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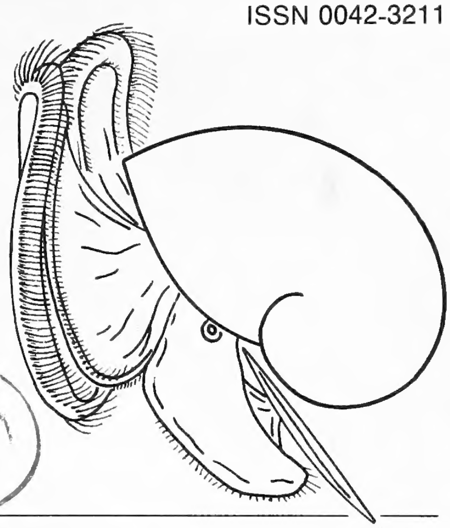
THE VELIGER



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THE VELIGER

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THE VELIGER

The Taxonomic Status of *Xerotropis* Monterosato, 1892, and Redescription of Its Type Species (Pulmonata: Hygromiidae)

by

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Abstract. The taxonomic status of the nominal genus *Xerotropis* Monterosato, 1892, was revised by studying its type species *Carocolla gargottae* Philippi, 1836. Anatomical research showed that the species belongs to the genus *Cernuella* Schlüter, 1838. Consequently, *Xerotropis* becomes a junior synonym of *Cernuella.*

A long taxonomic and nomenclatural controversy exists on the name of the type species of *Xerotropis. Carocolla gargottae* was considered to be a junior synonym of one of the following nominal species: "*Helix rugosa*" Chemnitz, 1786, *Helix corrugata* Gmelin, 1791, *Helix scabra* Salis Marschlins, 1793, "*Helix groyana*" Férussac, 1821, and *Helix rugosa* Lamarck, 1822.

Analysis of the literature showed that two of these names were not valid: "*Helix rugosa*" Chemnitz, 1786, being part of a polynomial name (*Helix scabra et rugosa*) and *Helix groyana* Férussac, 1821, being a *nomen nudum*; and that two others were not available for the Sicilian species: *H. corrugata* Gmelin, 1791, being introduced for the polynomial *Helix scabra et rugosa* but, despite Pfeiffer's claim, without objective evidence that the species illustrated by Chemnitz is the same as that of Philippi; and *H. scabra* Salis Marschlins, 1793, being introduced for material collected at Paestum in southern Italy, but with an original description insufficient for establishing its identity.

Examination of the type material of *Helix rugosa* Lamarck, 1822, demonstrated that it is the same species as *Carocolla gargottae* Philippi, 1836. Consequently, *Helix rugosa* Lamarck, 1822, is the correct name for the species.

INTRODUCTION

Monterosato (1892:23) established *Xerotropis* for a group of species of the so-called xerophilae having shells "depresse a forti rugosità interrotte da un orlo carenale [depressed, with marked ribs interrupted by a peripheral carina]." He placed six species in it: *Carocolla gargottae* Philippi, 1836, from Sicily; *Helix jolyi* Ancey, 1882, from Algeria; *Helix prietoi* Hidalgo, 1878, from the Balearic Islands; *Helix ledereri* Pfeiffer, 1857, from Jaffa; *Helix milaschewischi* [*sic*] Retowski, 1886, from Crimea; and *Helix spratti* Pfeiffer, 1846, from the Maltese Islands. In the same year, "*Hel*[*ix*]. *gargottae*" was designated as the type species of *Xerotropis* in an anonymous comment (presumably written by Kobelt, editor of the Nachrichtsblatt) (Kobelt, 1892:152) on Monterosato's paper.

Xerotropis was confirmed as a subgenus of *Xerophila* Held, 1837, by Kobelt (1904), who included *Helix corrugata* Gmelin, 1791 [= *Carocolla gargottae*], and *H. praeclara* Cafici, 1882, in it. The other species originally included in *Xerotropis* by Monterosato were moved to different subgenera of *Xerophila*: *Helix ledereri* and *H. spratti* to *Xeroamanda* Monterosato, 1892; *H. milachewitchi* [*sic*] and *Helix sigensis* Kobelt, 1883 [= *H. jolyi*], to *Jacosta* Gray, 1821; and *H. prietoi* to *Xeroplexa* Monterosato, 1892.

On the other hand, *Xerotropis* was regarded as a junior synonym of *Jacosta* by Pilsbry (1895) and Gude & Woodward (1921), and as a taxon of unclear and dubious status by Hesse (1926, 1934) and Thiele (1931).

The taxonomy of *Xerotropis* was subsequently discussed by Zilch (1960), Alzona (1971), and Richardson (1980). Zilch (1960) regarded *Xerotropis* as being of uncertain status due to a lack of anatomical information. Alzona (1971) regarded *Xerotropis* as a subgenus of *Helicella* Férussac, 1821, and assigned four Sicilian species to it. Finally, Richardson (1980) considered it to be a subgenus of the

Miocene genus *Titthodomus* Pfeffer, 1929, misinterpreting Zilch (1960), who listed two uncertain helicellid genus group taxa, *Xerotropis* and *Xeronexa* Monterosato, 1892, using the typographic character used for subgeneric names, after the last genus of the Helicellinae Ihering, 1909, i.e., *Titthodomus*!

In view of persisting uncertainty about the status of *Xerotropis* (as in the case of many other Monterosatian genus group taxa of the xerophilae), we asked some Sicilian colleagues for living specimens of *Carocolla gargottae,* the nominal species designated at its type species. V. E. Orlando and I. Sparacio succeeded in providing this material in 1987, so that we were able to perform anatomical study and publish the following revision.

MATERIALS AND METHODS

Whole shells were photographed under the optical microscope (Wild M5A). All dimensional parameters (shell height, maximum shell diameter, aperture height, and aperture diameter) were measured using a calipers.

Living specimens were drowned in water, then fixed and preserved in 75% ethanol buffered with $NaHCO_3$. The bodies were isolated after crushing the shells, and dissected under the optical microscope using very thin, pointed watchmaker's forceps. Anatomical details were drawn using a Wild camera lucida. The dimensions of anatomical tracts were measured using a millimetric lens on the same microscope.

Radulae were manually extracted from the buccal bulbs, washed in pure 75% ethanol, mounted on copper blocks with electronconductive glue, sputter-coated with gold, and photographed using a Philips 505 SEM.

The material examined is listed as follows: locality, municipality and province names in parenthesis, UTM reference, collector(s), date, number of specimens in parenthesis. Locality names and UTM references were according to the official 1:50,000 scale map of Italy (series M 792, sheets 593 and 626).

THE TYPE SPECIES OF *XEROTROPIS*

In the past century, much controversy arose over the correct name for the species selected as the type species of *Xerotropis.*

Many authors considered the name of the type species of *Xerotropis, Carocolla gargottae,* introduced by Philippi (1836:136–137; pl. 8, fig. 10; type locality: "prope Panormum et Termini") for a species of western Sicily, to be a junior synonym of one of the following species: "*Helix rugosa*" Chemnitz, 1786; *Helix corrugata* Gmelin, 1791; *Helix scabra* Salis Marschlins, 1793; "*Helix groyana*" Férussac, 1821; and *Helix rugosa* Lamarck, 1822.

The matter was raised by L. Pfeiffer (1841:17) who, on the basis of material in the Lamarck collection, claimed that Philippi's species was a junior synonym of both *Helix rugosa* Lamarck, 1822 (p. 90; type locality: ". . . en Italie, sur la rôute d'Ancône à Sinigaglia") and *Helix groyana* Férussac, 1821 (p. 44, *nomen nudum*!), the latter introduced for material collected by Ménard de la Groye "Entre Fiumesino et le case Brusciota, route de Sinigaglia, à Ancône."

Philippi (1844:110) denied this and alleged that there had been an exchange of material in the Lamarck collection. In fact, the original description of *Helix rugosa* did not appear to fit his *C. gargottae*: ". . . sed error manifestus collectionis Lamarchianae videtur; verba Lamarckii angle de son dernier tour est *un peu prononcé* minime quadrant."

Nevertheless, Pfeiffer (1845:23) persisted in his hypothesis. According to him, there was no doubt that Philippi's *C. gargottae* was Lamarck's *Helix rugosa* (on the basis of his examination of the material in the Lamarck collection and confirmed by the figures of Delessert, 1841–1842:pl. 26, fig. 4a–d), despite the fact that this evidence was in contrast with Lamarck's description.

Pfeiffer (1845) also claimed that the authorship of the species should be assigned to Chemnitz (1786) and not to Lamarck (1822). According to him, the species described and illustrated by Chemnitz (1786:152–153; pl. 133, fig. 1208) as "*Helix scabra et rugosa,*" for which Gmelin (1791: 3623) introduced the binomial name *Helix corrugata,* corresponded (at least in part, see below) to that later introduced by Lamarck under the name of *H. rugosa.* It was therefore not necessary to change its name, but to maintain a part of Chemnitz's original polynomial name.

In the second edition of Martini & Chemnitz's *Conchylien-Cabinet,* Pfeiffer again published the original description and figures by Chemnitz (Pfeiffer, 1846a:51–52, pl. 6, figs. 12, 13). However, since he realized that incongruities existed between the description and figure 1208, he wrote: "Bei einer spätern bessern Abbildung werde ich die vollständige Synonymik und Beschreibung geben" (Pfeiffer, 1846a:52). Two years later, Pfeiffer (1848a:173–174) gave a new description of the species and referred to new figures previously published by himself (Pfeiffer, 1843, pl. 23, figs. 3, 4). He also reintroduced Lamarck as the author of the species, by way of explanation offering only: "Ich halte diese Art für dieselbe Schnecke, welche als *H. rugosa* Chemn. früher gegeben word ist." In subsequent years, he curiously reverted to assigning the authorship of the species to Chemnitz (Pfeiffer, 1848b, 1853, 1859, 1868, 1876).

Pfeiffer created further confusion when he cited a different nominal species: *Helix groviana* Férussac, 1832 (Explication: ij, pl. 46A, fig. 1), which he reported in the synonymy of the Madeiran hygromiid *Leptaxis undata* (Lowe, 1831) as "*Helix groviana* (Helicogena) *Fér.* pr. 276. Hist. t. 46 A f. 1." (cf. Pfeiffer, 1848b:192; Pfeiffer, 1852: 154). "*Helix* (*Helicogena*) *groviana*" does not exist in the Prodromus: the species listed at number 276 is *Helix groyana,* not *Helix groviana*! *Helix groviana* is only reported in the "Explication des planches des livraisons XXII, XXIII, XXIV, XXV, XXVI et XXVII" of 1832.

Pfeiffer's (1845) hypothesis that *Helix corrugata* Gmelin, 1791, "*Helix groyana*" Férussac, 1821, *Helix rugosa* La-

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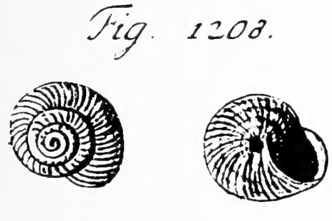


2

Figures 1, 2

Two illustrations involved in early taxonomic and nomenclatural history of *Cernuella rugosa* (Lamarck, 1822). 1. The reference to "*Lister Hist. Conchyl. tab. 55. fig. 51*" by Chemnitz (1786) and Gmelin (1791) corresponds to a figure in Lister's *Historiae sive Synopsis Methodicae Conchyliorum*. The fig. 51 of plate 55 of this book illustrates a Jamaican cyclophorid collected by H. Sloane and described as *Cochlea umbilicata minor, subrufa, ore circinnato et operculato*. 2. Die rauhe runzelhafte Schnirtelschnecke of Chemnitz (1786: pl. 133, fig. 1208). This shell was assigned by Draparnaud (1805) to his *Helix variabilis* [= *Cernuella virgata* (Da Costa, 1778)].

marck, 1822, and *Carocolla gargottae* Philippi, 1836, were junior synonyms of "*Helix rugosa*" Chemnitz, was accepted by many authors (Albers, 1850; Reeve, 1854; Benoit, 1862, 1882; Paulucci, 1878; Reuleaux, 1889; Westerlund, 1876, 1889; De Gregorio, 1896; Alzona, 1971).

Albers (1860:111) later preferred to use the name *Helix corrugata* Gmelin, 1791 (presumably because Chemnitz's name was polynomial) and Martens in Albers (1860:115), that of *Helix scabra* Salis Marschlins, 1793. While some authors followed Albers (1860) in using the name *H. corrugata* (Schaufuss, 1869; Kobelt, 1871, 1904; Tryon, 1887; Pilsbry, 1895), no one followed Martens in using Salis Marschlins's name.

The matter is obviously complex and requires detailed historical analysis from the beginning.

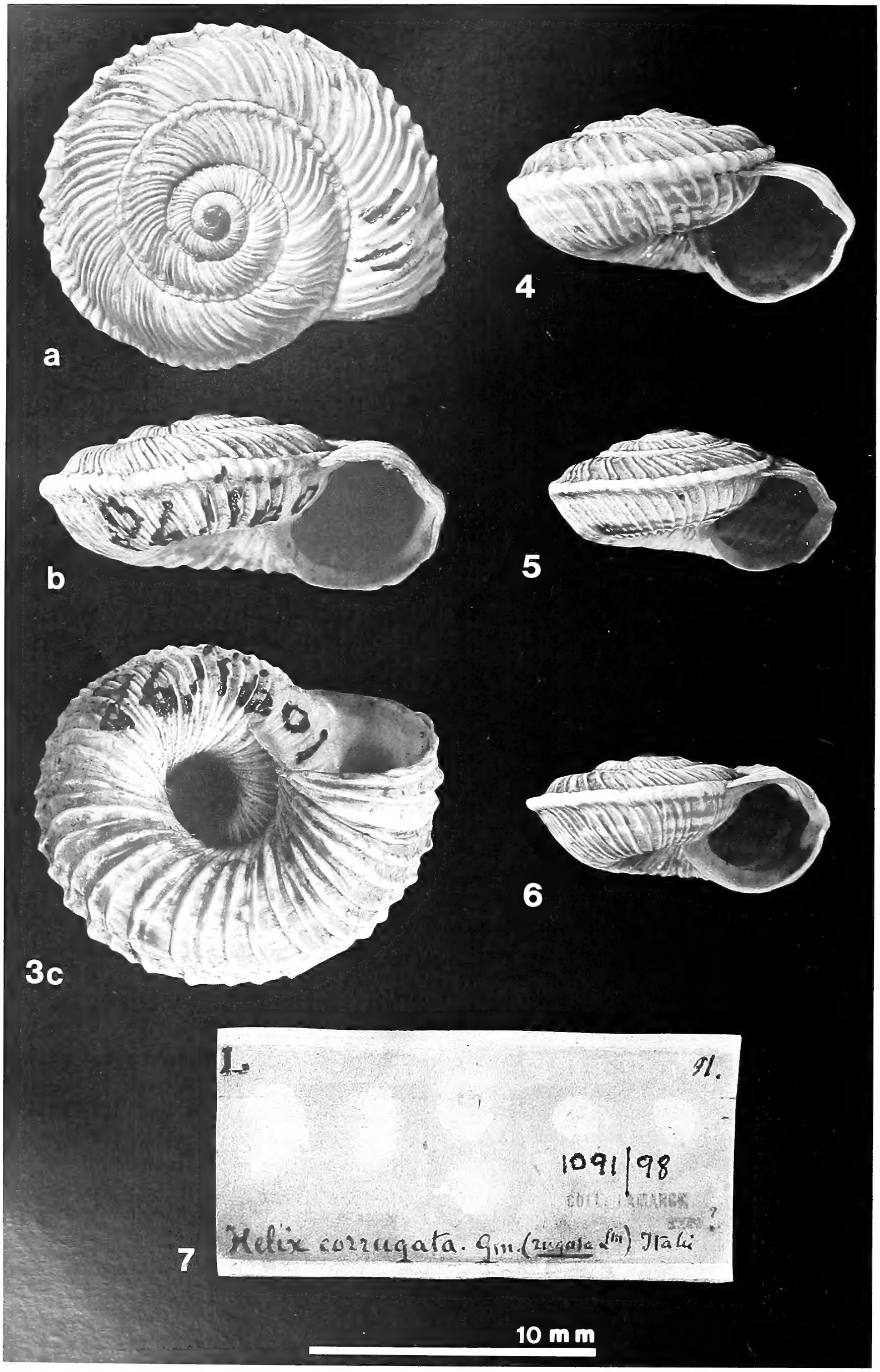
Chemnitz (1786:152–153; pl. 133, fig. 1208) described "Die rauhe runzelhafte Schnirtelschnecke" as follows "*Helix scabra et rugosa, testa umbilicata, carinata, cinereoalbida, longitudinaliter obliqua striata, anfractibus sex rotundis, apertura lunata, labro intus reflexo et incarnato.*"

He referred it to "Lister Hist. Conchyl. tab. 55. fig. 51. *Cochlea umbilicata minor, subrufa, ore circinnato et operculato.* Iamaic." and, in his remarks, listed a few differential features mentioning that "Lister nennet Jamaica als das wahre Vaterland dieser Schneche" and that "Eine fast völlig gleichförmige, die auf Otaheite [Haiti] gefunden worden, verwahre ich unter meinen Südlandischen Conchylien."

The bibliography of M. Lister (1638–1711/12) is very complex (Keynes, 1981), and Chemnitz's reference to "Lister Hist. Conchyl. tab. 55, fig. 51" concerns the *Historiae sive Synopsis Methodicae Conchyliorum* published in 1685–1692 and reprinted in 1770. As Pfeiffer (1840:89) was first to realize, Lister's description (*cochlea umbilicata, minor subrufa, ore circinato, et operculato*) and the figure (pl. 55, fig. 51) (Figure 1) clearly indicate a cyclophorid land snail. The indications "Iamac." and "SLOANE" which follow the figure indicate that the material was collected by H. Sloane on the island of Jamaica. When Sloane went to Jamaica in 1687, Lister asked him to collect terrestrial and freshwater snails (Dance, 1986). Descriptions of this material were published in the *Historiae sive Synopsis Methodicae Conchyliorum* and in its early versions (*De Cochleis* and *Historiae Conchyliorum*) (Keynes, 1981).

Chemnitz's figure 1208 (Figure 2) shows dorsal and umbilical views of a shell from the Chemnitz collection ("Ex Museo nostro"), but in what remains of the Chemnitz collection at the Zoologisk Museum of the University of Copenhagen (Denmark), the figured specimen no longer exists (J. Knudsen, personal communication, June 1993).

This shell has transverse striae, which could be growth lines or ribs, and a very small umbilicus. This feature does not agree with the description in the German text which speaks of a wide umbilicus ("Der Nabel ist rund gross und weit"). Although it is impossible to determine the exact shape of the shell (globose or depressed and carinated) from the figure, one can suppose it to be globose, as the figure is one of many in a plate (tab. 133) in which only species with globose shells ("*Helices rotundatae*") are illustrated (e.g., *Cepaea, Arianta, Cantareus, Acanthinula*). This conclusion seems to be supported by Draparnaud (1805:84) who considered the species identical to that of fig. 1207 and listed it as "*Helix variegata* Chemnitz" among



Figures 3–7

Syntypes of *Helix rugosa* Lamarck, 1822, and their old label. The type series is composed of six syntypes and is kept in the Lamarck collection at the Muséum d'Histoire Naturelle of Geneva (Switzerland). Photos by G. Dajoz, Muséum d'Histoire Naturelle of Geneva (Switzerland).

the synonyms of his *Helix variabilis* [= *Cernuella virgata* (Da Costa, 1778)]. Moreover, the periphery of the last whorl is linear and entire both in the original figure (Chemnitz, 1786:pl. 133, fig. 1208) and in the subsequent reproductions (Wood, 1825:pl. 33, fig. 38; Pfeiffer, 1846a: pl. 6, figs. 12, 13). On the contrary, the periphery of the shell of the Sicilian species in dorsal and umbilical view shows a crenulated rim, and this is evident both in our figures (Figures 3, 8, 12), and in the classic iconography of the species (Philippi, 1836:pl. 8, fig. 10; Rossmässler, 1837:pl. 26, fig. 357; Delessert, 1841–42:pl. 26, fig. 4a, b; Pfeiffer, 1843:pl. 23, fig. 4; Benoit, 1862:pl. 4, fig. 25; Tryon, 1887:pl. 61, figs. 79–81).

It is impossible to establish whether Chemnitz (1786) redescribed Lister's cyclophorid or another species. In any case, he included two (or three?) different species under the name "*Die rauhe runzelhafte Schnirtelschnecke*" that described with "der Nabel rund gross und weit" does not correspond to the one in fig. 1208 which has a very small umbilicus, but possibly to the Jamaican cyclophorid snail illustrated by Lister. The short description may be regarded as fitting the Sicilian species which Philippi (1836) named *Carocolla gargottae,* but the shell in figure 1208 does not correspond at all to this species, as Pfeiffer (1846a) realized.

Gmelin (1791:3623) introduced the binomial name *Helix corrugata* for a species, to be assigned to a sectio of his genus *Helix* including species "*carinatae*" i.e., with "*anfractuum margine acuto.*" This species, living "in Jamaica," was described as "*testa umbilicata rugosa cana oblique striata: apertura lunata, labro incarnato intus reflexo*" and was said to have been described and figured by "Chem. Conch. 9. p. 152. t. 133. f. 1208" and "List. Conch. t. 55 f. 51."

The name *Helix corrugata* Gmelin, 1791, was assigned to the Sicilian species for the first time by Pfeiffer (1845), and it was used as the latter's correct name by Albers (1860), Schaufuss (1869), Kobelt (1871, 1904), Tryon (1887), and Pilsbry (1895).

The Jamaican cyclophorid land snail *Cyclostoma corrugatum* Sowerby, 1843, has nothing to do with the Jamaican cyclophorid reported by Lister and assigned by Gmelin (1791) to his *Helix corrugata. Cyclostoma corrugatum* was introduced by Sowerby (1843a:30), without reference to the preceding literature (cf. also Sowerby, 1843b; Pfeiffer, 1846b, 1854; Kobelt, 1901).

Two years later, Salis Marschlins (1793:378 not seen; repeated on p. 472 of the English translation) used the name *Helix scabra* for an Italian land snail found at Paestum (southern Italy) and described as "*Testa umbilicata, depressiuscula transversim sulcata, aspera, apertura sublabiata ovata.*" Although Salis Marschlins referred it to "Mart. [i.e., Chemnitz] t. ix. tab. 133. fig. 1208," he should be regarded as having described it as a new nominal species (P. Tubbs, personal communication, 28 April 1994).

The name *Helix scabra* Salis Marschlins, 1793, was assigned to the Sicilian species only by Martens in Albers (1860).

Férussac (1821:44) also used the name *Helix scabra* for the species illustrated by Chemnitz (1786:fig. 1208), regarded *Helix corrugata* Gmelin, 1791 as its junior synonym and, without a line of description, cited "*Helix groyana,* nobis. *Habit.* Entre Fiumesino et le case Brusciota, route de Sinigaglia, à Ancône; *Comm.* Ménard de la Groye," as a different species.

Pfeiffer's (1845:24) statement "Dass *Hel. Groyana,* Fér. pr. 376 [*sic*] mit der Chemnitz'schen Figur 1208 identisch ist, hat Férussac, wahrscheinlich in Folge flüchtiger Prüfung des Textes, eben so gut übersehen, als alle folgende Auctoren" is unfounded. When Férussac realized this, he could no longer list the two species separately!

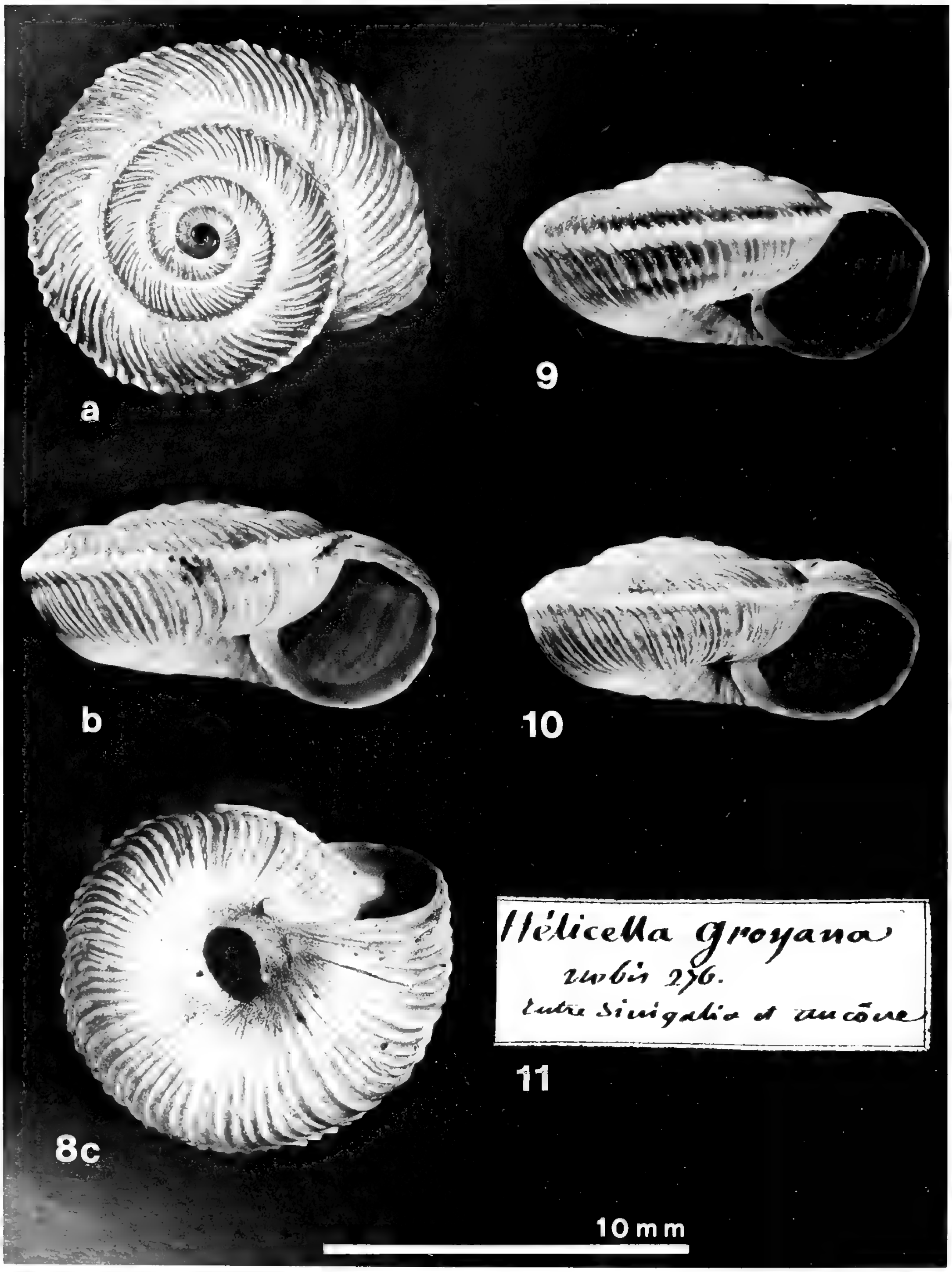
Lamarck (1822:90) introduced the name *Helix rugosa* for a species inhabiting "L'Italie, sur la route d'Ancône à Sinigaglia," previously cited as "*Helix groyana*" at no. 276 of Férussac's Prodromus. Finally, Philippi (1836) established his *Carocolla gargottae* on shells from "prope Panormum et Termini."

In conclusion, Chemnitz's name is not available because it is polynomial (ICZN, 1985:Art. 11c). The names *Helix rugosa* and *Helix scabra,* derived from different parts of Chemnitz's polynomial name, take the author (and date) of the publication in which they were first accompanied by a description, indication, or definition (ICZN, 1985:Art. 50a). Thus *Helix rugosa* "Chemnitz, 1786" is available from Pfeiffer, 1846a, and *Helix scabra* "Chemnitz, 1786" from Férussac, 1821. Since *Helix scabra* Férussac, 1821, and *Helix rugosa* Pfeiffer, 1846a, are junior primary homonyms of *Helix scabra* Salis Marschlins, 1793, and *Helix rugosa* Lamarck, 1822, respectively, they must be rejected.

Four names remain: *Helix corrugata* Gmelin, 1971, introduced for Chemnitz's "Die rauhe runzelhafte Schnirtelschnecke"; *Helix scabra* Salis Marschlins, 1793, introduced as a new species, though considered to be the same as that illustrated by Chemnitz; *Helix rugosa* Lamarck, 1822, and *Carocolla gargottae* Philippi, 1836, independently established without reference to Chemnitz.

The oldest available name is *Helix corrugata* Gmelin, 1791, but it is impossible to use it for the Sicilian species. Only the description fits the Sicilian species, but it also fits many other similarly shelled species. The specimens shown in fig. 51 by Lister and fig. 1208 by Chemnitz might constitute the type series of *Helix corrugata,* and one of them might be selected as lectotype according to art. 74(c) clarifying the identity of Gmelin's name. Nevertheless, the selection of fig. 1208, would not automatically provide a name for the Sicilian species because, despite Pfeiffer's claim, there is no objective evidence that the two correspond.

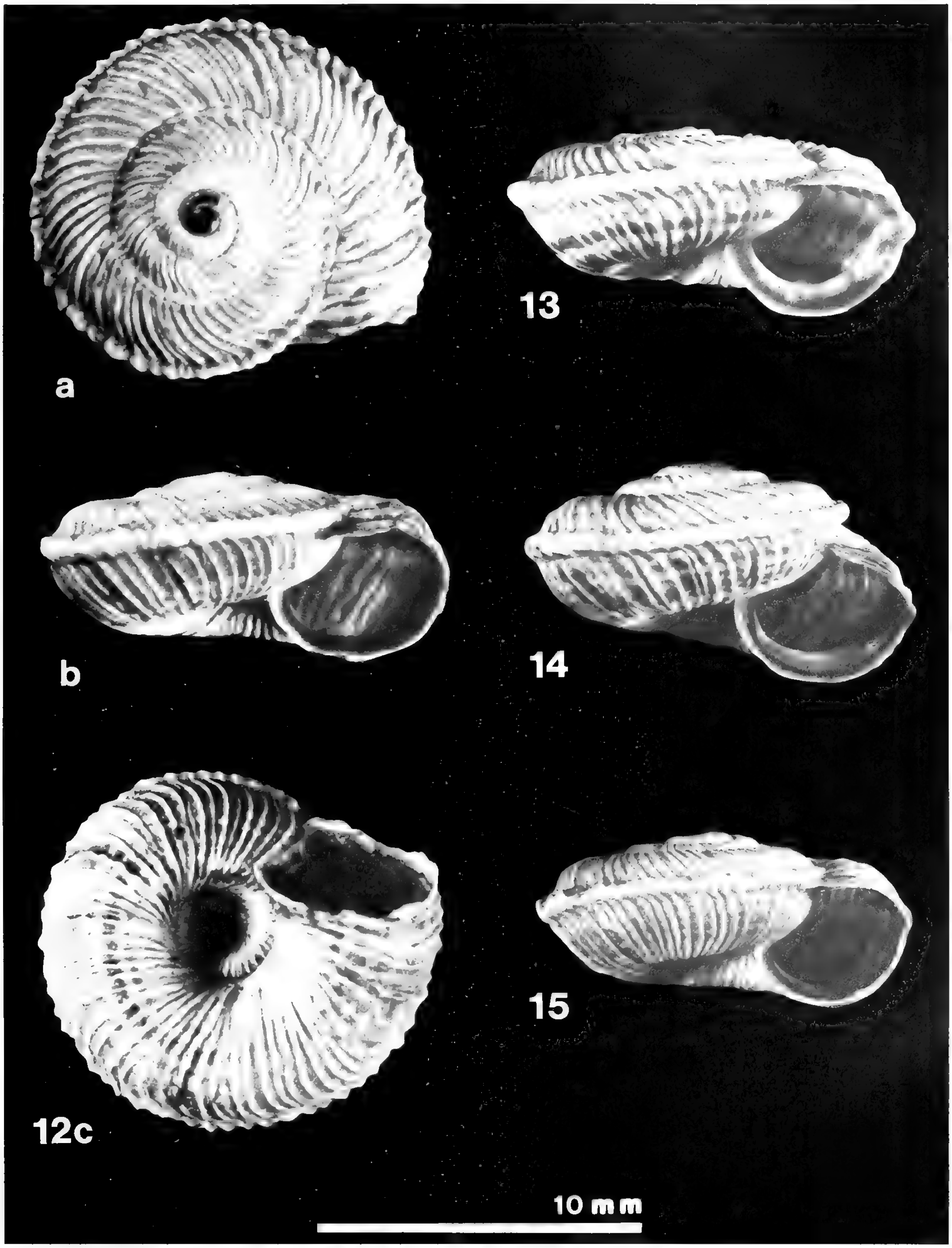
The identity of the species called *Helix scabra* by Salis Marschlins and found at Paestum is also uncertain. Férussac (1821:45) believed that it corresponded to his *Helix*



Hélicella groyana
nobis 276.
Entre Sinigaglia et Ancône

Figures 8–11

The three shells (and their original label) cited by Férussac as "*Helix groyana*" [*nomen nudum*] and reported as collected by M. de la Groye "Entre Fiumesino et le case Brusciota, route de Sinigaglia, à Ancône," present in the Férussac collection at the Muséum d'Histoire Naturelle of Paris (France).



Figures 12–15

Shells of *Cernuella rugosa* (Lamarck, 1822) from Comuni di Casteluzzo (San Vito Lo Capo, Trapani), 33SUC02, I. Sparacio leg. 3.4.87.

(*Helicella*) *simulata* (*nomen nudum*!) [= *Trochoidea simulata* (Ehrenberg, 1831)] from "Alexandrie d'Égypte." Again, however, there is no objective evidence, apart from the description (insufficient for diagnosis), to support hypotheses on its real nature.

Despite its poor original description, the identity of *Helix rugosa* Lamarck, 1822, is certain, as six syntypes have been traced in the Lamarck collection at the Muséum d'Histoire Naturelle of Geneva. The type locality of *Helix rugosa,* as indicated by Lamarck in the original description ("... en Italie, sur la rôute d'Ancône à Sinigaglia"), is probably derived from Férussac because the oldest label accompanying the syntypes reported only "Italie" (Figure 7), and, apart from the six syntypes, no other material of *Helix rugosa* exists in the Lamarck collection at Geneva.

Férussac reported that his material was collected by Ménard de la Groye, between Fiumesino and Casa Brusciote, along the road from Sinigaglia (Sinigaglia is a misspelling of Senigallia and Casa Brusciote of Casa Bruciata) to Ancona. However, it has always been impossible to accept that Ménard de la Groye could have found the shells studied by Férussac and Lamarck in this locality. Some Italian malacologists (Benoit, 1862; Paulucci, 1878; Alzona, 1971) and Kobelt (1898), in fact, have stressed that the species was endemic to Sicily and that it had never been found in central Italy. Benoit (1862:184) wrote: "dobbiamo confessarlo, non abbiamo finora contezza della italiana *H. rugosa* [we must confess, we do not yet have clear ideas on the Italian *H. rugosa*]." The presence of a species with shell corresponding to the syntypes of *Helix rugosa* of Lamarck in the area between Senigallia and Ancona is also excluded by data in the literature (cf. Piersanti, 1933) and by our research. We visited the site indicated by Férussac, which is between the right bank of the Esino River at its mouth and the town of Falconara Marittima (the area is now in the industrial outskirts of Falconara Marittima). We could find only populations of *Cernuella cisalpina* (Rossmässler, 1837), the shells of which correspond to those of well-known forms of the coastal regions of northeastern Italy (i.e., shell rather small, finely and densely ribbed, umbilicus rather small, with traces of peripheral carina).

Thus the fact that *H. rugosa* was reported in the area can only have two explanations: an exchange of material or a mistake in the original indication of the collecting site.

The hypothesis of an exchange of shell material in the Lamarck collection was first advanced by Philippi (1844). In support of this hypothesis, one could adduce the fact that the syntypes are not accompanied by a label handwritten by Lamarck and that Lamarck's description of *Helix rugosa* does not fully fit the Sicilian species, as stressed by Philippi (1844) and as Pfeiffer (1845) was obliged to admit.

When Lamarck died, his collection was bought by Prince Masséna who sold it to B. Delessert in 1840. The collection was later bought by the Muséum d'Histoire Naturelle of Geneva, where it still resides (Dance, 1986).

An exchange of material in the Lamarck collection is unlikely after 1840. Since Delessert's (1841–1842) figures of *Helix rugosa* correspond to the present syntypes (Figures 3–6), the *Helix rugosa* material in the collection was the same when he acquired it. A previous exchange of material also seems unlikey because in her copy of the *Animaux sans Vertèbres,* Ivet Rosalie de Lamarck listed the number of *Helix rugosa* syntypes in her father's collection as six, the same as the present syntypes.

As regards the absence of handwritten label by Lamarck, Y. Finet (personal communication, December 1987) told us that: "the lots of the Lamarck collection rarely contain the original labels with Lamarck's handwriting." To explain the poor correspondence between the original description and the syntypes, one can adduce the general lack of accuracy of Lamarck's (1822) descriptions. This lack of accuracy does not invalidate the descriptions but makes it possible to apply them to different species with similar shells.

We also sought the material cited by Férussac as "*Helix groyana.*" In the Férussac collection at the Muséum National d'Histoire Naturelle of Paris (France) there are two lots. One, labelled "*Helicella groyana,* nobis 276. Entre Sinigalia et Ancône" contains three shells, slightly smaller than those of the Sicilian species and with less marked ribbing (Figures 8–10). The other lacks the original label (the oldest label states "*Helix corrugata.* Italie") and contains four specimens (one very juvenile) perfectly corresponding to the Sicilian species and Lamarck's syntypes. The last tube also contains one shell of *Xerosecta explanata* (Müller, 1774) (a species absent from Italy!), and this is indicative of the frequent exchanges of material in old collections.

Férussac's specimens from the type locality mentioned in Lamarck's original description have not the status of type material, the type material being the six syntypes in the Lamarck collection at Geneva.

Helix rugosa Lamarck, 1822, must therefore be considered the same as *Carocolla gargottae* Philippi, a species the identity of which has never been uncertain and which clearly corresponds to the syntypes in the Lamarck collection. This seems to us the only possible solution, and consequently we conclude that *Carocolla gargottae* Philippi, 1836, is a junior synonym of *Helix rugosa* Lamarck, 1822, the oldest valid name for this species.

A statement of Deshayes (1830:220) that was completely overlooked by all subsequent authors is evidence that this is the correct interpretation: "C'est à Ménard de la Groye que l'on fut redevable de la connoissance de cette espèce; il la découvrit en Italie, près de Sinigalia: depuis elle fut retrouvée en Sicilie." This important statement, published no more than 8 years after Lamarck described *Helix rugosa* and 6 years before Philippi described *Carocolla gargottae*

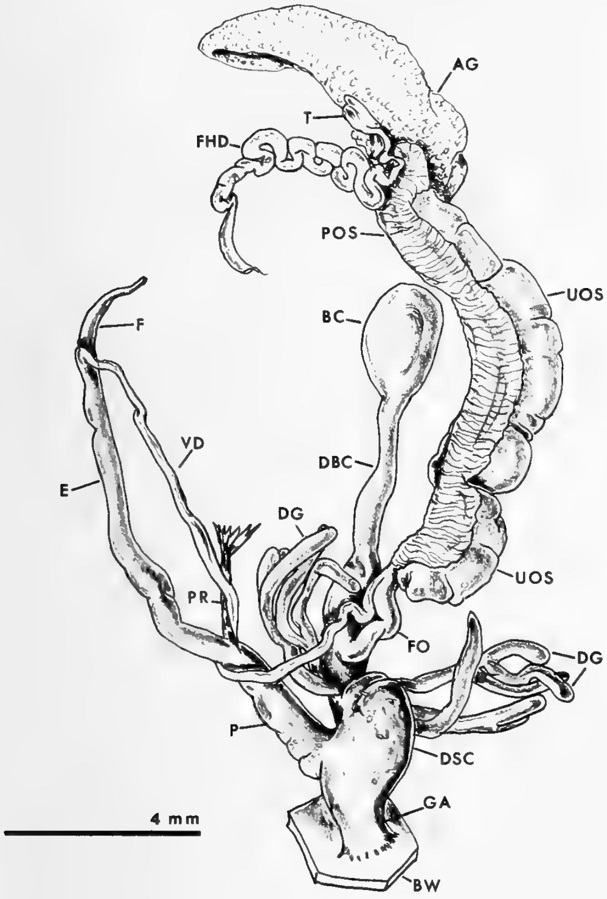


Figure 16

Genitalia (gonad excluded) of *Cernuella rugosa* (Lamarck, 1822) from San Vito Lo Capo (San Vito Lo Capo, Trapani), 33SUC02, V. E. Orlando leg. 10.87. Key: AG, albumen gland; BC, bursa copulatrix; BW, body wall; DBC, duct of bursa copulatrix; DG, digitiform glands; DSC, dart sac complex; E, epiphallus; F, flagellum; FHD, first hermaphodite duct; FO, free oviduct; GA, genital atrium; P, penis; POS, prostatic portion of ovispermiduct; PR, penial retractor muscle; T, talon; UOS, uterine portion of ovispermiduct; VD, vas deferens.

(but probably written when Lamarck, old and blind, was still alive) and accompanied by an excellent redescription of the species, clearly demonstrates the perfect correspondence between the Lamarckian *Helix rugosa* and the Sicilian snail.

Cernuella (*Cernuella*) *rugosa* (Lamarck, 1822)

[Figures 3–6, 8–10, 12–26]

Helix rugosa Lamarck, 1822:90.

Type locality: the locality reported in the original description: "... en Italie, sur la rôute d'Ancône à Sinigaglia" is certainly incorrect and taken from Férussac. The old label (Figure 7) accompanying the syntypes indicates only "Italie" and, on the basis of available data, the species is known to live only in Sicily.

Type series: six syntypes in the Lamarck collection at the Muséum d'Histoire Naturelle of Geneva (Switzerland) (Figures 3–6).

Carocolla gargottae Philippi, 1836:136–137; pl. 8, fig. 10.

Type locality: "prope Panormum et Termini."

Type series: according to R. Kilias (personal communication, May 1994) there is no syntype in the Philippi Collection, at the Zoologisches Museum und Institut für spezielle Zoologie of Berlin (Germany).

Helix pleurischura Bourguignat, 1876:44–45.

Type locality: "Habite la Sicile."

Type series: holotype in the Bourguignat collection at the Muséum d'Histoire Naturelle of Geneva (Switzerland) (Figure 26).

Helix chonomphala, Bourguignat, 1876:45–46.

Type locality: "La Sicile."

Type series: lost? No syntype is found in the Bourguignat collection at the Muséum d'Histoire Naturelle of Geneva (Switzerland).

Historical material examined: "Calatafimini, 1 esempl. ricev. 1877 dal Sig. Benoit col nome di *H. gargottae*" (1 det. *H. rugosa* var. *minor*; Coll. Paulucci, Museo di Zoologia dell'Università di Firenze, MZUF 6709); "Calatafimini, 2 esempl. ric. dal Sig. Benoit 1877" (2 det. *H. rugosa*; Coll. Paulucci, MZUF 6710); "Calatafimini, 2 esempl. ricev. dal Sig. Benoit 1877 col nome di *H. gargottae*" (2 det. *H. rugosa* var. *alba*; Coll. Paulucci, MZUF 6711); "Dintorni di Messina, 6 esempl. ricevuti 1870 dal Sig. Benoit a Messina" (6 det. *H. rugosa* var. *minor*; Coll. Paulucci, MZUF 6712); "Presso Messina" (4 det. *Helix gargottae*; Coll. Paulucci, MZUF 6713); "Redicofani" (15 det. *Helix rugosa*; Coll. Paulucci, MZUF 6714); "Sicilia, presso Messina, 12 esempl. 5 ricevuti dal Mse Monterosato 1870 da Trapani, 7 avuti stesso anno dal Sig. Benoit come raccolti presso Messina" (11 det. *Helix rugosa*; Coll. Paulucci, MZUF 6717); "Trapani e Messina, 6 esempl. ricevuti metà dal Mse Monterosato come provenienti da Trapani, metà dal Sig. Benoit come raccolti presso Messina- 1870" (6 det. *Helix rugosa* var. *alba*; Coll. Paulucci, MZUF 6718).

New material examined: San Vito Lo Capo (San Vito Lo Capo, Trapani), 33SUC02, V. E. Orlando leg. 10.87 (numerous specimens); S. Cianfanelli & M. Calcagno *leg.* 27.8.91 (5); Comuni di Casteluzzo (San Vito Lo Capo, Trapani), 33SUC02, I. Sparacio *leg.* 3.4.87 (numerous specimens); Torretta Granitola (Mazara del Vallo-Campobello di Mazara, Trapani), 33STB95, S. Cianfanelli & M. Calcagno *leg.* 21.8.91 (5).

Diagnosis: A species belonging to *Cernuella* (*Cernuella*) easily distinguishable from the two other, currently recognized species of the nominotypical subgenus of *Cernuella, C. virgata* (Da Costa, 1778) and *C. cisalpina* (Rossmässler, 1837), by virtue of medium-sized, robust, lenticular, shell,

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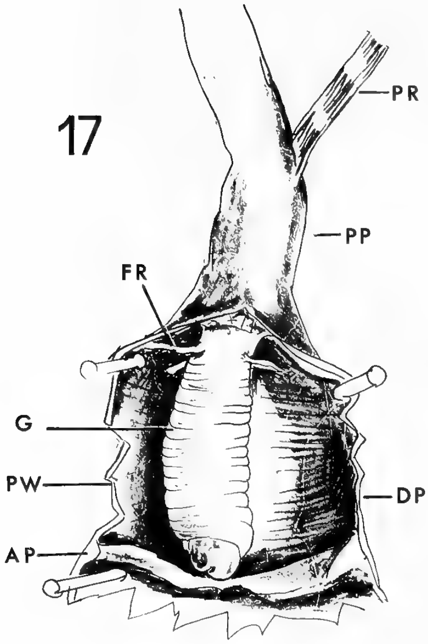

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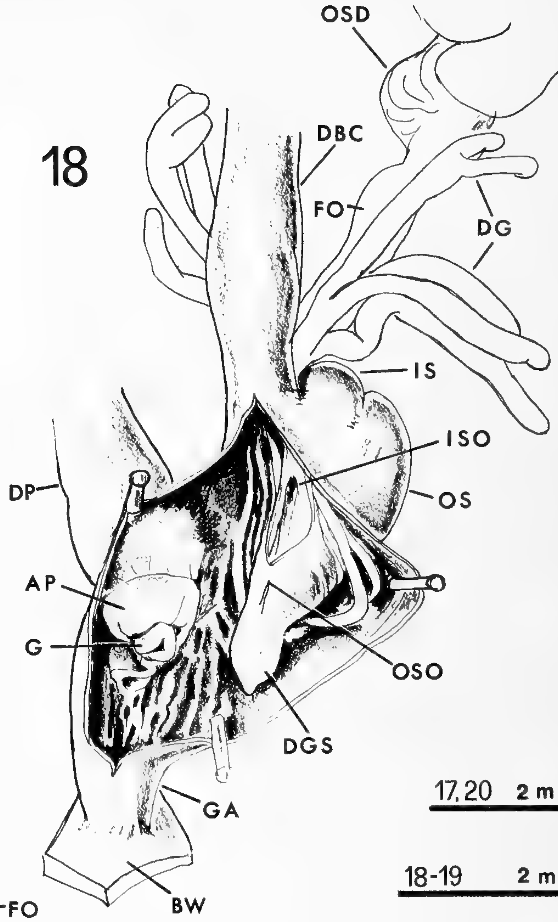

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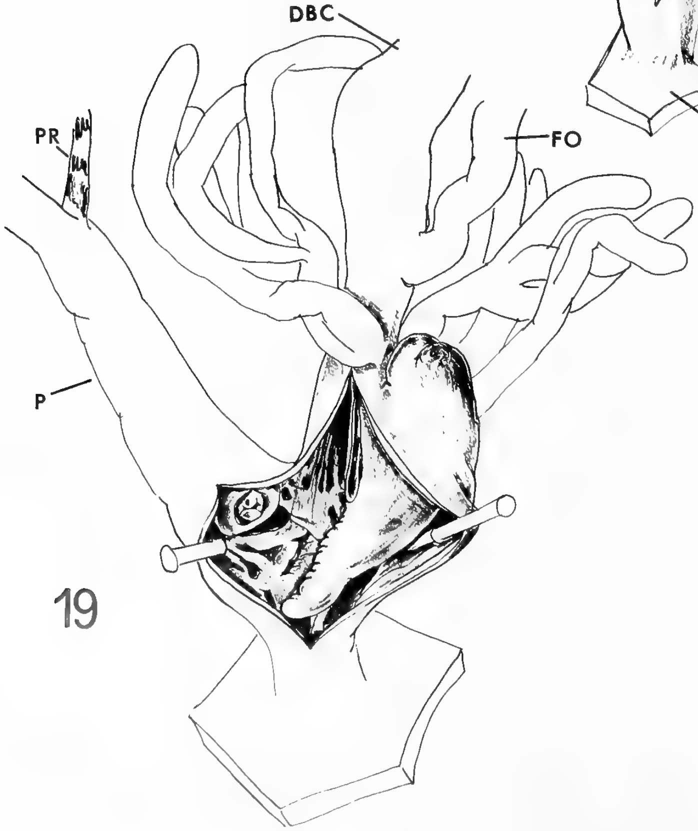

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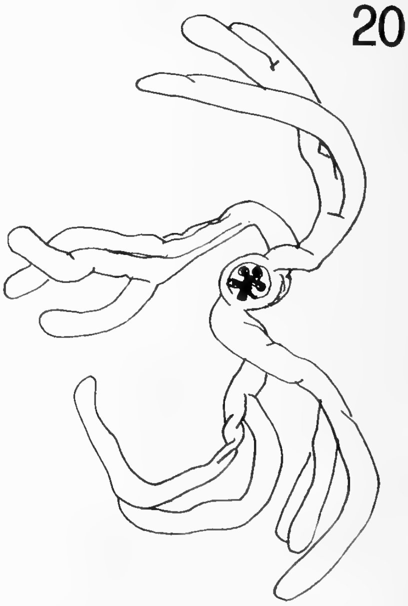

Table 1

Dimensions of the shell of *Cernuella rugosa*. For each parameter mean standard deviations and range are given.

Locality	Shell diameter	Shell height	Number of specimens
San Vito lo Capo	12.62 ± 0.58 (12.0–13.3)	6.28 ± 0.58 (5.3–7.0)	5
Comuni di Castelluzzo	12.35 ± 0.37 (11.6–13.1)	5.91 ± 0.66 (4.8–6.8)	10
Torreta Granitola	14.50 ± 0.75 (13.3–15.4)	5.56 ± 0.34 (5.2–6.2)	5

with raised, irregularly spaced ribs and evident, cordlike keel at periphery.

Shell (Figures 3–6, 8–10, 12–15): Shell dextral, medium-sized, robust, lenticular, uniformly yellowish-grey or with traces of pale brown bands most evident in lower half, opaque; external surface with evident raised ribs, rather irregularly positioned and spaced: spire depressed, sometimes almost flattened, consisting of 5–5½ clearly convex whorls, regularly and slowly enlarging; last whorl large, moderately dilated, sometimes descending near aperture, with evident, cordlike keel at periphery; sutures moderately deep, shouldered by keel of preceding whorls; umbilicus open, very large (about one-third of shell maximum diameter); aperture oval, its external margin angled at keel; peristome interrupted, simple, not reflected, with upper margin sometimes starting at keel, sometimes below keel, with well-developed, yellowish or brownish, internal callous rib.

Dimensions (Table 1). Height: 4.8–7.0 mm; maximum diameter: 11.6–15.4 mm.

Body: Animal blackish, darker above; retractor of right ommatophore independent of penis and vagina; kidney sigmurethrous; jaw odonthognathous; penial nerve originating from right pedal ganglion.

Genitalia (Figures 16–20): General scheme of the semidiaulic monotrematic type, characterized by: large hermaphrodite gonad (ovotestis) consisting of bunch of acini whose ducts converge into first hermaphrodite duct, its initial portion very slender, then widening to function as seminal vesicle; first hermaphrodite duct ending in clublike "talon" adhering to internal side of large, beanlike albumen gland; talon consisting of seminal receptacles (a treelike system of tubules, ending in three to five branches) and fertilization chamber; second hermaphrodite duct (ovispermiduct) arising from base of albumen gland, and consisting of female channel (uterine portion of ovispermiduct containing seminal groove) and prostate gland (with sperm groove) fused to define single cavity; short, wide free oviduct following female channel; duct of bursa copulatrix arising from where proximal vagina follows free oviduct, of medium length (about twice penis length), initially flared, ending in large, oval bursa copulatrix (gametolytic gland); proximal vagina very short; two tufts of sparsely branched, long, slender digitiform glands opening into initial portion of proximal vagina on opposite sides, level with apex of inner stylophore; distal vagina initiating from where dart-sac complex enters one side of vagina; dart-sac complex 0 + 2, i.e., consisting of one pair of stylophores, outer fused to external side of inner for most of its length; larger outer stylophore containing dart, smaller inner stylophore with small, empty cavity; dart slightly curved, circular in cross section near base and mid length, tip arrowhead-shaped, cross-shaped in section (two opposite arms of cross very short); cavities of stylophores opening independently one above other into groove along side of conical structure named "dart-gun" (Manganelli & Giusti, 1988); dart-gun constituting basal appendix of dart-complex projecting into distal vagina lumen; vaginal pleats variable in number along internal surface of vagina walls on both sides of dart-gun, two of them fusing below dart-gun and giving rise to sort of half-ring; vagina ending in genital atrium just after penis enters its far end; long slender vas deferens following sperm groove (inside prostate gland of ovispermiduct) and ending in penial complex; penial complex composed of flagellum, epiphallus and penis; flagellum relatively long (about two-thirds penis length), ending level with where vas deferens enters penial complex and epiphallus begins; epiphallus long (more than twice penis length), ending where penial retractor muscle contacts penial complex wall and penis begins; penis short,

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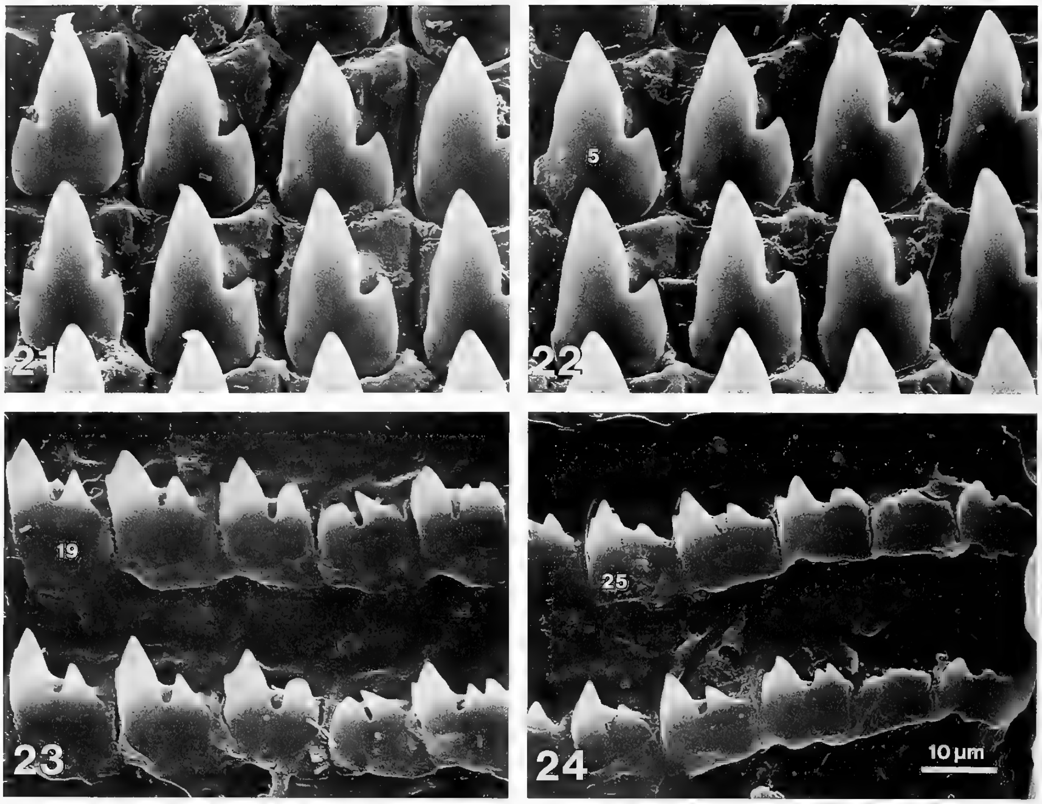
Figures 17–20

Details of distal genitalia of specimens of *Cernuella rugosa* (Lamarck, 1822) from San Vito Lo Capo (San Vito Lo Capo, Trapani), 33SUC02, V. E. Orlando leg. 10.87 (17, 19, 20) and from Comuni di Casteluzzo (San Vito Lo Capo, Trapani), 33SUC02, I. Sparacio leg. 3.4.87 (18). Distal penis opened to show penial papilla, frenula and annular pad (17); vagina opened to show dart gun structure; the apex of penial papilla protrudes from annular pad (18, 19); digitiform glands (20). Key: AP, annular pad; BW, body wall; DBC, duct of bursa copulatrix; DG, digitiform glands; DGS, dart gun; DP, distal penis; FO, free oviduct; FR, frenulum; G, glans or penial papilla; GA, genital atrium; IS, inner stylophore; ISO, inner stylophore opening; OS, outer stylophore; OSD, ovispermiduct; OSO, outer stylophore opening; PP, proximal penis; PR, penial retractor muscle; PW, penial wall.



Figures 21–24

Radula of *Cernuella rugosa* (Lamarck, 1822) from Comuni di Casteluzzo (San Vito Lo Capo, Trapani), 33SUC02, I. Sparacio leg. 3.4.87.

entering distal vagina level with apex of dart-gun and containing penial papilla (glans); penial papilla arising one-third of penis length from base, well-developed, slender, cylindrical, with apical opening bordered by two to three "lips," its base connected to penial walls by three small, symmetrically disposed muscles (frenula); penial papilla compact, its transverse section showing central duct (ejaculatory duct continuing directly from proximal penis and epiphallus lumen); penis opening into vagina bordered by sort of annular pleat, possibly a sphincter, usually contracted.

Radula (Figures 21–24): Similar to that of other *Cernuella* species (the radula in the various genera of the Hygromiidae and Helicidae does not usually have diagnostic characters), consisting of many rows each of about 57 teeth; central tooth with large tricuspid crown, mesocone long, twice ectocone height; first lateral teeth with bicuspid crown with long, robust mesocone and small (about half mesocone height) ectocone; small protuberance on internal side of mesocone (about two-thirds along mesocone height) of first lateral teeth possibly preluding small cusp evident on lateromarginal teeth; extreme marginal teeth with crown composed of very reduced mesocone with one to two small, sharp points and very reduced ectocone, frequently split into two small, sharp points.

Habitat: Xeroresistant species occurring in dune habitats on calcareous substrata. Found on soil, low vegetation, and stones. At Capo Granitola, live specimens were collected on *Thymelaea hirsuta* and *Asteriscus maritimus* (S. Cianfanelli, personal communication).

Distribution (Figure 25): According to Benoit (1862, 1882), this species is not present in the sites listed by Philippi (1836) for his *Carocolla gargottae* ("prope Panormum et Termini") or in the locality "Gesso près de Messine" reported by Cantraine (1841).

According to Benoit (1862, 1875, 1882), it is only known to live near "Redicofani" and particularly in a site known as "Portella dello Mpiso" (western Sicily). Our Sicilian colleague I. Sparacio thinks that the enigmatic localities indicated by Benoit as "Redicofani" and "Portella dello Mpiso" could be Golfo Cofano and Cala dello Mpiso, respectively, which are in the area inhabited by the species. Still, according to Benoit (1862, 1882), a population with a small shell was found by D. Pietro Campanella at Serranieri near Messina (eastern Sicily), along the "cammino

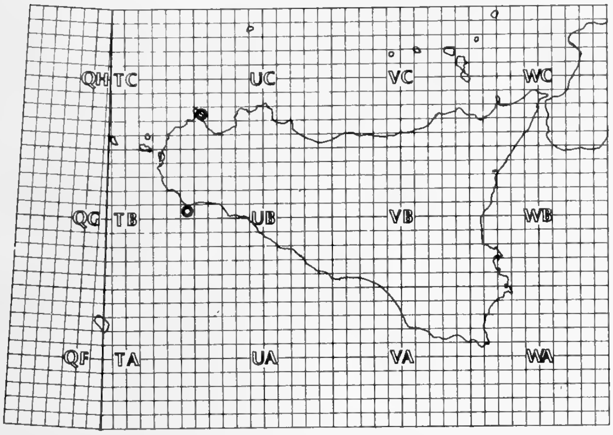


Figure 25

Distribution of *Cernuella rugosa* (Lamarck, 1822) on UTM map of Sicily plotted on 10 × 10 km squares.

coverto che dalla Cittadella mena al forte della Lanterna (the covered path which leads from the Cittadella to the Lanterna fortress)," where Benoit was never able to find it. De Gregorio (1896) also reported it at San Vito (San Vito Lo Capo, western Sicily) where the specimens studied by us were collected.

DISCUSSION

The true identity and status of the many taxa of the genus group introduced by Monterosato (1892) for the various "xerophilae" have posed a serious problem to anyone attempting to revise these small palaearctic helicoids in the last 100 years (cf. Pilsbry, 1895; Kobelt, 1904; Gude & Woodward, 1921; Hesse, 1926, 1934; Lindholm, 1927; Thiele, 1931; Germain, 1929; Zilch, 1960). Since these taxa were established on a conchological basis, in many cases they are artificial groups. The case of *Xerotropis* is a good example of this. Apart from its type species and the Algerian *Helix jolyi* Ancey, 1882, whose identity is uncertain, successive anatomical studies have shown that the other four species assigned to *Xerotropis* by Monterosato (1892) belong to different genera: *Helix spratti* Pfeiffer, 1846, from the Maltese Islands, belongs to *Trochoidea* (*Trochoidea*) Brown, 1827 (cf. Giusti et al., in press); *Helix prietoi* Hidalgo, 1878, from the Balearic Islands, and *Helix ledereri* Pfeiffer, 1857, from Jaffa, belong to *Trochoidea* (*Xerocrassa*) Monterosato, 1892 (cf. Ortiz de Zarate, 1963; Forcart, 1976); and *Helix milaschewitschi* Retowski, 1886, from Crimea, belongs to *Helicopsis* Fitzinger, 1833 (cf. Schileyko, 1978).

Until the old, conchological approach to gastropod taxonomy was superceded by the anatomical approach, it was impossible to create a natural classification. The work of P. Hesse was fundamental for understanding this group of taxa. The classification derived from his studies, based on the organization of the distal genitalia and position of the right ommatophore retractor, proved to be a satisfactory framework for nearly 50 years.

Research gained new momentum thanks to A. Schileyko's study of the inner structure of the distal genitalia (dart-sac complex and penis), which had never been investigated in detail before. During the 1970s and 1980s, Schileyko (1972, 1978, 1991) revised many taxa of the genus group and proposed new classification of the helicoids, which, although criticized in some aspects (Giusti & Manganelli, 1987; Hausdorf, 1988; Manganelli & Giusti, 1988; Giusti et al., 1992; Nordsieck, 1993) were innovative and gave new impetus to revision of the helicoids.

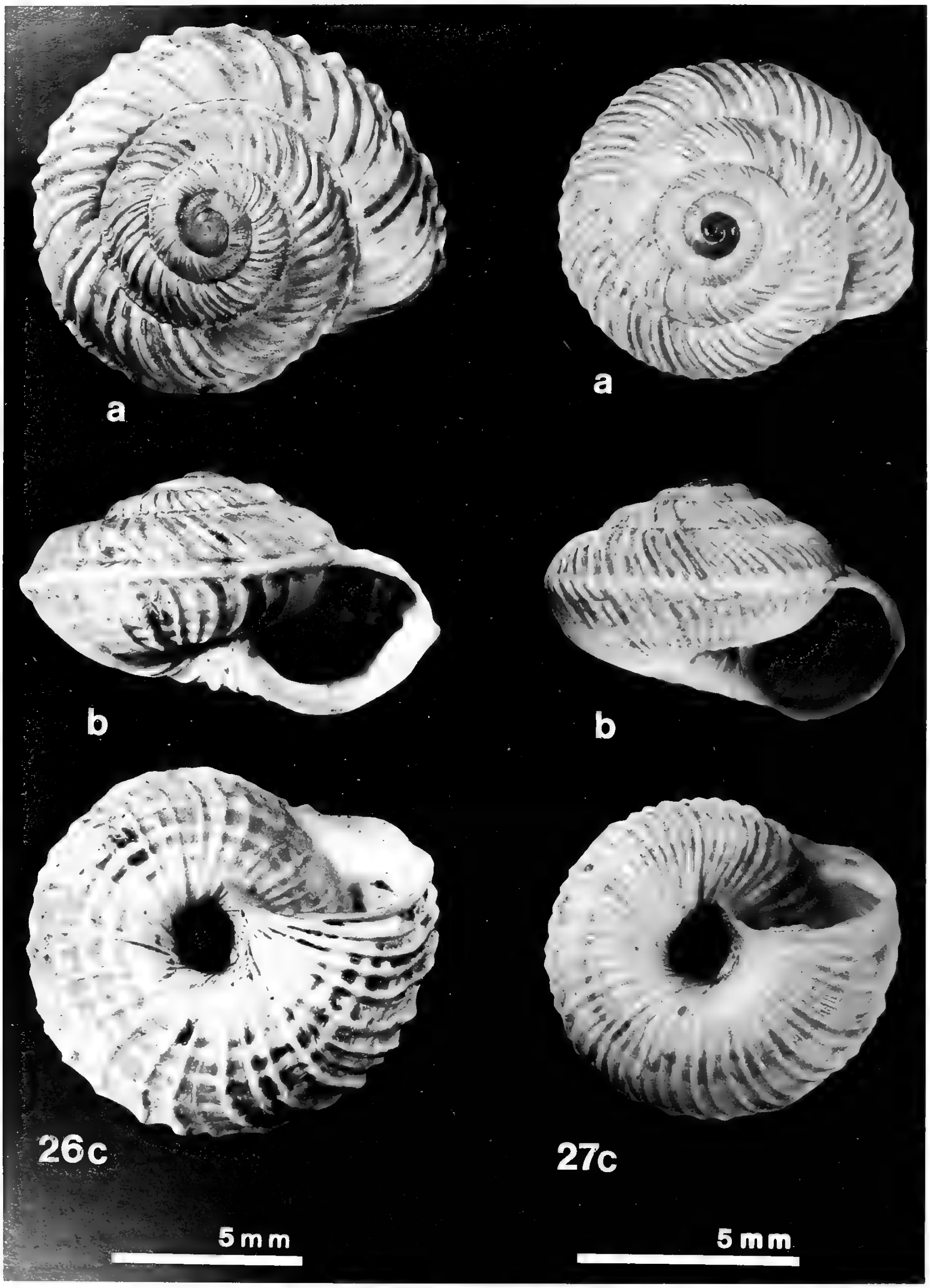
Anatomical study of the type species of *Xerotropis* showed that this taxon is characterized by the same distal genital structure as that of the subfamily Hygromiinae *sensu* Schileyko (dart sac complex with 0 + 2 stylophores).

The genus group taxa of the Hygromiinae with 0 + 2 stylophores and right ommatophore retractor independent of the genitalia was recently revised by Hausdorf (1988) and Manganelli & Giusti (1988, 1989). These studies showed that many subgenera or supposed synonyms of *Cernuella* Schlüter, 1838 (e.g., *Xerosecta* Monterosato, 1892, *Xeromagna* Monterosato, 1892, *Polloneriella* Alzona & Alzona Bisacchi, 1940, *Microxeromagna* Ortiz de Zárate López, 1950, *Xeromunda* Monterosato, 1892; cf. Zilch, 1960; Clerx & Gittenberger, 1977; Aparicio, 1982, 1985; Giusti & Castagnolo, 1982; Kerney et al., 1983; Manga Gonzales, 1983; Marquet, 1985; Prieto, 1986; Abbott, 1989) were distinct taxa of the genus group (*Xeroplana* Monterosato, 1892, *Xerofalsa* Monterosato, 1892, and *Xeroamanda* Monterosato, 1892, are still uncertain).

Cernuella is clearly characterized by the structure of the distal genitalia (dart sac complex wide and fused to inner walls of vagina for a long tract; penis joining distal vagina level with stylophores) (Manganelli & Giusti, 1988; Giusti et al., 1992), which is markedly different from that of the group *Xerosecta-Xeromagna-Polloneriella-Microxeromagna* (characterized by a smaller dart-sac complex entering vagina through a slender neck; penis joining vagina distally with respect to stylophores) (Manganelli & Giusti, 1988; Giusti et al., 1992) and that of *Xeromunda* (characterized by a dart-sac complex joined to vagina through large wide "basal portion" and with a very modified inner stylophore) (Manganelli & Giusti, 1989; Giusti et al., 1992).

As the above anatomical description demonstrates, *Xerotropis* corresponds to *Cernuella*. *Cernuella* includes two subgenera: *Cernuella* (*Cernuella*) (penial papilla with three basal frenula) and *Xerocincta* (penial papilla without frenula). Although this classification needs to be revised (Favilli, 1994), it is evident that *Xerotropis* corresponds to *Cernuella* (*Cernuella*), and must therefore be considered as a junior subjective synonym of *Cernuella* Schlüter, 1838.

At present, *Cernuella rugosa* (Lamarck, 1822) seems to be endemic to Sicily and is easily distinguishable on the basis of shell features from the two other, currently ac-



Figures 26, 27

Figure 26. Holotype of *Helix pleurischura* Bourguignat, 1876, from "Sicile." Bourguignat collection, Muséum d'Histoire Naturelle of Geneva (Switzerland). Figure 27. A syntype/topotype of *Helix praeclara* Cafici, 1882 from "Castelvetrano (Sicilia), determ. Cafici teste Monterosato." Pollonera collection, Museo Regionale di Scienze Naturali, Torino (Italy).

cepted *Cernuella* (*Cernuella*) species: *C. virgata* (Da Costa, 1778) and *C. cisalpina* (Rossmässler, 1837). This fact and the existence of populations with small shells, apparently similar to this species, such as those described as *Helix praeclara* Cafici, 1882 (type locality: "Abita Castelvetrano in provincia di Trapani") (Figure 27), and others of reduced size and ribbing from Sicily, very similar to Apennine populations of *C. cisalpina,* must be carefully evaluated if this group of species is to be classified correctly. *Cernuella* are remarkable for wide, intra- and interpopulation shell variability which caused an enormous amount of splitting in the second half of the last century, particularly, by French conchologists of the Nouvelle Ecole. For the Sicilian *Cernuella* alone, more than 60 nominal taxa of the species group were introduced (Favilli, 1994). The status of these taxa is problematical, and their revision complex, involving the location and study of original descriptions, syntypes, topotypes, and much living material for classical morphological (conchological and anatomical) and genetic (allozyme polymorphism) analysis.

Hence we synonymize only two species described by Bourguignat (1876): *Helix pleurischura* and *H. chonomphala.* We traced the holotype of the former in the Bourguignat collection at the Muséum d'Histoire Naturelle of Geneva (Switzerland) (Figure 26) and found that it corresponds perfectly to *C. rugosa.* On the contrary, there is no type material of the latter species in the Bourguignat collection (Y. Finet, personal communication, December 1987). It is here regarded as a junior synonym of *C. rugosa* on the basis of Benoit's (1875:142) statement that Bourguignat chose some shells from many *C. rugosa* sent to him by Benoit and attributed them to different species: "Il nostro dotto amico M. Bourguignat ritiene, che tra i molti esemplari da noi speditigli dell'*H. gargottae,* vi sieno, oltre la specie di Philippi, altre due specie distinte, cioè l'*H. conomphala,* e l'*H. plewischura* [*sic*]. Non dividiamo la sua opinione [my learned friend M. M. Bourguignat believes that, amongst the many specimens of *H. gargottae* sent to him by me, there are not only Philippi's species, but also two other distinct species, i.e., *H. conomphala* and *H. plewischura* [*sic*]. I do not share his opinion]."

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LITERATURE CITED

ABBOTT, R. T. 1989. Compendium of Landshells. A Full-color Guide to More than 2,000 of the World's Terrestrial Shells. American Malacologists, Inc.: Melbourne, Florida. 240 pp.

ALBERS, J. C. 1850. Die Helicen, nach natürlicher Verwandtschaft systematisch geordnet. Berlin. 262 pp.

ALBERS, J. C. 1860. Die Helicen nach natürlicher Verwandtschaft systematisch geordnet. Zweite Ausgabe nach dem hinterlassenen Manuskript besorgt von Eduard von Martens. Leipzig. xviii + 359 pp.

ALZONA, C. 1971. Malacofauna Italica. Catalogo e bibliografia dei molluschi viventi, terrestri e d'acqua dolce. Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano 111:1–433.

APARICIO, M. T. 1982. Observations on the anatomy of some Helicidae from central Spain. Malacologia 22:621–626.

APARICIO, M. T. 1985. Variabilidad de *Cernuella (Xeromagna) cespitum* (Draparnaud, 1801) en ejemplares españoles e italianos (Pulmonata, Helicidae). Bollettino malacologico 21: 281–288.

BENOIT, L. 1857–62. Illustrazione sistematica critica iconografica de' testacei estramarini della Sicilia Ulteriore e delle isole circostanti. i–xvi + Pp. 1–52 [? 1–9 pls.] (1857), Pp. 53–116 (1857), Pp. 117–180 (1859), Pp. 181–248 (1862) [pl. 10 has never been published; date of publication of pls. 11–12 unknown]. Napoli.

BENOIT, L. 1875. Catalogo delle conchiglie terrestri e fluviatili della Sicilia e delle isole circostanti. Bullettino della Società Malacologica Italiana 1:129–163.

BENOIT, L. 1882. Nuovo catalogo delle conchiglie terrestri e fluviatili della Sicilia o continuazione alla illustrazione sistematica critica iconografica dei testacei extramarini della Sicilia Ulteriore e delle isole circostanti. Messina. 176 pp.

BOURGUIGNAT, J. R. 1876. Species novissimae Molluscorum in Europaeo systemati detectae notis diagnosticis succinctis breviter descriptae. Lutetiae. 80 pp.

CANTRAINE, F. 1841. Malacologie méditerranéenne et littorale, ou description des mollusques qui vivent dans la Méditerranée ou sur le continent de l'Italie, ainsi que des coquilles qui se trouvent dans les terrains tertiaires italiens, avec des observations sur leur anotomie, leurs moeurs, leur analogie et leur gisement. Ouvrage servant de faune malacologique italienne et de complément a la *Conchiologia fossile subapennina* de Brocchi. Nouveaux Mémoires de l'Académie royale des Sciences et Belles-Lettres de Bruxelles, 13:175 pp., pls. 1–6.

CHEMNITZ, J. H. 1786. In F. H. W. Martini, Neues systematisches Conchylien-Cabinet geordnet und beschrieben von F. H. W. Martini und unter dessen Aufsicht nach der Natur gezeichnet und mit lebenden Farben erleuchtet, 9:xvi + 194 pp., pls. 103–136. Nürnberg.

CLERX, J. P. M. & E. GITTENBERGER. 1977. Eniger über *Cernuella* (Pulmonata, Helicidae). Zoologische Mededelingen (Leiden) 52:27–56, pls. 1–2.

Dance, S. P. 1986. A History of Shell Collecting. E. J. Brill-Dr. W. Backhuys: Leiden, xv + 265 pp., [1] + 32 pls.

De Gregorio, A. 1896. Appunti su talune conchiglie estramarine di Sicilia viventi e fossili con la spiegazione delle tavole dell'opera di Benoit. Il Naturalista Siciliano 14:183-212.

Delessert, B. J. P. 1841-1842. Recueil de coquilles décrites par Lamarck dans son "Histoire naturelle des animaux sans vertébres", et non encore figurées. Paris. 92 pp., 40 pls.

Deshayes, G. P. 1830. Histoire naturelle des Vers. Par Bruguière et De Lamarck, continuée par M. G. P. Deshayes in Encyclopédie Methodique (Dictionaire Encyclopédique Méthodique), ou par ordre de matières. Histoire naturelle des Vers, 2(1): Pp. 1-256. Paris. See: Sherborn, C. D. & B. B. Woodward, 1893. Proceedings of the Zoological Society, 1893:582-595.

Draparnaud, J. P. R. 1805. Histoire naturelle des mollusques terrestres et fluviatiles de la France. Montpellier et Paris. [12] + viii + 164 + [1] pp., 13 pls.

Favilli, L. 1994. Per una revisione nomenclaturistica e tassonomica del genere *Cernuella* in Italia (Gastropoda, Pulmonata, Hygromiidae). Unpublished doctoral dissertation, Università di Siena, Dottorato di Ricerca in Biologia Animale (Zoologia) VI Ciclo, 113 pp., 33 figs., 27 tables.

Férussac, J. B., d'Audebard de. 1821. Tableaux systématiques des Animaux Mollusques terrestres classés en familles naturelles, dans lesquels on a établi la concordance de tous les systèmes; suivis d'un prodrome générale pour tous les Mollusques terrestres ou fluviatiles vivants ou fossiles. Tableau systematique de la Famille des Limaçons, Cochleae: 25-48 [Quarto Edition]. Paris. See: Kennard, A. S., 1942. Proceedings of the Malacological Society of London, 25:12-17, 105-118.

Férussac, J. B., d'Audebard de. 1832. Histoire naturelle générale et particulière des Mollusques terrestres et fluviatiles. Livraisons 22-27 and "Explications des planches des livraisons XXII, XXIII, XXIV, XXV, XXVI, XXVII": pls. 50, 54A, 56, 56A, 117 (Livr. 22); pls. 8D, 9B, 27A, 64, 66*, 124A (Livr. 23); pls. 24A, 28B, 46A, 51A, 65, 68 (Livr. 24); pls. 67, 69, 69A, 140, 155 (Livr. 25); pls. 71, 74, 79, 109, 142, 153 (Livr. 26); pls. 80, 82, 141a, 142b, 148, 163 (Livr. 27). Paris. See: Kennard, A. S., 1942. Proceedings of the Malacological Society of London, 25:12-17, 105-118.

Forcart, L. 1976. Die Cochlicellinae und Helicellinae von Palästina und Sinai. Archiv für Molluskenkunde 106:123-189.

Germain, L. 1929. Les Helicidae de la faune française. Archives du Muséum d'Historie Naturelle de Lyon 13:4-482.

Giusti, F. & L. Castagnolo. 1982. I molluschi terrestri delle dune italiane: brevi cenni di ecologia, elenco delle specie e chiavi per il loro riconoscimento. Consiglio Nazionale delle Ricerche, Pubblicazione AQ/1/174. Quaderni sulla "Struttura delle zoocenosi terrestri", 3. Ambienti Mediterranei, 1. Le Coste Sabbiose: 51-102.

Giusti, F. & G. Manganelli. 1987. Notulae Malacologicae XXXVI. On some Hygromiidae (Gastropoda: Helicoidea) living in Sardinia and in Corsica. (Studies on the Sardinian and Corsican Malacofauna VI). Bollettino Malacologico 23: 123-206.

Giusti, F., G. Manganelli & P. Schembri. In press. The non-marine molluscs of the Maltese Islands. Museo Regionale di Scienze Naturali, Torino, Monografie, 15.

Giusti, F., G. Manganelli & M. G. Selmi. 1992. Spermatozoon fine structure in the phylogenetic study of the Helicoidea (Gastropoda, Pulmonata). Proceedings of the Tenth International Malacological Congress (Tübingen, 1989):611-616.

Gmelin, G. F. 1791. Caroli a Linné. Systema Naturae. Editio decima tertia. 1 (VI): Pp. 3021-3910 Lugduni. See: Hopkinson, J., 1908. Proceedings of the Zoological Society, 1907: 1035-1037.

Gude, G. K. & B. B. Woodward. 1921. On *Helicella*, Férussac. Proceedings of the Malacological Society of London 14:174-190.

Hausdorf, B. 1988. Zur Kenntnis der systematischen Beziehungen einiger Taxa der Helicellinae Ihering 1909 (Gastropoda: Hygromiidae). Archiv für Molluskenkunde 119:9-37.

Hesse, P. 1926. Beiträge zur genaueren Kenntnis der Subfamilie Helicellinae. Archiv für Molluskenkunde 58: 113-141.

Hesse, P. 1934. Zur Anatomie und Systematik der palaearktischer Stylommatophoren. Zweiter Teil. Zoologica (Stuttgart) 85:1-59, pls. 1-9.

International Commission on Zoological Nomenclature [shortened ICZN]. 1985. International code on zoological nomenclature. Third edition adopted by the XX general assembly of the International Union of Biological Sciences. Berkeley and Los Angeles. xx + 338 pp.

Keynes, G. 1981. Dr Martin Lister. A bibliography. St. Paul's Bibliographies 3: 52 pp.

Kerney, M. P., R. A. D. Cameron & J. H. Jungbluth. 1983. Die Landschnecken Nord- und Mitteleuropas. Hamburg und Berlin. 384 pp., 24 pls.

Kobelt, W. 1871. Catalog der im europäischen Faunengebiet lebenden Binnenconchylien. Cassel. xiv + 150 pp.

Kobelt, W. 1892. Literaturbericht. Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft 24:149-152.

Kobelt, W. 1898. Die Fauna der meridionalen Sub-Region. Studien zur Zoogeographie. 2: 368 pp. Wiesbaden.

Kobelt, W. 1901. Cyclophoridae. Das Tierreich. Eine Zusammenstellung und Kennzeichnung der rezenten Tierformen 16: xxxix + 662, 1 map.

Kobelt, W. 1904. in E. A. Rossmässler, Iconographie der Land- und Süsswasser-Mollusken, mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten. Neue Folge, 11: xii + 343 pp., 6 pls.

Lamarck, J. B. M. 1822. Histoire naturelle des animaux sans vertèbres, présentant les caractères géneraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent. Paris. 6(2): 232 pp.

Lindholm, W. A. 1927. Zur systematik und nomenklatur einiger Heliciden und ihrer verwandten. Archiv für Molluskenkunde 59:116-138.

Manga Gonzales, M. Y. 1983. Los Helicidae (Gastropoda: Pulmonata) de la provincia de Leon. Leon. 394 pp.

Manganelli, G. & F. Giusti. 1988. Notulae Malacologicae, XXXVIII. A new Hygromiidae from the Italian Apennines and notes on the genus *Cernuella* and related taxa (Pulmonata: Helicoidea). Bollettino Malacologico 23:327-380.

Manganelli, G. & F. Giusti. 1989. Notulae Malacologicae, XLIII. *Xeromunda* Di Maria di Monterosato in Italy (Pulmonata: Hygromiidae). Bollettino Malacologico 25:1-22.

Marquet, R. 1985. The land molluscs of the Antwerp harbour area, with a new record of *Cernuella cespitum* (Draparnaud, 1801) for western Europe. Basteria 49:3-10.

Monterosato, T., Di Maria di. 1892. Molluschi terrestri delle isole adiacenti alla Sicilia. Atti della Reale Accademia di Scienze, Lettere e Belle Arti Palermo, Serie III, 2:1-34.

Nordsieck, H. 1993. Das System der paläarktischen Hygromiidae (Gastropoda: Stylommatophora: Helicoidea). Archiv für Molluskenkunde 122:1–23.

ORTIZ DE ZARATE, A. 1963. Observaciones anatomicas y posicion sistematica de varios helicidos españoles. VI. Anotaciones sobre las species españolas del genero *Helicella,* subênero *Xeroplexa* (Monterosato) Hesse 1926. Boletín de la Real Sociedad de Historia Natural de Baleares 48:93–100.

PAULUCCI, M. 1878. Materiaux pour servir a l'étude de la faune malacologique terrestre et fluviatile de l'Italie et de ses îles. Paris. 54 pp.

PFEIFFER, L. 1840. Kritisches Register zu Martini und Chemnitz's systematischem Conchilien-Kabinet. Kassel. 113 pp.

PFEIFFER, L. 1841. Symbolae ad historiam Heliceorum. 1: 88 pp. Cassellis.

PFEIFFER, L. 1843–1852. Die Schnirkelschnecken (Gattung *Helix*). in F. H. W. Martini & J. H. Chemnitz, Systematisches Conchylien-Cabinet, Forgesetzt von Haofrath Dr. G. H. v. Schubert und Professor Dr. J. A. Wagner. In Verbindung mit Dr. Philippi, Dr. Pfeiffer und Dr. Dunker neu herausgegeben und vervollständigt von Dr. H. C. Küster. Ersten Bandes zwölfte Abtheilung [first part], (68): 73–96, pls. 22–27 (1843); (58): i–xv + 49–56, pls. 6, 9–11, 13–14 (1846a); (77): 153–176, pls. 40–45 (1848a); Zweiter Theil, (112): 137–184, pls. 126–131 (1852). Nürnberg. See: Smith, E. A. & H . W. England, 1937. Journal of the Society for the Bibliography of Natural History 1:89–99.

PFEIFFER, L. 1845. Kritische Bemerkungen. Zeitschrift für Malakozoologie 2:21–24.

PFEIFFER, L. 1846b–1854. Die gedeckelten Lungenschnecken. (Helicacea et Cyclostomacea). in F. H. W. Martini & J. H. Chemnitz, Systematisches Conchylien-Cabinet, Forgesetzt von Haofrath Dr. G. H. v. Schubert und Professor Dr. J. A. Wagner. In Verbindung mit Dr. Philippi, Dr. Pfeiffer und Dr. Dunker neu herausgegeben und vervollständigt von Dr. H. C. Küster. Zweite Abtheilung, (61): 1–24, pls. 1–3, 5–7 (1846b); (136): 309–356, pls. 43–48 (1854). Nürnberg. See: Smith, E. A. & H . W. England, 1937. Journal of the Society for the Bibliography of Natural History 1:89–99.

PFEIFFER, L. 1847–1876. Monographia Heliceorum viventium sistens descriptiones systematicas et criticas omnium huius familiae generum et specierum hodie cognitarum. 1: xxxii + 160 pp. (1847), Pp. 161–484 (1848b); 3: vii + 711 pp. (1853); 4: ix + 920 pp. (1859); 5: xii + 565 pp. (1868); 7: x + 674 pp. (1876). Lipsiae.

PHILIPPI, R. A. 1836. Enumeratio molluscorum Siciliae cum viventium tum in tellure tertiaria fossilium, quae in itinere suo observavit auctor. 1, xiv + 267 pp., pls. 1–12. Berolini.

PHILIPPI, R. A. 1844. Enumeratio molluscorum Siciliae cum viventium tum in tellure tertiaria fossilium, quae in itinere suo observavit. 2: iv + 303 pp., pls. 13–28. Halis Saxonum.

PIERSANTI, C. 1933. La fauna malacologica della Valle Esina (Iesi-Marche). Bollettino di Zoologia 4:75–100.

PILSBRY, H. A. 1895. Guide to the Study of Helices (Helicidae, Vol. 7). Manual of Conchology, Structural and Systematical, with the Illustrations of the Species. Second series: Pulmonata, 9 (36): iii–xlviii + 161–366, pls. 41–71.

PRIETO, C. P. 1986. Estudio sistematico y biogeografico de los Helicidae (sensu Zilch, 1959–60) (Gastropoda: Pulmonata: Stylommatophora) del Pais Vasco y regiones adyacentes. Universidad del Pais Vasco, Facultad de Ciencias, doctoral thesis, 393 pp., 10 pls.

REEVE, L. A. 1854. Conchologica Iconica or, illustrations of the shells of molluscous animals. Vol. VII. Containing a monograph of the genus *Helix.* Pls. 175–210, title p., index. See: Roth, B., 1987. The Veliger 30:95–86.

REULEAUX, C. 1889. Katalog für die Heliceen-Genera *Euparypha* Hartm. und *Xerophila* Held aufgestellt, nach Dr. C. A. Westerlund. München. 51 pp.

RICHARDSON, L. 1980. Helicidae: Catalog of species. Tryonia, 3: iii + 697 pp.

ROSSMÄSSLER, E. A. 1837. Iconographie der Land- und Süsswasser-Mollusken, mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten. 1 (5–6): 1–2 + 1–70 pp., pls. 21–30.

SALIS MARSCHLINS, C. U. 1793. Reisen in verschiedenen Provinzen des Königreichs Neapel. Zürich und Leipzig. 442 pp., 10 pls. Original German edition unobtainable; English translation consulted: Travels through various provinces of the Kingdom of Naples in 1789. Appendix: a catalogue of such shells as came to my knowledge out of the sea, that bounds the kingdom of Naples. Translated from the German by Anthony Aufere, London, 1795. iv + viii + 527 pp., 8 pls., 2 maps.

SCHAUFUSS, L. W. 1869. Molluscorum Systema et Catalogus. System und Aufzählung sämmtlicher Conchylien der Sammlung von Fr. Paetel. Dresden. xiv + 119 pp.

SCHILEYKO, A. A. 1972. Some aspect of study of recent nonmarine gastropod mollusks. Results of Sciences. Zoology of Invertebrates, 1: 188 pp.

SCHILEYKO, A. A. 1978. Molluscs. Land molluscs of the superfamily Helicoidea. Fauna SSSR, (N.S.), 17: 384 pp. [in Russian].

SCHILEYKO, A. A. 1991. Taxonomic status, phylogenetic relations and system of the Helicoidea sensu lato (Pulmonata). Archiv für Molluskenkunde 120:187–236.

SOWERBY, G. B. 1843a. [without title]. Proceedings of the Zoological Society, 1843:29–31.

SOWERBY, G. B. 1843b. Monograph of the genus *Cyclostoma.* Thesaurus Conchyliorum or Monographs of Genera of Shells, 1(3):83–156, pls. 23–31.

THIELE, J. 1931. Handbuch der systematischen Weichtierkunde. 2:377–778. Jena.

TRYON, G. W. 1887. Helicidae:—Vol. I. Manual of Conchology, Structural and Systematic, with Illustrations of the Species, 3(9–12):1–313, pls. 1–63.

WESTERLUND, C. A. 1876. Fauna Europaea. Molluscorum extramarinorum. Prodromus. Fasciculus 1: Pp. 1–160. Lund.

WESTERLUND, C. A. 1889. Fauna der in der paläarktischen Region (Europa, Kaukasien, Sibirien, Turan, Persien, Kurdistan, Armenien, Mesopotamien, Kleinasien, Syrien, Arabien, Egypten, Tripolis, Tunesien, Algerien und Marocco) lebenden Binnenconchylien. II. Genus *Helix.* Berlin. 473 + 31 pp.

WOOD, W. 1825. Index Testaceologicus. London. xxxii + 188 + [2] pp., 38 pls.

ZILCH, A. 1960. Euthyneura in O. H. Schindewolf (ed.), Handbuch der Paläozoologie 6(2):401–600. Gebrüder Borntraeger: Berlin.

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Homoplastic Loss of Dart Apparatus, Phylogeny of the Genera, and a Phylogenetic Taxonomy of the Helminthoglyptidae (Gastropoda: Pulmonata)

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Abstract. The pulmonate land snail clade Helminthoglyptidae is redefined as *Helminthoglypta tudiculata* (A. Binney, 1843) and all gastropods that share a more recent common ancestor with it than with the clade (Xanthonychidae,Bradybaenidae)—the first phylogeny-based, rather than character-based, definition of this taxon. Many prior definitions of the group included a geographic component. Maximum-parsimony cladistic analysis was performed on 22 terminal taxa (named and unnamed) conventionally referred to the Helminthoglyptidae. The data set includes 21 multi-state shell, integument, and reproductive system characters. The resulting phylogenetic hypothesis indicates that absence of a dart sac is a homoplasy, originating at least six times; total absence of mucus glands originated homoplastically at least five times. The taxa usually assigned to *Sonorella* form a basal clade (SONORELLAMORPHA) that is the sister group of the rest of the Helminthoglyptidae (HELMINTHOGLYPTAMORPHA). Because SONORELLAMORPHA and HELMINTHOGLYPTAMORPHA share no common ancestor not also shared by the presumptive sister group (Xanthonychidae,Bradybaenidae), the monophyly of Helminthoglyptidae of authors is open to question. More information is needed to determine whether SONORELLAMORPHA is contained within HELMINTHOGLYPTIDAE as defined herein. The results of the analysis are expressed in a rank-free, phylogeny-based taxonomy. Four new genus-group taxa and 11 suprageneric taxa are described.

INTRODUCTION

The pulmonate land snail taxa of western and southwestern North America belonging to the Helminthoglyptidae are numerically significant—46% of the species of native land mollusks in California (Roth, unpublished); 45% of the species in Arizona (Bequaert & Miller, 1973)—and potentially important for understanding regional climatic history and biogeography (Smith et al., 1990). Patterns of ancestry and descent among these taxa usually have been addressed only on a case-by-case basis, and published classifications have not had a phylogenetic underpinning. A rigorous phylogenetic hypothesis is needed for meaningful further study.

Supraspecific taxonomy of the group has been based largely on accessory reproductive structures, including mucus glands and dart sac, which function in courtship and mating (Webb, 1942, 1951, 1952a). Absence of these structures in many genera is widely thought to be due to secondary simplification, although this assumption remains basically untested. A lively debate exists as to how many times the loss of dart sac and/or mucus glands has occurred.

The purpose of this paper is to apply the methods of phylogenetic systematics (Hennig, 1966; see also Wiley, 1981; Brooks & McLennan, 1991) to the analysis of evolutionary relationships among the genera contained in Helminthoglyptidae as defined herein. I used the program HENNIG86 (Farris, 1988) to generate a set of maximum-parsimony cladograms based on 22 terminal taxa and 21 characters representing 61 character states; a strict consensus tree (Nelson, 1979) is presented to show the groups in common to the resulting cladograms and used as a basis for discussion of the taxonomy of the Helminthoglyptidae.

The cladograms allow an estimate of the extent of homoplasy represented by absence of dart sac and mucus glands, and also, for each case, whether that absence is apomorphic or plesiomorphic with respect to its ingroup. Absence of dart sac and absence of mucus glands were not included in the originally analyzed data set, but were mapped afterward on the consensus tree.

Historically, Helminthoglyptidae has undergone several definitions and redefinitions. Dart-bearing helicoids of the Americas were long included in a broadly construed family Helicidae Rafinesque, 1815, roughly equivalent to what conventional land snail taxonomy now designates as the suborder Holopoda. Pilsbry's (1893–1895) "Belogona Euadenia" contained taxa with "mucus glands sacculated, club-shaped, bulbous or flattened, glandular, inserted on dart sack or at its base . . ." (Pilsbry, 1893–1895:xxxvi), spread among 12 genera. The primary division of Belogona Euadenia was into American and Eurasian groups, without supporting characters (Pilsbry, 1893–1895:xxx). The taxa considered in the present paper were included in the "sections" *Micrarionta* Ancey, 1880, and *Helminthoglypta* Ancey, 1887, of genus *Epiphragmophora* Döring, 1875.

Pilsbry (1939:1, 24) named the family Helminthoglyptidae, typologically defined by the genus *Helminthoglypta* (type species *Helix tudiculata* A. Binney, 1843). His diagnosis, "dart sac or sacs and mucous glands present, the latter club-shaped, globular or irregular (not tubular or finger-shaped), inserted close to the base of the dart sac; talon short, concealed in the albumen gland; shell usually with a band above periphery, or sometimes with three or many bands, the lip from simple to reflected, not toothed" (Pilsbry, 1939:1), differentiated Helminthoglyptidae from Camaenidae, Sagdidae, and Polygyridae ("no dart apparatus, talon exposed") and from the remainder of the old Belogona (in which the mucus glands are tubular or fingerlike). He also provided an enumerative definition—that is, he pointed to the taxa he expected to conform to his character-based definition—stating that the family included "the American dart-bearing helices" (Pilsbry, 1939: 25).

Pilsbry (1939) also named the subfamily Sonorellinae (originally including only the genus *Sonorella* Pilsbry, 1900, but later amended [Pilsbry, 1948:1093] to include *Sonorelix* Berry, 1943) for species lacking the diagnostic dart sac and mucus glands but agreeing with the rest of the Helminthoglyptidae in shell, jaw, and talon characters. In an insight with lasting impact on helminthoglyptid taxonomy, he inferred that the reproductive system in Sonorellinae is secondarily simplified,[1] but he did not provide a test of whether the dartless condition is apomorphic or plesiomorphic.

For nearly 40 years Pilsbry's concept of Helminthoglyptidae was widely accepted and the taxa defined by its enumerative/geographic and character-based definitions assumed to be coextensive. Baker (1956, 1959) observed that the earliest family-group name based on a member of the group was Xanthonychidae Strebel & Pfeffer, 1879 (based on *Xanthonyx* Crosse & Fischer, 1867), and a minority of authors adopted Xanthonychidae as the name to use, but the family's diagnosis and scope went largely unchallenged. Richardson (1982) catalogued the species.

Schileyko (1978, 1979) removed the Humboldtianinae, in which multiple dart sacs subtend compact mucus glands surrounding the vagina, from Helminthoglyptidae. Miller (1987), Miller & Naranjo-García (1991), and Evanoff & Roth (1992) followed Schileyko in recognizing Humboldtianidae as a distinct taxon.

Nordsieck (1987; translation by Emberton, 1992) revised the systematics of the Helicoidea at the family level, using cladistic methods to derive a statement of relationships among Xanthonychidae, Sphincterochilidae Zilch, 1960, Hygromiidae Tryon, 1866, Helicidae, and Bradybaenidae Pilsbry, 1934. His classification below the level of family was not based on the principle of grouping by synapomorphy, but relied on arbitrary magnitude of difference and gradal criteria (e.g., his refusal [Nordsieck, 1987:19] to group shelled snails and semislugs in a single subfamily). It included numerous new subfamilies and tribes, many of them monotypic at the next lower category (e.g., Monadeniinae, new subfamily for genus *Monadenia* Pilsbry, 1895; Bunnyini, new tribe for *Bunnya* Baker, 1942) and apparently proposed as much for "bookkeeping" reasons as for their information content (cf. Simpson's [1961] advocacy of exhaustive subsidiary taxa, and critique of same by Farris [1976]). His taxon definitions were partly character-based and partly enumerative. The character-based component was not rigorously diagnostic (for Helminthoglyptini, "diverticulum present; stimulatory organ present, lacking in one group"; for Sonorellini, "diverticulum usually lacking; stimulatory organ lacking" [Nordsieck, 1987:20; Emberton translation]); the enumerative component was rather casually employed, as in references to the otherwise undefined "*Micrarionta*-Gruppe" and "*Sonorella*-Gruppe," and sometimes erroneous (*Micrarionta,* placed by Nordsieck in the Helminthoglyptini, lacks a spermathecal diverticulum).

Miller & Naranjo-García (1991) used magnitude of difference criteria to modify the cladistic family-level classification of Nordsieck (1987). They redefined Helminthoglyptidae as helicoid snails having, in dart-bearing species, one or both mucus glands consisting of wide membranes that wrap around parts of the anterior end of the reproductive tract. Under this definition, Helminthoglyptidae consists of a number of genera of the North American west and southwest, distinguished from Mesoamerican genera (Xanthonychidae) in which mucus glands are nodulose, tubular, or vesicular. They reassigned *Monadenia,* formerly considered a genus of Helminthoglyptidae, to Bradybaenidae. Like Pilsbry (1939), Miller & Naranjo-García (1991) included genera that lack mucus glands and dart apparatus through secondary simplification but did

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[1] It was not the first time he had done such a thing. In Pilsbry & Vanatta (1898:68), he referred to the absence of mucus glands in *Glyptostoma* Bland and Binney, 1873, as "a degenerative feature unique in *Belogona Euadenia.*" *Glyptostoma* is now assigned to the Megomphicidae. The possibility of a cultural predisposition to see taxa lacking certain organs as derived or degenerate belongs properly to the history of science; I will not pursue it further here, except to note that Roth (1981) remarked on a parallel case in the early taxonomy of *Monadenia.*

not specify other morphologic criteria for inclusion of these genera. They stated that loss of mucus glands and dart apparatus had happened multiple times (citing Miller, 1970, 1973, 1981a), so that Sonorellinae of Pilsbry and Sonorellini of Nordsieck were polyphyletic groups.[2]

Schileyko (1991) proposed a systematic revision of the Helicoidea *sensu lato* based entirely on the characters of the lower part of the reproductive tract. He hypothesized an archetypal, ancestral form and from there spun an imaginative evolutionary history for the superfamily. The narrative consists of a series of sketches explaining how certain configurations of the genitalia could have come about through changes to other (mostly existing) configurations; hypothetical configurations were introduced as necessary. Criteria of parsimony or independent characters supporting or falsifying these hypotheses of ancestry and descent were not considered.

Schileyko's (1991) innovations in classification included Eremariontinae, a new monotypic subfamily of Helminthoglyptidae, for *Eremarionta* Pilsbry, 1913; removal of all dartless genera from Miller & Naranjo-García's (1991) Helminthoglyptidae to subfamily Sonorellinae of Xanthonychidae; and new subfamily Micrariontinae of Xanthonychidae. A character-based and an enumerative definition were provided for each family-group taxon, but the arrangement of taxa was based largely upon the evolutionary narrative and gradal criteria. Because many genera were considered to be derived directly from other genera (e.g., Schileyko, 1991:fig. 7), the system included numerous paraphyletic groups.[3]

Emberton (1991) cladistically analyzed 17 family-group taxa of land snails, including Helminthoglyptidae, in a search for the closest outgroup of Polygyridae. *Helminthoglypta tudiculata* represented Helminthoglyptidae in the analysis; *Cepolis varians* (Menke, 1829) represented Xanthonychidae. Maximum-parsimony analysis generated a consensus tree containing the polytomy (Helminthoglyptidae, Xanthonychidae, Bradybaenidae, Polygyridae, (Thysanophoridae,(Camaenidae,Sagdidae))). This clade is united by the synapomorphies of descending ureter partly or variably roofed, ureteric interramus shallowly and broadly excavated, and left parietal and visceral ganglia fused.

The distinction between Xanthonychidae as restricted by Miller & Naranjo-García (1991) and Bradybaenidae needs further investigation. Schileyko (1991) reassigned *Monadenia* (as subfamily Monadeniinae) to Xanthonychidae, but it is pointless to argue the allocation until an objective morphological distinction between Xanthonychidae and Bradybaenidae is in place. In common with the Asian Bradybaenidae (Azuma, 1982) and apparently with Central American Xanthonychidae (e.g., *Trichodiscina* Martens, 1892), *Monadenia* has a fundamentally four-banded shell (Roth, in preparation). In the few multiple-banded helminthoglyptids (some species of *Xerarionta* Pilsbry, 1913), the banding is complex and not obviously fourfold. The lower, ductlike portion of the mucus gland in *Monadenia* may be homologous to the Nebensack in other Bradybaenidae (A. A. Schileyko, written communication, 1990). Xanthonychidae and Bradybaenidae both have a single dart sac, homoplastic with the single dart sac in Helicidae, according to Schileyko's (1991) narrative, but possibly homologous with that in Helminthoglyptidae.

I provisionally regard (Xanthonychidae,Bradybaehnidae) as the sister group of Helminthoglyptidae. Other groups, such as Helicostylidae Ihering, 1909, and Epiphragmophoridae Hoffman, 1928, are too poorly known to be considered at this time.

In recent years, it has become increasingly clear that conventional biological taxonomy (that is, the taxonomy of which the nomenclatural expression is the subject of the International Code of Zoological Nomenclature) is limited in its ability to express the evolutionary relations that are the concern of phylogenetic systematics. One radical solution, taxon definitions based on phylogenetic relationships, has been explored in several recent papers (Wiley, 1979, 1989; Rowe, 1987; de Queiroz, 1988; Gauthier, Estes & de Queiroz, 1988; de Queiroz & Gauthier, 1990, 1992). In this paper I propose a taxonomy of the Helminthoglyptidae (I deliberately avoid the term "classification" for reasons discussed by de Queiroz & Gauthier, 1990) that is based on the phylogenetic hypothesis generated by this study. Between the most inclusive taxon (Helminthoglyptidae) and the least inclusive (species), the system conflicts in many ways with the traditional ("Linnaean") classification. Because the taxa of the phylogenetic taxonomy are all monophyletic groups by definition, I believe this system will prove more useful for future analysis than the traditional classification.

For purposes of this study, I define Helminthoglyptidae as ***Helminthoglypta tudiculata*** **(A. Binney, 1843) and all gastropods that share a more recent common ancestor with it than with the clade (Xanthonychidae, Bradybaenidae).** This is the first phylogeny-based definition of the family; all previous definitions have been character-based. It is a stem-based definition (de Queiroz & Gauthier, 1990, 1992) (that is, one that specifies the meaning of a name by associating the name with a clade of all organisms sharing a more recent common ancestor with one designated descendant than with another).

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[2] This is not quite fair to Nordsieck, who had stated that groups resulting from parallel evolution ought not to be united in the single subfamily Sonorellinae and, citing Miller as authority, that there were additional groups without a dart sac, independent of the "*Sonorella*-Gruppe" that made up his Sonorellini (Nordsieck, 1987:19, 20). He placed the dartless genus *Greggelix* in Helminthoglyptini.

[3] Solem (1991) criticized the Schileyko classification as "malacological hyperinflation" because certain groups of taxa were recognized at higher categoric levels than was traditional. This comes down to an argument about taste in ranking: Solem did not maintain that the groups recognized by Schileyko were anything other than natural, monophyletic groups or propose any alternative set of relationships among them.

Under the present state of knowledge, an apomorphy-based definition (de Queiroz & Gauthier, 1990, 1992) that takes in the same membership is "the first helicoid snail to have one or more membranous mucus glands, and all of its descendants." Both definitions define monophyletic taxa (a monophyletic taxon [*sensu* Farris, 1974; = holophyletic, Ashlock, 1971] is composed of an ancestor and all of its descendants). Taxa could be discovered that are members of the stem-based taxon but not of the apomorphy-based taxon (Figure 1). Because at present both taxa seem to comprise the same array of subordinate taxa, I propose no separate name for the apomorphy-based taxon. This study can be viewed as a test of the hypothesis that Helminthoglyptidae of Miller & Naranjo-García (1991) and Helminthoglyptidae as defined herein are coextensive. As shown below, the inclusion of the taxa conventionally referred to *Sonorella* is problematical.

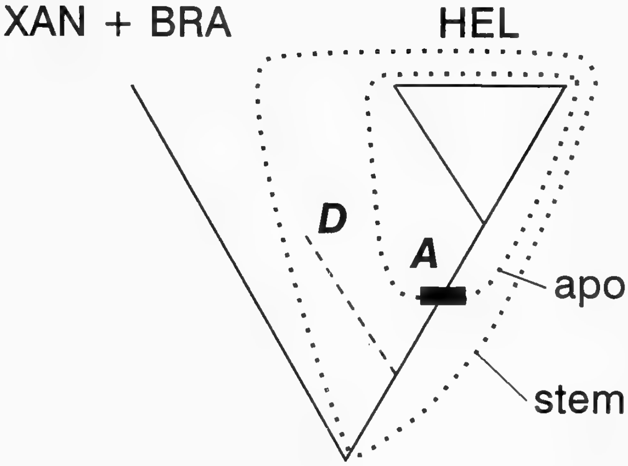

Figure 1

Relationship of apomorphy-based (apo) and stem-based (stem) definitions of HELMINTHOGLYPTIDAE (HEL). *A* = origin of autapomorphy; *D* = hypothetical newly discovered taxon; XAN+BRA = (Xanthonychidae,Bradybaenidae).

PREVIOUS WORK ON PHYLOGENY OF TAXA OF HELMINTHOGLYPTIDAE

Here follows a brief chronologic review of previous work touching on the phylogenetic relationships among taxa in the Helminthoglyptidae. Discussions in which "relationship" is equated with similarity or with membership in a particular character-based group, without explicit evolutionary implications (e.g., Berry, 1943, 1947) are omitted.

Webb (1952b) stated that the Sonorellinae evolved from *Micrarionta* by loss of dart and mucus gland systems.

Gregg (1960) briefly hypothesized reproductive system transformations: increased complexity in *Helminthoglypta* and loss of diverse structures in other genera.

The revisionary thesis of *Sonorella* by Miller (1967a) introduced the concept that the absence of dart sac and mucus glands was homoplastic, citing as examples (1) *Mohavelix micrometalleus* (Berry, 1930) from the El Paso Mountains, eastern Kern County, California, formerly assigned to *Sonorella* but conchologically more similar to *Chamaearionta aquaealbae* (Berry, 1922) and thought to be derived from a common ancestor with it; and (2) populations of *Eremarionta argus* (Edson, 1912) from the Argus Mountains, Inyo County, California, that lacked any trace of dart sac and mucus glands. He invoked "saltational" chromosomal reorganization (Lewis, 1966), occurring in marginal, intensely interbreeding populations, for the seemingly drastic and sudden loss of reproductive structures.

Gregg & Miller (1969) described *Sonorella allynsmithi* from the Phoenix Mountains, Maricopa County, Arizona, noting that the habitat was more typical of *Eremarionta* than of *Sonorella* and that certain shell and anatomical characters were also *Eremarionta*-like. They stated that the similarity might be due to convergent evolution or might "tend to point to *S. allynsmithi* as a relatively unchanged descendant of the ancestral *Sonorella* founder" (Gregg & Miller, 1969:92).

Miller (1970) described *Helminthoglypta micrometalleoides* from northern slopes of the El Paso Mountains, eastern Kern County, California, and suggested that it was ancestral to *Mohavelix micrometalleus* from southern slopes of the same range. He mentioned six genera as (presumably independent) instances of secondary simplification of reproductive structures.

Miller (1971:64) stated that *Sonorella* "probably arose from a marginal population of *Sonorelix* or *Eremarionta.*"

Miller (1972) proposed the new genus *Greggelix* for several species from Baja California, Mexico, and reaffirmed that evidence indicated that loss of dart apparatus had occurred more than once in Helminthoglyptidae.

Miller (1981a) proposed the new genus *Eremariontoides* for *Sonorella argus* Edson, 1912, of the Slate and Argus ranges, Inyo County, California, and suggested that it had "undergone major genetic changes from the populations in the Panamint and Avawatz ranges" (Miller, 1981a: 438–439) which he described as a new species, *Eremarionta greggi.*

Miller (1985:98) suggested that the new subgenus *Rothelix* "probably evolved from an *H*[*elminthoglypta*]. *traskii*-like ancestor and spread, during pluvial times, throughout the area that it now occupies."

Pearce (1990) was the first author to apply explicitly cladistic methods to the analysis of relations among any helminthoglyptid genera. (*Monadenia,* cladistically analyzed by Roth [1981], is no longer considered helminthoglyptid; Nordsieck's [1987] use of cladistic methodology was limited to taxa at the family level.) He presented (Pearce, 1990:figs. 5, 7) the tree (*Helminthoglypta,* ((*Plesarionta,Xerarionta*),(*Eremarionta,Micrarionta*))), with *Micrarionta* further analyzed into its component species. Pearce's results have little applicability to the present study for several reasons: The group he analyzed was not holophyletic; only the above genera were considered, for the limited purpose of polarizing character-state transformations within *Micrarionta.* The data set (Pearce, 1990:table 3) includes erroneous anatomical information (e.g., absence of a spermathecal diverticulum in *Eremarionta*; presence of a verge in *Xerarionta* and absence of a verge in *Plesarionta*; presence of a dart sac in *Micrarionta opuntia*). The codings for presence/absence of papillae on embryonic whorls differ from my observations presented herein. The concepts of *Helminthoglypta* and *Eremarionta* are based on few species, resulting in an underestimated range of form—excluding, for example, *Helminthoglypta* species with closed umbilicus or depressed shell. The data set for the consensus tree (Pearce, 1990:fig. 7) is based predominantly on shell dimensions, doubtfully useful for broader intergeneric comparison. Five of the eight character-states that define node 4 of the consensus tree (that is, *Micrarionta*) are size-related characters that show reversals within the *Micrarionta* clade.

In his revision of the Helicoidea, commented on above, Schileyko (1991) reasserted monophyly of the Sonorellinae. He presented a scenario based solely on characters of the lower reproductive tract, in which genera were derived sequentially from other contemporary genera (*Mohavelix* Berry, 1943, from *Sonorella*; *Sonorella* from *Sonorelix,* and so forth). His "family trees" used cartoons emphasizing the characters that supported his scenario; other characters were selectively excluded from the discussion (e.g., the penial sheath of *Sonorella*). All genera, whether the monotypic *Eremariontoides* or the speciose *Sonorella,* were treated as single entities—grades—along a few linear evolutionary paths; there was no representation of the diversity of side branches. Schileyko's (1991:223, fig. 5) depiction of *Eremarionta* and *Micrarionta* is incorrect in that mucus glands are shown inserting well up on the dart sac, remote from the vagina. In these genera the glands actually insert either on the vagina just above the opening of the dart sac or in the crotch between vagina and dart sac; the true condition is well illustrated by Pilsbry (1939) and Miller (1981a).

In summary, the present state of helminthoglyptid phylogenetics consists of two competing scenarios in which either one (according to Schileyko) or several (according to Miller) ancestral taxa with a "full kit" of accessory reproductive structures give rise to taxa lacking dart sac and/or mucus glands. Schileyko's (1991) work is an excellent example of conjectural, narrative (*sensu* Ball, 1976) history: a series of "how-possibly explanations" (Dray, 1957; O'Hara, 1988). It is not couched in testable propositions and therefore provides no objective way of dealing with new data. It uses the four devices—graphical and textual sequencing of contemporary taxa, pruning of side branches, recognition of paraphyletic taxa, and differential resolution of different parts of the tree—criticized by O'Hara (1992) as harmful to representations of the evolutionary past.

The papers of Miller look mainly to present geographic neighbors for ancestry of dartless taxa (*Helminthoglypta micrometalleoides* for *Mohavelix*; *Eremarionta greggi* for *Eremariontoides*; *Xerarionta* for *Greggelix*). This history is played out on a snail geography not very different to that of the present, and geological time, as far as it is considered, extends no farther back than "pluvial times" (Miller, 1985). Alternative theories of origin, and the extent to which other characters support or falsify them, are rarely considered. In this style of scenario-building, the fundamental assumption is of homoplasy—multiple origins of the dartless condition.

In contrast, the approach employed here starts with and maintains the assumption of homology until homoplasy is indicated by the weight of evidence from other, independent characters (Hennig, 1966; Brooks & McLennan, 1991). Since geography plays no part in the generation of the phylogenetic hypothesis, the hypothesis can be used to analyze biogeographic history of the group without introducing circularity into the argument. Similarly, excluding absence of dart sac and mucus glands from the data set analyzed and then mapping those absences on the consensus tree provides a non-circular approach to the number of independent origins of dartlessness.

MATERIALS AND METHODS

The terminal taxa entered in this analysis are listed alphabetically below, along with the representative species examined anatomically and references to published sources of information. I have examined shells of almost every species of the family, including at least one representative of every terminal taxon. Most reproductive system information is based on stained whole mounts prepared by the method of Miller (1967a). Emberton (1988) correctly pointed out limitations of the slide-mount method. I believe, in this instance, the ability to consult repeatedly numerous specimens permanently preserved in standard orientation justified reliance on whole mounts, as long as possible artifacts of the method were taken into account. Simultaneous dissection, recommended by Emberton (1991), was not possible in a situation where fresh material is unavailable for many scarce taxa.

The specimen lots consulted are too numerous for individual citation, but include material in my own reference collection, the Santa Barbara Museum of Natural History, the collection of Walter B. Miller, and the California Academy of Sciences.

Most of the terminal taxa originally were proposed as genera, subgenera, or informal groups (e.g., the *Sonorella hachitana* group of Pilsbry, 1939). Several nominal taxa were found to be diverse as to the characters analyzed and were divided into separate taxa (e.g., *Micrarionta*$_1$ and *Micrarionta*$_2$). In speciose terminal taxa of groups needing monographic revision (like *Charodotes,* where a verge is variably present or absent, or the subtaxa of *Sonorella*), separate taxa were considered early in the analysis, but were condensed into single taxa once it became clear that

Table 1

Distribution of character states among terminal taxa of Helminthoglyptidae and outgroup.

Terminal taxon	Symbol	Character no.			
		1–5	6–10	11–15	16–21
Chamaearionta	CHM	AABBA	EBDAB	ABCBB	BBCBAB
Charodotes	CHR	CBAAB	BBABB	AACAB	BBBBAB
Coyote	COY	CBAAB	BBAEB	ACCAB	BBCBAB
Eremarionta$_1$	ER1	AAABA	EBADB	ACCBB	BBBBBB
Eremarionta$_2$	ER2	AAABA	BBACB	AACBB	BBBBBB
Eremariontoides	ERO	AE?BC	BBBDB	ACCBB	BBBBBB
Greggelix	GRE	ADBBC	CBCAB	AECAB	BBCBBA
Helminthoglypta$_1$	HL1	CBAAB	BBABB	AACAB	BABBAB
Helminthoglypta$_2$	HL2	ABAAA	BBABB	AACAB	BABBAB
Herpeteros	HER	AE?BC	EBDAA	ADCAB	BBBBBA
Martirelix	MAR	ADBBC	BBCAA	AFCAB	BBCBBA
Micrarionta$_1$	MI1	AABBA	ABAAB	AECAB	BBBABB
Micrarionta$_2$	MI2	ACBBC	ABAAB	AECAB	BBCABB
Mohavelix	MOH	AE?BC	ABBAB	AACCB	BBCBAB
Myotophallus$_1$	MY1	AE?BC	ABBAA	ABBFB	BBABAB
Myotophallus$_2$	MY2	AE?BC	ABBAB	ABBBB	BBBBAA
Plesarionta	PLE	AABBA	CBCAB	AECDA	BAABAB
Rothelix	ROX	BBAAB	BBABB	BBCAB	BBBBAB
Sonorelix	SLX	AE?BC	DAAAB	AACCB	BBBBBB
Sonorella binneyi group	SNB	AE?BC	ABBAA	AAAFB	BBABAA
Sonorella granulatissima group	SNG	AE?BC	ABBAA	AGAGB	BBCBAA
Sonorella hachitana group	SNH	AE?BC	ABBAA	AGAFB	BBABAA
Xerarionta	XER	AABBA	CBCAB	ABCEA	AAABAB
outgroup	OUT	AABBA	ABAAB	AAABB	BBBBAB

they did not affect the framework of the cladograms being produced.

Analysis

Cladistic analysis of the taxon/character matrix (Table 1) was performed using the implicit enumeration algorithm of HENNIG86 (Farris, 1988) with the branch-breaking and successive approximations weighting procedures. From the set of minimum-length cladograms generated, a strict consensus tree (Nelson, 1979; Sokal & Rohlf, 1981) was computed. In the data matrix analyzed, character-state trees were represented by mixed coding (Brooks & McLennan, 1991). All character-states were treated as ordered. No weighting was assigned *a priori* to the characters of any one system; the successive approximations option of HENNIG86 reduced the number of equal-length cladograms by an iterative series of *a posteriori* weightings (Farris, 1969; Carpenter, 1988). Character-state transformations were polarized by outgroup comparison (Watrous & Wheeler, 1981; Brooks & McLennan, 1991). On the basis of Emberton's (1991) analysis of family-group taxa, (Xanthonychidae,Bradybaenidae) (represented by the genus *Monadenia*) was used as the outgroup for polarizing character-state transformations. Polygyridae was considered secondarily as an outgroup, with similar results.

Two aspects of land snail natural history influenced my evaluation of hypothesized character-state trees based on outgroup comparison. In the past, there has been some tendency to regard the variety in helminthoglyptid reproductive structures as a non-adaptive consequence of genetic drift in small populations (e.g., Miller, 1967a:228–229); but explanations involving sexual selection seem just as worthy of consideration. As Leonard (1991:45) stated, "where genital anatomy is varied sufficiently to be a useful taxonomic character at the levels of genus, subgenus and species . . . sexual selection is likely to have been important." Sexual selection does not rule out (and Eberhard [1985] argued that it tends to produce) rapid evolutionary divergence in genital characters, which may appear "saltational" in hindsight, because it leaves few intermediates.

I also considered water conservation. Desiccation may be the main cause of snail death worldwide (Solem, 1984). The cost in moisture (through mucus secretion and evaporative loss) during prolonged courtship leads to the prediction that, in semi-arid and arid habitats, structural modifications and behavior that reduce water-loss during reproduction should be selectively favored. *Monadenia* and *Helminthoglypta* species from mesic habitats undergo prolonged courtship before mating (Webb, 1942, 1951, 1952a, b; author's observations). In the Arizonan *Sonorella simmonsi* Miller, 1966, which lacks dart sac and mucus glands, the snails merely approach one another and mate (Webb, 1990); I regard this as the derived condition. Solem &

Christensen (1984) reported extreme cases of camaenid snail matings lasting less than 10 minutes in seasonally arid parts of northwestern Australia.

Taxa Included and Data Sources

Chamaearionta Berry, 1930. Originally proposed as a subgenus of *Micrarionta.* Monotypic; type species *Micrarionta aquaealbae* Berry, 1922, examined. Anatomy described and illustrated: Pilsbry (1939), Gregg (1960).

Charodotes Pilsbry, 1939. Originally proposed as a subgenus of *Helminthoglypta.* Type species *Helix traskii* Newcomb, 1861. Species examined: *Helminthoglypta* (*Charodotes*) *traskii* and 13 of the 15 other recognized species (Roth & Hochberg, 1992). Anatomy described and illustrated: Pilsbry (1939), Webb (1952a), Miller (1981c), Roth (1973, 1987a), Roth & Hochberg (1992).

Coyote Reeder & Roth, 1988. Originally proposed as a subgenus of *Helminthoglypta.* Type species *Helminthoglypta* (*Coyote*) *taylori* Reeder & Roth, 1988. Species examined: *H.* (*C.*) *taylori* and the 11 other recognized Recent species (Reeder & Roth, 1988). Anatomy described and illustrated: Pilsbry (1939), Miller (1970), Roth & Hochberg (1988), Reeder & Roth (1988).

Eremarionta Pilsbry, 1913. Originally proposed as a "section" of *Micrarionta*; separated as a genus by Bequaert and Miller (1973). Type species *Micrarionta desertorum* Pilsbry and Ferriss, 1908. Species examined: *Eremarionta greggi* Miller, 1981; *E. indioensis indioensis* (Yates, 1890); *E. i. cathedralis* (Willett, 1930); *E. i. wolcottiana* (Bartsch, 1903); *E. mexicana* (Pilsbry & Lowe, 1934); *E. rowelli* (Newcomb, 1865), subsp. indet., from Mohawk Mountains and Little Harquahala Mountains, Yuma County, Arizona. Anatomy described and illustrated: Pilsbry (1918, 1939), Miller (1981a).

In *Eremarionta rowelli,* the spermathecal diverticulum is short (Pilsbry [1907, 1939] reported it absent in *E. r. hutsoni* (Clapp, 1907) and *E. r. desertorum* (Pilsbry & Ferriss, 1908); but according to Gregg [1960] and in all dissections I have examined, a short diverticulum is present) and the verge consists of a short, broad papilla. This taxon was entered as *Eremarionta*$_1$. In *E. greggi, E. indioensis,* and *E. mexicana,* the spermathecal diverticulum is of moderate length and the verge is roughly cylindrical or conic. These taxa were entered as *Eremarionta*$_2$.

Eremariontoides Miller, 1981. Monotypic; type species *Sonorella argus* Edson, 1912, examined. Anatomy described and illustrated by Miller (1981a).

Greggelix Miller, 1972. Type species *Helix indigena* Mabille, 1895. Species examined: *Greggelix indigena*; *G. loehrii* (Gabb, 1868); *G. punctata* Miller, 1981. Anatomy described and illustrated: Miller (1972, 1981b).

Helminthoglypta Ancey, 1887. Type species *Helix tudiculata* A. Binney, 1843. Species examined: *Helminthoglypta tudiculata* and 36 of the 40 other recognized species (Roth, unpublished data). Anatomy described and illustrated: Pilsbry (1939), Berry (1959), Gregg & Miller (1976), Miller (1985), Reeder (1986), Reeder & Miller (1986a, b), Roth (1987b, 1988a). This terminal taxon is equivalent to *Helminthoglypta, sensu stricto* of Roth & Hochberg (1992).

Most species of *Helminthoglypta* have an atrial sac; these were entered as *Helminthoglypta*$_1$. In *Helminthoglypta intersessa* Roth, 1987, the atrial sac is absent and the dart sac inserts directly on the vagina (W. B. Miller, personal communication, 1992); this taxon was entered as *Helminthoglypta*$_2$.

Herpeteros Berry, 1947. Originally proposed as a subgenus of *Sonorelix.* Type species *Micrarionta* (*Eremarionta*) *inglesiana* Berry, 1928. Species examined: *Herpeteros inglesiana, H. peninsularis* (Pilsbry, 1916). Anatomy described and illustrated: Berry (1947), Gregg (1949), Miller (1972).

Martirelix Miller, 1982. Originally proposed as a subgenus of *Greggelix.* Type species *Greggelix* (*Martirelix*) *babrakzaii* Miller, 1982. Species examined: *G.* (*M.*) *babrakzaii*; *G.* (*M.*) *huertai* Miller & Roth, 1990. Anatomy described and illustrated: Miller (1982), Smith et al. (1990).

Micrarionta Ancey, 1880. Originally proposed as a subdivision of *Helix* Linnaeus, 1758; separated as a genus by Pilsbry (1913). Type species *Helix facta* Newcomb, 1864. Species examined: *Micrarionta facta*; *M. beatula* Cockerell, 1929; *M. feralis* (Hemphill, 1901); *M. gabbii* (Newcomb, 1864); *M. guadalupiana* (Pilsbry & Vanatta, 1898); *M. opuntia* Roth, 1975; *M. rufocincta* (Newcomb, 1864). Anatomy described and illustrated: Pilsbry (1927, 1939), Roth (1975). Pearce (1990) analyzed shell morphometrics. Most species of *Micrarionta* have a dart sac and two mucus glands; these were entered as *Micrarionta*$_1$. *Micrarionta opuntia* lacks a dart sac and has only one mucus gland; this taxon was entered as *Micrarionta*$_2$.

Pilsbry (1927) found the dart sac absent in one dissection of *Micrarionta guadalupiana* (Pilsbry & Vanatta, 1898); in other specimens a well-developed dart sac was present. The two specimens I dissected both had fully developed dart sacs. I suspect that Pilsbry's first specimen was immature; in his figures, the mucus glands do not seem fully developed. Further sampling is needed.

Mohavelix Berry, 1943. Originally proposed as a subgenus of *Sonorella*; separated as a genus by Miller (1967a, 1968). Monotypic; type species *Micrarionta* (*Eremarionta*) *micrometalleus* Berry, 1930, examined. Anatomy described and illustrated by Berry (1943), Miller (1970).

Myotophallus Pilsbry, 1939. Originally proposed as a subgenus of *Sonorella.* Type species *Sonorella fragilis* Pilsbry, 1939. Taxa examined: *Sonorella* (*Myotophallus*) *rooseveltiana fragilis*; *S.* (*M.*) *rooseveltiana rooseveltiana* Berry, 1922; *S.* (*M.?*) *allynsmithi* Gregg & Miller, 1969. Anatomy described and illustrated: Pilsbry (1939), Miller (1967a), Gregg & Miller (1969), Bequaert & Miller (1973). *Sonorella rooseveltiana* was entered as terminal taxon *Myotophallus*$_1$. *Sonorella allynsmithi,* grouped by Bequaert

& Miller (1973) with *S. rooseveltiana,* differs in penial retractor insertion, presence of a minute verge, and other characters and was entered as *Myotophallus*$_2$.

Plesarionta Pilsbry, 1939. Originally proposed as a subgenus of *Micrarionta*; separated as a genus by Miller (1981c). Type species *Helix stearnsiana* Gabb, 1868. Species examined: *Plesarionta stearnsiana, P. orcutti* (Dall, 1900), *P. tryoni* (Newcomb, 1864). Anatomy described and illustrated: Pilsbry & Vanatta (1898), Pilsbry (1939), Roth (1982).

In *Plesarionta stearnsiana* the spermathecal diverticulum is very short or absent, both conditions sometimes occurring in a population. In the rest of the clade ((*Plesarionta,Xerarionta*),(*Greggelix,Martirelix*)), both the spermathecal diverticulum, which receives the spermatophore in copulation, and the epiphallic caecum, which secretes it, are extremely long, suggesting an "arms race" between competing male and female systems. The epiphallic caecum in *P. stearnsiana* is long. The short or absent spermathecal diverticulum implies a different way of managing the received spermatophore; I regard it as an autapomorphy of *P. stearnsiana.*

Rothelix Miller, 1985. Originally proposed as a subgenus of *Helminthoglypta.* Type species *Epiphragmophora cuyamacensis lowei* Bartsch, 1918. Species examined: *Helminthoglypta* (*Rothelix*) *lowei, H.* (*R.*) *cuyamacensis* Pilsbry, 1895; *H.* (*R.*) *rhodophila* Reeder & Miller, 1987; *H.* (*R.*) *warnerfontis* Reeder & Miller, 1988. Anatomy described and illustrated: Pilsbry (1939; see commentary by Miller, 1985), Miller (1985), Reeder & Miller (1987, 1988).

Sonorelix Berry, 1943. Type species *Micrarionta* (*Eremarionta*) *borregoensis* Berry, 1929. Species examined: *Sonorelix borregoensis.* Anatomy described and illustrated: Berry (1943), Miller (1972).

Sonorella binneyi group. Originally proposed by Pilsbry (1939) as an informal subdivision of *Sonorella* Pilsbry, 1900; content amended by Miller (1967a). Species examined: *Sonorella binneyi* Pilsbry & Ferriss, 1910; *S. xanthenes* Pilsbry & Ferriss, 1923; and *S. sitiens sitiens* Pilsbry & Ferriss, 1915; 23 other recognized species (Bequaert & Miller, 1973; Christensen & Reeder, 1981; Miller, 1984; Naranjo-García & Miller, 1986; Naranjo-García, 1988b, 1989) were not examined firsthand but are well documented in the literature. Anatomy described and illustrated: Pilsbry (1939), Miller (1966, 1967a, c, d, 1968, 1969, 1984), Christensen & Reeder (1981), Naranjo-García & Miller (1986), Naranjo-García (1988b, 1989).

A short spermathecal diverticulum occurs in one species, *Sonorella reederi* Miller, 1984. Miller (1984) regarded it as the renewed expression of genes usually masked in *Sonorella.* The diverticulum in *S. reederi* arises low on the spermathecal duct, which is capacious below the origin (Miller, 1984:fig. 2), whereas in other Helminthoglyptidae except *Sonorelix* it arises remote from the base of the spermathecal duct, and the duct below the origin is not distended. The diverticulum in *S. reederi* may not be homologous with those of other taxa.

Sonorella granulatissima group. Originally proposed by Pilsbry (1939) as an informal subdivision of *Sonorella*; content amended by Miller (1967a). Species examined: *Sonorella granulatissima* Pilsbry, 1905, and five of the 25 other recognized species (Bequaert & Miller, 1973; Fairbanks & Reeder, 1980; Naranjo-García, 1989). Anatomy described and illustrated: Pilsbry (1939), Miller (1967a, b, c), Fairbanks & Reeder (1980). This terminal taxon includes the type species of *Masculus* Pilsbry, 1939 (*Sonorella virilis* Pilsbry, 1905), and of *Sonoranax* Pilsbry, 1939 (*Sonorella dalli* Bartsch, 1904); both of these names are available for use when the group(s) containing the type species is (are) accorded formal taxonomic recognition.

Sonorella hachitana group. Originally proposed by Pilsbry (1939) as an informal subdivision of *Sonorella*; content amended by Miller (1967a). Species examined: *Sonorella hachitana* (Dall, 1896), and 13 of the 34 other recognized species (Bequaert & Miller, 1973; Gregg & Miller, 1974; Miller, 1976; Fairbanks & Reeder, 1980). Anatomy described and illustrated: Pilsbry (1939), Miller (1966, 1967a, b, 1968, 1976), Gregg & Miller (1974), Fairbanks & Reeder (1980), Naranjo-García (1988a). This terminal taxon includes the type species of *Sonorella* Pilsbry, 1900 (*S. hachitana*); *Sonorella, sensu stricto* is the valid name when the group is accorded formal taxonomic recognition as a subset of *Sonorella.*

Xerarionta Pilsbry, 1913. Originally proposed as a "section" of *Micrarionta*; separated as a genus by Miller (1981c). Type species *Arionta veitchii* 'Newcomb' Tryon, 1866 [= *Xerarionta levis canescens* (Adams & Reeve, 1848)]. Taxa examined: *Xerarionta levis canescens*; *X. areolata* (Pfeiffer, 1845); *X. kellettii* (Forbes, 1850), *X. pandorae* (Forbes, 1850). Anatomy described and illustrated: Pilsbry & Vanatta (1898), Pilsbry (1939), Miller (1972).

Taxa Excluded

Ariolimax Mörch, 1860. Type species *Limax columbianus* Gould in A. Binney, 1851. Webb (1961) assigned this genus of large slugs to Xanthonychidae (*sensu* Baker, 1959) because he found the verge of *A. columbianus* "to be structurally as in most xanthonycids [*sic*], except that the outer epithelial layer of the verge is more prominent. . . . The verge develops almost exactly as in xanthonycid snails" (Webb, 1961:34–35). These comparisons are in the form of a two-taxon statement; no comparison was made with the structure or development of verges in other families. Webb's further comments on the development of the genitalia compared *Monadenia* (of Bradybaenidae) and *Leptarionta* Fischer & Crosse, 1872 (of Humboldtianidae or Xanthonychidae, restricted), not any taxa of Helminthoglyptidae as construed herein. In *Ariolimax* the penial retractor is broad, inserting on the summit or side of the penis; the spermatheca has a short duct; a caudal mucus pit and pronounced suprapedal grooves are present. I consider *Ariolimax* a genus of Arionoidea.

Cepolinae Ihering, 1909. Type genus *Cepolis* Montfort, 1810. In *Cepolis, Polymita* Beck, 1837, *Dialeuca* Albers, 1850, and *Setipellis* Pilsbry, 1926, a single globose mucus gland inserts on the summit of the dart sac, which in turn is seated on an atrial sac. A membrane encloses the atrial sac and other parts of the lower genitalia and bears a more or less bipartite gland consisting of numerous parallel tubules (Pilsbry, 1939; Baker, 1943). Webb's (1952a) observations on the structure of the mucus gland suggest that it is not homologous with the mucus bulbs of *Helminthoglypta,* as some authors suggested. Mucus glands inserting high on the dart sac are known in Xanthonychidae, restricted (e.g., *Metostracon* Pilsbry, 1900). No homology of the bipartite "sheath gland" with structures of the west American Helminthoglyptidae has been demonstrated. In *Cepolis* the seminal receptacle consists of a mass of tubercles; this condition has not been observed in Helminthoglyptidae as construed herein (Emberton, 1991). Nordsieck (1987) regarded Cepolinae as distinct from Helminthoglyptinae; Miller & Naranjo-García (1991) allocated it to Xanthonychidae, restricted.

Gliabates Webb, 1959. Type species *G. oregonia* Webb, 1959. Webb (1959, 1961) tentatively referred this monotypic genus of slugs to Xanthonychidae (*sensu* Baker, 1959) without specifying the characters supporting that assignment. The reproductive system includes a small spermatheca on a short, broad duct, and a globose penial sac with a lobate internal collar forming upper and lower cavities. The penial retractor muscle inserts on the summit of the penis, separated from the epiphallus. No dart apparatus is present (G. R. Webb, written communication, 1990). There are no obvious synapomorphies with Helminthoglyptidae, and I regard *Gliabates* as a genus of Arionoidea.

Glypterpes Pilsbry, 1893. Type species *Helix veterna* Meek & Hayden, 1861, a Tertiary fossil. No anatomical information available.

Mesoglypterpes Yen, 1952. Type species *M. sagensis* Yen, 1952, a Cretaceous fossil. No anatomical information available.

Tryonigens Pilsbry, 1927. Type species *Helix remondi* Tryon, 1863. Zilch (1960), followed by Miller (1967a), assigned this genus to Sonorellinae. Miller (1971) regarded it as more closely related to *Leptarionta.* Schileyko (1991) assigned it to a monotypic subfamily, Tryonigeninae, in Humboldtianidae. The short spermathecal duct, serrated dorsal keel, and smooth, practically unsculptured embryonic whorls are unlike anything in Helminthoglyptidae.

Characters

The data set consists of shell, integument, and reproductive system characters. Here are listed the characters, character states, and hypothetical character-state trees, along with comments on specific characters used in the analysis.

1. Atrial sac (fingerlike lateral outpouching of genital atrium): (A) absent (all taxa but *Charodotes, Coyote, Helminthoglypta*$_1$, and *Rothelix*); (B) present, with vagina inserting near summit of atrial sac (*Rothelix*); (C) present, with vagina inserting on atrium at base of atrial sac (*Charodotes, Coyote, Helminthoglypta*$_1$). A → B → C.

Outgroup comparison establishes absence of the atrial sac as plesiomorphic; the copulatory pad in *Monadenia* is probably not homologous, involving as it does a much larger part of the lower genital tract. The atrial sac appears to develop through a process of progressive stripping off of the dart sac-bearing part of the vaginal wall. Character-state (B) represents an intermediate stage of the sequence from (A) to (C).

Webb (1952a) proposed the term "neophore" for the atrial sac and similar structures, with reference to their being newly evolved organs. Since "newness" (i.e., apomorphy) is relative to the ingroup under study, I retain the phylogenetically neutral term, atrial sac.

2. Mucus glands: (A) paired, inserting individually on vagina (*Chamaearionta, Eremarionta*$_1$, *Eremarionta*$_2$, *Micrarionta*$_1$, *Plesarionta, Xerarionta*); (B) paired, feeding into common duct that inserts at base of dart sac (*Charodotes, Coyote, Helminthoglypta*$_1$, *Helminthoglypta*$_2$, *Rothelix*); (C) single, fully developed (*Micrarionta*$_2$); (D) vestigial (either 1 or 2 present) (*Greggelix, Martirelix*). B ← A → C; A → D.

An additional character state, (E) mucus glands absent (*Eremariontoides, Herpeteros, Mohavelix, Myotophallus*$_1$, *Myotophallus*$_2$, *Sonorelix, Sonorella binneyi* group, *Sonorella granulatissima* group, *Sonorella hachitana* group) was not entered in the analysis but was mapped on the resulting tree. Outgroup comparison establishes mucus gland insertion on the vagina at or near the base of the dart sac as plesiomorphic.

3. Bulbous reservoirs on mucus gland ducts: (A) present (*Charodotes, Coyote, Eremarionta*$_1$, *Eremarionta*$_2$, *Helminthoglypta*$_1$, *Helminthoglypta*$_2$, *Rothelix*); (B) absent (all others; coded as "?" in taxa without mucus glands or ducts [2E, above]). B → A.

Small swellings on the mucus gland ducts in *Eremarionta rowelli* and *E. greggi* probably are homologous with the mucus bulbs in *Charodotes, Coyote, Helminthoglypta,* and *Rothelix.* This character was noticed in *Eremarionta* first by Schileyko (1991). The bulbs are thin-walled in *Helminthoglypta*$_2$ but more thickly and muscularly walled in *Charodotes, Coyote, Helminthoglypta*$_1$, and *Rothelix,* in which they probably play a more active rôle in mucus ejection.

4. Membranous mucus gland tissue: (A) enveloping lower genitalia (*Charodotes, Coyote, Helminthoglypta*$_1$, *Helminthoglypta*$_2$, *Rothelix*); (B) not enveloping lower genitalia (all others). B → A.

Development of membranous mucus glands is probably related to an increase in secretory surface area. (The same thing is accomplished in Helicidae by development of multiple tubules.) The extreme elaboration of the membranous surface (character state B) in *Helminthoglypta* and the taxa conventionally regarded as its subgenera is a continuation of this trend; the driving force may be sexual selection. Miller & Naranjo-García (1991:fig. 1) assumed that membranous glands were ancestral to vesicular glands and on that basis proposed the tree (Helminthoglyptidae,(Humboldtianidae,Xanthonychidae)). However, that phylogeny runs counter to the biogeographic history proposed in the same paper, in which Helminthoglyptidae and Xanthonychidae have a vicariant relationship related to the breakup of the ancient continent "Pacifica," while Humboldtianidae is indigenous to the North American craton.

5. Dart sac: (A) present, seated on vagina (*Chamaearionta, Eremarionta*$_1$, *Eremarionta*$_2$, *Helminthoglypta*$_2$, *Micrarionta*$_1$, *Plesarionta, Xerarionta*); (B) present, seated on atrial sac (*Charodotes, Coyote, Helminthoglypta*$_1$, *Rothelix*). A → B.

An additional character state, (C) dart sac absent (all other taxa) was not entered in the analysis but was mapped on the resulting tree.

Nordsieck (1987) used the term "Reizapparat" ("stimulatory organ") as a near synonym of "Pfeilapparat" (dart apparatus), and other authors have assumed that the function of the dart sac in courtship was stimulatory, but dart emplacement apparently has more to do with mediating male and female rôles in the mating of these simultaneous hermaphrodites (cf. Chung, 1987). I retain the neutral descriptive term, dart sac.

6. Spermathecal diverticulum: (A) absent (*Micrarionta*$_1$, *Micrarionta*$_2$, *Mohavelix, Myotophallus*$_1$, *Myotophallus*$_2$, *Sonorella binneyi* group, *Sonorella granulatissima* group, *Sonorella hachitana* group); (B) of moderate length [0.7–2.0 times length of spermathecal duct above origin of diverticulum], arising well above base of spermathecal duct (*Charodotes, Coyote, Eremarionta*$_2$, *Eremariontoides, Helminthoglypta*$_1$, *Helminthoglypta*$_2$, *Martirelix, Rothelix*); (C) very long [>2.0 times length of spermathecal duct above origin of diverticulum], arising well above base of spermathecal duct (*Greggelix, Plesarionta, Xerarionta*); (D) of moderate length, arising near base of spermathecal duct (*Sonorelix*); (E) short [<0.7 times length of spermathecal duct above origin of diverticulum], arising well above base of spermathecal duct (*Chamaearionta, Eremarionta*$_1$, *Herpeteros*). A → B → C; A → D; B → E.

7. Muscular vaginal node: (A) present (*Sonorelix*); (B) absent (all others). B → A.

This character was first noticed by Miller (1972:134, fig. 2).

8. Epiphallic caecum: (A) of moderate length [0.3–2.0 times length of penis plus epiphallus] (*Charodotes, Coyote, Eremarionta*$_1$, *Eremarionta*$_2$, *Helminthoglypta*$_1$, *Helminthoglypta*$_2$, *Micrarionta*$_1$, *Micrarionta*$_2$, *Rothelix, Sonorelix*); (B) minute [<0.15 times length of penis plus epiphallus], free from vas deferens (*Eremariontoides, Mohavelix, Myotophallus*$_1$, *Myotophallus*$_2$, *Sonorella binneyi* group, *Sonorella granulatissima* group, *Sonorella hachitana* group); (C) very long [>2.0 times length of penis plus epiphallus] (*Greggelix, Martirelix, Plesarionta, Xerarionta*); (D) short [0.15–0.3 times length of penis plus epiphallus] (*Chamaearionta, Herpeteros*). A → B; A → C; A → D.

Monadenia has a moderately long epiphallic caecum. An epiphallic caecum that is minute and buried in connective tissues of the epiphallus occurs in three genera of Polygyridae—*Cryptomastix* Pilsbry, 1939; *Vespericola* Pilsbry, 1939; and *Hochbergellus* Roth & Miller, 1992; but the plesiomorphic condition in Polygyridae is an epiphallus without caecum (K. C. Emberton, personal communication, 1992).

9. Wall of lower portion of epiphallus: (A) single (all taxa but *Charodotes, Coyote, Eremarionta*$_1$, *Eremarionta*$_2$, *Helminthoglypta,* and *Rothelix*); (B) double; double-walled section more than 3/8 (0.4 times) as long as penis, not extending into verge, cylindrical or club-shaped (*Charodotes, Helminthoglypta*$_1$, *Helminthoglypta*$_2$, *Rothelix*); (C) double; double-walled section less than 3/8 (0.4 times) as long as penis, extending into verge at summit of penial chamber (*Eremarionta*$_2$); (D) double; double-walled section more than 3/8 (0.4 times) as long as penis, extending into verge, conical, expanding to prominent swelling at lower end that projects into penial chamber as a short, broad papilla (*Eremarionta*$_1$, *Eremariontoides*); (E) double; double-walled section more than 3/8 (0.4 times) as long as penis, not extending into verge, conical, expanding to prominent swelling at lower end that projects into penial chamber as a short, broad papilla (*Coyote*). A → B → C; B → D; B → E.

The portion of the male reproductive system in *Helminthoglypta* that has been called the preputial chamber (Gregg & Miller, 1976), the lower part of the penis (Miller, 1985), and the lower chamber of the penis (Reeder & Roth, 1988), is homologous with the penis of other genera, i.e., the saccular organ that is everted and performs intromission in mating. What has been called the penis (Gregg & Miller, 1976), the upper part of the penis (Miller, 1985), and the upper chamber of the penis (Reeder & Roth, 1988), is homologous with the lower portion of the epiphallus of other genera and is here referred to as such.

The transformation series proposed here (Figure 2) agrees with that of Schileyko (1991:194, fig. 4) in having the double walled condition originate above the verge. The fact that a double-walled lower portion of the epiphallus is widespread in *Eremarionta* was discovered in the course of this study; it was first depicted in Miller's (1981a:figs. 3C, 3D) figures of *E. greggi.*

10. Insertion of penial retractor muscle: (A) at or near base of epiphallus, close to or reaching summit of penis (*Herpeteros, Martirelix, Myotophallus*$_1$, *Sonorella binneyi* group; *Sonorella granulatissima* group; *Sonorella hachitana*

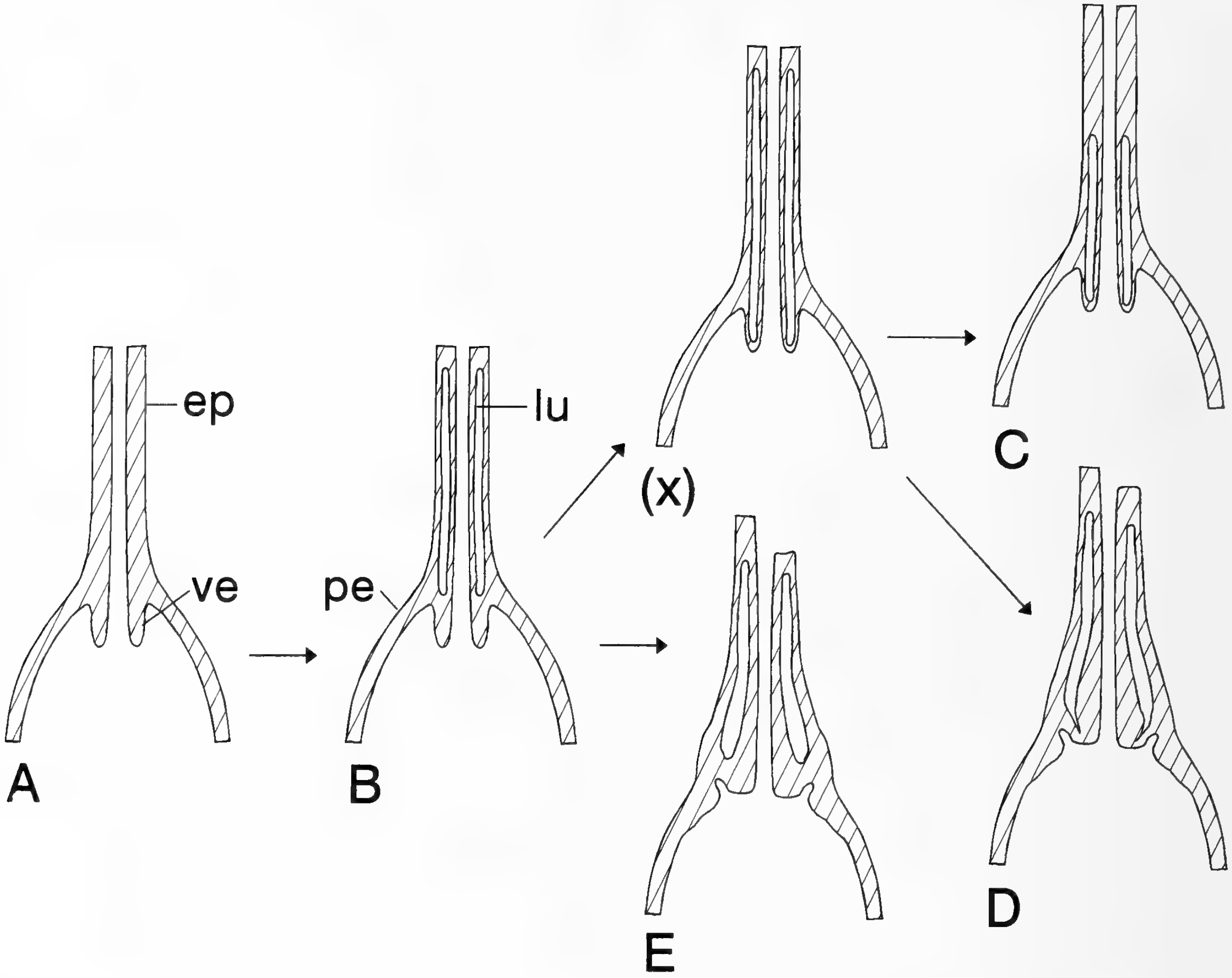

Figure 2

Diagrammatic lengthwise sections of lower portion of epiphallus and summit of penis showing transformation series for character 9. Abbreviations: ep, lower portion of epiphallus; lu, lumen of double-walled section of epiphallus; pe, summit of penis; ve, verge. (X) = intermediate grade with long lumen extending into verge.

group); (B) on epiphallus, remote from summit of penis (all others). B → A.

Outside of *Myotophallus*$_1$ and the *Sonorella* groups, a low insertion of the penial retractor muscle is associated with a large, heavy verge, possibly for reasons of mechanical efficiency.

11. Penial sac: (A) cylindrical to conic, single-chambered, without constriction setting off a separate chamber (all taxa but *Rothelix*); (B) sausage-shaped with post-medial constriction setting off a posterior chamber (*Rothelix*). A → B.

12. Verge: (A) roughly cylindrical or conic, small to medium-sized, occupying only upper end of penial sac, not markedly distending same (*Charodotes, Eremarionta*$_2$*, Helminthoglypta*$_1$*, Helminthoglypta*$_2$*, Mohavelix, Sonorelix, Sonorella binneyi* group); (B) minute or absent (*Chamaearionta, Myotophallus*$_1$*, Myotophallus*$_2$*, Rothelix, Xerarionta*); (C) consisting of a short, broad papilla developed from swelling of inner wall of double-walled lower portion of epiphallus (*Coyote, Eremarionta*$_1$*, Eremariontoides*); (D) roughly cylindrical or conic, very large, nearly filling swollen penial sac (*Herpeteros*); (E) broadly distending summit of penial sac, globose or hemispheric (*Greggelix, Micrarionta*$_1$*, Micrarionta*$_2$*, Plesarionta*); (F) broadly distending summit of penial sac, bullet-shaped to conical (*Martirelix*); (G) long, acicular, narrowly pointed, occupying much of length of penial sac (*Sonorella granulatissima* group, *Sonorella hachitana* group). A → B; A → C; A → D; A → E → F; A → G.

13. Penial sheath: (A) thin to moderately thick, not enveloping whole penis (*Sonorella binneyi* group, *Sonorella granulatissima* group, *Sonorella hachitana* group); (B) very

thick, enveloping whole penis (*Myotophallus*$_1$, *Myotophallus*$_2$); (C) absent (all others). B ← A → C.

The penial sheath in *Monadenia* is moderately thick, enveloping the basal part of the penis. The plesiomorphic condition in Polygyridae is a well-developed but not excessively thick sheath, enveloping the lower part of the penis (K. C. Emberton, personal communication, 1992).

14. Embryonic whorl sculpture: (A) radially wrinkled with overlay of sparse papillae, wrinkles usually weakly granulose (*Charodotes, Coyote, Greggelix, Helminthoglypta*$_1$, *Helminthoglypta*$_2$, *Herpeteros, Martirelix, Micrarionta*$_1$, *Micrarionta*$_2$, *Rothelix*); (B) first ≈ 0.5 whorl as in (A), thereafter papillose, papillae spirally elongated, discrete (*Chamaearionta, Eremarionta*$_1$, *Eremarionta*$_2$, *Eremariontoides, Myotophallus*$_2$); (C) first ≈ 0.5 whorl as in (A), thereafter papillose, papillae spirally elongated, confluent into network (*Mohavelix, Sonorelix*); (D) radially wrinkled, without overlay of papillae, wrinkles granulose (*Plesarionta*); (E) radially wrinkled, without overlay of papillae, wrinkles smooth (*Xerarionta*); (F) smooth or finely granulose, with spirally descending, sometimes divaricating, threads (*Myotophallus*$_1$, *Sonorella binneyi* group, *Sonorella hachitana* group); (G) coarsely granulose, with spirally descending, divaricating threads (*Sonorella granulatissima* group). C ← B → A → D → E; B → F → G.

In *Monadenia troglodytes* Hanna & Smith, 1933, sculpture of the first 0.25 whorl consists of wavy radial rugae with sparse, irregularly placed, round papillae. Over the next 0.5 whorl, the papillae become spirally elongated and tend to align in diagonal series; most of them remain discrete and do not fuse. Essentially the same pattern, character state (B), occurs in *Eremarionta, Eremariontoides,* and *Chamaearionta*; I hypothesize the origin of character state (A) by deletion of the elongation phase, and of character states (C), (F), and (G) by elaboration of it.

15. Shell color pattern: (A) including mottling and/or multiple banding (*Plesarionta, Xerarionta*); (B) not including mottling or multiple banding (all others). B → A.

16. Diagonal granulose sculpture on teleoconch: (A) present (*Xerarionta*); (B) absent (all others). B → A.

At least traces of diagonal granulose sculpture (Roth, 1984:fig. 32) occur in all species of *Xerarionta,* although they are faint and localized in some.

17. Malleation on teleoconch: (A) present (*Helminthoglypta*$_1$, *Helminthoglypta*$_2$, *Plesarionta, Xerarionta*); (B) absent (all others). B → A.

18. Papillation on teleoconch whorls: (A) absent (*Myotophallus*$_1$, *Plesarionta, Sonorella binneyi* group, *Sonorella hachitana* group, *Xerarionta*); (B) confined to spire, or mostly so (*Charodotes, Eremarionta*$_1$, *Eremarionta*$_2$, *Eremariontoides, Helminthoglypta*$_1$, *Helminthoglypta*$_2$, *Herpeteros, Micrarionta*$_1$, *Myotophallus*$_2$, *Rothelix, Sonorelix*); (C) extensive over shell, including body whorl (*Chamaearionta, Coyote, Greggelix, Martirelix, Micrarionta*$_2$, *Mohavelix, Sonorella granulatissima* group). A ← B → C.

19. Body whorl: (A) closely coiled [ratio of suture-to-periphery diameter of last whorl to diameter of adult shell <0.23] (*Micrarionta*$_1$, *Micrarionta*$_2$,); (B) not especially closely coiled [ratio of diameter of last whorl to diameter of adult shell ≥0.23] (all other taxa). B → A.

A ratio of < 0.23 occurs sporadically elsewhere as an autapomorphy (e.g., in some populations of *Helminthoglypta* (*Coyote*) *graniticola* Berry, 1926, and *Helminthoglypta* (*H.*) *arrosa* (W. G. Binney, 1858) and in *Plesarionta tryoni*); among other taxa the general range is 0.23 to 0.35.

20. Periostracum: (A) conspicuous (*Chamaearionta, Charodotes, Coyote, Helminthoglypta*$_1$, *Helminthoglypta*$_2$, *Mohavelix, Myotophallus*$_1$, *Myotophallus*$_2$, *Plesarionta, Rothelix, Sonorella binneyi* group, *Sonorella granulatissima* group, *Sonorella hachitana* group, *Xerarionta*; (B) inconspicuous to absent (*Eremarionta*$_1$, *Eremarionta*$_2$, *Eremariontoides, Greggelix, Herpeteros, Martirelix, Micrarionta*$_1$, *Micrarionta*$_2$, *Sonorelix*). A → B.

21. Body and mantle mucus: (A) highly colored (orange, yellowish, or chartreuse) (*Greggelix, Herpeteros, Martirelix, Sonorella binneyi* group, *Sonorella granulatissima* group; *Sonorella hachitana* group, *Myotophallus*$_2$); (B) colorless or milky (all other taxa). B → A.

Taxonomy

The results presented below document a partly nested, partly polytomous pattern of clades within the Helminthoglyptidae. This is sufficient to answer the questions posed by this study, but for systematists who would like to have the results expressed in the form of a list, I propose a taxonomy based on the following conventions. New taxon names are given phylogeny-based definitions in the Appendix.

In traditional biological taxonomy, taxon names are defined by lists of characters, regardless of whether the taxa are monophyletic, paraphyletic, or polyphyletic (de Queiroz & Gauthier, 1990). Decisions on naming or rank are often based on magnitude of difference criteria, recognizable by statements of the form, "[taxon X] is *different enough* from [taxon Y] that I recognize it as a [family, subfamily, etc.]." The phylogenetic taxonomy employed here uses three conventions not observed in traditional taxonomy: (1) no categorical ranks in the absolute sense are recognized; only relative rank, based on the phylogenetic hypothesis, with sister groups—the opposite branches of a fork in the tree—considered of equal dignity; (2) only monophyletic taxa are named, not paraphyletic or polyphyletic groups; and (3) monotypic groups are given no redundant names, except where necessary to keep an existing genus name from applying to a polyphyletic group (e.g., *Maricopella,* new genus for "*Sonorella*" *allynsmithi*). These conventions are more fully expounded by Gauthier et al. (1988). The names of previously recognized groups that are paraphyletic according to this analysis are enclosed in quotation marks.

The system proposed here intersects the traditional classification at two points: the most inclusive taxon retains the familiar name Helminthoglyptidae, not to express cat-

Table 2

Six maximally parsimonious trees based on analysis of data in Table 1.

Tree 1
(OUT,(MY2,(MY1,(SNB,(SNG,SNH)))),((MOH,SLX),((MI1,MI2),((CHM,HER),((GRE,MAR),(PLE,XER)),
((ER2,(ER1,ERO)),(HL2,(ROX,(CHR,COY,HL1))))))))
Tree 2
(OUT,(MY2,((MY1,SNB),(SNG,SNH))),((MOH,SLX),(MI1,MI2),((CHM,HER),((GRE,MAR),(PLE,XER)),
((ER2,(ER1,ERO)),(HL2,(ROX,(CHR,COY,HL1))))))))
Tree 3
(OUT,(MY2,(MY1,(SNB,(SNG,SNH)))),((MOH,SLX),((MI1,MI2),(((GRE,MAR),(PLE,XER)),((CHM,HER),
((ER2,(ER1,ERO)),(HL2,(ROX,(CHR,COY,HL1)))))))))
Tree 4
(OUT,(MY2,(MY1,SNB,(SNG,SNH))),((MOH,SLX),((MI1,MI2),((CHM,HER),((GRE,MAR),(PLE,XER)),
(ER2,(ER1,ERO)),(HL2,(ROX,(CHR,COY,HL1)))))))
Tree 5
(OUT,(MY2,((MY1,SNB),(SNG,SNH))),((MOH,SLX),((MI1,MI2),
(((GRE,MAR),(PLE,XER)),((CHM,HER),(ER2,(ER1,ERO)),(HL2,(ROX,(CHR,COY,HL1))))))))
Tree 6
(OUT,(MY2,(MY1,SNB,(SNG,SNH))),((MOH,SLX),((MI1,MI2),
(((GRE,MAR),(PLE,XER)),((CHM,HER),((ER2,(ER1,ERO)),(HL2,(ROX,(CHR,COY,HL1)))))))))

egorical rank but simply as a link to the traditional classification of pulmonate land snails. At the other end, I continue to use Latin binomina (set in italics) for the lowest, least inclusive taxa—species; I am not prepared to deal with the confusion that would result from abandoning ICZN Article 5.[4] However, for many of the generic names themselves, I introduce a global conversion according to the following formula: [genus-name] is defined as [type species of the genus] and all taxa that share a more recent common ancestor with it than with [name of sister group] (see Appendix). This form of definition is consistent with the International Code of Zoological Nomenclature, which specifies that a genus is defined by reference to its type species—as is the case here—but does not dictate the basis for assigning other species to a genus. Between these two tie points, the traditional formal suffixes, with their imputations of rank (-ini, "tribe"; -inae, "subfamily") are not used.

One typographical convention is introduced: the names of taxa that have phylogeny-based definitions (or are used with regard to their phylogeny-based definitions, if more than one definition exists) are set in SMALL CAPITAL LETTERS. This convention may have wider use in papers in which it is necessary to discuss both taxa with and without phylogeny-based definitions. Where I use an existing genus name in the sense implied by its phylogenetic redefinition, the name is set in small capitals; otherwise, it is set in italics.

RESULTS

The analysis produced 377 maximally parsimonious trees 76 steps in length, with consistency index 0.57, and retention index (Farris, 1989) 0.73. Iterations of the successive approximations weighting and branch-breaking procedures reduced the number of trees to six. Table 2 presents these trees in parenthetical notation. They differ from one another principally as shown in Figure 3. The strict consensus tree is shown in Figure 4. It is 76 steps long with consistency index 0.57 and retention index 0.73. This tree is used as the basis for the following taxonomy of Helminthoglyptidae. Because a consensus tree represents the information on grouping shared by all the competing cladograms, it is less resolved than any, and a taxonomy based on it should be viewed as conservative (Carpenter, 1988).

In the proposed taxonomy (Table 3), hierarchic relations among the taxa are indicated by successive indention.[5]

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[4] The so-called binominal system is in practice trinominal—genus, subgenus, and species—with a built-in three-tiered hierarchy of ranks. Not renaming the second level of taxa in clades with unresolved terminal polytomies (HELMINTHOGLYPTA) or numerous species (SONORELLA), but allowing the existing genus names to stand, nomenclaturally forces the subordinate terminal taxa into the rank of subgenus. This is in keeping with current usage and leaves the finer resolution to monographers of those genera. A wholly rank-free taxonomy would not utilize subgenera as such. I have steered a middle course that preserves many familiar names in their customary sense for the time being.

[5] A hypothetical systematist concerned with expressing these results within the Linnaean hierarchy would probably adopt the following measures: (1) call HELMINTHOGLYPTAMORPHA and SONORELLAMORPHA, primary subdivisions of the Helminthoglyptidae, "Helminthoglyptinae" (the earliest-proposed existing family-group name typologically based on an included taxon) and "Sonorellinae," respectively, or, with equally good reason, "Hel-

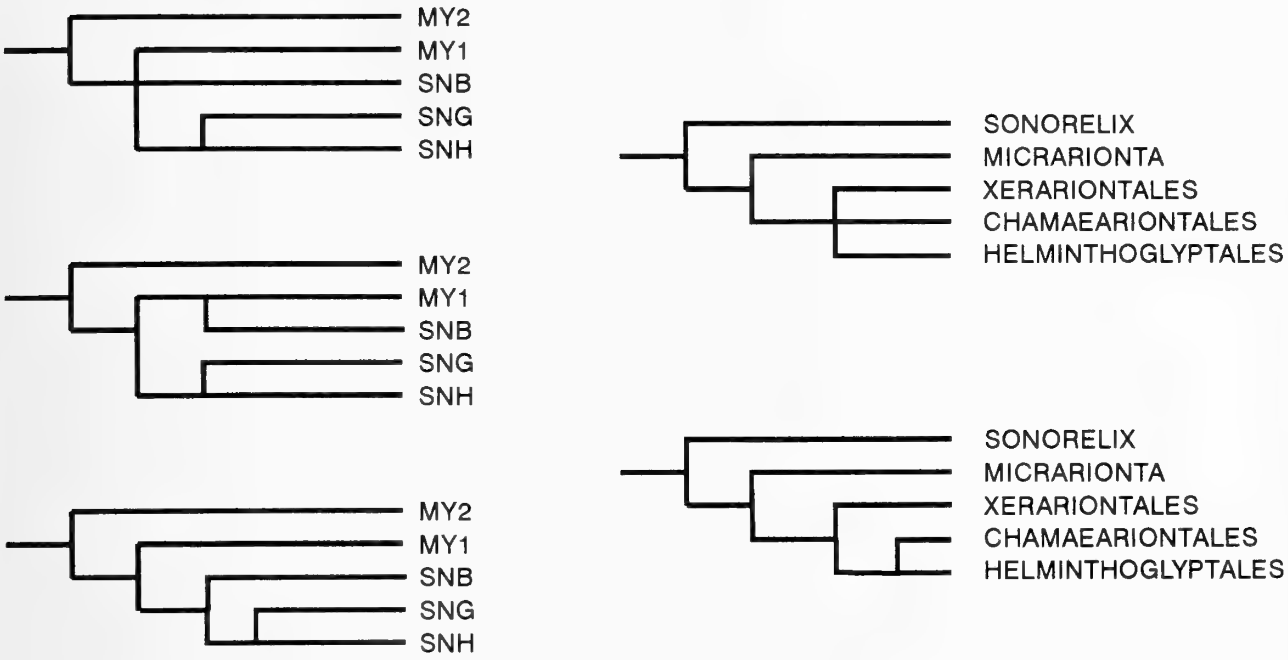

Figure 3

Differing components of trees in Table 2; left, in SONORELLAMORPHA (abbreviations as in Table 1); right, in HELMINTHOGLYPTAMORPHA (taxa defined in following text).

Table 4 compares the content of taxa proposed in this paper to the taxa recognized by Nordsieck (1987) and Schileyko (1991).

The tree exhibits a basal trichotomy among the outgroup, the taxa conventionally assigned to *Sonorella* (SONORELLAMORPHA), and the rest of the Helminthoglyptidae (HELMINTHOGLYPTAMORPHA). SONORELLAMORPHA is diagnosed by the synapomorphies of minute epiphallic caecum (character state 8B) (homoplastic in *Eremariontoides argus*) and colored mucus (21A). Mucus glands and dart sac are absent (2E, 5C). As discussed below, whether these absences are considered apomorphic or plesiomorphic depends on interpretation of the outgroup.

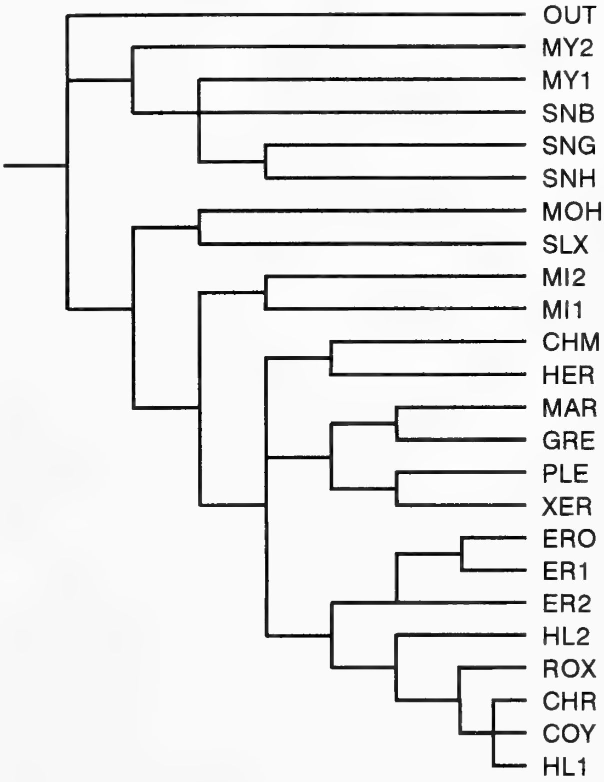

Figure 4

Strict consensus tree for taxa of Helminthoglyptidae. Abbreviations as in Table 1.

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minthoglyptidae” and “Sonorellidae”; (2) call CHAMAEARIONTALES, XERARIONTALES, and HELMINTHOGLYPTALES (major subdivisions of “Helminthoglyptinae”), “Chamaeariontini,” “Xerariontini,” and “Helminthoglyptini;” and (3) interpose taxa named “Sonorelicini” and “Micrariontini” hierarchically between SONORELIX and “Helminthoglyptinae” and MICRARIONTA and “Helminthoglyptinae,” respectively. I reject measures (1) and (2) because in the Linnaean system the suffixes-inae and-ini denote formal categorical ranks. There is no reason having to do with the biology or evolutionary history of the organisms why those names could not equally well be applied to other subdivisions containing their nominotypical genera. Any such decision is subjective and arbitrary. Measure (3) runs counter to the convention of no redundant names: “Sonorelicini” and SONORELIX would have identical membership, as would “Micrariontini” and MICRARIONTA.

Table 3

Phylogenetic taxonomy of the Helminthoglyptidae.

- HELMINTHOGLYPTIDAE
  - SONORELLAMORPHA
    - *Maricopella allynsmithi*
    - SONORELLALES
      - MYOTOPHALLUS
      - "*Sonorella binneyi* group"
      - SONORELLA
        - SONORANAX (*Sonorella granulatissima* group)
        - "*Sonorella, sensu stricto*"
  - HELMINTHOGLYPTAMORPHA
    - SONORELIX
      - *Mohavelix micrometalleus*
      - SONORELIX, SENSU STRICTO
    - HELMINTHOGLYPTAINA
      - MICRARIONTA
        - NICOLENEA
        - MICRARIONTA, SENSU STRICTO
      - HELMINTHOGLYPTOTES
        - CHAMAEARIONTALES
          - *Chamaearionta aquaealbae*
          - HERPETEROS
        - XERARIONTALES
          - GREGGELIX
            - MARTIRELIX
            - "*Greggelix, sensu stricto*"
          - XERARIONTA
            - XERARIONTA, SENSU STRICTO
            - "*Plesarionta*"
        - HELMINTHOGLYPTALES
          - EREMARIONTAPHIM
            - CAHUILLUS
            - EREMARIONTA
              - *Eremariontoides argus*
              - EREMARIONTA, SENSU STRICTO
          - HELMINTHOGLYPTAPHIM
            - *Noyo intersessa*
            - HELMINTHOGLYPTANIKI
              - ROTHELIX
              - HELMINTHOGLYPTA
                - *Helminthoglypta, sensu stricto*
                - *Coyote*
                - "*Charodotes*"

SONORELLAMORPHA consists of two primary component clades. The first, *Maricopella allynsmithi* (that is, *Myotophallus*$_2$ of the preceding data set), is diagnosed by minute verge (12B) (homoplastically derived in XERARIONTA, SENSU STRICTO and ROTHELIX) and thick penial sheath enveloping the whole penis (13B). A thick penial sheath is either homoplastically derived in *Myotophallus* or reversed in other SONORELLALES. The second primary component clade, SONORELLALES, is diagnosed by penial retractor inserting at base of epiphallus (10A) (homoplastically derived in HERPETEROS and MARTIRELIX); embryonic whorl sculpture of spirally descending, sometimes divaricating threads (14F); and general absence of papillation on the teleoconch whorls (18A) (also occurring in XERARIONTA; reversed in the *Sonorella granulatissima* group).

The component taxa of SONORELLALES plot as an unresolved trichotomy: MYOTOPHALLUS (that is, *Myotophallus*$_1$), diagnosed by thick penial sheath enveloping the whole penis (13B), the (homoplastic) absence of a verge (12B), and colorless mucus (21B) (a reversal); the "*Sonorella binneyi* group," which has no autapomorphies in the present phylogenetic hypothesis and is regarded as paraphyletic pending further study; and SONORELLA, diagnosed by a long, acicular verge (12G). SONORELLA consists of two subclades. The *Sonorella granulatissima* group is diagnosed by embryonic whorls coarsely granulose with spirally descending, divaricating threads (14G) and extensive papillation (18C) (homoplastically derived in several clades of HELMINTHOGLYPTAMORPHA). This clade contains the type species of SONORANAX, and I apply that name, in its phylogeny-based definition, to it. Whether *Masculus* is useful as the name for a component clade of SONORANAX will depend on the results of a monographic study of the species of the group. The second subclade, "*Sonorella, sensu stricto,*" has no autapomorphies in the present phylogenetic hypothesis and is regarded as paraphyletic pending further study.

HELMINTHOGLYPTAMORPHA is diagnosed by the absence of a penial sheath (13C). The periostracum is greatly reduced or absent on the teleoconch (20B), but this transformation shows at least one reversal in every principal clade of HELMINTHOGLYPTAMORPHA except MICRARIONTA, often in combination with other character states implying progenesis.

HELMINTHOGLYPTAMORPHA consists of two primary component clades. The first, SONORELIX, is diagnosed by netlike embryonic whorl sculpture (14C). Mucus glands and dart sac are absent (2E, 5C). SONORELIX consists of two subclades. The monotypic *Mohavelix micrometalleus* is diagnosed by a minute epiphallic caecum (8B), extensive papillation (18C), and a conspicuous periostracum (20A; a reversal). These apomorphies also occur elsewhere in HELMINTHOGLYPTAMORPHA. SONORELIX, SENSU STRICTO is diagnosed by the presence of a vaginal node (7A) and a spermathecal diverticulum in a basal position.

The second primary component clade of HELMINTHOGLYPTAMORPHA, HELMINTHOGLYPTAINA, is diagnosed by embryonic whorl sculpture of radial wrinkles overlain by sparse papillae (14A). HELMINTHOGLYPTAINA consists of two component clades. The first, MICRARIONTA, is diagnosed by globose verge (12E) (homoplastic in XERARIONTALES) and close coiling (19A). MICRARIONTA consists of two subclades. NICOLENEA, new subgenus (that is, *Micrarionta*$_2$), is diagnosed by absence of descending mucus gland and dart sac (2C, 5C) and extensive papillation (18C). MICRARIONTA, SENSU STRICTO (that is, *Micrarionta*$_1$) has no autapomorphies in the present data set. Pearce's (1990) cladistic analysis resolved a clade consisting of *Micrarionta facta* and six other species as the sister group of the clade here designated NICOLENEA. It

Table 4

Relationship of content of taxa of phylogenetic taxonomy proposed in this paper and classifications of Nordsieck (1987) and Schileyko (1991). Order of taxa same as in Table 3. Note that upon further analysis the membership (and hence the equivalence) of taxa of the phylogenetic system could change without the taxon definitions changing.

This paper	Nordsieck (1987)[1]	Schileyko (1991)
HELMINTHOGLYPTIDAE	Helminthoglyptinae	Helminthoglyptidae in part + Xanthonychidae in part
SONORELLAMORPHA	"*Sonorella*-Gruppe" (of Sonorellini) (in part?)	Sonorellinae (of Xanthonychidae) in part
Maricopella allynsmithi	not treated	not treated
SONORELLALES	["*Sonorella*-Gruppe" in part]	Sonorellinae in part
Myotophallus	["*Sonorella*-Gruppe" in part]	Sonorellinae in part
"*Sonorella binneyi* group"	["*Sonorella*-Gruppe" in part]	Sonorellinae in part
SONORELLA	"*Sonorella*-Gruppe" in part	Sonorellinae in part
SONORANAX	["*Sonorella*-Gruppe" in part]	Sonorellinae in part
"*Sonorella, sensu stricto*"	"*Sonorella*-Gruppe" in part	Sonorellinae in part
HELMINTHOGLYPTAMORPHA	Helminthoglyptini + "*Sonorella*-Gruppe" in part?	Helminthoglyptidae in part + Xanthonychidae in part
SONORELIX	"*Sonorella*-Gruppe" in part?	Sonorellinae in part
Mohavelix micrometalleus	not treated	Sonorellinae in part (as *Mohavelix*)
SONORELIX, SENSU STRICTO	"*Sonorella*-Gruppe" in part?	Sonorellinae in part
HELMINTHOGLYPTAINA	Helminthoglyptini	Helminthoglyptinae + Eremariontinae + Micrariontinae (of Xanthonychidae) + Sonorellinae in part
MICRARIONTA	"*Micrarionta*-Gruppe" (of Helminthoglyptini) in part	Micrariontinae in part
NICOLENEA	not treated	not treated
MICRARIONTA, SENSU STRICTO	"*Micrarionta*-Gruppe" in part	Micrariontinae in part
HELMINTHOGLYPTOTES	Helminthoglyptini in part	Helminthoglyptinae + Eremariontinae + Micrariontinae in part + Sonorellinae in part
CHAMAEARIONTALES	[Helminthoglyptini in part]	not treated
Chamaearionta aquaealbae	["*Micrarionta*-Gruppe" in part]	not treated
HERPETEROS	not treated	not treated
XERARIONTALES	Helminthoglyptini in part	Micrariontinae in part + Sonorellinae in part
GREGGELIX	Helminthoglyptini in part	Sonorellinae in part
MARTIRELIX	not treated	not treated
"*Greggelix, sensu stricto*"	Helminthoglyptini in part	Sonorellinae in part
XERARIONTA	["*Micrarionta*-Gruppe" in part]	Micrariontinae in part
XERARIONTA, SENSU STRICTO	["*Micrarionta*-Gruppe" in part]	Micrariontinae in part
"*Plesarionta*"	["*Micrarionta*-Gruppe" in part]	Micrariontinae in part
HELMINTHOGLYPTALES	Helminthoglyptini in part	Helminthoglyptidae + Sonorellinae in part
EREMARIONTAPHIM	["*Micrarionta*-Gruppe" in part]	Eremariontinae + Sonorellinae in part
CAHUILLUS	not treated	not treated
EREMARIONTA	["*Micrarionta*-Gruppe" in part]	Eremariontinae in part + Sonorellinae in part
Eremariontoides argus	not treated	Sonorellinae in part (as *Eremariontoides*)
EREMARIONTA, SENSU STRICTO	["*Micrarionta*-Gruppe" in part]	Eremariontinae in part
HELMINTHOGLYPTAPHIM	Helminthoglyptini in part	Helminthoglyptinae
Noyo intersessa	not treated	not treated
HELMINTHOGLYPTANIKI	*Helminthoglypta* in part	Helminthoglyptinae in part
ROTHELIX	[*Helminthoglypta* in part]	*Helminthoglypta* in part
HELMINTHOGLYPTA	*Helminthoglypta* in part	Helminthoglyptinae in part
Helminthoglypta, sensu stricto	*Helminthoglypta* in part	*Helminthoglypta* in part
Coyote	[*Helminthoglypta* in part]	*Helminthoglypta* in part
"*Charodotes*"	[*Helminthoglypta* in part]	*Helminthoglypta* in part

[1] The "*Micrarionta*-Gruppe" of Nordsieck (1987) is assumed to include the taxa that Pilsbry (1939) treated as subgenera of *Micrarionta*. Bracketed equivalences are inferred.

was defined by five measurements and ratios of the shell lip, lip convexity, and the presence of spiral lines on the shell. Lip convexity and one ratio show reversals within the clade. The other character states are synapomorphic with respect to the array of taxa considered. I accept this clade provisionally as MICRARIONTA, SENSU STRICTO pending further study. On Pearce's (1990:fig. 7) consensus tree, *Micrarionta guadalupiana* is the sister group of (NICOLENEA, MICRARIONTA SENSU STRICTO) but is paraphyletic, without a defining autapomorphy in the Pearce hypothesis.

The second component clade of HELMINTHOGLYPTAINA, HELMINTHOGLYPTOTES, is diagnosed by a spermathecal diverticulum of moderate length (6B). It consists of three primary component clades. The first, CHAMAEARIONTALES, is diagnosed by short epiphallic caecum (6E) and short spermathecal diverticulum (8D). CHAMAEARIONTALES consists of two subclades. The monotypic *Chamaearionta aquaealbae* is diagnosed by the absence of a verge (12B), extensive papillation (18C), and a conspicuous periostracum (20A; a reversal). These apomorphies also occur elsewhere in HELMINTHOGLYPTAMORPHA. The second subclade, HERPETEROS, is diagnosed by the absence of mucus glands and dart sac (2E, 5C), penial retractor inserting at base of epiphallus (10A), very large verge (12D), and embryonic whorl sculpture of radial wrinkles overlain by sparse papillae (14A). All except (12D) are homoplastic elsewhere in HELMINTHOGLYPTAMORPHA.

The second primary component clade of HELMINTHOGLYPTOTES, XERARIONTALES, is diagnosed by a very long epiphallic caecum (8C) (partly reversed in MARTIRELIX) and probably by a very long spermathecal diverticulum (6C) (also partly reversed in MARTIRELIX). In an equally parsimonious alternative interpretation, a long spermathecal diverticulum could have originated twice, in "*Greggelix, sensu stricto*" and in XERARIONTA. I favor the former interpretation, in which the transformations of spermathecal diverticulum and epiphallic caecum are correlated.

XERARIONTALES consists of two subclades. GREGGELIX is diagnosed by vestigial mucus glands (2D) (lost in some species of "*Greggelix, sensu stricto*"), absence of a dart sac (5C), extensive papillation (18C) (homoplastic), and colored mucus (21A) (also occurring in SONORELLAMORPHA). GREGGELIX consists of two subclades. MARTIRELIX is diagnosed by penial retractor inserting at base of epiphallus (10A) (homoplastic in HERPETEROS and SONORELLAMORPHA), bullet-shaped to conical verge (12F), and moderately long spermathecal diverticulum (6B) (a probable reversal). Unless a very long spermathecal diverticulum (6C) is considered to have originated anew, homoplastically with that in XERARIONTA, the second subclade, "*Greggelix, sensu stricto*," has no autapomorphies in this phylogenetic hypothesis and is regarded as paraphyletic pending further study.

The second subclade of XERARIONTALES, XERARIONTA, is diagnosed by mottling or multiple banding (15A), malleation (17A) (homoplastic in *Helminthoglypta, sensu stricto* and *Noyo intersessa* [that is, *Helminthoglypta*$_2$]), and embryonic whorl sculpture of radial wrinkles without an overlay of papillae (14D); papillation is absent from teleoconch whorls (18A) (homoplastic in SONORELLALES). XERARIONTA consists of two subclades. XERARIONTA, SENSU STRICTO is diagnosed by smooth embryonic whorl wrinkles (14E), diagonal granulose sculpture (16A), and the (homoplastic) absence of a verge (12B). "*Plesarionta*" has no autapomorphies in this phylogenetic hypothesis and is regarded as paraphyletic pending further study.

The third primary component clade of HELMINTHOGLYPTOTES, HELMINTHOGLYPTALES, is diagnosed by bulbous mucus gland reservoirs (3A) (secondarily lost in *Eremariontoides argus*) and the double wall of the lower part of the epiphallus (9B). HELMINTHOGLYPTALES consists of two subclades. EREMARIONTAPHIM is diagnosed by embryonic whorl sculpture of spirally elongated, discrete papillae (14B; a reversal); it also shows extension of the double-walled section of the epiphallus into the verge, a component in common of states 9C and 9D. EREMARIONTAPHIM consists of two subclades. CAHUILLUS, new genus (that is, *Eremarionta*$_2$), is diagnosed by a double-walled section of the epiphallus less than 0.4 times the length of the penis (9C). EREMARIONTA is diagnosed by a conical double-walled section of the epiphallus (9D) and a short, broad, papillar verge (12C) (homoplastic with that in *Coyote*). EREMARIONTA consists of two subclades. *Eremariontoides argus* is diagnosed by the absence of mucus glands and dart sac (2E, 5C) and by minute epiphallic caecum (8B) (homoplastic in SONORELLAMORPHA and *Mohavelix micrometalleus*). EREMARIONTA, SENSU STRICTO (that is, *Eremarionta*$_1$) is diagnosed by a short spermathecal diverticulum (6E) (homoplastic in CHAMAEARIONTALES).

The second subclade of HELMINTHOGLYPTALES, HELMINTHOGLYPTAPHIM, is diagnosed by the common duct of the mucus glands (2B), membranous tissue enveloping the lower genitalia (4A), embryonic whorl sculpture of radial wrinkles overlain by sparse papillae (14A) (also occurring in HERPETEROS and MICRARIONTALES), and the presence of a conspicuous periostracum (20A; a reversal). HELMINTHOGLYPTAPHIM consists of two subclades. *Noyo intersessa* (that is, *Helminthoglypta*$_2$) is diagnosed by the presence of malleation on the teleconch (17A) (homoplastic in *Helminthoglypta, sensu stricto,* and XERARIONTA). Malleation apparently tends to be associated with large, more or less globose, capacious-whorled shells and is evidently not a good indicator of phylogeny in this context. HELMINTHOGLYPTANIKI is diagnosed by the presence of an atrial sac (1B), with the dart sac seated on it (5B).

HELMINTHOGLYPTANIKI consists of two subclades. ROTHELIX is diagnosed by penial chamber with post-medial constriction (11B) and the (widely homoplastic) absence of a verge (12B). HELMINTHOGLYPTA is diagnosed by vagina inserting on atrium at base of atrial sac (1C). The component taxa of HELMINTHOGLYPTA plot as an unresolved trichotomy: *Helminthoglypta, sensu stricto,* diagnosed by malleation (17A) (homoplastic in XERARIONTA

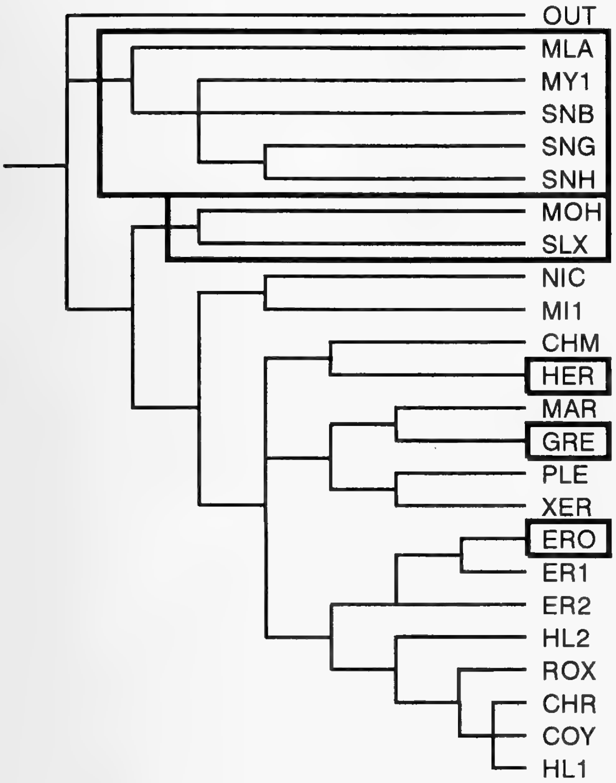

Figure 5

Absence of mucus glands mapped on consensus tree. Abbreviations as in Table 1, except for new taxa: MLA, *Maricopella allynsmithi*; NIC, NICOLENEA; CAH, CAHUILLUS; NOY, *Noyo intersessa*. Absence is variable in GREGGELIX.

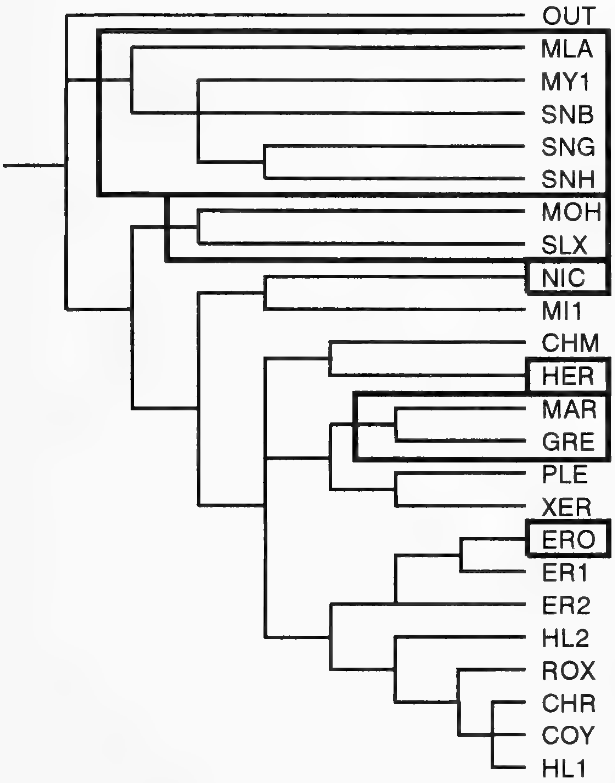

Figure 6

Absence of dart sac mapped on consensus tree. Abbreviations as in Figure 5.

and *Noyo intersessa*); *Coyote,* diagnosed by conical double-walled section of epiphallus (9E) and papillar verge (12C) (homoplastically derived in EREMARIONTA); and "*Charodotes,*" which has no autapomorphies in the present phylogenetic hypothesis and is regarded as paraphyletic pending further study. A verge is absent homoplastically in some species of "*Charodotes*" and *Helminthoglypta, sensu stricto.* Phylogeny-based definitions of the component taxa of HELMINTHOGLYPTA are left for a monographic study of the group.

Figure 5 plots the distribution of the total absence of mucus glands (2E) on the consensus tree. This character state occurs as an apomorphy in SONORELLAMORPHA, HERPETEROS, SONORELIX, *Eremariontoides argus,* and some species of "*Greggelix, sensu stricto.*" If the absence in SONORELLAMORPHA is accepted as due to loss, a minimum of five independent origins of the condition is indicated.

Figure 6 plots the distribution of the absence of dart sac (5C) on the consensus tree. This character state occurs as an apomorphy in SONORELLAMORPHA, HERPETEROS, SONORELIX, NICOLENEA, GREGGELIX, and *Eremariontoides argus.* If the absence in SONORELLAMORPHA is accepted as due to loss, a minimum of six independent, homoplastic origins of the condition is indicated.

DISCUSSION

This analysis falsifies the proposition that absence of dart sac and/or mucus glands originated only once (Schileyko, 1991) as the most parsimonious account of helminthoglyptid evolution. It provides evidence against most other ancestor-descendant relationships suggested by previous authors.

All the taxa of HELMINTHOGLYPTAMORPHA have apomorphies (including the synapomorphic absence of penial sheath) that eliminate them as potential ancestors of the taxa of SONORELLAMORPHA.

Maricopella allynsmithi is the sister group of all other taxa conventionally referred to *Sonorella* (that is, of SONORELLALES), but the autapomorphies of minute verge (12B) and thick penial sheath (13B) rule it out as "a relatively unchanged descendant of the ancestral *Sonorella* founder" (Gregg & Miller, 1969:92). Its similarities to EREMARIONTA are symplesiomorphies.

Embryonic whorl sculpture (14C) and the absence of mucus glands (2E) support *Mohavelix micrometalleus* as the sister group of SONORELIX, SENSU STRICTO rather than of *Helminthoglypta micrometalleoides* as Miller (1970) suggested.

GREGGELIX is the sister group of **XERARIONTA**, not the derivative of any population assignable to **XERARIONTA** as surmised by Miller (1972).

Eremariontoides argus is the sister group of **EREMARIONTA SENSU STRICTO**. This relationship rules out the simple common ancestry with "*Eremarionta*" *greggi* suggested by Miller (1981a); based on the moderately long spermathecal diverticulum and conic verge, "*E.*" *greggi* is a species of CAHUILLUS.

Roth (1987b) stated that in *Noyo intersessa* the muscularized common duct of the mucus glands had (apomorphically) taken over the function of mucus ejection performed by muscular mucus bulbs in most species of *Helminthoglypta*. The present phylogenetic hypothesis indicates that the muscular common duct and thin-walled mucus bulbs of *N. intersessa* are plesiomorphic with respect to the muscular bulbs and slender common duct in HELMINTHOGLYPTANIKI.

ROTHELIX, regarded by all previous authors as a subgenus of *Helminthoglypta,* is the sister group of all other taxa conventionally assigned to *Helminthoglypta*. Its position on the consensus tree does not suggest recent evolution from "an *H*[*elminthoglypta*]. *traskii*-like ancestor" (Miller, 1985) but rather an origin preceding the radiation of HELMINTHOGLYPTA into its component clades. It preserves an intermediate state in the stripping off of the atrial sac from the vagina (1B). At the same time, the male system shows the apomorphies of a post-medial constriction setting off a posterior chamber of the penial sac and the absence of a verge.

The differences between my results and those of Pearce (1990) and Schileyko (1991) are adequately accounted for by character coding and argumentation (in the case of Pearce) and method (in the case of Schileyko), and will not be belabored here.

Since Pilsbry's (1939) monograph, the taxa here assigned to **SONORELLAMORPHA** have been regarded as secondarily simplified from a dart-bearing ancestor. However, **SONORELLAMORPHA** is a basal clade, the sister group of **HELMINTHOGLYPTAMORPHA**, and not derivable from any other clade of Helminthoglyptidae. **SONORELLAMORPHA** and **HELMINTHOGLYPTAMORPHA** share no common ancestor not also shared by the presumptive sister group (Xanthonychidae,Bradybaenidae). If the taxa of **SONORELLAMORPHA** are in fact secondarily simplified, they may as readily have lost a xanthonychid-bradybaenid type of dart apparatus as a helminthoglyptid type. Or they may never have had one. If Polygyridae is regarded as the outgroup (which does not greatly affect the structure of the consensus tree) then absence of dart apparatus in **SONORELLAMORPHA** is plesiomorphic. Therefore, the monophyly of Helminthoglyptidae of authors (e.g., Miller & Naranjo-García, 1991) remains open to question, and more information is needed to determine whether **SONORELLAMORPHA** is contained within HELMINTHOGLYPTIDAE as defined herein.

The use of fossils to calibrate a phylogeny in time, especially one as strongly based on soft anatomical characters as this one, is not without risks. The situation is made worse by the rampant parallelism and convergence in shell form among land snails. I accept the following generic identifications, which constrain the time scale of helminthoglyptid evolution. *Xerarionta waltmilleri* Roth, 1984, from the Vieja Group of Trans-Pecos Texas, is between 39.6 and 37.7 Ma (late Eocene) in age (Roth, 1984). It shows the diagonal granulose sculpture diagnostic of XERARIONTA, SENSU STRICTO. Two undescribed species of XERARIONTA, SENSU STRICTO occur in the Brule Member of the White River Formation in the Douglas area, Wyoming (E. Evanoff & Roth, in preparation); the stratigraphically lowest occurrence is near a bed dated 33.9 Ma (early Oligocene).

Helminthoglypta bozemanensis Roth, 1986, from the Bozeman Group of western Montana, about 36 Ma in age (latest Eocene or earliest Oligocene), and *Helminthoglypta martini* (Hanna, 1920), from the John Day Formation of Oregon, with age bracketed loosely between 20 and 30 Ma (late Oligocene to early Miocene), show shell sculpture of collabral rugae cut into elongate granules, similar to that found in *Noyo intersessa* and some Recent species of *Helminthoglypta, sensu stricto* (Roth, 1986, 1988a).[6] A species of *Helminthoglypta* probably assignable to *Coyote* occurs in Pliocene rocks of the Tehachapi Mountains, California (Roth & Hochberg, 1988). The origins of **NOYO**, *Helminthoglypta, sensu stricto* and **XERARIONTA, SENSU STRICTO** occur well out on their respective limbs of the consensus tree. The substantial radiation of the **HELMINTHOGLYPTIDAE** that underlies the framework of the tree must have taken place before the end of the Eocene.

Other fossils that have been assigned to **HELMINTHOGLYPTIDAE** probably are not referrable to any modern genus of the clade. "*Helminthoglypta*" *alfi* Taylor, 1954, from the Barstow Formation (middle Miocene), southern California, has been assigned to *Coyote* (Reeder & Roth, 1988; Roth & Hochberg, 1988), but the description of its embryonic whorl sculpture (Taylor, 1954:76–77) does not accord well with any Recent taxon. *Greggelix? hochbergi* Roth & Megaw, 1989, from rocks of probable middle Eocene age in Chihuahua, Mexico (Roth & Megaw, 1989; Megaw, McDowell, & Roth, 1994), does not show any characters here regarded as diagnostic of terminal taxa; it could belong to **SONORELLAMORPHA** or **HELMINTHOGLYPTAMORPHA**. "*Helminthoglypta*" *obtusa* Anderson & Hanna, 1925, and "*Helminthoglypta?*" *stocki* G D. Hanna, 1934, from the Eocene of southern California, are ca-

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[6] Assigning *H. bozemanensis* and *H. martini* to *Noyo* rather than to *Helminthoglypta* requires fewer assumptions about soft-part apomorphies not in evidence. The most conservative assignment is merely to **HELMINTHOGLYPTAPHIM**; cf. usage by Roth (1988b) of [Camaenidae] *stocki* and by Pierce (1992) of [Succineidae] *montana*. Including this type of sculpture as a character in the data set does not affect the relative positions of *Noyo intersessa* and *Helminthoglypta, sensu stricto* on the trees generated.

maenid land snails (Roth, 1988b). "*Micrarionta*" *dallasi* M. A. Hanna, 1927, from the Eocene of southern California, is a helicinid snail (Roth & Pearce, 1988). The referrals of *Glypterpes* and *Mesoglypterpes* to HELMINTHOGLYPTIDAE rest on tenuous readings of non-diagnostic shell characters.

By placing much of helminthoglyptid evolution in an early Tertiary time frame, this hypothesis obviates the need for scenarios of sudden or recent (e.g., post-Pleistocene) loss of reproductive structures. Of course, phylogenetic systematics does not rule out saltational speciation or any other evolutionary mechanism; at most it assumes only that evolution has occurred (Brooks & McLennan, 1991). Both *Helminthoglypta, sensu stricto* and XERARIONTA, SENSU STRICTO occur in settings of mesic paleoclimate (there is other climatic evidence, besides the presence of those genera, so this argument is not circular) and both have replete reproductive systems. Three of the instances of secondary simplification, *Mohavelix micrometalleus, Chamaearionta aquaealbae,* and *Eremariontoides argus,* are monotypic clades with their origins not constrained in time by any nodes farther up the tree. The phylogenetic hypothesis does not falsify a scenario of recent origins for these taxa, perhaps related to water conservation in an increasingly arid environment.

In contrast, the origins of SONORELLAMORPHA and the primary clades of HELMINTHOGLYPTAMORPHA must precede the origins of XERARIONTA, SENSU STRICTO and HELMINTHOGLYPTAPHIM in time. Even if the absence of accessory reproductive structures in SONORELLAMORPHA is apomorphic, it is not related to the late Tertiary onset of widespread aridity in the American Southwest (Axelrod, 1979). Pleistocene climatic fluctuations may be involved in the allopatric species diversity within SONORELLAMORPHA, but not in its origin as a clade.

From correspondence between the distribution of Bradybaenidae, Xanthonychidae, and Helminthoglyptidae and the tectonically accreted terranes around the Pacific rim, Miller & Naranjo-García (1991) drew the conclusion that those taxa had a common ancestry on a Mesozoic Gondwanan land mass ("Pacifica"; see Nur & Ben-Avraham, 1977; Jones et al., 1982) and were dispersed passively to the Americas on rafting fragments of continental crust. The present analysis impacts little on that model, except that, when fossil distribution is included, the range of HELMINTHOGLYPTIDAE is less congruent with accreted terranes than Miller & Naranjo-García (1991) assumed. (Schileyko [1991] reasserted the older alternative scenario of trans-Beringian dispersal, without offering any new reasons for preferring one story over the other.) The phylogenetic relations among the above taxa (and Epiphragmophoridae and Helicostylidae) are critical to the historical biogeography and still remain to be analyzed. Geographic components of taxon definitions, as noted above in the early concepts of Helminthoglyptidae, should be deleted when found, and future taxonomy be grounded in characters of the organisms themselves.

The rôle of heterochrony in bringing about the range of genital configurations should be investigated. For example, *Chamaearionta aquaealbae* may be neotenic with respect to CHAMAEARIONTALES in loss of (i.e., failure to develop) a verge and retention of periostracum and papillation into adulthood, and progenetic in its small size, low whorl number, and angular periphery. *Mohavelix micrometalleus* may be neotenic with respect to SONORELIX in failure to develop a spermathecal diverticulum, reduction of epiphallic caecum, and retention of periostracum and papillation into adulthood.

Here I remind myself that a hypothesis is a beginning, not an end in itself, and that my phylogenetic hypothesis is based on relatively few characters from only three systems. Future studies of the excretory, nervous, and alimentary systems will provide additional characters. The radula seems practically to have been written off for use in helminthoglyptid taxonomy, but should be reconsidered. Molecular data is potentially a rich field. Cladistic analysis should be extended to relations among species in speciose clades like SONORELLA and HELMINTHOGLYPTA, in which many new synapomorphies will have to be found if the trees are not to resemble the Ace comb I used to carry in my back pocket.

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LITERATURE CITED

ASHLOCK, P. D. 1971. Monophyly and associated terms. Systematic Zoology 20:63–69.

AXELROD, D. I. 1979. Age and origin of Sonoran Desert vegetation. Occasional Papers of the California Academy of Sciences 132:1–74.

AZUMA, M. 1982. Colored Illustrations of the Land Snails of Japan. Hoikusha Publishing Company, Ltd.: Osaka. xv + 333 pp.

BAKER, H. B. 1943. Some Antillean helicids. The Nautilus 56: 81–91, pls. 9–11.

BAKER, H. B. 1956. Family names in Pulmonata. The Nautilus 69:128–139.

BAKER, H. B. 1959. Xanthonychidae (Pulmonata). The Nautilus 73:25–28.

BALL, I. R. 1976. Nature and formulation of biogeographic hypotheses. Systematic Zoology 24:407–430.

BEQUAERT, J. C. & W. B. MILLER. 1973. The Mollusks of the Arid Southwest, with an Arizona Check List. University of Arizona Press: Tucson. xvi + 271 pp.

BERRY, S. S. 1943. On the generic relationships of certain Californian xerophile snails. Transactions of the San Diego Society of Natural History 10:1–24.

BERRY, S. S. 1947. On the generic relationships of certain Lower Californian helicoid snails. Leaflets in Malacology 1:9–12.

BERRY, S. S. 1959. Two Californian mountain snails of the genus *Helminthoglypta*—a problem in the relationship of species. Transactions of the San Diego Society of Natural History 11:329–344.

BROOKS, D. R. & D. A. MCLENNAN. 1991. Phylogeny, Ecology, and Behavior: a Research Program in Comparative Biology. University of Chicago Press: Chicago. 434 pp.

CARPENTER, J. M. 1988. Choosing among multiple equally parsimonious cladograms. Cladistics 4:291–296.

CHRISTENSEN, C. C. & R. L. REEDER. 1981. New records of *Sonorella* (Pulmonata: Helminthoglyptidae) from the Table Top Mountains, Pinal County, Arizona, with a description of *Sonorella milleri,* new species. The Southwestern Naturalist 26:341–344.

CHUNG, D. J. D. 1987. Courtship and dart shooting behavior of the land snail *Helix aspersa.* The Veliger 30:24–39.

DE QUEIROZ, K. 1988. Systematics and the Darwinian Revolution. Philosophy of Science 55:238–259.

DE QUEIROZ, K. & J. GAUTHIER. 1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. Systematic Zoology 39:307–322.

DE QUEIROZ, K. & J. GAUTHIER. 1992. Phylogenetic taxonomy. Annual Review of Ecology and Systematics 23:449–480.

DRAY, W. 1957. Laws and Explanation in History. Oxford University Press: Oxford.

EBERHARD, W. G. 1985. Sexual Selection and Animal Genitalia. Harvard University Press: Cambridge, Massachusetts.

EMBERTON, K. C. 1988. The genitalic, allozymic, and conchological evolution of the eastern North American Triodopsinae (Gastropoda: Pulmonata: Polygyridae). Malacologia 28:159–273.

EMBERTON, K. C. 1991. Polygyrid relations: a phylogenetic analysis of 17 subfamilies of land snails (Mollusca: Gastropoda: Stylommatophora). Zoological Journal of the Linnean Society 103:207–224.

EMBERTON, K. C. 1992. A translation of Hartmut Nordsieck's (1987) "Systematic revision of the Helicoidea (Gastropoda: Stylommatophora)". Museum of Comparative Zoology Special Occasional Publication 8:1–79.

EVANOFF, E. & B. ROTH. 1992. The fossil land snail *Helix leidyi* Hall and Meek, 1855, a member of a new genus of Humboldtianidae (Gastropoda: Pulmonata). The Veliger 35: 122–132.

FAIRBANKS, H. L. & R. L. REEDER. 1980. Two new species of *Sonorella* (Gastropoda: Pulmonata: Helminthoglyptidae) from the Pinaleno Mountains, Arizona. Proceedings of the Biological Society of Washington 93:395–404.

FARRIS, J. S. 1969. A successive approximations approach to character weighting. Systematic Zoology 18:374–385.

FARRIS, J. S. 1974. Formal definitions of paraphyly and polyphyly. Systematic Zoology 23:548–554.

FARRIS, J. S. 1976. Phylogenetic classification of fossils with Recent species. Systematic Zoology 25:271–282.

FARRIS, J. S. 1988. HENNIG86, Version 1.5. Computer program distributed by author. Port Jefferson Station, New York.

FARRIS, J. S. 1989. The retention index and the rescaled consistency index. Cladistics 5:417–419.

GAUTHIER, J., R. ESTES & K. DE QUEIROZ. 1988. A phylogenetic analysis of Lepidosauriomorpha. Pp. 15–98 in R. Estes & G. K. Pregill (eds.), Phylogenetic Relationships of the Lizard Families. Stanford University Press: Stanford, California.

GREGG, W. O. 1948 [1949]. A new and unusual helicoid snail from Los Angeles County, California. Bulletin of the Southern California Academy of Sciences 47:100–102.

GREGG, W. O. 1960. Derivation of the Helminthoglyptinae with particular reference to the desert forms. American Malacological Union Bulletin 26:45–46.

GREGG, W. O. & W. B. MILLER. 1969. A new *Sonorella* from Phoenix, Arizona. The Nautilus 82:90–93.

GREGG, W. O. & W. B. MILLER. 1974. Two new species of land snails from the Pinaleno Mountains, Arizona. Bulletin of the Southern California Academy of Sciences 73:146–151.

GREGG, W. O. & W. B. MILLER. 1976. Two new species of *Helminthoglypta* (Mollusca: Pulmonata) from San Diego County, California. Bulletin of the Southern California Academy of Sciences 75:10–16.

HENNIG, W. 1966. Phylogenetic Systematics. University of Illinois Press: Urbana. 263 pp.

JONES, D. L., A. COX, P. CONEY & M. BECK. 1982. The growth of western North America. Scientific American 247:70–84.

LEONARD, J. L. 1991. Sexual conflict and the mating systems of simultaneously hermaphroditic gastropods. American Malacological Bulletin 9:45–58.

LEWIS, H. 1966. Speciation in flowering plants. Science 152: 167–172.

MEGAW, P. K. M., F. W. MCDOWELL & B. ROTH. Refinement of the age of certain Tertiary land mollusks (Gastropoda: Pulmonata): based on new U-Pb zircon ages from the Sierra Santa Eulalia, Chihuahua, Mexico. Malacological Review 27:109.

MILLER, W. B. 1966. Three new *Sonorella* from southwest Arizona. The Nautilus 80:46–52, pls. 1, 2.

MILLER, W. B. 1967a. Anatomical revision of the genus *Sonorella* (Pulmonata: Helminthoglyptidae). Ph.D. dissertation, Department of General Biology, University of Arizona, Tucson.

MILLER, W. B. 1967b. Two new *Sonorella* from Rincon Mountains of Arizona. The Nautilus 81:54–61.

MILLER, W. B. 1967c. Two new *Sonorella* from Sonora, Mexico. The Nautilus 80:114–119, 121–122.

MILLER, W. B. 1967d. Two new *Sonorella* from Sonora, Mexico, with notes on southern limit of the genus. The Nautilus 81:1–6, 9.

MILLER, W. B. 1968. New Sonorella from Arizona. The Nautilus 82:50–63.

MILLER, W. B. 1969. A new *Sonorella* from the Salt River Mountains of Phoenix, Arizona. The Nautilus 82:87–89.

MILLER, W. B. 1970. A new species of *Helminthoglypta* from the Mojave Desert. The Veliger 12:275–278.

MILLER, W. B. 1971. The reproductive anatomy of *Tryonigens remondi* (Tryon, 1863): Helminthoglyptidae. The Nautilus 85:61–65.

MILLER, W. B. 1972. *Greggelix,* a new genus of autochthonous land snails (Helminthoglyptidae) from Baja California. The Nautilus 85:128–135.

MILLER, W. B. 1973. Saltational specieation in American Helminthoglyptidae. American Malacological Union Bulletin 1973:44.

MILLER, W. B. 1976. New species of *Sonorella* (Pulmonata: Helminthoglyptidae) from New Mexico and Texas. The Nautilus 90:70–73.

MILLER, W. B. 1981a. A new genus and a new species of helminthoglyptid land snail from the Mojave Desert of California. Proceedings of the Biological Society of Washington 94:437–444.

MILLER, W. B. 1981b. A new *Greggelix* (Mollusca: Pulmonata: Helminthoglyptidae) from Baja California Sur, Mexico. Proceedings of the Biological Society of Washington 94:731–738.

MILLER, W. B. 1981c. *Helminthoglypta reederi* spec. nov. (Gastropoda: Pulmonata: Helminthoglyptidae) from Baja California, Mexico. The Veliger 24:46–48.

MILLER, W. B. 1982. A new subgenus and a new species of *Greggelix* (Gastropoda: Sigmurethra: Helminthoglyptidae) from the Sierra San Pedro Martir, Baja California, Mexico. The Veliger 24:345–348.

MILLER, W. B. 1984. Three new species of *Sonorella* (Gastropoda: Pulmonata: Helminthoglyptidae) from Arizona. Proceedings of the Biological Society of Washington 97:681–687.

MILLER, W. B. 1985. A new subgenus of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae). The Veliger 28:94–98.

MILLER, W. B. 1987. A new species of *Bunnya* (Gastropoda; Pulmonata: Humboldtianidae) from western Mexico, with notes on its life cycle and familial relationships. The Veliger 29:308–312.

MILLER, W. B. & E. NARANJO-GARCÍA. 1991. Familial relationships and biogeography of the western American and Caribbean Helicoidea (Mollusca: Gastropoda: Pulmonata). American Malacological Bulletin 8:147–153.

NARANJO-GARCÍA, E. 1988a. Four new *Sonorella* (Gastropoda: Pulmonata: Helminthoglyptidae) from northwestern Sonora, Mexico. The Veliger 31:80–86.

NARANJO-GARCÍA, E. 1988b. *Sonorella cananea,* a new species of land snail (Gastropoda: Pulmonata: Helminthoglyptidae) from Sonora, Mexico. The Southwestern Naturalist 22:81–84.

NARANJO-GARCÍA, E. 1989. Four additional species of *Sonorella* (Gastropoda: Pulmonata: Helminthoglyptidae) from Sonora, Mexico. The Veliger 32:84–90.

NARANJO-GARCÍA, E. & W. B. MILLER. 1986. A new species of Sonorella (Gastropoda: Pulmonata: Helminthoglyptidae) from Sonora, Mexico. The Veliger 29:166–168.

NELSON, G. 1979. Cladistic analysis and synthesis: principles and definitions, with a historical note on Adanson's Familles des Plantes (1763–1764). Systematic Zoology 28:1–21.

NORDSIECK, H. 1987. Revision des Systems der Helicoidea (Gastropoda: Stylommatophora). Archiv für Molluskenkunde 118:9–50.

NUR, A. & Z. BEN-AVRAHAM. 1977. Lost Pacific continent. Nature 279:41–43.

O'HARA, R. J. 1988. Homage to Clio, or, toward an historical philosophy for evolutionary biology. Systematic Zoology 37: 142–155.

O'HARA, R. J. 1992. Telling the tree: narrative representation and the study of evolutionary history. Biology and Philosophy 7:135–160.

PEARCE, T. A. 1990. Phylogenetic relationships of *Micrarionta* (Gastropoda: Pulmonata) and distinctness of the species on San Nicolas Island, California. Malacological Review 23:1–37.

PIERCE, H. G. 1992. The nonmarine mollusks of the late Oligocene-early Miocene Cabbage Patch fauna of western Montana. II. Terrestrial gastropod families other than Pupillidae (Pulmonata: Stylommatophora). Journal of Paleontology 66:610–620.

PILSBRY, H. A. 1893–1895. Guide to the study of helices. Manual of Conchology, (2), 9:1–48, pls. 1–14 (1893); 49–160, pls. 15–40 (1894); 161–336, i–xlviii, pls. 41, 71, frontis. (1895).

PILSBRY, H. A. 1907. On the soft anatomy of *E.* (*Micrarionta*) *hutsoni.* The Nautilus 20:138–139, pl. 9.

PILSBRY, H. A. 1913. Notes upon some Lower Californian helices. Proceedings of the Academy of Natural Sciences of Philadelphia 65:380–393, pls. 15, 16.

PILSBRY, H. A. 1918. On the generic position of *Sonorella wolcottiana* Bartsch. Proceedings of the Academy of Natural Sciences of Philadelphia 70:139–140.

PILSBRY, H. A. 1927. Expedition to Guadalupe Island, Mexico, in 1922. Land and freshwater mollusks. Proceedings of the California Academy of Sciences, (4), 16:159–203, pls. 6–12.

PILSBRY, H. A. 1939. Land Mollusca of North America (north of Mexico). Academy of Natural Sciences of Philadelphia, Monograph 3, 1(1):i–xvii, 1–573.

PILSBRY, H. A. 1948. Land Mollusca of North America (north of Mexico). Academy of Natural Sciences of Philadelphia, Monograph 3, 2(2):i–xlviii, 521–1113.

PILSBRY, H. A. & E. G. VANATTA. 1898. Anatomical notes on certain west American helices. Proceedings of the Academy of Natural Sciences of Philadelphia 50:67–71, pl. 1.

REEDER, R. L. 1986. A new species of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae) from the Cuyamaca Mountains of southern California. The Veliger 28: 444–447.

REEDER, R. L. & W. B. MILLER. 1986a. A description of a new *Helminthoglypta s.s.* (Gastropoda: Pulmonata: Helminthoglyptidae) from San Diego County, California. The Veliger 29:129–131.

REEDER, R. L. & W. B. MILLER. 1986a. A new species of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae) from San Diego County, California. Proceedings of the Biological Society of Washington 99:137–139.

REEDER, R. L. & W. B. MILLER. 1987. A new *Helminthoglypta* (*Rothelix*) (Gastropoda: Pulmonata: Helminthoglyptidae) from southern California with comments on its probable evolutionary relationships. The Southwestern Naturalist 32: 261–265.

REEDER, R. L. & W. B. MILLER. 1988. A new *Helminthoglypta* (*Rothelix*) (Gastropoda: Pulmonata: Helminthoglyptidae) from Warner Springs, San Diego County, California. The Veliger 31:87–90.

REEDER, R. L. & B. ROTH. 1988. A new subgenus of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae) with the description of a new species from San Bernardino County, California. The Veliger 31:252–257.

RICHARDSON, L. 1982. Helminthoglyptidae: catalog of species. Tryonia 6. 117 pp.

ROTH, B. 1973. The systematic position of *Helminthoglypta traskii fieldi* Pilsbry, 1930 (Gastropoda: Stylommatophora). Bulletin of the Southern California Academy of Sciences 72: 148–155.

ROTH, B. 1975. Description of a new terrestrial snail from San Nicolas Island, California (Gastropoda: Stylommatophora). Bulletin of the Southern California Academy of Sciences 74: 94–96.

ROTH, B. 1981. Distribution, reproductive anatomy, and variation of *Monadenia troglodytes* Hanna and Smith (Gastropoda: Pulmonata) with the proposal of a new subgenus. Proceedings of the California Academy of Sciences 42:379–407.

ROTH, B. 1982. The identity of "*Helminthoglypta*" *tularica* (Bartsch) (Gastropoda: Pulmonata). Bulletin of the Southern California Academy of Sciences 81:101–105.

ROTH, B. 1984. *Lysinoe* (Gastropoda: Pulmonata) and other land snails from Eocene-Oligocene of Trans-Pecos Texas, and their paleoclimatic significance. The Veliger 27:200–218.

ROTH, B. 1986. Land mollusks (Gastropoda: Pulmonata) from early Tertiary Bozeman Group. Montana. Proceedings of the California Academy of Sciences 44:237–267.

ROTH, B. 1987a. A new and polytypic species of *Helminthoglypta* (Gastropoda: Pulmonata) from the Transverse Ranges, California. The Veliger 30:184–189.

ROTH, B. 1987b. A new species of *Helminthoglypta* (Gastropoda: Pulmonata) from the North Coast Ranges of California, with observations on the spermatophore. Wasmann Journal of Biology 44:57–65.

ROTH, B. 1988a. A new Recent species of *Helminthoglypta* (Gastropoda: Pulmonata) from the Klamath Mountains, California, and redescription of an Oligo-Miocene species from Oregon. Wasmann Journal of Biology 45:16–25.

ROTH, B. 1988b. Camaenid land snails (Gastropoda: Pulmonata) from the Eocene of southern California and their bearing on the history of the American Camaenidae. Transactions of the San Diego Society of Natural History 21:203–220.

ROTH, B. & F. G. HOCHBERG, JR. 1988. A new species of *Helminthoglypta* (*Coyote*) (Gastropoda: Pulmonata) from the Tehachapi Mountains, California. The Veliger 31:258–261.

ROTH, B. & F. G. HOCHBERG, JR. 1992. Two new species of *Helminthoglypta* (Gastropoda: Pulmonata) from southern California, with comments on the subgenus *Charodotes* Pilsbry. The Veliger 35:338–346.

ROTH, B. & P. K. M. MEGAW. 1989. Early Tertiary land mollusks (Gastropoda: Pulmonata) from Sierra Santa Eulalia, Chihuahua, Mexico, and the origins of the North American arid-land mollusk fauna. Malacological Review 22:1–16.

ROTH, B. & T. A. PEARCE. 1988. "*Micrarionta*" *dallasi,* a helicinid (prosobranch), not a helminthoglyptid (pulmonate) land snail: paleoclimatic implications. The Southwestern Naturalist 33:117–119.

ROWE, T. 1987. Definition and diagnosis in the phylogenetic system. Systematic Zoology 36:208–211.

SCHILEYKO, A. A. 1978. Land mollusks of the superfamily Helicoidea. Fauna of the U.S.S.R., Mollusks, 3(6):1–384.

SCHILEYKO, A. A. 1979. The system of the order Geophila (=Helicida) (Gastropoda Pulmonata). Pp. 44–69 in O. A. Scarlato (ed.), Morphology, Systematics and Phylogeny of Mollusca. Proceedings of the Zoological Institute, Academy of Sciences of the U.S.S.R. 80.

SCHILEYKO, A. A. 1991. Taxonomic status, phylogenetic relations and system of the Helicoidea sensu lato (Pulmonata). Archiv für Molluskenkunde 120:187–236.

SIMPSON, G. G. 1961. Principles of Animal Taxonomy. Columbia University Press: New York.

SMITH, A. G., W. B. MILLER, C. C. CHRISTENSEN & B. ROTH. 1990. Land Mollusca of Baja California, Mexico. Proceedings of the California Academy of Sciences 47:95–158.

SOKAL, R. R. & F. J. ROHLF. 1981. Taxonomic congruence in the Leptopodomorpha re-examined. Systematic Zoology 30:309–325.

SOLEM, A. 1984. A world model of land snail diversity and abundance. Pp. 6–22 in A. Solem and A. C. van Bruggen (eds.), World-Wide Snails: Biogeographical Studies on Non-Marine Mollusca. E. J. Brill/Dr. W. Backhuys: Leiden.

SOLEM, A. 1991. The next challenge: life styles and evolution. American Malacological Bulletin 8:173–175.

SOLEM, A. & C. C. CHRISTENSEN. 1984. Camaenid land snail reproductive cycle and growth patterns in semiarid areas of north-western Australia. Australian Journal of Zoology 32: 471–491.

TAYLOR, D. W. 1954. Nonmarine mollusks from Barstow Formation of southern California. U. S. Geological Survey Professional Paper 254-C:67–80, pl. 20.

WATROUS, L. E. & Q. D. WHEELER. 1981. The out-group comparison method of character analysis. Systematic Zoology 30:1–11.

WEBB, G. R. 1942. Comparative observations of the mating habits of three California landsnails. Bulletin of the Southern California Academy of Sciences 41:102–108.

WEBB, G. R. 1951. An instance of amixia between two species of landsnails (Pulmonata, Helminthoglyptidae). American Naturalist 85:137–139.

WEBB, G. R. 1952a. Pulmonata, Helminthoglyptidae: sexological data on the land snails, *Cepolis maynardi* & *Helminthoglypta traski fieldi* and their evolutionary significance. Gastropodia 1:4–5.

WEBB, G. R. 1952b. Pulmonata, Xanthonycidae: comparative sexological studies of the North American land-snail, *Monadenia fidelis* (Gray)—a seeming ally of Mexican helicoids. Gastropodia 1:1–3.

WEBB, G. R. 1959. Two new north-western slugs, *Udosarx lyrata,* and *Gliabates oregonia.* Gastropodia 1:22–23.

WEBB, G. R. 1961. The phylogeny of American land snails with emphasis on the Polygyridae, Arionidae, and Ammonitellidae. Gastropodia 1:31–44.

WEBB, G. R. 1990. Notes on the sexology of *Sonorella simmonsi* Miller. Gastropodia 2:22–24.

WILEY, E. O. 1979. An annotated Linnean hierarchy, with comments on natural taxa and competing systems. Systematic Zoology 28:308–337.

WILEY, E. O. 1981. Phylogenetics: the Theory and Practice of Phylogenetic Systematics. John Wiley and Sons: New York.

WILEY, E. O. 1989. Kinds, individuals, and theories. Pp. 289–300 in M. Ruse (ed.), What the Philosophy of Biology Is. Kluwer Academic Publishers: Dordrecht.

ZILCH, A. 1959–1960. Gastropoda, Teil 2, Euthyneura. Handbuch der Paläozoologie, 6(2):1–400 (1959), 401–834 (1960).

APPENDIX: NEW TAXA AND PHYLOGENETIC DEFINITIONS OF NAMED TAXA

New Taxa of the Genus Group

CAHUILLUS, new genus. Type species: *Sonorella wolcottiana* Bartsch, 1903. Definition: CAHUILLUS consists of *Cahuillus indioensis wolcottianus* (Bartsch, 1903) and all other taxa that share a more recent common ancestor with it than with EREMARIONTA. Diagnostic character states: double-walled section of epiphallus cylindrical, less than 0.4 times as long as penis, extending into verge (9C). Additional referred taxa: *Cahuillus indioensis indioensis* (Yates, 1890), *Cahuillus indioensis cathedralis* (Willett, 1930), *Cahuillus greggi* (Miller, 1981), *Cahuillus mexicanus* (Pilsbry & Lowe, 1934). Many nominal species and subspecies conventionally referred to *Eremarionta* have not yet been dissected; some may prove to belong to CAHUILLUS. The conventional subspecific relationship of *C. i. indioensis, C. i. wolcottianus,* and *C. i. cathedralis* is retained pending further study of the group. *Cahuillus mexicanus* formerly was regarded as a subspecies of *Eremarionta rowelli,* but its anatomy is that of CAHUILLUS. Etymology: named for prehistoric Lake Cahuilla, which formerly occupied much of the Salton Trough in southern California.

MARICOPELLA, new genus. Type species: *Sonorella allynsmithi* Gregg & Miller, 1969. Definition: MARICOPELLA consists of *Maricopella allynsmithi* (Gregg & Miller, 1969) and all other species that share a more recent common ancestor with it than with SONORELLALES. Diagnostic character states: minute verge (12B); thick penial sheath enveloping whole penis (13B). Etymology: named for Maricopa County, Arizona.

NICOLENEA, new subgenus. Type species: *Micrarionta opuntia* Roth, 1975. Definition: NICOLENEA consists of *Micrarionta* (*Nicolenea*) *opuntia* Roth, 1975, and all other species that share a more recent common ancestor with it than with MICRARIONTA, SENSU STRICTO. Diagnostic character states: descending mucus gland absent (2C); dart sac absent (5C); papillation extensive over shell, including body whorl (18C). Tight coiling of the body whorl (19A) and absence of spermathecal diverticulum (6A) are synapomorphies shared with MICRARIONTA, SENSU STRICTO. Additional referred taxa: *Micrarionta sodalis* (Hemphill, 1901), *Micrarionta micromphala* Pilsbry, 1939. *Micrarionta opuntia, M. sodalis,* and *M. micromphala* form a clade diagnosed by the synapomorphies of translation rate slope > 0.05 (more domed spire), upper lip not reflected or recurved, and aperture wider than high (Pearce, 1990). Although *M. micromphala* and *M. sodalis* are extinct and their anatomy unknown, I refer them to NICOLENEA on the basis of these shell characters. Etymology: named for San Nicolas Island, California.

NOYO, new genus. Type species: *Helminthoglypta intersessa* Roth, 1987. Definition: NOYO consists of *Noyo intersessa* (Roth, 1987) and all other species that share a more recent common ancestor with it than with HELMINTHOGLYPTANIKI. Diagnostic character states: malleation (17A) and granular sculpture formed by collabral rugae cut by striae nearly parallel to suture; y-shaped, heavily muscularized common duct of mucus glands. Roth's (1987b) observations of an atrial sac in *N. intersessa* were incorrect; the dart sac inserts directly on the vagina. Malleated and granular sculpture occur as homoplasies in *Helminthoglypta, sensu stricto,* which has an atrial sac with vagina inserting at its base (1C). Additional referred taxa: the fossil *Helminthoglypta bozemanensis* Roth, 1986, and *H. martini* (Hanna, 1920) may be species of NOYO. Etymology: named for the Noyo River, a major stream in the region of *N. intersessa*; gender feminine.

New Suprageneric Taxa

CHAMAEARIONTALES, new taxon, consists of *Chamaearionta aquaealbae* and all taxa that share a more recent common ancestor with it than with HELMINTHOGLYPTALES.

EREMARIONTAPHIM, new taxon, consists of *Eremarionta rowelli desertorum* and all taxa that share a more recent common ancestor with it than with HELMINTHOGLYPTAPHIM.

HELMINTHOGLYPTAINA, new taxon, consists of *Helminthoglypta tudiculata* and all taxa that share a more recent common ancestor with it than with SONORELIX.

HELMINTHOGLYPTALES, new taxon, consists of *Helminthoglypta tudiculata* and all taxa that share a more recent common ancestor with it than with CHAMAEARIONTALES.

HELMINTHOGLYPTAMORPHA, new taxon, consists of *Helminthoglypta tudiculata* and all taxa that share a more recent common ancestor with it than with SONORELLAMORPHA.

HELMINTHOGLYPTANIKI, new taxon, consists of *Helminthoglypta tudiculata* and all taxa that share a more recent common ancestor with it than with *Noyo intersessa.*

HELMINTHOGLYPTAPHIM, new taxon, consists of *Helminthoglypta tudiculata* and all taxa that share a more recent common ancestor with it than with EREMARIONTAPHIM.

HELMINTHOGLYPTOTES, new taxon, consists of *Helminthoglypta tudiculata* and all taxa that share a more recent common ancestor with it than with MICRARIONTA.

SONORELLALES, new taxon, consists of *Sonorella hachitana* and all taxa that share a more recent common ancestor with it than with *Maricopella allynsmithi.*

SONORELLAMORPHA, new taxon, consists of *Sonorella hachitana* and all taxa that share a more recent common ancestor with it than with HELMINTHOGLYPTAMORPHA.

XERARIONTALES, new taxon, consists of *Xerarionta levis canescens* and all taxa that share a more recent common ancestor with it than with HELMINTHOGLYPTALES.

Phylogeny-Based Definitions of Existing Taxa

EREMARIONTA Pilsbry, 1913, consists of *Eremarionta rowelli desertorum* and all taxa that share a more recent common ancestor with it than with CAHUILLUS.

EREMARIONTA, SENSU STRICTO consists of *Eremarionta rowelli desertorum* and all taxa that share a more recent common ancestor with it than with *Eremariontoides argus.*

GREGGELIX Miller, 1972, consists of *Greggelix indigena* and all taxa that share a more recent common ancestor with it than with XERARIONTA.

HELMINTHOGLYPTA Ancey, 1887, consists of *Helminthoglypta tudiculata* and all taxa that share a more recent common ancestor with it than with ROTHELIX.

HELMINTHOGLYPTIDAE consists of *Helminthoglypta tudiculata* and all taxa that share a more recent common ancestor with it than with the clade (Xanthonychidae, Bradybaenidae).

HERPETEROS Berry, 1947, consists of *Herpeteros inglesiana* and all taxa that share a more recent common ancestor with it than with *Chamaearionta aquaealbae.*

MARTIRELIX Miller, 1982, consists of *Martirelix babrakzaii* and all taxa that share a more recent common ancestor with it than with "*Greggelix, sensu stricto*".

MICRARIONTA Ancey, 1880, consists of *Micrarionta facta* and all taxa that share a more recent common ancestor with it than with **HELMINTHOGLYPTOTES**.

MICRARIONTA, SENSU STRICTO consists of *Micrarionta facta* and all taxa that share a more recent common ancestor with it than with **NICOLENEA**.

MYOTOPHALLUS Pilsbry, 1939, consists of *Myotophallus rooseveltiana fragilis* and all taxa that share a more recent common ancestor with it than with **SONORELLA**.

ROTHELIX Miller, 1985, consists of *Rothelix lowei* and all taxa that share a more recent common ancestor with it than with **HELMINTHOGLYPTA**.

SONORANAX Pilsbry, 1939, consists of *Sonoranax dalli* and all taxa that share a more recent common ancestor with it than with "*Sonorella, sensu stricto*".

SONORELIX Berry, 1943, consists of *Sonorelix borregoensis* and all taxa that share a more recent common ancestor with it than with **HELMINTHOGLYPTAINA**.

SONORELIX, SENSU STRICTO consists of *Sonorelix borregoensis* and all taxa that share a more recent common ancestor with it than with *Mohavelix micrometalleus.*

SONORELLA Pilsbry, 1900, consists of *Sonorella hachitana* and all taxa that share a more recent common ancestor with it than with **MYOTOPHALLUS**.

XERARIONTA Pilsbry, 1913, consists of *Xerarionta levis canescens* and all taxa that share a more recent common ancestor with it than with **GREGGELIX**.

XERARIONTA, SENSU STRICTO consists of *Xerarionta levis canescens* and all taxa that share a more recent common ancestor with it than with "*Plesarionta*".

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Lecithotrophic Development in *Doto amyra* (Nudibranchia: Dendronotacea), with a Review of Developmental Mode in the Genus

by

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Abstract. *Doto amyra* from Cape Arago, Oregon fed on *Abietinaria* sp. and laid eggs averaging 152 μm in diameter on the basal portions of the hydroid. Veliger larvae with large eyespots, well-developed propodium, small velum, and type 1 shells averaging 239 μm in length hatched after an embryonic period of 28–29 days at 11–13°C or 19–21 days at 15–17°C. Newly hatched larvae alternated between crawling and swimming; in the presence of *Abietinaria* sp., most settled and began metamorphosis 1 to 2 days after hatching (at 15–17°C). Shell loss occurred 3–5 days after hatching, and the juvenile shape was attained after another 1 to 2 days. Feeding on *Abietinaria* sp. was first observed in juveniles about 300 μm long 7 days after hatching. Twelve days after hatching, juveniles ranged in length from 280 to 390 μm and had two pairs of cerata buds, but lacked rhinophores.

Of the 33 species of *Doto* for which data are available, between 82 and 91% have planktotrophic development, at least as high a proportion as known for the Nudibranchia as a whole. *Doto ussi,* with reportedly large eggs, may have direct development; the remaining species have lecithotrophic development (with *Doto acuta* sometimes hatching as newly metamorphosed juveniles). No relationship was found between adult size and development type. Long-term persistence of individual patches of *Abeitinaria* sp., combined with a patchy distribution of this hydroid over meso scales, are proposed as having been important in the evolution of lecithotrophic development in *Doto amyra.*

INTRODUCTION

Lecithotrophic and direct modes of development have been described for only a few opisthobranchs from the cold temperate waters north of Point Conception, California (Bridges, 1975; Goddard, 1984, 1990; Gibson & Chia, 1989). This paper describes in greater detail than Goddard (1984) aspects of the larval development, metamorphosis, and post-larval growth of the nudibranch *Doto amyra. Doto amyra* occurs from northern Baja California to Vancouver Island (McDonald, 1983; Millen, 1983) and preys suctorially on the coenosarc of thecate hydroids such as *Abietinaria* sp. and *Sertularia furcata* Trask, 1857 (Goddard, 1977, 1984).

Based on observations of adults, larvae, and prey of specimens of *Doto* from central California to northern Oregon, as well as on information provided by other workers, the concept of *D. amyra* currently accepted by Beeman & Williams (1980), McDonald & Nybakken (1980), McDonald (1983), and Behrens (1991) may include at least two, and possibly as many as four, distinct species. Aspects of the external morphology, color, prey, and larval development of these forms are briefly described (see Appendix) in order to distinguish which specimens I regard as *D. amyra.*

Consideration of the evolution and adaptive significance of lecithotrophic development in *Doto amyra* led to an examination of the data available on mode of development in other members of the genus. These data, not previously examined as a whole, are summarized and analyzed. Patterns of development in the genus are compared to some of those described for the Nudibranchia as a whole by Hadfield & Miller (1987).

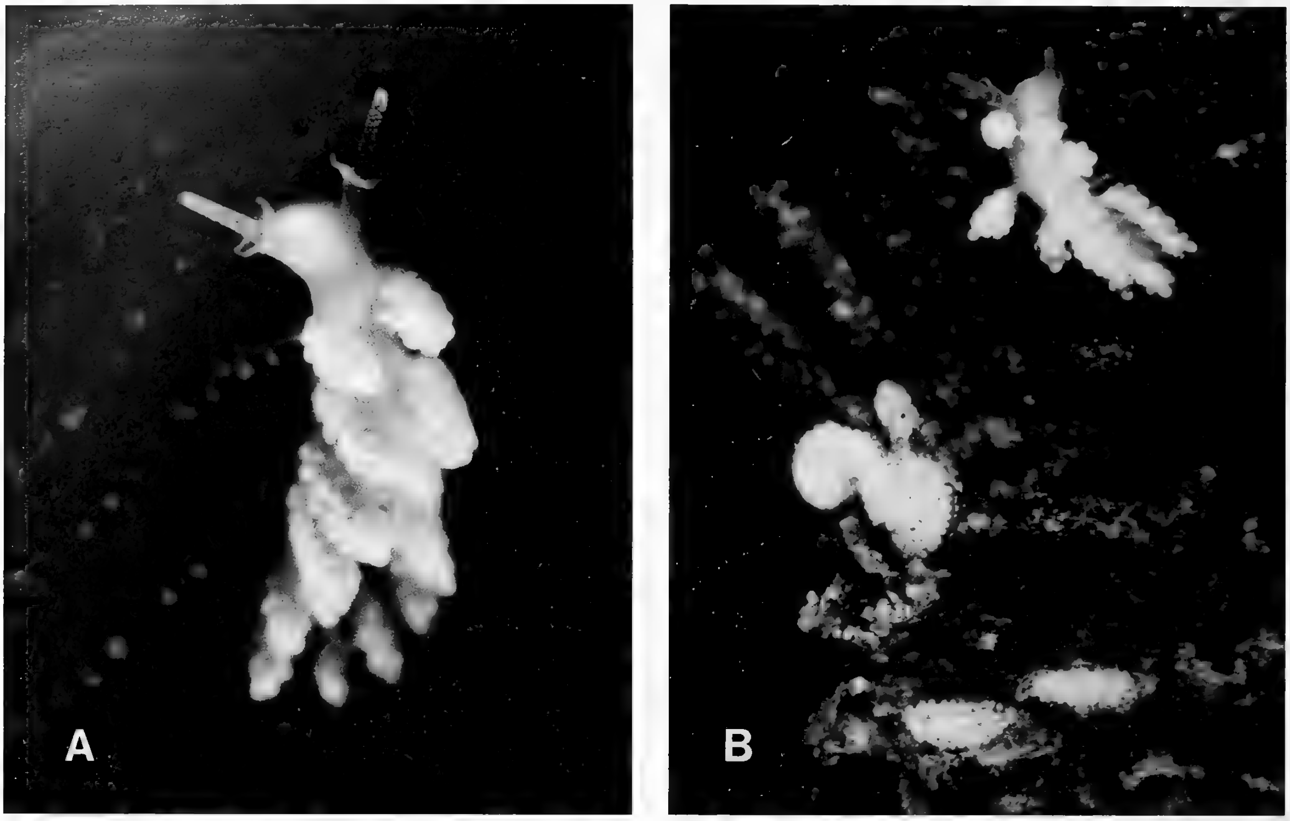

Figure 1

Doto amyra from Middle Cove, Cape Arago, Oregon, June, 1985. A. Specimen 12 mm long. B. Specimen 7 mm long with egg masses on heavily fouled *Abietinaria* sp.

MATERIALS AND METHODS

Adults and egg masses of *Doto amyra* were collected, along with their hydroid substrate and prey *Abietinaria* sp. (*A. anguina* of Ricketts et al., 1985), from semi-protected, low intertidal pools at Middle Cove, Cape Arago during spring and summer of 1983 and 1985 (see Goddard, 1984 for a description of this area). Nudibranchs and hydroids were maintained together in small wide-mouth jars containing 50–90 mL of unfiltered seawater and held in seawater baths at either 12–15°C (spring 1983), 15–17°C (summer 1983), or 11–13°C (spring and summer, 1985). Water in these jars was changed once or twice daily. Small pieces (~1 cm long) of hydroid colonies on which egg masses had been laid were removed and maintained in separate vials containing 30–90 mL of unfiltered seawater. A few newly deposited egg masses were completely removed from the hydroids and held separately. Water in all vials was changed once or twice daily until the veliger larvae hatched and every 2 or 3 days thereafter. All adults, egg masses, and larvae were exposed to indirect natural lighting in the laboratory. Observations of development, measurements of size, and photomicrographs were made using live material, a Zeiss compound microscope equipped with a calibrated ocular micrometer and bright field optics.

OBSERVATIONS

Egg Masses and Eggs

At Cape Arago, *Doto amyra* (Figure 1) laid their egg masses primarily on the stolons and basal portions of the hydrocaulus of *Abietinaria* sp. The egg masses (Figure 1B) are short, inflated ribbons laid on edge and broadly rounded at the ends. They are attached to the hydroid by a translucent white, tough, gelatinous sheet. Longer ribbons usually fold or curve back on themselves a few times; smaller masses are kidney- or crescent-shaped. The pale yellow eggs number one per capsule and give the egg masses their color. Egg masses observed in this study were up to 6 mm long and 1.8 mm high, with a mean of 79 eggs per mm^2 of ribbon (SD = 8, four samples from two egg masses). One typical egg mass, 2 mm long and 1.7 mm high, contained 240 eggs. The mean diameter of zygotes in eight egg masses varied from 145.1 μm in one egg mass (SD = 3.1 μm, n = 10) to 157.6 μm in another (SD = 3.3 μm, n = 20), with a grand mean of 151.8 μm.

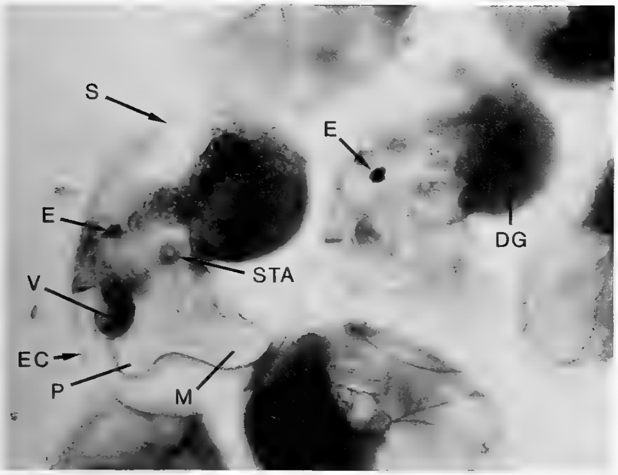

Figure 2

Live embryonic veligers of *Doto amyra* 2 days before hatching. Shell of specimen on left is 250 μm long. List of abbreviations used in Figures 2–4: A, anus; BM, buccal mass; CA, ciliary arc; DD, digestive diverticulum; DG, digestive gland; E, eye; EC, egg capsule; ESO, esophagus; INT, intestine; LK, larval kidney; M, metapodium; OP, operculum; P, propodium; RAD, radula; RCG, right cerebral ganglion; RH BUD, rhinophore bud; S, shell; STA, statocyst; STOM, stomach; V, velum.

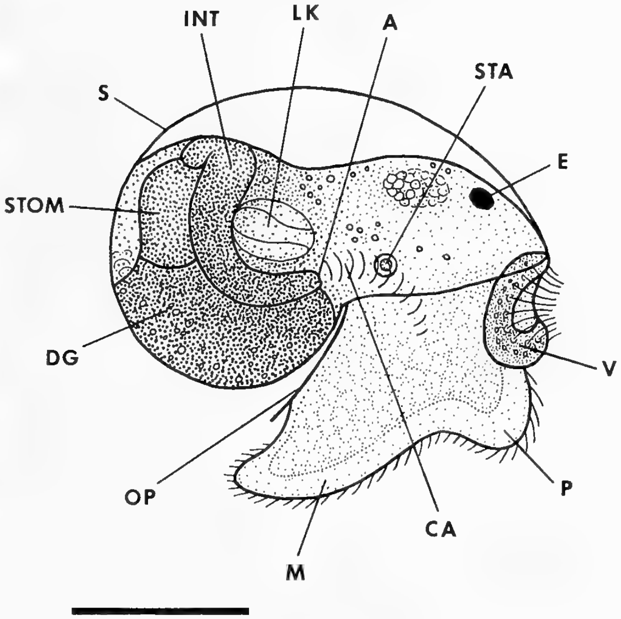

Figure 3

Newly hatched veliger larva of *Doto amyra,* right lateral aspect. Drawn from photographs and life. Scale bar = 100 μm.

Larvae

Veliger larvae hatched after an embryonic period of 19 to 21 days at 15–17°C, and 28–29 days at 11–13°C. They had large eyespots, a large foot with a well-developed propodium, and a relatively small velum (Figures 2, 3). The clear shells (type 1 of Thompson, 1961) ranged in length from 233.6 μm in one egg mass (SD = 4.6 μm, *n* = 10) to 246.1 μm in another (SD = 4.1 μm, *n* = 7), with a grand mean of 238.6 μm. I did not observe a mantle fold in the newly hatched larvae (it recedes from the shell aperture late in embryonic development and appears to fuse with the peri-visceral membrane), and the shell appeared to be attached to the body only in the region of the visceral mass, particularly on the left side. The large digestive gland was well endowed with yolk reserves, and consequently quite opaque. No radula was observed at this stage. A large, clear larval kidney was present on the right side next to the anus, and appeared to be composed of a number of large, flask-shaped cells.

A band of cilia originated just anterior to the anus, curved and tapered anterio-ventrally, and terminated on the right side of the foot (ciliary arc (CA), Figure 3). The cilia in this band were observed beating rapidly in wavelike synchrony, creating a current that ventilated the space between the shell and body, and probably removed wastes. Bonar & Hadfield (1974:236) described a similar band of cilia on the lecithotrophic larvae of the aeolid nudibranch *Phestilla sibogae* Bergh, 1905.

Larvae hatching in the presence of *Abietinaria* sp. crawled out of the egg mass and onto the hydroid or bottom of the vials. Many were then observed alternately crawling and then swimming just above the bottom of the vials. Some became trapped in the surface film of the water within 1 day of hatching, presumably after swimming there. No morphological or qualitative behavioral differences were observed between hatching larvae that had developed in the presence of *Abietinaria* and those that had developed in its absence. However, a higher proportion of the latter became trapped in the water surface film within a day of hatching, suggesting they had spent more time swimming.

Metamorphosis, Feeding, and Post-Larval Growth

The following description is based on observations made in 1983 at temperatures of 15–17°C.

Within 1 day of crawling and swimming in the presence of *Abietinaria* sp., some of the larvae anchored themselves to the hydroid perisarc, presumably with pedal gland secretions, and began metamorphosis. They appeared to prefer newly grown (and relatively unfouled) basal stolons for attachment sites, but some were also observed on the branches and stalks of the hydrocaulus. Two days after hatching, these larvae were in the same positions, had lost the velum, and had developed a small radula. Shell loss occurred 3 to 5 days after hatching. At this stage, the visceral mass was still in a posteriorly directed hump, the ciliary arc was still visible on the right side, and the radula of one individual was 80 μm long and had 11 teeth (Figures 4A, B). Examination of the eyespots revealed them to be

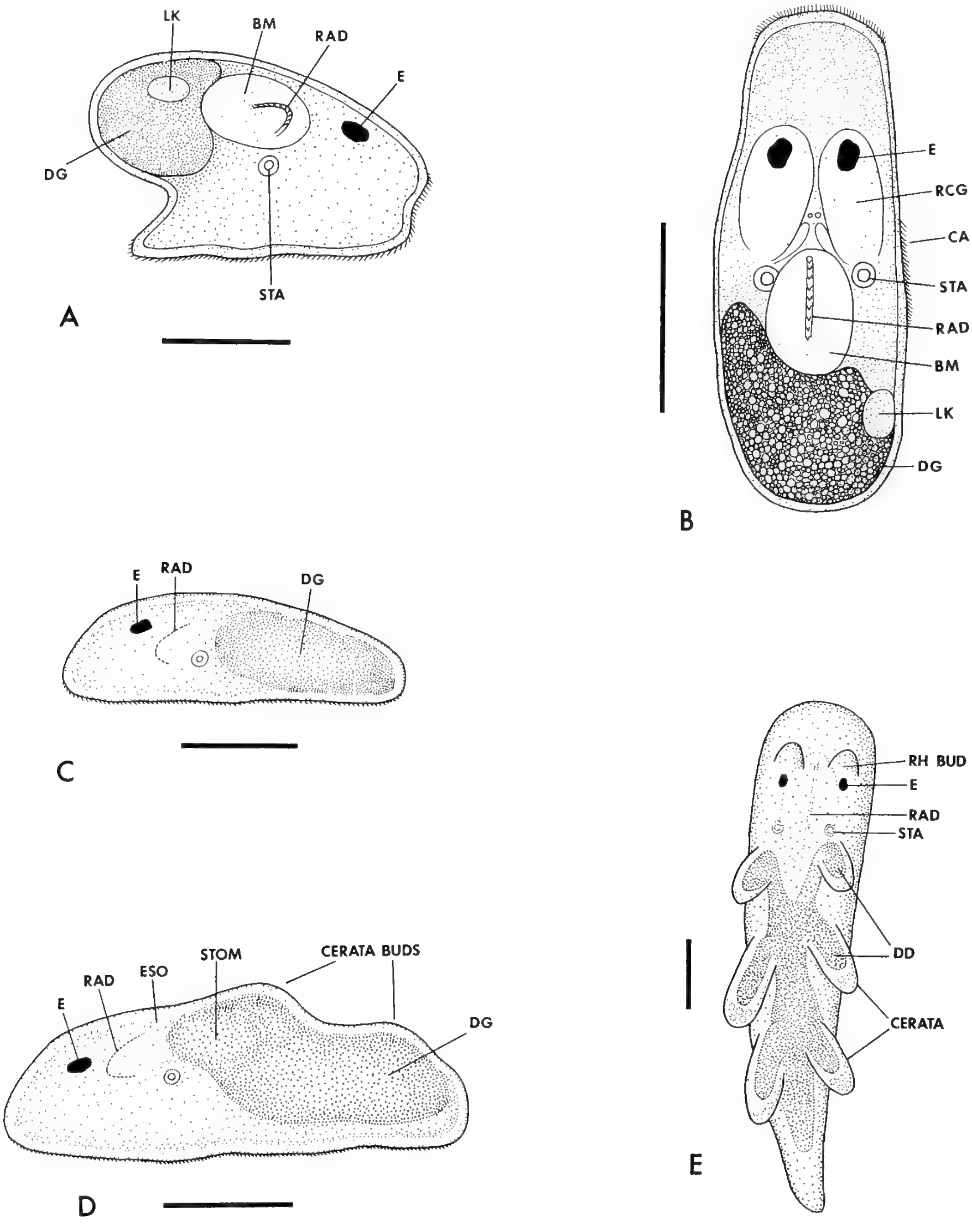

Figure 4

Stages in the post-larval growth of *Doto amyra*. Drawn from life; scale bars = 100 μm. A. Post-larva recently after exit from shell, right lateral aspect. B. Post-larva recently after exit from shell, dorsal aspect; same specimen (at same time) as in figure 4A. C. Juvenile *Doto amyra,* 290 μm long, 7 days after hatching, left lateral aspect. D. Juvenile *Doto amyra,* 360 μm long, 12 days after hatching, left lateral aspect; the radula of this specimen had 47 teeth. E. Juvenile *Doto amyra,* 750 μm long, 38 days after hatching, dorsal aspect.

composed of minute grains of dense black pigment overlain with a clear lens one-fourth the diameter of the pigmented area. Metamorphosis appeared complete 1 to 2 days after shell loss and resulted in a typical vermiform juvenile about 275 μm long (Figure 4C).

Feeding on *Abietinaria* sp. was first observed in juveniles about 290 μm long 7 days after hatching. Feeding entailed repeated protraction of the radula to drill a hole in the hydroid perisarc, followed by retraction of the radula and rhythmic contractions of muscles in the foregut and buccal mass to suck out hydroid coenosarc. Feeding did not appear very efficient in recently metamorphosed individuals: as soon as contractions of the foregut ceased, ingested coenosarc was observed to reverse direction and run out of the nudibranch's alimentary canal and back into the hydroid.

Twelve days after hatching, four juveniles ranged in length from about 280 μm to 390 μm and possessed two pairs of cerata buds, but no external signs of the rhinophores (Figure 4D). One of these individuals (390 μm long) had a radula 214 μm long with 47 teeth.

Only one individual was examined at a post-hatching age of more than 12 days. Twenty-five days after hatching, this specimen was 480 μm long and had small rhinophore buds and two pairs of cerata. After 38 days, it had a third pair of cerata (each ceras had a visible extension of the digestive gland) and measured 750 μm in length (Figure 4E). At an age of 46 days, it was still about 750 μm long, but had four pairs of cerata, longer rhinophores (still sheathless), and a fuller body with a more adultlike appearance.

DISCUSSION

Larvae virtually identical to those described above hatched from *Doto amyra* egg masses collected on the open coast of Santa Cruz County, California and Tillamook County, Oregon (personal observations); and S. Millen (personal communication) describes similar development in *Doto amyra* from the Vancouver Island region. She observed eggs 140 μm in diameter that developed into hatching larvae after 38 days (at 10°C). Newly hatched larvae alternated every few minutes between swimming and crawling, and shell loss occurred 3 days after hatching.

In the presence of *Abietinaria* sp., some of the larvae observed in this study began metamorphosis within a day of hatching (at 15–17°C). Other larvae did not appear to begin metamorphosis for another day or two, and in one case, some larvae (in the presence of a small amount of *Abietinaria* and recently metamorphosed siblings) had not metamorphosed after 9 days. This variation in onset of metamorphosis might have resulted from normal variation in the length of the pre-competent phase or from delays in metamorphosis related to laboratory conditions. Morphologically, the larvae of *Doto amyra* appear competent to metamorphose upon hatching. The propodium and eyespots are well developed, and the mantle fold has disappeared, having already withdrawn from the shell and apparently fused with the peri-visceral membrane. Other lecithotrophic larvae do not lose their mantle fold until either late in the precompetent stage or until metamorphosis itself (Thompson, 1958; Bonar & Hadfield, 1974; Todd, 1981; Rose, 1983).

Larvae held in the absence of *Abietinaria* sp. generally became trapped in the surface film within a day of hatching and were not observed further. Consequently, I do not know if this hydroid is necessary to induce metamorphosis. Little is known about the ability of the larvae to delay metamorphosis and disperse by swimming, or their ability to feed in the plankton as has been observed in some other lecithotrophic larvae (e.g., Kempf & Hadfield, 1985). Larvae hatching in the absence of *Abietinaria* did appear to swim more than those hatching in its presence, and, as suggested by the observation of healthy-looking larvae up to 9 days after hatching, the extensive yolk reserves in the digestive gland probably can support competent veligers for days and possibly weeks. In addition, an extended swimming phase is not necessarily precluded by the size of the hatching larvae. Some nudibranch larvae cannot settle and metamorphose until they are considerably larger than the larvae of *Doto amyra* (Hadfield & Miller, 1987: fig. 12).

During the present study, few *Doto amyra* survived more than 1 or 2 weeks beyond metamorphosis. Holding conditions in the laboratory might have depressed early survivorship, or early feeding efficiency and juvenile survivorship of *Doto amyra* might be higher on different species of prey. *Doto amyra* is known to consume other hydroids in other localities (see Appendix), but has only been found feeding on *Abietinaria* at Cape Arago.

The observation of hydroid tissue running out of the foregut of feeding, recently metamorphosed *Doto amyra* and back into the hydrocauli of *Abietinaria* sp. suggests that feeding by young individuals is not very efficient. It also raises the intriguing possibility that hydroids, using their gastrodermal cilia, may be capable of forming localized, internal negative pressures as one defense against small suctorial predators. Alternatively, could *Doto amyra* utilize these backflows to inject into the hydroids enzymes or other substances that actually facilitate ingestion? Diet composition and interactions between post-metamorphic *Doto amyra* and their prey warrant further study.

Developmental mode is currently known for 70 species of nudibranchs from the northeastern Pacific Ocean north of Point Conception, California (Goddard, 1992, and unpublished data). Excluding the introduced *Tenellia adspersa* (Nordmann, 1845), all but *Doto amyra* have planktotrophic development, begging questions about the origin and adaptive significance of lecithotrophic development in this species. As shown below, mode of development in *Doto amyra* does not reflect phylogenetic constraints within the genus, or constraints on absolute fecundity imposed by small adult size. Most species of *Doto,* including those sympatric with *D. amyra,* are smaller than *Doto amyra* and have planktotrophic development. Based on limited observations of its hydroid prey (and ignoring for now any nonadaptive explanations), I propose that lecithotrophic development in *Doto amyra* is adaptive in specializing as a partial predator on hydroids that are spatially and temporally persistent on minute and local scales and patchily distributed over larger or meso scales (10s to 100s of kms).

Although *Abietinaria* sp. is subject to seasonal fouling by epifauna and flora (Ricketts et al., 1985; personal observations), as well as predation by *Doto amyra* and other dendronotacean nudibranchs (McDonald & Nybakken, 1978; Goddard, 1990), small patches of this hydroid (< 0.25 m^2) have persisted for at least 12 years at Middle Cove, Cape Arago (personal observations made during all seasons). Predation by *Doto amyra* appears to be partial; the thick perisarc of the hydroid is damaged little, and only coenosarc is consumed (Goddard, 1984; present study). In addition, the stolons of *Abietinaria* sp. are often overgrown (but not damaged) by sponges, colonial ascidians, and other encrusting invertebrates (personal observations) and thus effectively shielded from predation by *Doto.* Enough coenosarc may remain after bouts of predation to fuel either the growth of new stolons and hydrocauli or the regeneration of existing ones (e.g., see Hughes, 1977, 1986), especially if population densities of *Doto amyra* are kept low by other factors, such as predation on juveniles.

Doto amyra therefore appear likely to hatch close to exploitable *Abietinaria,* at least at Cape Arago. If this predictability in local food supply had once been combined with a very patchy distribution in the hydroid over a larger scale so that a larva's chances of successfully finding new patches of prey declined sharply with increasing dispersal distance, selection might have favored the reduced obligatory planktonic periods associated with lecithotrophic development. When the abundance or quality of local prey declined far enough, resulting in a lack of appropriate settlement cues, pelagic lecithotrophic larvae could postpone metamorphosis and traverse longer distances in search of fresh patches of prey (Hadfield & Switzer-Dunlap, 1984; Kempf & Hadfield, 1985).

Long-term persistence and accessibility of individual patches of its prey, even in the face of predation, may then have been important in the evolution of lecithotrophic development in *Doto amyra.* In order to evaluate this hypothesis further, more information is needed on: (1) the distribution and population dynamics of *Abietinaria* sp., (2) the effects of predation on this hydroid by *D. amyra,* and (3) the dietary composition of juvenile and adult *D. amyra* over a larger portion of their range.

Development in the Genus

Species of *Doto* prey suctorially on the coenosarc of hydroids (Goddard, 1984; Thompson & Brown, 1984) and are smaller than most other nudibranchs (adults rarely exceed 10–15 mm in length) (Lemche, 1976; Todd, 1981; Thompson & Brown, 1984). Because small adult size is associated with a reduced pelagic phase in the life history of many benthic marine invertebrates (e.g., Chia, 1974; Menge, 1975; Strathmann & Strathmann, 1982; Strathmann, 1985), one might expect a higher incidence of lecithotrophy and/or direct development in the genus *Doto* compared to the Nudibranchia as a whole, more than two-thirds of which produce planktotrophic larvae (Hadfield & Miller, 1987). On the other hand, the opportunistic and ephemeral nature of many hydroids (Clark, 1975; Hughes, 1977, 1983, 1986; Boero, 1984; Harris, 1987) might be exploited best by predators with short generation times and good powers of dispersal. For small benthic predators with limited dispersal abilities, the latter can be facilitated by planktotrophic or pelagic lecithotrophic larvae adapted for locating the prey of the adults.

Data presented in recent analyses of developmental patterns in the Opisthobranchia (Ros, 1981; Hadfield & Switzer-Dunlap, 1984; Hadfield & Miller, 1987) suggest that most species of *Doto* have planktotrophic development. However, patterns of development have not been examined in detail in this genus, and considerably more data (some new, some previously overlooked) are available for analysis.

Based on observations of the size, morphology, and behavior of hatching veliger larvae, developmental mode can be determined for 11 species of *Doto* (Table 1). Nine of these have planktotrophic larvae; *D. amyra* produces short-term lecithotrophic larvae from eggs averaging 152 μm in diameter (present study); and *D. acuta* hatch as either short-term lecithotrophic larvae or as newly metamorphosed juveniles (both from eggs 110 to 120 μm in diameter) (Schmekel & Kress, 1977). All larvae have coiled type 1 shells (see Thompson, 1961).

Egg diameter appears to be a relatively good predictor of shell size at hatching in the genus (Figure 5). However, of the planktotrophic species, *Doto yongei* is reported to produce the largest hatching veligers from the smallest eggs—if omitted from the regression analysis summarized in Figure 5, R^2 would increase to 0.98. The eggs and hatching larvae of this species should be re-examined for idiosyncrasies in morphology and development as well as to confirm the original size measurements.

Egg diameter varies widely within different taxonomic groups of Nudibranchia, including genera, and if small enough, can be used to distinguish between planktotrophic and non-planktotrophic modes of development (Hadfield & Switzer-Dunlap, 1984; Hadfield & Miller, 1987). Egg diameters are known for a total of 26 species of *Doto* (Table 2) and range from 64 to 230 μm. Their frequency distribution is skewed to the right and has a mode of 75 μm (Figure 6). Twenty-one (81%) of these species produce eggs under 100 μm, the minimum diameter known for nudibranch species with lecithotrophic or direct modes of development (Hadfield & Miller, 1987).

Of the five species of *Doto* with eggs larger than 100

Table 1

Development in the genus *Doto*. Values for egg diameter and shell length at hatching are means or grand means. P = planktotrophic, L = lecithotrophic, D = direct (capsular metamorphic or ametamorphic). Inferred developmental types in brackets.

Species	Egg diameter (µm)	Embryonic period (days)	Temp. (°C)	Shell length at hatching (µm)	Type of devel.	Reference
D. japonica Odhner, 1936	80	5	26–30	145	(P)	Hamatani (1963)
D. yongei Thompson, 1972	64	—	—	168	P	Thompson (1972)
D. coronata (Gmelin, 1791)	72	13	10–12	116	(P)	Kress (1975)
D. fragilis (Forbes, 1838)	83	18	10–12	145	(P)	Kress (1975)
D. pinnatifida (Montagu, 1804)	95	16	10–12	160	(P)	Kress (1975)
D. acuta Schmekel & Kress, 1977	117	16–20	16	—	L or D	Schmekel & Kress (1977)
D. amyra Marcus, 1961	152	19–21 28–29	15–17 11–13	239	L	Goddard (1984, present study)
D. kya Marcus, 1961	78	7	15–17	133	P	Goddard (1992)
D. lancei Marcus & Marcus, 1967[1]	—	—	—	—	P	personal observation
D. form A[2]	76	12	11–13	123	P	Goddard (1992)
D. form B[2]	70	11	11–13	122	P	Goddard (1992)

[1] Specimens from Bahía de Concepción, Baja California Sur, and Matanchen Beach, Nayarit, Mexico.

[2] See Appendix.

µm, *D. amyra* and *D. acuta* have already been discussed, and development has not been described for *D. fragaria, D. tuberculata,* and *D. ussi.* Based on the egg size distributions reported by Thompson (1967) and Hadfield & Miller (1987:fig. 1), *D. fragaria* and *D. tuberculata* most likely have planktotrophic or lecithotrophic development, and *D. ussi* probably has direct development (however, regarding the latter species see Table 2, note 3).

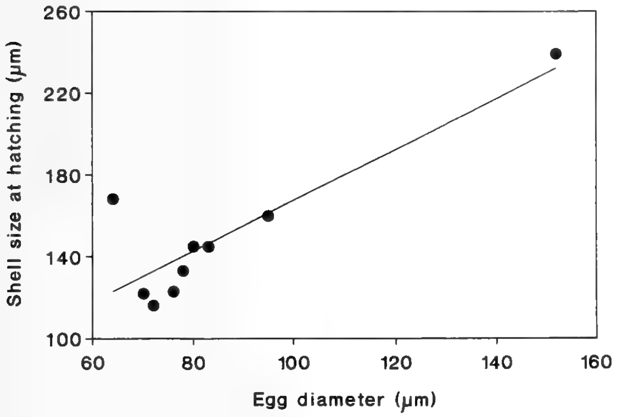

Figure 5

Relationship between mean egg diameter and mean shell size at hatching for nine species of *Doto* ($y = 1.24x + 43.65$, $R^2 = 0.76$). Data from Table 1.

Species of *Doto* usually deposit one egg per capsule, but pairs are occasionally seen, especially in *D. fragilis* (Kress, 1975:696). There are no reports of egg masses containing extra-zygotic yolk.

Intraspecific variation in egg size in the genus is generally small. The largest range in egg size reported for a species of *Doto* (all localities and egg masses combined) is 40 µm for *D. ussi,* followed by 25 µm for *D. pinnatifida* and 22 µm for *D. amyra, D. coronata,* and *D. maculata*

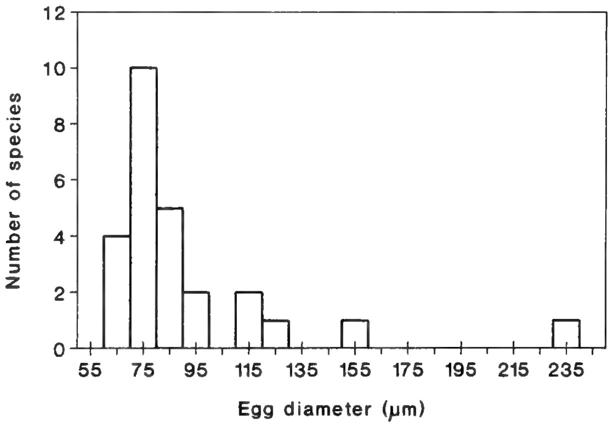

Figure 6

Egg size distribution for 26 species of *Doto*. Data from Table 2.

Table 2

Egg size and maximum reported adult length in the genus *Doto*. Values given for eggs are means or, if more than one mean was available for a species (i.e., from different egg masses, localities, or references), grand means.

Species of *Doto*	Egg diameter (µm)	Maximum adult length (mm)	Source[1]	
			egg size	adult size
acuta Schmekel & Kress, 1977	117	7	17	17
amyra Marcus, 1961	152	14	6, 23	23
chica Marcus & Marcus, 1960	77	10*	4	12
coronata (Gmelin, 1791)[2]	70	15	5, 10, 17, 19	21
doerga Marcus & Marcus, 1963	83	6	17	18
eireana Lemche, 1976	81	7	5, 11	21
fluctifraga Ortea & Perez, 1982	97	8	15	15
fragaria Ortea & Bouchet, 1988	110	8	14	14
fragilis (Forbes, 1838)	81	40	10, 17	17
japonica Odhner, 1936	80	12	9	1
koenneckeri Lemche, 1976	68	8	5	16
kya Marcus, 1961	78	10	7	2
lemchei Ortea & Urgorri, 1978	74	10	5, 22	21
maculata (Montagu, 1804)	72	9	5	21
millbayana Lemche, 1976	66	14	5	21
oblicua Ortea & Urgorri, 1978	73	9.5	16	16
paulinae Trinchese, 1881	70	7	17	17
pinnatifida (Montagu, 1804)	97	29	5, 10, 17	21
rosea Trinchese, 1881	70	12	17	17
tuberculata Lemche, 1976	127	19	5	21
ussi Ortea, 1982[3]	230	10	13	13
verdicioi Ortea & Urgorri, 1978	67	6	16	16
yongei Thompson, 1972	64	6	20	20
form A[4]	76	7	7	23
form B[4]	70	11	7	23
sp. (*coronata* of Clark, 1975)[5]	89	12	3	8

[1] 1, Baba (1949); 2, Behrens (1991); 3, Clark (1975); 4, Clark & Goetzfried (1978); 5, Frenandez-Ovies & Ortea (1981); 6, Goddard (1984); 7, Goddard (1992); 8, Gosner (1971); 9, Hamatani (1963); 10, Kress (1975); 11, Lemche (1976); 12, Marcus (1972); 13, Ortea (1982); 14, Ortea & Bouchet (1988); 15, Ortea & Perez (1982); 16, Ortea & Urgorri (1987); 17, Schmekel & Kress (1977); 18, Schmekel & Portmann (1982); 19, Thompson (1967); 20, Thompson (1972); 21, Thompson & Brown (1984); 22, Thompson et al. (1990); 23, present study (see Appendix).

[2] *Doto coronata* as described by Thompson & Brown (1984) and Lemche (1976); however, see Morrow et al. (1992).

[3] Ortea (1982) clearly states that the eggs of *Doto ussi* average 230 µm in diameter, but the scale bar and depiction of eggs in his figure 3 imply an average diameter of about 140 µm. The former value therefore requires confirmation.

[4] See Appendix.

[5] According to Thompson & Brown (1984:29) *Doto coronata* reported from the east coast of the United States are "distinctive and may be another species." The large differences in egg size between European *D. coronata* and the *D. coronata* of Clark (1975) (see above) support this hypothesis. *D. coronata* of Clark (1975) is therefore here considered a separate species.

* Length of a preserved specimen (an estimate of 15 mm was used in statistical analyses).

(Fernandez-Ovies & Ortea, 1981; Kress, 1975; present study). Using standard deviations in egg diameter reported for individual egg masses or eggs from a given locality by Kress (1975), Clark (1975), and the present study, the average coefficient of variation in egg diameter for a species of *Doto* is about 3% (range, 0.8%–9.4%; data for eight species), a value similar to those for other nudibranchs (Goddard, 1992; and see means and standard deviations in egg diameter reported by Clark, 1975; Eyster, 1980; Williams, 1980; and Ros, 1981).

As might be expected, given the limited intraspecific variation in egg size, no examples of poecilogony or polymorphism in type of development (Hoagland & Robertson, 1988) have been reported in the genus. Although *Doto acuta* from different egg masses hatch as either short-term lecithotrophic larvae or newly metamorphosed juveniles (Schmekel & Kress, 1977), this variation appears to result more from extrinsic factors affecting the embryonic period rather than significant differences in egg size and/or developmental pathways (both types developed at the same temperature from eggs of the same size, and individuals hatching as juveniles had a longer embryonic period than those hatching as larvae).

Developmental mode can be inferred for six additional species of *Doto*. Based on egg capsule sizes (early in development) reported by García Gómez et al. (1988) for *D. furva,* and on ratios of capsule length to egg diameter that can be derived from Kress (1975) and Schmekel & Kress (1977) for five other European species of *Doto, D. furva* most likely has eggs between 80 and 95 µm in diameter and thus probably has planktotrophic development. Descriptions and depictions of egg masses (especially their size and approximate number of eggs) in Just & Edmunds (1985) suggest that *D. columbiana* O'Donoghue, 1921, *D. dunnei* Lemche, 1976, *D. onusta* Hesse, 1872, and their *Doto* sp. E have planktotrophic development, and that development in *Doto* sp. C is either planktotrophic or lecithotrophic. Just & Edmund's *Doto* sp. D, which has "small eggs," is probably the same as the *Doto* form B of the present study (see Table 2 and Appendix) and therefore has already been included in the present analysis.

Based on the data in Tables 1 and 2, and including the inferences for the above six species, between 82% (27/33) and 91% (30/33) of species of *Doto* have planktotrophic development, at least as high a proportion as the 66 to 80% reported by Hadfield & Miller (1987) for the Nudibranchia as a whole. There is no relationship between maximum reported adult length and egg diameter (and thus mode of development) for the species listed in Table

2 ($R^2 = 0.003$, $n = 26$, $P > 0.25$). Moreover, the maximum reported adult lengths of the planktotrophic species ($n = 27$ or $n = 30$) do not differ significantly from those of the non-planktotrophic species ($n = 6$ or $n = 3$, respectively) ($P > 0.4$ for both comparisons; Mann-Whitney U test).[1]

The high incidence of planktotrophic development observed in *Doto* compared to nudibranchs as a whole could be an artifact of sample size ($n = 33$ species), as well as the non-random nature of the sample (also see below). However, as mentioned at the beginning of this section, planktonic modes of development could be advantageous in exploiting hydroids by facilitating dispersal. Planktonic larvae, especially those capable of feeding and delaying metamorphosis for long periods, might also be important in surviving seasonal or unpredictable lows in hydroid abundance. Given these advantages, planktotrophy, which is assumed to be the ancestral mode of development in opisthobranchs (Hadfield & Miller, 1987), should predominate among hydroid-feeding nudibranchs as long as larval mortality rates do not offset the gains in fecundity associated with this mode of development (Strathmann, 1985; Hadfield & Miller, 1987; Levin & Hugget, 1990). Where larval mortality rates are consistently higher, we would expect evolutionary shifts toward the reduced obligatory planktonic periods associated with pelagic lecithotrophic development (this is the essence of what was argued earlier for *Doto amyra*). Non-feeding modes of development in *Doto* and other hydroid-feeding nudibranchs might also be expected (1) where high juvenile mortality rates select for increases in juvenile size attained primarily through ametamorphic development (Hadfield & Miller, 1987); and (2) in members of lineages in which feeding larval stages have already been lost (Strathmann, 1978).

Factors affecting larval and juvenile mortality of marine benthic invertebrates can vary regionally (Thorson, 1950; Rumrill, 1990), with (as alluded to above) implications for their life histories and mode of development (Strathmann, 1985; Hines, 1986). Most of the species of *Doto* included in the present review are from the northwest Mediterranean Sea and the cool temperate waters of the northeast Atlantic and northeast Pacific oceans. Nudibranchs from all three of these regions show a high incidence of planktotrophic development compared to those from other regions, where conditions appear to favor non-feeding types of development (Goddard, 1992). This pattern could also hold true for *Doto*, lowering the percentage of planktotrophic development ultimately observed in the genus as a whole.

The predominance of planktotrophic development and lack of relationship between adult size and mode of development in *Doto* indicate that fecundities, even in the smallest species, have not been limited in a way that might have favored (owing to planktonic mortality and relatively low densities of settling larvae) an evolutionary shift toward the reduced larval periods and reduced dispersal associated with non-planktotrophic modes of development. Either reproduction is synchronous enough to ensure adequate densities of settling larvae, or benthic populations are dense and widespread enough (and juvenile mortality rates low enough) that recruits from the plankton, however few, have a good chance of reaching maturity, encountering mates, and successfully reproducing. Early maturity, a relatively prolonged reproductive period, and overlapping generations would probably enhance an individual's chances even more under the latter circumstances. Individuals appear to begin mating at small sizes (Miller, 1962; Clark, 1975; personal observations), and Miller (1962) suggests that *Doto coronata* from Britain live from 5 to 10 months, depending on the season, and have up to four overlapping generations per year.

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LITERATURE CITED

BABA, K. 1949. Opisthobranchia of Sagami Bay Collected by His Majesty the Emperor of Japan. Iwanami Shoten: Tokyo. 194 pp.

BEEMAN. R. D. & G. C. WILLIAMS. 1980. Opisthobranchia and Pulmonata: the sea slugs and allies. Pp. 308–354 in R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal Invertebrates of California. Stanford University Press: Stanford, California. 690 pp.

BEHRENS, D. W. 1991. Pacific Coast Nudibranchs. Sea Challengers: Monterey, California. 107 pp.

BOERO, F. 1984. The ecology of marine hydroids and effects of environmental factors: a review. Marine Ecology 5:93–118.

BONAR, D. B. & M. G. HADFIELD. 1974. Metamorphosis of the marine gastropod *Phestilla sibogae* Bergh (Nudibranchia: Aeolidacea): I. Light and electron microscopic analysis of larval and metamorphic stages. Journal of Experimental Marine Biology and Ecology 16:227–255.

BRIDGES, C. B. 1975. Larval development of *Phyllaplysia taylori* Dall, with a discussion of development in the Anaspidea (Opisthobranchia: Anaspidea). Ophelia 14:161–184.

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[1] Adult lengths used for *Doto columbiana*, *D. dunnei*, *D. furva*, *D. onusta*, and *D.* spp. C and E of Just & Edmunds (1985) were 14, 25, 15, 11, 4, and 10 mm, respectively (see García-Gómez et al., 1988; Just & Edmunds, 1985).

CHIA, F.-S. 1974. Classification and adaptive significance of developmental patterns in marine invertebrates. Thalassia Jugoslavica 10:121–130.

CLARK, K. B. 1975. Nudibranch life cycles in the northwest Atlantic and their relationship to the ecology of fouling communities. Helgolander wissenschaftliche Meeresuntersuchungen 27:28–69.

CLARK, K. B. & A. GOETZFRIED. 1978. Zoogeographic influences on development patterns of north Atlantic Ascoglossa and Nudibranchia, with a discussion of factors affecting egg size and number. Journal of Molluscan Studies 44:283–294.

EYSTER, L. S. 1980. Distribution and reproduction of shell-less opisthobranchs from South Carolina, USA. Bulletin of Marine Science 30:580–599.

FERNANDEZ-OVIES, C. L. & J. A. ORTEA. 1981. Contribucion al conocimiento de las masas de huevos de los opistobranquios (Mollusca: Gastropoda). 1. El género *Doto* (Oken, 1815) en el norte y noroeste de España. Revista Facultad de Cienceas, Universidad Oviedo (Ser. Biologia) 22:41–51.

GARCÍA GÓMEZ, J. C., C. M. LÓPEZ DE LA CUADRA & M. B. BALBUENA MARCILLA. 1988. Adiciones al conocimiento de *Doto furva* García Gómez y Ortea Rato, 1983 (Gastropoda: Nudibranchia: Dendronotacea). Bolletino Malacologico 24: 173–178.

GIBSON, G. D. & F.-S. CHIA. 1989. Developmental variability (pelagic and benthic) in *Haminoea callidegenita* (Opisthobranchia: Cephalaspidea) is influenced by egg mass jelly. Biological Bulletin 176:103–110.

GODDARD, J. H. R. 1977. Observations on the natural history and occurrence of nudibranch molluscs at Scott Creek, Santa Cruz County. Senior Thesis, Biology, University of California: Santa Cruz, California. 56 pp.

GODDARD, J. H. R. 1984. The opisthobranchs of Cape Arago, Oregon, with notes on their biology and a summary of benthic opisthobranchs known from Oregon. The Veliger 27: 143–163.

GODDARD, J. H. R. 1987. Observations on the opisthobranch mollusks of Punta Gorda, California, with notes on the distribution and biology of *Crimora coneja*. The Veliger 29:267–273.

GODDARD, J. H. R. 1990. Additional opisthobranch mollusks from Oregon, with a review of deep water records and observations on the fauna of the south coast. The Veliger 33: 230–237.

GODDARD, J. H. R. 1992. Patterns of development in nudibranch molluscs from the northeast Pacific Ocean, with regional comparisons. Unpublished Ph.D. Dissertation, University of Oregon, Eugene, Oregon. 237 pp.

GOSNER, K. L. 1971. Guide to the Identification of Marine and Estuarine Invertebrates. Wiley-Interscience: New York. 693 pp.

HADFIELD, M. G. & S. E. MILLER. 1987. On developmental patterns of opisthobranchs. American Malacological Bulletin 5:197–214.

HADFIELD, M. G. & M. SWITZER-DUNLAP. 1984. Opisthobranchs. Pp. 209–350 in A. S. Tompa, N. H. Verdonk & J. A. M. van den Biggelaar (eds.), The Mollusca, vol. 7, Reproduction. Academic Press: New York.

HAMATANI, I. 1963. Notes on the veligers of Japanese opisthobranchs. Publications of Seto Marine Biological Laboratory 11:125–130.

HARRIS, L. G. 1987. Aeolid nudibranchs as predators and prey. American Malacological Bulletin 5:287–292.

HINES, A. H. 1986. Larval problems and perspectives in life histories of marine invertebrates. Bulletin of Marine Science 39:506–525.

HOAGLAND, K. E. & R. ROBERTSON. 1988. An assessment of poecilogony in marine invertebrates: phenomenon or fantasy? Biological Bulletin 174:109–125.

HUGHES, R. G. 1977. Aspects of the biology and life-history of *Nemertesia antennina* (L.) (Hydrozoa: Plumulariidae). Journal of the Marine Biological Association of the United Kingdom 57:641–658.

HUGHES, R. G. 1983. The life-history of *Tubularia indivisa* (Hydrozoa: Tubulariidae) with observations on the status of *T. ceratogyne*. Journal of the Marine Biological Association of the United Kingdom 63:467–479.

HUGHES, R. G. 1986. Differences in the growth, form and life history *Plumularia setacea* (Ellis & Solander) (Hydrozoa: Plumulariidae) in two contrasting habitats. Proceedings of the Royal Society of London (B) 288:113–125.

JUST, H. & M. EDMUNDS. 1985. North Atlantic Nudibranchs (Mollusca) Seen by Henning Lemche. Ophelia Publications: Marine Biological Laboratory: Helsingor, Denmark. 150 pp.

KEMPF, S. C. & M. G. HADFIELD. 1985. Planktotrophy by the lecithotrophic larvae of a nudibranch, *Phestilla sibogae*. Biological Bulletin 169:119–130.

KRESS, A. 1975. Observations during embryonic development in the genus *Doto* (Gastropoda, Opisthobranchia). Journal of the Marine Biological Association of the United Kingdom 55:691–701.

LEMCHE, H. 1976. New British species of *Doto* Oken, 1815 (Mollusca: Opisthobranchia). Journal of the Marine Biological Association of the United Kingdom 56:691–706.

LEVIN, L. A. & D. V. HUGGETT. 1990. Implications of alternative reproductive modes for seasonality and demography in an estuarine polychaete. Ecology 71:2191–2208.

MARCUS, ER. 1961. Opisthobranch mollusks from California. The Veliger 3 (Supplement) 1–85.

MARCUS, EV. 1972. On some opisthobranchs from Florida. Bulletin of Marine Science 22:284–308.

MCDONALD, G. R. 1983. A review of the nudibranchs of the California coast. Malacologia 24:114–276.

MCDONALD, G. R. & J. W. NYBAKKEN. 1978. Additional notes on the food of some California nudibranchs with a summary of known food habits of California species. The Veliger 21: 110–119.

MCDONALD, G. R. & J. W. NYBAKKEN. 1980. Guide to the Nudibranchs of California. American Malacologists, Inc.: Melbourne, Florida. 72 pp.

MENGE, B. A. 1975. Brood or broadcast? The adaptive significance of different reproductive strategies in the two intertidal seastars *Leptasteria hexactis* and *Pisaster ochraceus* Marine Biology 31:87–100.

MILLEN, S. V. 1983. Range extensions of opisthobranchs in the northeastern Pacific. The Veliger 25:383–386.

MILLER, M. C. 1962. Annual cycles of some Manx nudibranchs, with a discussion of the problem of migration. Journal of Animal Ecology 31:545–569.

MORROW, C. C., J. P. THORPE & B. E. PICTON. 1992. Genetic divergence and cryptic speciation in two morphs of the common subtidal nudibranch *Doto coronata* (Opisthobranchia: Dendronotacea: Dotoidae) from the northern Irish Sea. Marine Ecology Progress Series 84:53–61.

ORTEA, J. A. 1982. Una nueva especie de *Doto* (Mollusca, Dendronotacea) de las Islas Comores. Cahiers de Biologie Marine 23:1–7.

ORTEA, J. A. & P. BOUCHET. 1988. Description de deux nouveaux *Doto* de Méditerranée occidentale (Mollusca: Nudibranchia). Bolletino Malacologico 24:261–268.

ORTEA, J. A. & J. PEREZ. 1982. Una nueva especie de *Doto*

Oken, 1815 (Mollusca: Opisthobranchia: Dendronotacea) de las Islas Canarias. Iberus 2:79–83.

ORTEA, J. A. & V. URGORRI. 1978. El género *Doto* (Oken, 1815) en el Norte y Noroeste de España. Boletin de la Estación Central de Ecología 7:73–92.

RICKETTS, E. F., J. CALVIN & J. W. HEDGEPETH. 1985. Between Pacific Tides. 5th ed. Revised by D. W. Phillips. Stanford Univ. Press: Stanford, California. 652 pp.

ROS, J. 1981. Desarrollo y estrategias bionómicas en los Opistobranquios. Oecologia aquatica 5:147–183.

ROSE, R. A. 1983. Lecithotrophic development of *Hoplodoris nodulosa* (Angas) (Opisthobranchia, Gastropoda). Journal of the Malacological Society of Australia 6:63–70.

RUMRILL, S. S. 1990. Natural mortality of marine invertebrate larvae. Ophelia 32:163–198.

SCHMEKEL, L. & A. KRESS. 1977. Die Gattung *Doto* (Gastropoda: Nudibranchia) in Mittelmeer und Armelkanal, mit Beschreibung von *Doto acuta* n. sp. Malacologia 16:467–499.

SCHMEKEL, L. & A. PORTMANN. 1982. Opisthobranchia des Mittelmeeres, Nudibranchia und Saccoglossa. Springer-Verlag: Berlin. 410 pp.

STRATHMANN, R. R. 1978. The evolution and loss of feeding larval stages of marine invertebrates. Evolution 32:894–906.

STRATHMANN, R. R. 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. Annual Review of Ecology and Systematics 16:339–361.

STRATHMANN, R. R. & M. F. STRATHMANN. 1982. The relationship between adult size and brooding in marine invertebrates. American Naturalist 119:91–101.

THOMPSON, T. E. 1958. The natural history, embryology, larval biology and post-larval development of *Adalaria proxima* (Alder & Hancock) (Gastropoda, Opisthobranchia). Philosophical Transactions of the Royal Society of London (B) 242:1–58.

THOMPSON, T. E. 1961. The importance of the larval shell in the classification of the Sacoglossa and Acoela (Gastropoda, Opisthobranchia). Proceedings of the Malacological Society of London 34:233–238.

THOMPSON, T. E. 1967. Direct development in the nudibranch *Cadlina laevis,* with a discussion of developmental processes in Opisthobranchia. Journal of the Marine Biological Association of the United Kingdom 47:1–22.

THOMPSON, T. E. 1972. Eastern Australian Dendronotoidea (Gastropoda, Opisthobranchia). Zoological Journal of the Linnean Society 51:63–77.

THOMPSON, T. E. & G. H. BROWN. 1984. Biology of Opisthobranch Molluscs, Vol. II. Ray Society: London. 229 pp.

THOMPSON, T. E., R. CATTANEO, & Y. M. WONG. 1990. Eastern Mediterranean Opisthobranchia: Dotidae (Dendronotoidea), Arminidae and Madrellidae (Arminoidea). Journal of Molluscan Studies 56:393–413.

THORSON, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews 25:1–45.

TODD, C. D. 1981. The ecology of nudibranch Mollusca. Oceanography and Marine Biology. An annual Review 19: 141–234.

WILLIAMS, L. G. 1980. Development and feeding of larvae of the nudibranch gastropods *Hermissenda crassicornis* and *Aeolidia papillosa.* Malacologia 20:99–116.

APPENDIX: FORMS OF *DOTO* CURRENTLY REFERRED TO AS *DOTO AMYRA*

The four forms of *Doto* that in my opinion would be identified as *Doto amyra* based on the descriptions and synonymies given by Beeman & Williams (1980), McDonald & Nybakken (1980), McDonald (1983), and Behrens (1991), are characterized below (descriptions are of living adults). Two or more of these may represent distinct species.

Because Marcus's (1961) description of *Doto amyra* was based on preserved specimens and only touches on the color of the living animals, it is difficult to state using external characters which of the following four forms best fits the original description of *D. amyra.* However, of the four, specimens of the one that I refer to as *D. amyra* appear to fit best the *D. amyra* of Marcus (1961) based on his description of the cerata tubercles and adult size. However, it should be noted that Marcus (1961) reported *D. amyra* as occurring on *Obelia,* a genus of hydroid on which I have not observed *D. amyra.*

1) *Doto amyra* of Goddard (1977, 1984, 1987, 1990, and present study). The following description of the external morphology and color of this form expands on that given by Goddard (1984) for specimens from Cape Arago, Oregon and is based on additional specimens from that locality.

Adults (Figure 1, present study) feed on the hydroid *Abietinaria* sp. (*A. anguina* of Ricketts et al., 1985) and reach a length of 14 mm, though most are under 10 mm. The body and head are translucent white and occasionally have an irregular scattering of fine-grain, subcutaneous brown to black pigment. The gonads are yellow and show clearly through the body wall. The rest of the viscera are cream-colored. The five to eight pairs of cerata have pale yellow to light pinkish-orange or orange-brown colored cores, possess four to seven rings of tubercles, and lack dark pigment. The tubercles vary from low to elongate in different individuals and contain semi-translucent white glands (possibly defensive in nature). Longer tubercles point upward; all are rounded at their ends. The tubercles stand out as white against darker colored cerata cores and tend to blend in against yellowish cores. The accessory gills (pseudobranchs) interrupt the lower rings of tubercles and are clear, branched, and often contain a few minute, opaque white grains. The rhinophores and their sheaths are translucent like the body and contain opaque white grains, especially distally. The anal papilla is distinct and located between the right members of the first and second pairs of cerata. Specimens closely resemble *Doto amyra* as described and depicted by McDonald & Nybakken (1980: 58–59) and McDonald (1983:183–184).

In addition to Cape Arago, I have also found this form at (1) Scott Creek, Santa Cruz County, California where it feeds on *Sertularia furcata* growing on an unidentified, foliose red alga and on the lower portions of the leaves of the surfgrass *Phyllospadix torreyi* Watson; these specimens have development virtually identical to that described in the present paper (Goddard, 1977; personal observations); (2) Punta Gorda, Humboldt County, California (Goddard, 1987); (3) southern Oregon (Goddard, 1990); and (4) northern Oregon, where it has been found feeding on

Abietinaria sp. and *Garveia* sp. (personal observations). Specimens feeding on *Garveia* sp. were orange in color. This form has also been found in the Vancouver Island region where it also has swimming larvae and lecithotrophic development (see discussion) and has been observed on the hydroids *Coryne, Abietinaria,* and *Garveia* (S. Millen, personal communication).

2) *Doto* form A. Specimens of this form were found among small athecate hydroids on the undersides of intertidal boulders at the mouth of Drake's Estero, Marin County, California. They measured up to 7 mm long and were similiar to the previous form in color (including the presence distally of opaque white grains in the rhinophores and their sheaths), but none had dark pigment. They closely resemble "*Doto amyra*" as pictured by Behrens (1991: species number 149). There are five to six pairs of cerata, usually with orange to pinkish cores, and with longer tubercles than the previous form. Owing to the color of the cerata cores, the length of the tubercles, and the presence of semi-translucent white glands in the tubercles, the tubercles generally stand out as whiter than in the previous form. *Doto* form A produces small planktotrophic larvae from eggs averaging 76 μm in diameter (see Table 1). Seven specimens of this form have been deposited in the invertebrate collection of the California Academy of Sciences (voucher number CAS 056222).

3) *Doto* form B. This form occurs on several species of *Aglaophenia* growing on various algae, especially species of *Laminaria.* I have observed it at the mouth of Drake's Estero, Marin County, California; on the southern Oregon coast; and at the south jetty of Coos Bay, Oregon. Specimens from Drake's Estero and the south jetty have been deposited in the California Academy of Sciences (voucher numbers CAS 056216 and CAS 056217 respectively).

This form differs from the above two in having cerata with dark pigment and low to medium-length tubercles (the cerata of some individuals are almost smooth). The dark pigment may be scattered over the entire cerata, including the tubercles, or concentrated between the tubercles. Specimens lack the opaque white grains found in the accessory gills, rhinophores, and rhinophore sheaths of the above two forms (however, one larger specimen from the south jetty did have these grains in the rhinophore sheaths). The ground color of the body and cerata is pale yellow; the cerata of specimens from south jetty were pinkish-orange. The body, head, and rhinophore sheaths of most individuals have subcutaneous brown to black pigment. Specimens from Drake's Estero measured up to 8 mm in length and produced small planktotrophic larvae from eggs averaging 70 μm in diameter (Table 1).

This may be a light form of *Doto columbiana* O'Donoghue, 1921 [which is how I referred to specimens from the southern Oregon coast (Goddard, 1990)] and may also be the same as the *Doto amyra* reported by McDonald (1983) on *Aglaophenia struthionides* (Murray, 1860). Individuals of *Doto* form B closely resemble the individual pictured by McDonald & Nybakken (1980:59, pl. 74) for *Doto columbiana,* and their morphology and egg masses also are very similar to those of *Doto* sp. D described by Just & Edmunds (1985:40–41). Specimens of the latter were found on *Aglaophenia* sp. at Friday Harbor, Washington.

4) A form from the La Jolla, California area that James Lance (personal communication) refers to as *Doto amyra,* but which he states produces planktotrophic larvae. In addition, Dr. Hans Bertsch has sent me a photograph of what he calls *D. amyra,* also from the La Jolla area. The photograph shows adults (very similar in appearance to *Doto* form A above) and their egg masses among short hydroids. These egg masses contained small embryos that clearly developed into planktotrophic larvae. This form may be the same as *Doto* form A above or may be a different species.

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THE VELIGER

Redescription of *Nembrotha megalocera* Yonow, 1990 (Gastropoda: Nudibranchia: Polyceratidae) from the Red Sea

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Abstract. *Nembrotha megalocera* Yonow, 1990, is redescribed from one specimen from Al-Ghardaqah (Egypt) collected during the expedition to the Red Sea organized by the Marine Biology Laboratory of the University of Sevilla in 1992. New data on its internal anatomy are presented. Moreover, a comparison between this species and others similar to it, *N. rutilans* Pruvot-Fol, 1931, *N. purpureolineata* O'Donoghue, 1924, and *N. lineolata* Bergh, 1905, is provided.

INTRODUCTION

One specimen of a polyceratid nudibranch of the genus *Nembrotha* Bergh, 1877, was collected by researchers from the Marine Biology Laboratory of the University of Sevilla in the Red Sea in April 1992. We later concluded that this specimen belongs to the species *N. megalocera* Yonow, 1990. The original description of this species is short and does not provide schemes or drawings of the animal's external or internal anatomy; it does provide a color photograph of one specimen.

In this paper, we redescribe the species, supplementing Yonow's data with ours.

SYSTEMATICS

Family Polyceratidae Alder & Hancock, 1845

Nembrotha Bergh, 1877

Nembrotha megalocera Yonow, 1990

Material: Al-Ghardaqah (Egypt) (27°32′24″N, 33°48′06″E): 1 specimen of 70 mm in length collected, April, 1992, at 20 m depth on colonies of the coral genus *Acropora* Oken, 1815. The specimen was deposited at the Laboratorio de Biología Marina at the University of Sevilla.

Description: Specimen limaciform, elongate, and slightly undulate. Foot linear and tail pointed. Cephalic veil inconspicuous, rounded and without lobes (Figure 1A). Rhinophores perfoliate, retractile in their sheaths, with 54 and 51 laminae (Figure 1B). Strong oral tentacles, grooved dorsolaterally along part of their length. Small and blunt foot corners. Branchial tuft composed of three large multipinnate and non-retractile trunks (Figure 1C). Dorsum black, except head and area around gills that are yellow lemon. Two pale grey areas also situated on head at rear of rhinophores. Flanks mostly orange; area closest to foot is whitish. Foot edge, oral and propodial tentacles, base of

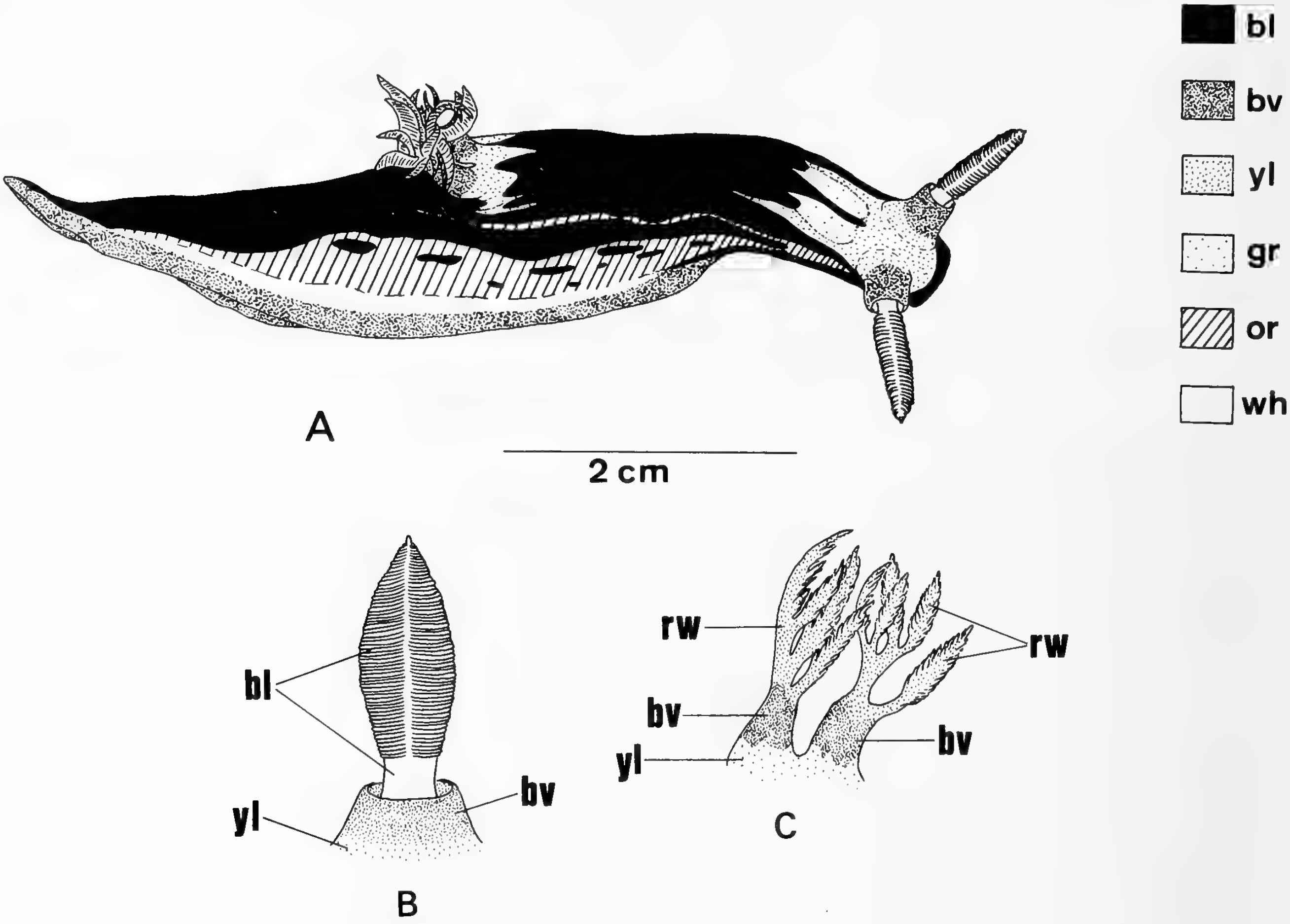

Figure 1

A. General view of the specimen. B. Detail of one rhinophore. C. Detail of the gills. Key: bl, black; bv, bluish violet; gr, grey; or, orange; rw, red wine; wh, whitish; yl, yellow lemon.

gills and rhinophoral sheaths are blue or bluish violet. Gills are red-wine and rhinophores are black.

A general view of the internal anatomy can be seen in Figure 2. The radular formula of the specimen is 27 × 7-8.1.1.1.7-8. The rachidian tooth is square, with four strong denticles, of which the innermost on the right side is bifid (Figure 3C, D). This is probably an aberration in our specimen, and not taxonomically significant. The well-developed innermost lateral teeth are hooked, and they have a spur at their base (Figure 3A, B). The remaining radular teeth are very poorly developed. The thin and delicate labial cuticle has a central and two lateral areas on which a weak armature appears. The genital system (Figure 4A) is characterized by a big and rounded gametolytic gland, largely covered by a well-developed prostate. The size of the seminal receptacle is not very big. We have not seen the presence of a vestibular gland. The efferent duct is relatively elongate and coiled over itself. The penis is very elongate, and it is armed with spines (Figure 4B).

Discussion: The ground color of our specimen agrees with that of the specimens described by Yonow (1990). The radular formula described by this author is similar to that

→

Figure 3

Radula: A. general view; B. Detail of the lateral teeth; C. Detail of the rachidian tooth to SEM; D. Detail of the rachidian tooth with camera lucida.

of our specimen; however, that animal had three denticles on the rachidian tooth, as opposed to the four observed in our specimen. Yonow (1990) did not describe any more anatomical details. This author commented that *Nembrotha rutilans* Pruvot-Fol, 1931, from the Western Australia coasts (Willan & Coleman, 1984; Coleman, 1989), is similar to *N. megalocera*. A comparison between these two species and two others from the Indo-Pacific area (*N. purpureolineata* O'Donoghue, 1924, and *N. lineolata* Bergh, 1905) is given in Table I. All four species share similar features, and hence should be compared. The descriptions of the ground color of the specimens attributed to *N. purpureolineata* by Baba (1976) and Gosliner (1987) show differences from that of the specimen photographed by Wells & Bryce (1993). According to Gosliner (personal communication), this last specimen probably belongs to *N. purpureolineata,* whereas Baba's and Gosliner's specimens probably belong to one or more undescribed species.

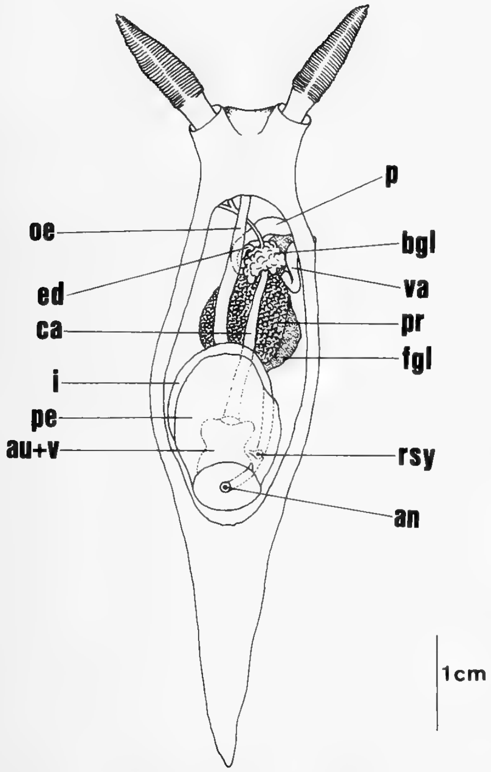

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Figure 2

Gross internal anatomy. Key: an, anus; au, auricle; bgl, blood gland; ca, cephalic arteria; ed, efferent duct; fgl, female gland; i, intestine; oe, esophagus; p, penis; pe, pericardium; pr, prostate; rsy, renal syrinx; v, ventricle; va, vagina.

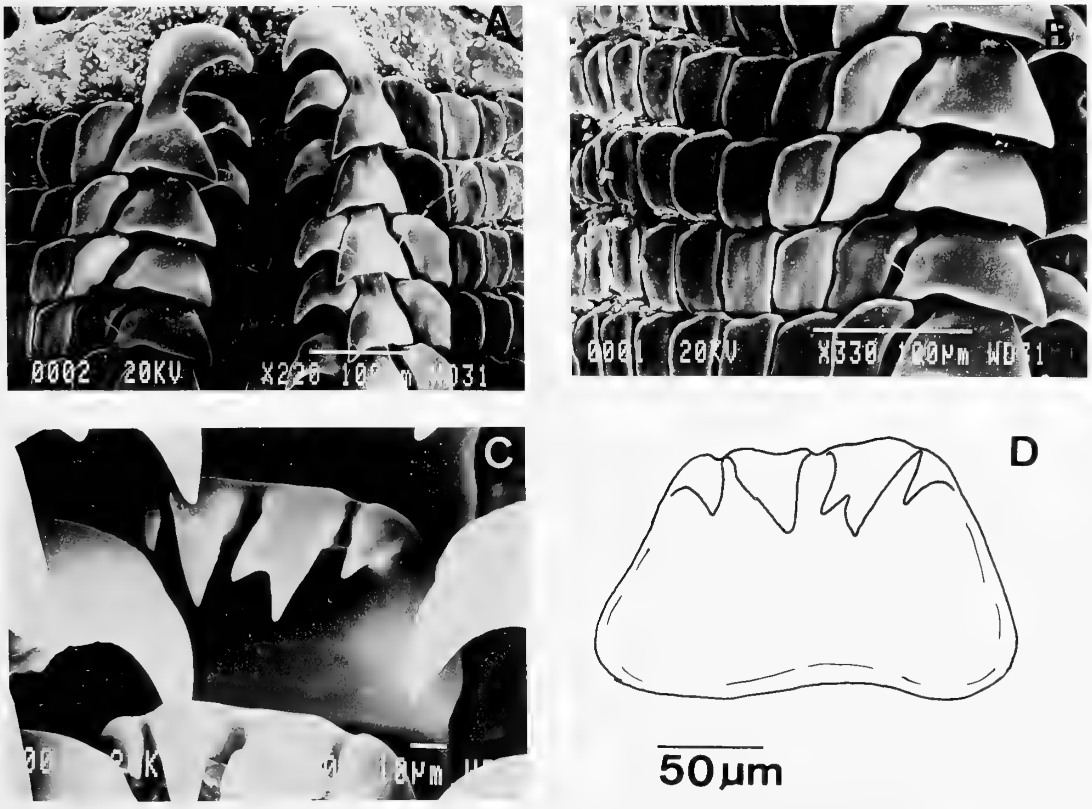

Table 1

Comparison of the features of the Indo-Pacific species *Nembrotha lineolata*, *N. purpureolineata*, *N. rutilans*, and *N. megalocera*.

	N. lineolata Bergh, 1905	*N. purpureolineata* O'Donoghue, 1924	*N. rutilans* (Pruvot-Fol, 1931)	*N. megalocera* Yonow, 1990
Color of the dorsum	White or yellowish white with brown or red-brown straight lines	Translucent slate-grey and dark purple-brown bands,* or milky white with a big red-brown area on the middle	White or whitish yellow/cream with very wide chocolate brown bands, fused in many cases	Black, with the head and the surrounding gill area of a yellow lemon color
Color of the flanks	The same as on the dorsum	Translucent slate-grey and dark purple-brown bands,* or milky white with few red-brown wide bands	The same as on the dorsum, but with more white/whitish yellow/cream surface	Orange, with some black lines
Foot color	Edged with two bands, one violet and other yellow	Edged bluish-violet	Violet	Bluish-violet or blue
Color of the oral tentacles	Violet	Blue or violet	Violet	Bluish-violet or blue
Color of the rhinophores	Red or vermillion; edge of rhinophoral sheaths violet. Below it, there is another yellow band	Orange-red, with bluish-violet tips. The sheaths are bluish-violet, except their bases that are yellow lemon	Blood-red. Edge of rhinophoral sheaths violet	Black. Rhinophoral sheaths bluish-violet or blue
Gills	3 bipinnate. Red or vermillion color. Bases of each gill rachis are violet and yellow	3 bipinnate. Orange-red color. The lower part of the bigger rachis are bluish-violet. Bases of these are yellow lemon	3 multipinnate. Blood-red color, with a violet band at the base of each gill	3 multipinnate. Dark blood red color, with a violet base at each gill
Radula	27 × 5-6.1.1.1.5-6. Rachidian tooth with 4 denticles, the innermost of the right side bifid	32 × 7-8.1.1.1.7-8. Rachidian tooth with 4 denticles, the innermost of the right side bifid	?	27-21 × 6-8.1.1.1.6-8. Rachidian tooth with 3 or 4 denticles (the innermost of the right side can be bifid)
Labial armature	Absent	Absent	?	Present
Reproductive system	?	?	?	Gametolytic gland big, rounded and surrounded by a very developed prostate. Seminal receptacle medium-sized. No vaginal (vestibular) gland. Armed penis
References	Baba (1976); Willan & Coleman (1984); Coleman (1989); Wells & Bryce (1993)	O'Donoghue (1924); Wells & Bryce (1993)	Pruvot-Fol (1931); Willan & Coleman (1984); Coleman (1989); Wells & Bryce (1993)	Yonow (1990); present study

* The ground color provided by O'Donoghue (1924) is based on preserved specimens, although he stated in the same paper: "Professor Dakin informs me that in life the body-colour of the animal was a translucent slate-grey and the dark bands were purple-brown."

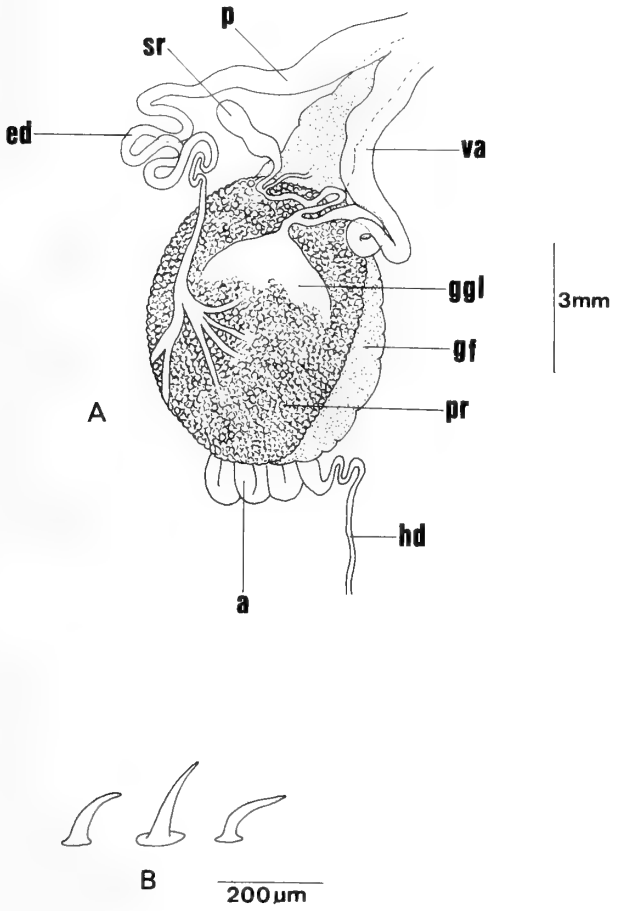

Figure 4

A. Reproductive system (the prostate is partially removed to show the gametolytic gland). B. Detail of the penial spines. Key: a, ampulla; ed, efferent duct; fgl, female gland; ggl, gametolytic gland; hd, hermaphroditic duct; p, penis; pr, prostate; sr, seminal receptacle; va, vagina.

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LITERATURE CITED

BABA, K. 1976. Two species of *Nembrotha* (s.s.) new to Japan (Nudibranchia: Doridoidea: Polyceridae). The Veliger 19: 131–134.

COLEMAN, N. 1989. Nudibranchs of the South Pacific. Vol. I. Ed. Neville Coleman's Sea Australia Resource Centre. 64 pp.

GOSLINER, T. M. 1987. Nudibranchs of Southern Africa. A Guide to Opisthobranch Molluscs of Southern Africa. Sea Challengers: Monterey, California. 136 pp.

O'DONOGHUE, C. H. 1924. Report on opisthobranchiata from the Albrolhos Islands, Western Australia, with description of a new parasitic copepod. Journal of the Linnean Society of London, Zoology 35(237):521–579, pls. 27–30.

PRUVOT-FOL, A. 1931. Nudibranches australiens figurés par Saville Kent dans son grand ouvrage "The great Australian barrier-reef," et qui ne sont ni décrits ni nommés. Bulletin du Muséum Nationale d'Histoire Naturelle, Paris, 2éme Serie, 3(8):754–755.

WELLS, F. E. & C. W. BRYCE. 1993. Sea Slugs of Western Australia. Western Australian Museum: Perth, Australia. 184 pp.

WILLAN, R. C. & N. COLEMAN. 1984. Nudibranchs of Australasia. Australasian Marine Photographic Index. 56 pp.

YONOW, N. 1990. Red Sea Opisthobranchia 3: the orders Sacoglossa, Cephalaspidea, and Nudibranchia: Doridacea (Mollusca: Opisthobranchia). Fauna of Saudi Arabia 11: 286–299.

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THE VELIGER

Embryonic and Larval Development of *Spisula solidissima similis* (Say, 1822) (Bivalvia: Mactridae)

by

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Abstract. Larvae of the southern surf clam, *Spisula solidissima similis* (Say, 1822), were reared in the laboratory at a salinity of 25 ppt and a temperature of 20–22°C through the embryonic and early larval development period. Unfertilized eggs averaged 58.5 ± 0.32 (SE) μm, with the size-frequency of eggs being normal. First polar body was observed 22 minutes after fertilization with 50% of eggs exhibiting polar bodies after 26 minutes. Ciliated blastula and trochophore stages occurred at 6 hours and 16.8 hours, respectively. Straight-hinge veligers appeared 39.2 hours after fertilization. Larvae grew to a mean size of 172 μm in the pediveliger phase (range 119 to 212 μm). Larvae were exhibiting active foot-probing by day 8 and continued to do so until day 13 when the cultures suffered heavy mortalities. Early life-history traits of *Spisula solidissima similis* larvae are compared to those for *Spisula solidissima solidissima* and *Spisula sachalinensis.*

INTRODUCTION

Unlike the commercially important Atlantic surf clam, *Spisula solidissima solidissima* (Dillwyn, 1817), the biology and ecology of the southern subspecies of the surf clam, *Spisula solidissima similis* (Say, 1822), has not been studied until recently. The southern surf clam has a maximum life span of 5 years (Walker & Heffernan, 1994) as compared to 37 years for the Atlantic surf clam (Sephton & Bryan, 1990), and attains a maximum size of 127 mm (Andrews, 1977) as compared to 226 mm in shell length for the Atlantic surf clam (Ropes & Ward, 1977). Southern surf clams mature sexually at age 1 year and at shell lengths of 40 mm (Kanti et al., 1993); whereas the Atlantic surf clam matures at 2 years of age and at a shell length of 67 mm (Belding, 1910). Southern surf clams from St. Catherines Sound, Georgia population spawned from February to May depending upon water temperature (Kanti et al., 1993). The Atlantic surf clam spawns in early summer to fall (Ropes, 1968; Jones, 1981). No early life-history data exists pertaining to larval development of this subspecies.

This study describes the embryonic and early larval development of *Spisula solidissima similis* reared within the laboratory. It compares the findings with the published life-history traits of *Spisula solidissima solidissima* (which is referred to in most shellfisheries literature as "*Spisula solidissima*") and *Spisula sachalinensis* (Schrenk, 1862).

MATERIALS AND METHODS

Southern surf clams, *Spisula solidissima similis,* were collected from a field population occurring in St. Catherines Sound, Georgia, on February 6, 7, and 8, 1994. Animals were dredged from a depth of approximately 8 m. Animals were planted in 12 mm mesh 1 × 1 × 0.25 vinyl-coated wire cages partially buried in a sandy-mud substrate on an intertidal flat located at the mouth of House Creek, Wassaw Sound, Georgia, on 9 February 1994. Cages with animals were positioned at the spring low-water mark. On 9 March 1994, clams were brought into the hatchery and placed in conditioning tanks (450 L) which were maintained at 25 ppt and 20–21°C. Animals were fed *Isochrysis galbana* (Tahitian isolate) on a daily basis.

On 7 April 1994, 10 animals were injected with 0.2 mL of serotonin in the anterior adductor muscle. After injection, each animal was placed in a separate container. Eight individuals (four males and four females) began spawning within 1 to 2 minutes after injection. The remaining two clams did not spawn. Samples of eggs from each spawned female were obtained, and 30 eggs per female measured

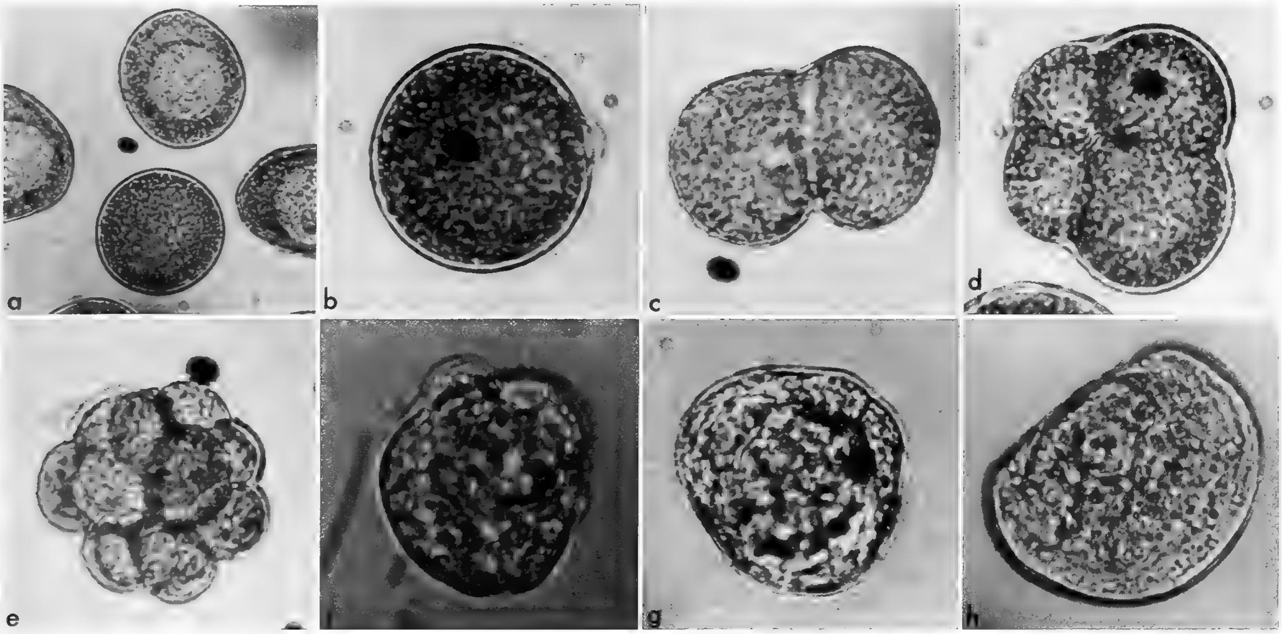

Figure 1

Photomicrograph of the various embryonic and larval stages of the southern surf clam, *Spisula solidissima similis* a) Unfertilized egg (approx. 58 mm); b) First polar body; c) First cleavage; d) Second cleavage; e) Multi-Cellular; f) Trochophore (approx. 78 mm); g) Gastrula; and h) Veliger (approx. 80 mm).

for size. Sperm and eggs were pooled into separate containers.

A 10 liter egg suspension was fertilized with sperm. Embryonic development was observed by placing a 1 mL subsample of eggs on a Zeiss Axiovert 10 microscope (at ×10 and ×32 and visually monitoring development. Various embryonic stages were compared to those described for *Spisula sachalinensis* by Imai et al. (1983). Fresh samples were observed every 15 minutes for the first two hours, with fresh samples observed every 30 minutes for the next 20 hours, after which the larvae were monitored on a daily basis. Once trochophore stages were reached, larvae were set up in three 10 L buckets at a density of 53 larvae per mL. Larvae were fed 100,000 cells per mL of *Isochrysis galbana* daily, and culture water exchanged every 48 hours. Every 24 hours, a 1 mL sample was visually checked to determine developmental stage, and 50 individuals were measured for shell length. Replicate ($n = 3$) 1 mL samples were taken, and the number of larvae per sample was enumerated every second day to give the mean stocking density per culture container.

RESULTS

A schedule of the main embryonic events is given in Table 1 with corresponding photomicrographs given in Figure 1. The mean diameter of the eggs prior to fertilization was 58.5 ± 0.32 (SE) μm. Germinal vesicle breakdown within the eggs was first observed 8 minutes after fertilization. The majority of the fertilized eggs had vesicle breakdown 10 minutes after fertilization. Hereafter, all of the times given are post-fertilization ($t = 0$ minutes), and the term "majority" refers to the fact that > 50% of the larvae displayed the described characteristic. First polar body formation occurred at 22 minutes with the majority of

Table 1

Embryonic development event times of *Spisula solidissima similis* cultured in 25 ppt and 20–22°C seawater.

Stage description	First occurrence time	> 50% occurrence time
Fertilization	0	0
Germinal vesicle breakdown	8 min	10 min
First polar body	22 min	26 min
First division	26 min	41 min
Second division	75 min	89 min
Third division	96 min	115 min
Ciliated blastula	5.5 hr	6 hr
Gastrula	8 hr	8.7 hr
Early trochophores	15.1 hr	15.1 hr
Trochophores	16.4 hr	16.8 hr
Veliger	28.5 hr	39.2 hr
Rudimentary foot		7 days
Probing foot		7.5 days

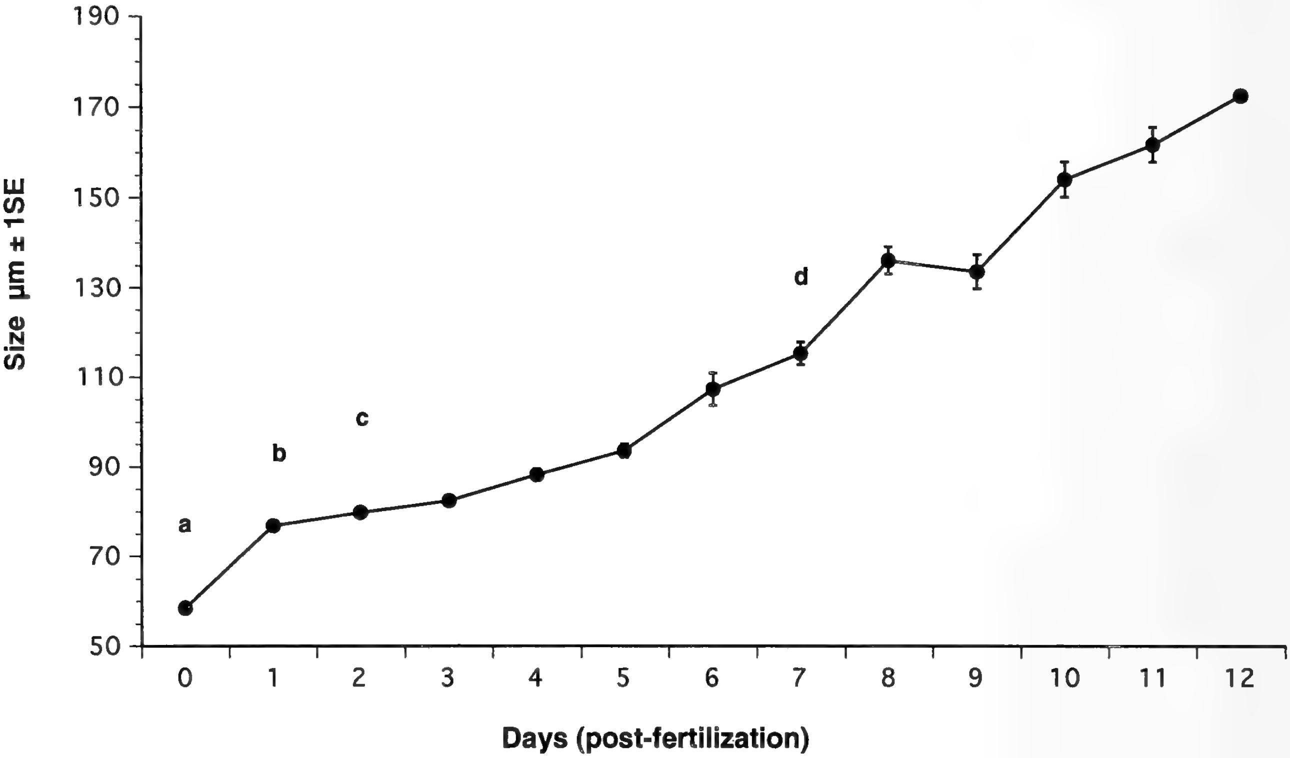

Figure 2

Growth of *Spisula solidissima similis* larvae and juveniles in µm ± one standard error (SE) from egg to day 12. a) Eggs; b) Trochophores; c) D-Shaped larvae; and d) Foot-Probing first exhibited.

individuals displaying polar body formation at 26 minutes. The majority of the larvae displayed first cleavage, second cleavage, and third cleavage at 41 minutes, 89 minutes, and 115 minutes, respectively. Free-swimming blastula larvae were observed at 6 hours, and first invagination of the archenteron occurred at 8 hours, with the majority displaying gastrula characteristics (multicellular, actively motile with rudimentary gut formation) at 8.7 hours. The first early trochophores were observed at 15.1 hours. The majority of the larvae were trochophores at 16.1 hours. At this stage, the larvae had a mean size of 76.8 ± 0.11 (SE) µm. Straight-hinged larvae were first observed at 28.5 hours with the majority D-shaped at 39.3 hours. A rudimentary foot was observed at 7 days, when the clams had a mean size of 107.3 ± 3.62 (SE) µm. A partially developed foot was observed probing (extending beyond the margin of the shell) at 7.5 days. The larvae continued as motile pediveligers until 12 days after fertilization. During this time, the larvae were primarily observed as swimmers. Some larvae exhibited foot-probing behavior on the surface of the slide, i.e., moving about with the aid of foot extension and velar activity. However, at 13 days, heavy mortality of the larvae was experienced due to contamination within the culture vessels by protozoans, probably brought in with food. The experiment was then terminated. Growth of the larvae through the 12 days of the study is recorded in Figure 2. Larval densities in the rearing containers ranged from mean values of 53, 47, 46, 33, and 26 larvae per mL on days 1, 3, 5, 7, and 9, respectively.

Table 2

Mean egg diameter in µm and egg size range of various species of *Spisula*.

Species	Mean egg diameter	Range in µm	Reference
Spisula sachalinensis		70–75	Imai et al., 1953
S. s. solidissima	56.5		Loosanoff & Davis, 1963
S. s. solidissima	53		Schechter, 1941
S. s. solidissima	56		Allen, 1853
S. s. solidissima		53–56	Costello et al., 1957
S. s. solidissima	58.3	50–69	Walker, unreported data
S. s. similis	58.5	44–78	This study
Spisula subtruncata		50–55	Jorgensen, 1946

Table 3

Embryonic and larval development event times of various *Spisula* species.

Stage description	*S. sachalinensis* Imai et al., 1983	*S. s. solidissima* Allen, 1953	*S. s. solidissima* Ropes, 1980	*S. s. solidissima* Schechter, 1941	*S. s. similis* This study
Fertilization	0	0	0	0	0
First polar body	40–50 min	29 min		30 min	26 min
First division	1.5 hr	74 min		65 min	41 min
Second division	2.5 hr	99 min	90 min	95 min	89 min
Third division	3.5 hr		110 min		115 min
Ciliated blastula		< 1 day		5 days	6 hr
Gastrula	12 hr		5.25 hr		8.7 hr
Trochophores	21 hr		9 hr		16.8 hr
Straight-hinge stage	40 hr		19–20 hr		39.2 hr
Pediveliger			18–21 days		> 8 days

DISCUSSION

The embryonic development of the southern surf clam, *Spisula solidissima similis,* is similar to that for *Spisula solidissima solidissima* and *Spisula sachalinensis.* The mean oocyte diameter for *S. s. similis* from this study was 58.5 ± 0.32 µm and did not differ significantly ($P = 0.5260$) in size from eggs spawned by *S. s. solidissima* ($\bar{x} = 58.3 \pm 0.13$ µm) cultured over winter in Georgia and induced to spawn via serotonin on the same day as *S. s. similis* in this study (Table 2). In addition, *S. s. similis* oocyte diameter was slightly larger than oocyte measurements reported for *S. s. solidissima* by Allen (1953), Loosanoff & Davis (1963), and Costello et al. (1957), but larger than that reported by Schechter (1941) (Table 2). *Spisula s. similis* oocyte diameters were larger than that reported for *S. subtruncata* (da Costa, 1778) (Jorgensen, 1946), but smaller than that for *S. sachalinensis* (Table 2).

Spisula solidissima similis embryonic development seems to occur at a comparable rate to that of *S. s. solidissima* through the third division, but seems to move at a slower rate for the gastrula through straight-hinge stages (Table 3). Yet it is unclear if the embryonic development times of Allen (1953), Schechter (1941), Ropes (1980), or Imai et al. (1983) are times at first occurrence or 50% occurrence. If they are first occurrence times, then *S. s. similis* embryonic development times from egg through third division proceeded at a slightly faster rate (Table 1) than that of *S. s. solidissima* (Table 3). *Spisula s. similis* appears to go through embryonic development up to the straight-hinge stage at a faster rate than *S. sachalinensis* (Table 3), while both attain the straight-hinge stage at approximately 40 hours, roughly twice the time described for *S. s. solidissima* by Ropes (1980). As pointed out by Costello et al. (1957) and Loosanoff & Davis (1963), culture temperatures play an important role in developmental times for marine bivalve larvae. *Spisula s. solidissima* attained ciliated blastula stage in < 24 hours when cultured at 21°C (Allen, 1953), but required 5 days to attain this stage when cultured at 25°C (Schechter, 1941). When cultured at 14°C, the straight-hinge stage for *S. s. solidissima* was attained in 72 hours, while at 22°C the stage was reached in 28 hours (Loosanoff & Davis, 1963). In a parallel study, *S. s. similis* larval development was faster at 25°C than at 20°C (Walker et al., in press).

Unfortunately, the pediveliger stage and size were not described for *S. sachalinensis* (Imai et al., 1983) or for *S. s. similis* in this study. For *S. s. similis,* 50% of animals were pediveligers at 107.3 µm in 7 days, whereas for *S. s. solidissima* a foot was observed in animals as small as 160 µm, with 80% of 215 µm and 100% of 240 µm animals possessing a foot (Loosanoff & Davis, 1963). *Spisula s. solidissima* metamorphoses at 280 µm in size and at 18 to 21 days (Costello et al., 1957). Loosanoff & Davis (1963) stated that *S. s. solidissima* metamorphoses at a size between 230 and 250 µm; while Chanley & Andrews (1971) reported that *S. s. solidissima* metamorphoses at 220–275 µm. Imai et al. (1983) stated 270 µm as the size that *S. sachalinensis* metamorphoses. In this study, *S. s. similis* had attained 50% pediveliger stage by day 7.5 with larvae at a mean size of 107.3 µm (Figure 2). Thus it appears that *S. s. similis* were close to setting before the cultures died at day 13 and that *S. s. similis* may metamorphose earlier and at a smaller size than *S. s. solidissima.* In previous and subsequent studies, *S. s. similis* was estimated to have metamorphosed between 18 to 19 days (Walker et al., 1995).

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LITERATURE CITED

ALLEN, R. D. 1953. Fertilization and artificial activation in the egg of the surf clam, *Spisula solidissima.* Biological Bulletin 105:213–239.

ANDREWS, J. 1977. Shells and Shores of Texas. University of Texas Press: Austin, Texas and London. 365 pp.

BELDING, D. L. 1910. The growth and habits of the sea clam (*Mactra solidissima*). Report to the Commissioner of Fish and Game Massachusetts, 1909. Public Document 25:26–41.

CHANLEY, P. & J. D. ANDREWS. 1971. Aid for identification of bivalve larvae of virginia. Malacologia 11:45–119.

COSTELLO, D. P., M. E. DAVIDSON, A. EGGERS, M. H. FOX & C. HENLEY. 1957. Methods for Obtaining and Handling Marine Eggs and Embryos. Marine Biological Laboratory, Woods Hole, Massachusetts. 247 pp.

IMAI, T., M. HATANAKA, R. SATO & S. SAKAI. 1983. Tank breeding of the Japanese surf clam, *Mactra sachalinensis* Schrenk. Science Reports, Research Institutes, Tohoku University 4:121–131.

JONES, D. S. 1981. Reproductive cycles of the Atlantic surf clam *Spisula solidissima* and the ocean quahog *Arctica islandica* off New Jersey. Journal of Shellfish Research 1:23–32.

JORGENSEN, C. B. 1946. Reproduction and larval development of Danish marine bottom invertebrates. 9. Lamellibranchia. Meddeleser fra Kommissionen for Danmarks fisheri- og Havundersoegelser, Series (d.) Plankton 4:277–311.

KANTI, A., P. B. HEFFERNAN & R. L. WALKER. 1993. Gametogenic cycle of the southern surf clam, *Spisula solidissima similis* (Say, 1822), from St. Catherines Sound, Georgia. Journal of Shellfish Research 12:255–261.

LOOSANOFF, V. L. & H. C. DAVIS. 1963. Rearing of bivalve mollusks. Advances in Marine Biology 1:1–136.

ROPES, J. W. 1968. Reproductive cycle of the surf clam, *Spisula solidissima,* in offshore New Jersey. Biological Bulletin 135: 394–365.

ROPES, J. W. 1980. Biological and fisheries data on surf clam, *Spisula solidissima* (Dillwyn). Northeast Fisheries Center, U.S. National Marine Fisheries Service, Technical Report Series No. 24. 88 pp.

ROPES, J. W. & G. E. WARD, JR. 1977. The Atlantic surf clam fishery—1974. U.S. National Marine Fisheries Service, Marine Fisheries Review 39:18–23.

SCHECHTER, V. 1941. Experimental studies upon the egg cells of the clams, *Mactra solidissima,* with special reference to longevity. Journal of Experimental Zoology 76:461–477.

SEPHTON, T. W. & C. F. BRYAN. 1990. Age and growth determinations for the Atlantic surf clam, *Spisula solidissima* (Dillwyn, 1817), in Prince Edward Island, Canada. Journal of Shellfish Research 9:177–186.

WALKER, R. L. & P. B. HEFFERNAN. 1994. Age, growth rate, and size of the southern surf clam, *Spisula solidissima similis* (Say, 1822). Journal of Shellfish Research 13:433–442.

WALKER, R. L., F. X. O'BEIRN & D. H. HURLEY. In press. Embryonic and larval development of the southern surf clam, *Spisula solidissima similis* (Say, 1822). Journal of Shellfish Research.

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THE VELIGER

A New Species of *Abyssochrysos* (Gastropoda: Loxonematoidea) from a Middle Eocene Cold-Seep Carbonate in the Humptulips Formation, Western Washington

by

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Abstract. A very small, localized, authigenic carbonate deposit within the lower part of the middle and early late Eocene Humptulips Formation in Grays Harbor County, Washington, preserves a molluscan fauna that is unique among recognized ancient chemosynthetic assemblages because the dominant faunal member is a large loxonematoidean gastropod, *Abyssochrysos* ***raui,*** sp. nov. The associated megafauna includes an unidentified neritiform gastropod, modiolid, thyasirid, and lucinid bivalves, numerous specimens of the bivalve *Vesicomya* sp., worm tubes, and crustacean fragments.

This is the first record of the genus *Abyssochrysos* from the northeastern Pacific Ocean, the oldest record for the genus, and the first report of *Abyssochrysos* from a chemosynthetic environment.

INTRODUCTION

The gastropod superfamily Loxonematoidea Koken, 1889, has a diverse pre-Cretaceous fossil record worldwide (Hoare & Sturgeon, 1985), but is almost unknown in Tertiary rocks. The Loxonematoidea contains only two surviving families; the Provannidae Warén & Ponder, 1991, and the Abyssochrysidae Tomlin, 1927. The Provannidae presently includes four genera (Warén & Bouchet, 1993), and almost all are exclusively from hydrothermal vents or cold seeps. The only fossil record for the Provannidae is *Provanna antiqua* Squires, 1995, from late Eocene and Oligocene cold-seep deposits in Washington State (Goedert & Campbell, 1995; Squires, 1995).

The Abyssochrysidae includes five living species, and all are rare: *Abyssochrysos bicinctum* Bouchet, 1991, from the Makassar Strait, Indonesia; *A. brasilianum* Bouchet, 1991, from the continental slope, southeastern Brazil; *A. eburneum* (Locard, 1897), from off of northwestern Africa; *A. melanioides* Tomlin, 1927, from bathyal depths off South Africa (Houbrick, 1979) and southeast Asia (Bouchet, 1991); and *A. melvilli* (Schepman, 1909) from bathyal depths in the Indo-West-Pacific (Figure 1). The only previous fossil record for the genus *Abyssochrysos* was from early Miocene strata at Suva, Fiji, where fossils of *A. melvilli* have been found (Ladd, 1977; Houbrick, 1979). Little is known about the ecology of *Abyssochrysos,* and *Abyssochrysos* has not been reported previously from chemosynthetic environments.

A fossil molluscan assemblage preserved in an authigenic carbonate deposit within the Humptulips Formation in western Washington was first described by Goedert & Squires (1990). We have discovered another previously unrecognized paleocommunity within a cold-seep carbonate (CSUN loc. 1583) in the lower part of the Humptulips Formation (Figure 2), and the purpose of this paper is to

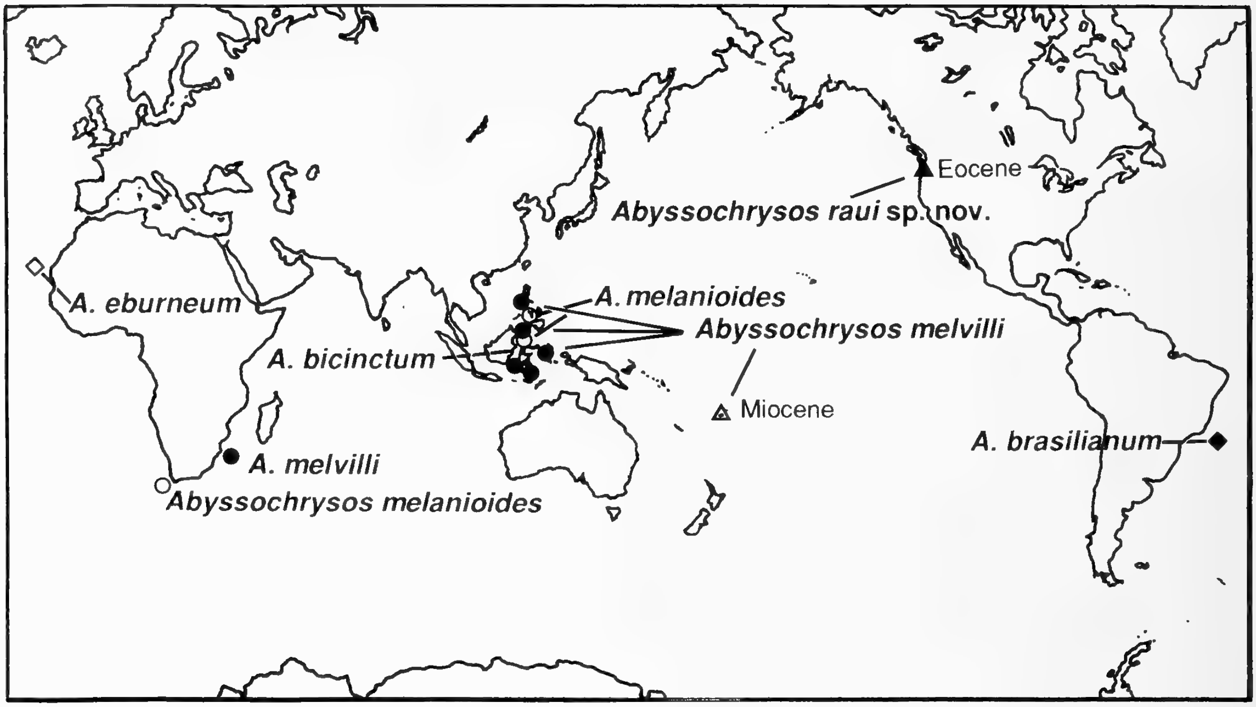


Figure 1

World map showing distribution of living and fossil *Abyssochrysos* species.

describe a new species of the gastropod *Abyssochrysos* from this assemblage.

Acronyms used for locality and specimen numbers are: CSUN, California State University, Northridge, California; and LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section, Los Angeles, California.

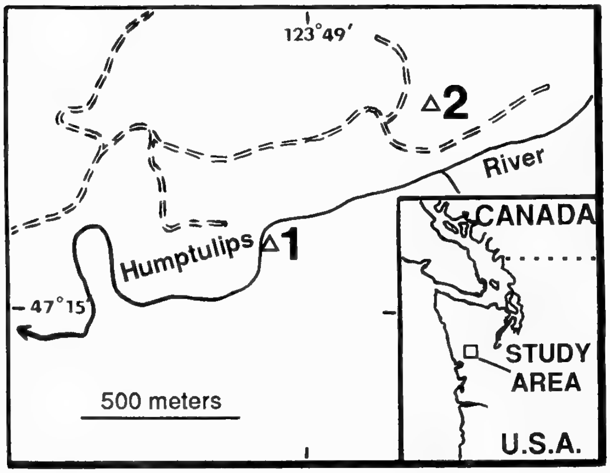


Figure 2

Maps showing location of study area and location of cold-seep carbonate deposits (*1* = CSUN loc. 1583; *2* = LACMIP 12385) along the east fork of the Humptulips River, Grays Harbor County, Washington (base maps: Burnt Hill & Railroad Camp, USGS 7.5 minute quadrangles, Prov. Editions 1990).

Geology

Exposures of siltstone, mudstone, and sandstone along the east fork of the Humptulips River in the study area were selected by Rau (1984, 1986) as the type section for the Humptulips Formation. The contact between the Humptulips Formation and the underlying early to middle Eocene Crescent Formation is a thrust fault (Rau, 1986), and in the study area, the formation is unconformably overlain by Pleistocene? gravels and younger fluvial deposits. The stratigraphy of this part of the Humptulips Formation is complicated by faults and limited exposures (Rau, 1984, 1986), and because of the nearly vertical attitude of the rocks, there is uncertainty regarding the superpositional relationships of some beds (W. W. Rau, written communication).

Age and Depositional Environment

Benthic Foraminifera are well represented in most samples from the Humptulips Formation, and they represent the Narizian Stage (middle and early late Eocene) and indicate bathyal depths, between 150 and 2500 meters

(Rau, 1984, 1986). Foraminifera in three samples (Rau, 1986:samples S–1011, S–1022, S–1021) from strata near CSUN loc. 1583 are characteristic of the middle Eocene part of the Narizian Stage as applied by Rau (1981) and clearly indicate bathyal conditions, perhaps within a lower middle bathyal range of 1500 to 2000 m (W. W. Rau, written communication).

Cold-Seep Carbonates

Rau (1984, 1986) reported that the type section of the Humptulips Formation included at least one thick "calcareous zone" (= LACMIP loc. 12385), and this limestone had earlier been described by Hodge (1938) and Danner (1966), but these authors did not recognize that it contained a diverse megainvertebrate assemblage. This calcareous zone was recently recognized as being an ancient cold-seep deposit (Goedert & Squires, 1990; Squires & Goedert, 1991), and the invertebrate assemblage was interpreted as having been supported by chemosynthesis via the bacterial oxidation of methane at a cold seep. This interpretation was later corroborated by Campbell & Bottjer (1993). Detailed petrographic and isotopic studies of these carbonates are not yet published, and are beyond the scope of this paper.

Lithologically, the carbonates at LACMIP loc. 12385 and CSUN loc. 1583 are broadly similar to each other, and they are similar to other recognized ancient cold-seep carbonates. At LACMIP loc. 12385, the carbonate is fossiliferous micrite in places; some parts of the outcrop are composed of fossiliferous carbonate breccia, and others are wavy, laminated, carbonate crusts. The entire outcrop at LACMIP loc. 12385 is more than 30 m thick (Danner, 1966; Rau, 1986).

At CSUN loc. 1583, the carbonate outcrop is only 2 m long and 1 m wide. The carbonate mound was about 1 m high, but the maximum thickness is unknown because the carbonate is completely surrounded by gravels in the riverbed. We excavated to a depth of 0.5 m (below water level) without finding the carbonate/siltstone contact, and therefore its stratigraphic location is uncertain. Most of the carbonate is highly indurated fossiliferous micrite, but it grades outward(?) into a breccia composed of small (≤3 cm) subrounded fragments of indurated micrite within a siltstone matrix. Wavy, laminated carbonate crusts, common at LACMIP loc. 12385, are only very weakly developed at CSUN loc. 1583. Gastropods and closed-valved bivalves are randomly oriented and are most common in the indurated carbonate; crustacean fragments are most abundant in the breccia. The gastropods are difficult to extract from the indurated carbonate, and preservation of the shell is generally poor; however, external molds do preserve surface sculptural detail. This carbonate preserves a fauna that is distinct from that in carbonate at LACMIP loc. 12385 (Table 1); therefore, it is not an allochthonous block derived from the carbonate deposit at LACMIP loc. 12385.

Table 1

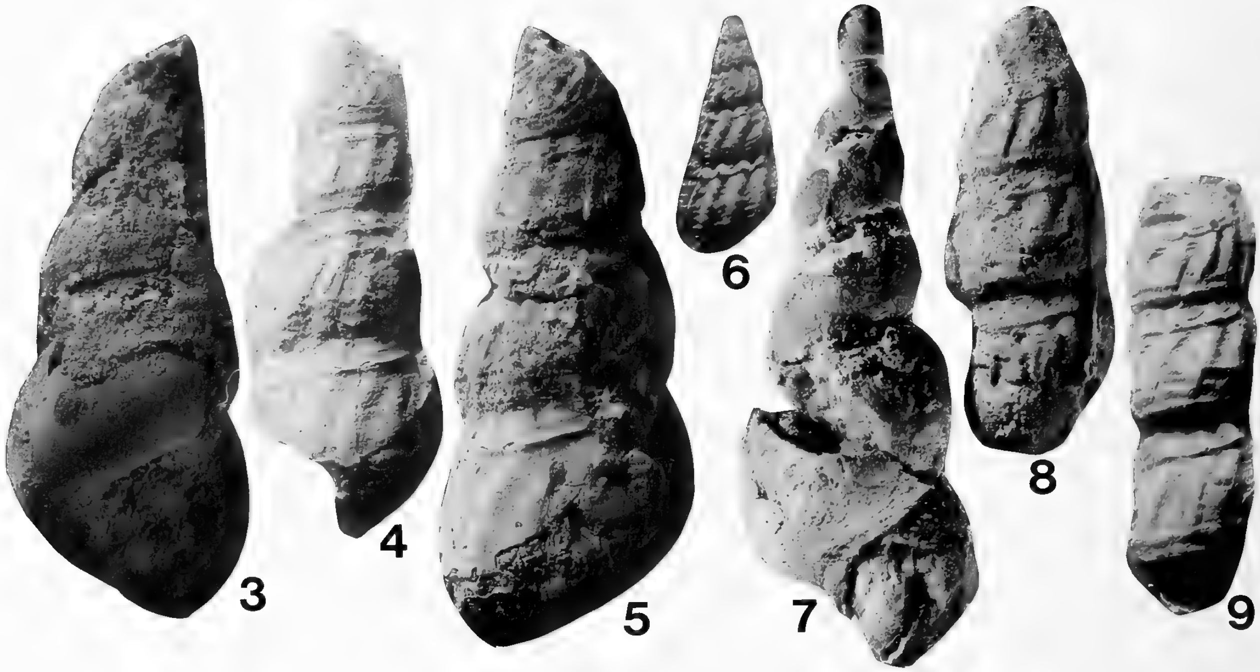
Faunal checklist for authigenic cold-seep carbonates within the lower part of the Humptulips Formation, east fork of the Humptulips River, Grays Harbor County, Washington. Data for LACMIP loc. 12385 is from Goedert & Squires (1990) and Squires & Goedert (1991, 1995).

Fauna	LACMIP loc. 12385	CSUN loc. 1583
Bivalvia:		
Acharax sp.	X	X
Calyptogena (*Calyptogena*) *chinookensis*, Squires & Goedert	X	—
Modiolus (*Modiolus*) *willapaensis*, Squires & Goedert	X	X
Thyasira (*Conchocele*) *folgeri*, Wagner & Schilling	X	X
Vesicomya sp.	—	X
lucinid (new genus?)	—	X
Gastropoda:		
Abyssochrysos ***raui***, sp. nov.	—	X
Homalopoma? sp.	X	—
limpets	X	—
naticid	X	—
neritiform gastropod	—	X
Other:		
Leptochiton (*Leptochiton*) *alveolus* (Lovén)	X	—
serpulid worm tubes	X	—
vestimentiferan? worm tubes	X	X
"*Callianassa*" sp. (crustacean)	X	X

Megapaleontology

Throughout this part of the Humptulips Formation, megafossils are extremely rare except in the authigenic cold-seep carbonates. The only megafossils found in the nearly barren strata were two unidentified shark teeth, some crinoid stem fragments, some poorly preserved specimens of a raninid crab, and a few wood fragments.

The carbonate deposits in the Humptulips Formation contain fossil invertebrate assemblages (Table 1) with large numbers of individuals and low taxonomic diversity, characteristic of those found in other modern and ancient chemosynthetic environments. All of the bivalve genera reported herein are either present in other ancient cold-seep assemblages, or have species represented in modern seep and vent communities. The bivalve *Vesicomya* sp. has been reported from one other seep deposit of Oligocene age in Washington (Goedert & Campbell, 1995), and a species of *Vesicomya* was reported from a probable cold-seep deposit in late Eocene rocks of the Wagonwheel Mountain area in central California (Squires & Gring, in press). The lucinid (new genus?) is up to 90 mm long and may be conspecific with the unidentified lucinid reported by Goe-



Figures 3–9

Abyssochrysos ***raui*** Goedert & Kaler, sp. nov., from CSUN loc. 1583, lower part of the Humptulips Formation, Grays Harbor County, Washington. Figures 3–5, Holotype, LACMIP 12363; Figure 3, apertural view, ×1.6; Figure 4, latex peel of external mold, ×1.4; Figure 5, abapertural view, ×1.7. Figure 6, Paratype, LACMIP 12364 latex peel of external mold, ×2.9. Figure 7, Paratype LACMIP 12365, apertural view, ×1. Figure 8 & 9, Paratype LACMIP 12366, ×1.6. Figure 9, latex peel of external mold, ×1.6. All coated with ammonium chloride.

dert & Campbell (1995) from a cold-seep carbonate on the northwestern Olympic Peninsula, Washington.

The cold-seep carbonate at CSUN loc. 1583 is unique faunally in that it preserves the only known Paleogene chemosynthetic assemblage that is dominated by a single large gastropod species. This gastropod was up to 90 mm long, and they are randomly oriented, complete individuals representing a new species of *Abyssochrysos.* A chiton was reported from LACMIP loc. 12385 and several other cold-seep carbonates in Washington (Squires & Goedert, 1995), and chitons are associated with modern methane-derived authigenic carbonates on the continental shelf off the coast of Oregon (Kulm & Suess, 1990). None of the mollusks from the Humptulips Formation seep sites show evidence of predation by other mollusks.

Serpulid and vestimentiferan? worm tubes are common at LACMIP loc. 12385 (Goedert & Squires, 1990), and vestimentiferan? tubes were found at CSUN loc. 1583 (Table 1). Tubes of these worms are common in many modern and ancient chemosynthetic assemblages. The crustacean "*Callianassa*" sp. was found at both LACMIP loc. 12385 and CSUN loc. 1583, and callianassid fragments were reported from cold-seep carbonate on the north side of the Olympic Peninsula by Goedert & Campbell (1995).

SYSTEMATIC PALEONTOLOGY

Superfamily LOXONEMATOIDEA Koken, 1889

Family ABYSSOCHRYSIDAE Tomlin, 1927

Genus *Abyssochrysos* Tomlin, 1927

Type species: *Abyssochrysos melanioides* Tomlin, 1927, by monotypy, Recent, off Cape Point, South Africa.

Abyssochrysos ***raui*** Goedert & Kaler, sp. nov.

(Figures 3–9)

Diagnosis: An *Abyssochrysos,* much larger and less elongate than any other known species.

Description: Shell large, elongate, turriform, up to 90 mm long and 2.5 mm thick on inner lip, with up to nine whorls (as preserved). Whorls inflated, slightly overhanging at bases; suture impressed; sculpture variable, with both spiral cords and opisthocline axial ribs, prominent spiral cord intersecting axial ribs near top of each forming small nodes; two spiral cords cross bases of ribs; on very large specimens axial ribs less prominent so upper spiral cord is bold; on last whorls both spiral cords and/or axial ribs lacking or faint. Spiral cords more numerous on smaller specimens; axial ribs can vary in number on the same specimen, most specimens having about 12 per whorl.

Types: Holotype, LACMIP 12363; Paratypes: LACMIP 12364, 12365, 12366.

Type locality: CSUN loc. 1583.

Material: More than 50 specimens were found; most are poorly preserved.

Remarks: *Abyssochrysos* ***raui*** sp. nov. is strikingly similar to *A. melanioides* (Tomlin, 1927:78–79, figs. 1–3; Barnard, 1963:141–143, fig. 27a–c; Houbrick, 1979:3–10, fig. 1a–i; Bouchet, 1991:311, figs. 8, 12–17) in sculptural variability, but *A.* ***raui*** differs in being less elongate and much larger, with whorls more inclined.

Abyssochrysos ***raui*** differs from *A. melvilli* (Schepman, 1909:170, pl. 12, fig. 1; Barnard, 1963:143–144, fig. 27f; Ladd, 1977:15–16, pl. 1, fig. 3, pl. 21, fig. 8; Houbrick, 1979:10–14, figs. 7a–j, 8, 9; Bouchet, 1991: 311, figs. 18–20) in being much less elongate and much larger, and by having only one row of nodes on axial ribs, more inflated whorls, whorls more inclined, with a more elongate aperture.

The shells of *Abyssochrysos bicinctum* Bouchet, 1991 (Bouchet, 1991:311–312, figs. 21, 22) differ from those of *A.* ***raui*** by being smaller, more elongate, with slightly concave whorls ornamented by two prominent noded spiral cords. Those of *A. brasilianum* Bouchet, 1991 (Bouchet, 1991:306–310, figs. 1–4, 9–11) are much smaller and more elongate that those of *A.* ***raui***. *Abyssochrysos eberneum* (Locard, 1897:389–390, pl. 19, figs. 7, 8; Bouchet, 1991:310–311, figs. 5–7) differs from *A.* ***raui*** in having a smaller, more elongate shell, with large nodes only on the basal part of each whorl.

The smallest available specimen of *Abyssochrysos* ***raui*** (LACMIP 12364; Figure 6) is 14 mm long, and its upper spire appears to have a smooth protoconch of about 1.5 whorls. The upper spire of some large specimens of *Abyssochrysos* ***raui*** is flat-sided and smooth, possibly corroded during life. The shells of gastropods from chemosynthetic environments are commonly corroded (Warén & Bouchet, 1993:81).

Etymology: The species is named for Weldon W. Rau in recognition of his pioneering work on the Foraminiferal biostratigraphy of Tertiary marine rocks in the Pacific Northwest.

DISCUSSION

Abyssochrysos ***raui*** from the middle to early late Eocene Humptulips Formation in Washington is the oldest record for the genus, the first report of *Abyssochrysos* from the northeastern Pacific Ocean, and the first report of *Abyssochrysos* from a chemosynthetic environment. The earliest and first fossil records for the related genus *Provanna* are also from Eocene and Oligocene cold-seep deposits in western Washington (Goedert & Campbell, 1995; Squires, 1995).

Houbrick (1979) recognized that the Abyssochrysidae represented a relict family of the superfamily Loxonematoidea, thought to have been extinct since the end of the Jurassic. Subsequently, Warén & Ponder (1991) have classified the Provannidae as a relict family of the Loxonematoidea as well. Some other invertebrates found at modern hydrothermal vents and cold seeps are also relict taxa having Paleozoic and Mesozoic ancestors (Newman, 1985). These taxa may have survived mass extinction events by using deep-water vent and seep environments as refugia, functioning independent of global climatic changes (Yamaguchi & Newman, 1990; Tunnicliffe, 1992). This idea seems to be reinforced by the discovery of *Abyssochrysos* and *Provanna* in Eocene cold-seep deposits in Washington, the only Paleogene record of the once widespread and diverse Loxonematoidea. The convergent margin of western North America, with a record of deep-water, cold-seep environments from Jurassic to Recent time (Campbell & Bottjer, 1993), may have provided refuge for many of these ancient groups.

ACKNOWLEDGMENTS

Gail H. Goedert assisted with field work. Weldon W. Rau (Division of Geology and Earth Resources, Olympia, Washington) allowed the use of unpublished information on the geology of, and Foraminifera from, the Humptulips Formation. We thank Richard L. Squires (California State University, Northridge), for help with artwork and for reviewing the manuscript. We thank Philippe Bouchet (Muséum national d'Histoire naturelle, Paris, France) and Kathleen A. Campbell (University of Southern California, Los Angeles) for critically reviewing various drafts of the manuscript.

LOCALITIES CITED

CSUN 1583. Small (1 m × 1 m × 2 m) limestone deposit exposed on east side of east fork of the Humptulips River, 600 m south and 110 m west of NE corner of sec. 5, T. 20 N, R. 9 W, Burnt Hill USGS 7.5 minute quadrangle, Provisional Edition 1990, Grays Harbor County, Washington. Humptulips Formation. Age: Middle Eocene. Collectors: J. L. & G. H. Goedert, K. L. Kaler, July and August 1994.

LACMIP 12385. Small hill in abandoned meander of the east fork of the Humptulips River, northwest part of sec. 4, T. 20 N, R. 9 W, Burnt Hill USGS 7.5 minute quadrangle, Provisional Edition 1990, Grays Harbor County, Washington. Humptulips Formation. Age: Middle Eocene. Collectors: J. L. & G. H. Goedert, 1990.

LITERATURE CITED

BARNARD, K. H. 1963. Contributions to the knowledge of South African marine Mollusca, part III: Gastropoda, Prosobranchiata; Taenioglossa. Annals of the South African Museum 47:1–199.

BOUCHET, P. 1991. New records and new species of *Abyssochrysos* (Mollusca, Caenogastropoda). Journal of Natural History 25:305–313.

CAMPBELL, K. A. & D. J. BOTTJER. 1993. Fossil cold seeps. National Geographic Research and Exploration 9:326–343.

DANNER, W. R. 1966. Limestone resources of western Washington. State of Washington, Department of Conservation, Division of Mines and Geology Bulletin 52:474 pp.

GOEDERT, J. L. & K. A. CAMPBELL. 1995. An early Oligocene chemosynthetic community from the Makah Formation, northwestern Olympic Peninsula, Washington. The Veliger 38:22–29.

GOEDERT, J. L. & R. L. SQUIRES. 1990. Eocene deep-sea communities in localized limestones formed by subduction-related methane seeps, southwestern Washington. Geology 18:1182–1185.

HOARE, R. D. & M. T. STURGEON. 1985. The Pennsylvanian gastropod *Pseudozygopleura* (*Pseudozygopleura*) from the Appalachian Basin: II. Journal of Paleontology 59:60–78.

HODGE, E. T. 1938. Market for Columbia River hydroelectric power using Northwest minerals. Section III, v. 1, pt. 1 of Limestones of the Northwest States. United States Corps of Engineers, North Pacific Division, Portland, Oregon, 312 pp.

HOUBRICK, R. S. 1979. Classification and systematic relationships of the Abyssochrysidae, a relict family of bathyal snails (Prosobranchia: Gastropoda). Smithsonian Contributions to Zoology 290:1–21.

KOKEN, E. 1889. Über die Entwickelung der Gastropoden von Cambrian bis zun Trias. Neues Jahrbuch für Mineralogie, Geologie und Paleontologie 6:305–484, pls. 10–14.

KULM, L. D. & E. SUESS. 1990. Relationship between carbonate deposits and fluid venting: Oregon accretionary prism. Journal of Geophysical Research 95(B6):8899–8915.

LADD, H. 1977. Cenozoic fossil mollusks from western Pacific Islands: Gastropods (Eratoidea through Harpidae). United States Geological Survey Professional Paper 533:1–84, 23 pls.

LOCARD, A. 1897. Mollusques Testacés, I. Expéditions scientifiques du Travailleur et du Talisman. Masson: Paris. 516 pp.

NEWMAN, W. A. 1985. The abyssal hydrothermal vent invertebrate fauna: a glimpse of antiquity? Pp. 231–242, in M. L. Jones, (ed.), Hydrothermal Vents of the Eastern Pacific: An Overview. Bulletin of the Biological Society of Washington 6. 545 pp.

RAU, W. W. 1981. Pacific Northwest Tertiary benthic foraminiferal biostratigraphic framework—an overview. Pp. 67–84 in J. M. Armentrout (ed.), Pacific Northwest Cenozoic Biostratigraphy. Geological Society of America Special Paper 184.

RAU, W. W. 1984. The Humptulips Formation—a new Eocene formation of southwest Washington. Washington Geologic Newsletter 12:1–5.

RAU, W. W. 1986. Geologic map of the Humptulips quadrangle and adjacent areas, Grays Harbor County, Washington. Washington State Department of Natural Resources Geologic Map GM-33.

SCHEPMAN, M. M. 1909. The Prosobranchia of the Siboga Expedition; Part 2, Taeniglossa and Ptenoglossa. Siboga Expeditie 49:100–231.

SQUIRES, R. L. 1995. First fossil species of the chemosynthetic-community gastropod *Provanna:* Localized cold-seep limestones in upper Eocene and Oligocene rocks, Washington. The Veliger 38:30–36.

SQUIRES, R. L. & J. L. GOEDERT. 1991. New late Eocene mollusks from localized limestone deposits formed by subduction-related methane seeps, southwestern Washington. Journal of Paleontology 65:412–416.

SQUIRES, R. L. & J. L. GOEDERT. 1995. An extant species of *Leptochiton* (Mollusca: Polyplacophora) in Eocene and Oligocene cold-seep limestones, Olympic Peninsula, Washington. The Veliger 38:47–53.

SQUIRES, R. L. & M. P. GRING. In press. Late Eocene chemosynthetic? bivalves from suspect cold-seeps, Wagonwheel Mountain, central California. Journal of Paleontology.

TOMLIN, J. R. LE B. 1927. Reports on the marine Mollusca in the collections of the South African Museum, II: families Abyssochrysidae, Oocorythidae, Haliotidae, Tonnidae. Annals of the South African Museum 25:77–83.

TUNNICLIFFE, V. 1992. The nature and origin of the modern hydrothermal vent fauna. Palaios 7:338–350.

WARÉN, A. & P. BOUCHET. 1993. New records, species, genera, and a new family of gastropods from hydrothermal vents and hydrocarbon seeps. Zoologica Scripta 22:1–90.

WARÉN, A. & W. F. PONDER. 1991. New species, anatomy, and systematic position of the hydrothermal vent and hydrocarbon seep gastropod family Provannidae fam. n. (Caenogastropoda). Zoologica Scripta 20:27–56.

YAMAGUCHI, T. & W. A. NEWMAN. 1990. A new and primitive barnacle (Cirripedia: Balanomorpha) from the North Fiji Basin abyssal hydrothermal field, and its evolutionary implications. Pacific Science 44:135–155.

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A New Species of Eastern Pacific *Fissidentalium* (Mollusca: Scaphopoda)

by

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Abstract. *Fissidentalium* ***erosum*** sp. nov. is described morphometrically from specimens collected from deep water off California. It is distinguished from *F. megathyris* primarily on the basis of soft-body-part proportions and radular characteristics. Shell differences are slight; the ventral aperture of *F.* ***erosum*** is approximately circular, whereas in *F. megathyris* the aperture is distinctly wider than high. The posterior portion of *Fissidentalium* ***erosum*** shells is often eroded, in contrast to the uneroded condition of most *F. megathyris* shells collected at the same station.

INTRODUCTION

During an examination of 38 scaphopod specimens collected from one station and tentatively identified as *Fissidentalium megathyris* Dall, 1890, 19 were noted to have a series of slight, but consistent differences from the other "typical" *F. megathyris.* In addition to minor differences in the shell, these specimens had evident and statistically significant differences in many soft body parts and radular characteristics.

Fissidentalium megathyris was originally described from specimens collected near the Galapagos Islands from depths greater than 1000 m (Dall 1890). Subsequent collections have generally confirmed that this species is characteristically collected at depths from about 1000 to 2500 m (Pilsbry & Sharp 1897). *Fissidentalium megathyris* is a large scaphopod, probably the largest in waters adjacent to North America. Large animals are relatively uncommon in collections, and unlikely to be examined as quantitatively as were the ones in our samples.

The first of the two groups found in this study closely matched the description of *F. megathyris.* The shells of the second group were consistently highly eroded and often stained with a tightly adherent black material which made those shells visually distinct from the uneroded, "typical" *F. megathyris.* These differences indicate that the two groups of specimens likely occupy two distinct habitats, with differing sediment chemical characteristics. Given that the two groups have consistent differences of shape, and in radular and soft-body-part proportions, and given that they likely occupy two chemically distinctive habitats, we think that both groups warrant species status and name the second taxon *Fissidentalium* ***erosum*** herein.

Sea anemones (of a currently undescribed species; D. Fautin, personal communication) were found on some of the *F. megathyris* shells, but never on *F.* ***erosum*** shells. It is possible that *F.* ***erosum*** may live deeply buried in the sediment, whereas *F. megathyris* may live very near the sediment surface. This relationship with the sea anemone appears to be opportunistic rather than species-specific; specimens of another deep-water scaphopod from south-central California are also found carrying sea anemones that appear to be the same species (Shimek, in preparation).

MATERIALS AND METHODS

Specimens examined for both descriptive and comparative purposes came from the collections of the Moss Landing

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Table 1

Specimens examined. For museum lots with more than one specimen, we designated the specimens. For the Moss Landing Marine Laboratories (MLML) specimens, the designations were FM1–FM22 and NS1–NS19. For all other specimens, the designations were alphabetic, in order, starting with A in each new lot number. Type specimens are noted, but these data were taken from specimen label information. Station data for FM20–FM22 from Nybakken, et al., 1992.

	Specimen				
Species	Designation	Lot	Collection	N	Comments
A. *Fissidentalium megathyris*	FM1–FM15	P3	MLML	15	Station P3, Collected with: Beam Trawl. 37°03.27′N, 123°26.30′W (on bottom) to 37°03.97′N, 123°25.26′W (off bottom). 29 February 1992. Depth = 3090–3300 m.
	FM16–FM19	M4	MLML	4	Station M4, Collected with: Beam Trawl. 36°20.30′N, 122°36.44′W (on bottom) to 36°19.77′N, 122°35.71′W (off bottom). 1 March 1992. Depth = 2630–2790 m.
	FM20–FM22	LIIT14	MLML	3	Station LIIT14, Collected with: Beam Trawl. 37°35.0′N, 123°30.1′N (on bottom) to 37°35.0′N, 123°28.8′N (off bottom). 30 July 1991. Depth = 3015–2690 m.
	A–B	085479	CAS	2	Off Santa Barbara.
		87558	USNM	1	Station 2789; 1342 fm. (2446 m), Off Chiloe Is.
		594262	USNM	1	Station 2807; 812 fm. (1496 m) "Lectotype".
	A–J	265901	USNM	10	Station 5673; 1090 fm. (1195 m), 31°26′N, 117°42′W.
	A–R	95851	USNM	18	Station 2807; Specimen A = "Figure Type".
	A–W	266823	USNM	23	Station 5693; 868 fm. (1588 m). S.W. of San Diego.
B. *Fissidentalium* ***erosum***	NS1–NS19	P3	MLML	19	Station P3, Pioneer Canyon, 3090–3300 m. (See above.)

Marine Laboratories (MLML). Additional specimens of nominal *F. megathyris,* for comparative purposes, were loaned from the California Academy of Sciences, San Francisco (CAS) and the National Museum of Natural History, Washington (USNM) (Table 1). Type specimens designated in this paper were deposited in the Los Angeles County Natural History Museum (LACM); United States Natural History Museum; and the British Natural History Museum (BMNH).

Shell Measurements and Morphometrics

Shell measurements were made following Shimek (1989), with the following changes (Figure 1). Shimek's (1989) measurement of Aperture Width is actually a measure of Aperture Height. The measure of Aperture Height in this study is the same as that measure designated Aperture Width in the earlier study (Shimek 1989). Aperture Width in this study refers to the maximum apertural distance between the two lateral sides of the shell.

For the shell description, we used an approach of quantitative shell morphometric analyses based on the mathematical properties of shell shape (Raup 1966). The morphometric analyses ideally require "perfect" undamaged shells. Such shells are rare, and to increase statistical reliability, we found it necessary to examine and measure shells with minor fractures, apertural lip breaks, and apical fractures. We tried to be as conservative as possible in the use of these shells, but their use undoubtedly increased variance in the analyses. For detailed derivations of the indices and measurements, see Shimek (1989).

Only 14 of the *F.* ***erosum*** specimens had intact shells which were used for shell comparisons. Most of the museum specimens were from distant localities; for example, the type locality for *F. megathyris* is the Galapagos Islands (Dall 1890). Given that scaphopods develop from demersal

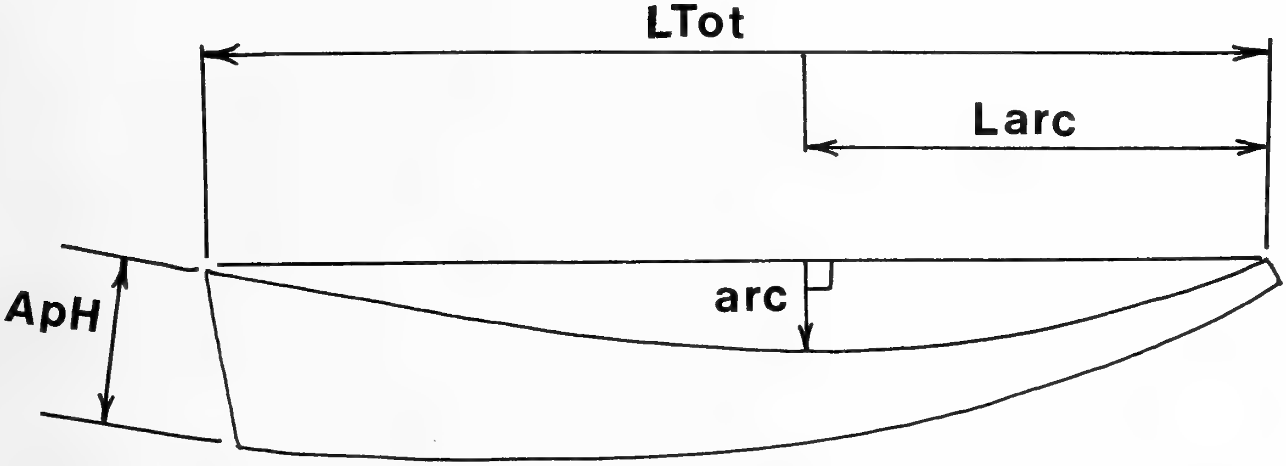


Figure 1.

Shell measurements of all specimens; all orientations labeled anatomically, i.e., the foot is ventral. Abbreviations: ApH = interior height of the ventral aperture, measured perpendicular to the anteriormost shell surface; arc = maximum perpendicular distance from a line connecting the anteriormost margin of the dorsal aperture to the anteriormost margin of the ventral aperture; Larc = distance from the anteriormost margin of the dorsal aperture to the point where measurement "arc" was taken; LTot = total length, from anteriormost margin of the dorsal aperture to the anteriormost margin of the ventral aperture. Measurement ApW (not shown) is taken perpendicular to measurement ApH across the widest part of the ventral aperture.

larvae, with short planktonic periods (Shimek & Steiner, in press), we thought local and distant populations of individuals assigned to *F. megathyris* might have different characteristics. Consequently, where possible, data from *F.* ***erosum*** were compared to the data from the total *F. megathyris* data set and to those data obtained from the nearby California populations.

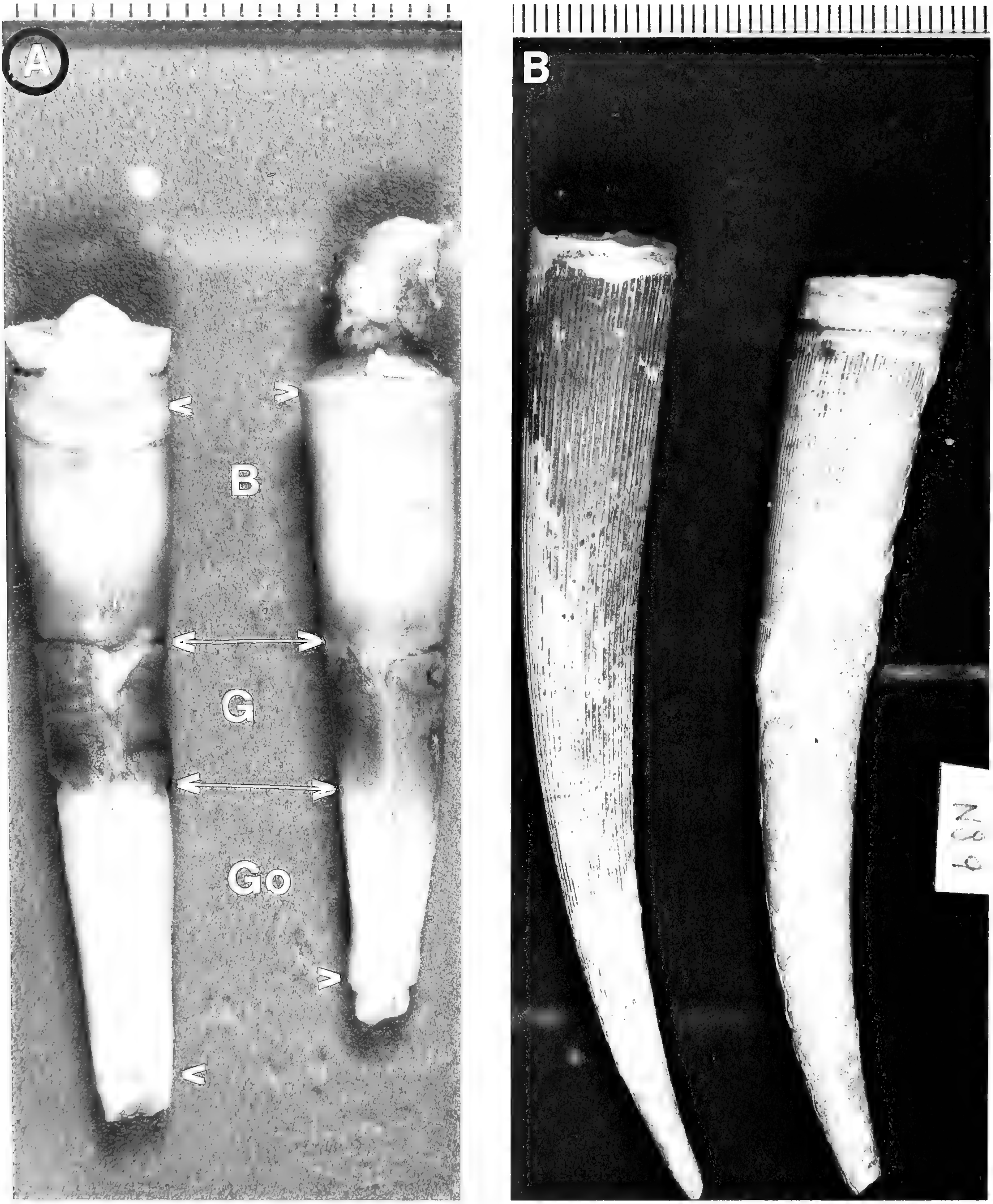
Fissidentalium megathyris was described from Galapagos Island specimens. We did a discriminant analysis classification for the factor of collection location to verify that the Californian *F. megathyris* specimens we used for comparisons were indistinguishable from the Galapagos type specimens. This analysis was based on the data variables of total length (LTot), length to maximum arc (Larc), aperture width (ApW), and aperture height (ApH). For this analysis we used the 56 California *F. megathyris* specimens from the Moss Landing Marine Laboratories collection (Lots P3, M4, and LIIT14), the United States National Museum collection (Lots 265901, 266823), and the California Academy of Sciences (Lot 085479) (Table 1). One specimen from the Moss Landing Marine Laboratories collection could not be measured because of shell fractures. These California specimens were compared with the two specimens collected from the Galapagos with label designations as the "lectotype" and the "figured type" (from USNM lots 594262 and 95851 respectively). Although the two Galapagos specimens were, on the average, larger than the California specimens, the calculated χ^2 probability that these specimens could be drawn from the same population was 0.14. Consequently, the specimens from California designated as *F. megathyris* could not be statistically distinguished, with an α probability of < 0.05, from those specimens designated as the *F. megathyris* lectotype or figured type.

Soft-Body-Part Measurements

Soft-body-part proportions were measured from fixed material, which has been shown to provide reliable quantitative data (Figure 2A) (Voight, 1991). Three basic soft-body-part components were measured. The first was the bucco-pedal region, for brevity referred to here as the buccal region, measured ventrally from the so-called periostracal groove on the outside of the mantle surrounding the ventral aperture to the groove separating this ventral component from the remaining soft body parts. This groove is formed in the region of the bifurcation of the mantle sinus and may be a fixation artifact (Steiner, personal communication). Nevertheless, it was a consistent landmark. The second was the gut region, measured ventrally from the groove separating the gut area from the buccal region to the position of the anus. The third was the gonadal region. This was measured ventrally from the anus to the mantle attachment ring on the mantle surrounding the dorsal aperture, and dorsally from the most posterior margin of the stomach to the mantle attachment ring surrounding the dorsal aperture.

Radular Morphometrics

Whole radulae were dissected from preserved animals, and teeth separated prior to measuring. The following


A
B
G
Go
B

measurements were taken: rachidian tooth width (RW) and length (RL); lateral tooth height (LH) and width (LW); and marginal tooth height (MH) and three width measurements, upper (MUW), middle (MMW), and lower (MLW) (Figures 3, 4, 5). All measurements were made using an image analysis system (Image 1.2 for Macintosh) through an Olympus SZ40 dissecting microscope.

Five animals of each type and six rows/animal (one tooth of each type/row) were measured for 30 measurements/axis/type. All measurements were compared using the Mann-Whitney U test.

Scanning Electron Microscopy

Measurements were made from whole radulae and individual teeth which were hand-cleaned with forceps and water, cleaned of tissue residue in 5% sodium hypochlorite, and ultrasonically treated. They were then dehydrated to 100 percent ethanol, air dried, mounted with silver paint on aluminum stubs, and gold plated. Micrographs were taken with an ISI SX 30 Scanning Electron Microscope (SEM) at 14 KeV. Additional samples for subsequent examination were examined with a JEOL JCS-100 at 20 KeV.

Shell Microstructure

Shells were either hand-broken or cut with a Buehler Isomet (diamond blade) saw in cross section and longitudinally. Some shells were etched in a 5% sodium hypochlorite solution to allow for more distinct differentiation of the various layers. All shells were viewed with an SEM with preparations as indicated above. Surveys of shell edges, inside, and outside surfaces were conducted. Due to shell erosion, numerous shells and locations had to be examined to describe the number and type of layers.

Statistics

The means and standard errors of the measurements or the derived indices were computed, except for the whorl expansion rate (Ws). The whorl expansion rate is a logarithmic function, and calculations of this index are sensitive to small changes of shape. We used the mean of the natural logarithm of this index for comparative purposes. The mean of a logarithmically transformed numerical array is the median of the untransformed array. The median is a better indicator of the central tendency of that array than the mean, as it is less sensitive to extreme values (Sokal & Rohlf, 1981). The mean Ws is also given for comparative purposes.

The morphometric factors and indices were compared between and within populations by using standard statistical graphics software (Manugistics, 1992). When small samples were compared or when the assumptions inherent in parametric tests could not be met, distribution-free or non-parametric tests (such as the Mann-Whitney U) were used, even though they were less powerful. The data were examined between the species with regard to homogeneity of variance using Cochran's and Bartlett's tests. Similarly, all data were tested with a Kolomogorov test for their fit to a normal distribution. Parametric tests, such as Analysis of Variance, were only used when the inherent assumptions of normality and homogeneity of variance could be met (Zar, 1984).

With the exception of the whorl expansion rate, all of the data sets showed non-significant differences in variance and were not significantly different from a normal distribution. Because the conditions of normality and homogeneity of variance could be met, the data were examined using a one-way Analysis of Variance for each of the measured factors. The proportional data were arc-sin transformed prior to these analyses.

We used five basic measurements and nine calculated values to describe the shell (Tables 2, 3). Throughout this study, statistical significance was defined as $P = \alpha \leq 0.05$.

Tabular Data Appendix

The numerous morphometric comparisons and statistical procedures used in this study generate large amounts of tabular data that are necessary for the analyses leading to the species description. Nonetheless, many of those data are superfluous to the actual species description, and are expensive to publish. All of the statistically significant differences determined from the comparisons are summarized in Table 4. All of the comparisons of differences, including both statistically significant and insignificant data, are grouped in the following tables in an electronically available data appendix.

Appendix Table 1. Summary of meristic factors for *Fissidentalium megathyris* and *F.* ***erosum.***

←

Figure 2.

Soft body parts and shells of California *Fissidentalium* ***erosum*** Shimek & Moreno, sp. nov. and *F. megathyris* collected from MLML Station P3. A. Left: Soft body parts from *F. megathyris* (Specimen FM-7), Right: Soft body parts from *F.* ***erosum*** Shimek & Moreno, sp. nov. (Specimen NS-16). Arrowheads indicate measuring points. B = Bucco-pedal region, G = Gut region, Go = Gonadal region. B. Left: Shell from *F. megathyris* (Specimen FM-20), Right: Shell from *F.* ***erosum*** Shimek & Moreno, sp. nov. (Specimen NS-9; LACM # 2755). Scale bar is in millimeters.

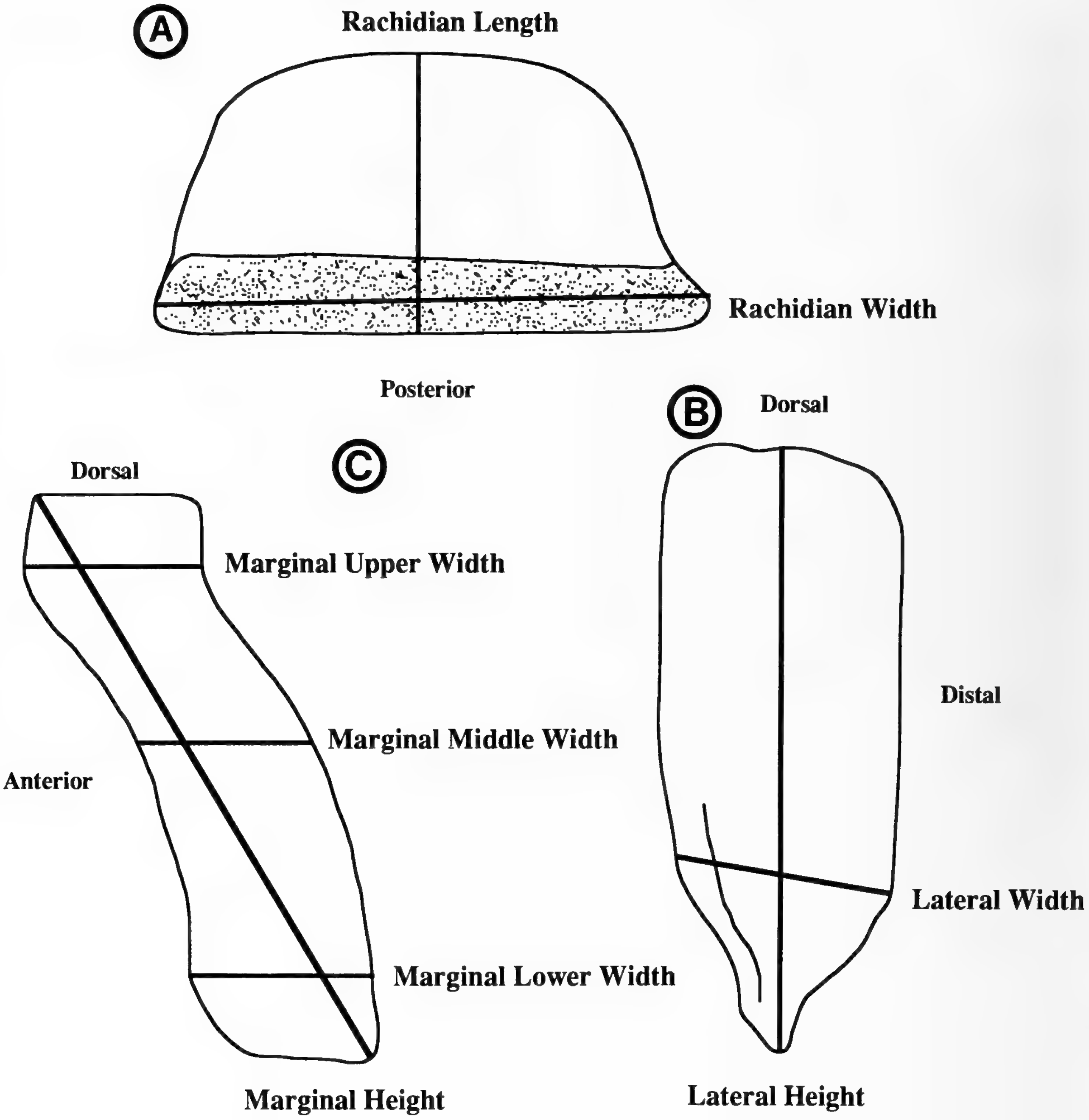


Figure 3.

A. Dorsal view of a typical rachidian tooth. Measurements taken were Rachidian Length (RL) and Rachidian Width (RW). B. Anterior view of a typical lateral tooth. Measurements taken were Lateral Length (LH) and Lateral Width (LW) of the tooth at the tooth "handle" (See Figure 4A). C. Distal view of a typical marginal tooth. Measurements taken were Marginal Height (MH), Marginal Upper Width (MUW), Marginal Middle Width (MMW), and Marginal Lower Width (MLW). MUW and MLW were taken at the curvatures of the teeth.

Appendix Table 2. Results of two factor comparisons of soft body part length measurements of *Fissidentalium megathyris* and *F.* ***erosum*** using the Mann-Whitney U test.

Appendix Table 3. Results of One-way ANOVAs testing factor differences by species for *F. megathyris* and *F.* ***erosum.***

Appendix Table 4. Results of two-sample compari-

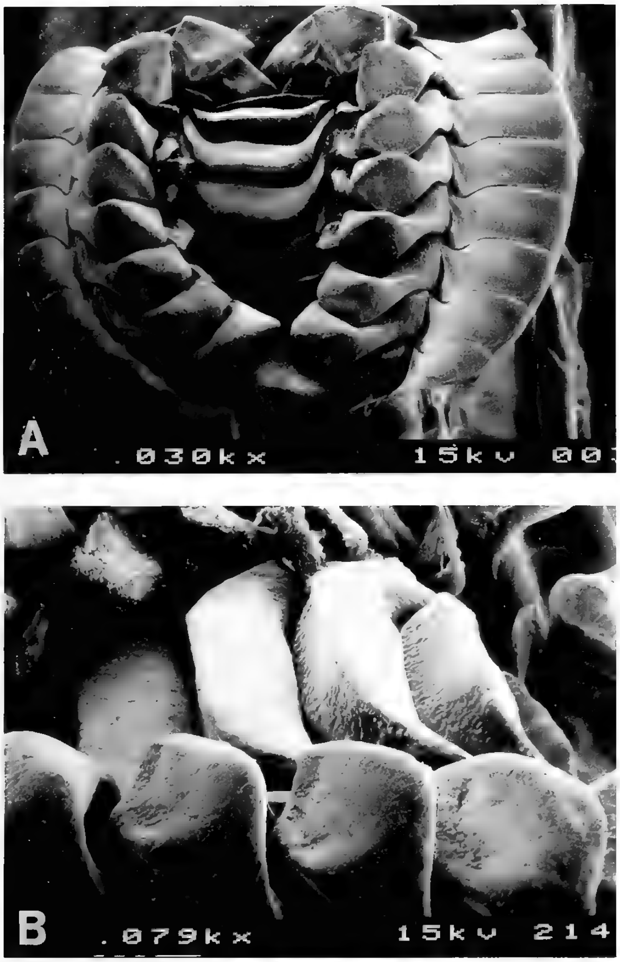


Figure 4.

Radula of *Fissidentalium* ***erosum*** Shimek & Moreno, sp. nov. Specimen NS-3. A. Whole radula. Figures 4B, 5A and 5B are oblique views from the right side of this preparation. B. Lateral view of rachidian and heads of lateral teeth.

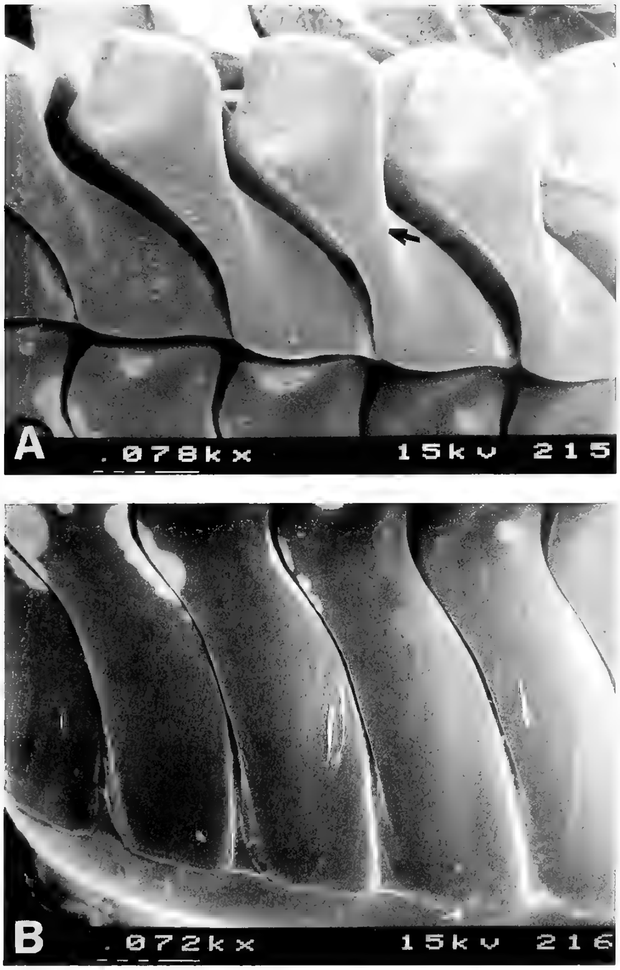


Figure 5.

Radula of *Fissidentalium* ***erosum*** Shimek & Moreno, sp. nov. Specimen NS-3. A. Dorso-lateral (oblique) view of the lateral teeth. Arrow indicates "tooth handle". B. Dorso-lateral oblique view of the marginal teeth.

sons made with a Mann-Whitney U test for the measurement indicated.

These data may be useful for other comparative taxonomic work, and are available electronically by anonymous FTP from ucmp1.berkeley.edu.

SYSTEMATICS

Class Scaphopoda Bronn, 1862

Order Dentaliida Da Costa, 1776

Family DENTALIIDAE Gray, 1834

Fissidentalium P. Fischer, 1885

Type species: *Dentalium ergasticum* P. Fisher, 1882 (designation by monotypy).

Fissidentalium contains numerous large, deep-water species. The shells are robust, and generally possess many longitudinal ribs or striae. The generic name refers to the presence of a narrow posterior (on the convex side) slit proceeding ventrally from the dorsal aperture (Emerson, 1962; Palmer, 1974b; Steiner, 1992). This slit is found in many *Fissidentalium* species, but is lacking in a few, notably *F. megathyris*. *Fissidentalium* is easily recognized and widespread; however, most of the species have been described on the basis of limited collections and are relatively similar in gross morphology (Pilsbry & Sharp 1897; Palmer 1974a).

Fissidentalium ***erosum***
Shimek & Moreno, sp. nov.

Type Material: Holotype: LACM # 2755 (Figure 1B);

Table 2

Shell measurements taken of *F. megathyris* and *F. erosum.* See Figure 1.

Basic measurements	
LTot	= Total length
Larc	= Length from the posterior aperture forward to the point of maximum distance to the shell from a chord running between the dorsal edges of both apertures.
ApW	= Aperture width
ApH	= Aperture height
arc	= Maximum distance to the shell from a chord running between the dorsal edges of both apertures.
Derived indices	
lnLtot	= Natural logarithm of (LTot)
lnLarc	= Natural logarithm of (Larc)
lnApW1	= Natural logarithm of ((ApW) + 1)
lnApH1	= Natural logarithm of ((ApH) + 1)
lnWmax1	= Natural logarithm of ((Wmax) + 1)
Lindex	= Natural logarithm of ((LWmax) + 1)/natural logarithm of (LTot)
whratio	= (ApW)/(ApH)
Apratio	= Natural logarithm of ((ApW) + 1)/natural logarithm of ((ApH) + 1)
Ws	$= {\frac{LTot}{\sqrt{(LTot - Larc)^2 + (\mathrm{arc})^2}}}^{\frac{1}{atan\left(\frac{(\mathrm{arc})}{LTot-Larc}\right)}}$

Paratypes: LACM # 2756, USNM # 880041, BMNH # 199405.

Type locality: Station P3 (Moss Landing Marine Laboratories Designation), Pioneer Canyon, off Central California. Collected with a beam trawl at 37°03.27′N, 123°26.30′W (trawl on bottom) to 37°03.97′N, 123°25.26′W (trawl off bottom), on 29 February 1992, at depths ranging from 3090 m to 3300 m.

Material examined: We examined 19 specimens of *Fissidentalium* ***erosum.*** The same number of *F. megathyris*

Table 3

Type specimen measurements. Specimen BMNH 199405 had a fractured shell; consequently no shell measurements are listed. All measurements are in millimeters. Measurements and derivations are described in Table 2 and Figure 1.

Category Museum Lot Number	Holotype LACM 2755	Paratype USNM 880041	Paratype LACM 2756	Paratype USNM 880041	Paratype BMNH 199405	Paratype BMNH 199405
A. Shell Measurements						
LTot	77.8	72.2	74.2	76.0		62.2
Larc	36.6	28.9	36.1	39.1		28.0
ApW	11.9	11.5	12.7	11.8		11.3
ApH	11.9	11.4	12.5	12.0		11.2
arc	5.1	2.9	6.4	5.4		5.2
B. Derived Indices						
lnLtot	4.4	4.3	4.3	4.3		4.1
lnLarc	3.6	3.4	3.6	3.7		3.3
lnApW1	2.6	2.5	2.6	2.5		2.5
lnApH1	2.6	2.5	2.6	2.6		2.5
Apratio	1.0	1.0	1.0	1.0		1.0
Ws	167.1	2244.0	50.6	133.1		49.7
whratio	1.0	1.0	1.0	1.0		1.0
C. Soft Body Part Length Measurements						
Total soft body parts	38.9	30.0	33.8	35.1	31.2	33.9
Buccal region	12.1	15.4	14.9	17.0	12.0	15.6
Gut region	9.6	4.3	6.1	5.6	8.3	7.8
Gonadal regions						
(Ventral)	17.2	10.3	12.8	12.5	10.9	10.5
(Dorsal)	16.7	11.4	15.0	11.7	13.0	14.6

Table 4

Significantly different characteristics and the test determining their differences. P = probability that the characteristic values in the *F. megathyris* and *F. erosum* are drawn from the same population. * = Proportions were Arc-Sin transformed prior to the ANOVA.

Characteristic	P	Test
Shell Characteristics		
LTot	< 0.001	ANOVA
lnLtot	< 0.001	ANOVA
Apratio	< 0.01	Mann-Whitney U
ApW/ApH	< 0.01	Mann-Whitney U
Soft Body Part Characteristics		
Total soft body part length	< 0.01	Mann-Whitney U
Total soft body parts length	< 0.001	ANOVA
Gut region length	0.05	Mann-Whitney U
Gonadal region, dorsal length	< 0.01	Mann-Whitney U
Gonadal region, dorsal length	< 0.001	ANOVA
Gonadal region, ventral length	< 0.01	Mann-Whitney U
Gonadal region, ventral length	< 0.001	ANOVA
Proportion of Total Soft Body Part Lengths		
Buccal region length	< 0.01	Mann-Whitney U
Buccal region length	0.001	ANOVA*
Gonadal region, ventral length	< 0.01	Mann-Whitney U
Gonadal region, ventral length	< 0.01	ANOVA*
Radular Tooth Characteristics		
Rachidian tooth width	0.012	Mann-Whitney U
Lateral tooth width	0.036	Mann-Whitney U
Marginal tooth height	0.012	Mann-Whitney U
Marginal tooth middle width	0.033	Mann-Whitney U
Marginal tooth lower width	0.020	Mann-Whitney U

was also collected from the site. Additional museum lots of *F. megathyris* specimens, including the type material, were examined for comparative purposes (Tables 1, 3).

Etymology: The epithet *erosum* refers to the shell erosion that characterizes this species.

Diagnosis: Shell large, over 65 mm long and 13 mm in ventral aperture diameter, evenly curved, point of maximum curvature posterior to, but near, shell middle. Outer shell layers, particularly near the dorsal aperture, eroded. Shell white, often with adherent black material. Ventral aperture oblique, slightly wider than high. Preserved, unrelaxed, soft-body-part mass divisible into the buccal (ventral), gut (middle), and gonadal (dorsal) portions and less than half total shell length; buccal and gonadal lengths approximately equal and each about 2/5 of total length.

Detailed description: Specific measurements of the holotype and paratypes are given in Table 3. Unless otherwise noted, all measurements in the description are means ± one standard error of all *F.* ***erosum*** specimens and were taken from Appendix Table 1.

Shell large, mean total shell length 69.20 ± 1.40 mm, evenly curved; shell length from dorsal aperture to point of maximum curvature 31.67 ± 1.17 mm; point of maximum arc posterior to, but near, the shell middle (Figure 2B).

Ventral aperture slightly oblique to dorso-ventral axis; approximately circular; aperture width 11.89 ± 0.15 mm; aperture height 11.74 ± 0.15 mm. Although not significantly different, most ventral apertures are wider than high.

Shell curvature moderate; maximum curvature 4.43 ± 0.33 mm; whorl expansion rate 615 ± 284.

Length of preserved, unrelaxed, soft-body-part mass 31.42 ± 1.10 mm; length of buccal region 14.32 ± 0.57 mm; gut region 6.96 ± 0.39 mm. Ventral gonadal region length 10.14 ± 0.61 mm; dorsal gonadal region length 12.23 ± 0.49 mm.

Radula of "*Antalis* type" (Chistikov 1975); lateral teeth convex anteriorly and concave posteriorly with sharply pointed forward projections where bent (Figures 3B and 4A); marginal teeth with wavy contours and three curvatures (Figure 4B), rachidian teeth concave dorsally, with transverse ridges, and "S"-shaped, allowing the teeth to fit tightly together (Figure 4B). Rachidian and lateral teeth movable on radular ribbon; marginal teeth immobile, imbedded in ribbon.

Radular tooth measurements were from five animals slightly smaller than sample mean size; aperture width 11.62 ± 0.20 mm., aperture height 11.42 ± 0.15 mm. Rachidian tooth length 61.00 ± 1.10 μm, width 100.8 ± 1.28 μm; lateral tooth height 105.6 ± 1.20 μm, width 53.2

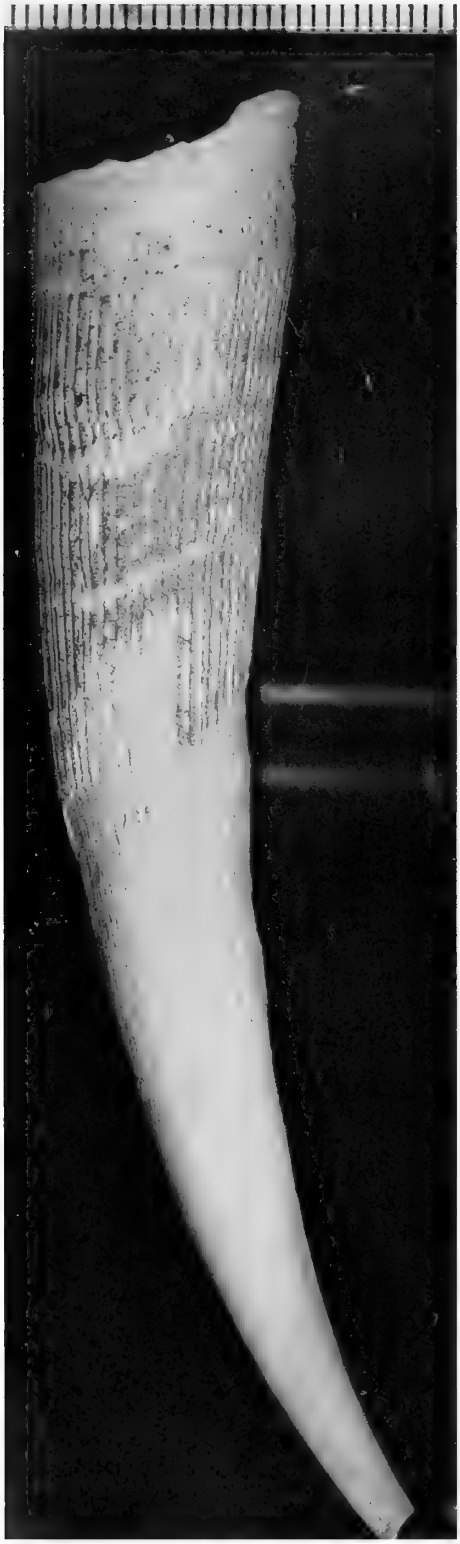


Figure 6.

Fissidentalium megathyris. Specimen F from USNM lot 95851, labeled paratypes, figured types. Scale bar is in millimeters.

± 1.77 μm; marginal tooth height 118.2 ± 3.84 μm, top width 37.8 ± 1.93 μm, middle width 33.6 ± 1.69 μm, lower edge width 35.0 ± 1.38 μm.

Shell with three layers; ribbed outer aprismatic layer, partially or completely eroded particularly near dorsal aperture, 20–40 μm thick; middle prismatic layer, 750 μm thick; inner aprismatic layer, 50 μm thick.

Shell white, adherent black material found on some specimens. Shell dorsal apical end often missing, due to decollation (Reynolds, 1992) or predation (Shimek, 1990).

Remarks: All of the *F.* ***erosum*** examined were adults, although a few small *F. megathyris* shells were examined during the comparisons. No *F.* ***erosum*** juveniles were collected, probably due to the sampling method. The gender of all the animals was not determined when the animals were measured, but an examination of eight haphazardly selected individuals indicated three males, four females, and one whose gender was indeterminate due to poor preservation; consequently the differences between *F.* ***erosum*** and *F. megathyris* were not likely due to sexual characteristics. Gametes filled each gonad; the animals gave no appearance of having recently spawned.

Fissidentalium ***erosum*** was externally similar in most regards to *F. megathyris* (Figures 2B, 6), and could easily be confused with it. The major differences were the amount of erosion, and the dorsoventrally flattened ventral aperture. We attempted to determine if the erosional difference was due to some structural difference in the shell. No significant differences were apparent; however, the *F.* ***erosum*** shells were too eroded to draw definitive conclusions.

We compared shell, soft-body-part, and radular meristic characters to determine if the two morphologies were actually statistically distinct species. On the basis of shells alone, these two morphologies were statistically distinct only as regards the ratios of the ventral aperture width to aperture height (Table 4, Appendix Table 1), as examined with the nonparametric tests. Using the Mann-Whitney U test, both the untransformed and the logarithmically transformed aperture ratios were different between the two species; *Fissidentalium* ***erosum*** apertures were significantly wider for a given height than were the ventral apertures of *F. megathyris* (Apratio, $Z = -3.536$, probability of ratios being different < 0.01; ApW/ApH, $Z = -3.602$, probability of ratios being different < 0.01).

On the basis of gross soft-body-part morphology, the species were more clearly distinct (Table 4, Appendix Tables 1, 2, Figure 2). The total soft body part length was significantly shorter for *F.* ***erosum*** than for *F. megathyris.* This difference was largely due to significant differences in the lengths of the gut and gonadal lobes. The buccal region was a significantly greater proportion of the total soft body parts in *F.* ***erosum*** than in *F. megathyris,* while the gut and the dorsal measurements of gonadal lobes were not proportionally different in size. The ventral measurement of the gonadal region was proportionally larger in *F. megathyris* than in *F.* ***erosum.***

Of the untransformed or transformed shell parameters, only total length was statistically significantly different between the two species (Table 4, Appendix Table 3). As the apertural measurements were not statistically different, this indicates that *F. megathyris* is longer for a given aperture measurement than is *F.* ***erosum.***

The total soft-body-part lengths were significantly different utilizing the one-way analysis of variance. This significant difference was due primarily to the differences in the length of the gonadal region, which was larger in *F. megathyris.* The dorsal and ventral gonadal region proportions of the soft body part components were statistically significantly different between the two species, utilizing this test as well (Table 4, Appendix Table 3).

We interpreted these data to indicate that *F.* ***erosum*** individuals were "stubbier" than those of *F. megathyris,* being shorter for a given width. This subtle truncation in length was reflected in the soft body part anatomy, where the gonadal component of the soft body parts was confined in a smaller space in *F.* ***erosum.*** The middle or gut region, which contained the radula and radular musculature, was not different between the two species, possibly indicating a similar food.

Examination of radular characteristics from paired animals showed significant differences as well. These data were too few to be sure that the assumptions for an analysis of variance could be met, so the comparisons were made utilizing the non-parametric Mann-Whitney U test. The animals were chosen to provide as close a match as we could get between the paired animals. The aperture widths were not significantly different. As expected however, the aperture heights were significantly different (Table 4, Appendix Table 4). The rachidian and lateral teeth were significantly wider in *F. megathyris* than in *F.* ***erosum,*** although the heights were not significantly different. Most of the marginal tooth measurements were significantly different between the two species; only the upper marginal tooth width was not significantly different. In all significantly different cases, the *F. megathyris* radular teeth were larger or more robust.

The significant differences between these two morphologies were related to both relative and proportional differences in size, and were reflected in both internal and some external meristic factors (Table 4). Additionally, there were radular differences, possibly reflecting differences in either prey eaten, or the method of eating it. Finally some of the more qualitative shell morphological differences, such as the amount of shell erosion, may indicate differential habitat utilizations. Because of all of these differences, we concluded that the two morphologies were from two distinct species: the larger, more elongate *F. megathyris,* and the smaller, stubbier *F.* ***erosum.***

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LITERATURE CITED

CHISTIKOV, S. D. 1975. Some problems in the classification of the order Dentaliida (Mollusca: Scaphopoda). Science [Nauka] Leningrad Section. -:18–21. Abstract translated in Emerson, W. K., 1978. Malacological Review 11:71–73.

DALL, W. H. 1890. Scientific results of the explorations by the U. S. Fish Commission steamer Albatros. No. VII.-Preliminary report on the collection of mollusca and brachiopoda obtained in 1887–88. Proceedings of the U. S. National Museum 12:219–363, 13 pl.

EMERSON, W. K. 1962. A classification of the scaphopod mollusks. Journal of Paleontology 36:76–80.

MANUGISTICS, INC. 1992. *Statgraphics Plus* v. 6.0. Rockville, Maryland.

NYBAKKEN, J., L. SMITH-BEASLEY, A. SUMMERS, S. CRAIG & L. WEETMAN. 1992. Invertebrate megafauna collected from the proposed U. S. Navy ocean disposal site as determined from beam and otter trawls and camera sled samples. Unpublished report prepared for PRC Environmental Management, Inc. 2828 Paa Street, Suite 3080, Honolulu, Hawaii 96819.

PALMER, C. P. 1974a. A supraspecific classification of the Scaphopod Mollusca. The Veliger 17:115–123.

PALMER, C. P. 1974b. Rectification of nomenclature in the molluscan class Scaphopoda. The Veliger 17:124–125.

PILSBRY, H. A. & B. SHARP. 1897–1898. Class Scaphopoda. Pp. xxxii+144 [1897]; Pp. 145–280 [1898], pls. 1–39 in G. W. Tyron, Jr. & H. A. Pilsbry, Manual of Conchology: Ser. 1, Vol. 17.

RAUP, D. 1966. Geometric analysis of shell coiling: general problems. Journal of Paleontology 40:1178–1190.

REYNOLDS, P. D. 1992. Mantle-mediated shell decollation increases posterior aperture size in *Dentalium rectius* (Scaphopoda: Dentaliida). The Veliger 35:26–35.

SHIMEK, R. L. 1989. Shell morphometrics and systematics: A revision of the slender, shallow-water *Cadulus* of the Northeastern Pacific (Scaphopoda: Gadilida). The Veliger 32:233–246.

SHIMEK, R. L. 1990. Diet and habitat utilization in a Northeastern Pacific Ocean scaphopod assemblage. American Malacological Bulletin 7:147–169.

SHIMEK, R. L. & G. STEINER. In press. Scaphopoda in F. Harrison & A. J. Kohn, eds. *Mollusca. Microscopic Anatomy of the Invertebrates.* Volume 6.

SOKAL, R. R. & F. J. ROHLF. 1981. *Biometry.* W. H. Freeman and Company. New York. 859 pp.

STEINER, G. 1990. Beiträge zur vergleichenden Anatomie und Systematik der Scaphopoda (Mollusca). Ph. D. Dissertation, University of Vienna. 174 pp.

STEINER, G. 1992. Phylogeny and classification of scaphopoda. Journal of Molluscan Studies 58:385–400.

VOIGHT, J. R. 1991. Morphological variation in octopod specimens: reassessing the assumption of preservation-induced deformation. Malacologia 33:241–253.

ZAR, J. H. 1984. *Biostatistical Analysis,* 2nd ed. Prentice-Hall, Inc.: Englewood Cliffs, New Jersey. 718 pp.

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Egg Capsules and Development of *Prunum prunum* (Gmelin, 1791) (Prosobranchia: Marginellidae) from the Venezuelan Caribbean

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Abstract. *Prunum prunum,* a common marginellid of Venezuelan sandy beaches has a plano-convex egg capsule that is attached to the substrate by an oval base. An ellipsoidal suture at the middle top of the egg capsule could act as a preformed escape aperture. A single, large, bright yellow egg develops within each egg capsule. The egg measures between 0.895 and 1.075 mm in diameter, being the largest egg recorded for the Marginellidae. Hatching takes place as a crawling juvenile, 55–60 days after oviposition. The shell length at hatching is 2.7 to 3.0 mm. Differences in protein and carbohydrate concentrations in the intracapsular fluid between early and pre-hatching stages suggest that, despite the enormous amount of yolk contained in the egg, the embryo may require extraembryonic food to complete development.

INTRODUCTION

The spawn of the Marginellidae were first described by Knudsen (1950) for a number of species from West Africa. Knudsen described two different types of egg capsules. The first type is lens-shaped, compressed, and attached to the substrate by a stalk. The second is plano-convex and attached to the substrate along one flat side. There are very few references regarding the reproduction of Caribbean marginellids [*Prunum apicinium* Menke, by Raeihle (1965), D'Asaro (1970), and Winner (1983); *Hyalina avena* Kiener, by Bandel (1976); and *Marginella aureocincta* Stearns and *Granulina ovuliformis* Orbigny, by D'Asaro (1986)]. Coovert (1986) summarized the information on marginellid egg capsules, including several Caribbean species.

Prunum prunum (Gmelin, 1791) is the most common shallow-water marginellid that inhabits non-calcareous shallow sandy beaches of Venezuela. In this paper, characteristics of the spawn and development of *Prunum prunum* are described. The protein and carbohydrate concentrations of the intracapsular fluid were measured in order to evaluate the contribution of extraembryonic food resources during development.

MATERIAL AND METHODS

Adults and egg capsules of *Prunum prunum* were collected from the sandy beaches of Tucacas, Quizandal, and Higuerote-Mercedes Paparo in western and central Venezuela at depths of 0.5 to 2 m. Egg capsules were found attached to different hard substrates depending on locality. On Las Mercedes Paparo beaches, they are laid almost exclusively on shells of live *Tivela mactroides,* a very abundant bivalve. Polychaete tubes and dead shells of bivalves and gastropods are frequently used as substrates in Tucacas and Quizandal. Part of the adult and egg material was preserved in 6% formalin in seawater, and some was taken alive to the lab and maintained in aerated seawater at 26°C. The first spawning observations were made in 1976, but most of

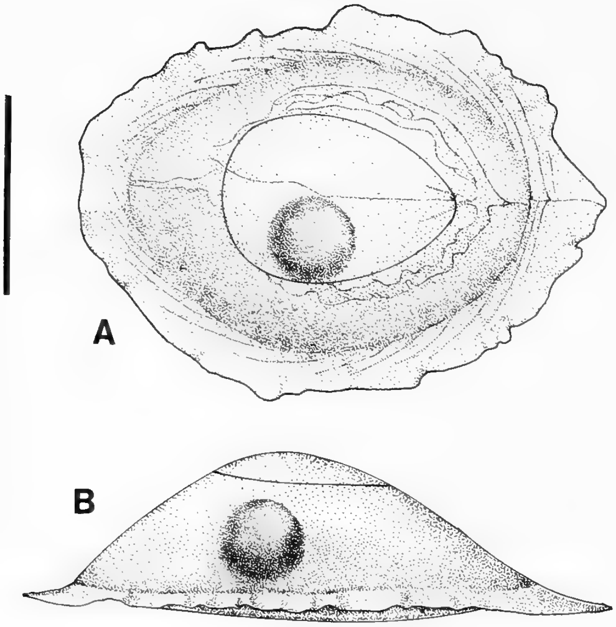

Figure 1

Prunum prunum (Gmelin, 1791). Dorsal (A) and lateral (B) views of an egg capsule. (Scale bar = 2 mm).

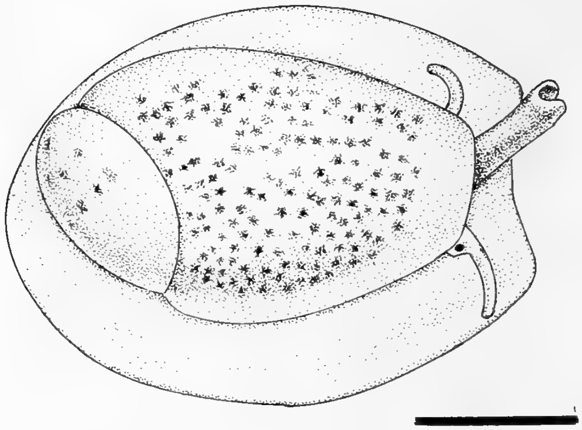

Figure 2

Prunum prunum (Gmelin, 1791). Hatching juvenile. (Scale bar = 1 mm).

the work herein presented was carried out between 1981–1983.

The intracapsular liquid was removed by means of a 25 μL Hamilton microsyringe. The protein content of the intracapsular fluid was determined using the method of Lowry et al. (1951), using bovine serum albumin as a standard. Carbohydrates were measured using the method of Dubois et al. (1956); the results are reported as mg/mL of D-glucose.

RESULTS

In the field, *Prunum* reproduced throughout the year. In Las Mercedes-Paparo, there were two periods of maximum spawning activity, May–June and October–November, which are the beginning and end of the rainy season, respectively. The warmest water temperature during these months ranges from 27 to 29°C. In June 1982, 50% of the live *Tivela* collected had egg capsules of *Prunum* attached to them. In September 1982, this number decreased to 5.4%.

In the laboratory, the egg capsules were deposited on the aquarium walls, on live and dead *Tivela* shells, and on other hard substrates. Observations of animals in aquaria indicated that oviposition is stimulated when the water temperature is raised to 27°C. The spawn consisted of several (2–6) egg capsules which were attached individually to the substrate; sometimes the egg capsules were attached very close to one another so that they appeared to form masses similar to those of small prosobranchs. The egg capsule (Figure 1) was plano-convex, relatively tall, and fixed to the substrate by a flattened oval base. The basal wall extended beyond the capsule walls. Immediately after oviposition, the wall was soft. Within 3–4 hours it became harder. The egg capsules ($n = 100$) measured 3.3–4.9 mm long, 3.2–4.1 mm wide, and 1.2–2.8 mm tall. An ellipsoidal suture line 2.1–3.0 mm long (mean 2.7 ± 0.2 mm) and 1.5–2.6 mm wide (mean 1.8 ± 0.2 mm) which served as a preformed hatching aperture was observed in about the middle of the capsule.

A single, large, bright yellow egg developed within each capsule. The egg measured 0.895–1.075 mm in diameter ($n = 142$). The egg capsule was filled with a viscous fluid that was completely translucent at oviposition. The volume of the egg capsule did not vary during development, but the viscosity of the intracapsular fluid diminished markedly.

The first division of the zygote occurred 2 hr after deposition and yielded two equal blastomeres. The second division occurred after 6 hr, and four blastomeres of the same size were seen. The gastrula stage was reached in a few days. By day 10, the embryo had enlarged and showed signs that torsion had begun. By day 12, the organic matrix for the future shell began to form. At this stage, the embryo measured 1.8 mm in length. Growth was very rapid in this phase; embryos reached a mean shell length of 2.6 mm by day 15, although the embryos varied greatly in size at each developmental stage. By 40 days after oviposition, the embryos measured up to 3.0 mm in shell length. From this point to hatching, external changes were not very noticeable, except for the pigmentation of the body with black dots, and shell calcification. The embryo never developed a velum. Hatching as a crawling juvenile took place 55–60 days ($n = 62$) after oviposition (Figure 2). Field and laboratory observations of the hatching process indicated that it occurred by the opening of the preformed exit aperture and sometimes by the mechanical destruction of the egg capsule by the embryo. The juvenile shell length at hatching was 2.7–3.0 mm (mean 2.8 ± 0.1 mm; n = 42).

The volume of intracapsular liquid obtained from the egg capsules varied between 6 and 11 μL.

The initial total protein concentration of the intracapsular fluid varied between 11.6 and 39.8 mg/mL (mean 23.4 ± 6.4 mg/mL; n = 45). At the pre-hatching stage (55–60 days after oviposition), the total protein concentration decreased to 0.2–5.6 mg/mL (mean 2.7 ± 1.7 mg/mL, n = 14). Protein concentration began to drop gradually in the period between 15 and 50 days after oviposition; after this point, it fell dramatically in the few days prior to hatching.

Carbohydrate concentration in the intracapsular fluid was 19.7–34.6 mg/mL (mean 32.3 ± 12.2 mg/mL; n = 14) at the initial stage, but in the pre-hatching stage, it decreased to 1.4–10.2 mg/mL (mean 4.6 ± 1.8 mg/mL; n = 7). Carbohydrate dropped significantly only in the final period of development (after 45 days from oviposition).

DISCUSSION

The egg capsules of *Prunum prunum* are very similar to many other marginellids in having a plano-convex shape. A single egg within each egg capsule seems to be the rule for all marginellids studied, with a few exceptions. Raeihle (1965) found two eggs per capsule as a rare case (0.5% of the egg capsules, the other contained a single egg) in *Prunum apicinium:* Bandel (1976) reported "about" five eggs per egg capsule in *Hyalina avena,* and Ponder (1970) reported one or two eggs per capsule in *Volvarinella cairoma* Brookes. The egg size of *Prunum prunum* (0.895 to 1.075 mm) is the largest ever recorded for a marginellid and one of the largest among prosobranchs. Other recorded egg diameters are: *Marginella aureocincta,* 240 microns (D' Asaro, 1986); *Prunum apicinium,* 250 microns (Raihle, 1965); *Microginella minutissima* Tenison-Woods, 300 microns (Murray, 1970); *Granulina ovuliformis,* 310 microns (D'Asaro, 1986); *Marginella marginata.* Born, 500 microns (Knudsen, 1950). At hatching, *Prunum prunum* juveniles measure between 2.7 and 3.0 mm in shell length. This size is surpassed only by two West African species: *Marginella cornea* Lamarck (7 mm in shell length) and *Marginella goodalli* Sowerby (4.5 mm in shell length) (Knudsen, 1950).

The observed changes in concentrations of protein and carbohydrates in the intracapsular fluid between early and pre-hatching stages in *Prunum prunum* suggest that despite the enormous amount of yolk contained within the egg, extraembryonic food resources could be necessary for development. The uptake of nutritional substances by the embryo has not been demonstrated in marginellids. The protein concentration of the intracapsular liquid of *Prunum prunum* (11.6 to 39.8 mg/mL) is high, compared with the initial developmental stage for other prosobranchs [*Busycon carica* Gmelin: 3–4 mg/mL (Harasewych, 1978); *Busycon canaliculatum* Linné: 9 mg/mL (Harasewych, 1978); *Nucella lapillus* Linné: 7.4 mg/mL (Stöckmann-Bosbach & Althoff, 1989); *Adelomelon brasiliana* Lamarck: 20 mg/mL (de Mahieu et al., 1974)]. Nevertheless, because the fluid volume contained in the egg capsule is small (6–11 μL), the total protein contained in the intracapsular fluid in *Prunum prunum* is less than that reported for other species. For instance, de Mahieu et al. (1974) reported a mean volume of 77 mL per capsule in *Adelomelon brasiliana,* which results in 1.540 g of protein per egg capsule. With a mean number of embryos per capsule of 22, this results in 70 mg of protein available per embryo in *A. brasiliana* vs. 0.140 to 0.257 mg for the single embryo in *P. prunum.* On the other hand, the egg diameter of *Adelomelon brasiliana* (0.240 mm; Penchaszadeh & de Mahieu, 1976) is much smaller than that of *Prunum prunum* (0.895 to 1.075 mm).

When comparing early stages of development of species without nurse eggs with species with nurse eggs, the protein concentration values in the intracapsular fluid of the latter are generally lower [initial stage in *Buccinum cyaneum* Bruguière: 0.61 mg/mL (Miloslavich & Dufresne, personal communication); initial stage in *Fasciolaria tulipa hollisteri* Weisbord: 2.06 mg/mL (Miloslavich & Penchaszadeh, unpublished data); gastrula stage in *Nucella lapillus:* 7.4 mg/mL (Stöckmann-Bosbach & Althoff, 1989)]. This suggests that the nutritional value of the intracapsular fluid is generally less important in the embryonic development of species with other extraembryonic food resources.

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LITERATURE CITED

Bandel, K. 1976. Spawning, development and ecology of some higher Neogastropoda from the Caribbean Sea of Colombia (South America). The Veliger 19(2):176–193.

Coovert, G. A. 1986. A review of marginellid egg capsules. Marginella Marginalia 1(4):13–19.

D'Asaro, C. N. 1970. Egg capsules of prosobranch mollusks from the South Florida and the Bahamas and notes on spawning in the laboratory. Bulletin of Marine Science 20(2): 414–440.

D'Asaro, C. N. 1986. Egg capsules of eleven marine prosobranchs from northwest Florida. Bulletin of Marine Science 39(1):76–91.

de Mahieu G., P. E. Penchaszadeh & A. B. Casal. 1974. Algunos aspectos de las variaciones de proteínas y aminoácidos libres totales del líquido intracapsular en relación al desarrollo embrionario en *Adelomelon brasiliana* (Lamarck, 1811) (Gastropoda, Prosobranchia, Volutidae). Cahiers de Biologie Marine 15:215–227.

Dubois, M., K. A. Gilles, J. R. Hamilton, P. A. Rebers & P. Smith. 1956. Colorimetric methods for determination of sugar and related substances. Ann. Chem. 28:250–256.

Harasewych, M. G. 1978. Biochemical studies of the hatching process in *Busycon*. M. Sc. Thesis, University of Delaware, 52 pp.

Knudsen, J. 1950. Egg capsules and development of some marine prosobranchs from tropical West Africa. Atlantide Report 1:85–130.

Lowry, O. H., N. Rosenbrough, A. C. Farr & R. S. Randall. 1951. Protein meassurement with the Folin Phenol reagent. Journal of Biological Chemistry 193:265–275.

Murray, F. V. 1970. The reproduction and life history of *Microginella minutissima* (Tenison-Woods, 1876) (Gastropoda. Marginellidae). Memoirs of the National Museum of Victoria 31:31–35.

Penchaszadeh, P. E. & G. de Mahieu. 1976. Reproducción de Gasterópodos Prosobranquios del Atlántico Suroccidental. Volutidae. Physis, secc. A 35(91):146–153.

Ponder, W. F. 1970. Some aspects of the morphology of four species of the neogastropod family Marginellidae with a discussion on the evolution of the toxoglossan poison gland. Journal of the Malacological Society of Australia 2(1):55–81.

Raeihle, D. 1965. Studies of captive *Prunum apicinium* Menke. Annual Reports for 1965; American Malacological Union 32:21–22.

Stöckmann-Bosbach, R. & J. Althoff. 1989. A correlated morphological and biochemical study of capsular fluid of *Nucella lapillus* (Gastropoda: Prosobranchia: Muricidae). Marine Biology 102:283–289.

Winner, B. E. 1983. The direct development of *Marginella* (*Prunum*) *apicinum.* Of Sea and Shore 13(1):37–38.

The Veliger 39(1):87–97 (January 2, 1996)

THE VELIGER

NOTES, INFORMATION & NEWS

Probable Pupillid Land Snail of Early Cretaceous (Hauterivian) Age in Amber from Lebanon

by
Barry Roth,[1] George O. Poinar, Jr.,[2]
Aftim Acra,[3] and Fadi Acra[4]

A terrestrial snail preserved in amber of Early Cretaceous (Hauterivian) age from southern Lebanon represents the first known occurrence of the stylommatophoran pulmonate clade Pupilloidea in that time period and is tentatively assigned to the family Pupillidae Turton, 1831. The specimen was collected from nonmarine beds in an unnamed formation located near the mountain villages of Jezzine and Dar Al-Baidhar. At those sites, amber occurs *in situ* in Hauterivian strata, while reworked amber of the same age also occurs in Barremian and Aptian deposits (Schlee & Dietrich, 1970; Schlee & Glockner, 1978). The age of the Hauterivian Stage is currently reported to range from 131.8 to 135 Ma (Harland et al., 1990). The amber was washed and then polished, by rubbing first with wet emery paper and then with a towel containing cesium oxide. The piece of amber containing the fossil snail is designated as JG 260/01 and is deposited in the Acra collection of Lebanese amber maintained by Fadi Acra.

Pulmonata Cuvier, 1817

Stylommatophora Schmidt, 1855

Orthurethra Pilsbry, 1900

PUPILLOIDEA Turton, 1831

(?) PUPILLIDAE Turton, 1831

?Pupillid sp.

(Figures 1, 2)

Description: Shell convexly conic, approximately 3.2 mm in diameter and 3.1 mm in length parallel to axis of coiling, consisting of approximately 4.7 whorls. Columella apparently hollow. Embryonic whorls about 1.5, smooth, without perceptible sculpture, with glossy luster. Post-embryonic whorls moderately convex, profile of successive whorls becoming more flattened; suture deeply impressed. Whorls crossed by slender, threadlike, collabral ribs separated by flat interspaces normally about 2–4 times as wide as ribs; ribs convex-forward to shallowly sinuous, continuing across base into umbilical region. Periphery subangulate; base almost flat.

Remarks: In height/diameter ratio, spire profile, and subangulate periphery defining a relatively flat base, the specimen resembles the juvenile growth phase ("phase 1" of Gould, 1984:175, fig. 4) of a cylindrical or elongate-ovate pulmonate shell. In this phase the shell is roughly triangular in longitudinal section, and its growth adds width before entering a phase of adding height but no width. This specimen's moderate positive allometry of the rate of translation along the coiling axis (producing a convexly conic profile) hints at a probable cylindrical phase of growth to come.

The lip of the aperture, although broken, shows no tendency toward thickening or turning outward, and the coiling trajectory shows no modification behind the aperture. The absence of such features is consistent with a juvenile specimen.

The ribs rise sharply from the surface of the whorl. There are no buttressing microsculptural elements, such as occur in discid and other arionoid land snails (Solem, 1977; Solem & Yochelson, 1979). The ribs are rounded, not mere fins of periostracum, such as occur in some taxa of Pupillidae. Breakage patterns suggest that the ribs were brittle, but because the specimen is enclosed in amber we did not attempt a finer shell structure analysis.

On the basis of the apex and spire growth patterns pointed out by Solem & Yochelson (1979), this specimen is more likely to be a pupillid than a tornatellinid. No apertural barriers are present, which is consistent with juvenile Pupillidae; many species of Tornatellinidae show apertural barriers present in juveniles. Among recognized genera of Pupillidae, the most similar is probably *Orcula* Held, 1837, which has a reported range from Paleocene to Recent in middle and southern Europe and the Middle East (Zilch, 1959–1960).

All previous uncontroversial records of Pupillidae are Paleocene or younger (Zilch, 1959–1960; including families Vertiginidae, Pupillidae, Orculidae, and Chondrinidae of his classification). Paleozoic and other Mesozoic fossil taxa that have at times been referred to Pupillidae are now assigned to other families. Solem & Yochelson (1979) assigned the middle Pennsylvanian to early Permian *Dendropupa* Owen, 1859, to Enidae and the middle Pennsylvanian to early Permian *Anthracopupa* Whitfield, 1881 (synonym: *Maturipupa* Pilsbry, 1926), to Tornatellinidae. Solem & Yochelson (1979) accepted "*Pupa*" *bigsbii* Dawson, 1880, from Pennsylvanian strata in Nova Scotia,

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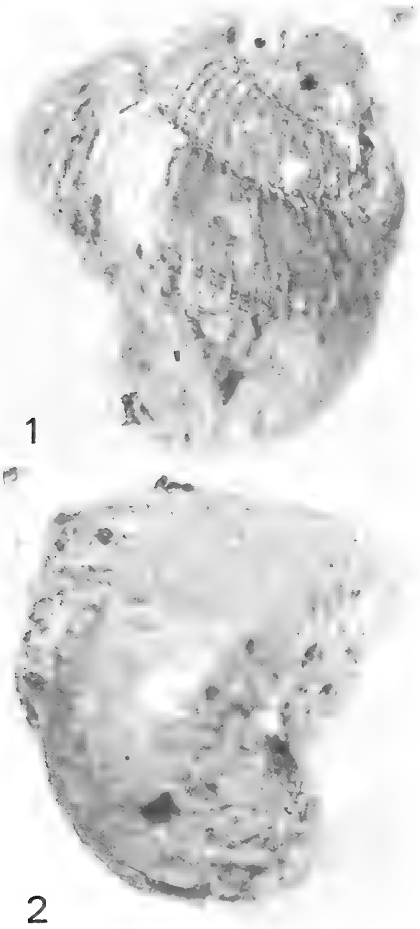

Figures 1, 2

Pupillid (?) sp. in amber. JG 260/01, Acra collection. Diameter approximately 3.2 mm.

as a member of the superfamily Pupilloidea on the basis of the apex and spire growth pattern but declined to assign it to a specific family.

The "*Pupa* sp. indet." of Dyer (1930:14, pl. 3, fig. 13), from the St. Mary River Formation (Maastrichtian) of southern Alberta, Canada, is an incomplete internal mold of about five whorls, measuring approximately 14 mm long and 8 mm in diameter (measurements from illustration). On the basis of size alone, it is unlikely to be a pupillid. Tozer (1956) regarded the specimen as assignable to his new species of Urocoptidae, *Holospira dyeri* Tozer, 1956, which is also known from the St. Mary River Formation.

The Lebanese specimen is approximately twice as old as the earliest Tertiary pupillids. This occurrence is well before the Aptian to Early Cenomanian onset of the angiosperm vegetational revolution (Upchurch & Wolfe, 1987) that profoundly affected the composition and diversity of the world's land snail fauna (Roth, in preparation).

Two previous records of pupillid land snails preserved in amber are *Vertigo hauchecornei* Klebs, 1886, and *Vertigo kuenowii* Klebs, 1886, both from the Eocene of the Baltic region (Klebs, 1886).

We thank Joseph H. Hartman, and David R. Lindberg, who reviewed drafts of the manuscript, and members of the MOLLUSCA List (mollusca@ucmp1.berkeley.edu) who responded to the senior author's posted query about Cretaceous records of the family Pupillidae. This is Contribution No. 1635 from the Museum of Paleontology, University of California, Berkeley.

Literature Cited

DYER, W. S. 1930. New species of invertebrate fossils from the non-marine formations of southern Alberta. National Museum of Canada Bulletin 63:7–14, pls. 3, 4.

GOULD, S. J. 1984. Morphological channeling by structural constraint: convergence in styles of dwarfing and gigantism in *Cerion,* with a description of two new fossil species and a report on the discovery of the largest *Cerion.* Paleobiology 10(2):172–194.

HARLAND, W. B., R. L. ARMSTRONG, A. V. COX, L. E. CRAIG, A. G. SMITH & D. G. SMITH. 1990. A Geologic Time Scale 1989. Cambridge University Press: Cambridge. 263 pp.

KLEBS, R. 1886. Gastropoden im Bernstein. Jahrbuch der Preussische Geologischen Landesanstalt für 1885:366–394.

SCHLEE, D. & W. GLOCKNER. 1978. Bernstein. Stuttgarter Beiträge zur Naturkunde, Serie C, 8:1–72.

SCHLEE, D. & H.-G. DIETRICH. 1970. Insektenfuhrender Bernstein aus der Unterkreide des Lebanon. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1970(1): 40–50.

SOLEM, A. 1977. Shell microsculpture in *Striatura, Punctum, Radiodiscus,* and *Planogyra* (Pulmonata). The Nautilus 91(4): 149–155.

SOLEM, A. & E. L. YOCHELSON. 1979. North American Paleozoic land snails, with a summary of other Paleozoic nonmarine snails. U.S. Geological Survey Professional Paper 1072:1–42, pls. 1–10.

TOZER, E. T. 1956. Uppermost Cretaceous and Paleocene nonmarine molluscan faunas of western Alberta. Geological Survey of Canada Memoir 280. 125 pp.

UPCHURCH, G. R., JR. & J. A. WOLFE. 1987. Mid-Cretaceous to early Tertiary vegetation and climate: evidence from fossil leaves and woods. Pp. 75–105 in E. M. Friis, W. G. Chaloner & P. R. Crane (eds.), The Origins of Angiosperms and Their Biological Consequences. Cambridge University Press: Cambridge.

ZILCH, A. 1959–1960. Gastropoda, Teil 2, Euthyneura. Handbuch der Paläozoologie 6(2):1–400 (1959); 401–834 (1960).

Uptake of Copper by *Biomphalaria glabrata* (Gastropoda: Planorbidae) as Determined by Atomic Absorption Spectrometry

by

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Introduction

Biomphalaria glabrata (Say, 1818) is a medically important freshwater planorbid snail because it is the major vector of the trematode parasite *Schistosoma mansoni* in the Western Hemisphere. This parasite is responsible for a serious blood-liver disorder in humans called schistosomiasis (also known as bilharziasis). This waterborne disease is transmitted from the *B. glabrata* snail to man by water contact with the free-living larval stage, the cercaria. The cercaria can actively penetrate the skin of man in endemic tropical and subtropical areas. Current estimates indicate that 200 to 300 million people are infected with schistosomes, either *S. mansoni* or the other two species that can cause the disease in humans, *Schistosoma haematobium* and *S. japonicum.*

Although copper sulfate has been used as a molluscicide to control *B. glabrata,* little information is available on the accumulation of copper in this snail. Sullivan & Cheng (1976) reported the detection of only negligible amounts of copper by atomic absorption spectrometry (AAS) in the tissues of *B. glabrata* exposed to either 0.10 or 1.00 ppm of copper as copper sulfate for 2 hr. The purpose of our study was to determine copper accumulation in *B. glabrata* snails exposed to 1.00 ppm of copper as copper sulfate for 24 hr. Because the Sullivan & Cheng (1976) paper did not provide any information on the AAS techniques they used, we report below the details of our study using AAS methods not previously described in the malacological literature. Our analyses were done on either hemolymph and other body fluids (mainly mantle and extrapallial fluids) or snail tissue minus the shell, including the epithelial surface of the snail. These categories are henceforth referred to as either hemolymph or snail tissues in this note. Because of the open circulatory system of planorbid snails, contamination of the hemolymph with other fluids is likely, hence the designation of the sample as hemolymph and other body fluids.

Materials and Methods

Stock cultures of *Biomphalaria glabrata* were maintained as described previously (Boston et al., 1994). Ten snails with shell diameters of 12–18 mm were removed from the stock cultures and placed in a beaker containing 500 mL of 1.00 ppm of copper as copper sulfate in deionized water, prepared by dilution from a 1000 ppm stock solution containing 2.51 g of anhydrous copper sulfate in 1 L of deionized water (experimentals). An additional 10 snails of the same size were placed in beakers containing 500 mL of deionized water (controls). Five separate experiments were performed on a total of 100 snails in order to obtain sufficient samples for replicate analysis of copper in the tissues and hemolymph of experimental and control snails and statistical evaluation of the data.

Experimental and control snails were maintained for 24 hr at 22–24°C before they were analyzed. To examine survival of the experimental snails after exposure to copper, each snail was prodded with a needle to determine body withdrawal into the shell. All experimental snails survived the 1.00 ppm copper treatment for 24 hr. Use of higher copper concentrations or exposure times, i.e., 2.00 ppm for 24 hr or 1.00 ppm for 36 hr, resulted in snail mortality under our experimental conditions. Likewise, use of snails with shell diameters of 6–10 mm resulted in snail mortality in 1.00 ppm of copper after 24 hr.

The snails were rinsed several times in deionized water prior to sample preparation. The snails' shells were also blotted dry with filter paper prior to sample preparation. Hemolymph and tissue were obtained by gently crushing snails' shells with a forceps in a Petri dish. Hemolymph was pooled from 10 snails for a sample size of 100–700 μL. Each pool was centrifuged at 8000 × g for 2 min in a microcentrifuge tube to separate the hemolymph and other body fluids (supernatant) from the precipitated residual snail tissue and amoebocytes. The supernatant was removed with a Pasteur pipet and used for analysis. The pellet was discarded. To obtain body tissue, whole bodies minus shells and hemolymph from 10 experimental or control snails were pooled to produce a sample size of 0.47–1.45 g.

A 1000 ppm stock analytical copper solution was prepared by dissolving 1.00 g of pure copper metal in 10 mL of concentrated nitric acid and diluting to 1.00 L with deionized water in a volumetric flask. Standard solutions for AAS containing 0.00 (blank), 0.50, 1.00, 2.00, 5.00, and 10.00 ppm of copper were prepared by appropriate dilution of the stock solution with 1% aqueous nitric acid. Tissue and hemolymph samples were extracted by immersion in a beaker containing 10 mL of concentrated nitric acid for 24 hr at room temperature. The extracts were filtered through glass wool held in a 10 cm × 9 mm i.d. glass disposable pipet, quantitatively transferred to a 100 mL volumetric flask, and diluted to the line with deionized water. The standards and samples were analyzed for copper against the reagent blank using a Varian SpectrAA-10 computer-controlled flame atomic absorption spectrometer operated with the following parameters: copper hollow cathode (wavelength 324.8 nm), 0.5 nm slit, air/acetylene flame. Concentration readings (ppm) from the instrument computer were converted by calculation to μg/g for snail bodies and μg/mL for hemolymph.

Table 1

Copper in snail samples.

Trial number	Tissue* (μg/g)		Hemolymph** (μg/ml)	
	E	C	E	C
1	11.3	6.9	17.9	3.6
2	12.0	9.7	17.9	4.2
3	11.9	5.3	12.5	0.0
4	9.7	3.9	10.7	8.3
5	12.3	7.3	15.4	3.8
Mean	11.4	6.6	14.9	4.0
SE	0.5	1.0	1.4	1.3
P	0.007		0.0009	

E = experimental snails; C = control snails; SE = standard error of the mean; P = probability value from Student's t-test.

* Minus the shell, but including the epithelial surface of the snail.

** Includes other body fluids such as mantle and extrapallial fluids.

Results and Discussion

The results of the analyses are shown in Table 1. The concentrations of copper in the hemolymph and tissues of snails exposed to 1.00 ppm of copper for 24 hr were significantly higher than those of the control snails as determined using Student's t-test ($P < 0.05$). Information on the accumulation of copper or the exact mechanism by which snails are killed through exposure to copper are not available (see Sullivan & Cheng, 1975), but it is apparent from our study that *B. glabrata* snails can survive treatment with 1.00 ppm of copper as copper sulfate for 24 hr and accumulate significant amounts of this ion in their hemolymph and other body fluids and in tissues, including the epithelial surface of the snail. Quantitative data based on AAS for copper levels in *B. glabrata* following exposure to this metal are presented for the first time in this paper.

Literature Cited

BOSTON, C. J., L. R. LAYMAN, B. FRIED & J. SHERMA. 1994. Calcium content of planorbid snails maintained in artificial spring water on leaf lettuce with and without chalk. The Veliger 37:121–123.

SULLIVAN, J. T. & T. C. CHENG. 1975. Heavy metal toxicity to *Biomphalaria glabrata* (Mollusca: Pulmonata). Annals of the New York Academy of Sciences 226:437–444.

SULLIVAN, J. T. & T. C. CHENG. 1976. Comparative mortality studies on *Biomphalaria glabrata* (Mollusca: Pulmonata) exposed to copper internally and externally. Journal of Invertebrate Pathology 28:255–257.

New Records of the Genus *Ancula* Lovén, 1846 (Nudibranchia: Goniodorididae) on the American Pacific Coast

by

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Introduction

The genus *Ancula* Lovén, 1846, is composed of species with a smooth body, a small frontal velum, rhinophores with two anterior digitiform appendages, and gills arranged in a semicircle around the anus, with one pair of elongate extrabranchial appendages.

The armature of the labial disc consists of rows of hooks, the radula is narrow, with the formula (1.1.0.1.1) or (1.1.1.1.1), and the penis is armed with small hooks.

Two species of the genus *Ancula* Lovén, 1846, are known from the Pacific Coast of North America—*Ancula pacifica* MacFarland, 1905, in Monterey Bay and *Ancula lentiginosa* Farmer in Farmer & Sloan, 1964, in Los Angeles. In the Atlantic Ocean, there are three other species: *Ancula gibbosa* Risso, 1818 (synonym *A. cristata* Alder, 1841), which is distributed on both sides of the North Atlantic Ocean, from the Arctic to Massachusetts in America, and the Mediterranean Sea in Europe, *Ancula fuegiensis* Odhner, 1926, in Tierra del Fuego of the South Atlantic Coast, and *Ancula evelinae* Marcus, 1961, in Beaufort, North Carolina.

This paper presents new data about the geographic distribution of two species of the genus *Ancula* in the Pacific Ocean and some aspects of their anatomy. The color pattern of *Ancula fuegiensis* is described for the first time.

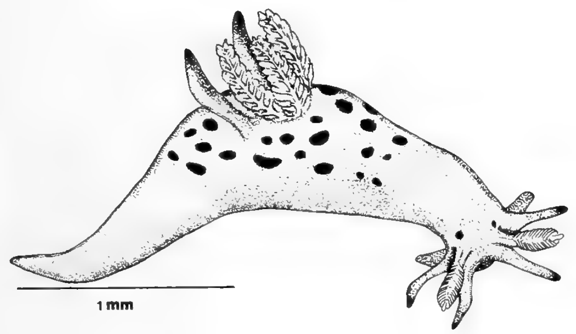
Materials and Methods

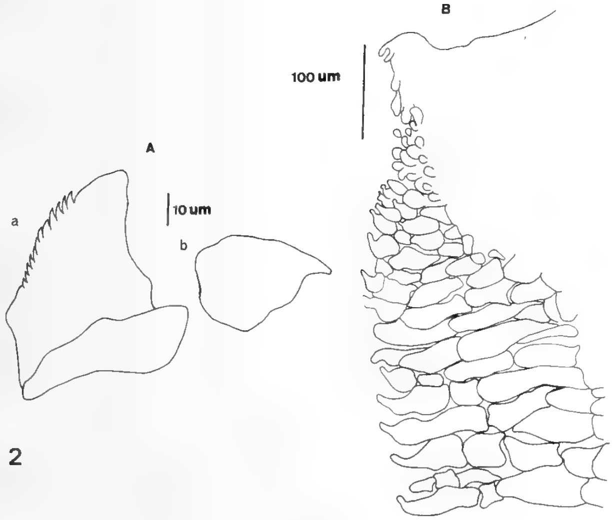
The specimens of *Ancula lentiginosa* were collected under rocks with bryozoans and hydrozoans in the intertidal zone.

The specimen of *Ancula fuegiensis* was collected by means of scuba, in the sheltered subtidal zone at 3 m depth, on acrylic plates with bryozoans and hydrozoans.

Both species were studied only externally owing to their small size. The mandible and radula were removed, cleared in Sosa, observed with a light microscope (Nikon), and drawn with camera lucida.

The studied material was deposited in two museums, Museo Nacional de Historia Natural de Santiago de Chile (MNHN) and Museo Nacional de Ciencias Naturales de Madrid, Spain (MNCN).





Explanation of Figures 1 and 2

Figures 1 and 2. *Ancula fuegiensis.* Figure 1. Lateral view of one specimen (MNHN 201620). Figure 2. A, View of radular teeth; a, lateral tooth; b, marginal tooth; B, armature of the labial disc (MNHN 201620).

Systematics and Descriptions

Suborder Doridacea Odhner, 1934

Family Goniodorididae H & A. Adams, 1859

Genus *Ancula* Lovén, 1846

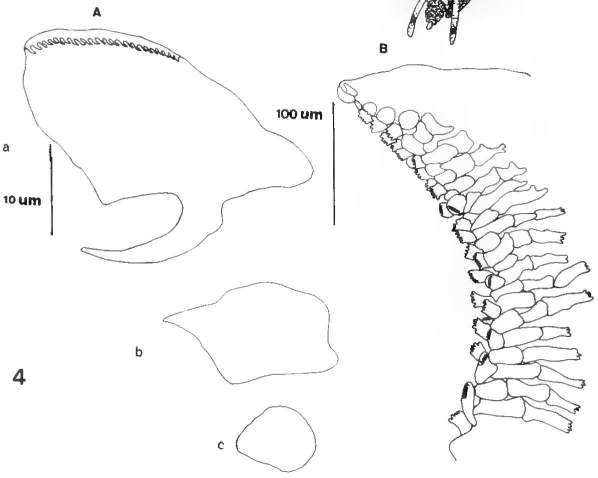
Type species. *Ancula cristata* (*Polycera* Alder, 1841) by monotypy.

Ancula fuegiensis Odhner, 1926

(Figures 1, 2)

Ancula fuegiensis: Odhner, 1926: 45–46, pl. I, figs. 20, 21.

Distribution: Ushuaia (type locality), Tierra del Fuego (55°18′S, 68°33′W) Argentina, collected between 22 and 27 m.



Explanation of Figures 3 and 4

Figures 3 and 4. *Ancula lentiginosa.* Figure 3. Lateral view of one specimen (MNCN 15.05-20.501). Figure 4. A, View of radular teeth; a, lateral tooth; b, marginal tooth; c, central plate; B, armature of the labial disc (MNCN 15.05-20.501).

Material examined: Punta El Lacho, Las Cruces (33°59′S, 71°20′W) Chile. 1 specimen collected 11 January 1992, M. A. Fischer coll. (MNHN, 201620).

Description: Body elongate and smooth. Size is 9 mm in length alive and 3 mm fixed. Ground color white, center of dorsum covered with reddish-brown dots.

Rhinophores pale yellow, with 12 slender lamellae (Figure 1). There are three bipinnate gills.

Radular length 0.53 mm, its formula is 24 (1.1.0.1.1). Lateral tooth hook-shaped, with 11 to 19 denticles (Figure 2A, a); marginal tooth rectangular, slightly flattened (Figure 2A, b). Armature of labial disc has rows of three or four elongate, rectangular plates, joined in compact form. Masticatory plate terminates in rounded end, which is slightly curved and lacks denticles (Figure 2B).

Ancula lentiginosa Farmer in Farmer & Sloan, 1964

(Figures 3, 4)

Ancula lentiginosa: Farmer in Farmer & Sloan, 1964: 148–150, pl. 18, figs. 1, 2, text figs. 1, 2; Lance, 1966:78; Sphon & Lance, 1968:76; Roller & Long, 1969:425;

Keen, 1971:829; Abbott, 1974:364; Nybakken, 1978: 135; Jaeckle, 1981:240; McDonald, 1983:143–144, fig. 44a, b, text fig. 128.

Previous known distribution: Bahía de los Angeles, Gulf of California to Marin County, California (Behrens, 1991).

Material examined: Islote Mosquera, Islas Galápagos (0°30′S, 90°15′W) Ecuador. 11 specimens collected 29 April 1994, J.A. Ortea coll. (MNCN 15.05–20.501).

Description: Body 2 to 3.7 mm. General ground color hyaline yellow, with small brown dots distributed in varying densities. Areas of body without color around rhinophores, gills, and center of lateral zone of flanks (Figure 3).

Rhinophores have long basal stem and four thick lamellae. There are three bipinnate gills. Between extrabranchial process and tail, one conspicuous dorsal keel is extended. Radular length 0.51 mm, its formula is 32 (1.1.0.1.1), lateral tooth has 28 denticles (Figure 4A, a), marginal tooth rectangular, (Figure 4A, b) in central zone there is a flat plate (Figure 4A, c). Armature of labial disc shows imbricate plates, with one to four elongated denticles and 19 rows (Figure 4B).

Discussion

Odhner (1926) described the species *Ancula fuegiensis* based on a preserved single 3 mm specimen. In this work, we present the second record of this species and the color pattern of a living specimen for the first time. The specimens are very similar, exhibiting small differences in radular features. In the Odhner specimen, the radula is 1.2 mm long [its formula is 34 (1.1.0.1.1)], with 20 denticles on the lateral tooth, whereas in our specimen, it is 0.53 mm long and its formula is 24 (1.1.0.1.1), with 11–19 denticles in the lateral tooth.

The record of our specimen extends the known geographic distribution from Ushuaia, Argentina, (Atlantic Ocean) to the central coasts of Chile (Pacific Ocean).

On the other hand, *Ancula lentiginosa* was described with tripinnate gills (Farmer & Sloan, 1964; Abbott, 1974; McDonald, 1983), whereas our specimens have bipinnate gills.

Moreover, one conspicuous keel after the extrabranchial process, the presence of a central plate in the radula, and the number and disposition of armature lip plates are features not described previously.

The known geographic distribution of *Ancula lentiginosa* is extended from the California and Mexican Pacific coasts to the Islas Galápagos.

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We would like to thank Prof. Dr. Juan Carlos Cancino of the Pontificia Universidad Católica de Chile for letting us collect specimens in the area of the marine station at Punta El Lacho. Also, we are grateful to Dr. Terrence Gosliner for his critical review of the manuscript, and Dr. Bernard Métivièr for sending us information from the Muséum National d'Histoire Naturelle de Paris. Finally, Dr. Lucas Cervera and Lic. Ángel Valdés are acknowledged for their critical comments.

Literature Cited

ABBOTT, R. T. 1974. American Seashells. 2nd ed. Van Nostrand Reinhold: New York. 633 pp., 24 pls.

BEHRENS, D. 1991. Pacific Coast Nudibranchs. A Guide to the Opisthobranchs Alaska to Baja California. Sea Challengers: Monterey, California. 107 pp.

FARMER, W. & A. J. SLOAN. 1964. A new opisthobranch mollusk from La Jolla, California. The Veliger 6(3):148–150.

JAECKLE, W. 1981. New distributional records for two California Nudibranchs. The Veliger 23:240.

KEEN, A. 1971. Sea Shells of Tropical West America. 2nd ed. Standford University Press: Stanford, California. xiv + 1066 pp.

LANCE, J. 1966. New distributional records of some northeastern Pacific Opistobranchiata with descriptions of two new species. The Veliger, 9:69–81.

McDONALD, G. 1983. A review of the nudibranchs of the California coast. Malacologia 24(1–2):114–276.

NYBAKKEN, J. 1978. Abundance, diversity and temporal variability in a California intertidal nudibranchs assemblage. Marine Biology 45:129–146.

ODHNER, N. H. 1926. Die Opisthobranchien in Further Zoological Results of the Swedish Antartic Expedition 1901–1903. 2:1–100, pls. 1–3.

ROLLER, R. A. & S. J. LONG, 1969. An annotated list of opisthobranchs from San Luis Obispo County, California. The Veliger 11(4):424–430.

SPHON, G. & J. LANCE, 1968. Annotated checklist of the nudibranchs and their allies from Santa Barbara County, California. Proocedings of the California Academy of Sciences, ser. 4, 36:73–84.

New Records of Two Uncommon Sacoglossans (Gastropoda: Opisthobranchia) from the Coasts of the Iberian Peninsula

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Introduction

Four specimens of two uncommon sacoglossan species, *Elysia gordanae* Thompson and Jaklin, 1988, and *Ercolania lozanoi* Ortea, 1981, were collected from several samples along the coasts of the southwestern Iberian Peninsula, during the development of the project "Fauna Ibérica II."

Results and Remarks

Elysia gordanae Thompson and Jaklin, 1988

Two specimens, 8.5 and 8.0 mm in length, were collected in the intertidal zone at Caños de Meca, Spain (southwestern Iberian Peninsula; 36°11′N, 06°01′W) (February, 1990). An additional third specimen, 14 mm in length, was collected on the green algae *Derbesia* sp., also in the intertidal zone at Playa de Santa Maria del Mar, Spain (southwestern Iberian Peninsula, 36°31′N, 06°17′W) (May, 1995). The specimens were deposited at the Laboratorio de Biología Marina of the University of Sevilla. The head and the foot are rounded anteriorly. The rhinophores are inrolled, straight, and relatively short. The dorsal vessels are inconspicuous. The anus is not situated at the end of a papilla. The edge of the parapodia is characterized by the presence of eight to thirteen opaque white protuberances (Figure 1). The 8.5 mm specimen was teratological, as it had partially fused parapodia. The ground color is greenish. A pinkish-white coloration, similar to that which covers the edge of the parapodia, covers the head, rhinophores, and the mid-dorsal region. A small amount of sky-blue pigmentation is scattered on the sides of the head and on the parapodial surface (Figure 1). The radular formula of the smaller specimen was 12 × 0.1.0. Moreover, five discarded preradular teeth were observed in the ascus. The radular teeth have minute, but conspicuous, denticles all around the edge (Figures 2A, B, 3A). An egg mass was laid in the laboratory, and two more were collected close to the larger specimen. The most remarkable feature is the possession of orange extracapsular yolk.

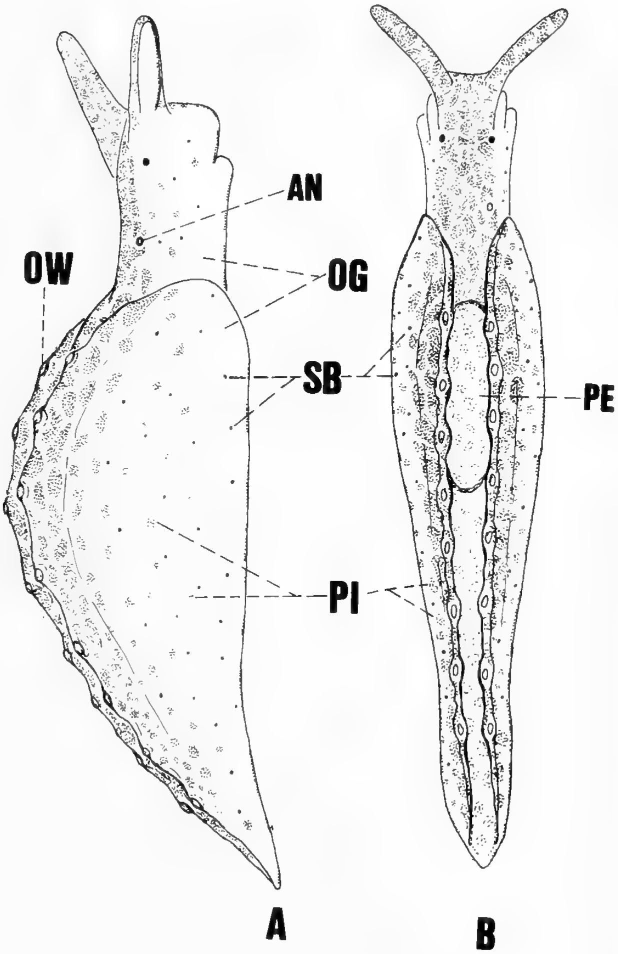

Figure 1

Elysia gordanae. General view of one specimen: lateral (A) and dorsal (B). Length 8.0 mm. AN, anus; OG, olive greenish; OW, opaque white; PE, pericardium; PI, pinkish; SB, sky-blue.

Discussion: *E. gordanae* has been recorded exclusively on the Slovenian coasts (ex-Yugoslavia) (Thompson & Jaklin, 1988) and on the Mediterranean coast of the Iberian Peninsula (Marín & Ros, 1988; García-Raso et al., 1992). Our specimens constitute the first record from the Atlantic Ocean and the westernmost record of this species.

Ercolania lozanoi Ortea, 1981

One specimen, 4.5 mm in length, was collected on the green alga, *Valonia utricularis* (Roth) C. Agardh at the

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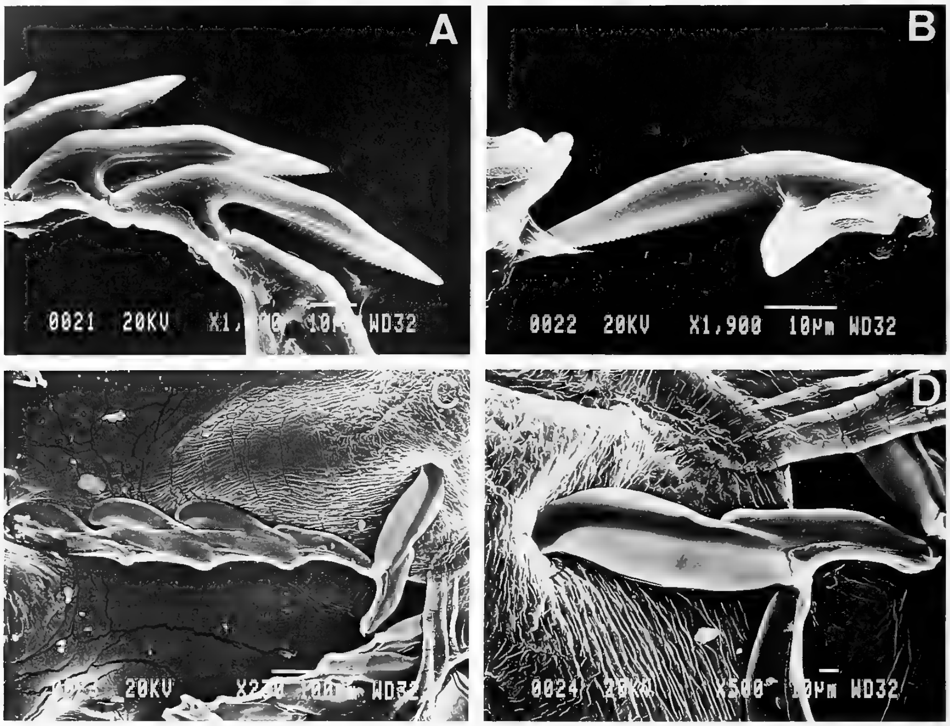

Figure 2

Detail of the radular teeth of *Elysia gordanae* (A, B) and *Ercolania lozanoi* (C, D) from the SEM.

intertidal zone at Caños de Meca (February, 1990). The specimen was deposited at the Laboratorio de Biología Marina of the University of Sevilla. The rhinophores were long, cylindrical, and somewhat widened at their base. The foot was notched and slightly bilobed. The cerata were distributed almost symmetrically, with 25 on the right side and 24 on the left side. The anal papilla was prominent and located on the pericardium (Figure 4A). The ground color of the body is yellowish white. A large, dark, violaceous black spot is present between the rhinophores. It continues on both sides of the head to shape into the midlateral zone of the animal. Both extensions of the pigment are interrupted at the level of the genital papilla. There are also two dorsal fringes of this color running from the pericardium to the posterior region of the body where the pigment bands join. The back also has two opaque white fringes, joined at the posterior region of the specimen, that continue to both sides of the anal papilla (Figure 4A). The elongate, globular cerata are olive green. At a greater magnification, the internal ochre green color of the digestive gland branch and its ramifications can be seen, as well as a large number of translucent granules (opaque white at the cerata apex) all around the ceratal surface (Figure 4C). The radular formula was 9 × 0.1.0 (excluding the discarded teeth of the ascus). The radular teeth have a smooth edge (Figures 2C, D, 3B). Data on the reproductive system were provided by Fernández-Ovies et al. (1984).

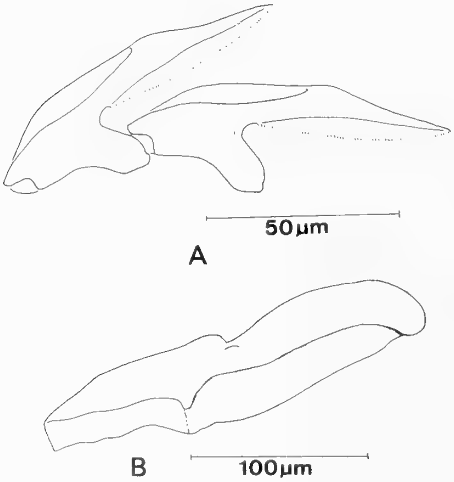

Figure 3

Detail of the radular teeth of *Elysia gordanae* (A) and *Ercolania lozanoi* (B) with camera lucida.

Discussion: Recently, K. Jensen (personal communication) has stated that she considers it possible that *E. lozanoi* is simply a color variation of *E. funerea* (Costa, 1867). According to her, this may be one of the cases where

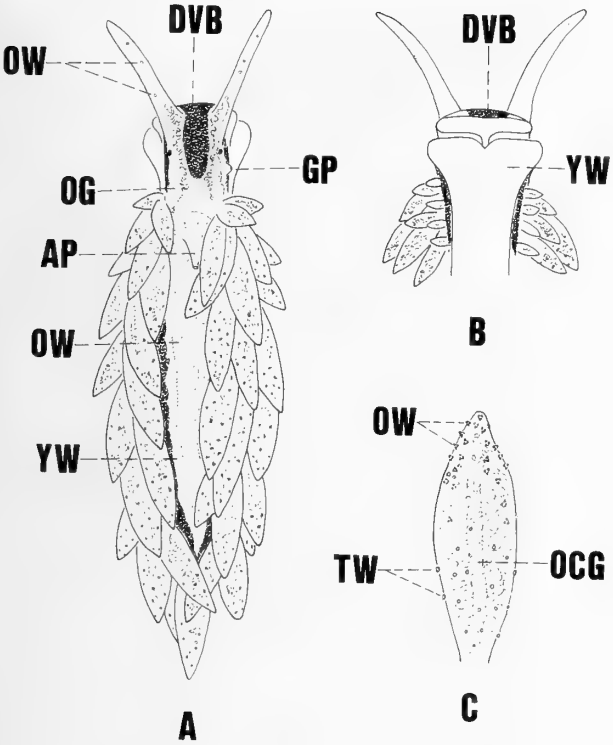

Figure 4

Ercolania lozanoi. A. Dorsal view of specimen. B. Ventral view of the anterior region. C. Detail of one ceras. Length 4.5 mm. AP, anal papilla; DVB, dark violaceous black; GP, genital papilla; OCG, ochre green; OG, olive green; OW, opaque white; TW, translucent white; YW, yellowish white.

molecular biology could prove useful. However, we agree with Ortea (1981) that the body and ceratal coloration of *E. lozanoi* is sufficiently different from *E. funerea* [= *E. viridis* (Costa, 1866)]. Moreover, these color differences were consistently observed when comparing Canarian and Iberian specimens with those attributed to *E. funerea* (as *E. viridis*) by García-Gómez (1987) from the Algeciras Bay (Strait of Gibraltar). We prefer to retain *E. lozanoi* as a separate species until additional material can be examined.

To date, *E. lozanoi* has been recorded exclusively from the Canary Islands (Ortea, 1981; Fernández-Ovies et al., op. cit.). Our specimen constitutes the first record of this species from the Iberian Peninsula and European mainland and the northernmost record of this species.

Acknowledgments

We thank Dr. Kathe Jensen for her valuable comments and Dr. Terrence M. Gosliner for improving the manuscript. This paper has been supported by the project "Fauna Ibérica" DGICYT PB89-0081.

Literature Cited

FERNANDEZ-OVIES, C. L., J. A. ORTEA & J. M. PEREZ-SANCHEZ. 1984. Nuevos datos anatómicos y biológicos de *Ercolania lozanoi* Ortea, 1981 (Opisthobranchia: Ascoglossa). Cuadernos del Crinas 6:39–44.

GARCIA-GOMEZ, J. C. 1987. Adiciones a la fauna de opistobranquios del estrecho de Gibraltar (Sur de España). I. Iberus 7(2):197–209.

GARCIA-RASO, J. E., A. A. LUQUE, J. TEMPLADO, C. SALAS, E. HERGUETA, D. MORENO & M. CALVO. 1992. Fauna y flora marinas del parque natural de cabo de Gata-Nijar, Madrid. 288 pp.

MARIN, A. & J. ROS. 1988. Los sacoglosos (Mollusca, Opisthobranchia) del sudeste ibérico. Catálogo de las especies y presencia de cloroplastos algales en las mismas. Iberus 8(1): 25–49.

ORTEA, J. A. 1981. Moluscos opistobranquios de las Islas Canarias. Primera parte: Ascoglosos. Boletín del Instituto Español de Oceanografía 6:180–199.

THOMPSON, T. E. & A. JAKLIN. 1988. Eastern Mediterranean Opisthobranchia: Elysiidae (Sacoglossa = Ascoglossa). Journal of Molluscan Studies 54:59–69.

Preference of Adults of the Dorid Nudibranchs *Archidoris montereyensis* (Cooper, 1862), *Diaulula sandiegensis* (Cooper, 1862), and *Triopha catalinae* (Cooper, 1863) for Shaded over Lighted Conditions

by

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Biermann et al. (1992) discovered higher mortality rates among embryos of the dorid nudibranch *Archidoris montereyensis* (Cooper, 1862) in egg masses exposed to the light than in the shade. This conclusion suggests that the location of egg mass deposition may have profound effects on populations and life histories of at least one kind of dorid nudibranch.

If light-dependent differential survival is a long-term selective force, then adults may respond to this pressure by showing preference for shaded areas over unshaded ones. This idea led us to the following question: Do adult *Archidoris montereyensis* and other dorid nudibranchs prefer shaded conditions over unshaded ones? We tested the null hypothesis that adult dorid nudibranchs show no preference for either shaded or unshaded conditions. We here report on a laboratory experiment testing that null hypothesis.

In January 1995, we collected three species of dorid nudibranchs from the floating dock and pier pilings at the Friday Harbor Laboratories, San Juan Island, Washington, USA. *Archidoris montereyensis* and *Diaulula sandiegensis* (Cooper, 1862) were collected primarily from tires attached to the laboratory's floating dock, and *Triopha*

Table 1

Preference for shaded versus unshaded conditions by adults of three species of dorid nudibranchs based on the number of test specimens in shaded conditions at the end of 60-minute test runs.

Species	n	No. in shaded end of tank	χ^2 value	Level of significance
A. montereyensis	12	11	8.34	$P < 0.005$
D. sandiegensis	5	5	5.00	$P < 0.05$
T. catalinae	18	15	8.00	$P < 0.005$

Table 2

Effect of drain location on the final location of test specimens in the experimental apparatus for each species tested.

Species	n	No. in drain end of tank	χ^2 value	Level of significance
A. montereyensis	12	5	0.33	$P > 0.50$
D. sandiegensis	5	2	0.20	$P > 0.50$
T. catalinae	18	10	0.22	$P > 0.50$

catalinae (Cooper, 1863) were collected from pilings supporting the laboratory's pier. All specimens were kept in a holding tank with running seawater, in the laboratory, until they were tested, usually within a day or two. We know that our *A. montereyensis* specimens were adults because we observed several pairs of them copulating in the holding tank. We have no such supporting observations for the other species, but we believe that our *D. sandiegensis* and *T. catalinae* specimens were also most likely adults due to their size.

The apparatus used to test for light versus shade preferences comprised an opaque seawater table approximately 60 cm wide by 130 cm long, with a drain at one end and a tygon tube supplying water to the center of the table. One end of the seawater table was covered with an opaque black plastic sheet so that half of the tank received light from the overhead fluorescent lights of the laboratory, and the other half of the tank was shaded. Windows of the laboratory were covered during testing so that the only light entering the seawater table was from overhead lights.

An experimental run began when we placed three individuals of the same species in the middle of the experimental seawater table. The nudibranchs were oriented so that the longitudinal axis of each specimen coincided with the line where the shaded and unshaded areas of the tank met. Thus, at the beginning of a run, one side of each nudibranch was in the shade and the other side was in the light. In addition, we randomized the anterior-posterior orientation of each specimen along that line in order to eliminate possible confounding effects of genetic predispositions for turning to the left or right. A run ended 60 minutes later when the location of each individual was recorded. We did four runs of three individuals each for *Archidoris montereyensis,* one run of three individuals and one run of two individuals for *Diaulula sandiegensis,* and six runs of three individuals for *Triopha catalinae.*

The seawater table was drained and cleaned with a rubber squeegee after every run in order to remove mucous trails and any residual scents left by test specimens from prior runs. The black plastic cover was then moved to the opposite end of the tank so that the shaded and unshaded halves of the tank alternated from one run to the next. This was done in order to minimize possible effects of water flow due to the location of the drain at one end of the tank.

We used the chi-square analysis to test for differences between the number of individuals that moved to the shaded end of the tank versus the unshaded end, for each species. We also tested for water-flow effects on slug movement via chi-square analysis by comparing the number of individuals that moved to the drain-end of the tank to the number moving to the non-drain end.

Significantly more individuals of each of the three species tested moved to the shaded end of the tank than to the unshaded end: 11 of 12 (91.7%) *Archidoris montereyensis,* 5 of 5 (100%) *Diaulula sandiegensis,* and 15 of 18 (83.3%) *Triopha catalinae* (Table 1). These results led us to reject our null hypothesis, that equal numbers of animals would move to the light and dark areas, and to accept an alternative hypothesis—that the nudibranch species tested prefer shaded conditions over unshaded conditions. The effect of drain location on final location of test specimens was not significant for any of the three species (Table 2). This is, to our knowledge, the first time a preference for shaded conditions has been reported for adult dorid nudibranchs.

Explaining this preference remains problematic, especially since the species tested may move into sunlit areas of intertidal pools from time to time. However, the findings of Biermann et al. (1992) suggest a possible explanation for the tendency of dorid nudibranchs to move into shaded areas—that for at least *Archidoris montereyensis,* there appears to be selection against progeny of individuals that deposit egg masses in unshaded areas compared to those that do so in shaded areas. This differential survivorship may have an evolutionary effect on the reproductive ecology of *A. montereyensis* by favoring individuals that stay in darker areas and deposit their egg masses there. Another possible explanation could be related to the feeding ecology of some dorid nudibranchs. For example, *A. montereyensis* and *Diaulula sandiegensis* prey on sponges, primarily *Halichondria* spp. and *Haliclona* spp. (Bloom, 1976; Elvin, 1976). *Haliclona* spp. prefer shaded microhabitats (Bakus & Abbott, 1980), and nudibranchs that feed on them may consequently move into darker areas to search for sponge prey. *Triopha catalinae,* on the other hand, preys on erect bryozoans (Beeman & Williams, 1980 and references therein). There are no strong data showing that erect bryozoans, as a group, are more common in shaded areas than in unshaded ones. Therefore, a testable hypothesis for the shade preference by *T. catalinae* has yet to be developed.

Literature Cited

BAKUS, G. J. & D. P. ABBOTT. 1980. Porifera: the sponges. Pp. 21–39 in R. H. Morris, D. P. Abbott & E. C. Haderlie (eds), Intertidal Invertebrates of California. Stanford University Press: Stanford, California.

BEEMAN, R. D. & G. C. WILLIAMS. 1980. Opisthobranchia and Pulmonata: the sea slugs and allies. Pp. 308–354 in R. H. Morris, D. P. Abbott & E. C. Haderlie (eds), Intertidal Invertebrates of California. Stanford University Press: Stanford, California.

BIERMANN, C. H., G. O. SCHINNER & R. R. STRATHMANN. 1992. Influence of solar radiation, microalgal fouling, and current on deposition site and survival of embryos of a dorid nudibranch gastropod. Marine Ecology Progress Series 86: 205–215.

BLOOM, S. A. 1976. Morphological correlations between dorid nudibranch predators and their sponge prey. The Veliger 18:289–301.

ELVIN, D. W. 1976. Feeding of a dorid nudibranch, *Diaulula sandiegensis,* on the sponge *Haliclona permollis.* The Veliger 19:194–196.

International Commission on Zoological Nomenclature

The following applications were published on 30 June 1995 in Volume 52, Part 2 of the *Bulletin of Zoological Nomenclature.* Comment or advice on these application is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Case 2903—*Tropidoptera* Ancey, 1889 (Mollusca, Gastropoda): proposed designation of *Endodonta wesleyi* Sykes, 1896 as the type species.

Case 2946—PLUTONIINAE Bollman, 1893 (Arthropoda, Chilopoda) and PLUTONIINAE Cockerell, 1893 (Mollusca, Gastropoda): proposed removal of homonymy.

The following Opinions concerning mollusks were published on 30 June 1995 in Volume 52, Part 2 of the *Bulletin of Zoological Nomenclature.* Copies of these Opinions can be obtained free of charge from the Executive Secretary at the address given above.

Opinion 1805—*Doris grandiflora* Rapp, 1827 (currently *Dendrodoris grandiflora*) and *Doridopsis guttata* Odhner, 1917 (currently *Dendrodoris guttata*) (Mollusca, Gastropoda): specific names conserved.

Opinion 1806—*Ammonites nodosus* (currently *Ceratites nodosus*; Cephalopoda, Ammonoidea): specific name attributed to Schlotheim, 1813, and a lectotype designated.

MOLLUSCS 97

Symposium on the Mollusks of the Indo-West Pacific and Australasian Region

Rottnest Island, Western Australia
February 1–4, 1997

Organized by The Malacological Society of Australasia Ltd.

The huge Indo-West Pacific and Australasian region has a tremendous diversity of mollusks in all environments—marine, freshwater, and terrestrial. This will be the first meeting to bring together malacologists and other interested scientists working on the mollusks of the region.

The symposium will be held at the Rottnest Environmental Education Centre at Rottnest Island, off the coast of Perth, Western Australia from February 1–4, 1997.

The first two days of the conference, Saturday, February 1st and Sunday, February 2nd, will be devoted to scientific sessions, as will Tuesday, February 4th. Excursions will be held on Monday, February 3rd.

Rottnest Island is on the central coast of Western Australia, where there is a mixture of temperate, tropical, and Western Australian endemic mollusks. An island tour with the opportunity to explore the local rocky shore habitats will be organized for Monday, February 3rd.

The Malacological Society of Australasia expects to make limited travel support available to some student members living in Australasia who present a paper or poster.

Three symposia are planned:

- Mollusks of environmental or economic importance
- Evolutionary studies of mollusks
- Contributed paper sessions

Posters are welcomed as an alternative to papers. The symposium is open to papers and posters on all aspects of Indo-West Pacific and Australasian mollusks, whether marine, freshwater, or terrestrial.

Participants are encouraged, but not required, to publish the papers presented in *Molluscan Research,* the journal of The Malacological Society of Australasia. Papers submitted to *Molluscan Research* will be subject to the normal editorial review process.

Post-Conference Tours

Many of the delegates will be visiting Western Australia for the first time. There will be a five day post-conference tour to Albany on the south coast of the state, pending sufficient interest.

To register for the mailing list for further announcements, please contact:

Dr. F. E. Wells, Western Australian Museum, 1 Francis Street, Perth WA 6000 Australia, Phone: 61 9 427 2745, Fax: 61 9 328 8686.

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BOOKS, PERIODICALS & PAMPHLETS

Life History and Biogeography: Patterns in *Conus* Oxford Biogeography Series No. 9

by Alan J. Kohn & Frank E. Perron. 1994. Clarendon Press, Oxford. 106 pp.

This book is the ninth contribution to the Oxford Biogeography Series, which began publication in 1981 with *Wallace's Line and Plate Tectonics* (Whitmore, 1981). The goal of the series has been to provide dynamic syntheses of new developments and analytical techniques that reflect on biogeographical studies. To this end, Kohn & Perron's monograph on the genus *Conus* provides a wealth of detailed information concerning reproductive characteristics and relates them to Indo-Pacific biogeographic patterns within this speciose group. The authors intend to use this taxon for testing various hypotheses concerning the relationships among reproductive parameters and biogeographic patterns throughout the vast Indo-Pacific province. The detailed, comprehensive data presented represent over 55 combined years of research by the two authors on this genus of predatory gastropods. Such extensive, species-level work is essential to explore the fine-grained nature of biogeographic history.

The book tests two main hypotheses: (1) the overall pattern of life history variation in the genus *Conus* can be interpreted in terms of differences in egg size; and (2) the key attribute, egg size, as a determinant of developmental mode and dispersal ability, also explains observed patterns of geographic distribution in the genus. By concentrating on the genus *Conus,* the authors intend to stimulate others to test their hypotheses in other marine invertebrates that exhibit similar ecological and life history characteristics. The Indo-Pacific region represents the most diverse marine faunal province in the world, and many questions concerning its biogeographic history remain problematical (Rosen, 1988). The province covers approximately one quarter of the earth's ocean surface and is two-dimensional, in contrast to most other marine provinces, which are linear, usually across latitudes. The province is also very old; theories concerning the origins of its component taxa usually incorporate some Tethyan affinity. Kohn & Perron's book belongs in this biogeographic series because it is the first to analyze present distribution patterns within the region in relation to reproductive parameters.

The authors set up tests of their hypotheses in the first three chapters. The first chapter provides an introduction to the genus and includes a description of *Conus* biology and ecology. Most readers of this review are probably familiar with the extensive work by the authors on these subjects. The second chapter describes reproductive characteristics from mating through oviposition, embryonic development, larval development and metamorphosis. This review introduces the reproductive variability and terminology while laying the foundation for proposing working hypotheses on interrelationships among various reproductive parameters. The third chapter provides the bulk of the raw data used for comparative analyses in later chapters. Here they offer species accounts for 62 Indo-Pacific taxa, giving detailed observations of such reproductive parameters as egg diameter, eggs per capsule, capsule type, capsule size, prehatching period, hatching size, minimum pelagic period, and settling size. In many instances, the authors present multiple observations for the same species from disparate locales. This information is nicely summarized in Table 1 of the Appendix. The authors also describe the methods used to generate this information.

The next two chapters explore the interrelationships of reproductive parameters and biogeographic patterns. Chapter four analyzes the relationships between reproductive and life history parameters: egg size, fecundity, hatching size, adult size, and developmental mode. The crux of their argument falls here. The authors establish that egg diameter is constant within a species regardless of adult size, and that egg size has a strong correlation with all other reproductive characteristics so that it can be used as an accurate predictor of other attributes including maternal investment, prehatching duration, size at hatching, developmental mode, and larval growth rate. Although these relationships were documented only in 11 species reared through settlement and metamorphosis (19 species for hatching size), the correlations and subsequent predictions of other parameters are extremely valuable and can be tested by further research on other species. Chapter five tests the hypothesis that geographic range is correlated with dispersal potential, again using the predictor of egg size for 82% of their taxa (51 of 62). The minimum precompetent period explains 43% of the normalized variance in geographic range area.

The book is an excellent step toward teasing out the factors involved in the historical biogeography of the Indo-Pacific. The authors are first to admit that a phylogenetic framework is desperately needed. Unfortunately, as yet no hypothesis of species-level relationships has been proposed. The realization and justification of this is awkwardly addressed: at first the authors claim that because they are only dealing with one genus they automatically hold constant all variables shared by congeners; yet in the next sentence, they argue that because the results span 62 species from a number of independent lineages, they can explore correlated patterns (p. 72). The clade *Conus* encompasses over 500 extant species and 55 million years of history; it would be surprising if there was no phylogenetic signal.

passes over 500 extant species and 55 million years of history; it would be surprising if there was no phylogenetic signal.

The authors attempt to limit the effects of common ancestry by staying within one genus, yet the amount of variation among congeners is extreme and continuous in almost all reproductive categories. In using only one genus, the authors run a greater chance of violating statistical independence within their sampled data pool. A violation of independence might significantly reduce the degrees of freedom in their analyses. Additionally, this extreme variation (egg size, as an example, spans more than half the range known among all prosobranchs) would be interesting to explore within a phylogenetic framework. Such tests would help determine how much of this variation is independently derived in multiple groups (perhaps pointing to selection) and how much is shared because of common ancestry.

The authors set out to show that dispersal ability can explain biogeographic patterns, but do not set up a test that can falsify such a hypothesis. Instead they explore the correlation between dispersal potential (again estimated for 82% of their species) and geographic range area (computed from absolute area projections). Although the correlation explains up to 43% of the variance, this number might be significantly altered by incorporating the effects of oceanographic currents rather than using absolute area. Even so, one cannot always falsify dispersalist scenarios. Instead, dispersal might be what's left over as an appealing alternative after falsifying vicariance using a phylogenetic approach. Although described separately in Chapter six, information concerning species outside the Indo-Pacific province may play a significant role in understanding the biogeographical history within the region, particularly if, as seems likely, those regions contain sister-groups of clades that have diversified in the Indo-Pacific.

Obviously, a phylogenetic framework is the next step in this problem. A species-level phylogeny brings a more robust, testable framework. Nevertheless, the book appropriately focuses attention on those areas of biology that will be instrumental in unraveling the complex history of the Indo-Pacific and other faunal provinces. Such species-level investigations coupled with data on reproductive characteristics and robust phylogenies will undoubtedly elucidate many important biogeographic questions. Researchers concerned with how reproductive parameters are interrelated or with the historical biogeography of the Indo-Pacific should have Kohn & Perron's book on their shelves.

Christopher P. Meyer

Literature Cited

RÖCKEL, D., W. KORN & A. J. KOHN. In press. A Manual of Conidae, Vol. 1. Verlag Christa Hemmen: Wiesbaden.

ROSEN, B. R. 1988. Progress, problems and patterns in the biogeography of reef corals and other tropical marine organisms. Helgoländer Meeresuntersuchungen 42:269–301.

WHITMORE, T. C. (ED.). 1981. Wallace's Line and Plate Tectonics. Oxford Biogeography Series No. 1. Clarendon Press: Oxford.

Catalog of the Native Land and Freshwater Molluscs of the Hawaiian Islands

by ROBERT H. COWIE, NEAL L. EVENHUIS, and CARL C. CHRISTENSEN. 1995. Backhuys Publishers, Leiden, The Netherlands, vi + 248 pp. Price NLG 78,00, available from Backhuys Publishers, P.O. Box 321, 2300 AH Leiden, The Netherlands

Hawaiian land snails epitomize evolution by Darwinian natural selection, and they also played a seminal role in determining Darwin's conception of the role of geographic isolation in the process of new species formation. The naturalist John T. Gulick (1832–1923) was an American missionary in Hawai'i who made a huge collection of the genus *Achatinella* which is endemic to the island of O'ahu. Based on his experience with the numerous geographic variants of these Hawaiian land snails he concluded that geographic isolation is important in the origin of new species, and he corresponded with Charles Darwin on this topic. Gulick and his Hawaiian snails were largely responsible for convincing Darwin of the efficacy of isolation in producing new species, a notion that was downplayed by Darwin in the first edition of the *Origin of Species* (Lesch, 1975; Sulloway, 1979; Young, 1992). Geographic isolation has now largely become *sine qua non* in evolutionary thinking about speciation.

This catalog of Hawaiian terrestrial gastropods is a compendium of all the species-group and genus-group names that have been applied in the literature to these taxa. It is not a taxonomic revision *per se* or an identification guide or a phylogenetic analysis. This catalog contains no illustrations because the authors are using the most recent taxonomic revisions of the various groups from the literature and are not making many new taxonomic judgments themselves. Even if a previous author introduced a plethora of subspecies names for what a reasonable taxonomist today would consider intraspecific variants and polymorphic populations, the names are listed in their proper taxonomic context in this catalog. The Hawaiian land snail fauna is so diverse and taxonomically complicated that this catalog is essentially a first step for further taxonomic revision and ultimately for phylogenetic analysis. To this end it succeeds admirably.

Particular attention has been paid to the subtle details of synonyms, homonyms and unavailable names (*nomina nuda*, etc.). Type localities and type designations have been extensively documented.

The catalog consists of several sections: introductory information, the systematic catalog itself, a complete checklist of the fauna, and a substantial bibliography. There is also a thorough systematic index to all listed taxa. For example, I was able to find easily all references to *moomomiensis,* to check on how many species had been named from the region called Mo'omomi on the north shore of Moloka'i, an area I visited in 1993.

For the order of families, the authors (p. 5) chose to follow Vaught (1989)—a wholly derivative work—even while mentioning the existence of *primary* works on the classification of land mollusks, such as Tillier (1989) and Zilch (1959-60). This probably does not have much consequence for the families that Cowie, Evenhuis, and Christensen deal with, but Vaught's work contains some serious errors elsewhere regarding land snails (B. Roth, personal communication).

The authors have done a great service to malacology in the format and content of their extensive bibliography compiled by Evenhuis and Cowie. The 30 pages of this well-researched bibliographic compendium stand alone for its attention to detail in reporting the precise date of publication of taxonomic monographs issued in multiple parts, particularly those from the 19th and early 20th centuries.

A recent revival of interest over the past 20 years in correctly writing the Hawaiian language using the diacritical marks called the glottal stop and macron has appeared in some scientific and some popular publications. These grammatical subtleties are sometimes best appreciated by a "local" audience in the islands and often unappreciated by an international audience. Cowie, Evenhuis, and Christensen have chosen not to write the numerous geographic localities in the text using the diacritical marks, but rather to transliterate the names from previous publications and museum records (R. H. Cowie, personal communication) where the diacritical marks were not used. For this essentially historical catalog of Hawaiian land snail names, the decision was warranted because adding the diacritical marks could have introduced unnecessary interpretation of the identity of a particular geographic locality. Future scientific studies (of land snails or any other taxa) that do not rely heavily on transliteration of published works should use the diacritical marks; to do otherwise is a disservice to the Hawaiian language because the meanings of words change with the presence/absence of the marks (Pukui & Elbert, 1971). Realizing that the International Code of Zoological Nomenclature does not permit diacritical marks in generic names or specific epithets (and many endemic Hawaiian land snails have Hawaiian species names), the marks should nonetheless be used (correctly) whenever possible. For example, Hawai'i is correct and Hawai'ian is incorrect.

It is interesting to note that the most widely known group of Hawaiian land snails (in terms of the popular literature of Hawaiian biodiversity; see, for example, color photos in Kay, 1983, and color plate in Young, 1992), the genus *Achatinella,* contains no full species named after 1914 and no subspecies named after 1958. This is a testament to how intensively and extensively this diverse group of gastropods was collected and studied primarily in the mid- to late-19th century. Previous authors overindulged in formally naming color variants, providing a difficult historical background for any future taxonomic revision. Sadly, many species of *Achatinella,* and species of other genera, are now extinct in the islands due to habitat alteration and destruction, introduced snail predators, rats, and ants.

Discussions of Hawaiian biodiversity often make reference to the subfamily Achatinellinae (and the genus *Achatinella* in particular) because of their relatively large size and striking shell color patterns. With just over 200 species names in 12 genera, one would also get the impression that this is also the most diverse group of native terrestrial gastropods in the islands. However, the lesser-known ground-dwelling family Amastridae consists of 325 species in eight genera. Ironically, as the authors state on page 37, *Achatinella* might only consist of a dozen or so valid species, suggesting the remaining taxa could be potentially subsumed as intraspecific and polymorphic variants in a future taxonomic revision.

This catalog is a very important contribution in bringing the Hawaiian land snail fauna onto an equal phylogenetic footing with the numerous other exemplars of Hawaiian-style insular evolution, such as Hawaiian *Drosophila,* Hawaiian crickets, and Hawaiian silverswords. Both John T. Gulick and Charles R. Darwin would be proud of this new treatment of Hawaiian terrestrial gastropods.

Matthew J. James

Literature Cited

KAY, E. A. 1983. Land snails. p. 83 in R. W. Armstrong & J. A. Bier (eds.), Atlas of Hawaii, 2nd ed. University of Hawaii Press: Honolulu. 238 pp.

LESCH, J. E. 1975. The role of isolation in evolution: Georges J. Romanes and John T. Gulick. Isis 66:483–503.

PUKUI, M. K. & S. H. Elbert. 1971. Hawaiian Dictionary. University of Hawaii Press: Honolulu. xxxix + 402 pp.

SULLOWAY, F. J. 1979. Geographic isolation in Darwin's thinking: The vicissitudes of a crucial idea. Studies in the History of Biology 3:23–65.

TILLIER, S. 1989. Comparative morphology, phylogeny and classification of land snails and slugs (Gastropoda: Pulmonata: Stylomatophora). Malacologia 30 (1–2):1–303.

VAUGHT, K. C. 1989. A Classification of the Living Mollusca. American Malacologists Inc.: Melbourne, Florida. xii + 195 pp.

YOUNG, D. 1992. The Discovery of Evolution. Cambridge University Press: Cambridge, Massachusetts. 256 pp.

ZILCH, A. 1959–1960. Handbuch der Paläozoologie. Band 6 Gastropoda. Teil 2: Euthyneura. Gebrüder Borntraeger: Berlin. xii + 835 pp.

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c) Composite works:

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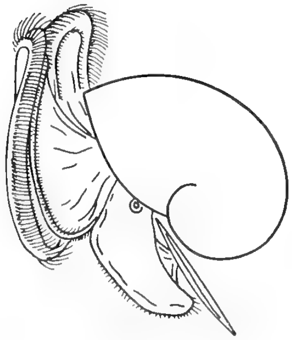

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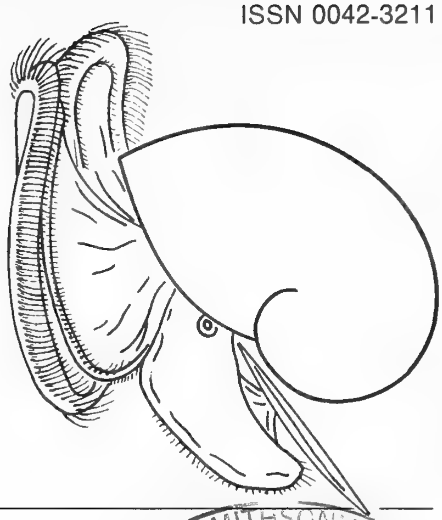

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Fine Structure of Caeca and Mantle of Arcoid and Limopsoid Bivalves (Mollusca: Pteriomorpha)

by

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Abstract. Shell pores with cellular content (caeca) are present in various molluscan groups. Up to now, the functions of the caeca are speculative, and also homology is questionable. To clarify the caeca of bivalve shell pores (tubules), the ultrastructure of the mantle of several species of arcoid and limopsoid bivalves has been investigated using microwave supported fixation and transmission electron microscopy.

In general, the outer mantle epithelium is composed of several cell types: caecal cells have processes that extend to the periostracum; supporting cells have prominent tonofilaments that attach the mantle to the shell, many mucous cells, and enigmatic microvillar pads that may have a photoreceptive function. The hemocoel is vascularized and contains cells that are typical of the bivalve hemocoel such as amoebocytes, rhogocytes (pore-cells), muscle and nerve fibers, and gliointerstitial cells. The inner mantle epithelium is quite homogeneously composed of a partly ciliated, squamous epithelium with a brush border suggesting metabolic and respiratory functions.

Structure (monocellular) and mode of development (secondary etching) contradict speculation concerning homology of bivalve caeca with those of other molluscan groups.

INTRODUCTION

The molluscan mantle is a multifunctional organ playing a crucial role in the formation of the mineralized exoskeleton (spicules, shell), in regulation of the pallial water currents, and in reception of sensory information (Beedham, 1958; Stasek & McWilliams, 1973). Whereas the ultrastructure of the molluscan and especially the bivalve mantle edge has been studied in great detail (see Table 1), the epithelium of the inner (toward the mantle cavity) and outer (toward the shell) surface of the mantle has received considerably less attention.

Shell pores (often called tubules) with cellular content (caeca) have been reported in several molluscan groups (see below), as well as in lophophorates (Brachiopoda and Bryozoa: Owen & Williams, 1969; Tavener-Smith & Williams, 1972; Reindl et al., 1995) and ostracod and cirripedian Crustacea (e.g., Klepal & Barnes, 1975; Keyser, 1980, 1981). The ultrastructure of the polyplacophoran caeca (so-called aesthetes) is well documented (see review by Eernisse & Reynolds, 1994), whereas caeca of conchiferan mollusks are poorly known. The ultrastructure of fissurellid caeca (Vetigastropoda) was described recently (Reindl & Haszprunar, 1994). Salvini-Plawen (1985) proposed homology of the conchiferan caeca with the polyplacophoran aesthetes and the mantle papillae of the aplacophoran groups. Up to now, the ultrastructure of the organic content of bivalve tubules, the caeca, has been completely unknown.

Most bivalve tubules, including those of the Arcoidea and Limopsoidea, penetrate all shell layers except the outermost organic layer, the periostracum. They are known

Table 1

EM-studies on the bivalve mantle (including LM-studies on caeca).

Group–species	Method	Subject	Reference
Arcoidea			
Arcidae (6 species)	SEM	Shell; mantle	Waller (1980)
Glycymeris glycymeris (Linnaeus, 1767)	Physiology	Whole mount	Shibata (1971)
Glycymeris pectinata (Gmelin, 1791)	LM; TEM; SEM	Shell; mantle	Waller (1980)
Pterioidea			
Pinctada margaritifera (Linnaeus 1758)	TEM; histochemistry	Whole mantle	Jabbour-Zaheb et al. (1993)
Ostreoidea			
Crassostrea virginica (Gmelin, 1791)	LM; TEM; SEM	Mantle lobes	Morrison (1993)
Unionoidea			
Amblema plicata perplicata Conrad, 1841	SEM; (LM)	Whole mantle	Petit et al. (1978)
Anodonta cygnea (Linnaeus, 1758)	TEM/SEM; X-ray; cytochemistry	Whole mantle	Machado et al. (1988)
Anodonta cygnea (glochidium)	TEM	Whole mantle	Durfort (1984, 1985)
Margaritifera margaritifera (Linnaeus, 1758) *Anodonta cygnea* (Linnaeus, 1758)	TEM; histochemistry	Mantle edge epithelium	Aleksandrova (1987)
Corbiculoidea			
Corbicula fluminea (Müller, 1774)	SEM; LM	Mantle; caeca	Araujo et al. (1994)
Musculium lacustre (Müller, 1774)	LM	Mantle; caeca	Schröder (1907)
Veneroidea			
Mercenaria mercenaria (Linnaeus, 1758)	TEM; histochemistry	Outer mantle epithelium	Neff (1972)
Ruditapes philippinarum (Adams & Reeve, 1850)	LM; TEM; SEM	Mantle edge; periostracum	Paillard & Le Pennec (1993)

to be secondarily formed, meaning that the caeca penetrate the previously formed shell (Waller, 1980). By contrast, members of the Mytilidae, Lucinidae, and Chamidae possess tubules which penetrate only the endostracum. The tubules of Carditidae and Lyonsidae extend through both the endostracum and the mesostracum. The tubules of the Spondylidae pierce all shell layers including the periostracum (Taylor et al., 1969, 1973). The mode of formation is unknown in these cases.

In order to increase our knowledge of the bivalve mantle and in particular of its caecal processes, we describe here for the first time the ultrastructure of the mantle epithelium and caeca of arcoid and limopsoid bivalves. This study should illuminate the functional questions which depend upon detailed information of this structure. In addition, the data should provide evidence in favor of or against the proposed homology with other molluscan caeca (aesthetes).

MATERIALS AND METHODS

Species Investigated

Eight representatives (several specimens each) of the order Arcoida were investigated (systematics after Vaught, 1989):

ARCOIDEA-Arcidae: *Arca noae* Linnaeus, 1758; (juveniles); *Arca tetragona* Poli, 1795; *Arca ventricosa* Lamarck, 1819; *Anadara inaequivalvis* (Bruguière, 1789); and *Barbatia barbata* (Linnaeus, 1758) (juveniles).

ARCOIDEA-Noetiidae: *Striarca lactea* (Linnaeus, 1758); and *Arcopsis adamsi* (Dall, 1886) (juveniles).

LIMOPSOIDEA-Limopsidae: *Lissarca notorcadensis* (Melvill and Standen, 1907).

Specimens of *Barbatia barbata, Arca tetragona,* and *Anadara inaequivalvis* were collected by scuba diving in shallow water (5 to 25 m) in the Mediterranean Sea off Calvi (Corsica). *Arcopsis adamsi* was collected by scuba diving (6 m deep) in the Caribbean Sea 30 miles south of Cancun on the east coast of Yucatan (Mexico). Specimens of *Arca ventricosa* were taken from an aquarium with tropical conditions, where they had been introduced with corals from the Indo-Pacific. Several *Lissarca notorcadensis* were kindly provided by Dr. Stefan Hain (Alfred-Wegener-Institut, Bremerhaven, FRG) and were taken from an aquarium maintained at −1 to +1°C, where they had been kept alive for several months. They were originally collected in the Weddell Sea (Antarctic) (Hain, 1990).

Fixation Methods

Specimens were fixed according to the procedure of Eisenman & Alfert (1982). Pieces of various areas of the shell with the attached mantle epithelium were prefixed for 10 minutes on ice in a "cocktail" of 0.05% OsO_4 and 4% glutaraldehyde in 0.2 M cacodylate-buffer. To this, 0.1 M NaCl and 0.35 M sucrose were added to adjust the osmolarity. The solution was stabilized at pH = 7.2 by adding 0.1 M HCl. The pieces were then treated with the same solution but without the OsO_4 component (main-fixative) for at least 2 hours but usually overnight, followed by three rinses in 0.2 M cacodylate buffer. For the final osmification, the pieces were treated with 1% OsO_4 in 0.3 M NaCl and 0.2 M cacodylate buffer for about 2 hours. After this procedure, the pieces were again rinsed in buffer three times. Each time, the buffer solution was diluted 1:1 with distilled water. After dehydration in an ethanol series, the pieces were embedded in low viscosity resin (Spurr, 1969).

However, this fixation protocol did not provide optimal results. In particular, the fixation chemicals did not infiltrate sufficiently into the very long and thin caecal processes within the calcified part of the shell. Therefore, for the fixation of *Arca noae* and *Striarca lactea,* we subsequently used the Eisenman & Alfert (1982) procedure of fixation with additional application of a microwave oven with electronic control of temperature (H2500 by Energy Beam Sciences, Agawam, MA, USA). The temperature control of the oven was disabled, and a digital timer controlled the process.

In a microwave oven, a high frequency tube ("magetron") converts the electrical power into microwave energy. These electromagnetic waves reach the whole volume of the oven, because they are reflected by a rotating metallic reflector and also by the lateral walls of the oven. The high frequency microwave energy modifies the tissue samples so that infiltration of the fixatives is much quicker than usual (Kok & Boon, 1992). This fact enables one to (1) minimize the fixing time which leads to a considerable reduction of artifacts and (2) to preserve satisfactorily also very thin and long subjects as is the case in the arcoid caeca. Indeed, without the support of microwaves, we failed to fix these structures sufficiently.

Processing and timing of fixation for *Arca noae*:

(1) 10 min. "cocktail" on ice and 2 × 5 sec microwave, after which the temperature of the solution was 40°C.

(2) 1 × 8 sec. microwave in the main-fixative followed by main-fixation overnight on ice.

(3) 2 × 6 sec. microwave in the OsO_4-fixative and storage in this fixative for 2 hours on ice.

Processing and timing of fixation for *Striarca lactea*:

(1) 10 min. cocktail and 2 × 2 sec microwave, after which the temperature of the solution was 40°C.

(2) main-fixation overnight on ice.

(3) 2 sec microwave in the OsO_4 fixative (40°C), after which the tissue was stored in this fixative for 2 hours on ice.

Further Treatment

After dehydration, embedding, and polymerization, the resin blocks were prepared for decalcification. For this procedure a resin block was trimmed until the calcified shell appeared at the (cutting) surface. The trimmed block was then put into 15% acetic acid for about 12 hours. After rinsing with distilled water, drying at 60°C, and reinfiltration of the etched cavity with resin, the block was trimmed again to prepare it for sectioning. This method resulted in sufficient fixation of the very long, thin, fragile caeca within the shell.

Serial semithin sections (2 μm) were cut with "ralph-knives" according to the method of Smith & Tyler (1984), and single semithin sections (0.35 μm) were cut with diamond knives. Both were subsequently stained with methylene blue (Richardson et al., 1960) for about 1 minute at 80°C.

Ultrathin sections (75 nm) were cut with a diamond knife and put on slot grids covered with a pioloform-film (a polyvinyl formaldehyde dissolved in chloroform) to increase the stability of the sections. Sections were stained for 30 minutes at 40°C with saturated uranyl acetate and for 10 minutes with lead citrate (Reynolds, 1963) at 25°C. The sections were examined and photographed with a Zeiss EM 902 transmission electron microscope.

RESULTS

Because the fine structure of the mantle epithelium and of the caeca was very similar in all the species investigated, a common description is provided. Differences between species will be mentioned where they occur.

Gross Morphology of the Mantle

The mantle of all investigated species consisted of three main layers (see Figure 1):

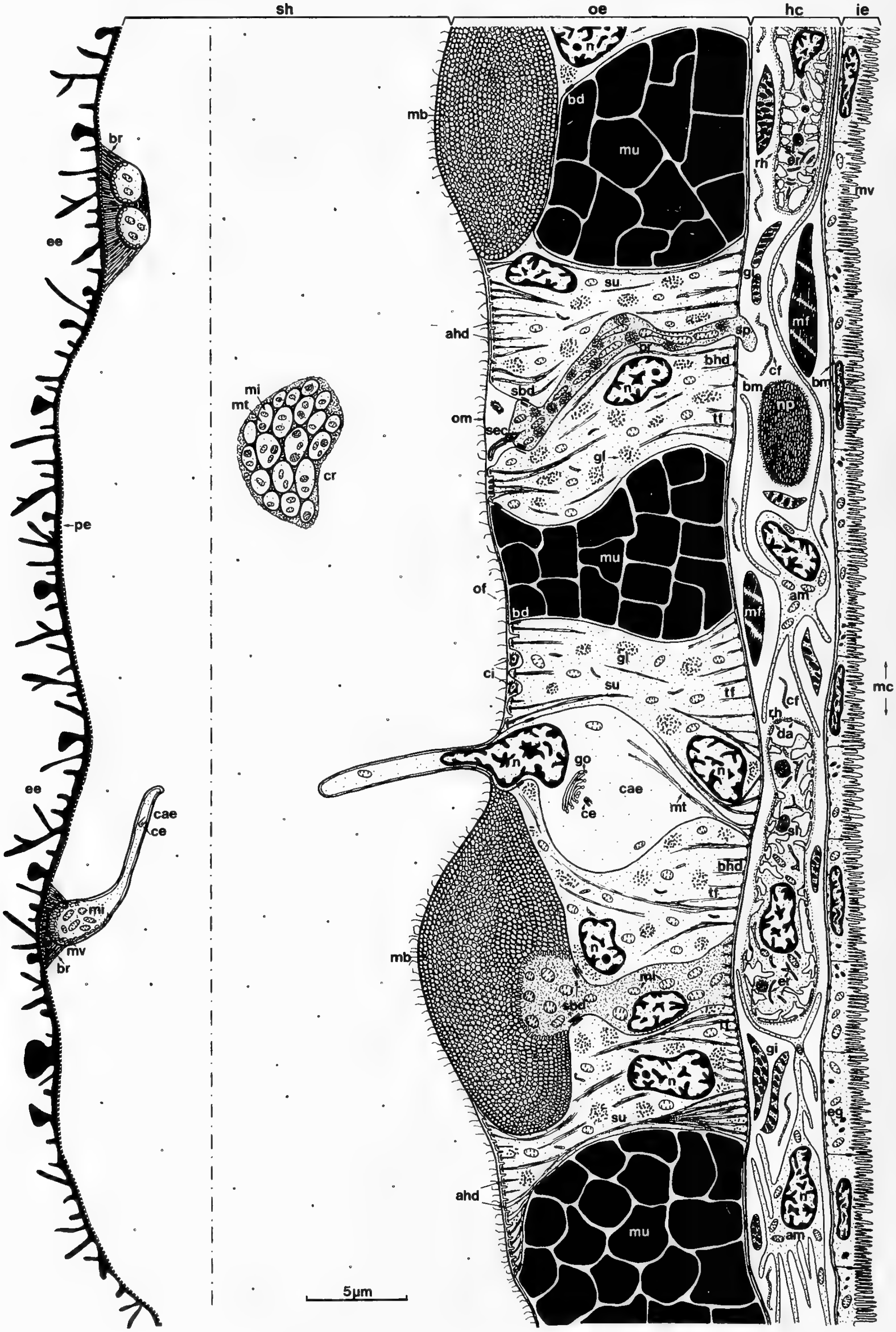
(1) The outer mantle epithelium underlay the shell. It was of variable height (8–20 μm) and was composed of several cell types (see below), including the caecal cells. Each caecal cell had an extension, the caecum, that penetrated the mineralized shell layers and contacted the periostracum.

(2) The hemocoel was bordered by the basement membranes of the outer and inner mantle epithelia and contained various cell types which did not form an epithelium.

(3) Finally, a squamous, relatively homogeneous layer formed the inner mantle epithelium, which bordered the mantle cavity.

Gross Morphology and Ultrastructure of the Caeca

Each caecum was an unbranched process of a single, specialized cell of the outer mantle epithelium. Usually caeca did not take the shortest route to the periostracum, but followed a curved course. Most proximally they grew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more or less parallel to the mantle epithelium, where some caeca contacted each other. In *Barbatia barbata,* and to a lesser extent in *Arca noae,* the caeca could contact each other and formed a reticulate construction about halfway across the shell section. At the outer third of the shell, the caeca lost contact again, and each of them connected individually with the periostracum. In all the other species investigated, the number of caeca without contacts outnumbered the reticulate constructions.

Each caecum consisted of a small, slightly extended, distal head (diameter 3–6 μm) and a very long and fragile proximal stalk (diameter 1.5–3 μm). Because the caecum extended across the entire mineralized part of the shell (its length depended upon the thickness of the shell [0.1–1 mm]), the diameter remained constant.

The whole caecum was surrounded by a thin, continuous organic matrix that was slightly thicker at the distal head of the caecum (Figure 2a). Any kind of perforation was lacking. The apical portion of the organic matrix was connected tightly to the periostracum by very fine, organic fibers called "brush" (Figure 2b). The periostracum of Arcidae usually consisted of two layers that were more (*Striarca lactea*) or less (*Arca noae*) distinct (Figure 2b). In *Lissarca notorcadensis* the periostracum consisted of more than two layers (Figure 4b).

The caecal head varied between species (Figures 2a–2d) and also within the same individual. It might contain many mitochondria and occasionally a Golgi body. Distally, a dense microvillar border was developed (see Figure 2a–c). In contrast to the head, mitochondria were only occasionally found in the caecal stalk. Instead, a distinct microtubular cytoskeleton (see Figure 2d) was present, and centrioles (diplosomes) occurred occasionally within the stalk (see Figure 1).

The cytoplasm of the cell body appeared more electronlucent than the cytoplasm of the adjacent cells (Figure 4d). The nucleus was usually located in the proximal cell body, but in some cases it extended slightly into the distal stalk (Figure 3d, e). Centrioles were present occasionally, as were Golgi bodies (Figures 1, 4d). The cells contacted the underlying basal matrix via a thin cellular process, as confirmed by means of semithin, serial sections.

Fine Structure of the Outer Mantle Epithelium

The outer mantle epithelium was composed of six (or occasionally seven) different cell types, which were interconnected via belt desmosomes: caecal cells (described above), mucous cells, supporting cells, interstitial cells and nerve processes, sensory processes, microvillar bodies, and occasionally "dark cells." All cells contacted the underlying basal matrix. The epithelium was separated from the mineralized shell by a thin layer of organic matrix and from the connective tissue by a basal membrane (for terminology see Pedersen, 1991).

Mucous or storage cells were filled with tightly packed, large (3–4 μm), globular and homogeneous granules (Figure 4d). The size and staining of the content of the mucous cells differed slightly between species.

Supporting cells had many prominent tonofilaments (Figure 3a). Many anchorlike, apical hemidesmosomes connected the cells with the organic matrix of the mineralized shell (see Figure 4a, c). In *Barbatia barbata* and the three *Arca* species studied, these hemidesmosomes were not as well defined as they were in the other species. In *Arcopsis adamsi, Arca tetragona* (Figure 3a), and *Anadara inaequivalvis,* the supporting cells had prominent apical microvilli, and each microvillus enclosed an apical hemidesmosome. The supporting cells of all other species investigated only occasionally exhibited a few, small microvilli, which always lacked hemidesmosomes. The supporting cells also contained oval mitochondria and many glycogen granules, which were concentrated in clusters of the α-type. In *Arca tetragona* and *Anadara inaequivalvis,* the glycogen formed large clusters that were situated adjacent to the organic matrix (Figure 3a).

Nerve processes and interstitial cells were occasionally present at the basis of the outer mantle epithelium (Figure 3a). Both were characterized by distinct neurosecretory vesicles of various types.

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Figure 1

Diagrammatic representation of a cross section of arcoid shell (including caeca) and mantle epithelium, based primarily on observations of *Arca noae.* External environment to the left, mantle cavity to the right, the thickness of the shell is reduced to 2% of original size.

ahd, apical hemidesmosomes; am, amoebocyte; bd, belt desmosome; bhd, basal hemidesmosomes; bm, basal matrix; br, brush; cae, caecum (cell body and process); ce, centriole; cf, collagen fibers; ci, cilia; cr, cross sections of caeca; da, diaphragmic area of rhogocyte; ecm, extracellular matrix; ee, external environment; eg, electron dense granules; er, endoplasmatic reticulum; gi, gliointerstitial cells; gl, glycogen; go, Golgi body; hc, hemocoel; ib, invaded bacteria; ie, inner mantle epithelium; mb, microvillar body; mc, mantle cavity; mf, muscle fiber; mi, mitochondria; mt, microtubules; mu, mucous cells; mt, microtubules; mv, microvillar border; n, nucleus; np, nerve process; oe, outer mantle epithelium; of, organic fibers of nacre; om, organic matrix; pe, periostracum; pr, free polyribosomes; rh, rhogocyte (pore cell); sbd, specialized belt desmosome; sec, sensory cilium; sh, mineralized part of shell; sl, secondary lysosome; sp, sensory process; su, supporting cell; tf, tonofilaments; va, vacuole.

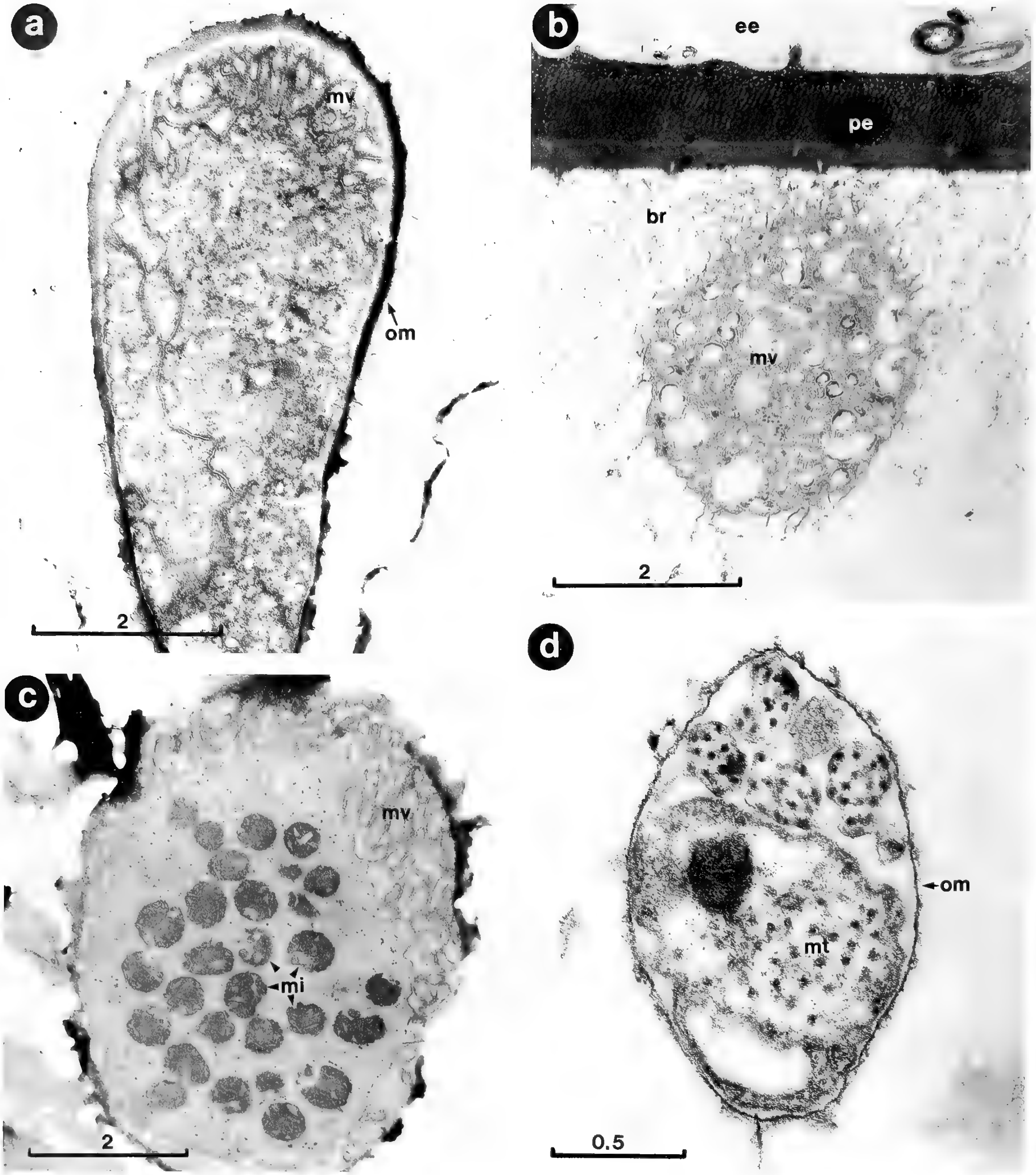

Figure 2

Ultrastructure of caecal processes (TEM). All scale bars in μm.

Figure 2a. *Barbatia barbata*: oblique section of caecal head with surrounding organic matrix (om) and microvillar border (mv).

Figure 2b. *Striarca lactea*: double-layered periostracum (pe) and most distal part of caecal head with microvillar border (mv) interconnected by organic fibers of the "brush" (br). ee, external environment.

Figure 2c. *Arca ventricosa*: caecal head with microvillar border (mv) and many mitochondria (mi).

Figure 2d. *Striarca lactea*: cross section of a caecal stalk with microtubular skeleton (mt) and is surrounded by organic matrix (om).

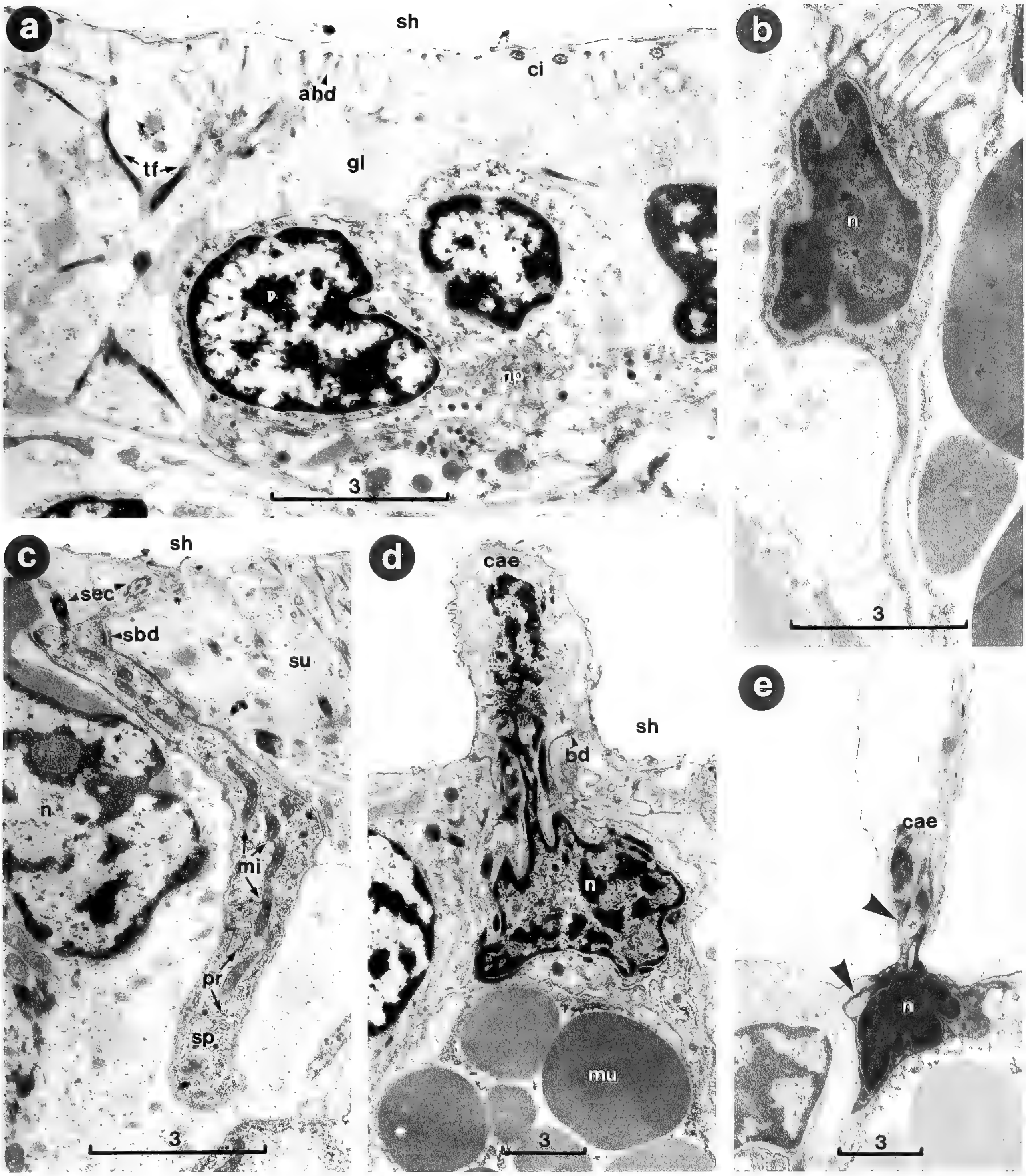

Figure 3

Ultrastructure of the outer mantle epithelium (TEM). All scale bars in μm.

Figure 3a. *Arca tetragona*: supporting cell (n, nucleus) with anchorlike hemidesmosomes (ahd), tonofilaments (tf) and glycogen deposits (gl). Note the presence of sensory cilia (ci) in the cleft below the organic matrix of the shell (sh), and the nerve process (np) and interstitial cells (i) at the bases of the outer epithelium.

Figure 3b. *Anadara inaequivalvis*: "dark cell" (n, nucleus).

Figure 3c. *Anadara inaequivalvis*: sensory process (sp) with neurotubuli, many mitochondria (mi), free polyribosomes (pr), and cilia (sec) below the shell (sh).

Figure 3d. *Barbatia barbata*: caecal cell with belt desmosomes (bd) and a nucleus (n) which extends into the caecal canal (cae) of the shell (sh).

Figure 3e. *Barbatia barbata*: caecum cell with electron-dense nucleus (n) and distinct lysosomes (arrowhead).

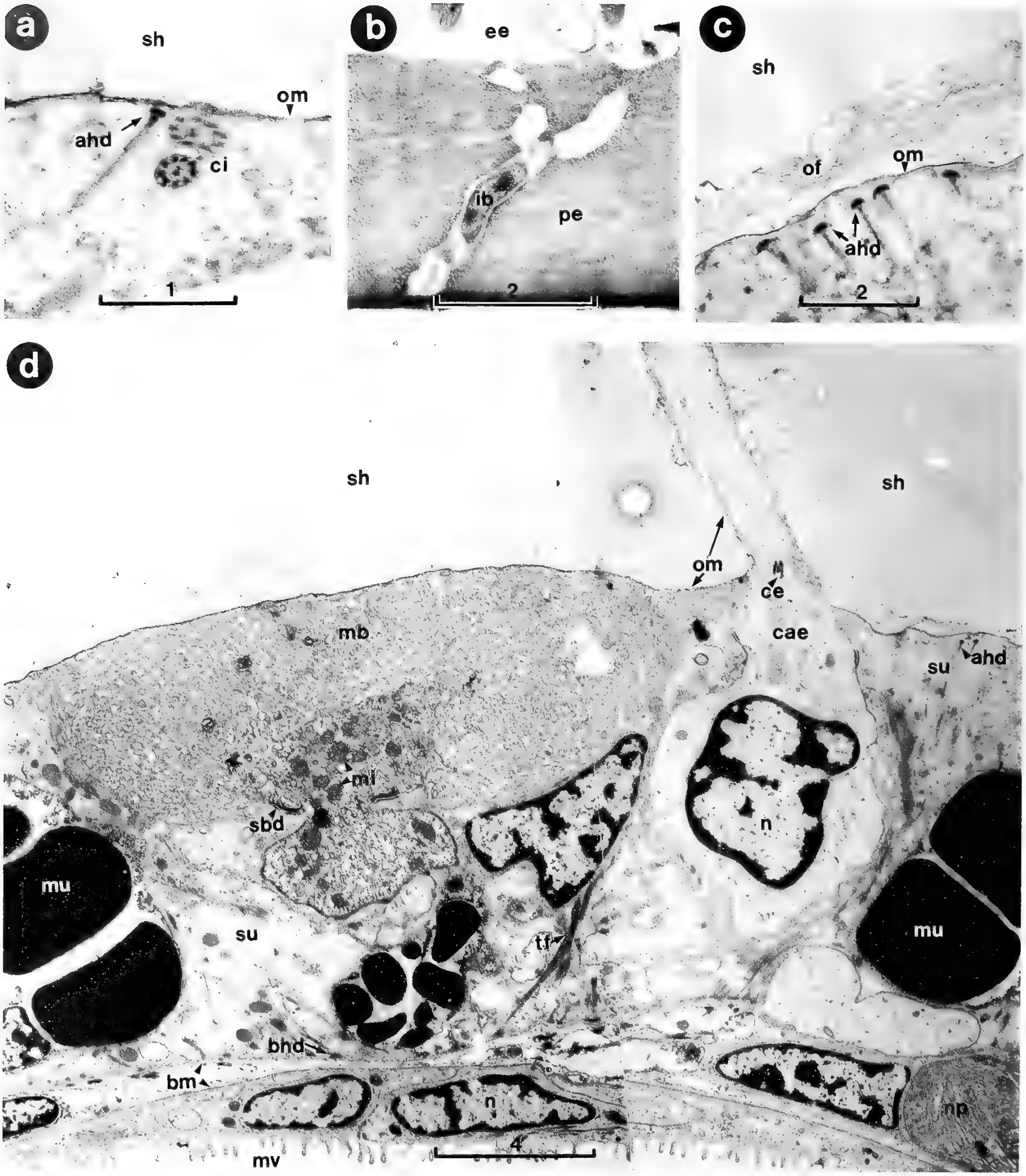

Figure 4

Ultrastructural details. All scale bars in µm.

Figure 4a. *Arca noae*: supporting cell of the outer mantle epithelium with anchorlike apical hemidesmosome (ahd) and two sensory cilia (ci) below the organic matrix (om) of the nacreous layer of the shell (sh).

Figure 4b. *Lissarca notorcadensis*: three-layered periostracum (pe) being invaded by bacteria (ib) from the external environment (ee).

Figure 4c. *Barbatia barbata*: supporting cell of the outer mantle epithelium with anchorlike hemidesmosomes (ahd) below the

Elongated sensory processes bearing cilia were also present in the outer mantle epithelium (Figure 3c). The sensory processes were characterized by many fine vesicles in their cytoplasm and by continuity with a nerve process from the underlying connective tissue. Belt desmosomes with a thickened inner portion were also characteristic of this cell type. The cilia of these cells usually occurred immediately below the organic matrix of the shell (Figures 3a, c, 4a). They laid just below the cell surface, being situated within an extracellular cleft between the surface of the mantle epithelium and the mineralized shell.

Microvillar bodies or pads were only observed in *Barbatia barbata* and *Arca noae,* where they were very common (Figures 1, 4d). These cells were easy to detect because of their prominent, apical, lens-shaped, microvillar border. Usually these cells were solitary, but sometimes two or three cells of this type were found adjacent to each other, and together they comprised a very prominent microvillar pad. These lens-shaped pads formed slight elevations into the mineralized part of the shell because the pads were slightly taller than the adjacent cells of the outer mantle epithelium. These cells also exhibited a special kind of belt desmosome, the inner side of which was strengthened by electron-dense material (Figure 4d). The oval nucleus was surrounded by many spherical pigment granules. As seen in light microscope sections, the cell contacted the basal matrix via a thin process. The microvillar bodies were usually bordered by supporting cells, sometimes also by mucous cells. There was a close positional relationship of the microvillar bodies to the caeca cells (Figures 1, 4d).

Occasionally special “dark cells,” with a very dense cytoplasm and characteristic protuberances, were detected in the outer mantle epithelium (Figure 3b). These cells had a very low nucleus-cytoplasm ratio.

Fine Structure of the Hemocoel

The connective tissue of the mantle was mainly filled by hemolymph and an extremely fine to nearly invisible extracellular matrix. Seven different cell types were found in this part of the tissue: rhogocytes, amoebocytes, elements of the gliointerstitial system, nerve processes, muscle cells, fibroblasts with collagen fibers, and phagocytes.

Rhogocytes or pore cells (see review by Haszprunar, in press) were very common (Figure 5a, c) and exhibited various shapes. These cells were characterized by a surrounding extracellular matrix and by distinct slit areas, which in cross section give the appearance of “pores.” The slits were provided with a fine diaphragm. The cell body contained a round nucleus, many vacuoles and mitochondria, an extensive endoplasmic reticulum, rarely residual bodies, and occasionally some electron-dense granules.

Amoebocytes (Figure 5b) were also very common in this layer of the mantle. The usually elongated cells were characterized by long pseudopodialike extensions which protruded in all directions. The cytoplasm appeared very homogeneous, containing many mitochondria; there were distinct areas of the cell showing tubular endoplasmic reticulum.

Elements of the gliointerstitial system (Figure 5a, b) were regularly found in the hemocoel in the vicinity of nerve processes and muscle fibers. The most characteristic elements of this system were oval granules (diameter 0.5 μm), which were filled with a very homogeneous, electron-dense material. No nucleus could be found in any of these cells.

Striated collagen fibers, which were produced by fibroblasts, were rare (Figure 5a), but small muscle fibers were common in the connective tissue (Figure 6a).

Prominent nerve processes were surrounded by a layer of extracellular matrix (Figures 4d, 5b). Occasionally also perikarya with nuclei were present in these distal nerves.

Phagocytes were detected only in *Lissarca notorcadensis.* This cell type phagocytosed invading bacteria (Figure 4d).

Fine Structure of the Inner Mantle Epithelium

The inner mantle epithelium was mainly composed of very flat, elongated cells (Figure 6a–c). These cells exhibited a prominent microvillar border, the height of which ranged from 0.4–2 μm. The epithelial cells contained oval nuclei, spherical mitochondria, and clusters of electron-dense granules. Cilia were occasionally observed between the microvilli (Figure 6b). In *Arca noae,* vacuoles were present in the epithelial cells (Figure 6c).

DISCUSSION

Caeca

Many authors have discussed the degree of penetration of shells by tubules. Taylor et al. (1969) remarked that tubules penetrate across the entire shell including the periostracum. Wise (1971) found that in the Anadarinae, a subfamily of Arcidae, the tubules penetrate all of the mineralized shell layers as well as the periostracum. However, in the species included in this study, the periostracum is

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organic matrix (om) and the organic fibers (of) of the nacreous layer of the shell (sh).

Figure 4d. *Arca noae*: cross section of whole mantle epithelium. Outer mantle epithelium with various cell types, hemocoel reduced, inner mantle epithelium with microvillar border. Abbreviations: ahd, apical hemidesmosomes; bhd, basal hemidesmosomes; bm, basement membrane; cae, caecum; ce, centriole; mb, microvillar body; mi, mitochondria; mu, mucous cells; n, nucleus; np, nerve process; om, organic matrix; sbd, specialized belt desmosome; sh, mineralized part of shell; su, supporting cell; tf, tonofilaments.

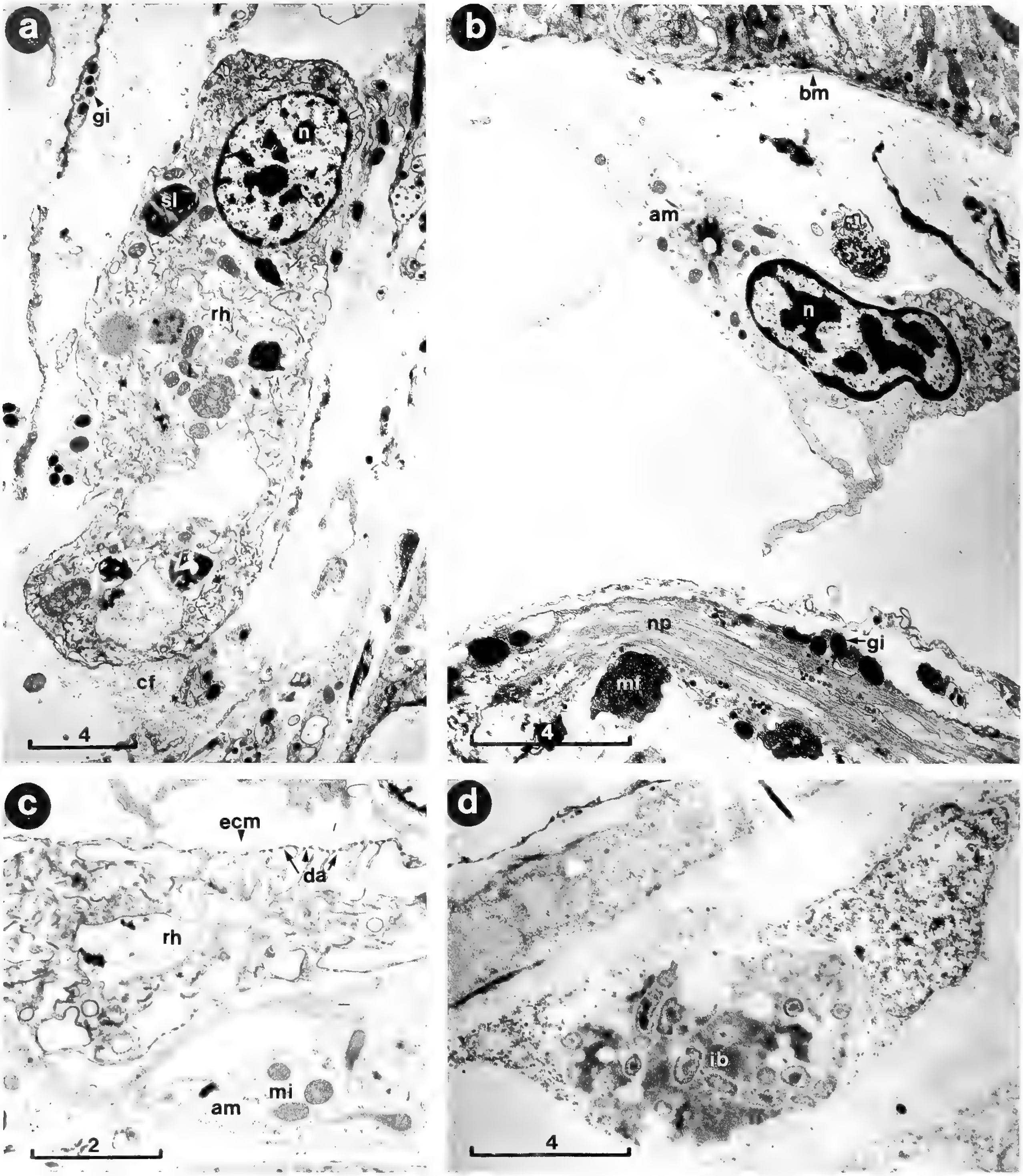

Figure 5

Ultrastructure of hemocytes (TEM). All scale bars in μm.

Figure 5a. *Barbatia barbata*: collagen fibers (cf) between gliointerstitial cell (gi) and rhogocyte (rh) with nucleus (n) and secondary lysosome (sl).

Figure 5b. *Barbatia barbata*: amoebocyte (am) with nucleus (n), nerve process (np), gliointerstitial cells (gi), and muscle fibers (mf) below the basement membrane (bm).

Figure 5c. *Barbatia barbata*: detail of a rhogocyte (rh) showing the slits with diaphragms (da) and the surrounding extracellular matrix (ecm).

Figure 5d. *Lissarca notorcadensis*: phagocyte with invaded bacteria (ib).

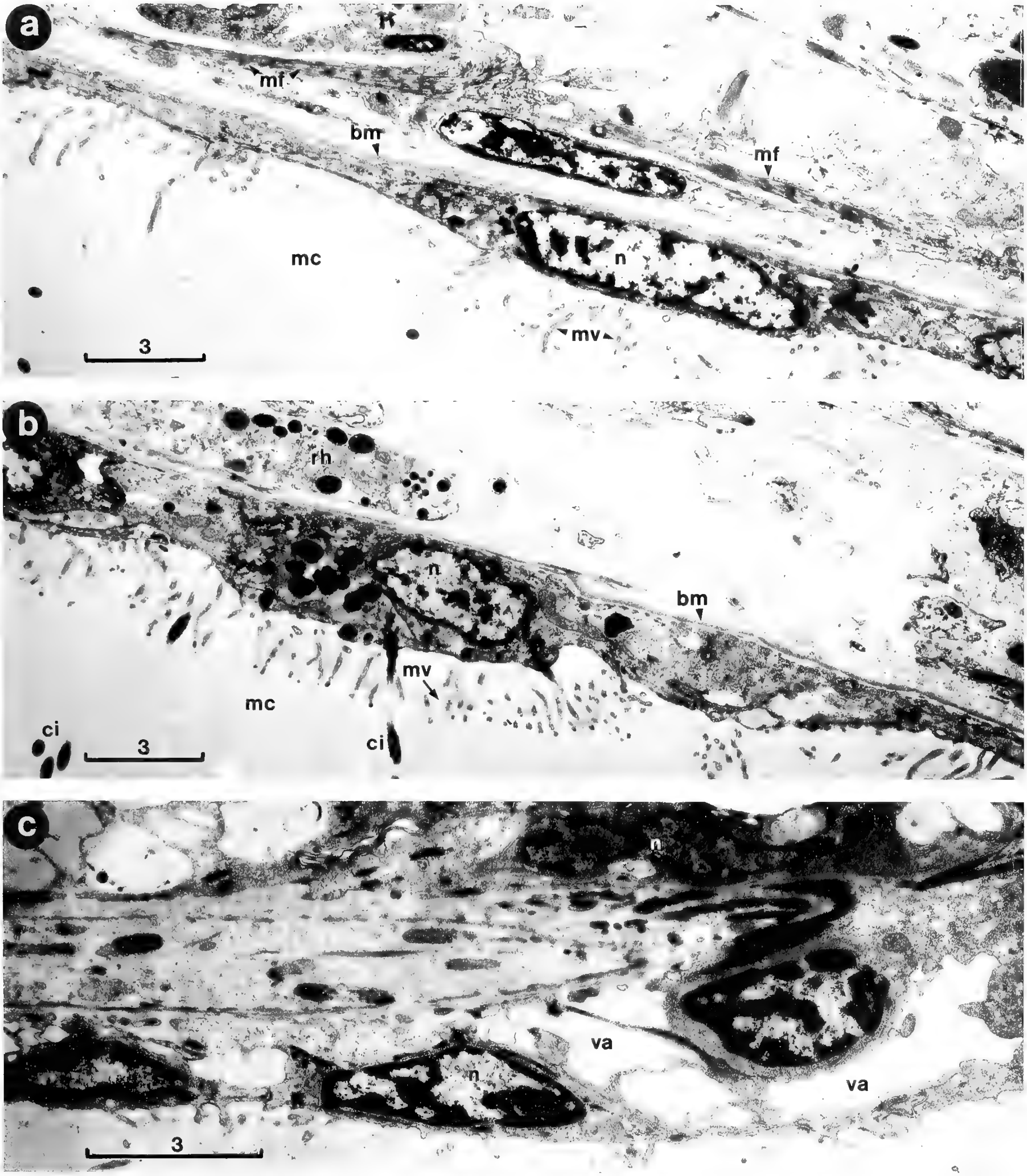

Figure 6

Ultrastructure of the inner mantle epithelium (TEM). All scale bars in μm.

Figure 6a. *Barbatia barbata*: cell with nucleus (n) and microvillar border (mv) of the inner mantle epithelium, which is underlain by a basement membrane (bm). Muscle fibers (mf) are present in the hemocoel.

Figure 6b. *Barbatia barbata*: ciliated (ci) cell with nucleus (n) and microvillar border (mv). The inner mantle epithelium is underlain by a basement membrane (bm). A rhogocyte (rh) is present in the hemocoel.

Figure 6c. *Arca ventricosa*: cells (n, nucleus) of inner mantle epithelium containing large vacuoles (va) with vacuoles of unknown function.

not perforated, which is in accordance with the data presented by Waller (1980) and Carter (1990).

We decalcified the shell after it was embedded in plastic to prevent shrinking of soft tissue. Nevertheless, the observed reticulate formation of caeca in *Barbatia barbata* and *Arca noae* might be a preparation artifact, because it does not agree with observations of non-decalcified shells in which all caeca are reported as solitary structures (Waller, 1980).

Salvini-Plawen (1985) considered conchiferan and polyplacophoran caeca to be homologous organs. The arcid caeca indeed share several structural similarities with the caeca of fissurellid limpets and with the aesthetes of the Polyplacophora. Particularly close resemblance is found between the arcoid caeca and the polyplacophoran microaesthetes, because both are unicellular structures, whereas the macroaesthetes and the fissurellid caeca are multicelluluar organs. However, many fine-structural similarities are also present in the clearly analogous caeca of brachiopods, probably due to similar function(s) (Reindl et al., 1995). Moreover, the fundamental developmental differences of the secondarily formed arcoid caeca (Waller, 1980) with the primarily formed caeca of the remaining groups suggest analogy rather than homology (Reindl & Haszprunar, in press).

Apart from the Arcoidea and Limopsoidea, where shell tubules have been reported in all species studied (Omori et al., 1962; Omori & Kobayashi, 1963; Oberling, 1964; Kobayashi, 1964, 1969, 1980; Shibata, 1970, 1976, 1979, 1980; Waller, 1980; see review by Carter, 1990), bivalve caeca have only been studied in the Corbiculoidea (Schröder, 1907; Robertson & Coney, 1979; Tan Tiu & Prezant, 1989; Adler & Fiechtner, 1992; Araujo et al., 1994). In both Arcoidea and Corbiculoidea, the caeca are unicellular structures that are secondarily formed by specialized cells of the outer mantle epithelium after the previously formed shell which is penetrated.

Although the phylogeny of bivalves is still a matter of much speculation, higher clades like the Pteriomorpha are accepted by most authorities (see reviews by Allen 1985, Vaught 1989). In light of the distant systematic relationship of Arcoida (Pteriomorpha) and Corbiculoidea (Heterodonta) the similarity of the structure and development of the caeca is remarkable. On the other hand, a general homology of the caeca within the bivalves is unlikely, first, because of the general rare presence of caeca among all bivalve groups, and second, because caeca of different structure and origin occur in more closely related groups (e.g., Mytilidae in Pteriomorpha, Chamidae in Heterodonta; Taylor et al., 1969, 1973).

Possible Functions of Caeca

Although it provides protection, a calcified shell may limit the exchange of materials and information between an organism and its environment (Watabe, 1984; Williams, 1984). Shell tubules may help to improve this exchange by extending the living cellular content (caeca) to the periostracum layer.

A photoreceptive function has been demonstrated for the aesthetes in polyplacophorans (Boyle, 1972) and has been assumed for bivalve caeca by Omori et al., (1976). However, we could not find any kind of photosensitive structures or pigments or nervous processes contacting the caeca to transmit the received information. Thus we agree with Waller (1980) that it is very unlikely that additional photoreceptors would be present beneath the shell, because those on the mantle margin can provide nearly 360° reception to slight changes in light intensity (Braun, 1954).

A second possible function is that tubulation serves to anchor the mantle to the shell in the region proximal to the pallial line. Indeed, the caeca considerably increase the area of adhesion of the mantle to the shell. However, shell attachment seems unlikely to be an important function, because it is already performed by specific adhesive cells (supporting or true tendon cells with tonofilaments; see Bubel 1984). In addition; if the attachment of the mantle to the shell is an important function, one would expect tonofilaments or actin fibers, which are suitable for mechanical stress, to extend into the tubules. This is not the case, however.

A third possible role of caeca is in gas exchange. Alekseev (1987) proposed this function for the caeca of Pisidiidae (Corbiculoidea). Tubulation certainly increases the contact area of the mantle epithelium with the free environment and thus facilitates gas exchange and the buffering of metabolic products that may result from anerobic metabolism when the valves are closed (Lutz & Rhoads, 1977). However, this hypothesis is in contrast to the results of Shibata (1971a, b, c), who investigated *Anadara subcrenata* by physiological methods and found no evidence for any role in gas exchange. In addition, the non-perforated periostracum contradicts this idea (see Waller, 1980 for detailed discussion).

A storage function, as discussed for Polyplacophora (Boyle, 1974; Fischer, 1988; Baxter et al., 1990) and Brachiopoda (Peck et al., 1989; Peck, 1992; Reindl et al., 1995), is improbable. We could not find any specific storage material such as mucus or glycogen within the caeca. Moreover, there is limited space for storage in the long and fragile caeca, and the restricted volume of all caeca within an animal argues against this possible function.

Because caeca penetrate the shell after its formation, a function with respect to shell secretion also appears unlikely.

The only function which seems acceptable at present is that the caeca are involved in chemical secretion for the purpose of deterring boring organisms. However, this secretion does not prevent settlement on the shell, because we found many epizoic and/or epiphytic organisms sitting on the periostracum immediately above a caecum. The caeca are certainly chemically active in order to perforate the shell and it is possible that they remain in this state after reaching the periostracum. This hypothesis is supported by the fact that in our investigated species we never found any kind of boring algae, fungi, or bacteria penetrating the mineralized shell. However, negative evidence always is unsatisfactory, and we must conclude that the function of arcoid caeca is far from being clarified.

Cilia of The Outer Mantle Epithelium

The cilia, which emerge from the sensory processes of the outer mantle epithelium, are situated in the narrow space between the apical surface of the outer mantle epithelium and the shell. These cilia lack roots, suggesting a sensory function in spite of their "normal" 9 + 2 construction (Barber, 1974, Moran & Rowley, 1983). They may detect invading debris and may induce defense reactions of the mantle epithelium.

Microvillar Pads

The ultrastructure of the microvillar pads suggests a sensory function because of the specialized desmosomes and the dense arrangement of the microvilli. However, we failed to detect an axon associated with any of these cells. The structure of the microvillar pads is very similar to rhabdomeric photoreceptors and therefore suggests photosensitivity of this cell type. On the other hand, photoreception is hard to accept because the pads are situated below the thick mineralized shell and the pigmented periostracum (see also above for caeca). Without further physiological studies, it is impossible to present a conclusive functional interpretation of the microvillar pads.

So far as is known, the microvillar pads are restricted to members of the subfamily Arcinae (*Arca noae*; *Barbatia barbata*), where they are very common in the outer mantle epithelium. In contrast, microvillar pads are lacking in the remaining species.

Mucous Cells

These cells are very common in the outer mantle epithelium, and only a narrow space is left between their apical surface and the mineralized shell. It is unknown whether distal or proximal secretion occurs, or whether storage is their main function. The mucous cells might also be involved in the production of the organic matrix of the shell.

Supporting Cells

This cell type has two functions. First, supporting cells work as a "pillar" for the entire outer mantle, because they are present in large numbers and are regularly interspersed between the other cell types of the outer mantle epithelium. In addition, this cell type is responsible for the attachment of the mantle to the shell by numerous prominent tonofilaments with their apical hemidesmosomes. Bubel (1984) reviewed the cell types which attach the various muscle fibers to the shell and called them "tendon cells." In our species, a smooth transition occurs between true tendon cells (with attached muscles) and supporting cells with very few tonofilaments.

Rhogocytes

Rhogocytes are diagnostic for mollusks. They have been described in the hemocoel of members of nearly all molluscan classes under many different terms such as "Plasmazelle," "Leydig cells," "brown cell," "vakuolisierte Rundzelle," "Blasenzelle," "cellule excrétrices du tissu conjonctif," and mostly as "pore cells" or "rhogocytes" (see recent review by Haszprunar, 1996). As outlined elsewhere (Haszprunar, 1996), the term "rhogocyte" (Greek: slit-cell) should be preferred, because actually slits are present rather than pores. As reviewed by Simkiss & Mason (1983), Mason et al. (1984), and Nott et al. (1993), pore cells are thought to play an important role in the metabolism of respiratory pigments and of metal ions in general. In general, the granules of the rhogocytes contain iron or copper ions according to the respective respiratory pigments. Rhogocytes also contain lysosomes, so it is possible that they are more catabolic than anabolic. Rhogocytes might also be involved in calcium metabolism. Most recently Morse & Cooper (1993) showed that rhogocytes take up hemolymph fluid via endocytosis. Without additional experiments, it is impossible to state any specific function of the rhogocytes in the arcoidan mantle.

Gliointerstitial System

According to Nicaise (1973), the molluscan gliointerstitial system forms a connection between muscles and nerves. These cells may be found at the base of the epidermis and also (as in this case) as "free" cells in the primary body cavity. It is supposed that the gliointerstitial system stores inorganic cations, thus participating in the ion regulation of neurons and perhaps also of muscle cells (Nicaise, 1973). In addition, this system is able to transport metabolites throughout the intercellular matrix (Nolte et al., 1976).

Amoebocytes

These cells, which are found throughout the hemocoel, are probably involved in defense against bacteria that have entered the animal's body. The rarely observed "phagocytes" might be amoebocytes in an active state, or might be another distinct cell type.

Inner Mantle Epithelium

The microvillar border of the squamous epithelium probably plays an important role in gas and metabolic exchange and therefore in respiration and excretion. Furthermore, Manahan et al. (1982) demonstrated transport of dissolved amino acids throughout the inner mantle epithelium by a demonstration of an uptake from natural seawater. The function of the few cilia is in all probability the maintenance of a continuous water flow over the epithelial surface.

General Remarks

The present investigations reveal that the mantle of arcoid and limopsoid bivalves is much more complicated and specialized than previously assumed. Nonetheless this study should encourage people to do comparative work on other bivalve groups. Such comparative data should enable us to increase our understanding of this important bivalve organ and to enlighten also phylogenetic relationship between the bivalve groups.

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LITERATURE CITED

ADLER, M. & S. FIECHTNER. 1992. Shell pores in European pill clams (genus *Pisidium*). Pp. 599–600 in C. Meier-Brook (ed.), Proceedings of the 10th International Malacological Congress, Tübingen 1989 (Tübingen, Germany).

ALEKSANDROVA, O. A. 1987. Histochemical and ultrastructural study of the mantle edge epithelium in two bivalve mollusc species *Margaritana margaritifera* and *Anodonta cygnea* (in Russian). Tsitologiya 29:995–1001.

ALEKSEEV, N. K. 1987. On the function of canals in shells of the molluscan superfamily Pisidoidea (in Russian, English summary). Proceedings of the Zoological Institute, Leningrad 171:169–173.

ALLEN, J. A. 1985. The recent Bivalvia: Their form and evolution. Pp. 337–403 in E. R. Trueman & M. R. Clarke (eds.), The Mollusca. Vol. 10: Evolution. Academic Press: London-New York.

ARAUJO, R., M. A. RAMOS & J. BEDOYA. 1994. Microtubules in the shell of the invasive bivalve *Corbicula fluminea* (Müller, 1774) (Bivalvia: Heterodonta). Journal of Molluscan Studies 60:405–413.

BARBER, V. C. 1974. Cilia in sensory organs. Pp. 403–433 in M. A. Sleight (ed.), Cilia and Flagella. Academic Press: New York.

BAXTER, J. M., M. G. STURROCK & A. M. JONES. 1990. The structure of the intrapigmented aesthetes and the periostracum layer in *Callochiton achatinus* (Polyplacophora). Journal of Zoology, London 220:447–468.

BEEDHAM, G. E. 1958. Observations on the mantle of the Lamellibranchia. Quarterly Journal of Microscopical Sciences 99:181–197.

BOYLE, P. R. 1972. The aesthetes of chitons. I. Role in the light response of the whole animals. Marine Behavior and Physiology 1:171–184.

BOYLE, P. R. 1974. The aesthetes of chitons. II. Fine structure in *Lepidochitona cinereus* (L.). Cell and Tissue Research 153: 383–398.

BRAUN, R. 1954. Zum Lichtsinn facettenaugentragender Muscheln (Arcacea). Zoologische Jahrbücher, Abteilung Physiologie 65:91–125.

BUBEL, A. 1984. Mollusca: Epidermal cells. Pp. 400–447 in J. Bereiter-Hahn, A. G. Matoltsy & K. S. Richards (eds.), Biology of the Integument. Vol. 1: Invertebrates. Springer Verlag: Heidelberg-New York.

CARTER, J. G. 1990. Shell microstructural data for the Bivalvia. Part III. Orders Praecardioida, Arcoida, Pterioida and Limoida. Pp. 321–345 in J. G. Carter (ed.), Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends. Van Nostrand Reinhold: New York.

DURFORT, M. 1984. Ultraestructura de les valves i del manto larvari d' *Anodonta cygnea* (L.). Biological Desenvolupament (Societad Catalana de Biologia) (Barcelona) 2:85–93.

DURFORT, M. 1985. Ultraestructura del manto lavario de *Anodonta cygnea* (L.) Iberus 5:43–52.

EERNISSE, D. J. & P. D. REYNOLDS. 1994. Polyplacophora. Pp. 55–110 in F. W. Harrison & A. J. Kohn (eds.), Microscopic Anatomy of Invertebrates. Vol. 5: Mollusca I. John Wiley and Sons: New York.

EISENMAN, E. A. & M. ALFERT. 1982. A new fixation procedure for preserving the ultrastructure of marine invertebrate tissues. Journal of Microscopy 125:117–120.

FISCHER, F. P. 1988. The ultrastructure of the aesthetes in *Lepidopleurus cajetanus* (Polyplacophora, Lepidopleurina). American Malacological Bulletin 6:153–159.

HAIN, S. 1990. Die beschalten benthischen Mollusken (Gastropoda und Bivalvia) des Weddellmeeres, Antarktis. Berichte zur Polarforschung (Bremerhaven) 70:1–181.

HASZPRUNAR, G. 1996. The molluscan rhogocyte (pore-cell, Blasenzelle, cellule nucales), and its significance for ideas on nephridial evolution. Journal of Molluscan Studies 62:185–211.

JABBOUR-ZAHEB, R., D. CHAGOT, F. BLANC & H. GRIZEL. 1993. Mantle histology, histochemistry and ultrastructure of the pearl oyster *Pinctada margaritifera* (L.). Aquatic Living Resources 5:287–298.

KEYSER, D. 1980. Auftreten und Konstanz von Poren und Borsten auf der Schale von *Podocopa* (Ostracoda, Crustacea). Verhandlungen des naturwissenschaftlichen Vereins Hamburg (NF) 23:175–193.

KEYSER, D. 1981. Aufbau der Tastsinnesorgane in den Schalen von Ostracoden (Crustacea). Beiträge zur elektronenmikroskopischen Direktabbildung von Oberflächen (Remy Verlag, Münster) 14:603–610.

KLEPAL, W. & H. BARNES. 1975. A historical and scanning electron microscopical study of the formation of the wall plates in *Chthamalus depressus* (Poli). Journal of Experimental Marine Ecology 20:183–198.

KOBAYASHI, I. 1964. Microscopical observations on the shell structure of Bivalvia. I: *Barbatia obtusoides* (Nyst). Science Reports of the Tokyo Kyoiku Daigaku, section C (Geology, Mineralogy and Geography) 8(82):295–301, pls. 1–3.

KOBAYASHI, I. 1969. Internal microstructure of the shell of bivalve molluscs. American Zoologist 9:663–672.

KOBAYASHI, I. 1980. Shell structure of *Bentharca asperula* (Dall) (in Japanese, English summary). Venus (Japanese Journal of Malacology) 39:178–185, pls. 1–2.

KOK, L. P. & M. E. BOON. 1992. Microwave Cookbook for Microscopists. Art and Science of Visualization (3rd Revised Edition), Coulomb Press: Leyden. 432 pp.

LUTZ, R. A. & D. C. RHOADS. 1977. Anaerobiosis and a theorie of growth line formation. Science 198:1222–1227.

MACHADO, J., F. CASTILHO, J. COIMBRA, E. MONTEIRO, C. SA & M. REIS. 1988. Ultrastructural and cytochemical studies in the mantle of *Anodonta cygnea.* Tissue and Cell 20:797–807.

MANAHAN, D. T., S. H. WRIGHT, G. C. STEPHENS & M. A. RICE. 1982. Transport of dissolved amino acids by the mussel *Mytilus edulis*: Demonstration of net uptake from natural seawater. Science 215:1253–1255.

MASON, A. Z., K. SIMKISS & K. P. RYAN. 1984. The ultrastructural localization of metals in specimens of *Littorina littorea* collected from clean and polluted sites. Journal of the Marine Biological Association of the United Kingdom 64:699–720.

MORAN, D. T. & J. C. ROWLEY. III. 1983. The structure and function of sensory cilia. Journal of Submicroscopical Cytology. 15:157–162.

MORSE, M. P. & M. S. COOPER. 1993. Endocytosis of hemolymph fluid in the connective tissue pore cells of the pectinid scallop, *Chlamys hastata.* American Zoologist 33(5): 22A.

MORRISON, C. M. 1993. Histology and cell ultrastructure of the mantle and the mantle lobes of the Eastern Oyster, *Crassostrea virginica* (Gmelin)—a summary atlas. American Malacological Bulletin 10:1–24.

NEFF, J. M. 1972. Ultrastructure of the outer mantle epithelium of the mantle in the clam, *Mercenaria mercenaria* in relation to the calcification of the shell. Tissue and Cell 4:591–600.

NICAISE, G. 1973. The gliointerstitial system of molluscs. International Review of Cytology 34:251–325.

NOLTE, A., M. REINECKE, D. KUHLMANN, E. J. SPECKMANN & H. SCHULTZE. 1976. Glia cells of the snail brain. Some remarks on morphology and function. Pp. 128–138 in J. Salanki (ed.), Neurobiology of Invertebrates: Gastropod Brain. Tihany 1975: Budapest.

NOTT, J. A., M. J. BEBIANNO, W. J. LANGSTON & K. P. RYAN. 1993. Cadmium in the gastropod *Littorina littorea.* Journal of the Marine Biological Association of the United Kingdom 73:655–665.

OBERLING, J. J. 1964. Observations on some structural features of the pelecypod shell. Mitteilungen der naturforschenden Gesellschaft Bern (N.S.) 20:1–63.

OMORI, M. & I. KOBAYASHI. 1963. On the microcanal structures of and in the shell of *Arca navicularis* Brugière and *Spondylus barbatus* Reeve (in Japanese, English summary). Venus (Japanese Journal of Malacology) 22:274–280; pls. 19–20.

OMORI, M., I. KOBAYASHI & M. SHIBATA. 1962. Preliminary report on the shell structure of *Glycymeris vestita* (Dunker) (in Japanese, English summary). Science Reports of the Tokyo Kyoiku Daigaku, section C (Geology, Mineralogy and Geography) 8(77):197–202; figs. 1–3; pls. 1–3.

OMORI, M., I. KOBAYASHI, M. SHIBATA, K. MANO & H. KAMIYA. 1976. On some problems concerning calcification and fossilization of taxodontid bivalves. Pp. 403–426. In: N. Watabe & K. M. Wilbur (eds.), The Mechanisms of Mineralization in the Invertebrates and Plants. University of South Carolina Press: Columbia.

OWEN, G. & A. WILLIAMS. 1969. The caecum of articulate Brachiopoda. Proceedings of the Royal Society of London B 172:187–201.

PAILLARD, C. & M. LE PENNEC. 1993. Ultrastructural studies on the mantle and the periostracal lamina in the mantle clam, *Ruditapes philippinarum.* Tissue and Cell 25:183–194.

PECK, L. S. 1992. Body volumes and internal space constraints in articulate brachiopods. Lethaia 25:383–390.

PECK, L. S., G. B. CURRY, A. D. ANSELL & M. JAMES. 1989. Temperature and starvation effects on the metabolism of the brachiopod, *Terebratulina retusa* (L.). Historical Biology 2:101–110.

PEDERSEN, K. J. 1991. Invited review: Structure and composition of basement membranes and other basal matrix systems in selected Invertebrates. Acta Zoologica (Stockholm) 72:181–201.

PETIT, H., W. L. DAVIES & R. G. JONES. 1978. Morphological studies on the mantle of the freshwater mussel *Amblema* (Unionidae): Scanning electron microscopy. Tissue and Cell 10:619–627.

REINDL, S. & G. HASZPRUNAR. 1994. Light and electron microscopical investigations on shell pores (caeca) of fissurellid limpets (Mollusca, Archaeogastropoda). Journal of Zoology, London 233:385–404.

REINDL, S. & G. HASZPRUNAR. 1995. Shell pores (Caeca, Aesthetes) of Mollusca: A case for polyphyly. Pp. 115–118 in J. D. Taylor (ed.), The Origin and Evolutionary Radiation of the Mollusca. Oxford University Press: Oxford.

REINDL, S., W. SALVENMOSER & G. HASZPRUNAR. 1995. Fine structure and immunocytochemical investigation of the cacea of *Argyrotheca cordata* and *Argyrotheca cuneata* (Brachiopoda, Terebratulida, Terebratellacea). Journal of Submicroscopical Cytology and Pathology 27:543–556.

REYNOLDS, E. S. 1963. The use of lead citrate at high pH as an electron-opaque stain in electron microscopy. Journal of Cell Biology 17:208–212.

RICHARDSON, K. C., L. JARRET & E. H. FINKE. 1960. Embedding in epoxy resins for ultrathin sectioning in electron microscopy. Stain Technology 35:313–323.

ROBERTSON, J. L. & C. C. CONEY. 1979. Punctal canals in the shell of *Musculium securis* (Bivalvia: Pisidiidae). Malacological Review 12:37–40.

SALVINI-PLAWÉN, L. 1985. Early evolution and the primitive groups. Pp. 59–150 in E. R. Trueman & M. R. Clarke (eds.), The Mollusca. Vol. 10: Evolution. Academic Press: London-New York.

SCHRÖDER, O. V. 1907. Beiträge zur Histologie des Mantels von *Calyculina (Cyclas) lacustris* Müller. Zoologischer Anzeiger 31:506–510.

SHIBATA, M. 1970. On the punctations scattered over the shell surface of *Glycymeris* (*Veletuceta*) *albolineata* (Lischke) (in Japanese, English summary). Earth Science (Chikyu Kagaku) 24:167–179; pls. 1–4.

SHIBATA, M. 1971a. The experimental researches on the function of the canals found on the shell of *Anadara* (*Scapharca*) *subcrenata* (Lischke) Part 1 (in Japanese, English summary). Research Institute for Natural Resources (Shigen Kagaku Kankyuio) Miscellaneous Report 75:103–108.

SHIBATA, M. 1971b. The experimental researches on the function of the canals found on the shell of *Anadara* (*Scapharca*) *subcrenata* (Lischke) Part 2 (in Japanese, English summary). Research Institute for Natural Resources (Shigen Kagaku Kankyuio) Miscellaneous Report 75:109–112.

SHIBATA, M. 1971c. The experimental researches on the function of the canals found on the shell of *Anadara* (*Scapharca*) *subcrenata* (Lischke). Part 3 (in Japanese, English summary). Earth Science (Chikyu Kagaku) 29:239–244; pls. 1–4.

Shibata, M. 1976. The microscopic structures of marginal area of the inner layer in eutaxodont shell. (in Japanese, English summary). Venus (Japanese Journal of Malacology) 35(1): 32–36.

Shibata, M. 1979. Tubules found in the arcoid shell. (in Japanese, English summary). Venus (Japanese Journal of Malacology) 38:48–60; pls. 1–3.

Shibata, M. 1980. On the function of tubules in the arcoid shell. Pp. 107–110 in M. Omori & N. Watabe (eds.), The Mechanisms of Biomineralization in Animals and Plants. Tokai University Press: Tokyo.

Simkiss, K. & A. Z. Mason. 1983. Metal ions: Metabolic and toxic effects. Pp. 102–163 in K. M. Wilbur & P. W. Hochachka (eds.), The Mollusca. Vol. 2: Environmental Biochemistry and Physiology. Academic Press: London.

Smith, J. P. S. III. & S. Tyler. 1984. Serial sectioning of resin-embedded material for light microscopy: Recommended techniques for micrometazoans. Mikroskopie (Wien) 41: 259–270.

Spurr, A. R. 1969. A low-viscosity epoxy resin embedding medium for electron microscopy. Journal of Ultrastructural Research 26:31–43.

Stasek, C. R. & W. R. McWilliams. 1973. The comparative morphology and evolution of the molluscan mantle edge. The Veliger 16:1–19.

Tan Tiu, A. & R. S. Prezant. 1989. Shell tubules in *Corbicula fluminea* (Bivalvia: Heterodonta): Functional morphology and microstructure. The Nautilus 103:36–39.

Tavener-Smith, R. & A. Williams. 1972. The secretion and structure of the skeleton of living and fossil Bryozoa. Philosophical Transactions of the Royal Society of London B 264: 97–160; pls. 6–30.

Taylor, J. D., W. J. Kennedy & A. Hall. 1969. The shell structure and mineralogy of the Bivalvia. Introduction. Nuculacea-Trigoniacea. Bulletin of the British Museum of Natural History, Supplement 3:1–125.

Taylor, J. D., W. J. Kennedy & A. Hall. 1973. The shell structure and mineralogy of the Bivalvia. II. Lucinacea-Clavigellacea. Conclusions. Bulletin of the British Museum of Natural History, Supplement 22:255–294.

Turbeville, J. 1991. Nemertinea. Pp. 285–328 in F. W. Harrison & B. J. Bogitsch (eds.), Microscopic Anatomy of Invertebrates. Vol. 3: Platyhelminthes and Nemertinea. John Wiley & Sons: New York.

Vaught, K. C. 1989. A Classification of the Living Mollusca. American Malacologists Inc.: Melbourne, Florida. 195 pp.

Waller, T. R. 1980. Scanning electron microscopy of shell and mantle in the order Arcoida (Mollusca, Bivalvia). Smithsonian Contributions of Zoology 313:1–58; figs. 1–46; tab. 1.

Watabe, N. 1984. Mollusca-Shell. Pp. 448–485 in J. Bereiter-Hahn, A. G. Matoltsy & K. S. Richards (eds.), Biology of the Integument. Vol. 1: Invertebrates. Springer Verlag: Heidelberg-New York.

Williams, A. 1984. Lophophorates. Pp. 728–745 in J. Bereiter-Hahn, A. G. Matoltsy & K. S. Richards (eds.), Biology of the Integument. Vol. 1: Invertebrates. Springer Verlag: Heidelberg-New York.

Wise, S. W. 1971. Shell ultrastructure of the taxodont pelecypod *Anadara notabilis* (Röding). Ecologiae Geologicae Helvetiae 64(1):1–12; pls. 1–9.

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THE VELIGER

The Hectocotylus and Other Reproductive Structures of *Berryteuthis magister* (Teuthoidea: Gonatidae)

by

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Abstract. Taxonomic studies of teuthoids have emphasized characters of the hectocotylus, a modified arm that male squids use in copulation. Although gonatid squids reportedly lack a hectocotylus, one of the arms in the fourth, or ventral, pair is reported here to be modified to form a hectocotylus in male specimens of *Berryteuthis magister magister* (Berry, 1913) collected in the eastern Pacific and Bering Sea. The stalks of the eighth to the seventeenth suckers from the beak are enlarged in both the dorsal and medial dorsal sucker rows. The hectocotylus may have remained undetected because the changes are comparatively subtle and affect the middle, rather than the distal, part of the arm. These factors and the small size of males in fishery trawls from the western Pacific seem more likely to explain the difference between these specimens and reports of western Pacific specimens of *B. magister* than does species-level separation of the populations. This hypothesis is supported by the similarity of spermatophores, sperm reservoirs, and ovarian eggs from eastern Pacific specimens reported here to those previously described from western Pacific specimens.

INTRODUCTION

The internal reproductive anatomy of oceanic squids is poorly known. Systematic studies of teuthoids, including those of the oegopsid family Ommastrephidae (Roeleveld, 1988) and the myopsid family Loliginidae (Natsukari, 1983, 1984), have extensively cited external characters associated with the hectocotylus, an asymmetrically modified arm which is known or presumed to aid in transferring spermatophores to females (Voss & Voss, 1983).

The terminology associated with the hectocotylus was reviewed by Voss & Voss (1983). Modified suckers, sucker stalks, or arm membranes are common specializations that form the hectocotylus; they may affect the entire arm or be restricted to a portion of the arm. The hectocotylus is inferred to transfer spermatophores to the female where the spermatophoric reaction generates a sperm reservoir that females carry until they spawn (reviewed by Arnold & Williams-Arnold, 1977), although exact mechanisms of sperm transfer and sperm storage are little known. The basic data concerning the taxonomic distribution of a hectocotylus and the morphological diversity of hectocotyli among the 27 recognized teuthoid families and among sepioids and octopods have been invoked as evidence that the modifications have evolved in polyphyly.

Among oegopsid squids are the gonatids, a monophyletic family identified by the presence of four rather than two sucker rows on each arm. Most of the family's 19 recognized species occur at high latitudes in the North Pacific Ocean; two species occur in the North Atlantic and one in the Antarctic Ocean (Nesis, 1987). The reproductive biology of *Berryteuthis magister* (Berry, 1913), which ranges from the Sea of Japan to the California Current, may be the best known of any gonatid species (Okutani et al., 1988). Females of *B. magister* with ovarian eggs up to 5 mm long carry sperm reservoirs imbedded in their inner mantle musculature (Nazumi et al., 1979).

The comparatively few males that have been studied have a small testis (< 2–3% of the body weight) through the life cycle (Kubodera, 1992), and are reported to lack a hectocotylus (Kasahara et al., 1978; Nesis, 1987). This paper, however, documents the presence of a hectocotylus in specimens of *Berryteuthis magister* from the eastern Pacific Ocean and the Bering Sea. The spermatophore, sperm

Table 1

Specimens closely examined, and in some cases dissected, by museum catalogue number, with locality, date of collection, sex, and mantle length in mm. Additional specimens from the Canada Museum of Nature (CMN 66-258, 45603), the United States National Museum (USNM 00814639, 00814640), and the holotype at the California Academy of Sciences (CAS 017965) were also consulted.

California Academy of Sciences, San Francisco, USA.

CAS 019834. 57°49.9′N; 173°38′W; 146–137.2 m. May 1976. 1♀ submature.
CAS 019962. 56°34.8′N; 172°3′W; 151.8–153.6 m. May 1976. 1♂ immature.
CAS 019989. 54°37.8′N; 166°54.0′W; 409 m. April 1976. n = 2 immature.
CAS 096135. 52°19.8′N; 174°7.58′E; 336–418 m. August 1980. n = 3 immature.
CAS 096140. 54°20′09″N; 167°40′06″W; 840–850 m. June 1979. 1♂, 249 mm (with right-handed hectocotylus); 1♀ 243 mm (copulated).

Field Museum of Natural History, Chicago, USA.

FMNH 278024. near Vancouver, British Columbia. No date. 1♀, 186 mm (with right-handed hectocotylus); 1♀ 156 mm.
FMNH 278036. 55°41.8′N; 168°47.52′W; 162 m. July 1994. 1♀, 251 mm (copulated).
FMNH 278037. 60°31.00′N; 171°53.39′E; 139 m. September 1994. 1♂, 203 mm (with left-handed hectocotylus); 2♀♀ 234 mm; 235 mm.
FMNH 278038. 59°40.97′N; 167°7.86′E; 265 m. September 1994. 1♂ 195 mm (with left-handed hectocotylus); 3♀♀ 244 mm; 240 mm; 245 mm.

reservoir, and ovarian eggs from females are also described. *Berryteuthis magister magister* (Berry, 1913), the subspecies considered here, contrasts with the apparently sympatric western Pacific taxon *B. magister nipponensis* Okutani and Kubodera, 1987, in the size of medial suckers on the club and its quasibenthic habits (Okutani & Kubodera, 1987).

MATERIALS AND METHODS

Specimens in nine lots of specimens of *B. magister magister* were closely examined; those that showed evidence of reproductive maturity, e.g., spermatophores visible within the mantle cavity, were dissected (Table 1). Most of the specimens studied were collected west of British Columbia and in the Bering Sea; these areas have been considered to be important spawning sites for the species (Kubodera & Jefferts, 1984; Okutani, 1988). The presence of spermatophores in the penis or eggs in the oviducts identifies reproductively mature specimens (Mangold, 1987).

RESULTS

On one of the fourth, or ventral, arms of mature males of *B. magister,* stalks of the suckers in the dorsal and medial dorsal sucker rows are enlarged to form papillae, and the suckers are reduced in size (Figure 1). The modified arm may be either the right (n = 4) or the left (n = 2) ventral arm of the male; the opposite arm appears entirely unmodified. Both ventral arms appear to be unmodified in specimens under 150 mm mantle length, although only two of these were closely examined.

The modifications that constitute the hectocotylus are restricted to the middle part of the arm. On the dorsal sucker row, the stalk of the eighth sucker from the arm base (at about half of the arm length from the beak) is subtly enlarged. Stalks of the nine succeeding suckers in both the dorsal and medio-dorsal rows are sufficiently enlarged to compress the area occupied by the ventral and medial ventral sucker rows (Figure 1b). The oral ring of the affected suckers is smaller in diameter than the cross section of the papilla, and smaller than the sucker ring of the ventral suckers, but the dorsal and ventral sucker rings carry the same number of teeth. On unmodified arms of females (Figure 1c), each of the four sucker rows occupies roughly an equal area of the arm's surface, and the diameter of the sucker ring exceeds the diameter of the sucker stalk. In males with a hectocotylus, the distal suckers and the arm membrane are unmodified.

Each male with a hectocotylus is fully mature, as documented by spermatophores densely packed in the spermatophore sac (Figure 2). The very short penis, which is the terminus of the spermatophore sac, ends far from the mantle opening (Figure 2). A muscle inserts medially on the penis near where the spermatophore sac tapers to form the penis. This muscle, judging from its medial and anterior origin on the visceral membrane, may help extend the penis when it transfers spermatophores to the hectocotylus prior to copulation. Despite the large number of spermatophores in the penis and spermatophore sac, the testis is very small.

A spermatophore extracted from the penis of the male specimen (CAS 096140) is illustrated in Figure 3a. The length of four spermatophores from this individual ranged in length from 17.25 to 19.5 mm, with a width of 0.75 mm. The length of most sperm masses ranged from 12.0 to 15.5 mm, although one spermatophore had a sperm mass only 6 mm in length. Spermatophores from the male

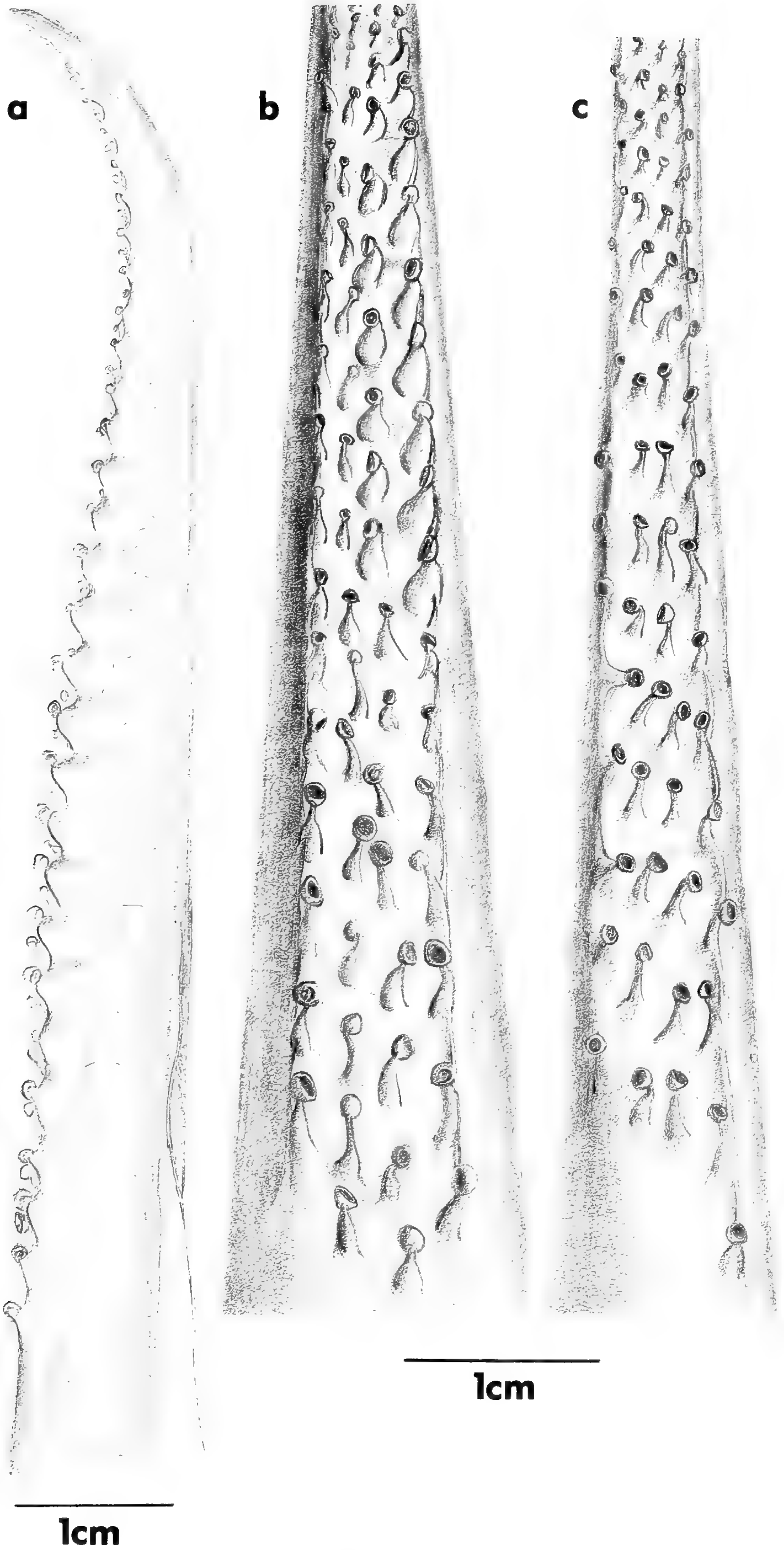

Figure 1

The hectocotylus of *B. magister* in lateral view (a) and oral views (b). The dramatic enlargement of the dorsal and medio-dorsal sucker stalks begins at the eighth sucker from the mouth. Compare with the oral surface of the fourth right arm of a female (c) (both CAS 096140).

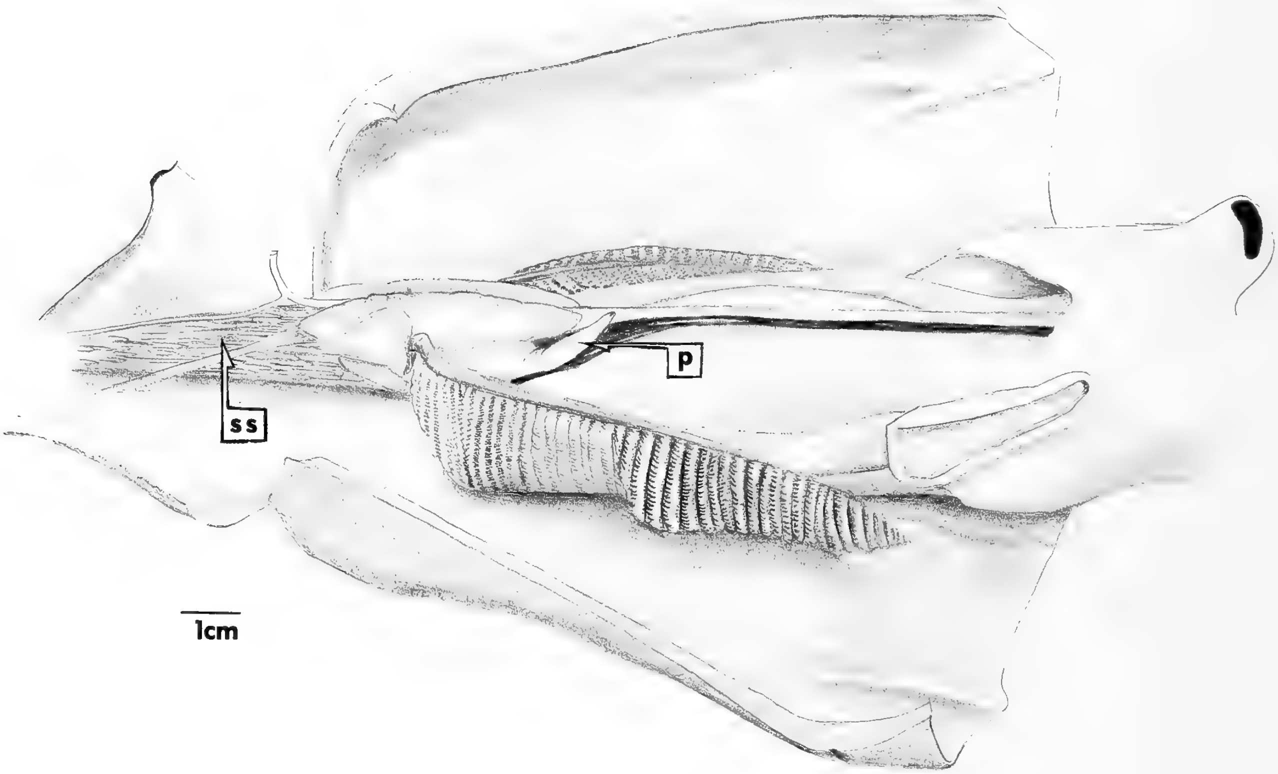

Figure 2

The mantle cavity of a male of *B. magister* (CAS 096140). Note the comparatively short penis (p), and the densely crowded spermatophore sac (ss) which covers the small testis.

specimens collected in the Bering Sea (Table 1), perhaps because they were frozen prior to fixation, could not be recovered intact.

Two females that had copulated, as evidenced by the presence of sperm reservoirs imbedded in their inner mantle musculature, were examined. Dorsally, the skin on the females' mantles is generally intact, and the consistency of the mantle muscle is firm. The dorsal mantle of one of the females, however, has a regular series of tears that appears to be consistent with damage from the arm hooks of a conspecific. The sperm reservoirs lodged in the internal mantle appear to have been inserted there rather than having penetrated the mantle wall (Figure 4); the outer mantle is intact, and removal of the sperm reservoirs from the inner mantle leaves only very faint circular scars.

Sperm reservoirs, measuring 13.0–17.8 mm in length, are firmly inserted into the inner mantle musculature slightly anterior to the base of each gill and immediately ventral to the opening of the distal oviducal gland (Figure 4). In the female specimen from CAS 096140, over three times as many reservoirs are lodged in the left (approx. 170) as are in the right (approx. 50) side of the mantle (Figure 4). Sperm reservoirs on the female's left side are flaccid, without what appear to be the distal white sperm storage areas that are conspicuous on those on the right side. In a second female (FMNH 278036), a total of 87 sperm reservoirs with distal white sperm masses and scars of implanted reservoirs are present only in the left side of the mantle.

Sperm reservoirs (Figure 3c), extracted from the mantle muscles of the females, have three distinct portions; the reservoir tip that was extracted from the mantle muscle has a thick, collar-type ring. The sperm reservoirs available did not allow the internal structure to be seen.

The large ovaries, nidamental glands, and the presence of eggs in the oviducts (Figure 4) indicate that these females have reached full reproductive maturity, although the ovary appears to occupy a lesser volume of the mantle than has been depicted in other fully mature female squids. The length of ovarian eggs varies from 0.9 to 4.0 mm (Figure 5); the largest eggs are free in the ovary or in the oviduct.

DISCUSSION

The enlargement of the stalks of the dorsal and medial dorsal sucker rows on one of the fourth arms of males of the gonatid squid, *B. magister,* constitutes a hectocotylus. Although Kasahara et al. (1978) stated explicitly that no male of *B. magister* examined had a hectocotylus, the presence of a hectocotylus may have been overlooked in western Pacific specimens of this species. The penis of west Pacific specimens of *B. magister,* as described by Okiyama (1970) and illustrated by Kasahara et al. (1978:figure 3) is as short as in specimens reported here. Squids with a hectocotylus typically have a very short penis (Nesis, 1987), as do specimens of *B. magister*. Squids without a hectocotylus typically have a very long penis that can be protruded far out of the mantle. Nesis (1987), in making this generalization, cited the gonatids as an example; the penis of *Gonatopsis borealis* Sasaki, 1923, extends nearly to the mantle opening (Sasaki, 1929:plate XXX; Young, 1972; Okiyama, 1970) as it does in *Gonatopsis octopedatus* Sasaki, 1920 (Okiyama, 1970).

Although the short penis may have suggested to researchers that males of *B. magister* had a hectocotylus, several factors likely contributed to its having remained undetected. Perhaps most significant among these factors is the small size of males studied by previous workers.

The males that Kasahara et al. (1978) and Nazumi et al. (1979) studied ranged in mantle length from 133 to 161 mm; the present study finds hectocotyli on specimens with mantle lengths of from 186 to 249 mm (Table 1). Kubodera (1992) documented that specimens from the Sea of Japan tend to be smaller than do those from more northern populations; he suggested that the population was genetically isolated by the presence of a shallow sill. The present results could be argued to support that hypothesis; however, the fact that hectocotyli were not found on specimens with mantle lengths less than 185 mm suggests that it develops late in ontogeny. Voss & Voss (1983) stated that asymmetric hectocotyli develop earlier in ontogeny than do symmetric modifications; this is consistent with their prediction that asymmetric hectocotyli contribute primarily to spermatophore transfer, and symmetric hectocotyli do not. Regardless of its ontogeny, if males living in warmer waters, such as the Sea of Japan, have smaller body sizes, their hectocotyli are also predicted to be smaller and less conspicuous.

Western Pacific males are also smaller than, and greatly outnumbered by, females (Kasahara et al., 1978; Nazumi et al., 1979; Yuuki & Kitazawa, 1986; Kubodera, 1992). That females live longer than males is a suggested means by which they reach larger sizes (Yuuki & Kitazawa, 1986). The size dimorphism, however, may be due to the sex-linked difference in growth rates estimated by authors. Statolith analysis, such as Jackson (1989) performed on

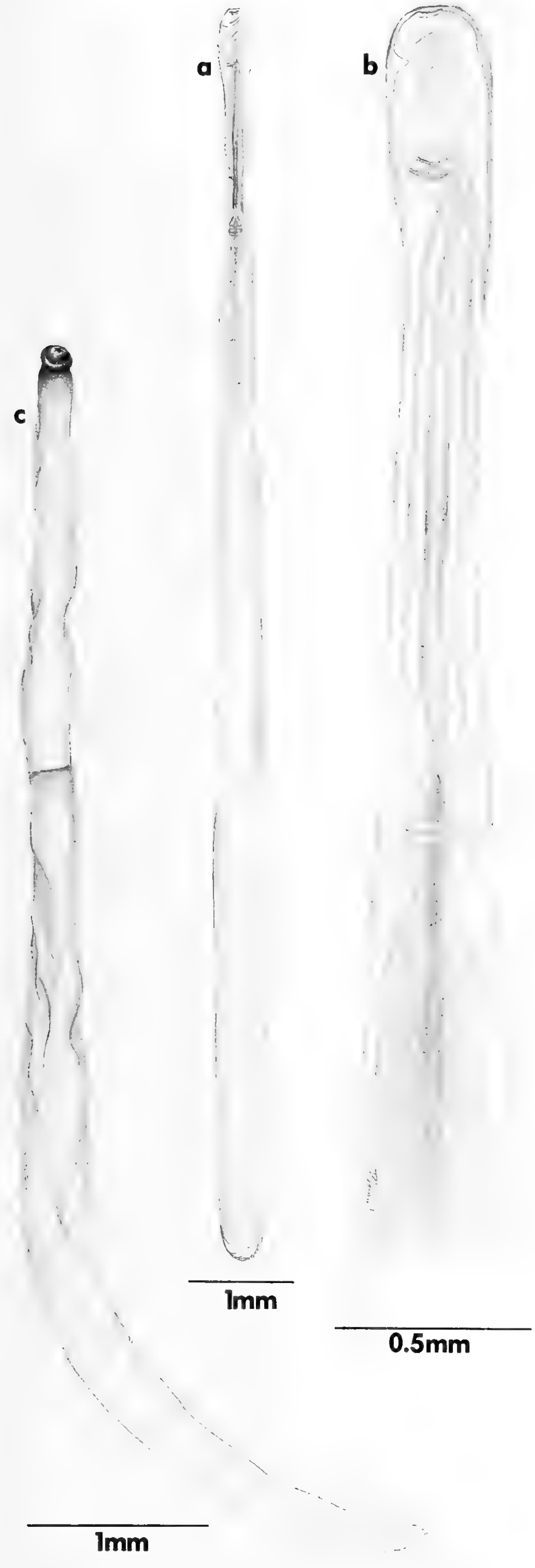

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Figure 3

(a) The spermatophore from the penis of *B. magister,* illustrated in its entirety; (b) a view of the head of the spermatophore (from CAS 096140). (c) Sperm reservoir from the mantle muscle of a gravid female of *B. magister* from the same lot.

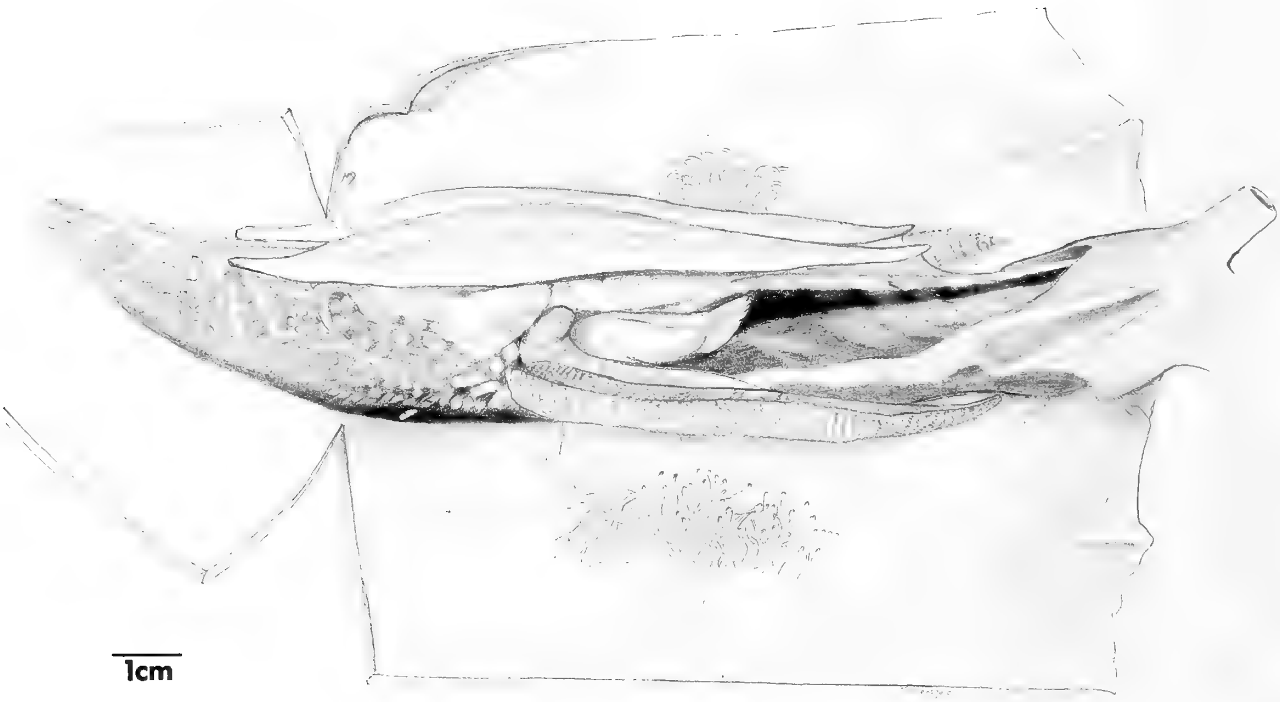

Figure 4

The mantle cavity of a female *B. magister* (CAS 096140). Note the enlarged ovary and nidamental glands and the presence of eggs in the oviducts. The sperm reservoirs imbedded in the left mantle are flaccid and lack sperm; those on the right are rigid with masses of white sperm.

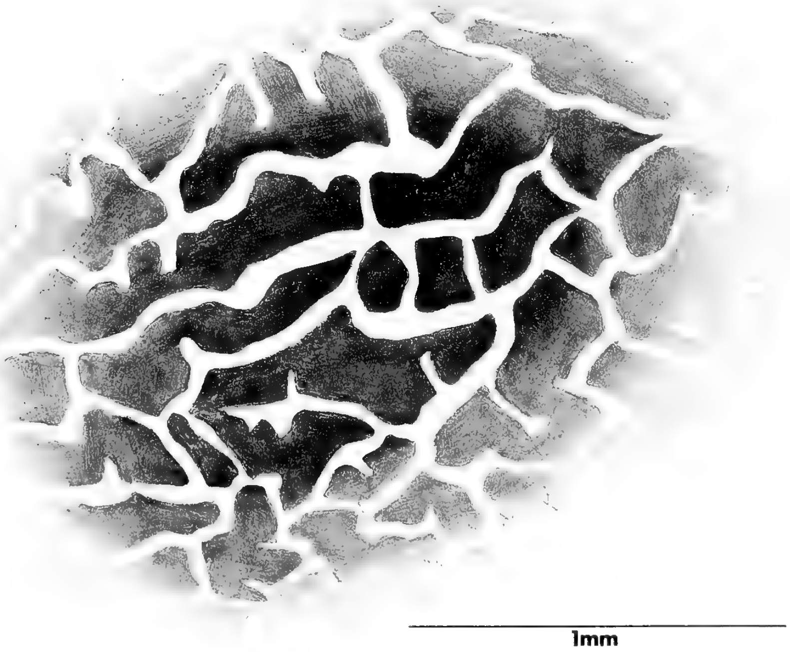

Figure 5

An ovarian egg of *B. magister* (CAS 096140).

the very strongly size-dimorphic species, *Idiosepius pygmaeus* Steenstrup, 1881, could be used to assess sex-linked differences in age and growth.

The very small testis and penis in *B. magister* (Yuuki & Kitazawa, 1986; Kubodera, 1992) may also have complicated the identification of mature males. The testis of *B. magister* weighs half of what it does in *G. borealis* and only a tenth of what it does in the onychoteuthid species *Onychoteuthis borealijaponicus* Okada, 1927 (Kubodera et al., 1983). The small size of these features could have suggested that males with spermatophores were less than maximally mature, despite the presence of spermatophores in the very small penis.

The position of the hectocotylus of *B. magister,* restricted to the middle portion of the arm, and the somewhat subtle modifications which constitute it may have also contributed to why it has been overlooked. Distal modifications and those affecting the arm membrane appear to be most common among oegopsids (Roeleveld, 1988). The restriction of modifications that form teuthoid hectocotyli to the middle portion of the arm, however, are known (e.g., Natsukari, 1983). The subtlety of the modifications reported here may be notable when compared to other oegopsids, but neither their subtlety nor their placement affects the arm's definition as a hectocotylus, following Voss & Voss (1983).

Because these potential problems have hindered the identification of the hectocotylus, and full demonstration that west Pacific specimens of *B. magister* lack a hectocotylus is wanting, defining a new taxon based on the presence of a hectocotylus would currently be inappropriate. As within-species variation in the "handedness" of the hectocotylus is also known (Roeleveld, 1988), this variation does not demonstrate the existence of species-level differences. Additional information concerning characters that could support or refute separation of the populations is required. For example, among the 19 species of gonatids, spermatophores have been previously illustrated only in the species description of *B. anonychus* Pearcy & Voss, 1963, and for *Gonatopsis octopedatus* by Okiyama (1970).

Sperm reservoir placement (Figure 4) in these females of *B. magister* is consistent with that reported for five specimens from the western Pacific (Nazumi et al., 1979). Females in both reports have sperm reservoirs on either the right or left side of their mantles. Whether the data available on sperm reservoir morphology (Figure 3c) are currently able to contribute to ascertaining taxonomic affiliation is somewhat questionable. The sperm reservoir illustrated by Nazumi et al. (1979) is inconsistent with the sperm reservoir measurements reported here. In addition, one of a single cluster of reservoirs illustrated has two rather than three divisions.

The presence of a hectocotylus in *B. magister,* considered to be one of the basal gonatids by Nesis (1973), may offer insight into higher order teuthoid phylogeny. An asymmetrical hectocotylus had been reported among six oegopsid families (Enoploteuthidae, Lycoteuthidae, Architeuthidae, Ommastrephidae, Thysanoteuthidae, Cranchiidae), both myopsid families (Loliginidae, Pickfordiateuthidae), most sepioids, and all incirrate octopods (Voss & Voss, 1983). That an asymmetric hectocotylus occurs across cephalopod orders and in both teuthoid suborders suggests that it may be a plesiomorphic character. Of the oegopsid families with this character, all, except the highly derived cranchiids (Voss & Voss, 1983), also share a primary conus that has been argued to be plesiomorphic (Toll, 1982; Donovan & Toll, 1988).

Whether the hectocotylus is a gonatid plesiomorphy, a remnant of an ancient common ancestor that was lost within the clade, as Voss & Voss (1983) postulated for the Cranchiidae, is shared by other gonatids, or is a unique adaptation to the quasibenthic habits of *B. magister magister* is unknown. To better our understanding of reproductive biology and evolution of the squids, we require additional insight into the occurrence and morphology of the hectocotylus and other phylogenetically informative characters among the diverse teuthoid families.

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LITERATURE CITED

ARNOLD, J. M. & L. D. WILLIAMS-ARNOLD. 1977. Cephalopoda: Decapoda. Pp. 243–290 in A. C. Giese & J. S. Pearse (eds.), Reproduction of Marine Invertebrates Vol. IV. Academic Press: New York.

DONOVAN, D. T. & R. B. TOLL. 1988. The gladius in coleoid (Cephalopoda) evolution. Pp. 89–101 in M. R. Clarke & E. R. Trueman (eds.), The Mollusca. Vol. 12. Academic Press: San Diego.

JACKSON, G. D. 1989. The use of statolith microstructures to analyze life-history events in the small tropical cephalopod *Idiosepius pygmaeus.* Fisheries Bulletin 87:265–272.

KASAHARA, S., T. NAZUMI, T. SHIMIZU & M. HAMABE. 1978. Contributions of biological information useful for development of inshore squid fishery in the Japan Sea. II. A note on reproduction and distribution of *Berryteuthis magister* (Berry) assumed from biological observations on trawl catches in the waters around Oki Islands, Japan Sea. Bulletin of the Japan Sea Regional Fisheries Research Laboratories 29: 159–178. (In Japanese, with English abstract).

KUBODERA, T. 1992. Biological characteristics of the gonatid squid *Berryteuthis magister magister* (Cephalopoda: Oegopsida) off Northern Hokkaido, Japan. Memoirs of the National Science Museum, Tokyo 25:111–123.

KUBODERA, T., W. G. PEARCY, K. MURAKAMI, T. KOBAYASHI, J. NAKATA & S. MISHIMA. 1983. Distribution and abundance of squids caught in surface gillnets in the subarctic Pacific, 1977–1981. Memoirs of the Faculty of Fisheries, Hokkaido University 30:1–49.

Kubodera, T. & K. Jefferts. 1984. Distribution and abundance of the early life stages of squid, primarily Gonatidae (Cephalopoda, Oegopsida), in the Northern North Pacific. Bulletin of the National Science Museum, Series A, 10:165–193.

Mangold, K. 1987. Reproduction. Pp. 157–200 in P. R. Boyle (ed.), Cephalopod Life Cycles II. Academic Press: London.

Natsukari, Y. 1983. Taxonomical and morphological studies on the loliginid squids-III. *Nipponololigo,* a new subgenus of the genus *Loligo.* Venus 42:313–318.

Natsukari, Y. 1984. Taxonomical and morphological studies on the loliginid squids-IV. Two new genera of the family Loliginidae. Venus 43:229–239.

Nazumi, T., S. Kasahara & M. Hamabe. 1979. Contribution of biological information useful for development of inshore squid fishery in the Japan Sea. III. Supplements and amendments to the previous paper on reproduction and distribution of *Berryteuthis magister* (Berry). Bulletin of the Japan Sea Regional Fisheries Research Laboratories 30:1–14. (In Japanese, English abstract).

Nesis, K. N. 1973. Taxonomy, phylogeny and evolution of squids of the family Gonatidae (Cephalopoda). Zoologichesky Zhurnal 52:1626–1638. [In Russian, English summary]

Nesis, K. N. 1987. Cephalopods of the World. TFR Press: Neptune City, New Jersey. 351 pp.

Okiyama, M. 1970. A record of the eight-armed squid, *Gonatopsis octopedatus* Sasaki, from the Japan Sea (Cephalopoda, Oegopsida, Gonatidae). Bulletin of the Japan Sea Regional Fisheries Research Laboratories 22:71–80.

Okutani, T. 1988. Evidence of spawning of *Berryteuthis magister* in the northeastern Pacific (Cephalopoda: Gonatidae). Bulletin of the Ocean Research Institute University of Tokyo 26:193–200.

Okutani, T. & T. Kubodera. 1987. *Berryteuthis magister nipponensis* Pp. 132–135 in T. Okutani, M. Tagawa & H. Horikawa (eds.), Cephalopods from the Continental Shelf and Slope around Japan. Japan Fisheries Resource Conservation Association: Tokyo.

Okutani, T., T. Kubodera & K. Jefferts. 1988. Diversity, distribution and ecology of gonatid squids in the subarctic Pacific: A review. Bulletin of the Ocean Research Institute University of Tokyo 26:159–192.

Pearcy, W. G. & G. L. Voss. 1963. A new species of gonatid squid from the northeastern Pacific. Proceedings of the Biological Society of Washington 76:105–112.

Roeleveld, M. A. 1988. Generic interrelationships within the Ommastrephidae (Cephalopoda). Pp. 277–291 in M. R. Clarke & E. R. Trueman (eds.), The Mollusca vol. 12. Academic Press: San Diego.

Sasaki, M. 1929. Dibranchiate cephalopods of the Japanese and adjacent waters. Journal of the Faculty of Agriculture Hokkaido Imperial University 20: Supplement 1–357.

Toll, R. B. 1982. The comparative morphology of the gladius in the order Teuthoidea (Mollusca: Cephalopoda) in relation to systematics and phylogeny. Unpublished Ph. D. Dissertation. University of Miami, Coral Gables, Florida 390 pp.

Voss, N. A. & R. S. Voss. 1983. Phylogenetic relationships in the cephalopod family Cranchiidae (Oegopsida). Malacologia 23:397–426.

Young, R. E. 1972. The systematics and areal distribution of pelagic cephalopods from the seas off southern California. Smithsonian Contributions to Zoology 97:1–159.

Yuuki, Y. & H. Kitazawa. 1986. *Berryteuthis magister* in the southwestern Japan Sea. Bulletin of the Japanese Society of Scientific Fisheries 52:665–672.

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Three New Turonian Muricacean Gastropods from the Santa Ana Mountains, Southern California

by

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Abstract. Three new species of *Praesargana, P.* ***argentea,*** *P.* ***confraga,*** and *P.* ***kennedyi,*** are the first sarganines reported from southern California. These rare muricacean gastropods of late Turonian age occur in the Baker Canyon Sandstone Member and the overlying lower part of the Holz Shale Member of the Ladd Formation in the Santa Ana Mountains, Orange County, California. Inclusion of *P.* ***argentea*** and *P.* ***kennedyi*** in *Praesargana* broadens the concept of the genus to include species that have spiny sculpture, and species that lack a strong axial component to the sculpture. One species of *Praesargana, P. condoni* (White, 1889), was previously known from the Turonian of northern California. This threefold increase in diversity in a more southern fauna suggests that *Praesargana* may be indicative of a warm-temperate to tropical climate. Sarganinae resemble predaceous Muricidae rather than ciliary-feeding Trichotropidae, but have a fold on the columella and a protoconch more like that of Pyropsinae. For these reasons, despite recent assignments to other families, Sarganinae are included in the family Tudiclidae of the Muricacea.

INTRODUCTION

Although gastropods of Cretaceous age from the Santa Ana Mountains, Orange County, California, have been described in several papers (e.g., Packard, 1992; Popenoe, 1937; Saul & Popenoe, 1993), the faunas are incompletely known. This paper describes three new muricacean species of late Turonian age from the Baker Canyon Sandstone Member and the overlying lower part of the Holz Shale Member of the Ladd Formation. Figure 1 plots the localities at which these species have been found on a geologic map.

At least 38 other molluscan taxa are present at the 10 localities that yielded these new species (Table 1). The ammonite *Subprionocyclus* sp. indicates a late Turonian age for these deposits (Matsumoto, 1959, 1960). Most of these fossiliferous beds may be storm deposits, but, at USGS loc. 2759, specimens of *Anchura (Helicaulax) tricosa* Saul & Popenoe, 1993, with elongate outer lip and rostral extensions preserved, suggest that these shells could not have undergone much transport or reworking by wave action. Saul (1982) considered the mollusks of these assemblages to have lived from the sublittoral to depths not greater than 40 m. At LACMIP 16644 the impression of a fragment (roughly 2 cm × 0.7 cm) of a coral colony was found. About 35 calices are present on the fragment, which possibly used a gastropod shell as substrate. Corals are rare in Pacific Slope Late Cretaceous deposits, and colonial corals even rarer. If this was a hermatypic coral, it suggests clear, normal salinity water above 18°C at a site of low sedimentation in water less than 50 m deep (Wells, 1956: F353). If the specimen was not transported downslope, it suggests a probable depth limit for these faunas.

These three new species have apertural features characteristic of the Late Cretaceous muricacean subfamily Sarganinae Stephenson, 1923. At present the subfamily comprises only *Sargana* Stephenson 1923, and *Praesargana* Saul & Popenoe, 1993, and each genus contains but few species. Additionally, *Rapana tuberculosa* Stoliczka, 1867, from near Serdamungalum, southern India may be a sarganine. In the illustrations and description of *R. tuberculosa* from the Trichinopoly Group of Turonian-Coniacian age (Acharyya & Lahiri, 1991), the description of the very narrow anterior siphonal canal is especially suggestive of Sarganinae. According to Stoliczka (1867:156), the description of this species was prepared before the specimen accidentally fell into acid, and the illustration was drawn after the spines had been partially etched away. Petuch (1988:12) has suggested that *Ecphora proquadricostata* Wade, 1917, should be placed in an as yet unnamed sub-

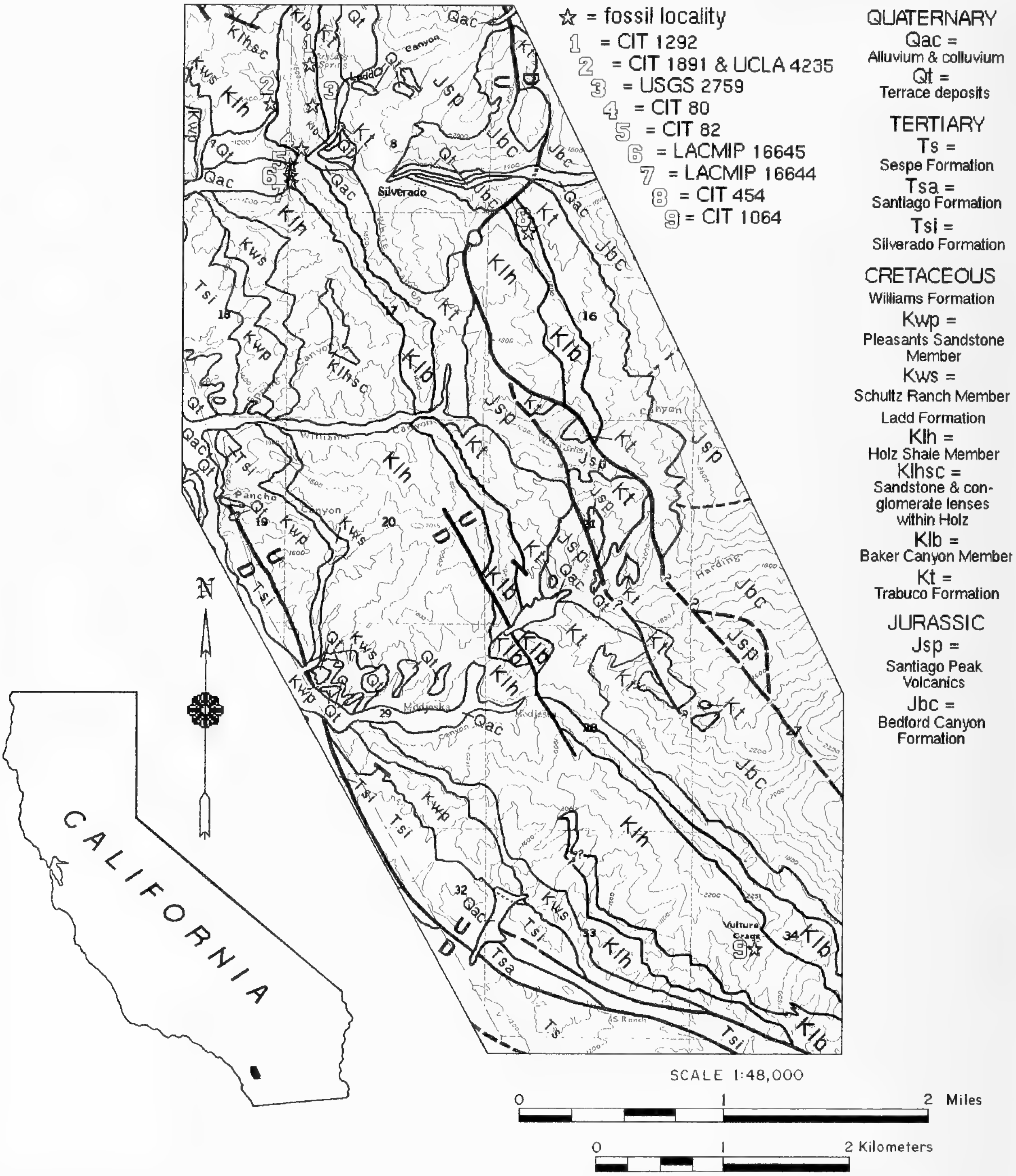


Figure 1

Geologic map of a portion of the northern Santa Ana Mountains, Orange County (after Morton, Miller, and Fife, 1973), with localities yielding specimens of *Praesargana* species. Map includes parts of Black Star Canyon (1967), Corona South (1967), El Toro (1968), and Santiago Peak (1954) USGS 7 ½-minute quadrangles.

Table 1

List of species associated with three *Praesargana* n. sp. Localities yielding *Praesargana* spp. are listed left to right in ascending stratigraphic order and toward deeper water deposits. Of the three species, *P.* ***kennedyi*** seems to have lived on shallowest bottoms and nearest to shore. *Praesargana* ***argentea*** and *P.* ***confraga*** are both associated with *Anchura (H.?) tricosa* in moderate depth shelfal assemblages that include ammonites. (See Saul, 1982, for listings of shallower and deeper water Santa Ana Mountains Cretaceous faunas).

Biota associated with *Praesargana* spp.	Map Number Locality	1	4	3	5	2	2	8	7	6	9	
	number	1292	80	2759	82	4235	1891	454	16644	16645	1064	
Trigonarca californica Packard, 1922		■	■			□	□					B
Pinna calamitoides Shumard, 1859		□						□				B
Lima beta Popenoe, 1937		□	▲		■		▲					B
Alleinacin sulcata (Packard, 1922)		▲				□						B
Ambocardia delta (Popenoe, 1937)		□			□		□					B
Callistalox arata (Gabb, 1864)		□	□		□							B
"*Aporrhais*" *vetus* Packard, 1922		□		□								G
Ampullina pseudoalveata (Packard, 1922)		□	□		□	□	□	□			?	G
Gyrodes dowelli White, 1859		□				□						G
Praesargana ***kennedyi***, sp. nov.		★	★				★					G
Varens formosus Saul & Popenoe, 1993		□	□		□			□				G
Glycymeris pacificus (Anderson, 1902)			■		□		▲				□	B
Pterotrigonia klamathonia (Anderson, 1958)			□		▲	□	□					B
Crassatella gamma Popenoe, 1937			□								■	B
Paraesa? zeta (Popenoe, 1937)			▲									B
Liopistha anaana (Anderson, 1902)			■									B
Latiala nodosa (Packard, 1922)			□		▲	□	□	□				G
Anchura (Helicaulax) tricosa Saul & Popenoe, 1993				▲	▲	■	□	▲	■	■	□	G
Praesargana ***argentea***, sp. nov.				★		★			★	★		G
Cucullaea (Idonearca) gravida (Gabb, 1864)					■	□		■			■	B
Tenea inflata (Gabb, 1864) small var.					▲	▲						B
Corbula sp.					□	□		□				B
Turritella hearni Merriam, 1941					▲	?						G
Varens anae Saul & Popenoe, 1993					□							G
Praesargana ***confraga***, sp. nov.					★			★			★	G
pycnodontid						▲			▲	▲		B
Pachycardium coronaense (Packard, 1922)						□	□				■	B
Calva regina Popenoe, 1937						□				□		B
?*Atira* sp.						□	□					G
Sciponoceras sp.						☆						C
Subprionocyclus sp.						☆			☆	☆		C
Inoceramus sp.							□					B
Neophylloceras sp.							☆					C
Cyprimeria moorei Popenoe, 1937								□				B
Aporrhais n. sp.								□			□	G
Carota dilleri (White, 1889)								□				G
Biplica cf. *B. isoplicata* Popenoe, 1957								□				G
Ellipsoscapha ? sp.								□				G
Eutrephoceras sp.								□				C
pachydiscid ammonite								☆				C
colonial coral									□			
Indogrammatodon sp.											□	B
Turritella iota Popenoe, 1937											□	G
Arrhoges sp. nov.											□	G

■ = abundant; ▲ = common; □ = rare; ★ = *Praesargana* spp., all are rare; ☆ = ammonite, all are rare; B = Bivalvia; C = Cephalopoda; G = Gastropoda.

genus of *Sargana,* but *E. proquadricostata* has an internally denticulate outer lip and a moderately wide siphonal canal. It lacks a columellar fold and a posterior notch at the suture.

Sargana has been recorded from the Senonian of Pondoland, South Africa, and the Campanian–Maastrichtian of the Gulf and Atlantic Coasts of North America. *Praesargana* was previously known from *P. condoni* (White,

Table 2

Characteristics of Tudiclidae, Tudiclinae, Pyropsinae, and Sarganinae.

Tudiclidae	Tudiclinae	Pyropsinae	Sarganinae
Shell Shape and Size			
Rapiform or pyriform, small to large size, commonly with moderate to long anterior siphonal neck	Medium to large size, with moderate to long anterior siphonal neck	Medium to large size, with moderate to long, tapering anterior siphonal neck	Small to medium size, with short to moderately long anterior siphonal neck, bent back to left, forming wide to moderte umbilicus
Whorl Shape			
Angulate, biangulate, or rounded	Angulate or biangulate with abrupt basal constriction	Angulate to rounded, abruptly to smoothly constricted basally	Angulate or subangulate, abruptly to smoothly constricted basally
Anterior Canal			
Commonly long	Long and narrow, nearly straight	Moderate to long, more or less narrow, nearly straight	Short to moderately long, very narrow
Protoconch			
Paucispiral, low	Low to papillate in earlier species becoming bulbous in late species	Low to nearly flattened	Low to flat
Aperture			
Rounded, commonly nearly as wide as high, commonly subangulate at shoulder	Rounded, nearly as wide as high, inside of outer lip lirate or smooth	Rounded to elongate, expanded, commonly subangulate at shoulder	Rounded, nearly as wide as high, some with angulation at shoulder
Columellar Fold			
One fold or swelling at entrance to siphonal canal or no fold	One fold at entrance to siphonal canal; inner lip wraps over fold leaving umbilical chink	One fold or swelling at entrance to siphonal canal or no fold; inner lip wraps over fold or swelling leaving umbilical chink	One fold at entrance to siphonal canal opposite projecting tubercle on inside of outer lip

1889) of Turonian age in northern California; this paper adds three species from southern California for a tripling of diversity in the more southern fauna. This is the first record of a possible latitudinal species diversity gradient within a sarganine genus. *Praesargana* and *Sargana* occurred both north and south of the equator in warm-temperate to subtropical faunas, and they apparently were more specifically diverse nearer the equator. Presently the sparse geological record of this group suggests that the Sarganinae may be a tropical to warm-temperate group.

California also provides, at present, the geologically earliest record of the sarganines, although the possible Indian record may be nearly contemporaneous. The geologically latest records are from the Gulf Coast of North America. The record is too meager to support a sarganine origin in the eastern Pacific or a direction of migration.

Abbreviations used in this paper include CIT, California Institute of Technology (collections at LACMIP); LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology; UCLA, University of California, Los Angeles (collections at LACMIP); USGS, United States Geological Survey; USNM, United States National Museum.

SYSTEMATIC PALEONTOLOGY

Superfamily MURICACEA Rafinesque, 1815

Family TUDICLIDAE Cossmann, 1901

Confusions resulting from orthographic meddling with the name *Tudicla* Röding, 1798, and resultant spellings of Tudiclidae were resolved by Rosenberg & Petit (1987). Composition and characteristics of the Tudiclidae were discussed by Saul (1988). With the placement of Sarganinae in Tudiclidae (Saul, 1995), the family comprises Tudiclinae Cossmann, 1901, Pyropsinae Stephenson, 1941, and Sarganinae. Table 2 lists and contrasts some of the characteristics of these three named subfamilies. Only the Tudiclinae is represented in a modern fauna, and the soft part anatomy of the sole living species, *Tudicla spiralis* (Linnaeus, 1767), is unknown. Although these subfamilies have not previously all been assigned to a single family, their shells are sufficiently similar to be confamilial. The type species of *Tudicla, T. spirillus* (Linnaeus, 1767), from the Bay of Bengal has an internally lyrate outer lip and a large mammillate protoconch of one and a half round, swollen, glossy whorls. Protoconchs of geologically older species of *Tudicla* are, however, smaller and much less bulbous, as, for instance, is that of *Tudicla rusticula* (Bastérot, 1825), a mid-Miocene species from the Vienna Basin of Austria. Protoconchs of Pyropsinae of Cretaceous and earliest Tertiary age consist of about one and a half round, smooth whorls, but they are smaller and lower than those of *Tudicla.*

Subfamily SARGANINAE Stephenson, 1923

The family Sarganidae was erected by Stephenson (1923: 377) to include *Sargana* and an undescribed genus from the Ripley Formation of Georgia and Alabama later described by Wade (1926:177) as *Schizobasis.* Stephenson (1952:181) formally included *Schizobasis* Wade and *Hillites* Stephenson, 1952, in the Sarganidae, but Sohl (1964: 174) disassociated *Hillites* and *Schizobasis* from *Sargana* and placed them in the Moreinae Stephenson, 1941. In addition, Sohl (1964:174) considered *Sargana* sufficiently similar to *Rapana* Schumacher, 1817, and other Rapaninae Gray, 1853, to be included in that subfamily of the Muricidae. Ponder & Warén (1988:305) resurrected the subfamily Sarganinae and placed it with a query in the Muricidae. Garvie (1991) placed *Sargana* in Trichotropidae and then in Cancellariidae (Garvie 1992). Tracey et al. (1993) suggested that *Lowenstamia* Sohl, 1964, and *Sargana,* which they comment upon under Coralliophilidae Chenu, 1859, are possibly neotaenioglossan muricacean homeomorphs. Saul (in press) proposed including the Sarganinae in the Tudiclidae.

Stephenson (1952) distinguished Sarganidae from Muricidae on the basis of its flattened spire and the columellar fold, but Sohl (1964), in assigning *Sargana* to the Rapaninae, pointed out that some Muricidae (e.g., *Murex* Linnaeus, 1758) have a similar fold on the columella and that, "*Sargana* itself is muricid in the character of its ornament and its siphonal canal." The muricid genera *Antinotrophon* Dall, 1902, *Ecphora* Conrad, 1843, and *Rapana* "have similar umbilical characters" (Sohl, 1964). An open umbilicus formed by a revolving, strongly deflected anterior canal is also present in *Poirieria* Jousseaume, 1880, and *Paziella* Jousseaume, 1880, two muricine taxa recognized from the Cretaceous (Garvie, 1991, 1992). The openness of the umbilicus is greatly exaggerated in *Sargana,* however. This feature, in conjunction with the shape of its protoconch (Figure 2) and early whorls, suggests that *Sargana* and *Praesargana* be placed not in Rapaninae but in Sarganinae.

Although Garvie (1991) indicated that *Sargana* is a close relative of trichotropids in the Neotaenioglossa on the basis of the protoconch, other characteristics suggest that it is muricacean in its affinities. Overall shape of the Sarganinae is very similar to that of the predaceous muricids. Sarganines have a very well defined, elongate anterior siphonal canal and a well-marked, posterior notch (Figures 7, 10). Both features, although not confined to predators, are unknown among ciliary feeders such as the trichotropids. Late Cretaceous trichotropids are sufficiently similar to modern species to suggest that they had already evolved a mode of life comparable to that of modern species.

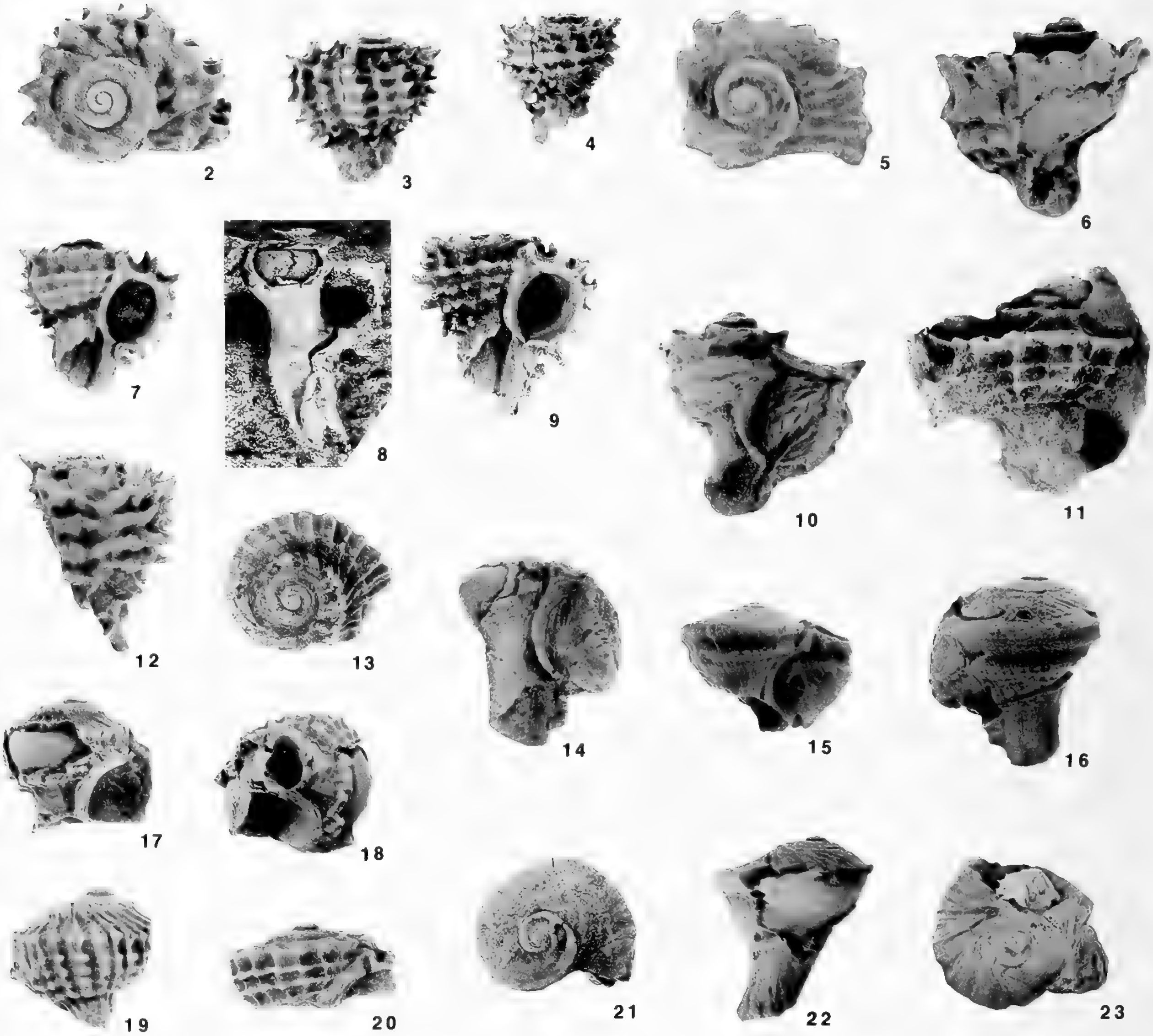
Garvie (1992) gave no reason for placing *Sargana* in the Cancellariidae. Shell shape, sculpture, and apertural features are sufficiently different that they can hardly have been the basis for this assignment, nor is the protoconch similar. For instance, the protoconch of *Cancellaria arnoldi* Dall, 1909, from the San Diego Formation of Pliocene age, San Diego, California, has more whorls and is higher than protoconchs of *Sargana* and *Praesargana,* and it lacks the carina present in sarganine protoconchs.

The protoconch of both *Sargana* and *Praesargana* is paucispiral, low, rapidly expanding, and becomes carinate after about one and a half whorls. In *Praesargana* the protoconch is slightly less flattened than in *Sargana.* In their paucispiral protoconchs, sarganines differ from the earliest representatives of most muricid groups in which multispiral protoconchs are present (Vokes, 1971). Whereas Muricinae and Rapaninae have multispiral protoconchs that probably indicate planktotrophic larvae (Kool, 1993b), the protoconchs of the Ocenebrinae, which appear slightly later in the geologic record, are paucispiral (Kool, 1993a, b). Kool (1993b) emphatically based his revision of the Rapaninae upon gross anatomy, radular, opercular, and protoconch morphology, and shell ultrastructure. He discussed placement of only one fossil genus, *Ecphora* Conrad, 1843, which he tentatively placed in Ocenebrinae Cossmann, 1903, because of its paucispiral protoconch, an assignment unequivocally endorsed by Vermiej & Kool (1994). The sarganine protoconch differs from that of rapanine, ocenebrine, and muricine protoconchs illustrated by Kool (1993a, b) in being very low-spired. Paucispiral protoconchs are also present in Pyropsinae (Sohl, 1964), and sarganine protoconchs are similar to those of the pyropsines *Pyropsis* Conrad, 1860, and *Napulus* Stephenson, 1941, in being paucispiral, rapidly expanding, and in becoming carinate after about one and a half whorls. Protoconchs of *Napulus* spp. and relatively high-spired *Pyropsis* spp. are not as flattened as the protoconch of *Sargana stantoni* (Weller, 1907). As pyropsines are included in Muricacea (Ponder & Warén, 1988), the protoconch of sarganines is similar to that of these muricaceans.

Sarganinae, comprising *Sargana* and *Praesargana,* have a paucispiral protoconch, a low spire, a rough-textured ornate shell, a fold on the columella, a very narrow anterior canal, the posterior siphonal notch adjacent to the suture rather than at the shoulder, and a moderate to wide umbilicus with a lacinate carina.

Genus *Praesargana* Saul & Popenoe, 1993

Type species: by original designation *Trophon condoni* White 1889, from the Turonian of northern California.



Figures 2–23

Figures 2–4, 7–9, 12 *Sargana stantoni* (Weller, 1907) hypotypes from LACMIP loc. 10326. 2–3, 7 LACMIP 12331, 2, apical view, ×2; 3, back view, ×1.5; 7, apertural view, ×1.5. 3, 9, 12 LACMIP 12332, 3, back view, ×1; 9, apertural view, ×1.5; 12, labral view, ×2. 8, LACMIP 12333, showing columellar fold, ×2. Figures 5–6, 10–11. *Praesargana* ***argentea*** Saul, sp. nov. all ×1.5. 5–6, 10, holotype, USNM 482399 from USGS loc. 2759; 5, apical view; 6, back view; 10, apertural view; 11, paratype, LACMIP 12324 from LACMIP loc. 16644, latex pull of back view. Figures 13, 17–20. *Praesargana* ***confraga*** Saul, sp. nov. all ×1. 13, 20, paratype LACMIP 12326 from LACMIP loc. 16524; 13, apical view, apparent rib on ramp is a crack formed during depression of the spire; 20, apertural view. 17–19, holotype LACMIP 12325 from CIT loc. 82; 17, apertural view; 18, umbilical view; 19, back view. Figures 14–16, 21–23. *Praesargana* ***kennedyi*** Saul, sp. nov. all ×1. 14, 16, 22, holotype LACMIP 12328 from CIT loc. 1292; 14, apertural view; 16, back view; 22, ablabral view. 15, 23, paratype LACMIP 12329 from CIT 1891; 15, apertural view; 23, apical view. 21, paratype LACMIP 12330 from CIT loc. 80, apical view.

Discussion: *Praesargana* was placed in Sarganidae because of its resemblance to *Sargana* Stephenson, 1923 (Saul & Popenoe, 1993) (Figures 2–4, 7–9, 12). As characteristic of *Praesargana* but not of *Sargana,* Saul & Popenoe (1993) listed: (1) no spiral sulcus at base of whorl; (2) finer, more regular, and not spiny sculpture; (3) smaller, shallower umbilicus; and (4) shorter, straighter, more open siphonal canal. Inclusion of the new species, *P.* ***argentea, P. con-***

fraga, and *P.* ***kennedyi,*** in *Praesargana* requires modification of this list of characteristics. The range of sculpture ascribed to *Praesargana* is expanded to include spines at the intersection of axial and spiral components as in *P.* ***argentea*** and spiral sculpture only, without any axial component, as in *P.* ***kennedyi.*** The length of the anterior siphon is a specific character. Width and depth of the umbilicus of *Praesargana* also vary by species, and the umbilicus may be as wide and deep as in *Sargana.*

Sargana and *Praesargana* are very similar. *Sargana* has a flatter protoconch. The whorl profile of *Praesargana* is angulate and widest at the shoulder, tapering toward the siphonal neck, rather than globose and abruptly constricted at the neck, as in *Sargana.* The spiral sulcus at the base of the whorl on *Sargana stantoni* is accentuated by spiral rows of spines above and below it. Stephenson (1923, 1952) and Sohl (1964) emphasized the importance of the spiral sulcus as characteristic of *Sargana.* Although on *Praesargana* ***confraga,*** a row of spines at the base of the whorl causes the neck to appear more abruptly constricted than in other *Praesargana, Praesargana* lacks the abrupt basal constriction and narrow spiral sulcus of *Sargana.*

Praesargana and *Sargana* have thus far been found in different areas. *Sargana stantoni* (Weller, 1907) is from the Campanian to early Maastrichtian (Sohl, 1964) of the Atlantic and Gulf Coasts of North America and *Sargana geversi* (Rennie, 1930) from the Senonian of Pondoland, South Africa (Sohl, 1964; Stephenson, 1941). *Praesargana* is thus far only known from Turonian deposits of the Pacific Slope of North America.

Praesargana ***argentea*** Saul, sp. nov.

(Figures 5–6, 10–11)

Diagnosis: A *Praesargana* with angular whorl profile and four strong spiral cords on the body whorl; suture not overlapping shoulder of previous whorl; varices foliate and forming spines at intersections with cords.

Description: Shell medium-sized, very low-spired; whorls angulate at shoulder, expanding rapidly; ramp barely sloping, concave to flat; suture abutting below shoulder of previous whorl; whorl sides slightly convex, sloping slightly inward from shoulder to anteriormost strong cord then strongly constricted; umbilicus moderately wide. Sculpture of four spinose, strong cords, strongest on shoulder, weakest at base of whorl; spiral cords crossed by about 14 foliate axials, forming spines at intersections with four major cords; shoulder spines strongest, flattened axially, elongate spirally, and bent apexward. Aperture rather quadrate, strongly constricted to form very narrow, bent, anterior siphonal canal; inner lip well demarked, detached from columella at base of body whorl, extending toward outer lip to form very narrow anterior canal; posterior siphonal notch well defined, at suture; outer lip apparently with denticle opposite columellar fold.

Type specimens: Holotype USNM 482399; paratype LACMIP 12324 from LACMIP loc. 16644.

Type locality: USGS loc. 2759, Ladd Canyon, near Silverado Canyon, Santa Ana Mountains, Orange County, California; Ladd Formation, basal Holz Shale Member.

Dimensions: Of holotype, height 21.8 mm; diameter 21.8 mm; spire height 3.6 mm.

Remarks: Description is based on the holotype, USNM 482399, the most complete of four available specimens. The paratype LACMIP 12324 is a rock mold. Some aspects of the sculpture show more clearly on a latex pull from this paratype than on the holotype. Two other poor but identifiable specimens are from LACMIP loc. 16645 and UCLA loc. 4235. The aperture of *P.* ***argentea*** is more angulate than that of *Praesargana condoni* or *Sargana stantoni* (Weller, 1907), especially at the shoulder, where the presence of a spine gives the aperture of *P.* ***argentea*** a more muricidlike aspect. Possibly a more mature specimen might develop a rounder aperture without an apparent siphon at the shoulder. The holotype of *P.* ***argentea*** is, however, larger than most specimens of *S. stantoni* and figured specimens of *S. geversi,* or *S.? tuberculosa* (Stoliczka, 1867). The sculpture of *P.* ***argentea*** differs from that of *P. condoni* and *S. stantoni* in having no spiral sculpture on the ramp and the axial elements and the spiral cords similarly spaced. *Praesargana* ***argentea*** lacks the secondary ribs of *P. condoni* and *S. stantoni* and has larger and fewer spines.

The protoconch is apparently present in the holotype, but the shell material is recrystallized, and no fine details are preserved. The early whorls resemble those of *S. stantoni* in being flattened and angulate. Among the four California *Praesargana* species, the spire of *P.* ***argentea*** is most like that of *S. stantoni* (Figures 3, 4, 7, 9, 12) in having the suture below the spinose shoulder. *Praesargana* ***argentea*** differs from *S. stantoni* in having a higher spire, a more angulate, straighter sided whorl with fewer cords, and no spiral sculpture or spines on the ramp. *Praesargana* ***argentea*** has a higher spire than either *P.* ***confraga*** or *P.* ***kennedyi.*** It differs from *P.* ***kennedyi*** in having foliate varices and four rather than two spiral cords. It differs from *P.* ***confraga*** and *P. condoni* in having fewer but stronger foliate varices, fewer but stronger spiral cords, and a whorl profile that is more strongly angulate and broader at the shoulder.

The holotype of *Praesargana* ***argentea*** was found in association with *Anchura (Helicaulax) tricosa* Saul & Popenoe, 1993, as were the two paratypes from the basal Holz Shale Member on the east side of Silverado Creek south of the old Holz Ranch.

Etymology: The specific name is from Latin, *argentum,* silver, and refers to the occurrence of this species in Silverado Canyon.

Praesargana **confraga** Saul, sp. nov.

(Figures 13, 17–20)

Diagnosis: A *Praesargana* with subangular whorl profile and four or five spiral cords on the body whorl; no spiral sculpture on ramp; suture overlapping the shoulder of the previous whorl; varices moderately foliate and forming low spines at intersection with cords.

Description: Shell medium-sized, very low-spired, whorl angulate at shoulder, expanding rapidly; ramp slightly sloping and concave; suture overlapping shoulder of previous whorl and forming nodular welt; whorl sides slightly convexly rounded below shoulder, constricted at base to form short, stout siphonal neck; umbilicus deep and moderately wide, bordered by a laciniate carina. Protoconch paucispiral, consisting of about two rapidly expanding whorls, becoming carinate, surrounding an apical dimple. Sculpture of four or five strong spiral cords, strongest on shoulder; spirals crossed by 23–28 foliate varices forming short spines at intersections with major cords. Aperture with posterior sinus and very narrow anterior canal; inner lip well demarked, thick; outer lip unknown.

Type specimens: Holotype LACMIP 12325 from CIT loc. 82; paratype LACMIP 12326 from LACMIP loc. 16524 Santa Ana Mountains; 12327 from LACMIP loc. 10873 (=CIT loc. 454) near Silverado Canyon, Santa Ana Mountains, Orange County, California.

Type locality: CIT loc. 82, south side Silverado Canyon, south of Holz Ranch, Santa Ana Mountains, Orange County, California, Ladd Formation, transition zone between Holz Shale and Baker Canyon Sandstone Members.

Dimensions: Of holotype LACMIP 12325, height 21.4 (lacking part of siphon), diameter about 23 mm, spire height 4.0 mm; of paratypes LACMIP 12326, height 9.8 (incomplete, lacks part of base and anterior siphon), diameter 26 mm, height of spire 3.4 mm (crushed); 12327 height 17.5 (incomplete, lacking anterior siphon), diameter 21 mm (lacking shell), height of spire 3.8 mm.

Remarks: *Presargana* **confraga** is described from four specimens. A specimen from CIT 454 is small and quite biangulate, suggesting that young *P.* **confraga** were biangulate, broader at the shoulder, and had the anterior angulation at the third spiral. A fifth specimen from CIT loc. 1064 is too poor to provide additional morphologic information. The most complete specimen is the holotype, which lacks the outer lip and part of the anterior canal. Paratype LACMIP 12326 also lacks the outer lip, and the base is broken off at the fourth spiral cord. Both of the other specimens lack most of the shell.

Praesargana **confraga** is similar to *P. condoni* in shape and sculpture, but *P.* **confraga** has a sharper shoulder, a wider and deeper umbilicus, fewer spiral cords and axial ribs, and spinier sculpture. It lacks spiral sculpture on the ramp. *Praesargana* **confraga,** which as an adult has a more rounded whorl and a more constricted base than other California species, has a whorl profile most like that of *S. stantoni.* The spires of these two are quite different, however, because the suture of *P.* **confraga** overlaps the shoulder of the earlier whorl rather than abutting below the shoulder spines. The spire of *P.* **confraga** also differs from that of *P.* **argentea,** which is similar to that of *S. stantoni. Praesargana* **confraga** has one more cord than *P.* **argentea** and two fewer than most *S. stantoni. Praesargana* **confraga** differs from *P.* **kennedyi** in having a more rounded shoulder, four or five strong cords rather than two on the body whorl, and varices that are spinose at the cords.

Etymology: The specific name is from Latin, *confragus,* broken, rough, uneven.

Praesargana **kennedyi** Saul, sp. nov.

(Figures 14–16, 21–23)

Diagnosis: A *Praesargana* with a very angulate whorl profile emphasized by a strong broad cord at the shoulder and having a second weak to moderately strong cord about 2 mm anterior to the shoulder and no axial varices.

Description: Shell of moderate size, thick, very low-spired; whorls strongly angulate at shoulder, rapidly expanding; ramp flat to barely sloping; suture at or barely below shoulder of previous whorl; whorl sides nearly flat, straightly sloping to siphonal neck; umbilicus deep, narrow. Protoconch paucispiral, consisting of about two rapidly expanding whorls, becoming flatly carinate, surrounding an apical dimple. Sculpture dominated by strong, broad cord at shoulder and lesser broad cord about 2 mm anterior to shoulder; fine axial and spiral threads forming fine cancellate pattern on whorl sides. Aperture roundish, subangulate at shoulder; inner lip thick, detached from columella at base of body whorl, rounding away from penultimate whorl toward outer lip; posterior siphonal notch well defined, at suture; outer lip bearing a strong denticulation at base of whorl opposite fold on columella; anterior siphonal canal very constricted, moderately long and deep.

Type specimens: Holotype LACMIP 12328, paratypes LACMIP 12329 from CIT loc. 1891, paratype LACMIP 12330 from CIT loc. 80.

Type locality: CIT loc. 1292, west side of Ladd Canyon approx. 0.8 km north of Silverado Canyon, Santa Ana Mountains, Orange County, California, Ladd Formation, Baker Canyon sandstone Member.

Dimensions: Of holotype, height 29 mm, diameter 25.4 mm (incomplete), spire height 3.8 mm; paratype 12329, height 20.7 mm (lacking anterior siphon), diameter 26.8 mm, spire height 3.7 mm; paratype 12330, height 14 mm (incomplete, lacking anterior siphon), diameter 24.7 mm, spire height 2.7 mm.

Remarks: Three specimens are assigned to this taxon; all are rather top-shaped and have a strong cord at the shoulder and a lesser, more anterior cord on the whorl flank. The spire varies from nearly flat to convex; sutures abut the shoulder flatly or are slightly stepped; strength of the cords differs between the three specimens. The absence of varices or axial ribs makes this species clearly distinct from other known *Praesargana.* The growth lines are very strong and give the surface a rough aspect. On all available specimens, the posterior portion of the outer lip is broken.

Etymology: The species is named for G. L. Kennedy.

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LITERATURE CITED

ACHARYYA, S. K. & T. C. LAHIRI. 1991. Cretaceous paleogeography of the Indian subcontinent; a review. Cretaceous Research 12:3–26, 5 figs.

ANDERSON, F. M. 1902. Cretaceous deposits of the Pacific Coast. California Academy of Sciences, Proceedings, Series 3, 2:1–154, pls. 1–12.

ANDERSON, F. M. 1958. Upper Cretaceous of the Pacific Coast. Geological Society of America, Memoir 71, 387 pp., 75 pls.

BASTEROT, M. B. DE. 1925. Description des Coquilles fossiles des environs de Bordeaux. Univalves. Société d'histoire naturelle de Paris, Mémoires 2:17–100, pls. 1–7.

CHENU, J. C. 1859–1862. Manuel de conchyliologie. Paris, v. 1, vii + 508 pp., 3707 figs. (1859); v. 2, 327 pp., 1236 figs. (1862).

CONRAD, T. A. 1843. Description of new genus and twenty-nine new Miocene and one Eocene fossil shells. Academy of Natural Sciences of Philadelphia, Proceedings 1:305–311.

CONRAD, T. A. 1860. Descriptions of new species of Cretaceous and Eocene fossils of Mississippi and Alabama. Academy of Natural Sciences of Philadelphia, Journal, Series 2, 4:275–298, 2 pls.

COSSMANN, M. 1901. Essais de Paléoconchologie Comparée. Vol. 4, 293 pp., 10 pls. Paris.

COSSMANN, M. 1903. Essais de Paléoconchologie Comparée. Vol. 5, 215 pp., 9 pls. Paris.

DALL, W. H. 1902. Illustrations and descriptions of new, unfigured, or imperfectly known shells, chiefly American, in the U.S. National Museum. United States National Museum, Proceedings, 24, number 1264:499–566, pls. 27–40.

DALL, W. H. 1909. Contributions to the Tertiary paleontology of the Pacific Coast. 1. The Miocene of Astoria and Coos Bay, Oregon. United States Geological Survey, Professional Paper 59, 278 pp., 23 pls.

GABB, W. M. 1864. Description of the Cretaceous fossils. California Geological Survey, Palaeontology 1:57–243, pls. 9–32.

GARVIE, C. L. 1991. Two new species of Muricinae from the Cretaceous and Paleocene of the Gulf Coastal Plain, with comments on the genus *Odontopolys* Gabb, 1860. Tulane Studies in Geology and Paleontology 24:87–92. 1 pl.

GARVIE, C. L. 1992. A second Cretaceous muricid from the Gulf Coastal Plain. Tulane Studies in Geology and Paleontology 25:187–190. 1 text-fig.

GRAY, J. E. 1853. On the division of ctenobranchous gasteropodous Mollusca into larger groups and families. The Annals and Magazine of Natural History, Series 2, 11 (57): 124–133, 10 figs.

JOUSSEAUME, F. 1880. Division méthodique de la famille des Purpuridés. Le Naturaliste, Année 2, no. 42:335–336.

KOOL, S. P. 1993a. The systematic position of the genus *Nucella* (Prosobranchia: Muricidae: Ocenebrinae). The Nautilus 107: 43–57, 65 figs.

KOOL, S. P. 1993b. Phylogenetic analysis of the Rapaninae (Neogastropoda Muricidae). Malacologia 35:155–259, 30 figs.

LINNAEUS, C. 1758. Systema naturae per regna tria naturae. Editio decima, reformata. Stockholm, v. 1, Regnum animale, 824 pp.

LINNAEUS, C. 1766–1767. Systema naturae per regna tria naturae. Editio duodecima, reformata. Stockholm, v. 1, Regnum animale. Pt. 1:1–532 (1766); pt. 2:533–1327 (1767).

MATSUMOTO, T. 1959. Upper Cretaceous ammonites of California. Part II. Kyushu University, Faculty of Science, Memoirs, Series D, Geology, Special Volume 1:1–172, 41 pls., 80 text figs.

MATSUMOTO, T. 1960. Upper Cretaceous ammonites of California. Part III. Kyushu University, Faculty of Science, Memoirs, Series D, Geology, Special Volume 2:1–204, 2 pls., 20 text figs.

MERRIAM, C. A. 1941. Fossil turritellas from the Pacific Coast region of North America. University of California Publications, Department of Geological Sciences, Bulletin 26:1–214, pls. 1–41, 19 figs.

MORTON, P. K., R. V. MILLER & D. L. FIFE. 1973. Preliminary geo-environmental maps of Orange County, California. California Division of Mines & Geology, Preliminary Report 15, 4 pls.

PACKARD, E. L. 1922. New species from the Cretaceous of the Santa Ana Mountains, California. University of California Publications, Department of Geological Science, Bulletin 13: 413–462, pls. 24–38.

PETUCH, E. J. 1988. Field Guide to the Ecphoras. Coastal Education and Research Foundation [CERF], Charlottsville, Virginia, 140 pp., pls. A1–A3, text figs. 1–52 + 10 unnumbered figs.

PONDER, W. F. & A. WARÉN. 1988. Classification of the Caenogastropoda and Heterostropha—a list of the family-group names and higher taxa. Malacological Review, Supplement 4, Appendix: 288–326.

POPENOE, W. P. 1937. Upper Cretaceous Mollusca from southern California. Journal of Paleontology 11:379–402, pls. 45–49.

POPENOE, W. P. 1942. Upper Cretaceous formations and faunas of Southern California. American Association of Petroleum Geologists, Bulletin 26:162–187, 4 text figs.

POPENOE, W. P. 1957. The Cretaceous gastropod genus *Biplica.* University of California Publications in Geological Sciences 30:425–454, pls. 50–51.

RAFINESQUE, C. S. 1815. Analyses de la nature ou tableau de l'universe et des corps organisées. Barravecchia, Palermo. 224 pp. [Reprinted, 1984, American Malacological Union].

RENNIE, J. V. L. 1930. New Lamellibranchia and Gastropoda from the Upper Cretaceous of Pondoland, with an appendix on some species from the Cretaceous of Zululand. South African Museum, Annals 28:159–260, pls. 16–31.

RÖDING, P. F. 1798. Museum Boltenianum. . .: pars secunda continens Conchylia . . . .J. C. Trappii, Hamburg, 109 pp.

ROSENBERG, G. & R. E. PETIT. 1987. Ryckholt's *Mélanges Paléontologiques,* 1851–1862, with a new name for *Tudicula* H. & A. Adams, non Ryckholt. Academy of Natural Sciences of Philadelphia, Proceedings 139:53–64.

SAUL, L. R. 1982. Water depth indications from Late Cretaceous mollusks, Santa Ana Mountains, California. Pp. 69–76, 3 text figs in D. J. Bottjer, I. P. Colburn & J. D. Cooper (eds.), Late Cretaceous Depositional Environments and Paleogeography, Santa Ana Mountains, Southern California. Society of Economic Paleontologists and Mineralogists, Pacific Section, Annual Convention field guidebook & volume.

SAUL, L. R. 1988. Latest Cretaceous and early Tertiary Tudiclidae and Melongenidae (Gastropoda) from the Pacific Slope of North America. Journal of Paleontology 62:880–889, 4 figs.

SAUL, L. R. 1995. Muricacean? gastropods of Late Cretaceous (Turonian) age from the Santa Ana Mountains, California. Western Society of Malacologists, Annual Report 27:9–11, 1 table.

SAUL, L. R. & D. J. BOTTJER. 1982. Late Cretaceous megafossil locality map, northern Santa Ana Mountains, California. Pp. 77–80, 3 maps in D. J. Bottjer, I. P. Colburn & J. D. Cooper (eds.), Late Cretaceous Depositional Environments and Paleogeography, Santa Ana Mountains, Southern California. Society of Economic Paleontologists and Mineralogists, Pacific Section, Annual Convention field guidebook & volume.

SAUL, L. R. & W. P. POPENOE. 1993. Additions to Pacific Slope Turonian Gastropoda. The Veliger 36:351–388, 138 figs.

SCHUMACHER, C. F. 1817. Essai d'un nouveau système des habitations de vers testacés. Copenhagen. 287 pp.

SHUMARD, B. F. 1859. Descriptions of new fossils from the Tertiary Formations of Oregon and Washington Territories and the Cretaceous of Vancouver's Island, collected by Dr. Jno. Ivans, U.S. Geologist, under instructions from the Department of the Interior. Academy of Sciences of St. Louis, Transactions 1:120–125.

SOHL, N. F. 1964. Neogastropoda, Opisthobranchia, and Basommatophora from the Ripley, Owl Creek, and Prairie Bluff Formations. United States Geological Survey, Professional Paper 331B: iv + 153–344, pls. 19–52, figs. 12–18.

STEPHENSON, L. W. 1923. The Cretaceous Formations of North Carolina. Part I. Invertebrate fossils of the Upper Cretaceous Formations. North Carolina Geological and Economic Survey 5:xii+ 604 pp., 102 pls., 6 figs.

STEPHENSON, L. W. 1941. The larger invertebrate fossils of the Navarro Group of Texas. University of Texas Publication 4101, 641 pp., 95 pls.

STEPHENSON, L. W. 1952. Larger invertebrate fossils of the Woodbine Formation (Cenomanian) of Texas. United States Geological Survey, Professional Paper 242, 226 pp., 59 pls.

STOLICZKA, F., 1867. Cretaceous fauna of southern India. Volume 2, The Gastropoda, pt. 1–4. India Geological Survey, Memoirs, Palaeontologia Indica, series V, Pp. 1–204, pls. 1–16.

TRACEY, S., J. A. TODD & D. H. ERWIN. 1993. Mollusca: Gastropoda. Pp. 131–167 in M. J. Benton (ed.), The Fossil Record 2. Chapman & Hall: London.

VERMEIJ, G. J. & S. P. KOOL. 1994. Evolution of labral spines in *Acanthais,* new genus, and other rapanine muricid gastropods. The Veliger 37:414–424, 9 figs.

VOKES, E. 1971. The geologic history of the Muricinae and the Ocenebrinae. The Echo (Annual Report of the Western Society of Malacologists) 4:37–54, 6 figs.

WADE, B. 1917. An Upper Cretaceous *Fulgur.* American Journal of Science, Series 4, 43:293–297, figs 1–2.

WADE, B. 1926. The fauna of the Ripley Formation on Coon Creek, Tennessee. United States, Geological Survey, Professional Paper 137, 272 pp., 72 pls.

WELLER, S. 1907. A report on the Cretaceous Paleontology of New Jersey. New Jersey Geological Survey, Paleontology series, v. 4, 871 pp. 111 pls.

WELLS, J. W. 1956. Scleractinia. Pp. F328–F369 in R. C. Moore (ed.), Treatise on Invertebrate Paleontology, Part F, Coelenterata. Geological Society of America and University of Kansas Press: Lawrence, Kansas.

WHITE, C. A. 1889. On invertebrate fossils from the Pacific Coast. United States Geological Survey, Bulletin 51:102 pp., 14 pls.

LOCALITIES CITED

CIT localities have been given LACMIP numbers. Most of the CIT and UCLA localities of the northern Santa Ana Mountains were plotted on Popenoe, 1942: fig. 2, and Saul & Bottjer, 1982: maps 1–3.

80 CIT (= LACMIP 8194): In sandstone above cgl., at fork of Silverado and Ladd Canyons on north side of Silverado Canyon, NW ¼, SW ¼ sec.8, T. 5 S, R. 7 W, El Toro quadrangle Santa Ana Mountains, Orange County, California. Coll: B. N. Moore, 1926. Ladd Formation, Baker Canyon Sandstone Member. Turonian

82 CIT (= LACMIP 8195): Limey sandstone bed near base of shale, south of roadcut at Holz's Ranch (locality may become obscured by slides), Silverado Canyon, east edge of SE ¼, SE ¼, sec.7, T. 5 S, R. 7 W, El Toro quadrangle, Santa Ana Mountains, Orange County, California. Coll: B. N. Moore, 1927 Ladd Formation, Holz-Baker Canyon transition. Turonian.

454 CIT (= LACMIP 10873): Cretaceous shale, fireline about Hough's 80 on south side of stream, about 400′ (?) above creek, Silverado Canyon, 450′S, 875′E of NW cor. sec.16, T. 5 S, R. 7 W, Santiago Peak quadrangle, Santa Ana Mountains, Orange County, California. Coll: B. N. Moore, August, 1929. Ladd Formation, lower Holz Shale Member. Turonian.

1064 CIT (= LACMIP 10893): Area south of Harding Canyon, Vulture Crags, lower part of shale section just north of first large canyon cutting across Cretaceous beds south of Harding Canyon, about 2 mi. S42°E of the dam in Harding Canyon and 6800′ N55°E of juncture of Santiago Creek and Trabuco Canyon Rds., 2600′N, 1625′E of SW cor. sec.34,

T. 5 S, R. 7 W, Santiago Peak quadrangle, Santa Ana Mountains, Orange County, California. Coll: W. P. Popenoe, October 14, 1934. Ladd Formation, lower Holz Shale Member. Turonian.

1292 CIT (= LACMIP 8177): Bluffs at base of Baker Canyon Sandstone, ½ mi. north of Silverado Canyon, west side Ladd Canyon, 1800′S, 600′E of NW cor. sec.8, T. 5 S, R. 7 W, Black Star Canyon quadrangle, Santa Ana Mountains, Orange County, California. Coll: W. P. Popenoe, April, 1936. Ladd Formation, Baker Canyon Sandstone Member, lowermost fossiliferous beds. Turonian.

1891 CIT (= LACMIP 10111): Just south across gully from locality CIT 1290, Holz Ranch Silverado Canyon, about 2675′S, 725′W of NE cor. sec.7, T. 54 S, R. 7 W, Black Star Canyon quadrangle, Santa Ana Mountains, Orange County, California. Coll: W. P. Popenoe, March 1939. Ladd Formation, transitional beds top of Baker Canyon Sandstone or base of Holz Shale Member. Turonian.

2759 USGS: Near Silverado Canyon, in lower part of Ladd Canyon, Santa Ana Mountains, Orange County, California. Coll: S. Bowers, April 24, 1903. Ladd Formation, Baker Canyon Sandstone Member. Turonian.

4235 UCLA: Dip slope of Baker Canyon Sandstone cropping out about 0.3 mi. NW of old Holz Ranch house, 2600′N, 700′W of SE cor. sec.7, T. 5 S, R. 7 W, Black Star Canyon quadrangle, Santa Ana Mountains, Orange County, California. Coll: W. P. Popenoe. Ladd Formation, Baker Canyon Sandstone Member. Late Turonian.

10386 LACMIP: Coon Creek, type locality, 36 inches to 51 inches above base, McNairy County, Tennessee. Coll: H. A. Lowenstam, October 23, 1955. Ripley Formation. Late Campanian, *Nostoceras hyatti* zone.

16524 LACMIP: Santa Ana Mountains (precise locality unknown), Orange County, California. Coll: UCLA summer field student, 1948. Ladd Formation, Baker Canyon Sandstone Member. Turonian.

16644 LACMIP: Silverado Creek, S of Holz Ranch, about 0.15 km S of Silverado Canyon Road, W side of narrows, E side of creek, near W line sec. 8, 0.23 km N of SW cor. sec.8, T. 5 S, R. 7 W, El Toro quadrangle, U.S.G.S., 1968, Santa Ana Mountains, Orange County, California. Coll: W. P. Elder, L. R. Saul, & W. V. Sliter, March 23, 1994. Ladd Formation, basal Holz Shale Member. Turonian.

16645 LACMIP: Silverado Creek S of Holz Ranch, about 90 m N of bend to W, E side of creek near E line of sec.7, 0.225 km N of SE cor. sec.7, T. 5 S, R. 7 W, El Toro quadrangle, U.S.G.S., 1968, Santa Ana Mountains, Orange County, California. Coll: L. R. Saul, March 23, 1994. Ladd Formation, basal Holz Shale Member. Late Turonian.

Note added in proof:

M. G. Harasewych has just written that he has recently dissected preserved specimens of the type species of *Tudicla*, and its anatomy is that of a buccinid.

The Veliger 39(2):136–141 (April 1, 1996)

THE VELIGER

Protoconch of the Rare Ovulid Gastropod *Cypraeogemmula warnerae* Effinger, 1938, from the Eocene of Western Washington

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Abstract. The protoconch of the small, rare gastropod *Cypraeogemmula warnerae* Effinger, 1938, is illustrated for the first time; the pattern of rhombs indicates that this genus belongs to family Ovulidae. Only well-preserved specimens of this species show the protoconch. This new information is based on recently collected specimens from lower Eocene rocks of western Washington.

The genus *Cypraeogemmula* is only known from two species, *C. warnerae* from the lower to upper Eocene of western Washington and *C. liliputana* (Schilder, 1922) from the lowermost Oligocene of northern Germany. Previously, *C. warnerae* was known only from the upper Eocene of western Washington.

INTRODUCTION

The small ovulid gastropod *Cypraeogemmula warnerae* Effinger, 1938, is a rare species from Eocene rocks in western Washington (Effinger, 1938; Durham, 1944; Squires & Goedert, 1995) (Figure 1). Recent collecting in western Washington has yielded a few additional specimens of this species. Some of these specimens are well preserved and show the protoconch, which has not been previously illustrated for the genus.

Only two species-level taxa are known for the genus *Cypraeogemmula*. Other than *C. warnerae* from Washington, the remaining taxon is *C. liliputana* (Schilder, 1922), from Lattorf, northern Germany. The Lattorf area is the stratotype of the Lattorfian Stage, and, based on studies of calcareous nannofossils, Berggren et al. (1985) assigned this stratotype to the lowermost Oligocene.

The molluscan stages for the Pacific coast of North America used in this report stem mainly from Clark & Vokes (1936), who proposed five mollusk-based Eocene stages, namely, "Meganos" (lowermost Eocene), "Capay" (middle lower Eocene), "Domengine" (upper lower to lower

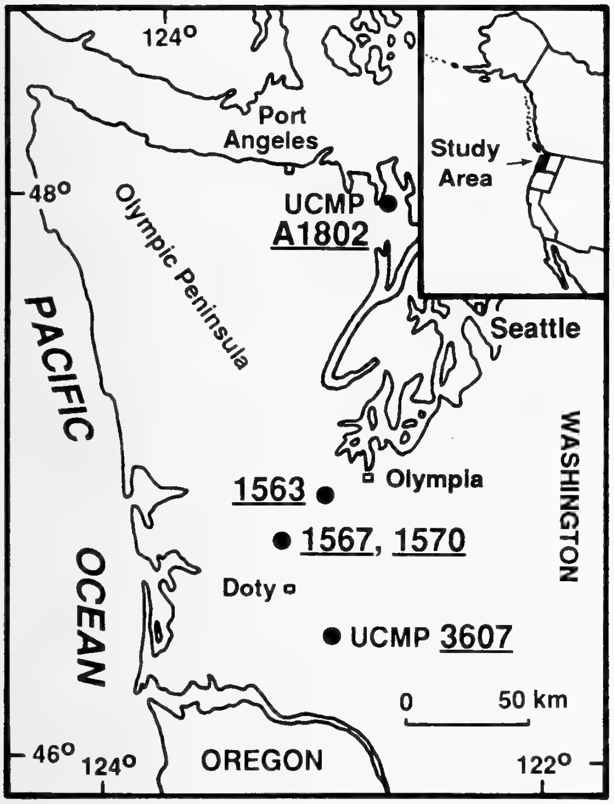


Figure 1

Index map to localities where *Cypraeogemmula warnerae* Effinger, 1938, has been found. Unless otherwise noted, localities are CSUN localities.

middle Eocene), "Transition" (lower middle Eocene), and "Tejon" (middle middle Eocene to upper Eocene). The stage names are placed in quotes because they are informal terms and generally the same as formation names. Givens (1974) modified the use of the "Capay Stage," and it is in this modified sense that the "Capay Stage" is used herein. The upper Eocene to lower Oligocene Pacific Northwest Galvinian Stage (= upper part of the "Tejon Stage") of Armentrout (1975) is also used in this report.

Abbreviations used for catalog and/or locality numbers are: CSUN, California State University, Northridge; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; UCMP, University of California Museum of Paleontology (Berkeley); UW, University of Washington, Seattle.

SYSTEMATIC PALEONTOLOGY

Superfamily CYPRAEACEA Rafinesque, 1815

Family OVULIDAE Fleming, 1822

Discussion: We use the classification of Ponder & Warén (1988) herein. Dolin (1991a) noted that the family Ovulidae is characterized by a multispiral planktotrophic protoconch with a sinusigeriform aperture and obliquely decussate sculpture. Bandel & Riedel (1994) confirmed that protoconch sculpture in the Ovulidae is distinguished by a pattern of rhombs, different from the coarsely cancellate protoconch found in the closely related family Cypraeidae. Bandel & Riedel (1994) also reported that, although the protoconchs of Ovulidae have a sinusigeriform aperture, this type of aperture is known from many gastropod taxa and usually cannot be used to characterize taxa higher than the species level.

We prefer not to assign *C. warnerae* to a subfamily until the diagnostic morphologic characters of the subfamilies of Ovulidae are more completely understood.

Genus *Cypraeogemmula* Vredenburg, 1920

Type species: *Trivia scabriuscula* Koenen, 1890 [non *Trivia scabriuscula* (Gray, 1827)], = *Cypraea liliputana* Schilder, 1922, by monotypy, early Oligocene, Lattorf, northern Germany.

Koenen's (1890) name *Trivia scabriuscula* is a secondary homonym because Gray's (1827) name *Cypraea scabriuscula* is known to belong to the genus *Trivia.* Vredenburg (1920:114) used Koenen's species name when he proposed the type species of genus *Cypraeogemmula.* The replacement name, *Cypraea liliputana* Schilder, 1922, for Koenen's name was allocated to genus *Cypraeogemmula* by Schilder (1927).

Cypraeogemmula warnerae Effinger, 1938

(Figures 2–8)

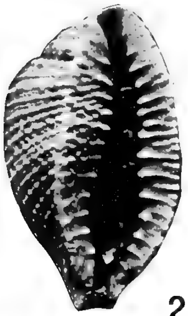
Cypraeogemmula warnerae Effinger, 1938:381, pl. 47, figs. 29, 35; Weaver, 1942 [1943]:394–395, pl. 77, fig. 2; Durham, 1944:117, 165; Schilder, 1961:147; Schilder & Schilder, 1971:22, 168; Groves, 1993:12; Squires & Goedert, 1995:table 1.

Holotype: UCMP 33588, lost (D. R. Lindberg, personal communication).

Type locality: "Gries Ranch beds" in the lower part of the Lincoln Creek Formation, UCMP loc. 3607, Lewis County, western Washington.

Geographic distribution: Jefferson, Thurston, and Lewis counties, western Washington.

Stratigraphic distribution: "Capay Stage" (middle lower Eocene) to Galvinian Stage (upper Eocene part). "CAPAY STAGE": Upper part of the Crescent Formation, Black Hills, Thurston County, western Washington (herein). MIDDLE EOCENE: Transition beds between the upper part of the Crescent Formation and the overlying lower part of the McIntosh Formation, northern Doty Hills, Lewis County, western Washington (Squires & Goedert, 1995). GALVINIAN STAGE: "Gries Ranch beds" in the lower part of the Lincoln Creek Formation, near Vader, Lewis County, western Washington (Effinger, 1938); lower part of the Quimper Sandstone, Discovery Bay,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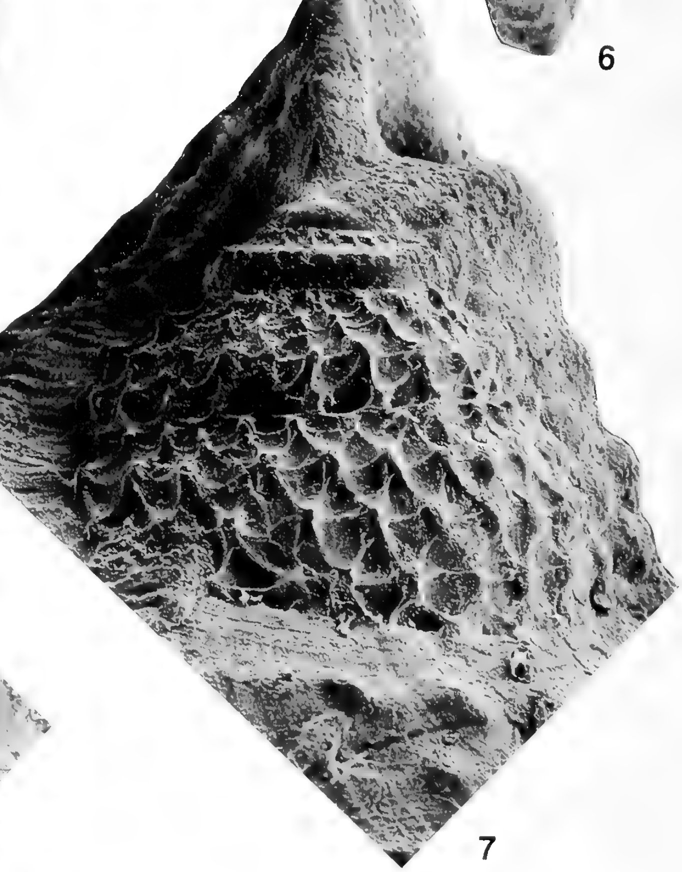
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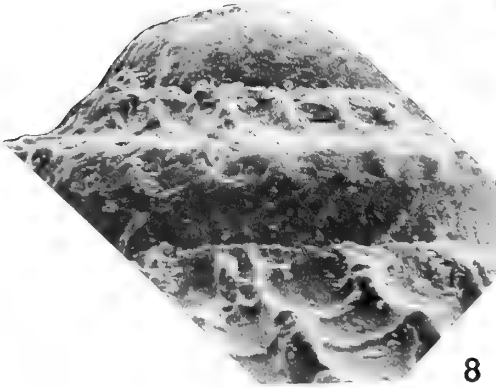
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Quimper Peninsula, Jefferson County, western Washington (Effinger, 1938; Durham, 1944).

Discussion: Ten specimens were found during the course of this present study. A single, exceptionally well preserved specimen 3 mm in height, was found at CSUN loc. 1563 in the upper part of the Crescent Formation in the Larch Mountain area, Black Hills, near Olympia, western Washington (Figures 2–8). Seven specimens were found at CSUN loc. 1567, and two were found at CSUN loc. 1570. Both of these localities are in the transition zone between the Crescent Formation and the McIntosh Formation in the northern Doty Hills area, Thurston County, western Washington. Preservation of the specimens at CSUN loc. 1567 is generally poor to good; two specimens show the protoconch. Preservation of the specimens at CSUN loc. 1570 is overall very good.

The specimens of *Cypraeogemmula warnerae* found during the course of this present study range from 2 to 5 mm in height. The spire is visible only on juvenile or early adult specimens. On more mature specimens between 4.5 and 5 mm in height, the spire is involute and completely obscured by the subsequent whorls. The lost holotype of *C. warnerae* measured 4.1 mm in height, and published illustrations of it (Effinger, 1938:pl. 47, figs. 29, 35; Weaver, 1942 [1943]:pl. 77, fig. 2) show no hint of a spire. Durham (1944:165) designated three non-figured referred specimens of *C. warnerae* (UCMP 35334–35336) from UCMP loc. A1802 in the lower part of the Quimper Sandstone, Quimper Peninsula, Jefferson County, western Washington. Specimen 35334 is 3.5 mm in height and shows a few of the spire whorls, although the shell is missing on the spire. Specimen 35335 is 5.5 mm in height and is the largest known specimen of *C. warnerae.* This poorly preserved specimen would have been involute if the posterior part of the shell had not been worn off, thereby exposing the spire. The third referred specimen is a worn fragment.

The holotype, Durham's three referred specimens, and specimens collected during the course of this present study indicate that adult specimens of *C. warnerae* are about 3 mm or greater in height, and the most mature specimens have an involute spire.

Effinger (1938) briefly described the spire of *C. warnerae,* so we assume that he observed juvenile or early adult specimens. Unfortunately, he did not illustrate any of them as paratypes, nor did he assign any of them catalog numbers for future study. Based on an extremely well preserved specimen from CSUN loc. 1563, as well as additional specimen from CSUN loc. 1567, the following additional information can now be added: protoconch (= spire in this species), approximately 0.4 mm long, multispiral (four whorls), inclined to the right side, and entire right side covered by the body whorl; initial whorl of protoconch low, rounded, smooth, and naticiform; second whorl of protoconch tabulate with oblique axial sculpture anterior to the tabulation and with no ornamentation posterior to the tabulation, third and fourth whorls of protoconch with oblique decussate (rhomboidal) axial sculpture crossed by four to five spiral ribs, each spiral rib bisecting a rhomb and thereby producing a distinctive triangular pattern; protoconch set off from rest of teleoconch by a smooth "shelf."

Effinger (1938) and Weaver (1942[1943]) assigned *C. warnerae* to family Cypraeidae, but the pattern of rhombs observable on the protoconch of *C. warnerae* indicates that this species is an ovulid rather than a cypraeid. The rhomb pattern of *C. warnerae* is very close to that in other ovulids (Pezant, 1910:pl. 14, figs. 14a–c; 1911:24; Liltved, 1989: fig. 226; Dolin, 1991b:fig. 2b; Bandel & Reidel, 1994:pl. 8, fig. 10; text fig. 10). The rhomb pattern of *C. warnerae* is very different from the cypraeid cancellate pattern, which is illustrated in Bandel & Reidel (1994:pl. 8, fig. 9).

The type locality of *C. warnerae* is in the "Gries Ranch beds." Durham (1944) assigned these beds to his *Molopophorus stephensoni* Zone. Armentrout (1975) assigned this zone to the middle part of his Galvinian Molluscan Stage of late Eocene age and included the "Gries Ranch beds" in the lower part of the Lincoln Creek Formation.

Effinger (1938:table 1) listed *C. warnerae* as also present at Woodman Wharf on the Quimper Peninsula, Jefferson County, western Washington. Durham (1944:112) reported that UCMP loc. A1802 is the same as "Woodman Wharf." Durham (1944:117), furthermore, found six specimens of *C. warnerae* at UCMP loc. A1802 and reported that this locality is from his *Molopophorus stephensoni* Zone.

The specimens of *C. warnerae* from CSUN loc. 1563 are from rocks in the upper part of the Crescent Formation that Squires & Goedert (1994, in press) assigned to the "Capay Stage" (middle lower Eocene). The specimens of *C. warnerae* from CSUN locs. 1567 and 1570 are from

←

Explanation of Figures 2 to 8

SEM micrographs = Figures 5–8. All non-SEM specimens coated with ammonium chloride. Figures 2–8. *Cypraeogemmula warnerae* Effinger, 1938, LACMIP catalog number 11372, CSUN loc. 1563 [= LACMIP 16655], height 3 mm. Figure 2. Apertural view, ×13.3. Figure 3. Oblique apical view, low-level lighting used to show "shelf" that separates protoconch from the teleoconch, ×15. Figure 4. Abapertural view, ×13.3. Figure 5. Abapertural view, ×40. Figure 6. Left-lateral view, ×40. Figure 7. Left-lateral view of protoconch, ×150. Figure 8. Left-lateral view of apical part of protoconch, ×400.

transition beds between the upper part of the Crescent Formation and the overlying lower part of the McIntosh Formation; Squires & Goedert (1995) assigned these transition beds to the middle Eocene.

Apparently *Cypraeogemmula warnerae* inhabited shallow-water marine environments even though its shells can be found in deep-water deposits. Although Effinger (1938) considered the "Gries Ranch beds" to represent a warm-water nearshore or littoral environment, Hickman (1984) believed that these beds, as well as the Quimper Sandstone, were probably deposited in deep water, subject to the influx of nearshore mollusks that were transported downslope. Squires & Goedert (1995) interpreted the depositional environment of CSUN locs. 1567 and 1570 as having been on the flank of an oceanic volcanic island in outer shelf to upper slope (bathyal) muds subject to the influx of shells of nearshore and shallow-marine megainvertebrates (mollusks, solitary corals, etc.) and pebbly basalt debris. Squires & Goedert (1994, in press) interpreted the depositional environment of CSUN loc. 1563 as adjacent to a rocky shoreline formed by the extrusion of basalt. Warm-water, shallow-marine mollusk shells and colonial corals were transported only a short distance and deposited in muddy matrix coquina that filled cracks between boulders of basalt. This last locality provides the best control as to the paleoecology of *C. warnerae*. We conclude that this species was a shallow-water marine species, even though it commonly ended up being transported into deeper waters. Its small size could have easily contributed to its being transported. Most extant species of ovulids are warm-water, shallow-marine forms that prey upon stony corals (either solitary or reef type) or on gorgonians (Keen, 1971).

The teleoconch morphology of *Cypraeogemmula liliputana* (Schilder, 1922) is very close to *C. warnerae*. The largest known specimens of *C. liliputana* are 3.2 mm in height. Based on illustrations and/or descriptions of the 3 mm-high holotype of *C. liliputana* (Koenen, 1890:565–566, pl. 39, figs. 8a–c; Wenz, 1941:1001, fig. 2874), the teleoconch of *C. liliputana* has a more projecting anterior canal, a more rectangular-shaped aperture, and more widely spaced primary spiral ribs. Although the spire is somewhat visible on the illustrations of the holotype of *C. liliputana*, the details are not discernible. Koenen (1890:565), in the description of this species, referred to the spire as consisting of four smooth, convex whorls that are inclined and attached to the body whorl. The relationship of the spire to the body whorl is the same as in *C. warnerae*. Koenen's (1890) description of the spire as smooth must have been based on observations without the aid of magnification. We concur with Schilder (1961) and Schilder & Schilder (1971) that *Cypraeogemmula liliputana* and *C. warnerae* both belong to the genus *Cypraeogemmula*. Vredenburg (1920) did not base his definition of this genus on protoconch characters, but knowing these characters is crucial in familial assignment. As discussed above, our studies of the protoconch of *C. warnerae* now allow assignment of the genus *Cypraeogemmula* to the family Ovulidae. If the whereabouts of the holotype of *C. liliputana* ever becomes known or when suitable material becomes available, it would be helpful to have SEM micrographs of the spire of this species. We predict that its spire will be found to show rhombs as in the otherwise similar *C. warnerae*.

ACKNOWLEDGMENTS

Gail H. Goedert helped collect the fossils. David R. Lindberg (UCMP) loaned hypotype specimens. Suzanne Henderson and Jean Crampon (Alan Hancock Foundation, University of Southern California) aided in locating rare and/or obscure references. Daniel Geiger (University of Southern California, Department of Biology) kindly translated parts of Koenen (1890) and Schilder (1961). James H. McLean (LACM Malacology) and LouElla Saul (LACMIP) reviewed early drafts of the manuscript. Two anonymous reviewers critically evaluated the manuscript and made valuable comments.

LOCALITIES CITED

CSUN 1563 [= LACMIP loc. 16655]. At elevation of 680 m (2230 ft.), exposed in roadcut on NE side of logging road, 300 m N and 50 m E of SW corner of section 1, T. 17 N, R. 4 W, and 500 m S32°E of Larch Mountain, 47°59′03″N, 123°8′W, U.S. Geological Survey, 7.5-minute, Capitol Peak Quadrangle, provisional edition 1986, Black Hills, Thurston County, western Washington. Crescent Formation. Age: Middle early Eocene ("Capay Stage"). Collectors: J. L. & G. H. Goedert, 1992–1994; J. L. Goedert & S. R. Benham, 1995 (Squires & Goedert, 1994).

CSUN 1567, 1570 [= LACMIP locs. 16849, 16850]. Localities are about 4 m apart, in ascending stratigraphic order, in a quarry at E end of bluff overlooking W side of Garrard Creek, 46 m N and 518 m W of SE corner of section 21, T. 15 N, R. 5 W, U.S. Geological Survey, 7.5-minute, Cedarville Quadrangle, 1986, northern Doty Hills, extreme NW corner of Lewis County, western Washington. Transition zone between the upper part of the Crescent Formation and the overlying lower member of the McIntosh Formation. Age: Middle Eocene. Collectors: J. L. & G. H. Goedert, 1993–1994 (Squires & Goedert, 1995).

UCMP 3607 [= UW 239]. South bank of Cowlitz River at old Gries Ranch, section 25, T. 11 N, R. 2 W, U.S. Geological Survey, 15-minute, Castle Rock Quadrangle, 1953, Lewis County, western Washington (Effinger, 1938:fig. 2; Weaver, 1942 [1943]). "Gries Ranch beds" in the lower part of the Lincoln Creek Formation. Age: Late Eocene. Collector: W. L. Effinger, circa middle 1930s.

UCMP A1802. On beach 0.4 km N of Woodman's Station (= Woodman Wharf), Discovery Bay, SW 1/4 of NE 1/4 of section 8, T. 29 N, R. 1 W, U.S. Geological

Survey, 7.5-minute, Port Townsend South Quadrangle, 1981, southwestern Quimper Peninsula, Jefferson County, western Washington (Effinger, 1938; Durham, 1944). Lower part of the Quimper Sandstone. Age: Late Eocene. Collector: W. L. Effinger?, circa middle 1930s (Effinger, 1938; Durham, 1944).

LITERATURE CITED

Armentrout, J. M. 1975. Molluscan biostratigraphy of the Lincoln Creek Formation, southwest Washington. Pp. 14–48, figs. 1–7 in D. W. Weaver, G. R. Hornaday & A. Tipton (eds.), Paleogene Symposium & Selected Technical Papers, Conference on Future Energy Horizons of the Pacific Coast. Pacific Sections, American Association of Petroleum Geologists, Society of Economic Paleontologists and Mineralogists, and Society of Economic Geologists.

Bandel, K. & F. Riedel. 1994. Classification of fossil and Recent Calyptraeoidea (Caenogastropoda) with a discussion on neomesogastropod phylogeny. Berliner Geowissenschaftliche Abhandlungen, Reihe A, 13:329–367, figs. 1–11b, pls. 1–8.

Berggren, W. A., D. V. Kent & J. J. Flynn. 1985. Jurassic to Paleogene: Part 2, Paleogene geochronology and chronostratigraphy. Pp. 141–195 in N. J. Snelling (ed.), The Chronology of the Geological Record. Blackwell Scientific Publications: Oxford, England.

Clark, B. L. & H. E. Vokes. 1936. Summary of marine Eocene sequence of western North America. Bulletin of the Geological Society of America 47:851–878, figs. 1–3, pls. 1–2.

Dolin, L. 1991a. *Cypraedia (Eucypraedia) multicarinata* (Dall, 1890); a late Eocene Ovulidae from Florida, Mississippi, Colombia, and Peru. Mississippi Geology 12(3–4):28–31, figs. 1–3.

Dolin, L. 1991b. Mollusca Gastropoda: *Cypraeopsis superstes* sp. nov., Pediculariinae relique du bathyal de nouvell-Calédonie et de la Réunion. Pp. 179–186, figs. 1–7 in A. Crosnier & P. Bouchet (eds.), Résultats des Campagnes MUSORSTOM, vol. 7. Muséum National d'Histoire Naturelle (Paris), Mémoire série A (Zoologie) 150. [English summary].

Durham, J. W. 1944. Megafaunal zones of the Oligocene of northwestern Washington. University of California Publications Bulletin of the Department of Geological Sciences 27(5):101–212, figs. 1–7, pls. 13–18.

Effinger, W. L. 1938. The Gries Ranch fauna (Oligocene) of western Washington. Journal of Paleontology 12(4):355–390, figs. 1–3, pls. 45–47.

Fleming, J. 1822. The Philosophy of Zoology; or a General View of the Structure, Functions, and Classification of Animals. Vol. 2. Archibald Constable & Co.: Edinburgh. 618 pp.

Givens, C. R. 1974. Eocene molluscan biostratigraphy of the Pine Mountain area, Ventura County, California. University of California Publications in Geological Sciences 109: 1–107, pls. 1–11.

Gray, J. E. 1827. Monograph on the Cypraeidae, a family of testaceous Mollusca. Zoological Journal 3(11):363–371.

Groves, L. T. 1993. Fossil and Recent species of eastern Pacific Cypraeacea (Pediculariidae, Cypraeideae, and Ovulidae). Western Society of Malacologists Annual Report 25:11–14.

Hickman, C. S. 1984. Composition, structure, ecology, and evolution of six Cenozoic deep-water mollusk communities. Journal of Paleontology 58(5):1215–1234, figs. 1–12.

Keen, A. M. 1971. Sea Shells of Tropical West America—Marine Mollusks from Baja California to Peru. 2nd ed. Stanford University Press: Stanford, California. xiv + 1064 pp., numerous figs., pls. 1–22.

Koenen, A. von. 1890. Das Norddeutsche unter-Oligocän und seine Mollusken-Fauna. Lieferung II: Conidae-Volutidae-Cypraeidae. Abhandlungen zur Geologischen Specialkarte von Preussen und den Thüringischen Staaten 10(2):281–574, pls. 24–39.

Liltved, W. R. 1989. Cowries and their Relatives of Southern Africa. Seacomber Publications: Cape Town, South Africa. 208 pp., 298 figs.

Pezant, A. 1910–1911. Coquilles fossiles des calcaires grossiers de Parnes, 1890–1910. La Feuille des Jeunes Naturalistes, série 4, 40(480):185–197, pl. 14 [1910]; série 5, 41: 23–33 [1911].

Ponder, W. F. & A. Warén. 1988. Appendix: Classification of the Caenogastropoda and Heterostropha—a list of the family-group names and higher taxa. Malacological Review, Supplement 4:288–326.

Schilder, F. A. 1922. Contributions to the knowledge of the genera *Cypraea* and *Trivia*. Proceedings of the Malacological Society of London 15:98–122.

Schilder, F. A. 1927. Revision der Cypraeacea (Moll., Gastr.). Archiv für Naturgeschte 91A(10):1–171.

Schilder, F. A. 1961. Nachträge zum katalog der Cypraeacea von 1941. Archiv für Molluskenkunde 90(4/6):145–153.

Schilder, M. & F. A. Schilder. 1971. A catalogue of living and fossil cowries. Taxonomy and bibliography of Triviacea and Cypraeacea (Gastropoda Prosobranchia). Institut Royal des Sciences Naturelles de Belgique Mémoires, series 2, 85: 1–246.

Squires, R. L. & J. L. Goedert. 1994. New species of early Eocene small to minute mollusks from the Crescent Formation, Black Hills, southwestern Washington. The Veliger 37(3):253–266, figs. 1–29.

Squires, R. L. & J. L. Goedert. 1995. New species of middle Eocene gastropods from the northern Doty Hills, southwestern Washington. The Veliger 38(3):236–251, figs. 1–18.

Squires, R. L. & J. L. Goedert. In press. New species of small to minute gastropods of early Eocene age from the Crescent Formation, Black Hills, southwest Washington. The Veliger.

Vredenburg, E. W. 1920. Classification of the Recent and fossil Cypraeidae. Records of the Geological Survey of India 51(2):65–152.

Weaver, C. E. 1942 [1943]. Paleontology of the marine Tertiary formations of Oregon and Washington. University of Washington Publications in Geology 5 (Parts 1–3):xiii + 1–789, pls. 1–104 [reprinted, 1958].

Wenz, W. 1941. Subfamilia Pediculariinae. Pp. 1000–1002, figs. 2873–2877 in O. H. Schindewolf (ed.), Handbuch der Paläozoologie, Band 6, Prosobranchia, Teil 6. Gebrüder Borntraeger: Berlin [reprinted 1960–1961].

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THE VELIGER

A Quantitative Study of Copulation and Spawning in the South American Apple-Snail, *Pomacea canaliculata* (Prosobranchia: Ampullariidae)

by

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Abstract. Copulation and spawning of male-female pairs of the South American apple-snail *Pomacea canaliculata* were periodically observed in aquaria. Copulation occurred under water (2.9 ± 0.3 times/week, mean ± SEM) and was more frequently recorded in the morning (45%) and afternoon (37%) than in the evening (18%). Most copulations were recorded in one or two subsequent observations, although some were recorded in up to five subsequent observations (encompassing more than 30 h); some of these long copulations were interrupted by spawning and then resumed, which suggests that some copulation may indeed be series of several copulatory episodes.

Spawning occurred above water level (1.4 ± 0.1 times/week) and mostly at night (93%). The number of eggs per spawn was 101.0 ± 6.8 eggs (mean ± SEM), its mean volume was 9.9 ± 0.2 mm^3, and the percentage of fertile eggs was 42.6 ± 2.7. The number of eggs produced, the mean egg volume, and the percent of fertile eggs did not differ significantly between the first and second spawn produced directly after copulation. When several spawns (up to five) were produced in succession, without intervening copulations, the number of eggs per spawn was within the normal range, but the fertility of the eggs produced varied from normal to null values. The adaptive significance of these findings in comparison with what is known in other ampullariid gastropods is discussed.

INTRODUCTION

The apple-snail *Pomacea canaliculata* (Lamarck, 1822) is a widespread freshwater snail in southern South America (Argentina, Bolivia, Paraguay, Uruguay, and Brazil) where it lives in lentic waters showing a rather wide range of salinity and hardness (Hylton-Scott, 1957; Bachmann, 1960; Castellanos & Fernández, 1976).

Ampullariid gastropods have received considerable attention in the past (Sachwatkin, 1920; Hägler, 1923; Prashad, 1925; Hylton-Scott, 1943, 1957; Bachmann, 1960; Andrews, 1964, 1965a, b) because of their exhibiting both "primitive" prosobranch characters and specializations, such as the combined occurrence of a ctenidium and a lung (the lung is used by the female of many ampullariid species while spawning above water level).

At present there is a revival of interest in this family, mainly because of its use as human food (Lum-Kong & Kenny, 1989) and/or its role as the biological antagonist of aquatic weeds (Thomas, 1975; Cazzaniga, 1981, 1983) and schistosome-bearing gastropods (Chernin et al., 1956; Ferguson & Palmer, 1958; Milward-de-Andrade, 1959; Milward-de-Andrade & Souza, 1979; Cazzaniga, 1990b). In particular, *Pomacea canaliculata* has received considerable attention because of the concern created by the anthropogenic spread of this species to Asia (Cazzaniga, 1987) where it may act as an intermediate host for *Angiostrongylus cantonensis* (Asaka & Sato, 1987; Kondo & Tanaka, 1989). It has also become a threat to rice crops (Leon-Dancel, 1970; Nishimura et al., 1987).

The core of the present paper is a quantitative study of some basic aspects of reproduction in *P. canaliculata,* and is part of a broader study of the environmental factors controlling the seasonality of reproduction in this species. Also, the results of some non-quantitative, but behaviorally detailed observations of copulation and spawning in this species, are reported.

MATERIALS AND METHODS

Sexually mature individuals of *Pomacea canaliculata,* of both sexes, were collected in Palermo Park (Buenos Aires, Argentina) during the spring and summer of 1993. The apple-snails were maintained in outdoor ponds until they were used for studies.

Non-quantitative observations of the behavior of the apple-snails during copulation and spawning were made in laboratory aquaria during the spring and summer months. Fresh lettuce was provided *ad libitum* (Estebenet & Cazzaniga, 1992); however, other environmental conditions, such as temperature and illumination, were largely uncontrolled.

The quantitative observations were conducted in four 56 × 41 × 20 cm aquaria. Each aquarium was divided with a plastic mesh into 10 11 × 20 × 20 cm compartments. The shell lengths of the individuals used ranged from 34 to 48 mm (sexual maturity is reached at about 25 mm shell length in this species: Martín, 1986; Estebenet & Cazzaniga, 1992). A pair comprising a male and a female individual (sex was determined by the shape of the operculum, according to Cazzaniga, 1990a, and confirmed at autopsy at the end of the experiments) was placed in each compartment. Individuals which died during the observations (one male and eight females) were replaced by other individuals of the same sex, since observations made in the course of another study (Albrecht & Castro-Vazquez, unpublished) indicated that replacement of the "familiar" partner did not modify the frequency of copulation thereafter.

Results are reported only of the 79 males and 71 females that remained alive and could be observed during the whole period of observation (2 weeks). Continuous water renewal (about 10 times/day) was ensured by a constant input flow (at 23–27°C) and by keeping water level 10 cm above the base of the aquarium. The aquaria were artificially illuminated (14 h/day) with 15 W white fluorescent tubes located 22 cm above water. The animals were fed fresh lettuce *ad libitum.*

Two replicate sets of observations were run, after at least 1 week of adaptation of the animals to the mesh compartments (starting on 8 February and 31 March 1994, respectively), and they were pooled for presentation. After the starting date, the animals were observed for copulation, and spawning during 14 days at 7:00–8:00 A.M., 1:30–2:30 P.M., and 8:00–9:00 P.M. A single episode of copulation was recorded if copulatory activity was recorded on one or more than one consecutive observation. An episode of spawning was recorded whether a female was seen during egg-laying or whether an egg mass was already deposited.

The spawns were collected as soon as they were observed, and the egg masses were dispersed in 2% sodium hydroxide, washed and air-dried thoroughly, and the eggs were counted. The mean egg volume was calculated on the basis of the mean diameter of a ten-egg sample of each spawn, as measured with a caliper to the nearest 0.1 mm. The spawn volume was calculated as the product between the mean egg volume and the number of eggs in the spawn. Later, the eggs were incubated in an air-conditioned room at 24–26°C for 10–15 days, when the percentage of fertile eggs (i.e., those with developing embryos) was determined for each spawn.

The correlation between the spawn measurements (number and mean volume of eggs, volume of the spawn, and percentage of fertile eggs) and the live mass of the female which laid the spawn were evaluated with the Spearman ranks test (Siegel, 1956). The same test was also used to evaluate correlations among the spawn measurements themselves.

RESULTS

Behavioral Patterns of Copulation and Spawning

During copulation, the male is attached to the last whorl of the female's shell while gripping its aperture with the muscular penial sheath. He remains there for the entire period of copulation (10–18 h), with his head partly withdrawn into the shell, and he does not loosen his grip even if the mating pair is lifted from the water. Although some decrease in locomotor activity of the female is also evident, she may still move around, hauling the male, with her head and palps extended, and she frequently feeds during copulation; she also responds to disturbances in the usual way, by withdrawing into her shell. Periods of immobility of the female occur mainly in proximity to the surface, either attached to the aquarium walls or floating, so that both partners are able to ventilate their lungs during copulation. In those cases in which the initial attempts at copulation could be observed, the male crawled over the female's shell, with his head partly withdrawn into the mantle cavity while thrusting out the penial sheath. Then he aimed to grip the female's shell aperture, first advancing the tip of the penial sheath over and alongside the female's head until the muscular penial sheath was finally inserted into the mantle cavity above the right nuchal lobe of the female. At that time, the thin and long penis is presumably stretched out and introduced into the pallial oviduct, but this cannot be ascertained during such direct observations.

Females laid their eggs several centimeters above water level, usually upon the aquarium walls. When the female attains the spawning place, she relaxes the columellar muscle while the foot remains firmly attached to the substratum, and the right nuchal lobe covers the opening of the pallial oviduct. Then the pink eggs appear (usually one by one, sometimes in pairs) from below the right nuchal lobe on the dark background of the female's body. No movements or contractions of the female are apparent, except that a groove is formed on the right side of the foot (termed the ovipositor by Andrews, 1964), as if between two bundles of the columellar muscle, and the eggs progress in order along the groove until reaching the proximity of

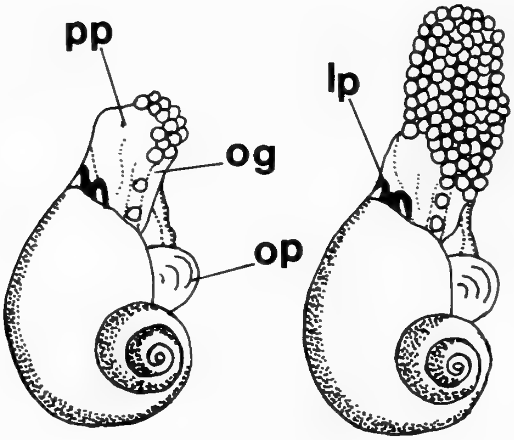

Figure 1

Sketches of a female *Pomacea canaliculata* laying eggs on a vertical surface, outside water. The head is partially retracted and only the labial palps (lp) are seen. An ovipositor groove (og) is formed on the right side of the foot, while movements of the upper edge of the propodium (pp) accomodate the eggs in rows. Finally (sketch on the right), the eggs accumulate on the right and upper part of the propodium. The operculum is indicated as op.

the foot's edge. The upper end of the groove swings slowly, thereby arranging the eggs along the edge of the propodium; also, fibrillar movements of this edge may accommodate the eggs in their final position in the spawn. Especially when the spawn being produced is a large one, the eggs start accumulating on the right part of the propodium (Figure 1). When spawning is ended, the female again contracts the columellar muscle; she detaches the propodium, dropping the lower part of the spawn on the substratum, and sometimes she turns left, facing water; finally, she drops or slides down into the water. The whole process may take from several minutes to more than 1 hour. The females crawling above water level may be easily induced to drop into the aquarium by any light or sound; however, once spawning begins, they are remarkably refractory to either light or sound stimulation.

Quantitative Aspects of Copulation

The frequency of copulation was 2.9 ± 0.3 times/week (mean ± SEM, computed for 73 couples and 422 episodes). Five males (out of 78) did not show any copulatory activity during the period of observation. Two additional males that were mistakenly put together in the same compartment showed four episodes of homosexual copulation during the 2 weeks of observation.

Most heterosexual copulations were recorded on either one (273/422, 64.7%) or two (126/422, 29.9%) consecutive observations; however, 14 couples were seen copulating on three consecutive observations, five couples on four observations, and four on five observations. Interestingly, in four of the latter nine cases, spawning occurred between the two last observations, indicating that the female must have interrupted copulation during egg-laying, but that she accepted the male again once she returned to water.

Copulatory activity showed a daily rhythm (Table 1), being more frequently observed in the morning (7:00–8:00 A.M.) and afternoon (1:30–2:30 P.M.) than in the evening (8:00–9:00 P.M.); all these differences were statistically significant (P < 0.001, χ^2 test).

Table 1

Records of copulation and spawning at different times of the day, in couples of *P. canaliculata*.

	7:00–8:00 AM	1:30–2:30 PM	8:00–9:00 PM
Copulating couples*	273 45%	225 37%	110 18%
Spawns deposited**	167 93%	10 6%	2 1%

* 78 couples; in 8 cases the female died during the observations and was immediately replaced.

** 62 females; 9 additional females did not lay eggs during the observation period.

Quantitative Aspects of Spawning

Most spawning activity occurred during the night since most egg masses were already found on the 7:00–8:00 A.M. observations (Table 1); however, some spawning also occurred in the morning (i.e., between the 7:00–8:00 A.M. and the 1:30–2:30 P.M. observations) and, occasionally, in the afternoon (i.e., between the 1:30–2:30 P.M. and the 8:00–9:00 P.M. observations). Although the period between the 7:00–8:00 A.M. and the 1:30–2:30 P.M. observations is shorter than the period between the 8:00–9:00 P.M. and the 7:00–8:00 A.M. observations (7 and 10 hours, respectively), this difference cannot account for the large difference between the number of spawns observed at 7:00–8:00 A.M. (93%) and that observed at 1:30–2:30 P.M. (6%).

Sixty-two out of 71 females laid eggs at least once during the period of observation; in total, 179 spawns were deposited by these females (frequency: 1.4 ± 0.1 times/week; mean ± SEM). Measurements of the spawns (i.e., the number and size of eggs produced and the percentage of fertile eggs) and of the female (i.e., the live mass) which laid the spawn are shown in Table 2. No correlation was found between the spawn measurements and the live mass. Also, weakly positive but significant correlations were found between the spawn volume and the percentage of fertile eggs in the spawn ($r_s = 0.4159$; $P = 0.001$; Spearman ranks test) and between the mean egg volume of a spawn and the percentage of fertile eggs ($r_s = 0.1886$; $P = 0.0222$); other correlations (between the spawn measurements themselves) were not significant.

Most spawning occurred as single episodes of egg-laying

Table 2

Live mass of female individuals of *P. canaliculata* and measurements of their laid spawns.

	Mean ± SEM	*n***
Live mass of the female (g)	16.6 ± 0.48	62
Number of eggs per spawn	101.0 ± 6.8*	62
Mean egg volume (mm^3)	9.9 ± 0.2*	60
Spawn volume (mm^3)	998.8 ± 66.7*	60
% of fertile eggs	42.6 ± 2.7*	56

* First, a mean value was calculated for each female, and then the "weighted" mean was calculated as the mean value of the means of all individual females.

** Number of females whose spawns were included in the mean.

Table 3

Number and fertility of the eggs produced by female *Pomacea canaliculata* during the first and second spawning occurring after an observed copulation.

Spawning order after the last observed copulation	Number of eggs per spawn	Percent of fertile eggs
1st spawning	107.4 ± 6.0 (147)	48.3 ± 2.2 (125)
2nd spawning	94.4 ± 18.4 (14)	50.6 ± 6.8 (12)

Figures between brackets indicate number of cases. Other figures indicate mean ± SEM.

between copulatory episodes ($n = 133$); however, 14 females showed two consecutive episodes of egg-laying (i.e., with no observed copulation in the intervening period), and four females (which did not copulate during the period of observation) did deposit eggs three to five times. An additional female neither deposited eggs nor copulated during the observation period. When the first spawn deposited after copulation (in those 14 females) was compared with the second one (deposited with no intervening, additional copulations by the same females), no significant differences in either the number of eggs or the percentage of fertile eggs were found (Table 3; Student's *t*-test). Also, two of the four females that produced eggs, but which were never observed copulating, showed numbers of eggs per spawn that were rather low (37–94 eggs) but still within the normal range; the fertility of those spawns was also within the normal range (32–70%). The remaining two females produced spawns of normal size (63–186 eggs) but of low fertility (0–21%).

DISCUSSION

Copulation and its Relation to Spawning

Copulation in *Pomacea canaliculata* was recorded more frequently in the morning and afternoon than in the evening, whereas spawning occurred mostly during the night. A similar daily rhythm for both processes has been mentioned by Guimarães (1981) for the congeneric species *P. haustrum* (Reeve, 1856). The behavioral patterns of copulation in *P. canaliculata* (Andrews, 1964; and this paper) are similar to those of another South American ampullariid species (*Marisa cornuarietis,* Linnaeus, 1758; Demian & Ibrahim, 1971) mainly in that the male starts crawling over the last whorl of the female's shell and finally secures her shell aperture with the penial sheath. A similar pattern of copulation was observed in the common Indian apple-snail *Pila globosa* (Swainson) (Bahl, 1928). Copulation in *P. canaliculata* is peculiarly long (10–18 h, vs. 1–3 h in *P. haustrum,* 1–6 h in *M. cornuarietis,* and 3 h "or more" in *Pila globosa*).

Previous studies (Bachmann, 1960; Andrews, 1964) have suggested that spawning in this species may be induced by the stimuli of copulation. Since fertilization is an internal process in *P. canaliculata,* the sequential occurrence of copulation and spawning may be important to ensure that eggs would not be laid without previous fertilization; otherwise, the female investment in spawning would be wasted. However, a simple hypothetical model relating each spawning to a previous copulation is in contrast to some of our present findings: (1) that the observed frequency of copulation was about double that of spawning (see Results), and (2) that several spawnings not directly preceded by copulation were observed (Table 3; see also Estebenet & Cazzaniga, 1993).

A parsimonious model that ensured fitness and that, in turn, was in agreement with the current data should be worked out. One can speculate that the development of the female's sexual attractiveness and receptivity (Beach, 1976) may occur in cycles that are entrained somehow by the ovarian cycle of oogenesis and spawning (Martín, 1986), thereby resulting in the temporal coordination of copulation and egg-laying. On an annual or seasonal time scale, the latter is certainly true, since copulation and spawning occur at the same time of the year (Hylton-Scott, 1957; Bachmann, 1960). Also, the ability of at least some females to produce several fertilized spawns after a single copulation (see Table 3) makes copulation unnecessary before each spawn. This suggests that a parallel, synchronic activation of oogenesis and spawning on one part, and of attractiveness and receptivity of the female for copulation on the other, may only be needed to attain optimal fertility.

Regarding the possibility of coordinating copulation and spawning on a smaller time scale (i.e., referring to cycles of both processes that would occur *within* the breeding season), it is worth mentioning that Andrews (1964) observed that when one male is attempting to copulate, other males also seem interested in the same female; this was be interpreted to mean that the female has become more attractive at that time, and one can further speculate that this attractiveness is entrained by the ovarian cycle. Unfortunately, our observations of the initiation of copulation were always made on isolated couples, so that we cannot confirm or reject Andrews's suggestion. But we did observe a strict coexistence of the drives to copulate and to spawn in the few cases in which copulation was interrupted by spawning and was immediately resumed (see Results). Incidentally, it should be noted that these cases also suggest that those copulations encompassing three to five observations (i.e., up to more than 30 h periods) might have indeed occurred in a series of several copulatory episodes.

Finally, regarding the case of homosexual mating that was reported here (see Results), we will also mention our recent observation of a triad composed of a medium-sized female, a large male, and a small male (in that order) that were found copulating in tandem in a heavily populated aquarium. When the triad was isolated in another aquarium and observed for several weeks, the small male was repeatedly observed copulating with either the large male or the female, while the large male copulated only with the female. These cases, and the observation mentioned by Andrews (1964) on the heterosexual attractiveness of females, clearly illustrate how far we are from understanding the factors influencing mate choice in this species. Additionally, since there is no evidence that homosexual mating is more than a male clasping another male with its penial sheath, one may consider that male snails may simply clasp any snail they can get a hold of, and that female receptivity may play little part in copulation.

Spawning Behavior and the Spawn

The act of spawning occurred mainly during the night since most egg masses were already found in the morning. In nature, spawning occurs either on the emergent stems of plants (mainly *Scirpus, Typha, Sagittaria*) or on banks. Spawning in *M. cornuarietis* is also nocturnal (Demian & Ibrahim, 1971); these females lay their eggs under water, but close below the surface and, as those of *P. canaliculata,* only interrupt spawning if stimulated strongly (such as being removed from the spawning place or being lifted from water). In *Pila globosa,* on the contrary, egg-laying usually takes place in the morning (Bahl, 1928).

Some of the spawn parameters (number of eggs per spawn and mean egg volume) that we reported here are partially in agreement with those mentioned by Andrews (1964), although apparently her data were not based on systematic counts or measurements. The percentage of fertile eggs reported by Estebenet & Cazzaniga (1993) is much higher than those reported here, which may be accounted for by differences in methodology to incubate the eggs. The measurements made on 30 spawns by Fujio et al. (1991) yielded a number of eggs per spawn that was much higher (230 ± 19, mean ± SEM) than ours, but a similar percentage of eggs with developing embryos (44.5 ± 3.6%). However, in another paper on the same group Fujio & von Brand (1990) mention a range of 200 to 700 eggs per spawn for their apple-snails. We think this suggests that their animals, which were from a closed colony whose origin is not mentioned, may in fact be *P. insularum* (Orbigny, 1835), which produces much larger spawns (Bachmann, 1960), or may be an aquaculture strain of *P. canaliculata* that was artificially selected for fecundity.

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LITERATURE CITED

ANDREWS, E. B. 1964. The functional anatomy and histology of the reproductive system of some pilid gastropod molluscs. Proceedings of the Malacological Society of London 36:121–140.

ANDREWS, E. B. 1965a. The functional anatomy of the gut of the prosobranch *Pomacea canaliculata* and some other pilids. Proceedings of the Malacological Society of London 145:19–36.

ANDREWS, E. B. 1965b. The functional anatomy of the mantle cavity, kidney and blood system of some pilid gastropods (Prosobranchia). Journal of Zoology, London 146:70–94.

ASAKA, A. & Y. SATO. 1987. Feeding inhibitory efficiency of cartap and bensultap against the apple snail *Pomacea canaliculata* [in Japanese, summary in English]. Japanese Journal of Applied Entomology and Zoology 31:339–343.

BACHMANN, A. O. 1960. Apuntes para una hidrobiología argentina. II. *Ampullaria insularum* Orb. y *A. canaliculata* Lam. (Moll. Prosobr. Ampullariidae). Observaciones biológicas y ecológicas. First South American Congress of Zoology 1:19–26.

BAHL, K. N. 1928. On the reproductive processes and development of *Pila globosa* (Swainson). Part I. Copulation and oviposition. Memoirs of the Indian Museum 9:1–11.

BEACH, F. A. 1976. Sexual attractivity, proceptivity and receptivity in female mammals. Hormones & Behavior 7:105–138.

CASTELLANOS, Z. J. A. DE & D. FERNANDEZ. 1976. La familia Ampullariidae en la República Argentina. Pp. 33 in R. A. Ringuelet (ed.), Fauna de agua dulce de la República Argentina. FECIC: Buenos Aires.

CAZZANIGA, N. J. 1981. Evaluación preliminar de un gasterópodo para el control de malezas acuáticas sumergidas. Pp. 131–165 in IIa. Reunión sobre Malezas Subacuáticas en Canales de Desagüe de CORFO. Comisión de Investigaciones Científicas: La Plata.

CAZZANIGA, N. J. 1983. Apple-snails eating *Chara.* Aquaphyte, Gainesville 3:1–4.

CAZZANIGA, N. J. 1987. Expansión de *Pomacea canaliculata* (Gastropoda: Ampullariidae) en Asia. Un comentario de bibliografía reciente. Comunicaciones de la Sociedad Malacológica del Uruguay 7:67–68.

CAZZANIGA, N. J. 1990a. Sexual dimorphism in *Pomacea canaliculata* (Gastropoda: Ampullariidae). The Veliger 33:384–388.

CAZZANIGA, N. J. 1990b. Predation of *Pomacea canaliculata* (Ampullariidae) on adult *Biomphalaria peregrina* (Planorbidae). Annals of Tropical Medicine and Parasitology 84: 97–100.

CHERNIN, E., E. H. MICHELSON & D. L. AUGUSTINE. 1956. Studies on the biological control of schistosome-snails. I. The control of *Australorbis glabratus* populations by the snail *Marisa cornuarietis* under laboratory conditions. American Journal of Tropical Medicine & Hygiene 5:297–307.

DEMIAN, E. S. & A. M. IBRAHIM. 1971. The egg mass, egg laying and mating behavior of the snail *Marisa cornuarietis* (L.). Bulletin of Zoology Society of Egypt 23:1–12.

ESTEBENET A. L. & N. J. CAZZANIGA. 1992. Growth and demography of *Pomacea canaliculata* (Gastropoda: Ampullariidae) under laboratory conditions. Malacological Review 25:1–12.

ESTEBENET A. L. & N. J. CAZZANIGA. 1993. Egg variability and the reproductive strategy of *Pomacea canaliculata* (Gastropoda: Ampullariidae). Apex 8:129–138.

FERGUSON, F. F. & J. R. PALMER. 1958. Biological notes on *Marisa cornuarietis,* a predator of *Australorbis glabratus,* the intermediate host of schistosomiasis in Puerto Rico. American Journal of Tropical Medicine & Hygiene 7:640–642.

FUJIO, Y. & E. VON BRAND. 1990. Two linked loci with a null allele for leucine aminopeptidase isozymes in apple snail *Pomacea canaliculata.* Nippon Suisan Gakkaishi 56:1039–1043.

FUJIO, Y., E. VON BRAND & M. KOBAYASHI. 1991. Apparent differential hatchabilities associated with degrees of heterozygosity at leucine aminopeptidase isozyme loci in the apple snail *Pomacea canaliculata.* Nippon Suisan Gakkaishi 57: 459–461.

GUIMARÃES, C. T. 1981. Algumas observações de laboratorio sôbre biologia e ecologia de *Pomacea haustrum* (Reeve, 1856). Memorias do Instituto Oswaldo Cruz 76:33–46.

HÄGLER, K. 1923. Anatomie von *Pachylabra (Ampullaria) cinerea* Reeve. Acta Zoologica, Stockholm, 4:313–410.

HYLTON-SCOTT, M. I. 1943. Sobre la organización de *Ampullaria (Asolene) megastoma* Sowerby. Notas del Museo de La Plata 8:269–280.

HYLTON-SCOTT, M. I. 1957. Estudio morfológico y taxonómico de los ampulláridos de la República Argentina. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" e Instituto Nacional de Investigación de las Ciencias Naturales, Ciencias Zoológicas 3:233–333.

KONDO, A. & F. TANAKA. 1989. An experimental study of predation of the larvae of the firefly, *Luciola lateralis* Motchulsky (Coleoptera: Lampyridae) on the apple-snail, *Pomacea canaliculata* Lamarck (Mesogastropoda: Pilidae) [in Japanese, summary in English]. Japanese Journal of Applied Entomology and Zoology 33:211–216.

LEON-DANCEL, D. 1970. On the experimental infection of *Pomacea australis* (d'Orbigny), refractive for *Fasciola hepatica* (Lin.) but receptive to *Angiostrongylus cantonensis* (Chen). Journal of Agriculture, University of Puerto Rico 54:411–412.

LUM-KONG, A. & J. S. KENNY. 1989. The reproductive biology of the ampullariid snail *Pomacea urceus* (Müller). Journal of Molluscan Studies 55:53–65.

MARTÍN, S. M. 1986. Ciclo reproductivo de *Ampullaria canaliculata* (Gastropoda; Ampullariidae) en el área rioplatense. Neotropica 32:171–181.

MILWARD-DE-ANDRADE, R. 1959. O problema da esquistossomose mansoni no lago artificial da Pampulha, Belo, Horizonte, Minas Gerais (Brasil). Revista Brasileira de Malariologia e Doenças Tropicais 11:653–674.

MILWARD-DE-ANDRADE, R. & C. SOUZA. 1979. *Pomacea haustrum* (Reeve, 1856) como engodo à infecção de *Biomphalaria glabrata* (Say, 1818) com *Schistosoma mansoni* Sambon, 1907. Revista Brasileira de Malariologia e Doenças Tropicais 31: 59–69.

NISHIMURA, K., M. MOGI, T. OKAZAWA, Y. SATO, H. TOMA & H. WAKIBE. 1987. *Angiostrongylus cantonensis* infection in *Ampullarius canaliculatus* (Lamarck) in Kyushu, Japan. Southeast Asian Journal of Tropical Medicine & Public Health 17:595–600.

PRASHAD, B. 1925. Anatomy of the common Indian apple-snail *Pila globosa.* Memoirs of the Indian Museum 8:91–154.

SACHWATKIN, V. A. 1920. Das Urogenitalsystem von *Ampullaria gigas* Spix. Acta Zoologica, Stockholm 1:67–130.

SIEGEL, S. 1956. Non-Parametric Statistics for the Behavioral Sciences. McGraw-Hill: New York. 347 pp.

THOMAS, K. J. 1975. Biological control of *Salvinia* by snail *Pila globosa* (Swainson). Biological Journal of the Linnean Society 7:243–247.

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Histology of Epithelia and Mantle Glands of Selected Species of Doridacean Mollusks with Chemical Defensive Strategies

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Abstract. Doridacean nudibranchs are known to use natural substances for chemical protection. In previous studies on the chemical defenses of several species of doridacean nudibranchs, we localized, isolated, and characterized diverse chemicals extracted from these animals. In this study, light and electron microscopic analyses of some mantle structures, which may be involved in the production or storage of these chemical defenses, were undertaken. The studied species of the genera *Hypselodoris* and *Chromodoris* presented mantle epithelia with ciliated cells and mucous cells, as well as mantle dermal formations (MDFs), in the subepithelial layer. *Doris verrucosa* presented a spiculate epithelium and clear vesiculated cells in the subepithelial layer. *Peltodoris atromaculata* and *Doriopsilla areolata* presented spicules in the subepithelial layer, and epithelia with ciliated cells and abundant mucous cells. In the borders of the mantle and gill epithelia of *Dendrodoris limbata,* three cell types were identified: ciliated cells, mucous glandular cells, and macrovacuolated cells. Only ciliated cells and mucous cells were observed in the rhinophore epithelium of *D. limbata.*

INTRODUCTION

Doridacean nudibranchs have been the subject of many studies concerning their defensive systems against potential predators. Their defensive mechanisms include mantle spicules, toxic and deterrent secretions, behavioral strategies, crypsis, and others (Thompson, 1960a; Edmunds, 1966, 1968, 1987; Ros, 1976; Faulkner & Ghiselin, 1983; Gosliner & Behrens, 1990). Furthermore, these nudibranchs provide an interesting source of natural products (Karuso, 1987; Cimino & Sodano, 1989; Avila, 1992, 1995; Faulkner, 1993, and references therein).

Defensive chemicals of the Doridacea have been anatomically located in only a few species: *Hexabranchus sanguineus* (Rüppell and Leuckart, 1828), *Dendrodoris* spp., *Doris verrucosa* Linnaeus, 1758, *Doriopsilla areolata* Bergh, 1880, *Hypselodoris* spp., and *Chromodoris* spp. (Pawlik et al., 1988; García et al., 1990; Avila et al., 1990a, 1990b, 1991a, 1991b; Gavagnin et al., 1992; Fontana et al., 1993, 1994; Spinella et al., 1994). Defensive metabolites in these species have been shown to be concentrated in the mantle (Table 1), although the origins of these chemicals are very different. In *Hypselodoris* spp. and *Chromodoris* spp., they are obtained from dietary sources, and in *Dendrodoris* spp. (and probably *Doris verrucosa* and *Doriopsilla areolata*), by *de novo* biosynthesis.

Surprisingly, the fine structure of the mantle in the Doridacea has received little attention in the past. The majority of studies have concentrated on the Eolidacea and their cerata (Edmunds, 1966; Schmekel & Wechsler, 1967; Harris, 1973; Todd, 1981; Porter & Rivera, 1980, 1983; Arias et al., 1984). Some other groups of opisthobranchs

Table 1

Location by anatomical dissection of the main natural products described in the doridacean species studied.

Species	Main chemicals	Location	References
Hypselodoris cantabrica	Longifolin Dendrolasin Nakafuran-9 Agassizin and other sesquiterpenoids	All in MDFs and digestive gland	Fontana et al. (1993)
Hypselodoris webbi	Longifolin Nakafuran-9 *Iso*-tavacfuran	All in MDFs and digestive gland	García et al. (1990) Avila et al. (1990b, 1991b) Fontana et al. (1994)
Hypselodoris villafranca	Longifolin Dendrolasin Nakafuran-9 Agassizin and other sesquiterpenoids	All in MDFs and digestive gland	Avila et al. (1991b) Fontana et al (1993)
Hypselodoris orsini	6-keto-deoxoscalarin	MDFs	Cimino et al. (1993) Avila (1993)
Chromodoris britoi	Several diterpenoids	MDFs and digestive gland	Avila (1993)
Doris verrucosa	Verrucosins	Mantle	Cimino et al. (1986, 1988) Avila et al. (1990a)
Peltodoris atromaculata	Petroformynes	Digestive gland only	Castiello et al. (1980) Cimino et al. (1982) Avila (1993)
Doriopsilla areolata	*Ent*-pallescensin-A Acetoxy derivatives of *ent*-pallescensin-A	Mantle Border of mantle	Avila (1993) Spinella et al. (1994)
Dendrodoris limbata	Olepupuane (and polygodial) 7-Deacetoxy-olepupuane	Border of mantle Gills	Avila et al. (1991a)

have also been examined (Herdman, 1890; Thompson & Slinn, 1959; Haefelfinger, 1961; Thompson, 1960a, 1960b, 1969, 1983; Thompson & Colman, 1984; Thompson & Gathercole, 1986; Marín et al., 1991). Examples also include the work of Herdman & Clubb (1892) on the structure of cerata and dorsal papillae of some Nudibranchia, and that of Kress (1981) and Foale & Willan (1987) on some dorids that present caryophyllid tubercles. Potts (1981) described the epithelial structure of the gills, mantle, and foot in the two dorids *Onchidoris bilamellata* (Linnaeus, 1767) and *Archidoris pseudoargus* (Rapp, 1827).

Recently, some studies have described the mantle of some cryptobranch dorids, and have tried to relate its structure to their chemical defensive mechanisms (Thompson, 1960a; Edmunds, 1968; García et al., 1990, 1991). García et al. (1991) studied the mantle dermal formations (MDFs) in some species of *Hypselodoris* and *Chromodoris*. Previously, these structures were simply called glands (Odhner, 1932), cream glands or white glands (Edmunds, 1981), mantle glands (Rudman, 1984), or subepidermal glands (Ortea, 1988).

In this paper we present a light and transmission electron microscopic (TEM) study of the mantle border and related structures in some chemically protected Doridacea (Table 1). In *Hypselodoris* and *Chromodoris* spp., the MDFs were studied because they contain the defensive allomones (Table 1). The epithelium was also examined. In *Dendrodoris limbata,* the borders of the mantle and the gills were analyzed, because different chemicals have been described in those regions (Table 1). These were compared with the rhinophores, which do not contain chemicals (Avila, 1993). To the best of our knowledge, this is the first study on the mantle histology of *D. limbata.* We have therefore provided a more detailed description. The mantle epithelia of *Doris verrucosa, Peltodoris atromaculata* Bergh, 1880, and *Doriopsilla areolata* were compared with those mentioned earlier.

MATERIALS AND METHODS

Doridacean mollusks were collected at various sites along the Spanish coast (Mediterranean and Atlantic shores) from 1987 to 1992 (Table 2). The animals were collected either by SCUBA (between 0 and 25 m depth) or by snorkeling. Several *Dendrodoris limbata* (Cuvier, 1804) and *Doriopsilla areolata* specimens were collected by trawling at about 80 m depth.

Specimens of all the collected species (Table 2) were relaxed in 7% $MgCl_2$ and dissected carefully to obtain the mantle border, mantle dermal formations (MDFs) (if present), as well as gills and rhinophores where appropriate. Tissue slices of all these structures were processed for electron microscopy by fixing them in 2.5% glutaraldehyde in seawater buffered with sodium cacodylate, for 24 h. Samples were postfixed for 2 h with 2% OsO_4, washed, dehydrated in a graded ethanol series, and embedded in Spurr's resin. Before ultrathin sections were cut, semithin sections (1 μm thick) were made and stained with methylene blue (0.5%)-borax (0.5%) to select appropriate areas, and for light photomicrography. Ultrathin sections were

Table 2

Localities of collection, dates and number of specimens of the species studied. (Atl: Atlantic Ocean; Med: Mediterranean Sea).

Species	Locality	Number of specimens	Date of collection
Hypselodoris orsini (Vérany, 1846)	Blanes (Med)	2	April 1992
Hypselodoris cantabrica Bouchet and Ortea, 1980	Santander (Atl)	6	April 1988
Hypselodoris webbi (d'Orbigny, 1839)	Palamós (Med)	2	April 1992
Hypselodoris villafranca (Risso, 1818)	Blanes (Med)	2	December 1987
Chromodoris britoi Ortea and Pérez, 1983	Blanes (Med)	7	July 1991
Doris verrucosa Linnaeus, 1758	Cubelles (Med)	4	August 1991
Peltodoris atromaculata Bergh, 1880	Blanes (Med)	2	May 1991
Doriopsilla areolata Bergh, 1880	Blanes (Med)	2	March 1992
Dendrodoris limbata (Cuvier, 1804)	Blanes (Med)	2	November 1987
	Blanes (Med)	3	March 1992

cut using a Reichert-Jung Ultracut ultramicrotome and glass knives. Sections were picked up on copper grids (200 mesh) and double stained with uranyl acetate 2% (30 min) and lead citrate (10 min). Observations and micrographs were made using a Philipps 301 Transmission Electron Microscope (TEM).

Samples of *Doris verrucosa* and *Hypselodoris villafranca* (Risso, 1818) were fixed in ethanol (70%), carefully dissected to obtain small pieces of mantle, and processed for light microscopy (LM) in order to provide a general view. These samples were embedded in paraffin, sectioned (7–12 μm), and stained with Schiff's reagent and toluidine blue, or with Mallory's triple stain.

Merck Universalindikator pH paper (pH 0–14) was used to determine the pH of mantle, foot, and mucous secretion. The secretion was obtained by slightly disturbing the animals.

RESULTS

Histological Descriptions

The MDFs of *Hypselodoris orsini* (Vérany, 1846) are located only in the posterior part of the mantle (Avila, 1993). The MDFs were irregularly shaped, with a matrix of vacuolated cells surrounded by a thin muscular layer. Aggregates of monovacuolated cells with peripheral nuclei were observed in the matrix by LM. Most of their cytoplasmic space was occupied by a very large, non-staining, frothy appearing vacuole. Some of these cells were also observed in the epithelium of the visceral face of the mantle.

Two cell types were identified in the epithelium of *H. orsini:* ciliated cells and mucous glandular cells. Ciliated cells were the most abundant cells in the epithelium (Figure 1). The cells were prismatic, more elongated, and possessed more microvilli than those of the other species studied, such as *Dendrodoris limbata* (see below). The nuclei occupied a mid-basal position, while characteristically the apical pole was extraordinarily vacuolated (Figure 1). Lysosomic structures and exocytotic formations were present. The external apical pole resembled the brush border of invertebrate and vertebrate enterocytes, and it probably has an absorptive function. The microvilli were uniformly sized and immersed in a well-developed glycocalyx. Cilia were seldom observed between the microvilli. Mucous glands were observed in a 1:10 proportion with respect to the other cells. Their secretion granules typically showed different degrees of condensation and electron densities, as they were probably released individually from the cell surface (Figure 1). Occasionally, the granules were fused before being excreted. Exocytosis seemed to be the secreting mechanism in that case.

The mantle epithelium of *Hypselodoris cantabrica* Bouchet and Ortea, 1980, presented ciliated cells and glandular mucous cells, with either basophilic or granulated contents (Figure 2). The MDFs were very voluminous in this species (Figure 3). The periphery of the MDFs was less basophilic than those in other *Hypselodoris* species (see below), displaying more fibrillar than cellular elements. The MDFs presented a unique and distinctive morphology. The internal vesicles were more polyhedric than in other species (see below). The vesicular boundaries were difficult to see by LM, but under TEM, the pattern reflected either the fusion of many vesicles, or the remains of entire vesicles which could have been disrupted during fixation (Figure 4).

The epithelium of the mantle of *Hypselodoris webbi* (d'Orbigny, 1839) (Figure 5) was quite similar to that of *H. orsini,* for which we provided a detailed description above. It was composed of ciliated cells and glandular mucous cells, while the MDFs were almost identical in their ultrastructure to those of *H. cantabrica* (see below). Aggregates of small numbers of cells were occasionally observed in the subepithelial layer. These cells contained a macrovesicle formed by a strongly electron-dense material, and peripherally, non-membrane-bound electron-lucent vesicles (Figure 6).

The MDFs of *Hypselodoris villafranca* were multicellular aggregates (Figure 7). These were surrounded by a

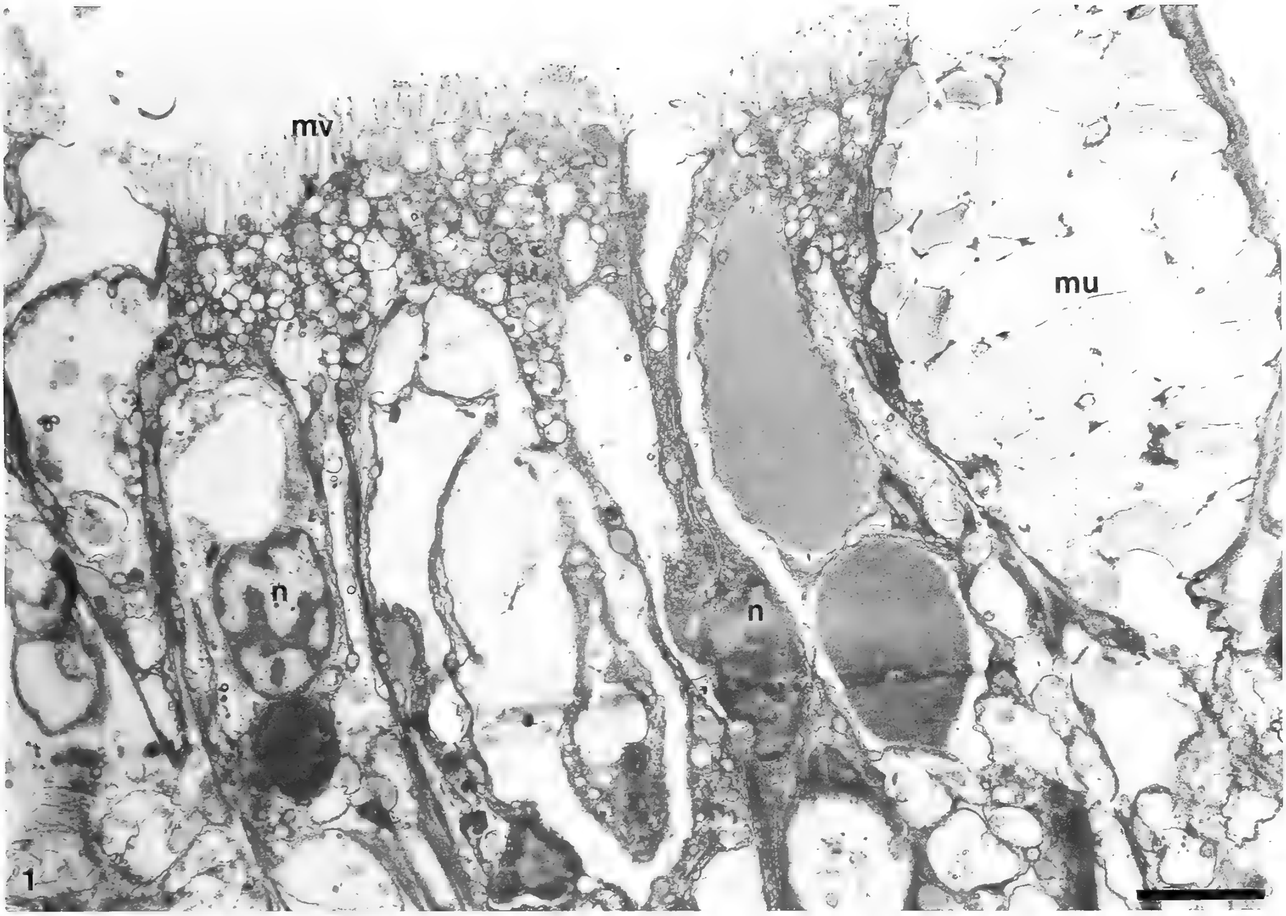


Figure 1

Hypselodoris orsini. TEM of the mantle epithelium showing ciliated cells with microvilli and a mucous glandular cell (scale bar = 5 μm). mu: mucous cell; mv: microvilli; n: nucleus.

group of mononucleated and occasionally, binucleated cells. By LM, the internal vesicles were delimited by a muscular basophilic sheath. These encapsulated vesicles were spherical or polygonal. Adjacent vacuolated cells appeared to coalesce. The epithelium presented ciliated cells and mucous glandular cells with no differences when compared with those reported above.

Ciliated cells bearing microvilli were observed in the epithelium of *Chromodoris britoi* Ortea and Pérez, 1983 (Figure 8). The microvilli were of larger diameter, and the fuzzy glycocalyx (Figure 9) was very developed, much more than observed, for instance, in *D. limbata.* A large number of mucous glandular cells was observed both in the epithelium and in the subepithelial layer. Inside the subepithelial mucous cells, granules in different phases of compaction were observed (Figure 10). A few cells containing electron-dense granules were also observed in the subepithelial layer (Figure 8).

The MDFs in *Chromodoris britoi* possessed smaller vacuolar cells than in *Hypselodoris* species. Inside the MDFs,

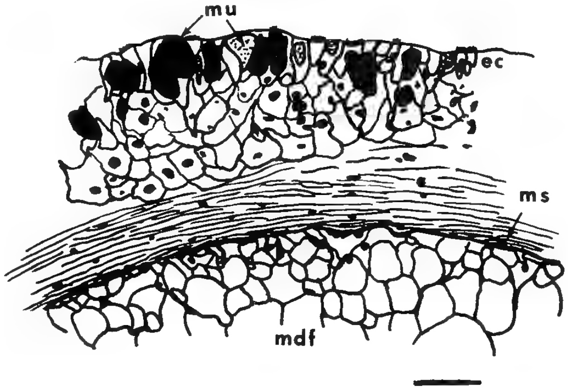
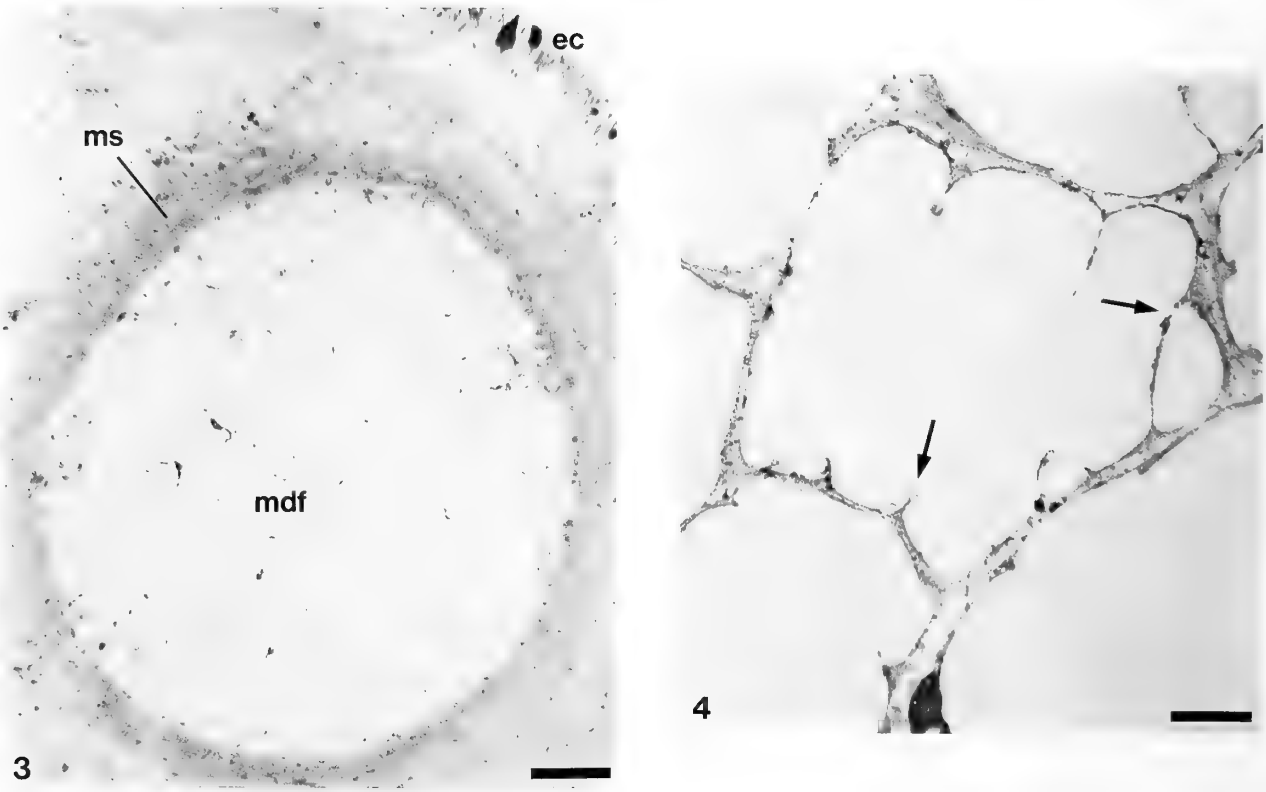


Figure 2

Hypselodoris cantabrica. Schematic representation of a section of the posterior part of the mantle showing epithelial cells and a mantle dermal formation (MDF) (scale bar = 25 μm). ec: epithelial ciliated cells; mdf: mantle dermal formation; ms: muscular capsule; mu: mucous cells.



Figures 3–4

Hypselodoris cantabrica. 3: Semithin section of a posterior mantle dermal formation (MDF) (scale bar = 50 μm). 4: TEM of the internal part of a MDF (arrows indicate points of either fusionated or broken vesicles; scale bar = 5 μm). ec: epithelial cells; mdf: mantle dermal formation; ms: muscular capsule.

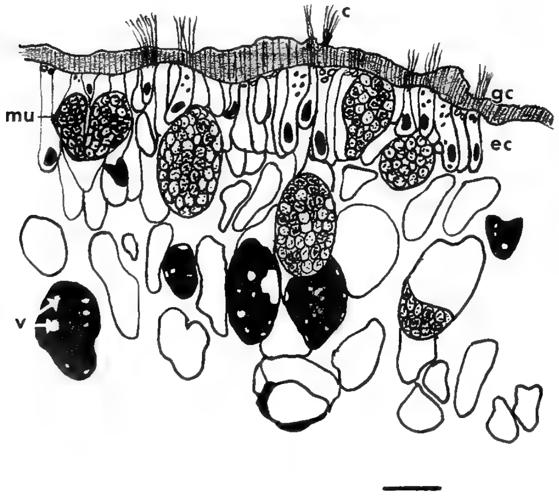


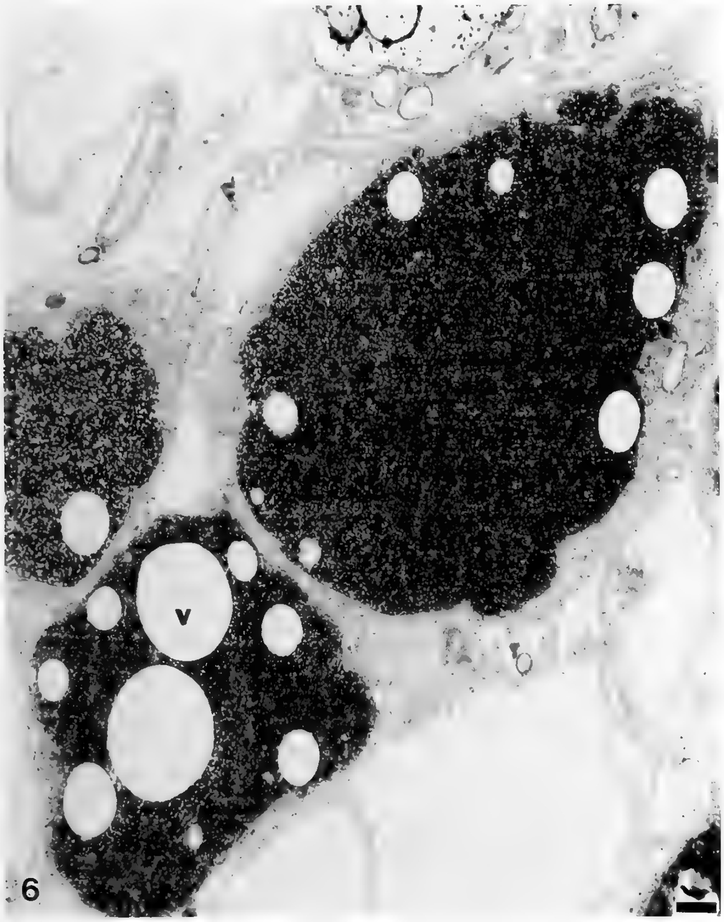
Figure 5

Hypselodoris webbi. Schematic representation of a mantle section showing the different types of cells in the epithelium and in the subepithelial layer (scale bar = 12.5 μm). c: cilia; ec: epithelial ciliated cells; gc: glycocalyx; v: non-membrane-bound electron-lucent vesicles included in a strongly electron-dense material.

the empty vacuolar cells were of different diameters, being irregular and closely packed (Figure 11). These vesicles presented a highly electron-dense peripheral area. The muscular capsule in the MDFs of *C. britoi* was thin with respect to that observed in *Hypselodoris* spp.

In the mantle protuberances of *Doris verrucosa,* a reticular middle area and a very thin epithelium were observed. Spicules were situated almost radially, with irregular distribution (Figure 12). The spicules originated in the subepithelial layer, and traversed the epithelium. Some cells containing clear vesicles were also observed in the subepithelial layer in different sections of the mantle.

The mucous secretion of *Peltodoris atromaculata* was a transparent fluid. Putatively, the cells responsible for this secretion were the epithelial mucous cells, which were very abundant (Figure 13). Large glandular mucous cells were present, with their granules in different degrees of condensation, and were situated both below and adjacent to the ciliated cells. Ciliated cells were also abundant, especially in the smaller mantle protuberances, and some presented microvilli (Figure 13). Spicules were observed in the subepithelial layer, where they were probably produced; these did not reach the epithelium (Figure 14).



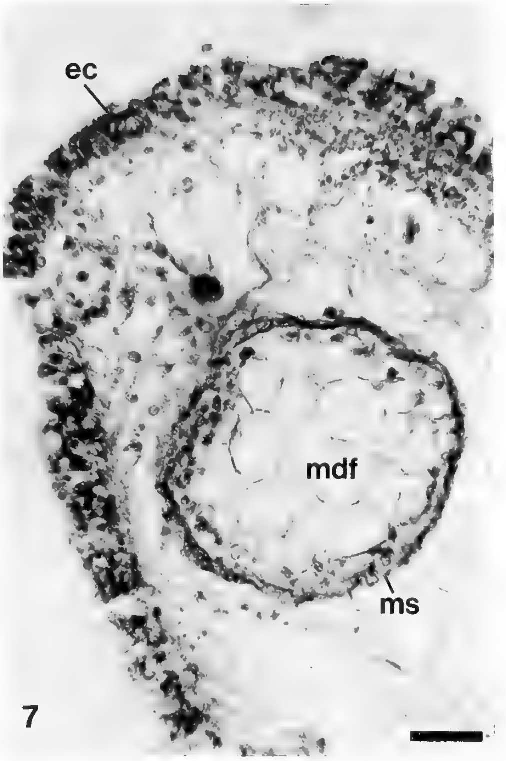


Figure 6, 7

Figure 6. *Hypselodoris webbi.* TEM of the highly electron-dense vesicles in the subepithelial layer cells (scale bar = 1 μm). v: non-membrane-bound electron-lucent vesicles included in a strongly electron-dense material.

Figure 7. *Hypselodoris villafranca.* Histological section (LM) of a posterior mantle dermal formation (MDF) and epithelium stained with Mallory's reagent (scale bar = 20 μm). ec: epithelial cells; mdf: mantle dermal formation; ms: muscular capsule.

Two types of epithelial cells were observed in the mantle border of *Doriopsilla areolata:* ciliated cells and numerous mucous glandular cells. Ciliated cells had basal nuclei and bore microvilli with rugose morphology (which could perhaps be a fixation artifact). Abundant vacuoles were observed in their apical zone. Mucous glandular cells contained secretion granules in different phases of condensation. Spicules were present in the subepithelial layer.

In the border of the mantle of *Dendrodoris limbata,* three cell types were distinguished in the epithelium (Figure 15). Ciliated cells were the most abundant. Mucous glandular cells and a small number of macrovacuolated cells were also present. Ciliated cells bore kinocilia alternating with microvilli, which occasionally showed rugose morphology, again possibly a fixation artifact. The typical basal nucleus was slightly elliptical. Contacts between ciliated cells and between ciliated cells and macrovacuolated cells were of the desmosome type. Mucous cells contained secretion vesicles in their apical regions.

Macrovacuolated cells (Figure 16) showed macroinclusion bodies that resembled monovacuolated adipose cells of vertebrates. In mature cells, the cytoplasm was displaced to one side where mitochondria, dictyosomes, and a poorly developed rough endoplasmic reticulum predominated. The nucleus was laterally displaced and in a position opposite the luminal face, thus conferring a strong polarity to the cell. Below this cell, there was usually a replacement cell. When the vacuole of the mature cell is liberated by macroexocytosis, the cell probably disintegrates, and the empty space is reoccupied by the newly developing basal cell.

Below the mantle epithelium, large glandular mucous cells were observed. These subepithelial cells were very apparent by their number and by their highly vesicular morphology. They presented at least two types of vesicles

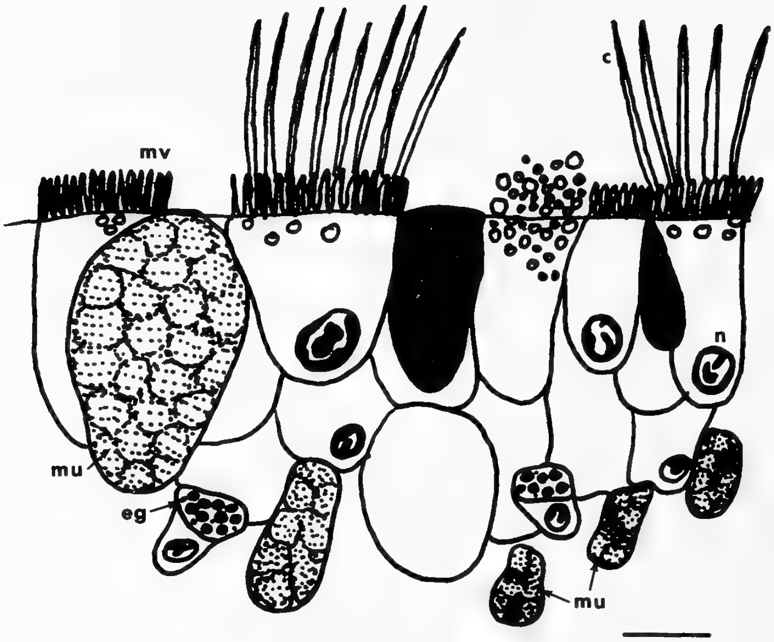


Figure 8

Chromodoris britoi. Schematic representation of the mantle epithelium and subepithelial layer showing the different types of cells found (scale bar = 5 µm). c: cilia; eg: electron-dense granules; mu: mucous glandular cells; mv: microvilli; n: nucleus.

(Figure 15). The first type contained granules with a reticular matrix that probably condensed with age, thus appearing highly electron-dense. The second one contained vesicles with secretion granules, which require further microanalysis.

Between the aggregates of glandular mucous cells in the subepithelial layer, some highly electron-dense cells resembling endocrine cells were observed (Figure 17). These cells were very conspicuous due to their unique morphology and to the presence of electron-dense granules.

In the gills of *D. limbata,* the epithelium showed the same basic cell types as those described from the border of the mantle, but with some differences. Ciliated cells (Figure 18) had a larger proportion of microvilli than the mantle cells. These microvilli were very long and showed a rugose aspect, which could again be a fixation artifact. Occasionally, some microvilli were observed divided into two or three branches (from their base or in their apical zone). In all cases, the microvilli were covered by a very evident glycocalyx.

Macrovacuolated cells were also conspicuous in the gill epithelium of *D. limbata.* In this tissue, it appears that the whole cell disrupts (holocrine secretion). Glandular mucous cells were also found both in the epithelium and in the subepithelial layer. In the subepithelial layer, they contained more abundant secretory granules than in the border of the mantle, and in this case, their vesicles typically formed a polylobulated structure (Figure 19). These vesicles were arranged both radially and circularly around the nucleus.

The epithelium of the rhinophores of *D. limbata* was formed mainly by prismatic ciliated cells. There was a voluminous nucleus basally and apical vesicles that seemed to correspond to lysosomes because of their aspect and contents (Figure 20). There were numerous ciliated pits on the surface separated by areas with dense microvilli

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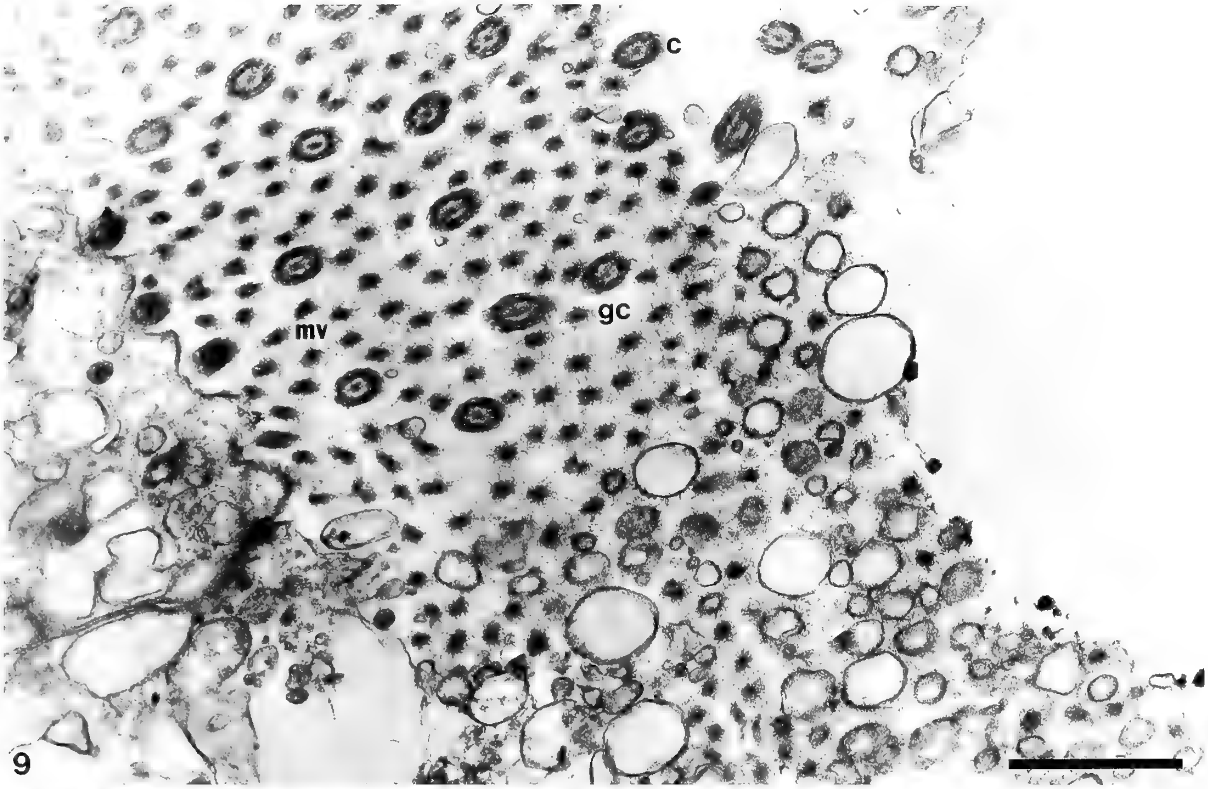
Figures 9–11

Chromodoris britoi. 9: TEM of the apical region of an epithelial mantle cell showing the fuzzy glycocalyx, cilia, and secretory vesicles. 10: Ultrathin section of the subepithelial layer showing a mucous cell with granules in different degrees of condensation. 11: TEM of a mantle dermal formation (MDF) showing the different-sized internal vacuolar cells. (Scale bars = 1 µm). c: cilia; gc: glycocalyx; mdf: mantle dermal formation; ms: muscular capsule; mu: mucous cell; mv: microvilli.



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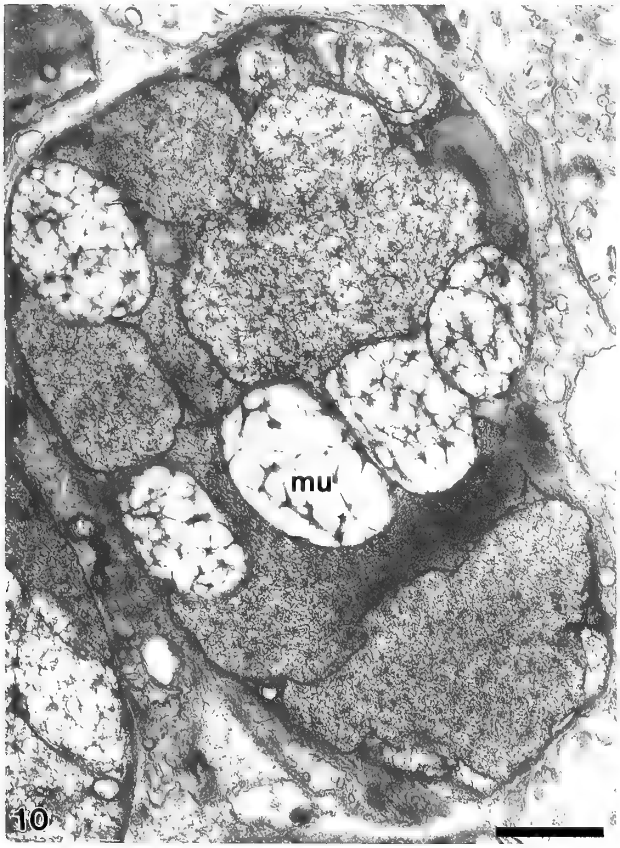

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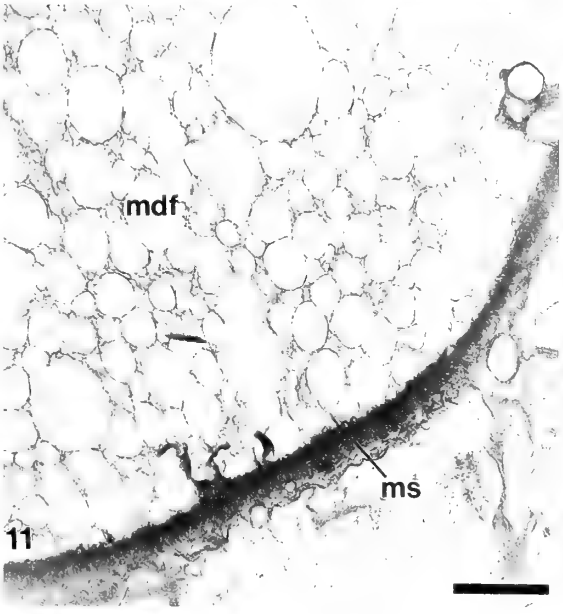

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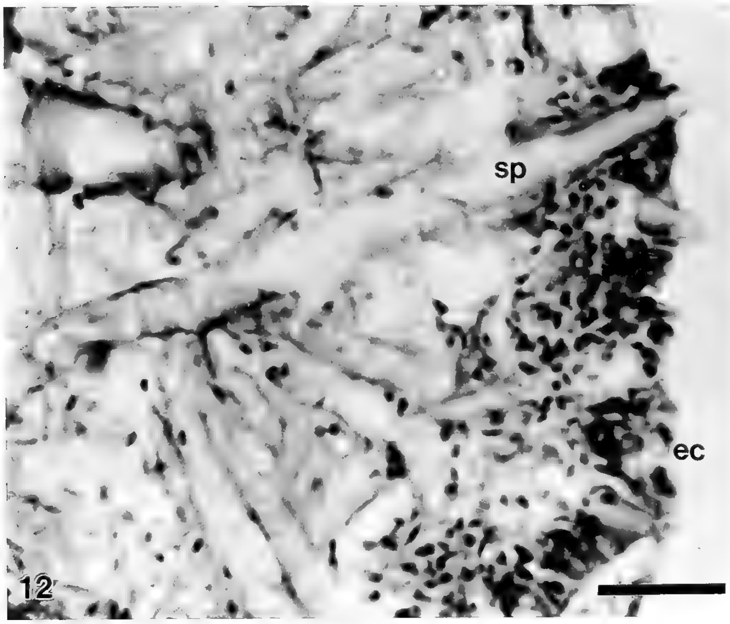
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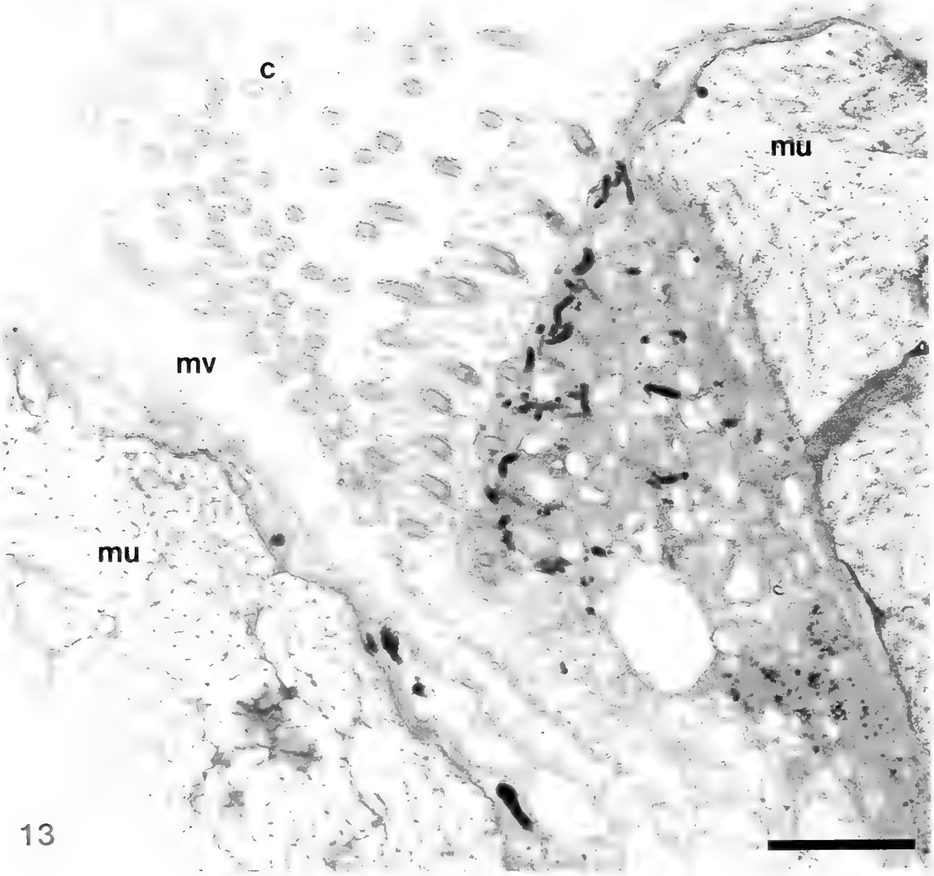
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Figure 14

Peltodoris atromaculata. Schematic representation of the mantle skin showing the different cells and structures observed (scale bar = 10 μm). c: cilia; mu: mucous cell; n: nucleus; sp: spicule.

(thin, rugose, and both simple and divided). Apical desmosomelike junctions were found between the cells, while tight junctions were found in the baso-lateral zones. Together with the abundant ciliated cells, mucous glandular cells were found in a proportion of 20:1. This proportion varied within different regions of the rhinophore.

pH Measurements

The secretion, mantle, and foot of all the species tested presented neutral pH (Table 3).

DISCUSSION

The results of the pH measurements (Table 3) are consistent with the histological data and with the chemical defense strategy of each particular species. For *Hypselodoris webbi* and *Hypselodoris villafranca,* these results agree with those previously reported by Ros (1976). However, our results disagree with those of Edmunds (1968) for *Doris verrucosa,* and Ballesteros & Ortea (1980) for *Doriopsilla areolata.* In both cases, the presence of natural products in the mantle (Table 1) is consistent with the absence of acid secretion. In the presence of acid, their chemical structure would certainly be affected. For the remaining species analyzed, there were no previous records of pH measurements in the literature.

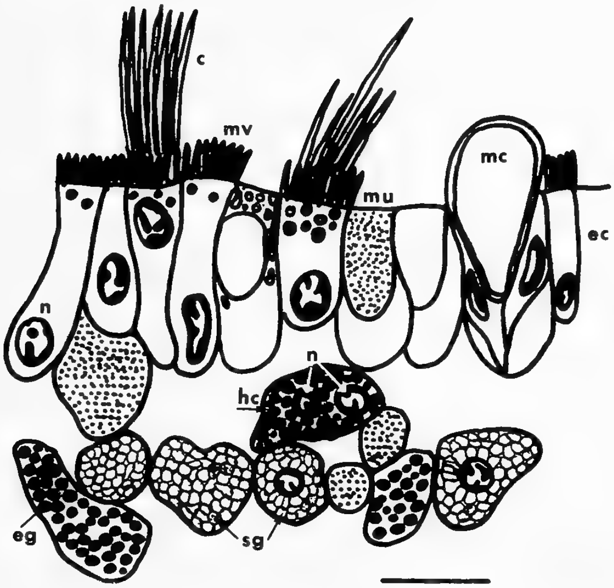

Figure 15

Dendrodoris limbata. Schematic representation of the border of the mantle showing the described types of cells. (scale bar = 10 μm). c: cilia; ec: epithelial cells; eg: electron-dense granules; mc: macrovacuolated cell; mu: mucous cell; mv: microvilli; n: nucleus; sg: secretory granules (see also Figure 16); hc: highly electron-dense cell (see also Figure 17).

The histological structures described in the different species are summarized in Table 3. A large number of mucous cells in the epithelia was common to all the species studied. This observation is consistent with the necessity for copious amounts of mucus, as has been suggested for other nudibranchs by Porter & Rivera (1983). As described by Potts (1981), *Archidoris pseudoargus* presented epithelial mucous cells, as well as dense granular cells. Potts (1981) also described some vacuolated cells on the edge of the mantle; in the gill epithelium, he found ciliated cells, vacuolated mucous gland cells, and some small wedge-shaped cells. The ciliated cells and the vacuolated mucous cells probably correspond to the cells described in our study. However, *Archidoris pseudoargus* possessed fewer ciliated cells in the dorsal mantle (Potts 1981) as compared with, for instance, *Dendrodoris limbata.* In our study of the rhinophores of *D. limbata,* we did not find any of the nonciliated, highly vacuolated cells described by Arias et al. (1984) in the rhinophoral epithelium of *Facelina coronata* (Forbes and Goodsir, 1839). The fact that these two species

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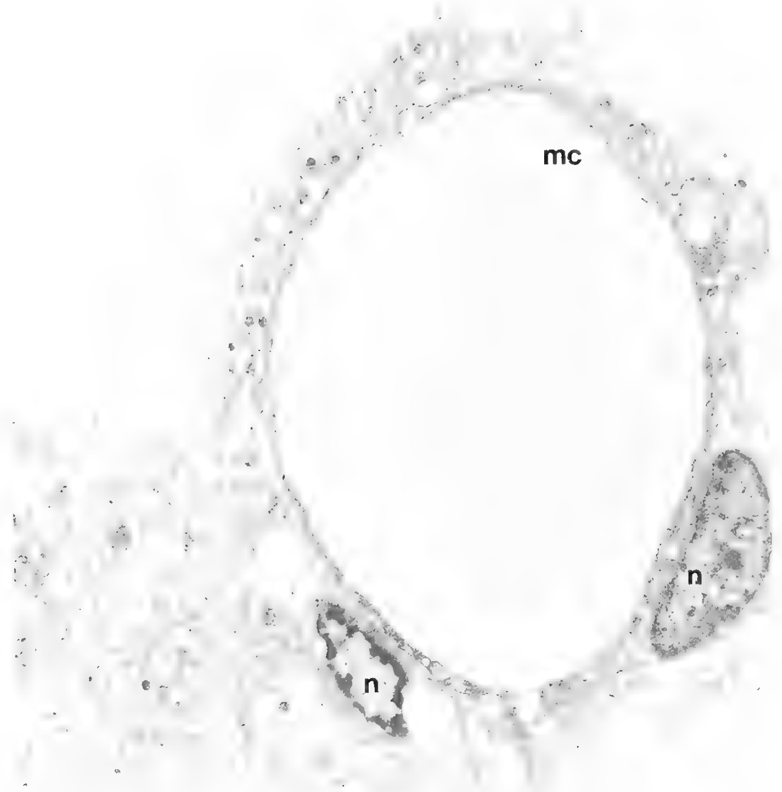
Figure 12, 13

Figure 12. *Doris verrucosa.* Histological section (LM) of a mantle protuberance, stained with Schiff's reagent and toluidine blue (scale bar = 10 μm). ec: epithelial cells; sp: spicules.

Figure 13. *Peltodoris atromaculata.* TEM of the mantle epithelium showing mucous cells and ciliated cells with microvilli (scale bar = 1 μm). c: cilia; mu: mucous cells; mv: microvilli.



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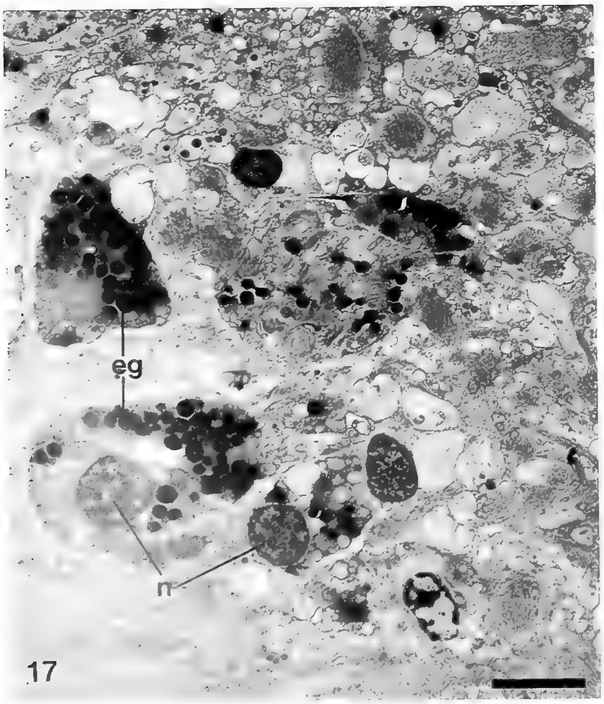

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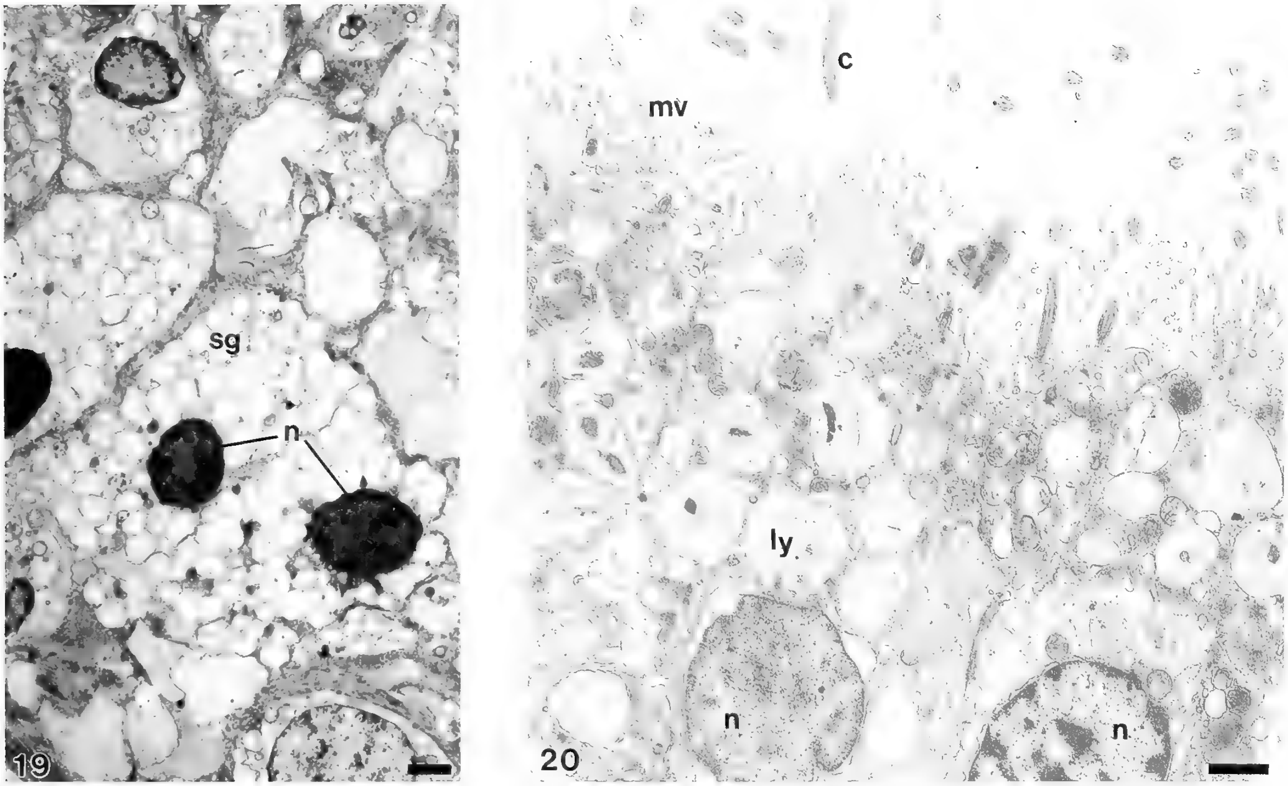

Figures 19–20

Dendrodoris limbata. 19: TEM of the gill subepithelial layer showing secretory granules around the nucleus (scale bar = 1 μm). 20: TEM of the rhinophore epithelium cells, with cilia, microvilli, and lysosomal vesicles (scale bar = 1 μm). c: cilia; ly: lysosome; mv: microvilli; n: nucleus; sg: secretory vesicles and granules.

belong to distinct nudibranch groups could account for this difference.

Defensive chemicals are not randomly distributed in the mantle, but are located in specific sites (Table 1). The first report on the localization of toxic substances in doridacean molluscs was probably that of Crozier (1916). He showed that the toxic substance in *Chromodoris zebra* Heilprin, 1888, was localized in the border of the mantle. Accumulation structures (MDFs of *Hypselodoris* and *Chromodoris* species) have been observed in species that obtain their products via their diet. Accumulation in the digestive gland is followed by transport (by unknown mechanisms) to MDFs, where the metabolites are stored. *Hypselodoris* and *Chromodoris* were recently studied by García et al. (1991) by LM of semithin sections. Our data on number, size, and distribution of MDFs (Avila, 1993) agree with their data. The MDFs are situated near the gills and the rhinophores, on the yellow (or white) line in the border of the mantle. The MDFs do not seem to open onto the surface of the mantle (García et al., 1991), and are formed by an accumulation of vacuolar cells. A closely related species, *Hypselodoris fontandraui,* accumulates similar compounds in the border of the mantle (Avila, 1993). Paradoxically, the mantle border of *H. fontandraui* does not present MDFs. Rudman (1984) described the distribution and possible evolution of MDFs in the different genera of chromodorids, and related their position in the body to their possible function as defensive glands.

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Figures 16–18

Dendrodoris limbata. 16: TEM of the mantle border showing a macrovacuolated cell (scale bar = 2 μm). 17: TEM of the mantle subepithelial layer showing highly electron-dense cells with their granules (scale bar = 5 μm). 18: TEM of gill epithelium cells with microvilli (scale bar = 1 μm). ec: epithelial cells; eg: electron-dense granules; mc: macrovacuolated cell; mv: microvilli; n: nucleus.

Table 3

Histological structures described in the mantle of selected doridacean mollusks, and their defensive strategies. Hc: *Hypselodoris cantabrica*; Hw: *Hypselodoris webbi*; Hv: *Hypselodoris villafranca*; Ho: *Hypselodoris orsini*; Cb: *Chromodoris britoi*; Dv: *Doris verrucosa* ([a] = biosynthesis of allomones is likely to occur; Avila et al., 1990a); Pa: *Peltodoris atromaculata* ([b] = dietary products are not likely to be related to defense); Da: *Doriopsilla areolata* ([c] = *ent*-pallescensin-A and its derivatives have not been tested for bioactivity yet; biosynthesis has been suggested to occur; Spinella et al., 1994). Dl: *Dendrodoris limbata* (me: mantle edge; gi: gills; rh: rhinophores). P: present; —: not detected; nm = not measured; MDFs: mantle dermal formations.

									Dl		
	Hc	Hw	Hv	Ho	Cb	Dv	Pa	Da	me	gi	rh
pH:	7	7	7	nm	7	7	6.5–7	7	7	7	7
Epithelia:											
Ciliated cells	P	P	P	P	P	P	P	P	P	P	P
Mucous glandular cells	P	P	P	P	P	P	P	P	P	P	P
Macrovacuolated cells	—	—	—	—	—	—	—	—	P	P	—
Monovacuolated cells	—	—	—	P	—	—	—	—	—	—	—
Subepithelial layer:											
Mucous glandular cells	—	—	—	—	P	—	P	—	P	P	—
Cells with electron-dense granules	—	P	—	P	P	—	—	—	P	—	—
Perinuclear vesiculated cells	—	—	—	—	—	—	—	—	P	P	—
Cells with clear vesicles	—	—	—	—	—	P	—	—	—	—	—
MDFs	P	P	P	P	P	—	—	—	—	—	—
Spicules	—	—	—	—	—	P	P	P	—	—	—
Defensive strategy:											
Mechanic defense (spicules)	—	—	—	—	—	P	P	P	—	—	—
Dietary allomones	P	P	P	P	P	—	—[b]	—	—	—	—
Biosynthetic allomones	—	—	—	—	—	P[a]	—	?P[c]	P	P	—

Hypselodoris orsini is able to chemically modify the native sponge compounds from its prey (Cimino et al., 1993). *H. orsini* presented irregularly shaped MDFs. Consequently, it differed from the rest of *Hypselodoris* species studied, which presented rounded, regular MDFs. *H. orsini* also differed from the rest of *Hypselodoris* species in that some monovacuolated cells were present in the epithelium of the visceral face of the mantle. The mantle epithelium presented similar characteristics in *Hypselodoris cantabrica, Hypselodoris webbi,* and *Hypselodoris villafranca. H. webbi,* however, presented some peculiar subepithelial vesiculated cells (Figure 6).

In the *Hypselodoris* species studied here, and in *Chromodoris britoi,* the general characteristics of the MDFs are in agreement with the fact that they contain the defensive allomones of each respective species (Table 1). However, histochemical tests are needed to demonstrate this fact at the cytological level.

Chromodoris luteorosea, Chromodoris purpurea, and *Chromodoris krohni* possess diterpenoid compounds, which are accumulated in the digestive gland and in the border of the mantle where MDFs are situated (Cimino et al., 1990a; Gavagnin et al., 1992; Avila, 1993). *C. britoi* also possess similar compounds stored in MDFs in the yellow mantle border (Avila, 1993). The MDFs in *C. britoi* (Figure 11) are slightly different from those of *Hypselodoris* spp. both in shape and structure, in agreement with the report of García et al. (1991).

In the remaining doridaceans studied here, there were no true accumulation structures comparable to MDFs, although some of them presented atypical secretory cells. *Peltodoris atromaculata, Doris verrucosa,* and *Doriopsilla areolata* possess epithelia with spicules. The spicules of *D. areolata* have been well studied by García et al. (1986). The presence of selected compounds in the border of the mantle of *D. areolata* (Table 1) does not seem to be related to the presence of a particular, distinctive type of cell in this area.

In *D. verrucosa,* the allomones are distributed in the mantle, and it is possible that the empty vesicular cells detected in the subepithelial layer do actually contain the verrucosins, although histochemical analysis is needed to demonstrate it. These empty vesicles probably correspond to the clear glands described by Edmunds (1968), although he interpreted them as containing inorganic acid.

Peltodoris atromaculata is able to obtain metabolites from a sponge; the metabolites are then accumulated in its digestive gland (Cimino et al., 1982; Avila, 1993). These compounds (petroformynes) showed strong toxic effects against *Artemia salina* (Cimino et al., 1990b), and inhibited pluteus larvae formation in sea urchin embryo bioassays (Avila, 1993). However, the petroformynes found in this species are not located in the mantle. Therefore, their effectiveness as a defensive mechanism is only possible if the animal dies. In *P. atromaculata,* the primary defense would then be restricted to spicules and perhaps coloration, but not chemicals. This is consistent with the fact that no distinctive accumulation structures or cells have been observed in the mantle epithelium of *P. atromaculata.* On the other hand, the mucous glandular cells observed in the mantle epithelium of *P. atromaculata* (Figure 13) could correspond to the "drüsenkörper" described by Haefelfinger (1961).

Defensive chemicals are selectively distributed in the mantle of *Dendrodoris limbata* (Table 1). These chemicals are biosynthesized by the nudibranch (Cimino et al., 1983). *D. limbata* presented an aspiculate epithelium. In the mantle epithelium of this species, ciliated, glandular, mucous, and other cells that we designated as macrovacuolated cells were found. These macrovacuolated cells were present in the yellow border of the mantle and in the gill epithelium. We suggest that these cells could be the sites of biosynthesis and storage of olepupuane and 7-deacetoxy-olepupuane, respectively. Their morphological characteristics support this hypothesis, although histochemical tests are needed in order to prove the presence of lipid substances inside the vacuole. Macrovacuolated cells were absent in other parts of the animal (i.e., rhinophore epithelium and the rest of the mantle), where no allomones were found.

Some subepithelial mucous cells of the border of the mantle of *D. limbata* contained granules of unknown composition. Further microanalyses are needed to ascertain the nature of their contents. Histochemical tests are necessary as well to investigate the peculiar electron-dense granules found between mucous glandular cells in the mantle subepithelial layer (Figure 17). These granules could be lipoprotein in nature.

Assuming that the various epidermal and subepidermal glands in doridaceans were homologous, Rudman (1984) hypothesized that cryptobranch dorids present glands that are small and spread widely over the whole mantle. In contrast, in chromodorids they would be concentrated, forming large compound glands, arranged only in some areas of the mantle. The only exception would be the macrovacuolated cells of *D. limbata,* which did not seem to be spread all over the mantle, but were located in specific areas, such as the mantle border and gill epithelium.

In summary, the doridaceans examined in this report seem to have developed different strategies that range from accumulation of defensive chemicals from prey (cleptochemodefenses) in specific structures, to the biosynthesis of defensive metabolites through multifunctional pathways in specific and selectively distributed cells. The authors hope that these results will encourage further studies of the mantle in doridaceans using histochemical techniques, in order to demonstrate specifically that the described cells contain the defensive allomones of these species.

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LITERATURE CITED

Arias, J. L., A. Menendez, M. Alvarez-Uria, D. Tolivia, C. Lopez, & H. Ramirez. 1984. Ultrastructural study of rhinophore epithelium in *Facelina coronata* (Mollusca: Opisthobranchia). Revista de Biología de la Universidad de Oviedo 2:51–57.

Avila, C. 1992. A preliminary catalogue of natural substances of opisthobranch molluscs from Western Mediterranean and near Atlantic. Scientia Marina 56(4):373–382.

Avila, C. 1993. Sustancias naturales de moluscos opistobranquios: Estudio de su estructura, origen y función en ecosistemas bentónicos. Ph.D. Thesis. 546 pp. University of Barcelona (Spain).

Avila, C. 1995. Natural products of opisthobranch molluscs: a biological review. Oceanography and Marine Biology, An Annual Review 33:487–559.

Avila, C., M. Ballesteros, G. Cimino, A. Crispino, M. Gavagnin, & G. Sodano. 1990a. Biosynthetic origin and anatomical distribution of the main secondary metabolites in the nudibranch mollusc *Doris verrucosa.* Comparative Biochemistry and Physiology 97B(2):363–368.

Avila, C., G. Cimino, A. Crispino, A. Fontana, M. Gavagnin, J. Ortea, & R. R. Vardaro. 1990b. Defensive strategies of Chromodorididae nudibranchs: origin, anatomical distribution and role of selected chemicals. Abstracts 25th European Marine Biology Symposium, Ferrara (Italy).

Avila, C., G. Cimino, A. Crispino & A. Spinella. 1991a. Drimane sesquiterpenoids in Mediterranean *Dendrodoris* nudibranchs: Anatomical distribution and biological role. Experientia 47:306–310.

Avila, C., G. Cimino, A. Fontana, M. Gavagnin, J. Ortea & E. Trivellone. 1991b. Defensive strategy of two *Hypselodoris* nudibranchs from Italian and Spanish coasts. Journal of Chemical Ecology 17(3):625–636.

Ballesteros, M. & J. Ortea. 1980. Contribución al conocimiento de los Dendrodorididae (Moluscos: Opistobranquios: Doridáceos) del litoral ibérico, I. Publicaciones del Departamento de Zoología (Univ. de Barcelona) 5:25–37.

Castiello, D., G. Cimino, S. De Rosa, S. De Stefano & G. Sodano. 1980. High molecular weight polyacetylenes from the nudibranch *Peltodoris atromaculata* and the sponge *Petrosia ficiformis.* Tetrahedron Letters 21(52):5047–5050.

Cimino, G., S. De Rosa, S. De Stefano & G. Sodano. 1982. The chemical defense of four Mediterranean nudibranchs. Comparative Biochemistry and Physiology 73B(3):471–474.

CIMINO, G., S. DE ROSA, S. DE STEFANO, G. SODANO & G. VILLANI. 1983. Dorid nudibranch elaborates its own chemical defense. Science 219:1237–1238.

CIMINO, G., A. CRISPINO, S. DE STEFANO, M. GAVAGNIN & G. SODANO. 1986. A naturally-occurring analog of methylthioadenosine (MTA) from the nudibranch mollusc *Doris verrucosa.* Experientia 42:1301–1302.

CIMINO, G., M. GAVAGNIN, G. SODANO, R. PULITI, A. MATTIA & L. MAZZARELLA. 1988. Verrucosin-A and-B, ichthyotoxic diterpenoic acid glycerides with a new carbon skeleton from the dorid nudibranch *Doris verrucosa.* Tetrahedron 44(8): 2301–2310.

CIMINO, G. & G. SODANO. 1989. The chemical ecology of Mediterranean opisthobranchs. Chemica scripta 29:389–394.

CIMINO, G., A. CRISPINO, M. GAVAGNIN & G. SODANO. 1990a. Diterpenes from the nudibranch *Chromodoris luteorosea.* Journal of Natural Products 53(1):102–106.

CIMINO, G., A. DE GIULIO, S. DE ROSA & V. DI MARZO. 1990b. Minor bioactive polyacetylenes from *Petrosia ficiformis.* Journal of Natural Products 53(2):345–353.

CIMINO, G., A. FONTANA, F. GIMENEZ, A. MARIN, E. MOLLO, E. TRIVELLONE & E. ZUBIA. 1993. Biotransformation of a dietary sesterterpenoid in the Mediterranean nudibranch *Hypselodoris orsini.* Experientia 49:582–586.

CROZIER, W. J. 1916. On the immunity coloration of some nudibranchs. Proceedings of the National Academy of Sciences, Washington 2:672–675.

EDMUNDS, M. 1966. Protective mechanisms in the Eolidacea (Mollusca, Nudibranchia). Zoological Journal of the Linnean Society 46:27–71.

EDMUNDS, M. 1968. Acid secretion in some species of Doridacea (Mollusca, Nudibranchia). Proceedings of the Malacological Society of London 38:121–133.

EDMUNDS, M. 1981. Opisthobranchiate Mollusca from Ghana: Chromodorididae. Zoological Journal of the Linnean Society 72:175–201.

EDMUNDS, M. 1987. Color in Opisthobranchs. American Malacological Bulletin 5(2):185–196.

FAULKNER, D. J. 1993. Marine natural products. Natural Products Report 10(5):497–539.

FAULKNER, D. J. & M. T. GHISELIN. 1983. Chemical defense and evolutionary ecology of dorid nudibranchs and some other opisthobranch gastropods. Marine Ecology Progress Series 13:295–301.

FOALE, S. J. & R. C. WILLAN. 1987. Scanning and transmission electron microscope study of specialized mantle structures in dorid nudibranchs (Gastropoda: Opisthobranchia: Anthobranchia). Marine Biology 95:547–557.

FONTANA, A., C. AVILA, E. MARTINEZ, J. ORTEA, E. TRIVELLONE & G. CIMINO. 1993. Defensive allomones in three species of *Hypselodoris* from the Cantabrian Sea. Journal of Chemical Ecology 19(2):339–356.

FONTANA, A., E. TRIVELLONE, E. MOLLO, G. CIMINO, C. AVILA, E. MARTINEZ & J. ORTEA. 1994. Further chemical studies of Mediterranean and Atlantic *Hypselodoris* nudibranchs: a new furanosesquiterpenoid from *Hypselodoris webbi.* Journal of Natural Products 57(4):510–513.

GARCIA, F. J., J. C. GARCIA & L. CERVERA. 1986. Estudio morfológico de las espículas de *Doriopsilla areolata* (Gastropoda: Nudibranchia). Malacologia 27(1):83–96.

GARCIA, J. C., G. CIMINO & A. MEDINA. 1990. Studies on the defensive behaviour of *Hypselodoris*: ultrastructure and chemical analysis of mantle dermal formations (MDFs). Marine Biology 106:245–250.

GARCIA, J. C., A. MEDINA & R. COVEÑAS. 1991. Study of the anatomy and histology of the mantle dermal formations (MDFs) of *Chromodoris* and *Hypselodoris* (Opisthobranchia: Chromodorididae). Malacologia 32(2):233–240.

GAVAGNIN, M., R. R. VARDARO, C. AVILA, G. CIMINO & J. ORTEA. 1992. Ichthyotoxic diterpenoids from the Cantabrian nudibranch *Chromodoris luteorosea.* Journal of Natural Products 55(3):368–371.

GOSLINER, T. M. & D. W. BEHRENS. 1990. Special resemblance, aposematic coloration and mimicry in opisthobranch gastropods. Proceedings of the Symposium of the American Society of Zoology, Galveston, Texas, USA pp. 127–145.

HAEFELFINGER, H. R. 1961. Beiträge zur kenntnis von *Peltodoris atromaculata* Bergh 1880 (Mollusca, Opisthobranchiata). Revue Suisse de Zoologie 68(3):331–343.

HARRIS, L. G. 1973. Nudibranch associations Pp. 213–315 in T. C. Cheng (ed.). Current Topics in Comparative Pathobiology. Academic Press: New York.

HERDMAN, W. A. 1890. On the structure and functions of the cerata or dorsal papillae in some nudibranchiate Mollusca. Quarterly Journal of Microscopical Science 31:41–63.

HERDMAN, W. A. & J. A. CLUBB. 1892. Third report upon the nudibranchiata of the L.M.B.C. district. Proceedings of the Biological Society of Liverpool III:131–169.

KARUSO, P. 1987. Chemical ecology of the nudibranchs. Pp. 31–60 in P. J. Scheuer (ed.), Bioorganic Marine Chemistry. Springer-Verlag: Berlin.

KRESS, A. 1981. A scanning electron microscope study of notum structures in some dorid nudibranchs (Gastropoda: Opisthobranchia). Journal of the Marine Biological Association of the United Kingdom 61:177–191.

MARIN, A., V. DI MARZO & G. CIMINO. 1991. A histological and chemical study of the cerata of the opisthobranch mollusc *Tethys fimbria.* Marine Biology 111:353–358.

ODHNER, N. 1932. Beiträge zur Malakozoologie der Kanarischen Inseln: Lamellibranchien, Cephalopoden, Gastropoden. Arkiv för Zoologi 23(14):1–116.

ORTEA, J. 1988. Moluscos Opistobranquios del Archipiélago de Cabo Verde: Chromodorididae. Publicações Ocasionais da Sociedade Portuguesa de Malacologia 11:1–16.

PAWLIK, J. R., M. R. KERNAN, T. F. MOLINSKI, M. K. HARPER & D. J. FAULKNER. 1988. Defensive chemicals of the Spanish dancer nudibranch *Hexabranchus sanguineus* and its egg ribbons: macrolides derived from a sponge diet. Journal of Experimental Marine Biology and Ecology 119:99–109.

PORTER, K. J. & E. R. RIVERA. 1980. The Golgi apparatus in epidermal mucoid and ellipsoid-vacuolate cells of *Aeolidia papillosa* and *Coryphella rufibranchialis* (Nudibranchia). Protoplasma 102:217–233.

PORTER, K. J. & E. R. RIVERA. 1983. Light and electron microscopic cytochemistry of the epidermal mucoid cells of *Aeolidia papillosa* and *Coryphella rufibranchialis* (Mollusca, Nudibranchia). Protoplasma 114(1–2):14–22.

POTTS, G. W. 1981. The anatomy of respiratory structures in the dorid nudibranchs *Onchidoris bilamellata* and *Archidoris pseudoargus,* with details of the epidermal glands. Journal of the Marine Biological Association of the United Kingdom 61:959–982.

ROS, J. 1976. Sistemas de defensa en los Opistobranquios. Oecologia Aquatica 2:41–77.

RUDMAN, W. B. 1984. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific a review of the genera. Zoological Journal of the Linnean Society 81:115–273.

SCHMEKEL, L. & W. WECHSLER. 1967. Elektronenmikroskopische Untersuchungen über Struktur and Entwicklung der Epidermis von *Trinchesia granosa* (Gastropoda Opisthobranchia). Zeitschrift für Zellforschung 77:95–114.

SPINELLA, A., L. A. ALVAREZ, C. AVILA & G. CIMINO. 1994. New acetoxy-*ent*-pallescensin-A sesquiterpenoids from the skin of the porostome nudibranch *Doriopsilla areolata*. Tetrahedron Letters 35(46):8665–8668.

THOMPSON, T. E. 1960a. Defensive adaptations in opisthobranchs. Journal of the Marine Biological Association of the United Kingdom 39:123–134.

THOMPSON, T. E. 1960b. Defensive acid-secretion in marine slugs and snails. The New Scientist 8:414–416.

THOMPSON, T. E. 1969. Acid secretion in Pacific Ocean gastropods. Australian Journal of Zoology 17:755–764.

THOMPSON, T. E. 1983. Detection of epithelial acid secretions in marine molluscs: review of techniques and new analytical methods. Comparative Biochemistry and Physiology 74A: 615–621.

THOMPSON, T. E. & D. J. SLINN. 1959. On the biology of the opisthobranch *Pleurobranchus membranaceus*. Journal of the Marine Biological Association of the United Kingdom 38: 507–524.

THOMPSON, T. E. & J. G. COLMAN. 1984. Histology of acid glands in Pleurobranchomorpha. Journal of Molluscan Studies 50:65–67.

THOMPSON, T. E. & L. J. GATHERCOLE. 1986. Histophysical demonstration of barium sulphate in acidic epithelia of molluscs and other organisms following irrigation *in vivo* with aqueous barium chloride. Journal of Molluscan Studies 52: 261–262.

TODD, C. D. 1981. The ecology of nudibranch molluscs. Oceanography and Marine Biology, An Annual Review 19:141–234.

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Morphological Differences between the Pedal Musculature of Patellogastropod and Fissurellid Limpets

by

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Abstract. In many of the rocky intertidal zones around the world, patellogastropods and fissurellid limpets live side-by-side. Although their external appearance is very similar, the allometry and organization of the pedal musculature of these gastropods are quite distinct. For temperate and tropical species pairs, allometric analyses indicate that the ratio of the area of the muscle scar to the area of the shell aperture is smaller in the species of patellogastropods studied than in the fissurellids studied. The foot of the patellogastropod *Acmaea antillarum* consists of one homogeneous muscular mass that resembles the columellar region of coiled prosobranch gastropods. In contrast, the foot of the fissurellid *Fissurella barbadensis* consists of columellar and tarsic regions like those of coiled prosobranchs. The majority of the muscle fibers in the foot of *A. antillarum* are oriented dorsoventrally; in *F. barbadensis* the muscle fibers do not show a tendency toward a particular orientation. The large mass of dorsoventral pedal muscles of patellogastropods should permit them to achieve stronger normal tenacities. The fewer dorsoventral muscle fibers found in fissurellids may be compensated for by the increase in the relative size of the surface area of attachment of the pedal musculature to the shell, which should increase the animal's ability to withstand shearing.

INTRODUCTION

Limpet-shaped gastropods are one of the most common organisms inhabiting the rocky intertidal region, due in part to the high tenacities of their muscular feet. The limpet shape has evolved independently many times within the Gastropoda (Fretter & Graham, 1994) and occurs in almost every order of the class. The muscular foot of a limpet-shaped gastropod carries out two paradoxically opposed functions: it permits the animal to move itself and prevents it from being moved by external forces. Patellogastropod and fissurellid limpets can be found living side-by-side in rocky intertidal communities around the world. Although superficially similar, the organization of the pedal musculature is quite distinct in these clades (Voltzow, 1988).

The foot of a limpet-shaped gastropod consists primarily of dorsoventral muscle fibers that extend ventrally from their origin at the U-shaped muscle scar on the ventral surface of the shell and ramify as they reach the sole (Jones & Trueman, 1970; Voltzow, 1988; Frescura & Hodgson, 1990). The muscle fibers are embedded in a matrix of collagenous connective tissue, which constitutes about 30% to 40% of the entire pedal volume of patellid limpets (Frescura & Hodgson, 1990).

Voltzow (1988) surveyed the gross organization of the pedal musculature of limpet-shaped gastropods from a diversity of taxonomic groups. The feet of patellogastropods are distinct from those of non-patellogastropods in that the muscle fibers that originate at each side of the foot do not cross the midline, whose dorsal surface is marked by a deep mid-sagittal cleft. Fissurellid limpets lack this cleft, and approximately one-third of the muscle fibers that originate at each side of the foot pass the midline and insert on the sole at the other side of the foot. These morphological differences are reflected in the locomotory patterns used by each group. Patellogastropods use ditaxic waves, in which two sets of waves travel along the sole, one on each side of the foot (Miller, 1974b; Voltzow, 1988). All other limpets studied use monotaxic waves, in which a single wave traverses the width of the sole.

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We compared the pedal musculature of representative species of Patellogastropoda and Fissurellidae to evaluate the differences in their pedal morphology and relate them to their ecology.

MATERIALS AND METHODS

Organisms

This study focused on four species of limpets, the patellogastropods, *Acmaea antillarum* (Sowerby, 1831) and *Tectura scutum* (Rathke, 1833), of the family Lottidae, and the "archaeogastropods" (*sensu* Hickman, 1988), *Fissurella barbadensis* (Gmelin, 1791) and *Diodora aspera* (Rathke, 1833), of the family Fissurellidae. Specimens of *A. antillarum* and *F. barbadensis* were collected from the rocky intertidal region of Piñones on the north coast of Puerto Rico. Specimens of *T. scutum* and *D. aspera* were collected at Lime Kiln Point and Cattle Point, San Juan Island, Washington, USA.

Allometric Analysis

Twenty-five individuals of each species were included in an allometric analysis. The length and width of the shell aperture were measured directly with calipers. The areas of the aperture, sole, and muscle scar (the site of attachment of the foot to the shell) were measured as follows: To minimize distortion, the outer margins of the shell and sole were traced on clear acetate sheets while the animals were attached to the wall of an aquarium constructed from 50 × 50 mm cover glass. These tracings were digitized and their areas were calculated with a Jandel Scientific 2210 digitizer and Sigma Scan 3.9 Scientific Measurement System (Jandel Scientific). After the animals were removed from the shells, the muscle scars on the shells were outlined with a fine permanent marker. These outlines were traced onto pieces of transparent tape that were placed over the muscle scars. The tape was removed, placed on a sheet of paper, and digitized and analyzed as above.

The use of Model II regression is recommended in allometric studies in which both variables are subject to measurement error (Niklas, 1994). McArdle (1988) concluded that reduced major axis (RMA) regression is less biased than major axis regression. For each species, we performed RMA regression between the length and width of the aperture (AL vs. AW), the log of the area of the aperture and the log of the area of the sole (log AP vs. log SO), and the log of the area of the aperture and the log of the area of the muscle scar (log AP vs. log MS) (McArdle, 1988; Niklas, 1994). The test proposed by Clarke (1980) was used to compare the slopes of the regression lines between species and between families.

Histology

The histology of the pedal musculature of 10 individuals each of *Acmaea antillarum* and *Fissurella barbadensis* were examined for this study. The feet of *Tectura scutum* and *Diodora aspera* were also analyzed for comparative purposes. The animals were relaxed in 7.5% magnesium chloride, and their shells and viscera were removed; only the feet were used for histology. The tissue was fixed in a solution of 2.5% glutaraldehyde and 4.0% formalin in a 0.1 M phosphate buffer at pH 7.2. The tissue was then dehydrated in an alcohol series.

Transverse and sagittal sections 5 to 10 μm thick were stained with Milligan trichrome stain (Humason, 1979). The sections were analyzed to determine the organization of the pedal musculature, the diameters of the muscle fibers, and the relative amounts of muscular and connective tissue throughout the foot.

Orientation of Muscle Fibers

Five specimens each of *Acmaea antillarum* and *Fissurella barbadensis,* prepared with the histological methods mentioned above, were analyzed to quantify the orientations of their muscle fibers. Immediately after fixation, a sagittal slice of approximately 3 to 5 mm was cut from the foot of each specimen using a razor blade. This slice was taken from the portion of the foot that included the complete length of the right side of the U-shaped shell muscle. Sagittal sections 7 μm thick were prepared from the slices as described above.

One section from each specimen was chosen for quantitative analysis on the basis of absence of scratches and folding and presence of even staining. The length and height of each section were measured with an ocular micrometer. The length of the section was defined as the distance between the anterior and posterior attachments of the mantle to the foot. The height of the section was defined as the distance between the sole and the dorsal edge. The dorsalmost 10% of the tissue was not included in this study to avoid analyzing musculature that might have been distorted or torn when the animal was removed from the shell. Each section was diagrammatically divided into three equal portions, the anterior, middle, and posterior. The central longitudinal axis of each section divided it into dorsal and ventral halves. Thus, each section was divided into six regions: anterodorsal, anteroventral, middorsal, midventral, posterodorsal, and posteroventral.

The orientations of the muscle fibers in each region were traced using a camera lucida mounted on an Olympus BHS compound microscope at a final magnification of 156.25×. A 72-point grid was prepared using graph paper with 20 squares to the inch. The grid was centered on each region of each section, and the slope of each muscle fiber that intersected a point on the grid was traced. If a grid point intersected with nervous, vascular, glandular, epithelial, or connective tissue, or with a muscle fiber oriented perpendicular to the plane of the section, the point was considered as missing data.

The angle of orientation of each muscle fiber traced on the grids with respect to the longitudinal axis of the foot was digitized as described above. The angle measured was

Table 1

Regression equations for the allometric relationships included in this study. Lines indicate analyses of covariance; those marked with two asterisks were significantly different ($P < 0.01$). AL = Aperture Length; AW = Aperture Width; AP = Aperture area; SO = Sole area; MS = Muscle Scar area.

	AL[1] vs. AW	log AP vs. log SO	log AP vs. log MS
Acmaea antillarum	$y = -0.0868 + 0.8972x$	$y = -0.2754 + 0.9251x$	$y = -0.8112 + 0.7064x$ **
Tectura scutum	$y = -0.0950 + 0.8677x$	$y = -0.2713 + 0.9633x$	$y = -0.9856 + 0.9736x$ **
Fissurella barbadensis	$y = -0.1206 + 0.7736x$	$y = -0.3467 + 1.2335x$	$y = -0.9776 + 1.4340x$ **
Diodora aspera	$y = -0.3664 + 0.5925x$	$y = -0.4965 + 1.3307x$	$y = -1.2345 + 1.4679x$
Pooled Patellids	$y = -0.0389 + 0.8531x$ **	$y = -0.2770 + 0.9680x$ **	not pooled
Pooled Fissurellids	$y = 0.3625 + 0.5943x$	$y = -0.3053 + 1.1561x$	$y = -0.7568 + 1.0350x$

that formed by the muscle fiber counterclockwise (toward the anterior end) with the longitudinal axis of the section. Twelve categories of angle of orientation at subsequent intervals of 15° each from 1° to 180° were established. The frequency distribution of the number of muscle fibers per specimen within each category was plotted and analyzed using the Kolmogorov-Smirnov (K-S) Goodness of Fit Test (Statistix 4.0 Statistical Analysis Program, Analytical Software). The probability values were adjusted for the number of simultaneous tests using the sequential Bonferroni test (Rice, 1989).

RESULTS

Allometric Analysis

The slopes of the regression lines as determined by RMA regression for aperture length (AL) vs. aperture width (AW) were not significantly different for each pair of species belonging to the same family (Table 1, Figure 1A). On the other hand, there was a significant difference ($P < 0.0001$) between the slope of the line for the two fissurellid species vs. that of the two patellogastropods (Table 1). Thus, the shells of the patellogastropods used in this study were relatively wider than those of the fissurellids.

In all four species, the log of the area of the sole (SO) increased linearly as a function of the log of the area of the shell aperture (AP) (Table 1, Figure 1B). There was no significant difference between the slopes of the RMA regression lines of log SO vs. log AP for the two species of patellogastropods or for the two fissurellids. In contrast, the slope of the line for the two fissurellid species was significantly different from that of the two patellogastropods (Table 1).

The slopes of the regressions of log AP vs. the log of the area of the muscle scar (MS) were not significantly different for the fissurellid species, but were different for the two patellogastropod species ($P < 0.001$) (Table 1, Figure 1C). However, the slopes were significantly different when the line for each fissurellid was compared with that of the patellogastropod from the same habitat (Table 1, Figure 1A).

Histology

Camera lucida drawings and histological sections (Figures 2, 3) revealed distinct differences between the organization of the pedal musculature of the patellogastropods and fissurellids studied.

Acmaea antillarum. Transverse sections of the foot of *A. antillarum* indicated that one bundle of muscle fibers originated at each side of the shell (Figure 2A). Each bundle ramified ventrally and laterally and inserted near the epithelium of the sole. Most of the muscle fibers were oriented dorsoventrally, although there were also transverse, longitudinal, and oblique muscle fibers throughout the foot.

Sagittal sections showed that the foot consisted of a solid mass of dorsoventral muscle fibers that extended from the dorsal surface to the sole (Figure 2B). There were distinct differences between the organization of the muscle fibers in the dorsal, central, and ventral areas of the foot. In the dorsalmost area near the attachment to the shell, the foot consisted of fine bundles of dorsoventral muscle fibers embedded in a dense matrix of connective tissue (Figure 3A). The diameters of the muscle fibers in this area ranged from 0.5 to 2.4 μm in a specimen whose aperture length was 19.5 mm. These bundles of muscle fibers extended ventrally into the central area of the foot, where they appeared to be thicker in diameter and surrounded by less connective tissue (Figure 3B). The diameters of the muscle fibers in this region ranged from 4.8 to 9.6 μm in the specimen mentioned above. In the ventral region, the muscle fibers continued ventrally as thick bundles until they reached the area directly above the sole (Figures 2, 3C). In this area the number of glands and thin transverse muscle fibers and the amount of connective tissue increased. The ventral region occupied approximately 10% to 15% of the total height of a section. The diameter of the muscle fibers in this region ranged from 3.2 to 5 μm in the same specimen mentioned above.

Fissurella barbadensis. The pedal musculature of *F. barbadensis* was distinct from that of *Acmaea antillarum* (Figures 2, 3). Mid-transverse sections showed that the bundles of muscle fibers that originated dorsally ramified ventrally,

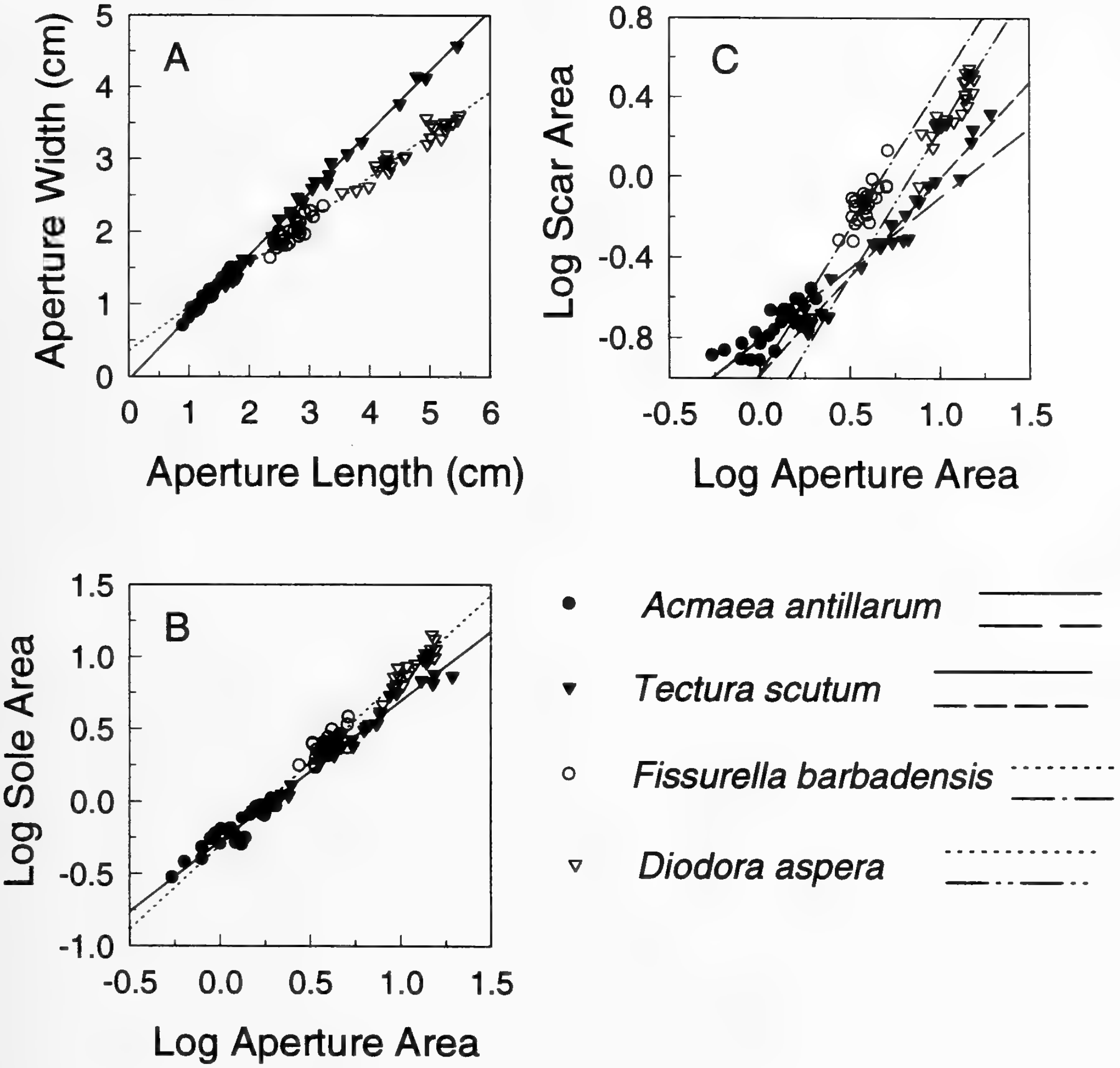

Figure 1

Relationships between (A) the length and width of the aperture of the shell; (B) the log of the area of the aperture of the shell and the log of the area of the sole; and (C) the log of the area of the aperture of the shell and the log of the area of the muscle scar of *Acmaea antillarum* (solid circles, long dash line), *Tectura scutum* (solid triangles, short dash line), *Fissurella barbadensis* (open circles, dot dash line), and *Diodora aspera* (open triangles, dot dot dash line). The solid lines indicate the regression for the pooled patellid data; the dotted lines for the fissurellid data.

laterally, and transversely into finer units, occupying approximately two-thirds of the pedal mass (Figure 2C). Many thick longitudinal and oblique muscle fibers lay between the bundles of dorsoventral muscles. A layer of thin transverse muscle fibers occupied the central portion of the foot. The ventral portion of the pedal musculature consisted of thin muscle fibers oriented in many directions and extending to the ventral epithelium.

In sagittal sections the foot of *Fissurella barbadensis* also appeared to be divided into regions based on the thickness of the muscle fibers and the relative amount of connective tissue (Figure 2D). Near the shell attachment site, there was a relatively large amount of connective tissue. The dorsalmost two-thirds of the pedal musculature consisted of thick bundles of muscle fibers oriented in virtually all directions (Figure 3D). In this region the diameters of the muscle fibers ranged from 3.1 to 4.8 μm in a specimen with an aperture length of 26.2 mm. This region contained a relatively small amount of connective tissue. In the central portion of the foot, the muscle fibers were less dense and lacked any obvious organization (Figure 3E). The ventral portion consisted of a loose network of very fine

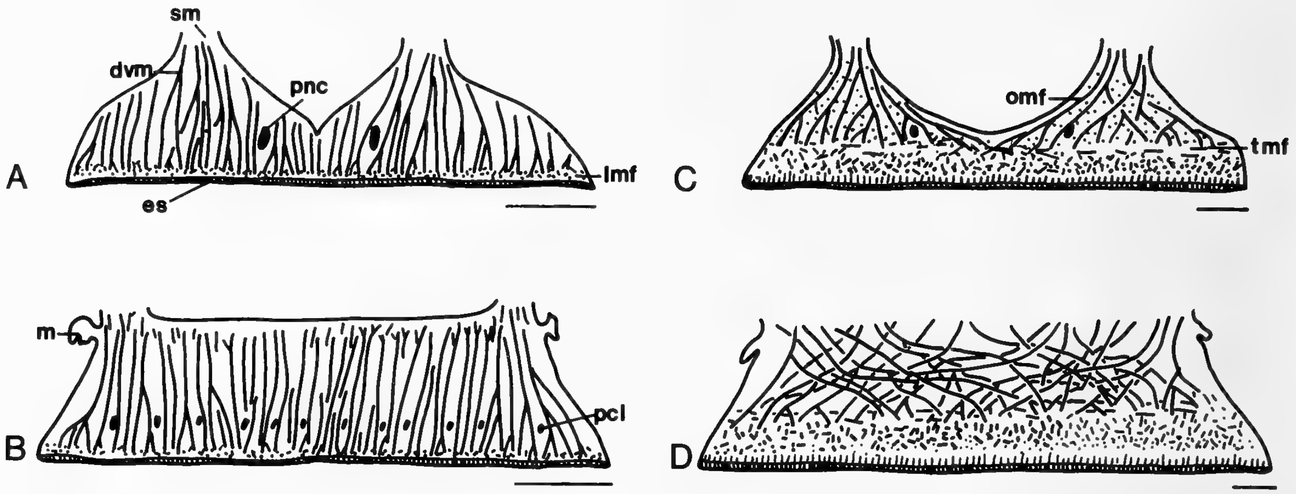

Figure 2

Diagrams based on camera lucida drawings and histological sections of the pedal musculature of *Acmaea antillarum* (A, B) and *Fissurella barbadensis* (C, D). A and C are from transverse sections; dorsal is at the top. B and D from sagittal sections; anterior is to the left. dvm, dorsoventral muscle fibers; es, epithelium of sole; lmf, longitudinal muscle fibers; m, mantle; omf, oblique muscle fibers; pcl, pedal cord lateral connectives; pnc, pedal nerve cord; sm, site of attachment of muscle to shell; tmf, transverse muscle fibers. Scale bars = 2 mm.

muscle fibers embedded in a dense matrix of connective tissue (Figure 3F). The diameters of the muscle fibers were much smaller, ranging from 1.5 to 1.8 μm in the central, transitional region to 0.4 to 1.0 μm in the ventral region in the same specimen mentioned above. A layer of thin dorsoventral muscle fibers appeared to insert at the basement membrane of the sole epithelium (Figure 3F). The muscle fibers that originated at the site of shell attachment did not appear to be the same ones that inserted at the sole.

Orientations of the Muscle Fibers

Acmaea antillarum. When the frequency distributions of the orientations of the muscle fibers for each region were compared across specimens, P-values were greater than or equal to 0.1000 (K-S test), demonstrating that all of the specimens had the same distribution in each part of the foot. Approximately 55% of the muscle fibers of *A. antillarum* were oriented perpendicular to the sole (Figure 4). From 58% to 62% of the muscle fibers in the anterodorsal, anteroventral, midventral, and posteroventral regions of the foot had an orientation of from 75° to 105°.

The muscle fibers of the middorsal region had a bimodal distribution; 45% of the muscle fibers were oriented from 70° to 105°, and 33% were oriented from 135° to 180° with respect to the longitudinal axis (Figure 4C). In the posterodorsal region, approximately half of the muscle fibers had a dorsoventral orientation (Figure 4E), and approximately 18% were oriented from 30° to 60° to the longitudinal axis.

Fissurella barbadensis. One specimen (FbN) of *F. barbadensis* had distributions of muscle fiber orientation that were significantly different (K-S test, $P < 0.0001$) from the other four specimens. These differences were found for the middorsal and posterodorsal regions only. The other four specimens were not significantly different from each other in any of the six regions. In all specimens the muscle fibers showed no strong tendency toward a particular orientation in any region (Figure 4). The muscle fibers were oriented similarly throughout the foot. Less than 15% of the muscle fibers of any region were oriented dorsoventrally. The anterodorsal region of *F. barbadensis* contained only a small number of muscle fibers that had an approximate orientation of 90° (Figure 4A). In the middorsal region (Figure 4C), approximately two-thirds of the muscle fibers were oriented from 105° to 165°.

The frequency distributions of the orientations of the muscle fibers of each region of the foot of *Acmaea antillarum* were significantly different ($P < 0.0001$) from that of the corresponding region of four specimens of *Fissurella barbadensis*. For the specimen FbN, the distributions were different ($P < 0.0002$) from *A. antillarum* for the anterodorsal and middorsal regions, but not for the other four regions.

DISCUSSION

Allometry

The patellogastropods studied had relatively wider shells than did the fissurellids of a given length (Figure 1A). The ratio of the log of the area of the aperture to the log of the area of the sole was greater in the fissurellids than in the patellogastropods studied. But the most interesting allometric differences involved the scaling of the muscle scar with respect to the area of the shell aperture (Figure 1C).

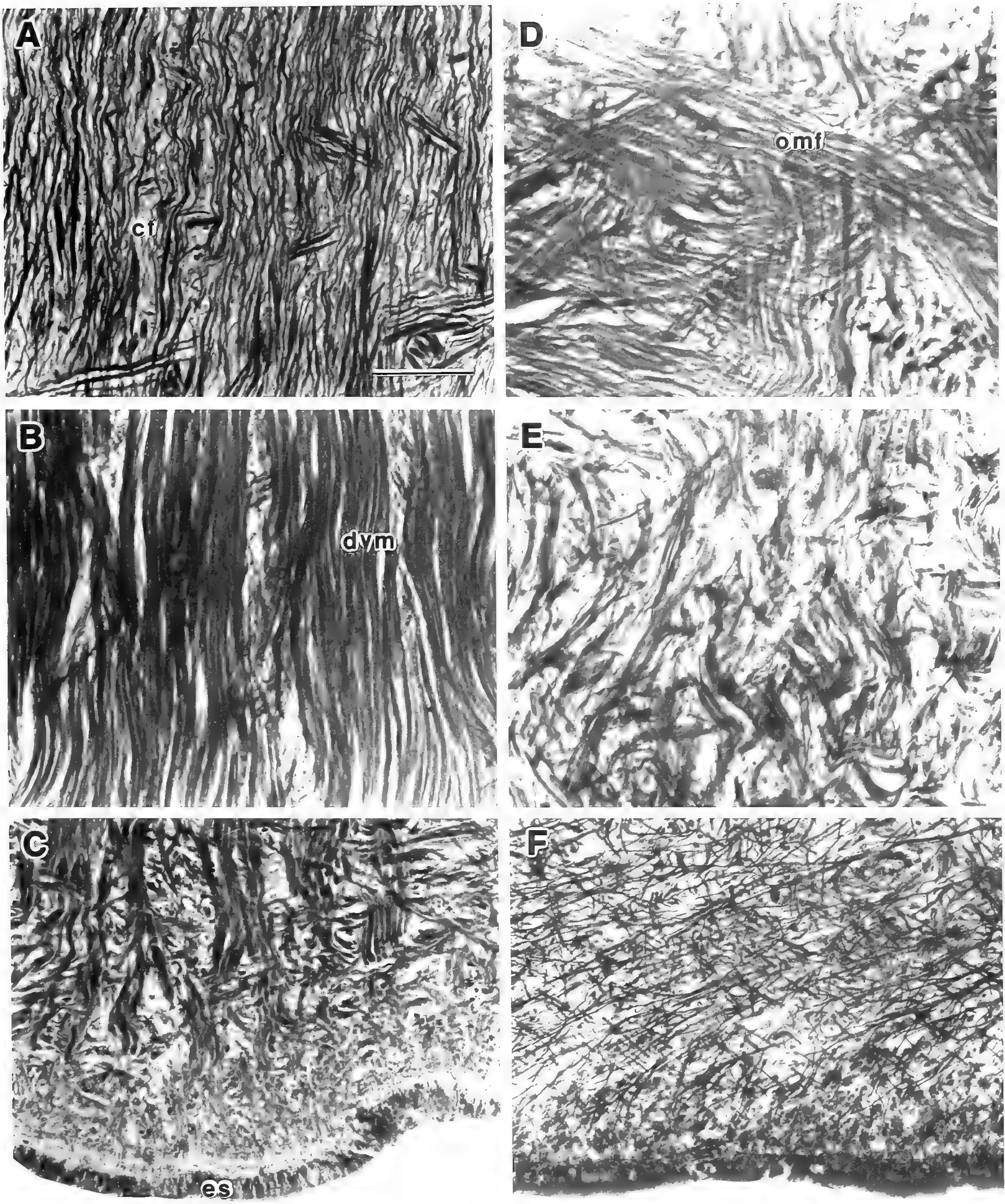

Figure 3

Photomicrographs of sagittal sections 7–8 μm thick of the feet of *Acmaea antillarum* (A, B, C) and *Fissurella barbadensis* (D, E, F). A and D are from the dorsal regions, B and E from the central regions, and C and F are from the ventral regions of the feet. ct, connective tissue; dvm, dorsoventral muscle fibers; es, epithelium of sole; omf, oblique muscle fibers. All photos to same scale, scale bar = 50 μm.

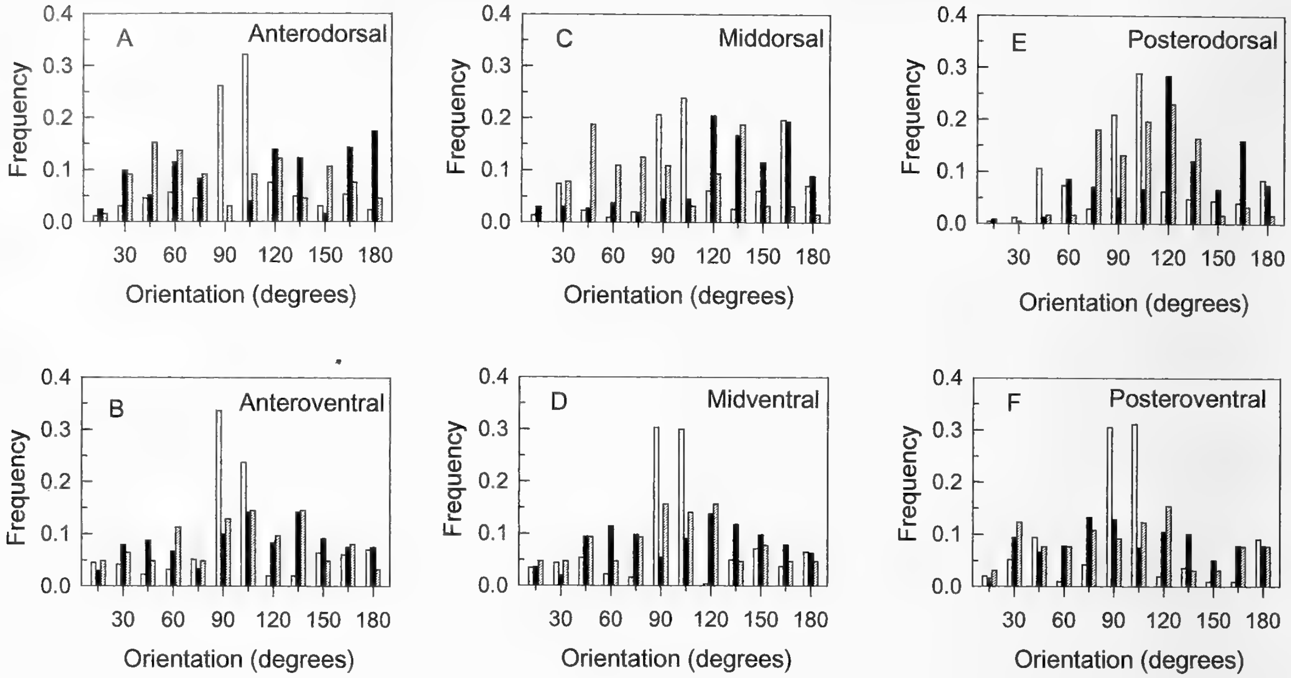

Figure 4

Frequency distributions of the orientations of the muscle fibers in the (A) anterodorsal, (B) anteroventral, (C) middorsal, (D) midventral, (E) posterodorsal, and (F) posteroventral regions of the feet of *Acmaea antillarum* (open bars) and *Fissurella barbadensis* (specimen FbN, shaded bars; all others, solid bars).

In each habitat, the fissurellid species studied had a larger muscle scar for a given shell size than did the patellogastropod studied. When the prying force exerted by crabs and birds or the drag and lift exerted by a wave acts on a limpet-shaped shell, the force is transmitted from the shell to the foot through the connective tissue at the site of the muscle scar. The relatively larger muscle scar of a fissurellid may help it transmit this force to a larger portion of its pedal musculature. This hypothesis could be tested by measuring the tenacities of a diversity of patellogastropod and fissurellid limpets.

Organization of Pedal Musculature

The feet of *Acmaea antillarum* and *Fissurella barbadensis* differed from each other in the orientation of their muscle fibers. The fibers of *A. antillarum* were primarily oriented dorsoventrally. The muscle fibers of *F. barbadensis* were less uniformly organized.

The pedal organization of the patellogastropods and fissurellids studied thus far differs in the arrangement and relative abundances of muscle and connective tissue. The pedal musculature of the patellogastropods, *Acmaea antillarum* (this study) and *Tectura scutum* (Voltzow, 1988; Cedeño Maldonado, 1993), and *Lottia strigatella* (Voltzow, 1994), consists of solid masses of thick bundles of dorsoventral muscle fibers embedded in a relatively small amount of connective tissue. The connective tissue is denser and the muscle fibers tend to be smaller in diameter at the dorsal surface of the foot near the shell attachment site and directly above the epithelium of the sole.

In contrast, the pedal musculature of *Fissurella barbadensis* (this study) and *Diodora aspera* (Voltzow, 1988; Cedeño Maldonado, 1993) consists of distinct regions. The dorsal region is composed of thick bundles of muscle fibers oriented in virtually all directions. These bundles of muscle are embedded in a relatively small amount of connective tissue. The central and ventral regions consist of loose networks of thinner muscle fibers embedded in dense connective tissue.

The pedal musculature of coiled prosobranch gastropods consists of two morphologically and functionally distinct regions, the columellar muscle and tarsos (Voltzow, 1985, 1986, 1990, 1991, 1994). The columellar muscle consists of a three-dimensional network of thick bundles of muscle fibers that are embedded in a relatively small amount of connective tissue. This region executes the gross movements of the animal, such as twisting and clamping the shell (Voltzow, 1990). The tarsic region consists of thinner bundles of muscle fibers oriented in many directions. The muscle fibers from the tarsos are surrounded by relatively denser connective tissue, and they are responsible for the finer movements of the foot, such as the formation and propagation of locomotor waves.

The morphology of the pedal musculature of the patellogastropods studied was very similar to that of the columellar region of coiled prosobranch gastropods as described by Voltzow (1990). No region with the morphological characteristics of the tarsic region has been found in patellogastropods, with the possible exception of a restricted area directly above the pedal epithelium. The feet of the fissurellids studied, however, consist of distinct regions similar to those found in coiled gastropods. The dorsal two-thirds of the foot of *Fissurella barbadensis* resembled the columellar region described for other prosobranch gastropods (Voltzow, 1990), and the ventral one-third resembled the tarsos.

In most prosobranch gastropods, the border between the columellar and tarsic regions is distinct (Voltzow, 1990, 1991, 1994; personal observations). In the fissurellids studied, however, this distinction was not so obvious. The central transition zone between the dorsal columellar muscle region and the ventral tarsic region occupied a larger proportion of the foot (approximately one-fourth of the height) than it does in coiled gastropods.

The patterns of orientations of muscle fibers in *Fissurella barbadensis* were less consistent than those of *Acmaea antillarum*. One specimen (FbN) showed a significantly different distribution of orientations than that of the other specimens. In general, the organization of the pedal musculature in this species appeared to be more variable than that of the patellogastropods studied.

Functional Implications

One functional implication of the differences between the orientations of the muscle fibers of *Acmaea antillarum* and *Fissurella barbadensis* is their effect on tenacity. Tenacity is defined as the maximum force of adhesion per unit area of the foot in contact with the substrate. The tenacity of limpets has been measured using three different pulling directions: perpendicular (normal tenacity), parallel (shear tenacity), and diagonal to the substrate (peel tenacity) (Miller, 1974a; Branch & Marsh, 1978; Grenon & Walker, 1981; Lowell, 1987; Smith, 1991, 1992). Because most of their pedal muscle fibers are oriented perpendicular to the substrate, patellogastropods should be able to exert higher normal tenacities than fissurellid limpets. On the other hand, their diverse array of muscle fibers might enable fissurellid limpets to exert higher tenacities under a diagonal pulling force than can patellogastropods.

Grenon & Walker (1981) found that for the patellogastropod *Patella vulgata*, shear tenacity is about 20–30% of normal tenacity, but peel tenacity is about 75% of normal tenacity. These results suggest that the tenacity under different pulling directions in *P. vulgata* may depend on the orientation of the muscle fibers in its foot. A comparative study between the tenacity of patellogastropod and fissurellid limpets under different pulling angles may reveal the functional implication of the differences of the orientation of their muscle fibers.

The constraints that the mechanical forces exert on *Acmaea antillarum* and *Fissurella barbadensis* apparently are not coupled with an increase in the areas of their soles, but rather with an increase in the surface area of attachment of the pedal musculature to the shell relative to the area of the aperture. These results help explain the results of Branch & Marsh (1978), who found that for several species of *Patella*, the larger the area of muscle attachment to the shell relative to the area of the sole, the higher the tenacity.

When patellogastropod and fissurellid limpets that are exposed at low tide are touched gently, they clamp even harder to the substrate (José Cedeño & Janice Voltzow, personal observation). In the patellogastropods studied, whose pedal muscle fibers are primarily oriented perpendicular to the substrate, the force produced by the contraction of the muscle fibers when the animal clamps will be exerted directly from the shell to the substrate. In the fissurellids studied, however, the contraction of a bundle of muscle fibers that is oriented at an angle to the substrate will exert a force that may be distributed through a range of angles. Only part of that force will be exerted perpendicular to the substrate, producing a clamp normal to the substrate that is less strong than that produced by the dorsoventral bundles of muscle fibers observed in patellogastropods. The relatively larger surface area of attachment of the pedal musculature to the shell in the fissurellids studied may compensate to strengthen the clamp.

ACKNOWLEDGMENTS

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LITERATURE CITED

Branch, G. M. & A. C. Marsh. 1978. Tenacity and shell shape in six *Patella* species: adaptive features. Journal of Experimental Marine Biology and Ecology 34:111–130.

Cedeño Maldonado, J. E. 1993. A histological and quantitative description of the pedal musculature of the limpets *Acmaea antillarum* (Patellogastropoda) and *Fissurella barbadensis* (Archaeogastropoda). MS thesis, University of Puerto Rico, Río Piedras.

Clarke, M. R. B. 1980. The reduced major axis of a bivariate sample. Biometrika 67:441–446.

Frescura, M. & A. N. Hodgson. 1990. The fine structure of the shell muscle of patellid prosobranch limpets. Journal of Molluscan Studies 56:435–447.

FRETTER, V. & A. GRAHAM. 1994. British Prosobranch Molluscs: Their Functional Anatomy and Ecology. Revised and updated edition. Ray Society: Andover, Hants. 820 pp.

GRENON, J. F. & G. WALKER. 1981. The tenacity of the limpet, *Patella vulgata* L.: an experimental approach. Journal of Experimental Marine Biology and Ecology 54:277–308.

HICKMAN, C. 1988. Archaeogastropod evolution, phylogeny and systematics: a re-evaluation. Malacological Review 4 (Supplement):17–34.

HUMASON, G. L. 1979. Animal Tissue Techniques. 4th ed. W. H. Freeman and Company: San Francisco. 661 pp.

JONES, H. D. & E. R. TRUEMAN. 1970. Locomotion of the limpet *Patella vulgata*. Journal of Experimental Biology 52: 201–216.

LOWELL, R. B. 1987. Safety factors of tropical versus temperate limpet shells: multiple selection pressures on a single structure. Evolution 41:638–650.

MCARDLE, B. H. 1988. The structural relationship: regression in biology. Canadian Journal of Zoology 66:2329–2339.

MILLER, S. L. 1974a. Adaptive design of locomotion and foot form in prosobranch gastropods. Journal of Experimental Marine Biology and Ecology 14:99–156.

MILLER, S. L. 1974b. The classification, taxonomic distribution and evolution of locomotor types among prosobranch gastropods. Proceedings of the Malacological Society of London 41:233–272.

NIKLAS, K. J. 1994. Plant Allometry: The Scaling of Form and Process. University of Chicago Press: Chicago. 395 pp.

RICE, W. M. 1989. Analyzing tables of statistical tests. Evolution 43(1):223–225.

SMITH, A. M. 1991. The role of suction in the adhesion in limpets. Journal of Experimental Biology 161:151–169.

SMITH, A. M. 1992. Alternation between attachment mechanisms by limpets in the field. Journal of Experimental Marine Biology and Ecology 1600:205–220.

VOLTZOW, J. 1985. Morphology of the pedal circulatory system of the marine gastropod *Busycon contrarium* and its role in locomotion (Gastropoda, Buccinacea). Zoomorphology 105: 395–400.

VOLTZOW, J. 1986. Changes in pedal intramuscular pressure corresponding to behavior and locomotion in the marine gastropods *Busycon contrarium* and *Haliotis kamtschatkana*. Canadian Journal of Zoology 64:2288–2293.

VOLTZOW, J. 1988. The organization of limpet pedal musculature and its evolutionary implications for the Gastropoda. Malacological Review 4 (Supplement):273–283.

VOLTZOW, J. 1990. The functional morphology of the pedal musculature of the marine gastropods *Busycon contrarium* and *Haliotis kamtschatkana*. The Veliger 33(1):1–19.

VOLTZOW, J. 1991. Gastropod pedal architecture: predicting function from structure and structure from function. Pp. 83–84 in C. Meier-Brook (ed.), Proceedings of the 10th International Malacological Congress, Tübingen, 1989. Vol. 1. Unitas Malacologica: Bajas, Hungary.

VOLTZOW, J. 1994. Gastropoda: Prosobranchia. Pp. 111–252 in F. W. Harrison & A. Kohn (eds.), Microscopic Anatomy of Invertebrates, Vol. 5: Mollusca I. Wiley-Liss, Inc.: New York.

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Schuchmanoceras hamicarinatum, Gen. Nov., Sp. Nov., a Keeled Heteromorph Ammonite from the Cretaceous (Albian) of California

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Abstract. **Schuchmanoceras hamicarinatum**, a new genus and species of Albian (Early Cretaceous) anisoceratid ammonite, is described on the basis of the unique combination of a ventral keel, distinctive sculpture, and anisoceratid coiling. Its late Albian age is established by the contemporaneous ammonite species *Anagaudryceras buddha, Pseudouhligella japonicum, Stoliczkaia notha,* and *Mesopuzosia colusaense.*

INTRODUCTION

A ventral keel is a common morphological feature of planispirally coiled ammonites such as the Upper Albian brancoceratid genera, *Mortoniceras* Meek, 1876, *Hysteroceras* Hyatt, 1900, and *Dipoloceras* Hyatt, 1900. However, in heteromorph ammonites, those forms with whorls not in contact or not planispirally coiled, a ventral keel is extremely rare. In some 150 named genera of lytoceratine heteromorphs, only three have previously been described as having some form of keel; none have been reported in the family Anisoceratidae. We herein describe a keeled heteromorph ammonite with anisoceratid coiling (body chamber in the shape of a hook), and a unique sculpture somewhat similar to that commonly observed in species of *Anisoceras* Pictet, 1854. This combination of features has not been reported previously in the same animal.

Although we have only a single specimen, the unique combination of morphological characters readily distinguishes this form from previously described ammonite genera, and in our judgment is sufficiently distinct to recognize this taxon as new at the generic level. In this we follow traditional morphologically based ammonite systematics. Phylogenetic classifications, while much needed for ammonites, are, in our opinion, still far away, and will require ontogenetic studies of well-preserved specimens with good stratigraphic control.

SYSTEMATIC PALEONTOLOGY

Mollusca

Cephalopoda

Ammonoidea

Family ANISOCERATIDAE Hyatt, 1900

Genus *Schuchmanoceras* Murphy & Rodda, gen. nov.

Type species: ***Schuchmanoceras hamicarinatum*** Murphy & Rodda, sp. nov.

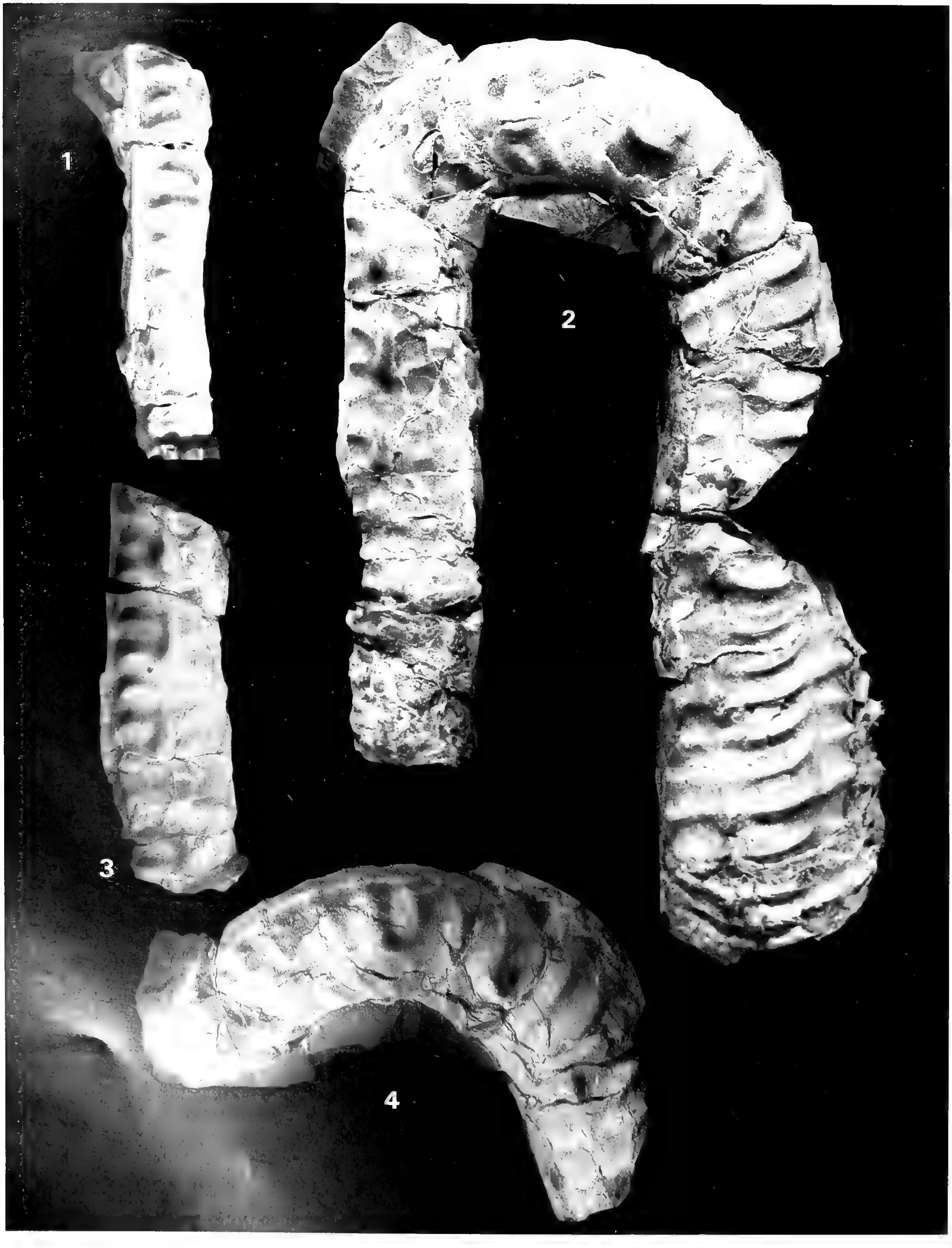
Derivation of the name: In honor of Clarence Schuchman, in recognition of his many contributions to the study of Cretaceous ammonites of California.

Diagnosis: A keeled heteromorph ammonite with anisoceratid coiling and strong ribs that are joined in pairs by a clavate lateral tubercle.

Schuchmanoceras hamicarinatum Murphy & Rodda, sp. nov.

(Figures 1–4)

Holotype: California Academy of Sciences Geology Type Collection CASG 66819.01.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Derivation of the name: From Latin *hami,* hook + *carina,* keel, hence, keeled hook.

Diagnosis: As for genus.

Material: One specimen consisting of deformed segments of shaft and hook.

Locality: North Fork of Cottonwood Creek, Ono quadrangle, 1/25,000, Shasta County, California. CASG Cottonwood Project, section NF Vla, at Stake 482 (Figures 5, 7). Upper part of Chickabally Mudstone Member, Budden Canyon Formation (Murphy, et al., 1969).

Description: Partial phragmacone of short (30 mm) section of shaft with clavate lateral tubercle elongate parallel to shaft; remaining shaft and hook comprise body chamber; dorsum smooth; cross section oval, slightly higher than wide; widely spaced, sharp-crested, curved ribs, mostly joined in pairs at midflank by clavate tubercle (spine base), from which they pass peripherally in a strong adapically directed curve; ribs die out ventrally near sharp ventral keel; one or two weak interribs between clavae with reverse sigmoidal curvature, commonly weaker at midflank; on latter part of body chamber tubercles more equant, and keel not apparent on poorly preserved venter. Segments of suture line visible on crushed and deformed partial phragmacone: E, part of first lateral saddle, and peripheral (?) half of L (Figure 6).

Measurements: Overall length of preserved specimen 175 mm; distance between shaft and body chamber 32–37 mm; height of the shaft 25 mm, width 21 mm; height of the body chamber near aperture 40–43 mm. Measurements approximate; specimen deformed by compaction, and parts somewhat rotated.

Discussion: This specimen, assigned to the family Anisoceratidae principally on the basis of it hooked shape and partial suture, is unique among anisoceratid heteromorphs in its distinctive ribbing and the presence of a keel on at least the earlier parts of the preserved shell. The small fragments of the septal suture line and the septal face partially preserved suggest an anisoceratid pattern like that found in the type species, *Anisoceras saussureanus* Pictet, 1847 (see also Spath, 1938, pp. 542, 552; Wright, 1957, p. L219).

The only other described keeled heteromorphs are *Phlycticrioceras* Spath, 1926, from the Coniacian of Europe and North America, *Prophlycticrioceras* Clark, 1965, from the Upper Albian of Texas, and *Boehmoceras* Riedel, 1931, from the Coniacian of Germany. These three genera (with *Boehmoceras* included questionably) constitute the family Phlycticrioceratidae (Spath, 1926; Wright, 1957; Clark, 1965). *Phlycticrioceras* and *Prophlycticrioceras* are generally similar and have a row of siphonal tubercules that in some specimens coalesce to form serrated keels; *Prophlycticrioceras* has broader ribs with fine intermediaries and a broader whorl section. Both of these genera resemble the anisoceratid genera *Idiohamites* Spath, 1925, and *Allocrioceras* Spath, 1926, in general shape, uniform ribbing, and ventro-lateral nodes, but with the addition of siphonal tubercules or serrate keel. ***Schuchmanoceras,*** by contrast, has a solid keel in the parts preserved, and the ornament is distinctly different, with clavate nodes elongate parallel to the shaft and strong, widely spaced, looped ribs connected in pairs to the nodes. This rib pattern is somewhat reminiscent of the "button and loop" rib pattern in some species of *Anisoceras,* but in that genus the nodes are smaller and equant, and the looped ribs, which are finer and much more narrowly spaced, connect paired ventro-lateral nodes, and additional loops extend to the dorso-lateral nodes. In *Anisoceras* the ribbing generally is finer and denser than in ***Schuchmanoceras.*** The "button and loop" pattern appears in *Anisoceras perarmatum* Pictet & Campiche, 1861, *A. armatum* (J. Sowerby, 1817), *A. phillipsi* Cooper & Kennedy, 1979, *A. haasi* Cooper & Kennedy, 1979, and in at least one species of *Protanisoceras* Spath 1923, *P. raulinianum* (d'Orbigny, 1842). See Spath (1938) and Cooper & Kennedy (1979) for illustrations and descriptions of these species and other anisoceratids.

Boehmoceras is characterized by a loose, open, expanding coil mainly in one plane, but without a hook or straight final shaft typical of *Anisoceratidae.* Compared with the ovate cross section of ***Schuchmanoceras,*** the whorl section of *Boehmoceras* is narrower with compressed, weakly inflated flanks and acutely tapered venter. Ornament on *Boehmoceras* consists of coarse, widely spaced, strongly curved ribs, bearing weak or no ventro-lateral nodes, and splitting ventrally into secondary ribs, which extend over the venter, forming weak serrations on the solid keel (Rie-

⟵

Explanation of Figures 1 to 4

Figure 1. ***Schuchmanoceras hamicarinatum*** Murphy & Rodda, gen. nov., sp. nov. Oblique view of shaft to show keel. CASG 66819.01. Length, 75 mm.

Figure 2. ***Schuchmanoceras hamicarinatum*** Murphy & Rodda, gen. nov., sp. nov. Lateral view of body chamber and small segment of shaft (lower left). CASG 66819.01. Maximum length, 175 mm; shaft length, 30 mm.

Figure 3. ***Schuchmanoceras hamicarinatum*** Murphy & Rodda, gen. nov., sp. nov. Lateral view of section of Figure 1 to show ornamentation on flank. CASG 66819.01. Length, 75 mm.

Figure 4. ***Schuchmanoceras hamicarinatum*** Murphy & Rodda, gen. nov., sp. nov. Oblique view of hook to show ribbing and keel. CASG 66819.01. Maximum height of flank, 30 mm.

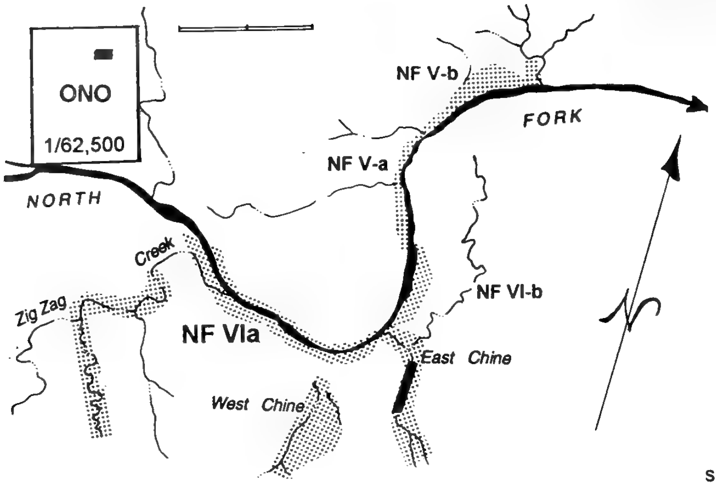

Figure 5

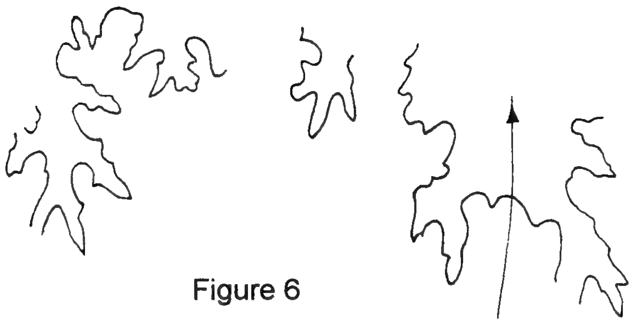

Figure 6

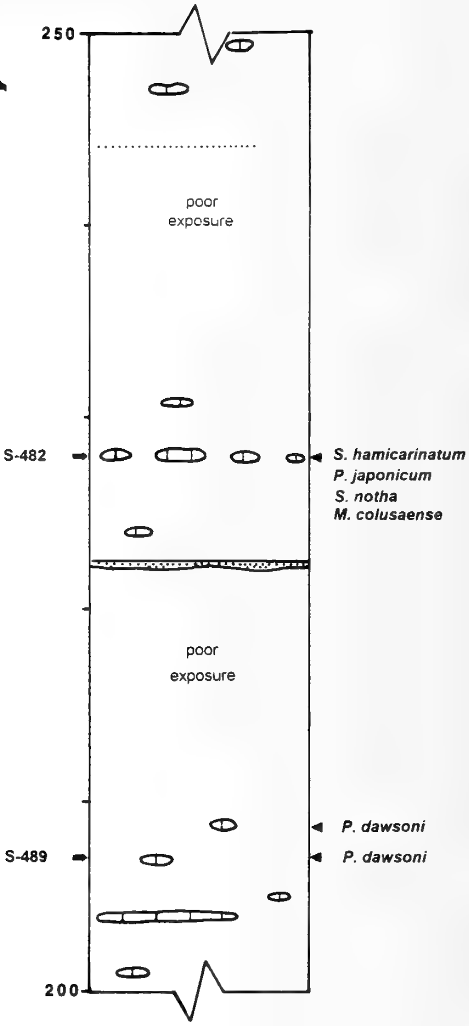

Figure 7

Explanation of Figures 5 to 7

Figure 5. Location map. Area of Figure 5 shown as black rectangle in inset of Ono quadrangle (1/62,500). Stippling indicates location of several measured stratigraphic sections. ***Schuchmanoceras hamicarinatum*** Murphy & Rodda, gen. nov., sp. nov., was found in upper part of section NF Vla in East Chine. Section NF Vla extends along North Fork of Cottonwood Creek from its base near the mouth of Zig Zag Creek to East Chine and up East Chine and its southern branch. Location of columnar section of Figure 7 indicated by thick line along East Chine. Scale bar 500 m long.

Figure 6. Partial suture of last septum of shaft of Holotype of ***Schuchmanoceras hamicarinatum*** Murphy & Rodda, gen. nov, sp. nov., CASG 66819.01.

Figure 7. Columnar section of upper part of section NF Vla (upper Chickabally Mudstone Member, Budden Canyon Formation) showing stratigraphic positions of ***Schuchmanoceras hamicarinatum*** Murphy & Rodda, gen. nov., sp. nov., and associated fossils, *Pseudouhligella japonicum* (Yabe, 1904), *Stoliczkaia notha* (Seeley, 1865), *Mesopuzosia colusaense* (Anderson, 1902), and *Pseudouhligella dawsoni* (Whiteaves, 1900). S-482 and S-489 indicate position of numbered stakes. Numbers at top and bottom of column indicate thickness in feet (200 ft. = 60.9 m; 250 ft. = 76.2 m). Lithologic symbols: Dots = sandstone, ovoids = limestone nodules, blank areas = mudstone.

del, 1931). In ***Schuchmanoceras,*** ribs are curved in a loop fashion and extend only from the flank clavae toward the venter, except on the outer part of the body chamber where ribs extend across the entire flank.

Age and correlation: The specimen was found in a stratigraphic interval that has also yielded *Anagaudryceras buddha* (Forbes, 1846), *Mesopuzosia colusaense* (Anderson, 1902), *Pseudouhligella japonicum* (Yabe, 1904), and *Sto-*

liczkaia notha (Seeley, 1865) (Figure 7). The latter species, recently reviewed by Wright & Kennedy (1994), suggests a correlation with the Upper Albian *dispar* Zone of Owen (1989) or the *perinflatum* Zone of Amédro (1992).

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LITERATURE CITED

Amédro, F. 1992. L'Albien du bassin Anglo-Parisien: ammonites, zonation phylétique, séquences. Bulletin Centres Recherche, Exploration-Production Elf-Aquitaine 16(1):187–233.

Anderson, F. M. 1902. Cretaceous deposits of the Pacific Coast. Proceedings of the California Academy of Sciences (4)23:1–34.

Clark, D. L. 1965. Heteromorph ammonoids from the Albian and Cenomanian of Texas and adjacent areas. Memoirs of the Geological Society of America 95:1–99.

Cooper, M. R. & W. J. **Kennedy**. 1979. Uppermost Albian (*Stoliczkaia dispar* zone) ammonites from the Angolan littoral. Annals of the South African Museum 77(10):175–308.

d'Orbigny, A. 1840–42. Paléontologie française. Terrains crétaces l. Céphalopodes. Paris. 662 pp.

Forbes, E. 1846. Report on the Cretaceous fossil invertebrates from southern India, collected by Mr. Kaye and Mr. Cunliffe. Transactions of the Geological Society of London (2)7: 97–174.

Hyatt, A. 1900. Cephalopoda. Pp. 502–604 in C. R. Eastman (transl. and ed.), K. A. von Zittel, Text-book of Paleontology, vol. 1. Macmillan: New York.

Meek, F. B. 1876. A report on the invertebrate Cretaceous and Tertiary fossils of the upper Missouri Country. Pp. 1–629 in F. B. Meek and F. V. Hayden, United States Geological and Geographical Survey of the Territories, volume 9.

Murphy, M. A., P. U. **Rodda** & D. M. **Morton**. 1969. Geology of the Ono quadrangle, Shasta and Tehama Counties, California. Bulletin of the California Division of Mines and Geology 192:1–28.

Owen, H. 1989. Late Albian (*Stoliczkaia dispar* Zone) ammonites from Misburg, Hannover. Geologisches Jahrbuch A 113:373–395.

Pictet, F. J. 1847. Pp. 257–412 in F. J. Pictet and W. Roux, Description des mollusques fossiles qui se trouvent dans les Grés Verts des environs de Genéve. Memoires Societe physique et historie naturelle Genéve 11(2).

Pictet, F. J. 1854. Traité de Paléontologie (2nd. ed.) 2, Céphalopodes. Paris. Pp. 583–716.

Pictet, F. J. & G. **Campiche**. 1860–64. Dêscription des fossiles du terrain crétacé des environs de Ste. Croix. Matériaux pour la Paléontologie Suisse 3 (1860–64):1–725.

Riedel, F. 1931. Zur Stratigraphie und Faciesbildung im Oberemscher und Untersenon am Südrande des Beckens von Münster. Jahrbuch Preussischen Geologischen Landesanstalt 51(2):605–713.

Seeley, H. G. 1865. On ammonites from the Cambridge Greensand. Annals and Magazine of Natural History (3)16: 225–247.

Sowerby, J. 1817. Mineral Conchology of Great Britain, vol. 2. Meridith: London. Pp. 1–245.

Spath, L. F. 1923. Excursion to Folkestone, with notes on the zones of the Gault. Proceedings of the Geologists Association 34:70–76.

Spath, L. F. 1925. On Upper Albian ammonoidea from Portuguese East Africa, with an appendix on Upper Cretaceous ammonites from Maputoland. Annals of the Transvaal Museum 11:179–200.

Spath, L. F. 1926. On the zones of the Cenomanian and uppermost Albian. Proceedings of the Geologists Association 37:420–432.

Spath, L. F. 1938. A monograph of the ammonoidea of the Gault, XIII. Palaeontographical Society. Pp. 541–608.

Whiteaves, J. F. 1900. On some additional or imperfectly understood fossils from the Cretaceous rocks of the Queen Charlotte Islands, with a revised list of the species from these rocks. Geological Survey of Canada, Mesozoic Fossils 1(4): 263–307.

Wright, C. W. 1957. Part L Mollusca, Cephalopoda, Mesozoic Ammonoidea superfamily Turrilitaceae. Pp. L214–L228 in R. C. Moore (ed.), Treatise on Invertebrate Paleontology. University of Kansas and Geological Society of America.

Wright, C. W. & W. J. **Kennedy**. 1994. Evolutionary relationships among Stoliczkaiinae (Cretaceous ammonites) with an account of some species from the English *Stoliczkaia dispar* Zone. Cretaceous Research 15(5):547–582.

Yabe, H. 1904. Cretaceous cephalopoda from Hokkaido, part 2. Journal of the College of Science, Imperial University, Tokyo 20(2):1–45.

The Veliger 39(2):178–183 (April 1, 1996)

THE VELIGER

Occurrence of the Tethyan Gastropods *Campanile* and *Gisortia* in the Lower Eocene Part of the Tepetate Formation, Baja California Sur, Mexico

by

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Abstract. The gastropods *Campanile* sp. and *Gisortia* sp. are warm-water faunal elements that occur in the Tepetate Formation (late early Eocene) in Baja California Sur.

The genus *Campanile* Fischer, 1884, has been known from the lower and middle Eocene strata in Baja California Sur, Mexico, and upper Paleocene and lower Eocene strata in California, USA. This gastropod shows close affinity with Old World Tethyan species. The genus *Gisortia* Jousseaume, 1884, has been known from the middle lower Eocene in Baja California Sur, this being the second report for Mexico. The genus is also known from lower and middle Eocene strata in India, Pakistan, Jamaica, and Florida, USA.

These molluscan genera are shallow-water tropical forms.

INTRODUCTION

The purpose of this paper is to report the presence of the gastropods *Campanile* sp. and *Gisortia* sp. from a late early Eocene locality in the Tepetate Formation, Baja California Sur, Mexico.

Squires & Demetrion (1991:A194) and Squires (1992: 10–11) mentioned the presence of *Campanile* sp. in the Tepetate Formation, but the poor preservation of the specimen prevented identification of the species. Also, Squires & Demetrion (1992:28, fig. 65) reported a *Campanile* sp. from the Bateque Formation; they mentioned that this specimen is poorly preserved, and no species identification is possible.

The *Campanile* specimens from the Tepetate Formation discussed in this paper show close affinity with the Old World Tethyan species *Campanile giganteum* (Lamarck, 1804).

This is the second record of the genus *Gisortia* Jousseaume, 1884, from Baja California. Squires & Demetrion (1994:129, fig. 8) mentioned *Gisortia* (*Megalocypraea*) cf. *G.* (*M.*) *clarki* (Ingram, 1940) from the Bateque Formation. The Tepetate Formation specimen shows affinities with described species from the lower and middle Eocene strata in India, Pakistan (Vredenburg, 1927), Jamaica (Trechmann, 1923), and Florida, USA. (Palmer, 1957).

STUDY AREA

The molluscan material discussed in this work comes from a stratigraphic section measured in the locality Cañada El Canelo (Figure 1), located at Km 100.5 of the Transpeninsular Highway 1 (24°20′08″N–111°01′00″W, Las Pocitas Quadrangle, Baja California Sur, Mexico, 1:50,000 topographic chart, CGSNEGI, 1983).

The measured section, 52.5 m thick, with the base not exposed, extends to the west of the highway and consists of nearly horizontal beds (5° dip). The sequence is made up of gray-yellow feldspathic and calcareous sandstone, interbedded with gray pebble to cobble conglomerate having a fine sandy matrix and siltstone with abundant siltstone concretions, gypsum veins (particularly in the base), graded beds, and some crossbeds associated with scour-and-fill structures and mud pebbles (Figure 2). *Pseudophragmina* (*Proporocyclina*) *advena* (Cushman) occurs parallel to bedding in discrete beds, or in chaotic arrangement interpreted tentatively as storm-bed deposits in channels in a shallow-marine environment deposited during the *Acarinina pentacamerata* Interval Zone of Toumarkine & Luterbacher (1985) of the late early Eocene (Carreño, written communication, 1995).

This section is part of the Tepetate Formation, which in the area is unconformably overlain by a Quaternary

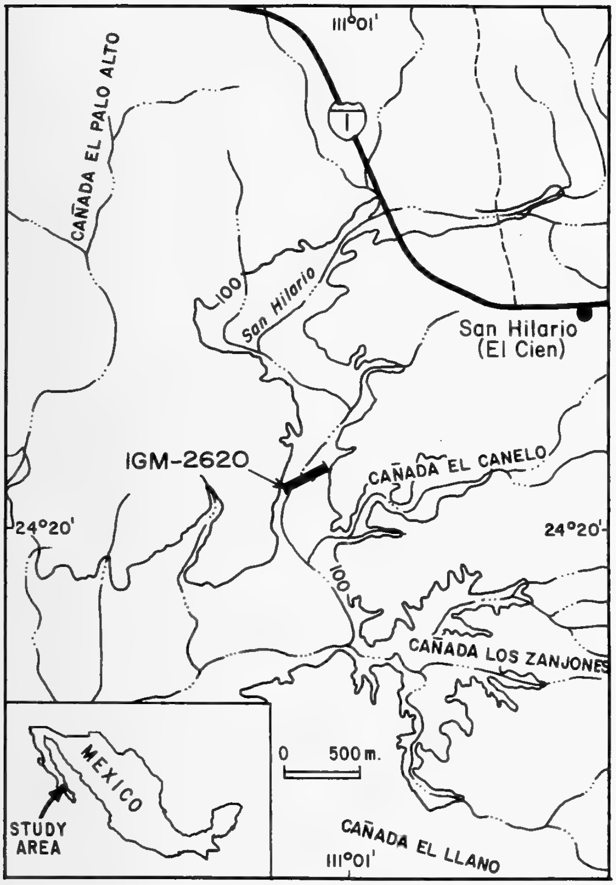

Figure 1

Location map showing the sampled locality of the Tepetate Formation: IGM 2620.

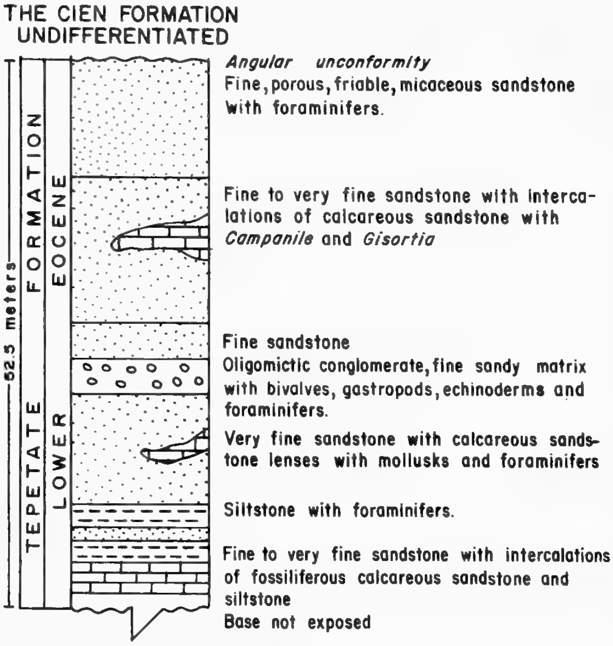

Figure 2

Composite stratigraphic section of the Tepetate Formation showing locations of *Campanile* and *Gisortia*.

conglomerate and alluvium. To the east, the formation is covered with angular unconformity by strata of the El Cien Formation (Carreño, 1992).

PREVIOUS STUDIES

Darton (1921) was the first to recognize a probable Eocene age for the soft to hard, light gray sandstone with argillaceous members that crops out to the west of the town of San Hilario. These rocks were later named by Heim (1922) as the Tepetate Formation with a type section in the bed of the Arroyo Colorado (3 km SW of the Tepetate ranch). Here, the Tepetate Formation is composed of beds of gray sandstone with a dip of 4°NE with ichnofossils and macroforaminifers.

Beal (1948) recognized the Tepetate Formation, but extended its distribution to the Vizcaíno region, and on the basis of a large invertebrate collection, assigned a Martínez to Tejón or Paleocene to upper Eocene age.

Mina-Uhink (1957) named the outcropping unit in the Vizcaíno region as a different formation. He recognized the Tepetate Formation as the unit outcropping to the south, in the area between El Conejo and Santa Rita, assigning it a late Paleocene to middle Eocene age and concluding that it accumulated in a neritic marine environment.

The first micropaleontological approach was that of Knappe (1974), later complemented by Fulwider (1976) who, on the basis of calcareous nannoplancton, assigned a Maastrichtian age to the base of the Tepetate Formation. On the basis of planktonic foraminifera, he extended its age up to the early Paleocene-early Eocene and inferred deposition in a middle to upper slope paleoenvironment, with possible low oxygen condition in a sub-sea fan complex.

Minch & Leslie (1979) referred to the Tepetate Formation as Paleocene and largely Eocene in age. On the basis of foraminifera, they assigned to some outcrops a lower and basal middle Eocene and middle lower Eocene age and inferred an upper to middle slope paleoenvironment.

Galli-Olivier et al. (1986) considered the Tepetate Formation as Late Cretaceous to lower Eocene in age and, based on a sedimentological study at the El Conejo locality, concluded that this part of the formation was deposited in a channel or submarine valley subenvironment of the mid slope environment.

AGE

At the El Canelo section, the presence of *Pseudophragmina* (*Proporocyclina*) *flintensis* (Cushman) and *Amphistegina* *lopeztrigoi* (Palmer), is indicative of a middle Eocene age (Butterlin, 1981). Nevertheless, the planktonic foraminifers represented by *Morozovella aragonensis* (Nuttall), *Morozovella caucasica* (Glaessner), *Acarinina pentacamerata* (Subbotina), *Acarinina primitiva* (Finlay), *Acarinina bulbrooki* (Bolli), *Acarinina broedermanni* (Cushman & Bermúdez) suggest deposition during the *Acarinina pentacamerata* Interval Zone of Toumarkine & Luterbacher (1985) during the late early Eocene (ca. 50.3 Ma). The absence of species belonging to the *Acarinina soldadoensis* and *Turborotalia cerroazulensis* groups prevents an assignment to the younger *Hantkenina nuttalli* Interval Zone of the early middle Eocene (Carreño, written communication, 1995).

The presence of the genera *Campanile* and *Gisortia* in the Canelo section corroborates a late early Eocene age, considering that these two genera are known in the middle lower Eocene ("Capay Stage") in California, and in the partly time-correlative Bateque Formation in Baja California Sur.

Abbreviations used for catalog and locality numbers are as follows: IGM, Instituto de Geología, Universidad Nacional Autónoma de México.

SYSTEMATIC PALEONTOLOGY

Superfamily CYPRAEACEA Rafinesque, 1815

Family Gisortiidae Schilder, 1930

Genus *Gisortia* Jousseaume, 1884

Type species: *Ovula gisortiana* Passy, 1859:948 by original designation. Middle Eocene, Lutetian Stage, Gisors, northern France. Classification of *Gisortia* in this report follows that of Schilder & Schilder (1971).

Gisortia sp.

(Figures 3, 4)

Description: Internal cast heavy, with a low spire of about five whorls not covered by the lip. Body whorl conical, anteriorly tapering. Aperture filled with matrix.

Dimensions: Hypotype IGM 6761, height 17.5 cm, width 13.0 cm.

Discussion: The description is based only on a single specimen. As many specimens of *Gisortia* are known as internal casts, they differ widely in appearance from specimens with completely preserved shells. *Gisortia* sp. is similar only to the internal casts of *Gisortia* (*Vicetia*) *murchisoni* (d'Archiac) (Vredenburg, 1927:64 pars, pl. 16, figs. 2a, 2b; pl. 22, figs. 1a, 1b) from a zone located at a fairly high horizon in the *Alveolina* limestone west of Ranikot in shape, but the specimen from the Tepetate Formation is larger than those figured by Vredenburg (1927).

Gisortia sp. also has similarities with *Gisortia,* cf. *murchisoni* d'Archiac (Trechmann, 1923:355, pl. 14, fig. 1) reported from the Eocene of Spring Mountain, Jamaica. Schilder & Schilder (1971:30) reported the same species from the middle Eocene Lutetian Stage of Jamaica, in the conical shape and in the spire that has five whorls, but the specimen from Baja California Sur is larger.

There are two known species in North America. *Gisortia harrisi* (Palmer, 1957:71, pl. 9, figs. 1–3) from the upper Eocene Crystal River Formation in Florida, has a large shell with sunken apical whorls, the spire flat with 4½–5 whorls, and the posterior lip raised above the spire, the body whorl rounded above, the left side straight and parallel to the right. The Tepetate Formation specimen differs from *G.* harrisi in that it does not show the sunken apical whorls and is smaller in size.

The other reported species of *Gisortia* from the Eocene of the Pacific Coast of North America is *Gisortia* (*Megalocypraea*) *clarki* (Ingram, 1940:376–377, fig. 1; 1942:19, pl. 4, fig. 1; 1947:63–64, pl. 3, fig. 1; Squires, 1987:35, figs. 39-41; Groves, 1992:figs. 3a, 3b; Squires & Demetrion, 1994:129–130, fig. 8) from the middle lower Eocene of south-central and southern California, and Baja California Sur, Mexico. But the specimen from Baja California Sur is larger and the spire presents five whorls; in *Gisortia clarki* the spire is almost totally submerged beneath outer enamel so that it cannot be compared with the internal cast of *Gisortia* sp.

From the Eocene of South America, there is a species reported from the Pale Gorda Formation of Peru. *Gisortia* (*Megalocypraea*) *thomasi* (Olsson, 1930:64, pl. 8, figs. 1, 2, 7).

Superfamily CERITHIACEA Fleming, 1822

Family Campanilidae Douvillé, 1904

Genus *Campanile* Fischer, 1884

Type species: *Cerithium giganteum* Lamarck, 1804 (by subsequent designation, Sacco, 1895:37). Eocene, Paris Basin, France.

→

Explanation of Figures 3 to 8

Figures 3, 4. *Gisortia* sp., hypotype IGM 6761 from IGM loc. 2620. Figure 3: internal mold, apertural view, ×0.52. Figure 4: internal mold, abapertural view, ×0.52. Figure 5. *Campanile* sp., plastotype IGM 6760 from IGM loc. 2620, internal mold, abapertural view, ×0.28. Figures 6, 8. *Campanile* sp., hypotype IGM 1213 from IGM loc. 2620. Figure 6: internal mold, apertural view, ×0.31. Figure 8: internal mold, abapertural view, ×0.31. Figure 7. *Campanile* sp., hypotype IGM 1214 from IGM loc. 2620. internal mold, abapertural view, ×0.25.


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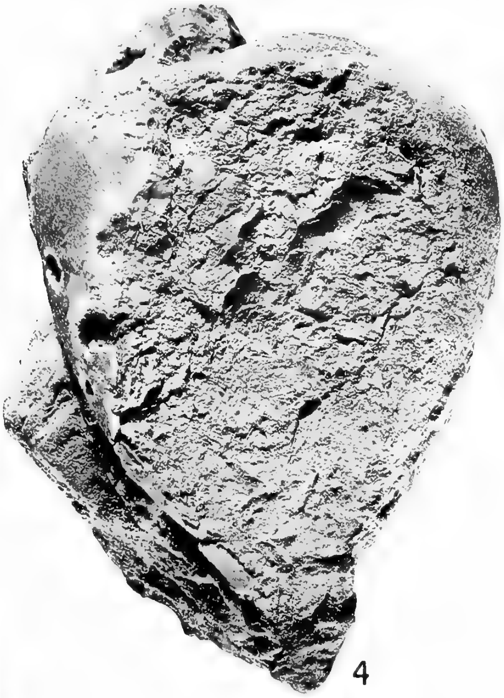
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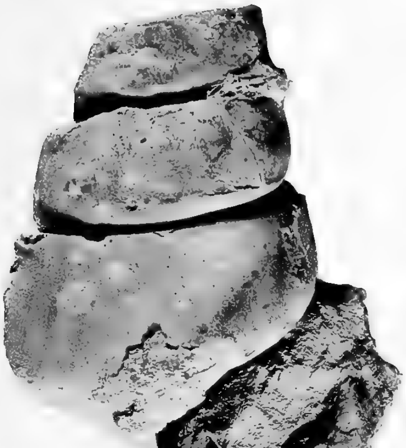
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Campanile sp.

(Figures 5–8)

Description: Shell large, turreted, elongated, with 17 straight-sided whorls. Suture moderately incised. Shell sculpture with one spiral row of eight nodes on posterior part of whorl. Apertural side missing.

Dimensions: Hypotype IGM 6760. A resin cast, height 33.5 cm, width 14.0 cm; hypotype IGM 1213, height 26.5 cm, width 16.5 cm; hypotype IGM 1214, height 30.3 cm, width 13.0 cm.

Discussion: In the collection there are 14 fragments that have from two to seven whorls, and the preservation is fairly good. Not all of them show nodes, but all are probably the same species. The largest such fragment is 30.3 cm in height.

Campanile sp. is similar to *Campanile giganteum* (Lamarck, 1804:95, pl. no. 12, fig. 1). The original description of this species is: "*57 Cérite géant. Cerithium (giganteum) turritum; longissimum, transversè striatum; anfractibus supernè tuberculato-nodosis; columellâ uniplicatâ.*"

"L. n. Grignon. Voici la plus singulière et la plus étonnante des espèces de ce genre, par sa grandeur énorme; car la plupart des individus ont 124 millimètres (un pied), et quelquefois beaucoup plus de longuer. Elle n'est pas rare à Grignon; mais presque toujours on la trouve fruste ou incomplète. Sous une forme turriculée ou pyramidale, elle offre plus de vingt tours de spire, garnis chacun près de leur bord supérieur, d'une rangée de gros tubercules qui rendent toute la moitié inférieure de la coquille hérissée de noeuds. La base de ces noeuds sélargit en-dessous en s'abaissant. Toute la coquille est légèrement striée en travers. Son ouverture est oblongue, oblique, terminé à la base par un canal dont l'extrémité se recourbe médiocrement: et la partie súpérieure du bord droit forme dans le lieu de la gouttière un prolongement latéral en manière d'oreillete. Il n'y a qu'un pli sur la columelle; malgré cela il en paroît deux, parce que le bord qui la termine inférieurement, est relevé en un bourrelet oblique qui borde le canal."

The species from the Tepetate Formation is similar to *C. giganteum* in the sculpture of the shell, the presence of the spiral row of eight nodes and the height of 33 cm—a size which is equal to that of a fully grown specimen of *Campanile giganteum* from the Paris Basin. Spiral cords are not evident, possibly due to the preservation.

The only Eocene species of *Campanile* described from the western coast of North America is *Campanile dilloni* (Hanna & Hertlein. 1949:393, pl. 77, figs. 2, 4; Givens, 1974:69, pl. 7, fig. 10; Squires & Advocate, 1986:853, fig. 2.1; Squires, 1987:31, figs. 32, 33) from south-central and southern California, and from the lower Eocene Juncal Formation of California.

Squires (1987:31, figs. 32, 33) described a *Campanile* new species?, but he considered that with better preserved material, this species and *Campanile dilloni* might prove to be the same.

The difference between *Campanile* sp. and the species mentioned above is that the Tepetate Formation specimen does not present such a pronounced projecting carina and that the number of pointed nodes is less.

Until we have better preserved complete specimens of *Campanile* sp. and *Campanile dilloni,* we will not know if the Baja California Sur specimens correspond to *C. dilloni* or are more similar to *C. giganteum.*

ACKNOWLEDGMENTS

This study was supported by CONACyT grant (2070-T9302). The author is indebted to Ana Luisa Carreño of the Instituto de Geología, U.N.A.M., who kindly offered the paleontological material for the present study and the information on the Cañada El Canelo area.

Technical assistance received from M. Alcayde-Orraca of the staff of the Instituto de Geología, U.N.A.M. was very valuable.

The author acknowledges Dr. Richard L. Squires (California State University at Northridge) and Dr. Barry Roth for critically reviewing the manuscript and offering helpful comments.

LOCALITY CITED

IGM 2620: Km 100.5 Highway La Paz-Constitución, Arroyo El Canelo, Municipio La Paz, Baja California Sur. 24°20′08″ N- 111°01′00″ W. Tepetate Formation. Age: late early Eocene. Collector: A. L. Carreño. 1991.

LITERATURE CITED

BEAL, C. 1948. Reconnaissance of the geology and oil possibilities of Baja California, Mexico. Geological Society of America, Memoir 31:137 pp.

BUTTERLIN, J. 1981. Claves para la determinación de macroforaminíferos de México y del Caribe, del Cretácico Superior al Mioceno medio. Instituto Mexicano del Petróleo, Subdirección de Tecnología y Exploración. 219 pp.

CARREÑO, A. L. 1992. Early Neogene Foraminifera and associated microfossils of the Cerro Tierra Blanca Member (El Cien Formation), Baja California Sur, Mexico. Pp. 39–93 in M. Alcayde-Orraca & A. Gómez-Caballero (eds.), Calcareous Neogene Microfossils of Baja California Sur, Mexico. Universidad Nacional Autónoma de México, Instituto de Geología, Paleontología Mexicana.

CGSNEGI. 1983. Las Pocitas G12C79, Baja California Sur, México: México, D. F. Secretaría de Programación y Presupuesto, Coordinación General de los Servicios Nacionales de Estadística, Geografía e Informática, Dirección General de Geografía, Topographic Chart scale 1:50,000.

DARTON, N. H. 1921. Geologic reconnaissance in Baja California Sur. Journal of Geology 29:720–748.

DOUVILLÉ, H. 1904. Mollusques Fossiles. Pp. 191–380 in J. de. Morgan, Mission Scientifique en Perse, Vol. 3, Etudes Géologiques, part 4, Paléontologie.

FISCHER, P. 1880–1887. Manuel de Conchyliologie et de Paléontologie Conchiliologique, ou histoire naturelle des mollusques vivants et fossiles. F. Savy: Paris. xxiv+1369 pp.

Fleming, J. 1822. The Philosophy of Zoology; or a General View of the Structure, Functions, and Classification of Animals. 2 Vols. Edinburgh. 1050 pp.

Fulwider, R. W. 1976. Biostratigraphy of the Tepetate Formation, Baja California Sur. Unpublished M.Sc. Thesis. University of Southern California. 111 pp.

Galli-Olivier, C., T. E. Márquez-Enríquez, J. A. Reyes-Sarabia & C. Rosas-Cortés. 1986. Estructuras sedimentarias primarias y litofacies de corrientes densas de un paleoambiente de talud. El Conejo, Baja California Sur, México. Ciencias Marinas 12(2):7–15.

Givens, C. R. 1974. Eocene molluscan biostratigraphy of the Pine Mountain area, Ventura County, California. University of California, Publications in Geological Sciences 109: 1–107, pls. 1–11.

Groves, L. T. 1992. California cowries (Cypraeacea): past and present, with notes on Recent tropical eastern Pacific species. The Festivus 24(9):101–107, figs. 1–3.

Hanna, G. D. & L. G. Hertlein. 1949. Two new species of gastropods from the middle Eocene of California. Journal of Paleontology 23(4):392–394, pl. 77.

Heim, A. 1922. Notes on the Tertiary of southern Lower California. Geological Magazine 59(702):529–547.

Ingram, W. M. 1940. A new *Gisortia*. Journal of the Washington Academy of Sciences 30(9):376–377, fig. 1.

Ingram, W. M. 1942. Type fossil Cypraeidae of North America. Bulletins of American Paleontology 27(104):6–32, pls. 1–4.

Ingram, W. M. 1947. Fossil and Recent Cypraeidae of the western regions of the Americas. Bulletins of American Paleontology 31(120):5–82, pls. 1–3.

Jousseaume, F. P. 1884. Etude sur la famille des Cypraeidae. Bulletin de la Société Zoologique de France 9:81–100.

Knappe, R., Jr. 1974. The micropaleontology of a section of the Tepetate Formation and a paleobiogeographic comparison with equivalent foraminifera along the west coast of the United States. Unpublished. M.Sc. Thesis, Ohio State University, 114 pp.

Lamarck, J. 1804. Suite des mémoires sur les fossiles des environs de Paris. Annales du Muséum National d'Histoire Naturelle 3:436–441.

Mina-Uhink, F. 1957. Bosquejo geológico del territorio de la Baja California. Boletín de la Asociación Mexicana de Geólogos Petroleros 9(3–4):139–269.

Minch, J. & T. A. Leslie. 1979. Geologic road log, La Paz to Tijuana. Pp. 159–189 in P. L. Abbott & G. Gastil. (eds.). Baja California Geology. Field Guides and Papers: San Diego State University: San Diego.

Olsson, A. A. 1930. Contributions to the Tertiary Paleontology of Northern Peru; Part 3, Eocene Mollusca. Bulletins of American Paleontology 17(62):1–96, pls. 1–12.

Palmer, K. V. W. 1957. A new *Gisortia* from the Crystal River Formation, Ocala Group, of Florida, with explanatory notes on the Tethyan influence on the Floridan Middle and Upper Eocene. Journal of the Palaeontological Society of India. Lucknow. D. N. Wadia Jubilee Number (2):69–72, pl. 9.

Passy, A. 1859. Note sur une grande ovule du calcaire grossier. Comptes Rendus Hebdomadaires de Séances de l'Académie des Sciences 48(1):948.

Rafinesque, C. S. 1815. Analyse de la nature, ou tableau de l'univers et des corps organisés. Palermo. 224 pp.

Sacco, R. 1895. I molluschi dei terreni Terziarii del Piemonte e della Liguria. Parte XVII (Cerithiidae, Triforidae, Cerithiopsidae e Diastomidae), Clausen: Torino. 93 pp.

Schilder, F. A. 1930. The Gisortiidae of the world Proceedings of the Malacological Society of London 19:118–138.

Schilder, M. & F. A. Schilder. 1971. A Catalogue of Living and Fossil Cowries. Taxonomy and Bibliography of Triviacea and Cypraeacea (Gastropoda Prosobranchia). Institut Royal des Sciences Naturelles de Belgique, Memoires, Deuxième Série 85:246 pp.

Squires, R. L. 1987. Eocene Molluscan Paleontology of the Whitaker Peak Area, Los Angeles and Ventura Counties, California. Natural History Museum of Los Angeles County, Contributions in Science 388. 93 pp.

Squires, R. L. 1992. Eocene mollusks from the Tepetate Formation, Baja California Sur, Mexico. American Conchologist 20(3):10–11, figs. 1–3.

Squires, R. L. & D. M. Advocate. 1986. New early Eocene mollusks from the Orocopia Mountains, Southern California. Journal of Paleontology 60(4):851–864, figs. 1–3.

Squires, R. L. & R. A. Demetrion. 1991. Early Eocene macrofaunal comparisons between the Tepetate and Bateque Formations, Baja California Sur, Mexico. Geological Society of America Abstracts with Programs:A194.

Squires, R. L. & R. A. Demetrion. 1992. Paleontology of the Eocene Bateque Formation, Baja California Sur, Mexico. Natural History Museum of Los Angeles County, Contributions in Science 434.55 pp.

Squires, R. L. & R. A. Demetrion. 1994. New reports of Eocene mollusks from the Bateque Formation, Baja California Sur, Mexico. The Veliger 37(2):125–135, figs. 1–22.

Toumarkine, M. & H. Luterbacher. 1985. Paleocene and Eocene planktic foraminifera. Pp. 87–154 in H. M. Bolli, J. B. Saunders & K. Perch-Nielsen (eds.). Planktonic Stratigraphy. Cambridge University Press: Cambridge.

Trechmann, C. T. 1923. The yellow limestone of Jamaica and its Mollusca. The Geological Magazine 60(8):337–367.

Vredenburg, E. 1927. A Review of the Genus *Gisortia* with descriptions of several species, Memoirs of the Geological Survey of India. Palaeontologia Indica, New Series 7: 7(3): 142 pp.

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The Veliger 39(2):184–186 (April 1, 1996)

BOOKS, PERIODICALS & PAMPHLETS

Annotated Checklist of Recent Marine Molluscs of Danish Waters

by KATHE R. JENSEN & JØRGEN KNUDSEN. 1995. Zoological Museum, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark. 73 pp. ISBN 87 7834 108 6. Price 70 DKr (US $12).

This work lists 377 Recent molluscan taxa and their distribution by geographic category (e.g., NK = Northern Kattegat; SR = Skagerrak) in the waters around Denmark. The most commonly used synonyms are cited, and references to other works in which more complete synonymies may be found. The introductory material includes remarks on the history of marine malacology in Denmark and the hydrography of the region.

The main species list consists simply of taxon names and their geographic categories. Intercalary notes call attention to open taxonomic questions (sometimes based on unpublished opinions of H. Lemche or other workers), geographic anomalies, nomenclatural decisions, and various other points of interest. Many of these notes give interesting insights, and lend a "working" quality to the list. It would be unfortunate if some of the taxonomic suggestions, as yet not fully documented, were to become accepted solely on the basis of their inclusion here.

The sources of the taxon records included in the list are not specified. There is no statement to the effect that, for example, records of species' occurrence in Danish maritime waters are documented by specimens in the collection of the Zoological Museum. Some quantity of the records may come from the references in the 7-page bibliography; but, again, this is not specified.

As the foreword indicates, the authors first compiled this checklist for biologists working locally on environmental or nature conservation issues; it undoubtedly succeeds in serving that and similar purposes. As an authoritative source for more wide-ranging biogeographic and ecological concerns, however, serious workers may well look forward to a more fully documented presentation.

B. Roth

Phylogeny and Biogeography of the Land Snail, *Sonorella,* in the Madrean Archipelago

by ROBERT D. MCCORD. 1995. Pp. 317–324 *in* L. F. DeBano et al. (Technical Coordinators), Biodiversity and Management of the Madrean Archipelago: the Sky Islands of Southwestern United States and Northwestern Mexico. USDA Forest Service General Technical Report RM-GTR-264.

Much current criticism of molluscan systematics focuses on the limitations of canonical, as opposed to phylogenetic, methods of taxonomy. But the mere ability to perform a cladistic analysis does not relieve one of one's other responsibilities as a biologist—to be well informed about the taxa under study, to perform the analysis correctly, and to know the limits of interpretation the results will support. This paper, using results from the phylogenetic program PAUP 3.0q (Swofford, 1990), is a crude effort marked by inadequate data, faulty methods, flawed execution, and unjustified interpretation.

Sonorella Pilsbry, 1900, is a speciose genus occurring in discontinuous habitat islands (the "Madrean Archipelago") in northern Mexico and the southwestern United States. This paper attempts to generate a phylogenetic hypothesis for 79 species plus five outgroup taxa and a hypothetical ancestor, based on 18 predominantly binary characters. For 79 ingroup taxa the minimum number of character states to allow for a fully resolved tree would be 157 states ($2n$-1, where n is the number of taxa); McCord's data set has only 50 states. This factor alone requires the analysis to report three times the homoplasy of a data set with the requisite 157 states.

The first three characters, presence/absence of dart sac, mucus glands, and spermathecal diverticulum, are monomorphic throughout the species of *Sonorella* and hence provide no basis for finer grouping.[1] Data on other characters (haploid chromosome number and color of mantle collar mucus) are known for very few of the taxa under consideration.

Two characters, precipitation and temperature, are coded not as amount of rainfall or degrees Celsius but as the names of vegetation communities. The actual precipitation or thermal parameters, and the extent to which those communities may be suitable proxies for them, are not discussed. The use of range, habitat, or environmental characters in a phylogenetic analysis is objectionable because (a) aspects of a species' history, not just its intrinsic tolerances, may influence its realized range; and (b) one cannot then turn around and use the phylogeny to investigate questions of biogeography without making a circular argument.

Values such as the ratio of verge length to penis length are said to be "based on population means" (pp. 318–319). The author claims that character states for *Sonorella* were determined by personal observation or from species de-

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[1] A spermathecal diverticulum is present in *Sonorella reederi* Miller, 1984, but that species is not among the taxa analyzed.

scriptions, but the amount of personal observation is not specified. Certainly the cited literature does not contain information that would allow the scoring of population statistics for these characters. Yet, since most *Sonorella* species are difficult to find in quantity, and laborious field search may yield only immature specimens (which then must be reared to maturity before they show diagnostic reproductive characters), it is hard to imagine that sample means adequate to characterize population means were newly obtained for very many species. Character states for the outgroups were taken from the literature, meaning that several characters are represented in the matrix only by question marks, when simple examination of museum specimens would have provided the needed information.

Character states for the hypothetical ancestor were assigned based on "characters generally recognized as being primitive for the Family" (p. 318), not by the method of outgroup comparison (e.g., Watrous & Wheeler, 1981).

To examine the distribution of homoplasy in the analysis we re-analyzed the data matrix with PAUP. Character state ordering, ancestral states, outgroups, branch swapping options, etc., followed McCord's specifications. We were unable to duplicate McCord's 146-step trees. The most parsimonious trees we found were 161 steps long. Shorter trees may exist; our analyses were terminated after saving 14,000 trees because of memory limitations. On several occasions, 14,000 trees greater than 161 steps were saved before any shorter trees were discovered. Hence, we are dubious of McCord's examining only 600 trees (setting MAXTREE = 600) in his study. Consistency index (Rohlf's CI) for our strict consensus tree of 14,000 trees is 0.025 and for the 50% majority rule tree, 0.336. McCord reported a CI of 0.43 for his 50% majority rule tree and a retention index of 0.75. This last statistic is puzzling as retention indices are not calculated for consensus trees. The small number of characters produces high levels of homoplasy and requires numerous reversals in some characters. To appraise this situation we examined character change lists for several of our 14,000 most parsimonious trees. In tree #12,156, for example, characters 4, 7, 9, 10, 11, 14, 15, and 16 had CI's of less than 0.278 (i.e., they are markedly homoplastic). Characters with high CI's (1.0–0.5) tended to be either basal (characters 1, 2, 3, 17) or autapomorphic (characters 5, 8, 12). Clearly, the mechanics of this analysis are so seriously flawed that the robustness of any putative relationships is highly suspect.

Most of the resulting interpretations are unsupported, or else are foregone conclusions given the nature of the data and coding. McCord states, "it is probable that *Sonorella*'s ancestors came from the west" (p. 321), but the only other taxa entered in the analysis (beside *Tryonigens,* which plots within the *Sonorella* clade[2]) *are* in the west. The relations shown by the analysis equally suggest that the common ancestor of *Sonorella* and its sister-taxa was distributed in the areas occupied by both; to choose between vicariance and dispersal scenarios requires additional information. The suggestion that the results contradict the model of multiple, independent reductions of genital structures is likewise unwarranted; Roth (1996) addressed the topic in much greater depth.

The finding that prior authors' infrageneric groups of *Sonorella* do not hang together as monophyletic groups is potentially interesting; but since "it is extremely unlikely that the tree presented here represents the true phylogeny of *Sonorella*" (p. 319), the indicated relationships are tentative at best.

The conclusion that *Sonorella eremita* Pilsbry & Ferris, 1915, is probably a junior synonym of *S. papagorum* Pilsbry & Ferris, 1915, is wholly unjustified. The data set employed is not competent to resolve specific versus subspecific differences, and the author's "detailed examination" (p. 320) of the question is a two-sentence throwaway. (Of several pairs of species that score as identical in this sketchy data set, only *S. eremita* and *S. papagorum* were singled out for comment and taxonomic conclusion.) *Sonorella eremita* is a federally listed candidate species, and this conclusion, which should not be accepted on such a flimsy basis, could have adverse management implications.

Barry Roth
David R. Lindberg

LITERATURE CITED

Miller, W. B. 1971. The reproductive anatomy of *Tryonigens remondi* (Tryon, 1863): Helminthoglyptidae. The Nautilus 85:61–65.

Roth, B. 1996. Homoplastic loss of dart apparatus, phylogeny of the genera, and a phylogenetic taxonomy of the Helminthoglyptidae (Gastropoda: Pulmonata). The Veliger 39: 18–42.

Schileyko, A. A. 1991. Taxonomic status, phylogenetic relations and system of the Helicoidea sensu lato (Pulmonata). Archiv für Molluskenkunde 120:187–236.

Swofford, D. L. 1990. Phylogenetic Analysis Using Parsimony (PAUP), version 3.0q. Illinois Natural History Survey, Champaign.

Watrous, L. E. & Q. D. Wheeler. 1981. The out-group comparison method of character analysis. Systematic Zoology 30:1–11.

Seashells of Central New South Wales: a Survey of the Shelled Marine Molluscs of the Sydney Metropolitan Area and Adjacent Coasts

by Patty Jansen. 1995. Privately published by the author. xii + 129 pp. ISBN 0.646.23760.8. A $40.00 + A $7 for

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[2] Miller (1971), Schileyko (1991), and Roth (1996) all give ample reasons to assign *Tryonigens* to another clade of Helicoidea, *sensu lato.* Its inclusion renders McCord's study group polyphyletic.

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This guide, produced by a shell collector for shell collectors, is clearly a labor of love. Its primary objective is to aid collectors in the identification of shells that wash up on the beaches around Sydney, and its special emphasis is on the small to minute shells that are customarily omitted from the lavish shell books with color plates featuring the taxa most sought after by collectors.

Each of the 484 species of shelled mollusks (380 gastropods, 99 bivalves, four scaphopods, and one cephalopod) is described concisely and illustrated with an excellent black-and-white line drawing. While the work is not revisionary in scope, the nomenclature does reflect the author's familiarity with the current literature, and she provides a good bibliography of references covering many of the major molluscan families. Authors and dates are listed for taxa, but there are no synonymies. There are brief family-level descriptions, but no characterization at the generic level.

The greatest strengths of this volume are its inclusion of micromollusks and the environmentally sound encouragement that it provides to beachcombing and the sorting of shell grit as exciting and enjoyable activities. It will serve as a useful general guide outside of Australia for collectors who have been frustrated by the upmarket shell books that omit the thousands of species with shells less than 5 mm in size. Such shells do not photograph well, and unless they are illustrated by scanning electron micrographs, line drawings are the only viable option. Patty Jansen has developed a remarkable facility for capturing the important features of shells, including color patterns, in her line drawings.

Another appealing thing about this book is its price.

I would have been pleased if the author had included even more introductory material on this kind of environmentally sound collecting. This volume was possible in large part because Patty Jansen was preceded by a unique host of amateur collectors in New South Wales who paid attention to the small and minute and who donated generously of their shells and their time building the research collections at the Australian Museum. It is a tradition well worth encouraging and perpetuating.

Carole S. Hickman

Résultats des Campagnes MUSORSTOM, Vol. 14

PHILIPPE BOUCHET, Coordinator. Mémoires du Muséum National d'Histoire Naturelle, Paris, Vol. 167 (Zoologie): 654 pp., 987 figs., 3 colored plates, 22 December 1995, US $120.

This substantial volume, dedicated to the memory of Richard Houbrick, is part of the continuing series on the offshore fauna of the Indo-Pacific. (Volume 7, 1991, also contained papers on the Mollusca.) The present volume contains 10 papers, three on bivalves, one on scaphopods, and six on gastropods. Henk H. Dijkstra, pp. 9–73, covers the Pectinoidea (Propeamussiidae, Entoliidae, and Pectinidae); nine new species are described. Akihiko Matsukuma and Tadashige Habe, pp. 75–109, treat *Meiocardia* (Glossidae) and *Glossocardia* (Trapeziidae); one new species of the former is described. Jean-Maurice Poutiers and the late Frank R. Bernard, pp. 107–187, discuss the carnivorous Anomalodesmata; eight taxa are described as new. This paper also provides a catalogue of the generic and Recent specific names that have been proposed for "septibranchs," a revised classification for this group, and a translation of the often overlooked 1983 paper by O. A. Scarlato & Ya. I. Starobogatov on the classification of the septibranchs.

A highlight of the volume is the substantial paper (pp. 189–379) on the Scaphopoda by Victor Scarabino. Some 139 species are discussed, of which 42 species are described as new, along with three new generic units. The paper also presents a reclassification of the entire class and illustrates the radulae of nearly all Recent genera.

Bruce A. Marshall, pp. 381–458, deals with the substantial diversity in the gastropod family Calliostomatidae. Of 30 species discussed, 27 are new. Four new genera and one new tribe are also proposed. Appendices discuss all generic units that belong or have been attributed to this family. Roland Houart, pp. 459–498, covers the Trophoninae (Muricidae); twenty-four of 32 species treated are new, along with two new genera. Philippe Bouchet and Guido T. Poppe review the volutid genus *Calliotectum*; the type species is the eastern Pacific *C. vernicosum* Dall, 1890, which occurs from Ecuador to Peru. Of the seven Recent species, two Indo-Pacific species are described as new. Fred E. Wells revises the drilliid genera *Splendrillia* and *Plagiostropha*, pp. 527–556; fourteen of 18 species of the former are new, as are four of the latter. Dieter Röckel, Georges Richard, and Robert G. Moolenbeek cover the deep-water Conidae, pp. 557–594; of the 39 species discussed, five are new. Finally, Rüdiger Bieler deals with the Mathildidae, pp. 595–641; thirteen species are covered, and four species are newly described. Other species are removed from the family.

E. V. Coan

The Veliger 39(2):187 (April 1, 1996)

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NOTES, INFORMATION & NEWS

International Commission on Zoological Nomenclature

The following Application was published on 28 September 1995 in Volume 52, Part 3 of the *Bulletin of Zoological Nomenclature.* Comment or advice on this application is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Case 2947—*Patella longicosta* Lamarck, 1819 (Mollusca, Gastropoda): proposed conservation of the specific name.

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In most cases, the parts of a manuscript should be as follows: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, footnotes, tables, and figures. The title page should be a separate sheet and should include the title, authors' names, and addresses. The abstract should be less than 200 words long and should describe concisely the scope, main results, and conclusions of the paper. It should not include references.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Phillips, 1981), for two authors (Phillips & Smith, 1982), and for more than two (Phillips et al., 1983). The reference need not be cited when author and date are given only as authority for a taxonomic name.

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a) Periodicals:

Hickman, C. S. 1992. Reproduction and development of trochacean gastropods. The Veliger 35:245–272.

b) Books:

Bequaert, J. C. & W. B. Miller. 1973. The Mollusks of the Arid Southwest. University of Arizona Press: Tucson. xvi + 271 pp.

c) Composite works:

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135 in R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal Invertebrates of California. Stanford University Press: Stanford, Calif.

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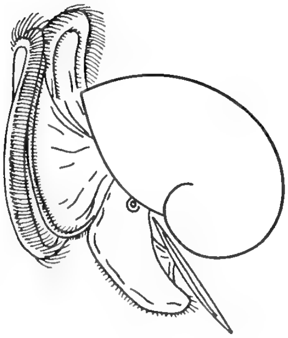

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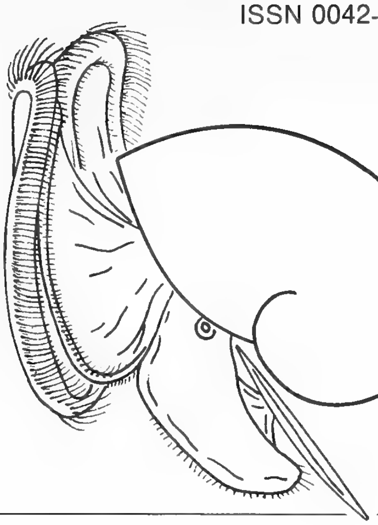

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THE VELIGER

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Very short papers, generally not over 750 words, will be published in a "Notes, Information & News" column; in this column will also appear notices of meetings and other items of interest to our members and subscribers.

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THE VELIGER

The Veliger 39(3):189–203 (July 1, 1996)

Argentine Species of *Pisidium* Pfeiffer, 1821, and *Musculium* Link, 1807 (Bivalvia: Sphaeriidae)

by

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Abstract. The Argentine Sphaeriidae (Mollusca, Bivalvia), in particular the Patagonian species, are reviewed. Seven species of *Pisidium* Pfeiffer, 1821, and two species of *Musculium* Link, 1807, have been recognized as distributed in east-central and southern Argentina.

Upon analysis of the type series of Pilsbry's Patagonian species, the original descriptions were improved and/or amended. Recent collections enlarged the known distributional ranges and allowed description of unknown features of soft-part anatomy, resulting in a more precise diagnosis of each species.

Pisidium ***inacayali,*** sp. nov. from Chubut Province (Patagonia) is described.

The presence of *Pisidium dorbignyi* Clessin, 1879, in Argentine inland waters is considered doubtful.

Cyclas paranensis d'Orbigny, 1846, quoted in the literature as a *Pisidium* species, actually belongs to the family Corbiculidae and corresponds to *Neocorbicula paranensis* (d'Orbigny, 1846).

After analysis of the type series of *Pisidium plenilunium* (Melvill & Standen, 1907), originally described in a marine genus and only known from a rather poor description, is here fully described and appropriately figured.

INTRODUCTION

Knowledge of the taxonomy, distribution, and biology of the Argentine representatives of the family Sphaeriidae, and particularly of the genera *Pisidium* Pfeiffer, 1821, and *Musculium* Link, 1807, is highly fragmentary and scanty.

The genus *Pisidium,* in our present knowledge, is represented in Argentina by seven species: *Pisidium sterkianum* Pilsbry, 1897, described from creeks in "el Prado," Montevideo, Uruguay; *Pisidium vile* Pilsbry, 1897, also described from creeks in "el Prado," Montevideo, Uruguay; *Pisidium magellanicum* (Dall, 1908), described from a single shell washed from some stream into the Magellan Strait; *Pisidium observationis* Pilsbry, 1911, from the "Monte Observación," south of the mouth of the Santa Cruz River, Province of Santa Cruz, Argentina; *Pisidium patagonicum* Pilsbry, 1911, from the Río Chico, Santa Cruz, Argentina; *Pisidium plenilunium* (Melvill & Standen, 1907) from Malvinas Islands; and *Pisidium dorbignyi* (Clessin, 1879) (*nomen novum pro Cyclas pulchella* d' Orbigny, 1835), described from the vicinity of Maldonado, Uruguay.

There are two known species of the genus *Musculium* in Argentina: *Musculium argentinum* (d' Orbigny, 1835), described from brooks in the vicinity of Montevideo Bay, Uruguay, and *Musculium patagonicum* Pilsbry, 1911, from springs along the Río Chico, Santa Cruz, Argentina.

Apart from all those original descriptions, further reports on Sphaeriidae species are rather scarce: Strobel (1874) reported *Musculium argentinum* from San Carlos (Mendoza), Bahía Blanca, and Carmen de Patagones (south of Buenos Aires Province); Olazarri (1983) reported *P. sterkianum* and *P. vile* from the environs of the Salto Grande Dam lake (Entre Rios); Fernandez & Schnack (1977) collected *P. sterkianum* from small brooks close to the Río de La Plata and, recently, Ituarte & Gordillo (1991) reported the presence of *P. observationis* and *Musculium patagonicum* at Isla Gable, Tierra del Fuego.

In a large number of ecological investigations on water courses and reservoirs along the Paraná and Uruguay River basins, the genus *Pisidium* (without species identification) has been reported as a relevant component of benthic associations (for a review see: Bonetto & Tassara, 1987). It must be noted that in none of them have *Musculium* species been reported.

The present paper focuses on the Sphaeriidae of east-central and southern Argentina, particularly on Patagonian species. The descriptions of known species of *Musculium* and *Pisidium* are enlarged and/or amended, and new data on soft-part anatomy are given. On the basis of museum collections and personal samplings on Patagonian water courses, the geographical distribution for each species is updated. A new species of *Pisidium* from Chubut Province is described.

MATERIALS AND METHODS

The present review of the genera *Pisidium* and *Musculium* in Argentina was undertaken upon the study of collections at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Museo de La Plata (MLP), and personal samplings which were deposited in the latter institution. The comparative study of the Patagonian species was made possible by the Academy of Natural Sciences of Philadelphia (ANSP) which provided most of the lots (including type series) collected by Dr. J. B. Hatcher (Princeton University expedition to Patagonia, 1896) and previously studied by H. A. Pilsbry. The study and description of the syntypes of *Pisidium plenilunium* was made possible by the cooperation of the Royal Museum of Scotland (RMS).

In the case of the collections made by the author, prior to fixation with 10% formalin (24 hr) and further preservation in 80% ethanol, specimens were relaxed by immersion in warm water (approx. 50°C) for a few minutes. Samples to be studied under scanning electron microscope were treated with a commercial sodium hypochlorite solution in order to eliminate soft parts, ligament, and periostracum adhering to shells. The specimens were then rinsed in distilled water, dried at room temperature, and coated with gold in a sputter coating unit.

Length measurements were taken with a Wild M_8 stereoscopic microscope provided with a micrometer eyepiece according to the following criteria: shell length (SL): maximum distance between the anterior and posterior margins parallel to the antero-posterior axis; shell height (H): maximum distance between dorsal and ventral margins, perpendicular to the antero-posterior axis; diameter (d): maximum distance across the valves. Shape indices based on shell measurements were calculated according to the following criteria (slightly modified from Holopainen & Kuiper, 1982; and Kuiper, 1983): Height index (I H/SL): percentage proportion of the height (H) over the shell length (SL); convexity index (Ci) or roundness: percentage proportion of the diameter (d) over the shell height (H); ratio hinge length and shell length (HiL/SL): distance between cusps of left anterior lateral (A_2) and left posterior lateral (P_2) as percentage of the shell length; pre-siphonal suture (PSS): distance between the base of the siphonal aperture (anal or branchial, according to the number of siphons the species have) and the origin of the pedal aperture; ligament-length index (Li): measured from the length of the ligamental pit and expressed as percentage of the shell length; and beak position: calculated as the percentage of the shell length left forward a perpendicular line that intercepts the central point of the beak and the antero-posterior axis.

RESULTS

Pisidium sterkianum Pilsbry

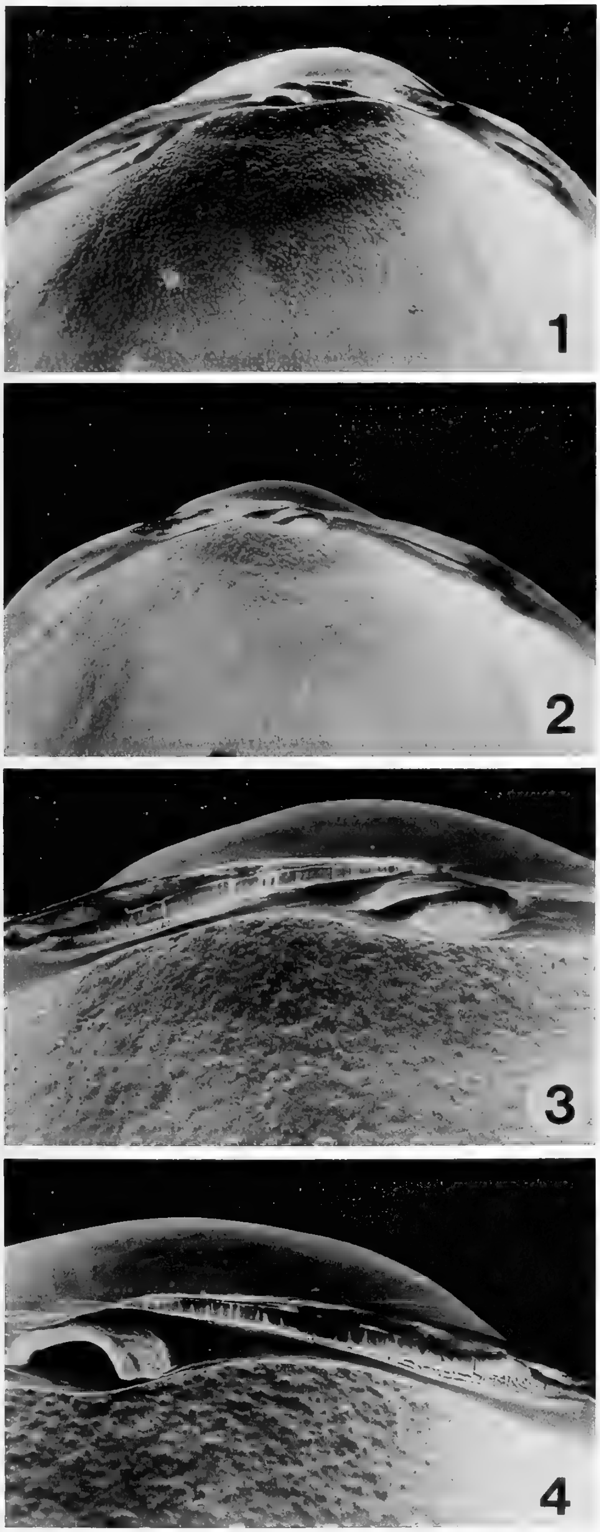
(Figures 1–4, 24)

Pisidium sterkianum Pilsbry, 1897:291, pl. 6, figs. 1–4.

Description: Shell inequilateral, medium to large, somewhat inflated (average I H/SL = 81.9 ± 1.8; average Ci = 69.3 ± 5.4). Surface glossy, straw-yellowish, and finely striated. Shell outline rounded-oval. Anterior end moderately produced; in certain specimens a slight but well-defined angle with the dorsal margin particularly evident. Posterior end decidedly truncate. Posterior margin broadly rounded or nearly straight. Anterior margin produced and obliquely rounded. Dorsal margin faintly curved and slightly concave in middle, just below beak. Dorsal and ventral margins about equally arcuate. Beak rather full but low and wide, not strikingly differentiated from shell surface or produced above dorsal margin; somewhat backwardly displaced (beak position: 53.1–64.7% of SL, average: 59.5%). Ligament extending from cardinal teeth to slightly beyond intersecting line of umbo with dorsal margin. From its origin, ligament inserting along a ridge at base of ligamental pit, being rather extroverted but not protruding from shell surface (average Li = 18.8 ± 2.7). Ligamental pit relatively long and slender, broadening out to posterior half.

Hinge plate solid. Hinge line broadly arcuated, strikingly narrowed behind cardinals (HiL/SL = 58 ± 2.7). Teeth well developed. In right valve: one cardinal tooth with anterior half straight or slightly arcuated, posteriorly thickened and deeply sulcated. Lateral walls of enlarged posterior end of C_3 sometimes appearing rugose due to presence of small circular hollows. Cardinal tooth arising from widest point of hinge plate. Lateral teeth arising just below intersection point of beak line with dorsal margin. Anterior and posterior lateral teeth solid, nearly straight and parallel. Inner posterior lateral (P_I) low, with nearly central cusp; P_{III} somewhat reduced, with distal cusps. Anterior laterals (A_I and A_{III}) with somewhat distally displaced cusps, A_{III} reduced when compared with A_I. Inner surface of laterals rugose. Left valve with two cardinal teeth, outer (C_4) just below central point of beak, slightly curved and oblique with respect to antero-posterior shell axis, overlapping C_2 at posterior half or a bit more. Inner cardinal (C_2) shorter, robust, broad at base and sharply curved at tip, displaced forward with respect to C_4 and parallel to antero-posterior axis. Left laterals strong, nearly straight, anterior lateral (A_2) with long inner slope and very short outer slope, posterior lateral (P_2) with more central cusp.

Anatomy. Only inner demibranchs present, short reflected lamella not much longer than one-fourth to one-third of length of descending one. Outer demibranchs entirely absent. Branchial opening absent. Anal opening, a slit bordered by muscular sphincter which does not extend into a siphon. Pre-siphonal suture relatively short (average PSS = 10.4 ± 2.7).



Figures 1–4

Pisidium sterkianum (MLP 5061). Figures 1, 4. Right valve, note the different shape of C_3 in Figure 4. Figures 2, 3. Left valve. Scale bars: Figures 1–2 = 2 mm; Figures 3–4 = 200 μm.

Variability. The solidness of the hinge plate may vary greatly. The anterior half of the right cardinal tooth may be in some individuals strongly arcuated (Figures 3, 4) and, in these cases, C_2 and C_4 are shorter, curved, and very close to one another, as shown in Figure 3.

Remarks: *P. sterkianum* is similar to *P. forense* Meier-Brook, 1967 (from Minas Gerais, Brazil), from which it differs in being larger, proportionally lower, and less globose. Moreover, the ligament is more decidedly extroverted in *P. sterkianum,* and the beak is less prominent.

In Kuiper's (1983, 1991) opinion, *P. gundlachi* Arango, 1865, and *P. consanguineum* Prime, 1865 (both from Cuba), may be considered synonymous with *P. sterkianum.*

Type locality: "el Prado," Montevideo, Uruguay.

Other localities: Several water courses that flow to the Uruguay River at Salto Grande Dam area, Concordia, Entre Rios (Olazarri, 1983); brooks and artificial channels flowing to the Río de La Plata: arroyo Miguelín, Ensenada, Buenos Aires (MLP 5058, 5059, 5061); Río Santiago, Ensenada, Buenos Aires (MLP 5060)).

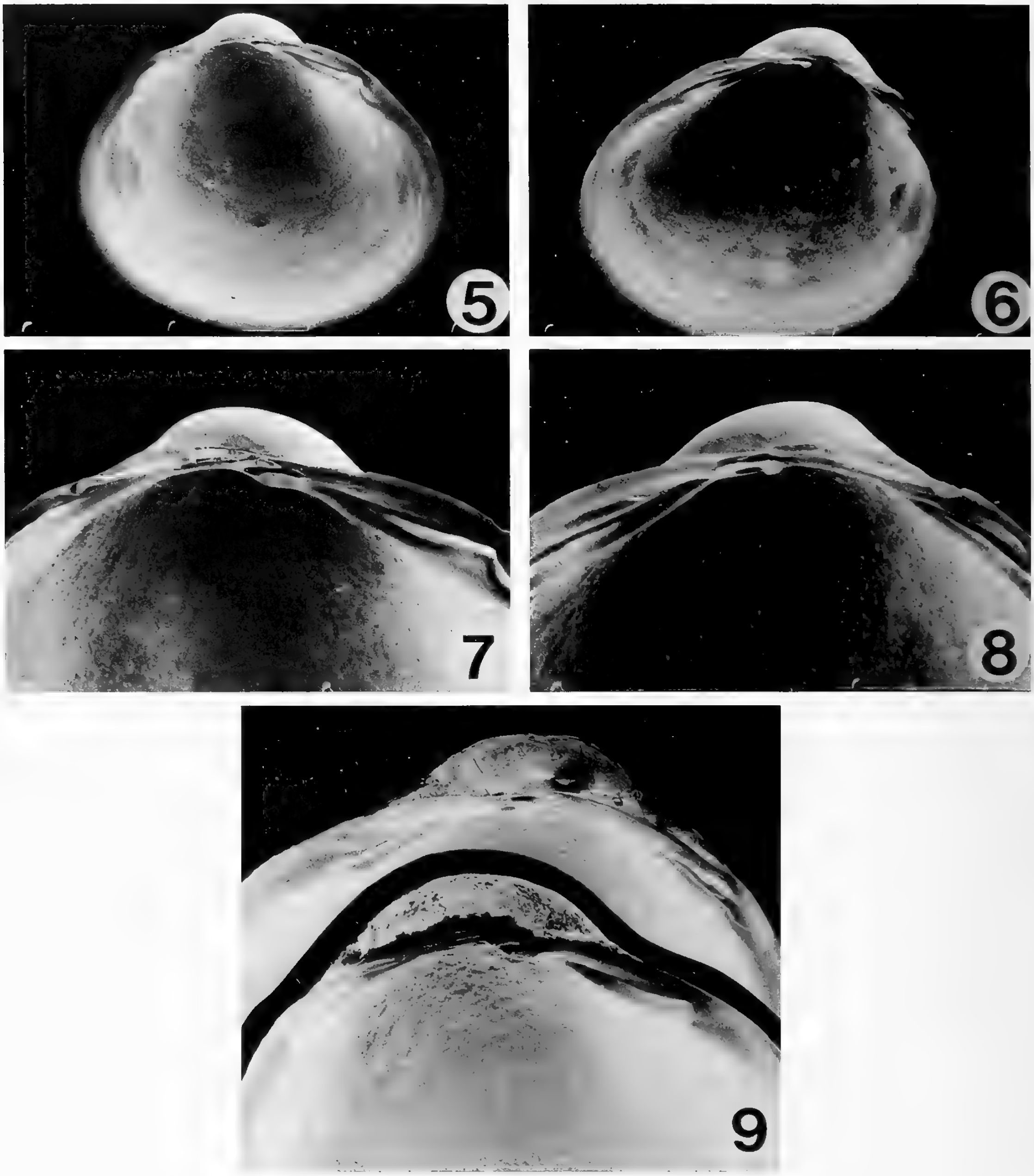
Pisidium vile Pilsbry

(Figures 5–9, 25)

Pisidium vile Pilsbry, 1897:292, pl.6, figs. 17–20.

Description: Shell small (maximum observed size: 3.4 mm), rather inequilateral, high, quite globose (average I H/SL = 89.2 ± 2.3; average Ci = 82.3 ± 4.6). Surface glossy, finely striated, white to pale yellowish; three or four concentric dark lines often well marked. Umbonal region frequently covered by sediments, forming thick crust masking external shell outline. Beak full, projecting above the dorsal margin and backward displaced (located at about 60% of shell length).

Posterior margin abruptly truncated, evenly curved or nearly straight. Anterior margin produced, oblique, and rounded. Dorsal margin rather short, about as strongly curved as ventral one. Hinge plate long, average HiL/SL = 55.7% ± 1.6) of shell length. Hinge plate sharply arcuate and narrow; cardinal teeth seeming to hang from dorsal margin. Hinge teeth well developed. In right valve, one cardinal tooth short, straight, or slightly curved, thickened and angled at its posterior end, forming a small weakly sulcated head. Anterior lateral teeth arising very close to cardinal ones. Inner anterior lateral (A_I) strong, wide, somewhat arcuated, with proximal slope long, distal slope relatively short. Outer anterior lateral (A_{III}) minute, nearly inconspicuous, narrow, straight, and displaced backward with respect to A_I. Posterior laterals delicate. Outer posterior lateral (P_{III}) short and straight, lower than P_I, and displaced forward. In left valve, one strong and large inner cardinal (C_2) and one outer cardinal (C_4) slender, straight, or evenly arcuate, very close to dorsal margin, overlapping C_2 at posterior end. Hinge plate very narrow at insertion of C_2, which seems to hang from its inner margin. Anterior lateral tooth strong, long, and straight, higher than P_2,



Figures 5–9

Pisidium vile (Figures 5–8: MLP 5062; Figure 9: MLP 5063). Figures 5 and 6. Interior view of left and right valves. Figures 7 and 8. Detail of hinge plates. Figure 9. Detail of beak covered by a thick crust of sediments. Scale bars = 2 mm.

with stippled cusp and long proximal slope; distal slope moderately short. Posterior lateral (P_2) rather short, as strongly curved as posterior margin, running very close to shell margin.

Ligament tending decidedly to be extroverted, inserting in a long and broad ligamental pit (average Li = 20.2% ± 1.4).

Anatomy. Only inner demibranchs present. Branchial opening absent. Pre-siphonal suture relatively short, representing about 8–12% of shell length (average 10.49%).

Remarks: *P. vile,* as stated in the original description, differs from *Pisidium dorbignyi* Clessin, 1879, in being smaller, shorter, with a much more projecting beak. In

Pilsbry's opinion, the very large size of the posterior left cardinal and the "greater reduction" of the anterior one, are conspicuous features.

Type locality: The species was described from a creek in "el Prado," Montevideo, Uruguay.

Other localities: Olazarri (1983) reported *P. vile* from the area of Salto Grande Dam lake (Entre Rios, Argentina; Salto, Uruguay). *P. vile* is a common species in water courses flowing to the Río de La Plata basin, frequently cohabiting with *P. sterkianum*. The studied specimens were dredged from "arroyo Miguelín" (MLP 5062) a small brook, and Río Santiago (MLP 5063), a moderately large stream, both at Ensenada, Buenos Aires.

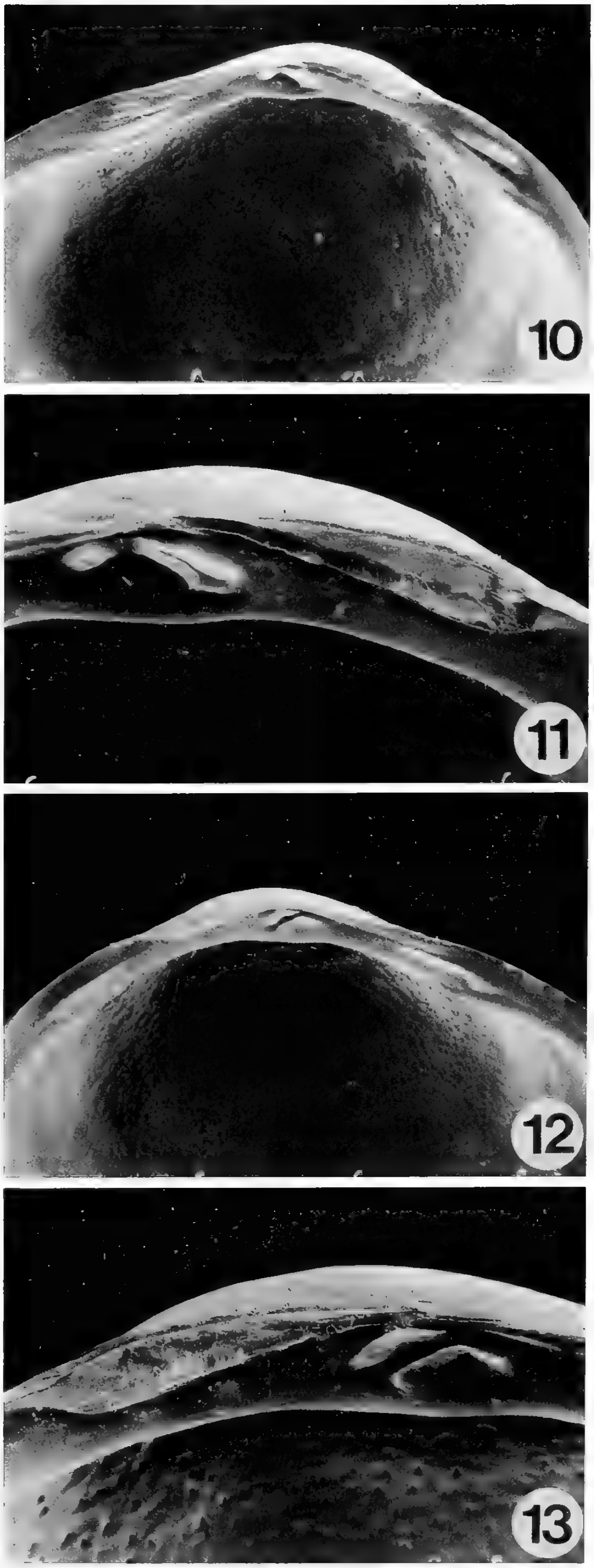
Pisidium magellanicum (Dall)

(Figures 10–13, 26)

Corneocyclas magellanicus Dall, 1908:411.
Pisidium magellanicum (Dall), Pilsbry, 1911:606, pl. 47, figs. 12–16.

Description: Species small to medium-sized, shell outline oval with antero-posterior axis rather enlarged, moderately inflated (average I H/SL = 80.5 ± 1.7; average Ci = 64.5 ± 3.7). Beak low and wide, not protruding, somewhat backwardly displaced (located at about 58% of the shell length). Posterior margin truncated, broadly rounded; anterior margin protruded, uniformly curved. Dorsal margin short, ventral margin broad, evenly arcuate. Shell surface polished, white-translucent. Shell surface sculptured with several resting-stage lines and fine concentric striation.

Hinge plate solid. Hinge line relatively long (HiL/SL about 54% of shell length). In left valve, two well-developed cardinal teeth. Inner cardinal tooth (C_2) strong, somewhat forward displaced; arising from a short and robust horizontal base, it twists at the apical end. Outer left cardinal (C_4) located exactly below central point of beak, oblique, overlapping C_2 at posterior half. C_4 short and slender, wedge-shaped, slightly arcuate. Lateral teeth arising just below intersection point of beak line with dorsal margin. Anterior lateral (A_{II}) triangular, with stippled distal cusp; posterior lateral (P_{II}) shorter, triangular, with nearly distal and blunt cusp. Right cardinal tooth (C_3) taking shape of wide inverted-V with posterior branch shorter, anterior branch slightly distally broadened, weakly sulcated. Anterior lateral teeth: A_{III} minute, cusp displaced backward with respect to cusp of inner one (A_I). Posterior lateral teeth strong, straight, shorter than anterior ones; P_I reduced, cusp quite distal. Inner surfaces of right lateral



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Figures 10–13

Pisidium magellanicum (MLP 5064). Figure 10. Right valve. Figure 11. Detail of C_3 and ligament. Figure 12. Left valve. Figure 13. detail of cardinal teeth and ligament of the left valve. Scale bars = 1 mm.

teeth rugose. Divergence angle between laterals varied from 122 to 125°.

Ligament internal, strong, relatively short and broad (ligament length about 17% of shell length); ligamental pit deep.

Anatomy. Outer and inner demibranchs present. Inner demibranchs well developed, shorter ascending lamella covering approximately one-third to one-fourth of descending ones. Outer demibranchs relictual, represented by a few short filaments close to posterior adductors. Both siphonal openings present (also observed on dry soft parts of individuals of ANSP lot 88811). Anal opening bordered by well-developed muscular ring, much reduced in branchial one. Inhalant and exhalant currents internally separated by pallial fold which forms horizontal septum between anal and branchial openings. Pre-siphonal suture short, representing about 5–10% (average: 7.7%) of shell length.

Type locality: Magellan Strait in 61 fathoms, "Albatross" station no. 2778 (the species was described upon a single valve washed into the sea from a stream in the continent).

Other localities: Pilsbry (1911) found *Pisidium magellanicum* ". . . in several springs a long the Río Chico, 15 miles (ANSP 88812, examined lot) and 25 miles above the Sierra Oveja (today known as "cerro Las Ovejas"), 48°46′S, 70°22′W; Río Blanco near the base of the Andes; and springs at the base of the Andes, 65 miles north of the Río Chico, 2400 ft. elevation (ANSP 88811, examined lot) . . ."; all sample sites mentioned above are at the Santa Cruz province. *Pisidium magellanicum* has been collected by the author from an unnamed brook, 3 km distance from Trevelin to Futaleufú hydroelectric power plant (Amutui-Quimei Lake), Chubut Province (MLP 5064).

Remarks: Following the original description in 1908 and later citation by Pilsbry in 1911, the species has never been reported until the present study. The specimens studied by Pilsbry (1911) from Río Chico (15 miles above Sierra Oveja) seem to be lower and with more prominent beaks than figured in his paper. The specimens of the lot ANSP 88811 (from the bottom of the Andes, 65 miles north to Río Chico) fit better with the original decription and with the specimens from Trevelin, Chubut, here described and figured.

Pisidium observationis Pilsbry

(Figures 14–19, 27)

Pisidium observationis Pilsbry, 1911:608, text fig. 19.

Description: Shell rather inequilateral, high, somewhat inflated (average I H/SL = 87.2 ± 2.3; average Ci = 60.3 ± 4.7). Shell outline rounded-ovate, posterior end decidedly truncated and widely arcuated; anterior end protruded in sharp curve. Shell surface glossy, straw-yellowish or pale brown. Several growth-arrest lines often well marked. Surface finely striated. Beak wide, low, not outstanding from shell surface, slightly visible above dorsal margin, located at about 57% of shell length. Dorsal margin short, slightly concave in middle. Ventral margin wide, evenly rounded.

Hinge plate solid, rather straight. Hinge length representing about 57% of shell length. Left cardinal teeth well developed. C_4 rather long, slender and low, slightly and evenly curved, nearly horizontal with respect to antero-posterior axis; overlapping C_2 at posterior end (Figure 17) or at both ends (Figure 18). C_2 shorter, more robust, slightly curved, sometimes oblique. External left cardinal (C_4) may appear as slightly sinuous. Lateral teeth not remote from cardinals, arising just below intersection of beak line with dorsal margin. A_2 and P_2 long, high, cusps distally displaced, blunt in P_2, stippled in A_2. Right cardinal tooth straight or slightly curved (somewhat distorted in cases), posterior end enlarged and sulcated, sometimes broadened in a small head. Right lateral teeth well developed, parallels. Inner anterior lateral (A_{I}) wide, broadly curved, cusp nearly central. Outer anterior lateral (A_{III}) straight, slender with distal cusp, shorter and lower than A_{I}. Posterior laterals: inner posterior lateral (P_{I}) long and low, slightly curved, cusp central or somewhat distal. Outer posterior lateral (P_{III}) shorter, straight, with distal cusp. Inner surface of laterals rugose. Divergence angle between lateral teeth ranging from 100 to 105°. Ligament internal; ligamental pit deep, curved at ventral margin, and evenly broadened to posterior end. Ligament length about 19% of shell length, surpassing a little the intersection point of beaks line with dorsal margin.

Anatomy. Anal aperture, only siphonal aperture present, a long slit. Pre-siphonal suture short, representing about 7 to 12% of shell length (average 9.3%) (pre-siphonal suture accessible for measurement in only five specimens). Analysis of dried soft parts of type series (ANSP lot 7799) permitted corroboration of the presence of a single siphonal aperture (only one specimen was available for measurement, PSS was 6.5% of SL). Only inner demibranchs present, ascending lamella half as long as descending one.

Remarks: *P. observationis* is the most distinctive species among the Patagonian Sphaeriidae described by Pilsbry in 1911. This species is easily distinguished from the rest of the Patagonian pisidia by the general shell outline, beak position, and hinge characteristics (particularly the morphology and position of the posterior right lateral teeth, which are long, slender, and parallel). The ligament length, the hinge-length ratio, and the short pre-siphonal suture distinguish *P. observationis* from other Patagonian species. In particular, the decidedly more internal ligament, the presence of only one siphonal aperture, only one branchial lamella, and the minor divergence angle of the lateral teeth are the main features that separate *P. observationis* from *P. magellanicum.*

Since the original description in 1911, *P. observationis* was only reported from Tierra del Fuego (Ituarte & Gordillo, 1991). Morphometric ratios of the type series and specimens from Laguna Verde, Neuquén here studied are coincident. The maximum shell size reported by Pilsbry in the original description (5.1 mm) exeeds the maximum sizes measured in the type-series lot (ANSP lot 7799), but that value is in agreement with the maximum size computed in the present study (5.2 mm) for specimens from Laguna Verde, Neuquén.

Type locality: "... near the Mount of Observation (below the mouth of Santa Cruz River) ...", today known as cerro Observación (50°22′S; 68°57′W), near "cañadón de las Vacas", department of Corpen Aike, Santa Cruz Province (ANSP 7799, examined lot).

Other localities: Laguna Verde (1600 m elevation), Cerro Chapelco, San Martín de los Andes, in the province of Neuquén (MLP 5065); Isla Gable, Tierra del Fuego (MLP 4988).

Pisidium patagonicum Pilsbry

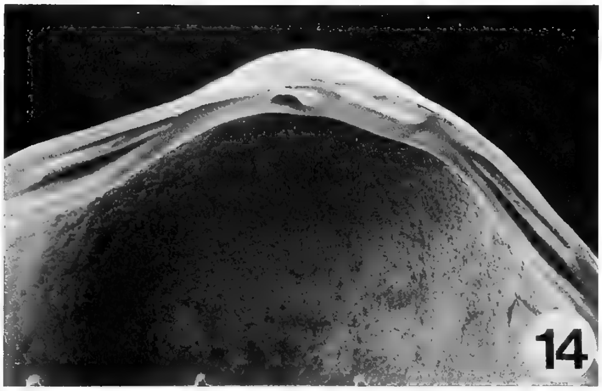
(Figure 28)

Pisidium patagonicum Pilsbry, 1911:607, pl.17, figs. 8–10.

This species has not been found or reported since the original description by Pilsbry (1911). The original description follows:

> "... The shell is pale buff, glossy, very finely striate, with low, wide, smooth and glossy beaks; strongly inequilateral, the anterior end very short and rounded, base evenly convex, posterior end narrow and somewhat produced. Interior white. Cardinal teeth are excessively weak and low, nearly effaced. There is a very low, horizontal, rudimentary tooth in the right valve, a low short one in the left, with the scarcely discernible trace of another anterior to it. ... Lateral teeth very short and moderately strong, distant from the beaks..."

Remarks on the type-series: (ANSP 88810). Shell moderately inflated, high (average I H/SL = 91.6 ± 1.6; average Ci = 63.9 ± 2.6). Shell outline rounded-oval, with posterior end bluntly truncate. Dorsal margin very short, uniformly arcuate; ventral margin wide, evenly curved; anterior end protruded, sharply curved. Beak central, moderately low and wide, somewhat protruding and readily visible above dorsal margin (located at about 54% of shell length). Hinge plate solid, sharply arcuate, relatively long (average HiL/SL = 58.5%). Strong ligament, broad and relatively long (ligament length is about 14.9% of shell length), located in a well-marked ligamental pit, and not



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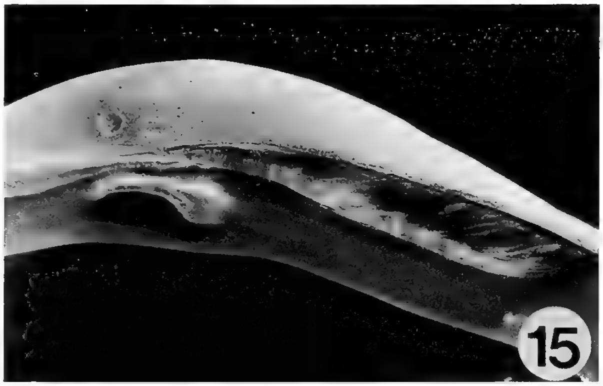

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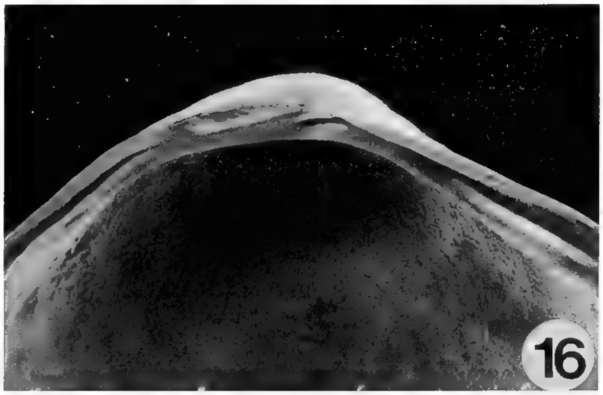

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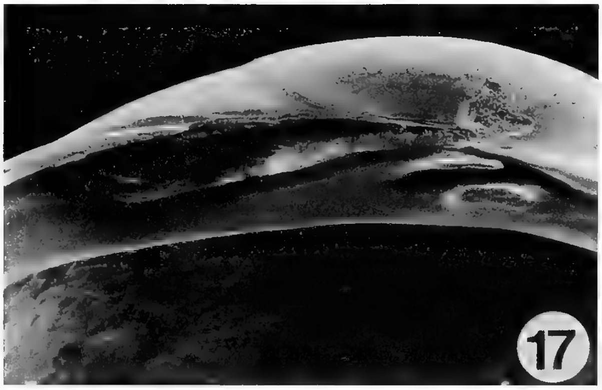

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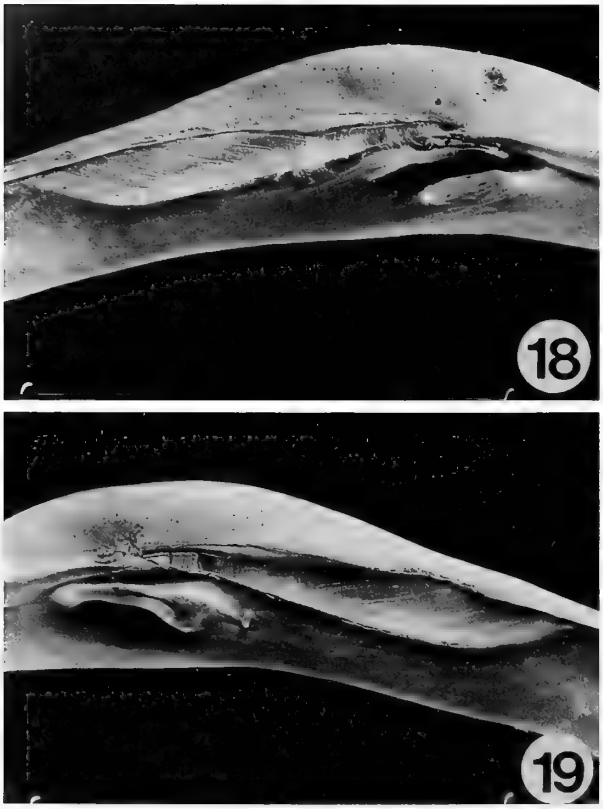
Figures 14–17

Pisidium observationis (MLP 5065). Figure 14. Hinge of the right valve. Figure 15. Detail of cardinal tooth and ligament. Figure 15. Hinge of the left valve. Figure 16. Detail of the cardinal teeth and ligament. Scale bars = 1 mm.



Figures 18 and 19

Pisidium observationis (MLP 5065), a second type of tooth arrangement. Figure 18. Detail of the left cardinal teeth showing C_4 overlapping C_2 at both ends. Figure 19. Right cardinal tooth (C_3) slightly curved, somewhat distorted and deeply sulcated. Scale bars = 1 mm.

discernible from exterior. Contrary to Pilsbry's original description, cardinal teeth seem to be rather well defined. Right valve: outer cardinal, C_4, slender, evenly curved, oblique and placed rather close to inferior margin of ligamental pit, not overlapping C_2. Inner cardinal tooth, C_2, very short (nearly columnar in several specimens), low and perpendicular to hinge plate, arising from a broad and strong base. Right cardinal tooth (C_3) irregular in shape, slender and short, slightly concave in middle, not distally enlarged. At both sides of right cardinal tooth, two fossettes serve to articulate C_2 and C_4. These fossettes are not as well developed in any other *Pisidium* species from Patagonia. Right and left laterals well defined, relatively short, and remote from cardinals; divergence angle of lateral teeth is about 100°, quite different from divergence angle found in *P. magellanicum:* 112° in Pilsbry's text figure 18, to 125° in specimens from Trevelin, Chubut, but closer to divergence angle in *P. observationis* (about 100–105°). Ligament proportionally shorter than in *P. observationis. P. patagonicum* resembles *P. observationis* in shell shape; however, the latter is lower and somewhat less convex.

Type locality: A spring on the Río Chico, 15 miles north of Sierra Oveja (today known as "cerro Las Ovejas," 48°46′S; 70°22′W, Río Chico Department, Santa Cruz Province) (ANSP 88810, examined lot).

Other localities: Pilsbry (1911) reported the species from ". . . springs on the Río Chico thirty miles above the Sierra Oveja; twenty-five miles below the Río Belgrano; Arroyo Eke, near the head waters of the Spring Creek, 2400 ft. elevation. . ."

Pisidium ***inacayali*** Ituarte, sp. nov.

(Figures 20–23, 29)

Description: Species medium-sized, shell elongated and moderately convex (average I H/SL = 80.3 ± 1.4; average Ci = 61 ± 3.6); translucent, periostracum white to yellowish, evenly fine-striated. Shell outline oval, rather inequilateral. Anterior margin produced, evenly curved, posterior margin abruptely truncated, widely rounded. Dorsal margin arcuate backward to beak, with marked depression or concavity in middle, nearly straight forward of the beak. A slightly marked angle connecting dorsal margin with anterior margin. Ventral margin uniformly arcuate. Beak wide, extremely depressed, displaced backward, located at about 59% of shell length, only slightly visible above dorsal line.

Hinge plate solid. Hinge line rather long (about 58% of shell length). In right valve, one cardinal tooth slender, with anterior half curved and not as thickened at posterior end, which is sulcated. Anterior lateral teeth strong, A_I broadly curved with cusp somewhat displaced forward, A_{III} reduced, with distal cusp slightly displaced backward. Posterior laterals delicate, straight, and parallel. P_I with nearly central cusp, P_{III} shorter, with distal cusp. In left valve, two slender cardinals, C_4 slightly sinuous or weakly curved, oblique, overlapping C_2 at least at posterior half. C_2 shorter, higher, more arcuated than C_4. Lateral teeth robust, high, inner slopes longer than outer ones. Divergence angle of lateral teeth from 113 to 122°.

Ligament robust, long (about 20% of shell length), surpassing, sometimes greatly, the beak line at intersection with dorsal margin. Ligament internal, enclosed, closely applied to dorsal margin. Well-defined ligamental pit, with inner margin curved, broadened, and slightly angled in middle.

Anatomy. Only inner demibranchs present, descending lamella well developed, ascending one shorter (about one-third of former). Only one siphonal aperture, the anal, as long slit encircled by weakly muscular sphincter. Presiphonal suture long (about 14% of shell length). Adductor scars and pallial line well marked.

Remarks: *P.* ***inacayali*** is close to *P. magellanicum* in general shell shape; however, the new species is less convex, the beak is more backward displaced, and the ligament is stronger, larger, and also different in shape. The hinge line length relative to shell length is larger in *P.* ***inacayali.*** The presiphonal suture is decidedly larger, in part because of the lack of the branchial opening. The right cardinal tooth morphology is also distinctive for each species. The new species differs from *P. observationis* in being much lower, with a much more depressed and backwardly displaced beak. The general shell shape is also distinctive, as well as the shape of the ligamental pit. The presiphonal suture is longer in *P.* ***inacayali.***

Type locality: An unnamed brook, at 3 km on the road from Trevelin (43°04′S; 71°29′W) to Futaleufú River Dam, Chubut province, Argentina.

Other localities: *P.* ***inacayali*** was also collected from an unnamed brook, 6.5 km before Tecka (on the intersection with the national route No. 40), Chubut, Argentine.

Type specimens: Holotype: in the collection of the Department of Invertebrate Zoology, Museo de La Plata (MLP 5066); Paratypes: MLP 5067; 5068; Department of Invertebrates MACN 33761; Muséum National d'Histoire Naturélle (Paris).

Etymology: The species is named in honor of Inacayal, one of the last Patagonian Indian Chiefs who surrendered at the end of the "Desert Campaign." Inacayal lived in the Tecka neighborhoods and spent the last years of his life at the Museum of La Plata where he died in 1888. His remains were repatriated in 1994.

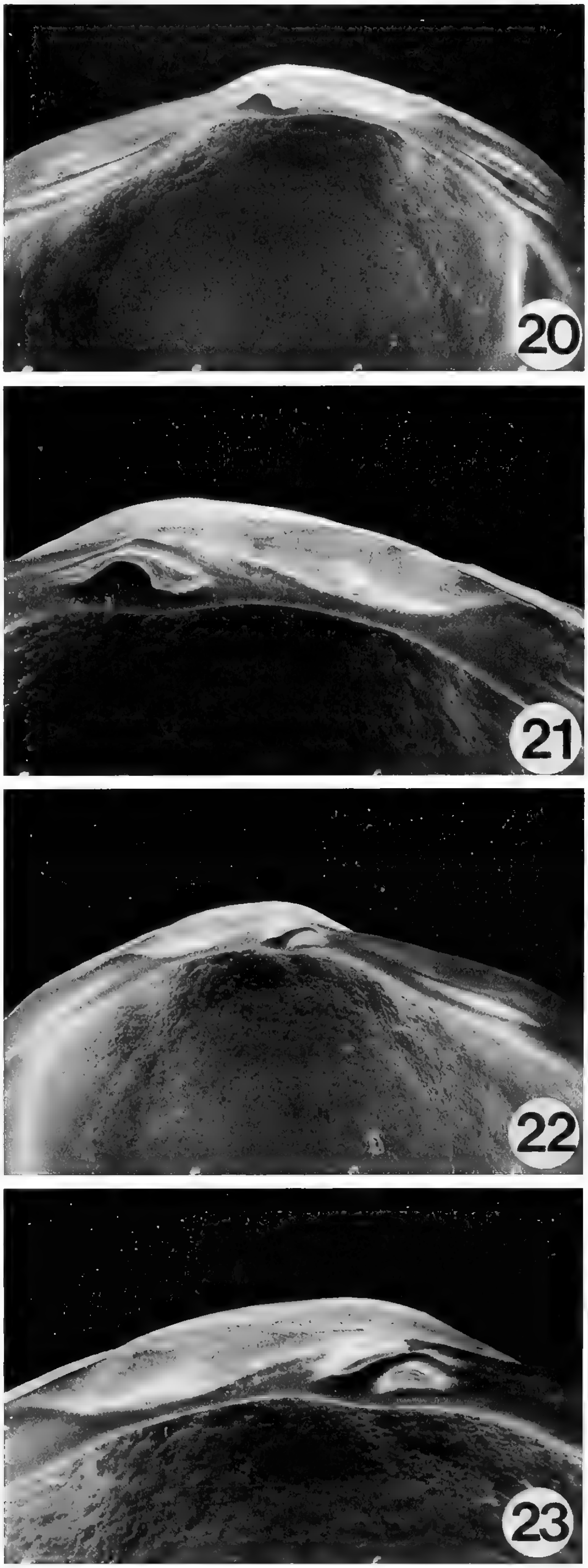
Pisidium Species Formerly Quoted in Marine Genera:

Pisidium plenilunium (Melvill & Standen)

(Figure 30)

Scacchia plenilunium Melvill & Standen, 1907:150, figs. 20, 20a. Carcelles & Willamson, 1951:339.
Sphaerium vallentinianum Melvill & Standen, 1914:132, pl. 7, figs. 3, 3a, 3b.
Pisidium plenilunium (Melvill & Standen), Dell, 1972:26, fig. 34.

Description of the two syntypes: (RMS 1921.143.724). Shell rounded-ovate, very high and moderately convex (I H/SL = 91.4 and 89.2; Ci = 65.9 and 60.6). Periostracum white-yellowish, shell semi-translucent, densely punctuated, surface finely striated. Shell not very inequilateral, posterior end truncated, anterior end somewhat produced and narrow. Postero-ventral angle of shell is withdrawn



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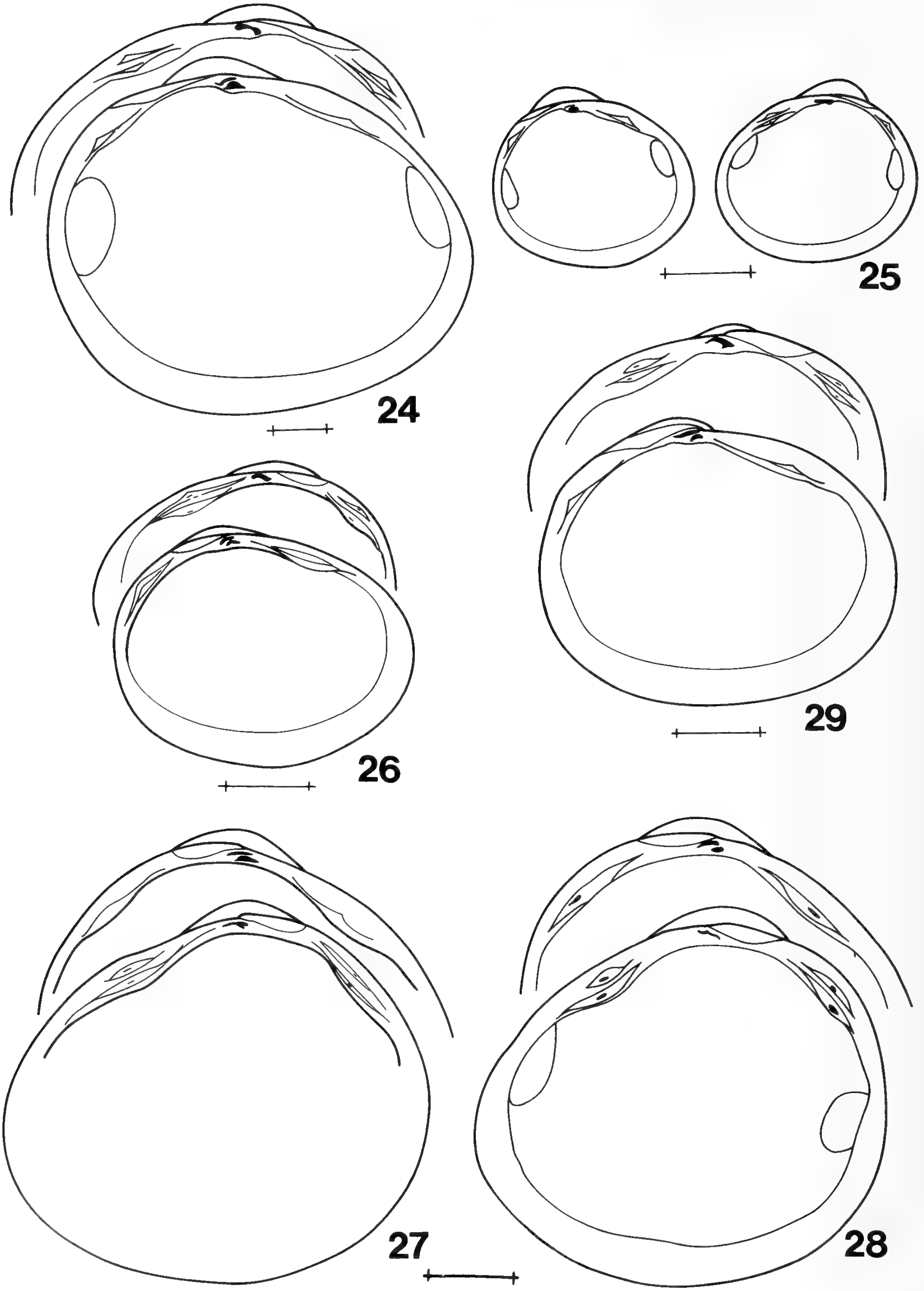
Figures 20–23

Paratype of *Pisidium* ***inacayali*** Ituarte, sp. nov. (MLP 5067). Figure 20. Hinge of the right valve. Figure 21. Detail of the right cardinal tooth and ligament. Figure 22. Hinge of the left valve. Figure 23. Left cardinal teeth and ligament. Scale bars = 1 mm.



Figures 24–29

Argentine species of *Pisidium*. Figure 24. *P. sterkianum* from Buenos Aires (MLP 5061). Figure 25. *P. vile* from Buenos Aires (MLP 5062). Figure 26. *P. magellanicum* from Chubut (MLP 5064). Figure 27. *P. observationis* from Neuquén (MLP 5065). Figure 28. *P. patagonicum* from Santa Cruz (from type-series ANSP 88810). Figure 29. Holotype of *P.* ***inacayali*** Ituarte, sp. nov. (MLP 5066). Scale bars for all figures = 1 mm.

forward. Beak low, moderately visible above dorsal margin, slightly displaced backward (located at 53.8 and 56.8% of shell length), nepionic shell well marked by a dark line, but not inflated.

Hinge plate solid, broadened in central part. Hinge line sharply arcuate, relatively long (HiL/SL = 57.6 and 61.6). Left cardinal teeth: outer (C_4) somewhat oblique, slender, evenly curved, overlapping C_2 at nearly its entire length. C_2 shorter, slender, and slightly curved. Left lateral teeth short, cusp of (A_{II}) stippled, somewhat distally displaced; $P(_{II})$ lower, cusp wide and rounded. Right cardinal tooth (C_3) low, slender, weakly curved, and thickened at posterior end. Lateral teeth well developed, very short. Anterior and posterior outer laterals reduced, half as long as inner ones. Ligament internal, rather long (representing, in the two syntypes, 21.5 and 20.3% of SL). Ligamental pit broad, ventral margin uniformly curved. Although soft parts have not been preserved in type lot, analysis of dried remains adhered to valves revealed the presence of only one siphonal aperture.

Type locality: Cape Pembroke, Malvinas islands (Scottish Antarctic Expedition 1902–1904, Station 118). Syntypes: one single valve and one complete shell, at the Royal Museum of Scotland, lot. nos. 1921.143.724.

Remarks: This species was originally described in a marine genus from valves collected from the marine shore. Undoubtedly, the authors failed to recognize the freshwater origin of the shells. Dell (1972) assigned the species to the genus *Pisidium* including *Sphaerium vallentinianum* Melvill & Standen, 1914, from Roy Cove, also Malvinas islands, in a synonymic list.

The original description is vague and not sufficient to assign certainly any specimen to this species. Dell (1972) did not give the description of the syntypes lodged at the Royal Museum of Scotland, but figured a right valve, suggesting the possibility that *P. plenilunium* and *P. magellanicum* were synonymous. However, taking into account the striking differences in shell shape—much more rounded, low, and less convex in *P. magellanicum*—this does not seem to be correct. Furthermore, the greater divergence angle of the lateral teeth, which are longer and not remote from cardinals, clearly separates that species from *P. plenilunium.*

In studying the syntypes of *Pisidium plenilunium,* it is evident that the shell outline (high and rounded-oval), the morphometric ratios, the morphology and position of the lateral teeth and beak position, closely approach those of *P. patagonicum* Pilsbry. This taxon may well be synonymous with *P. plenilunium,* but in order to preserve nomenclatural stability, the author postpones any conclusions until future studies allow more complete knowledge about the variability of Patagonian pisidia.

Species of *Pisidium* Doubtfully Distributed in Argentine Inland Waters:

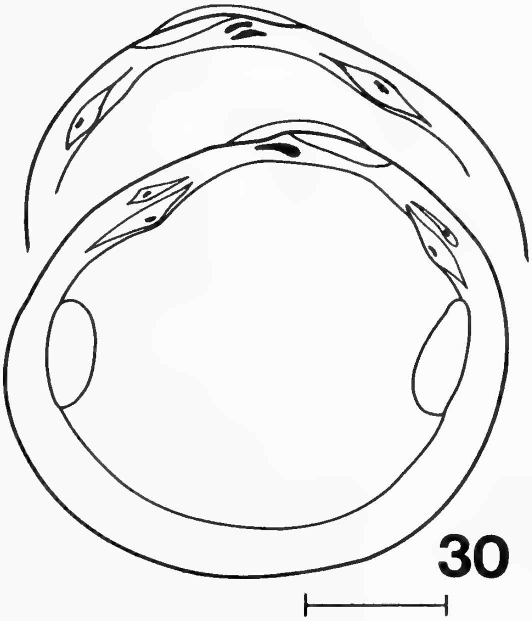


Figure 30

Syntype of *Pisidium plenilunium* (RMS 1921.143.724). Scale bar = 1 mm.

Pisidium dorbignyi (Clessin)

Cyclas pulchella d'Orbigny, 1835:44; 1846:568, pl.83 figs. 8–10

Pisidium dorbignyi Clessin, 1879:62 (*nomen novum pro Cyclas pulchella* d'Orbigny, 1846)

Sphaerium pulchellum (d'Orbigny), Formica Corsi, 1900:1–237

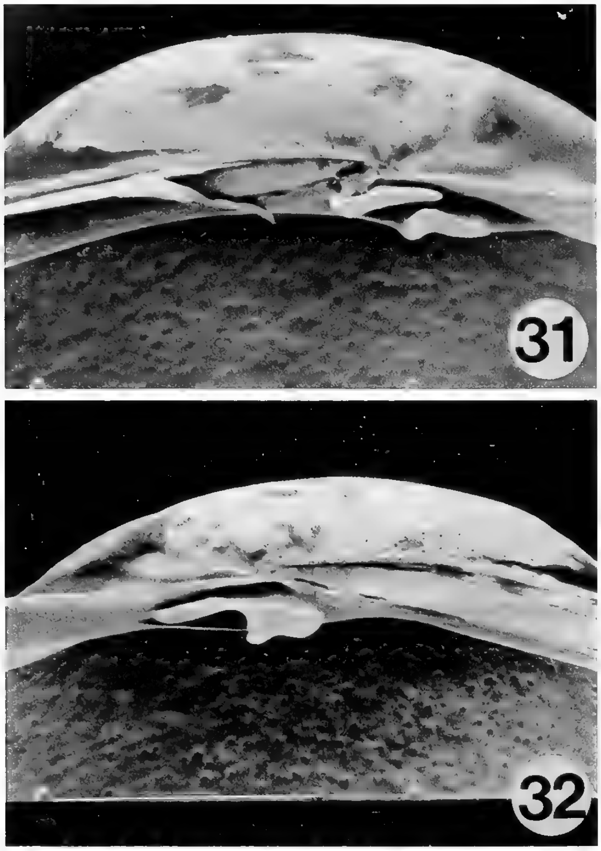
The original description reads (translated): ". . . Shell ovate, inflated, thin, inaequilateral, surface even. Externally olivaceous. 'Buccal' end elongated, rounded; 'anal' end short, obtuse. Interior white. Long. 3 mm . . . ."

Type locality: The type series was collected by d'Orbigny from water reservoirs among sand dunes in the neighborhood of Maldonado, Uruguay.

Other localities: Landoni (1992) reported *P. dorbignyi* from the Río de La Plata and related water courses, but he did not give precise collecting sites. *P. dorbignyi* was also reported from northern Brazil (Lange de Morretes, 1954 *fide* Figueiras, 1965).

Species Formerly Erroneously Quoted as *Pisidium* Species:

Bonetto & Tassara (1987) misquoted *Cyclas paranensis* d'Orbigny, 1846 as a *Pisidium* species from the Paraná river basin. d'Orbigny (1846) included under *Cyclas* the genera *Neocorbicula, Pisidium,* and *Musculium.* His reference to *Cyclas paranensis* actually corresponds to *Neocorbicula paranensis* (d'Orbigny, 1846) (Parodiz & Hennings, 1965; Figueiras, 1965), so *Pisidium paranensis* must be dropped from the *Pisidium* species list.



Figures 31 and 32

Musculium argentinum (MLP 5074). Interior view of right and left valves. Scale bars = 1 mm.

Other Misquoted Pisidia:

Mansur et al. (1991) reported *Sphaerium observationis* Pilsbry, 1911, from Río Grande do Sul, Brazil. Since there is no reason to refer the species to the genus *Sphaerium,* this is an obvious misquotation for *Pisidium observationis.* Furthermore, the occurrence of *P. observationis* in southern Brazil seems to need confirmation.

Some Remarks on the Argentine Species of *Pisidium*:

Attempts to define a natural subgeneric classification of the genus *Pisidium* have not been successful to date. As stated by Kuiper (1983), neither of the proposed subgeneric classifications proved to be valid for more than a very limited geographic region, and probably, further knowledge on soft anatomy, reproductive biology, and life histories is needed to determine a more appropriate system.

Kuiper's (1962) criteria—the occurrence of only one pair of gills, the lack of an anal opening, and the presence of an external ligament—suggest assignment of *P. sterkianum* and *P. vile* to the Ethiopic species group *Afropisidium* Kuiper, 1962, defined as a subdivision of the subgenus *Neopisidium* Odhner, 1921.

All Patagonian species of *Pisidium* here reported have an internal ligament. Among these, *P. magellanicum* is the only species, until now, for which the presence of two branchial openings and two demibranchs (the outer extremely reduced or vestigial) has been determined. The characteristics mentioned above indicate assignment of *P. magellanicum* to the subgenus *Cycladina* Clessin, 1871, a mainly Holarctic group with numerous species in the Southern Hemisphere (Kuiper, 1962). *P. observationis* and *P.* ***inacayali*** have an enclosed ligament and only one siphonal aperture (the anal) and one (the outer) demibranch, belonging, based on these features, to the subgenus *Neopisidium* Odhner, 1921 (a group, however, which includes small species).

The lack of knowledge of anatomical features for the remaining Patagonian species with internal ligament does not allow us to assign them to any of the proposed subgenus.

With regard to shell morphology, *P. observationis, P. patagonicum,* and *P. plenilunium* are characterized by a high shell, a centrally placed beak; a narrow anterior end, which is moderately protruded in a more or less sharp curve, and a very short posterior end. The anterior margin is oblique, the dorsal margin short, determining a shell outline which tends to a trigonal profile. Lateral teeth are short and more or less remote from the cardinal. The divergence angle between anterior and posterior laterals is low, no more than 105°. The remaining two species, *P. magellanicum* and *P.* ***inacayali,*** have lower shells, a rounded-oval shell outline, a very low and backward displaced beak, and a higher divergence angle between lateral teeth (up to 110° as a rule).

Musculium argentinum (d'Orbigny)

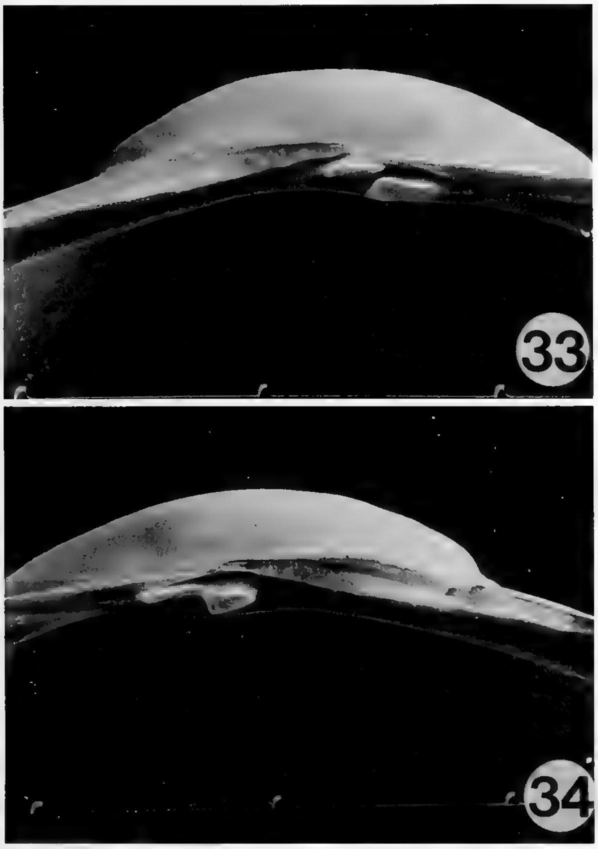
(Figures 31, 32, 35, 36)

Cyclas argentina d'Orbigny, 1835:44. d'Orbigny, 1846:568, pl. 83, figs. 5–7.

Sphaerium argentinum (d'Orbigny), Strobel, 1874:77.

Musculium argentinum (d'Orbigny), Pilsbry, 1911:605, pl. 46a, figs. 6–7a.

Description: Shell medium-sized to large (maximum size 12.6 mm in shell length), high, rather inequilateral, and moderately convex (average I H/L = 84 ± 2.6; average Ci = 62.4 ± 3.6). Shell outline quadrangular or sharply trapezoidal, dorsal margin quite extended, as large as ventral one; slightly arcuate or straight and broken in middle, just below beak. Dorsal margin connected with anterior and posterior margins by marked angles (sometimes smoothed). Anterior end projecting in markedly obtuse angle or sometimes rounded. Posterior end truncated, somewhat oblique, nearly straight. Beak median, prosogyrous. Prodissoconch minute (1.5–2 mm), inflated in marked nepionic cap. Beak projecting from shell surface to variable degree. In the typical form (Figure 35), lateral shell surface shows sharply marked median triangular hump arising from wide base and tapering to embryonic

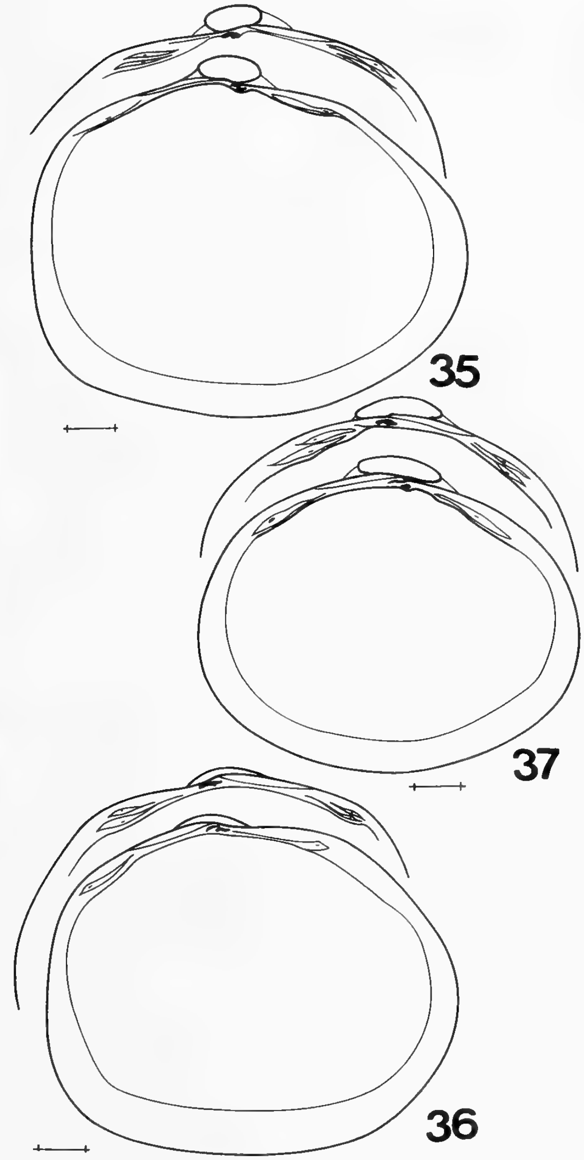


Figures 33–34

Musculium patagonicum (MLP 5077). Hinge plates of the right and left valves. Scale bars = 1 mm.

cap. In other specimens, beak is not so full, quadrangular appearance is smooth, and shells flatter (Figure 36).

Hinge line straight at anterior half, slightly curved at posterior one. Hinge plate extremely narrow in specimens with full and projected beak (cardinal teeth overhangs at inner margin of hinge). In specimens with lower beak, hinge plate is more solid, but always delicate. Hinge: two slender left cardinals, outer (C_4), oblique, slightly arcuated, thickened at posterior end, inner (C_2), shorter, higher, somewhat displaced forward, sharply curved at posterior half. C_4 overlapping C_2 at posterior end. Lateral teeth remote from cardinals. Anterior lateral (A_{II}) upward arcuate, triangular; cusp distally displaced to antero-dorsal angle. Posterior lateral (P_{II}) slightly curved downward, cusp distally displaced toward postero-dorsal angle. Right cardinal tooth (C_3) straight, broadening backward in small, sulcated, bell-shaped head. Lateral teeth rather short, straight, always low. Anterior laterals (A_I and A_{III}) curved upward, more developed than posterior ones (P_I and P_{III}). Divergence angle between lateral teeth always higher than 140°. Hinge length is about 58% of shell length, with maximum and minimum values ranging from 51% to 62%.



Figures 35–37

Argentine species of *Musculium.* Figure 35 (MLP 5092). Specimen of *M. argentinum* with markedly trapezoidal shell outline, very narrow hinge plate, and prominent beak. Figure 36 (MLP 5071). Specimen of *M. argentinum* with lower beak and more solid hinge plate. Figure 37. *M. patagonicum* from Chubut (MLP 5077). Scale bars for all figures = 1 mm.

Ligament long (representing about 20% of shell length) and narrow, extending from beak to short distance from beginning of posterior laterals. Ligament externally visible, not projecting above shell surface.

Variability. M. argentinum shows variation in shell outline (Figures 35, 36), convexity of shell (more convex in specimens with marked trapezoidal shell outline), degree of beak prominence (more marked in trapezoidal forms), and solidness of hinge plate (more solid in forms lacking accentuated contour). Morphology of cardinal teeth is also a variable characteristic which encompasses other variable features: C_3 may be more or less arcuate and, consequently, C_2 and C_4 more or less close to one another.

The range of morphological and morphometric variation has not been described up to date. Because of this, Pilsbry (1911) considered d'Orbigny's (1846) figures (pl. 83, figs. 5–7) of *M. argentinum* as very unsatisfactory. Certainly, d'Orbigny's figure corresponds to an individual without an accentuated trapezoidal outline and without full beaks. The topotypes studied and figured by Pilsbry (1911) correspond to the form here called typical, shown in Figure 35.

Remarks: *M. argentinum* differs from *M. patagonicum* Pilsbry, 1911, in being sharply quadrangular or trapezoidal in shell outline, with the posterior end bluntly truncated, and in having full beaks. The hinge plate is always less solid, and the hinge line always nearly straight or weakly curved. The ratio Hinge Length/Shell Length tends to be constantly greater in *M. argentinum.* In Pilsbry's (1911) opinion, the teeth are decidedly more delicate and compressed than in *M. patagonicum*

Type locality: A brook at the bottom of the Cerro ("arroyo Pantanoso" *fide* Figueiras, 1965), Montevideo, Uruguay.

Other localities: Argentina: Mendoza province: San Carlos; Buenos Aires province: Bahía Blanca, Carmen de Patagones, (Strobel, 1874); arroyo del Azul, Azul (MLP 5073); arroyo Primera Estancia, Magdalena (MLP 5074, 5075); Río Santiago, Ensenada (MLP 5071, 5076); arroyo Miguelín, Ensenada (MLP 5069, 5070, 5072); río Quequén (MLP 5055); Laguna Cami, Tierra del Fuego (MLP 5016).

Musculium patagonicum Pilsbry

(Figures 33, 34, 37)

Musculium patagonicum Pilsbry, 1911:605, pl. 46a, fig. 8, pl. 47, figs. 1–7.

Description: Shell medium-sized to large, fragile, slightly inequilateral. Moderately inflated (average I H/SL = 82.3 ± 1.7; average Ci = 66.3 ± 4.2). Surface glossy, straw-yellowish, somewhat olivaceous, sometimes changing to grey violaceous. Interior bluish. Shell outline from subquadrangular, with no marked angles, to rounded-oval. Dorsal and ventral margins about equally curved. Anterior end slightly protruded, evenly curved or very slightly angled. Posterior end weakly truncated; ventral margin always uniformly curved. Shell outline of half-grown specimens tending to be more trapezoidal. Beak prosogyrous, median, wide, not full, with well-marked embryonic cap.

Hinge plate rather solid, hinge line arched, relatively long (hinge length is about 58% of shell length, ranging from 53% to 68%. Hinge: left valve, cardinal teeth delicate, outer cardinal (C_4) a slender lamella, somewhat oblique, inner one (C_2) short, acute, displaced forward with respect to C_4. Lateral teeth rather close to cardinals, slender, triangular and relatively short, cusps median to distal. Right valve: one low cardinal tooth (C_3), nearly straight, posteriorly thickened and sulcated, sometimes showing a median sinking separating anterior and posterior ends. Anterior lateral teeth low, slender. Inner lateral (A_I) slightly curved, with distal cusp; outer lateral (A_{III}) strongly reduced, low, displaced backward. Posterior laterals (P_I and P_{III}) low, nearly straight. Maximum divergence angle between lateral teeth: 130° (more frequent values were: 120°–130°). Ligament externally visible but not protruding. Ligamental pit relatively long and uniformly narrow, pointed at both ends (ligament length is about 20% of shell length).

Variability. Among different lots, the shell shape may be more or less subquadrangular. The shell height represents about 81–83% of the shell length, varying slightly according to the origin of the lots. The shell diameter shows greater dispersion in values and represents about 55–66% of shell height.

Remarks: *M. patagonicum* is similar to *M. argentinum,* from which it differs in having a smaller maximum size, less relative height, and larger diameter. The beak is not as full, and the shell outline is never markedly trapezoidal as in *M. argentinum*; the posterior margin is less abruptely truncate (especially in larger specimens), and the shell outline not sharp-cornered as is typical for *M. argentinum.* The hinge plate is always more solid than in *M. argentinum.* The divergence angle of lateral teeth is constantly lower than in *M. argentinum.* The upper margin and the hinge line are curved, never straight or a broken line as in *M. argentinum.* The morphometric ratios of both species are very close.

Type locality: Santa Cruz province: río Chico, 50 miles above the Sierra Oveja (today: cerro Las Ovejas, 48°46′S; 70°22′W), department of Río Chico (ANSP 88807).

Other localities: Santa Cruz province: many springs along the río Chico, 15, 25, 30, y 35 miles above the Sierra Oveja (Pilsbry, 1911) (ANSP 88808 and 88809 lots were studied); Las Horquetas, Rio Coyle (MLP 5056); Lago San Martín (MLP 5057); arroyo Chico, Rio Gallegos (MLP 5053); Calafate, Lago Argentino (MLP 5083). Chubut province: arroyo Nant y Fall, national Road 259 between Trevelin and the Andean cordilleran pass toward Futaleufú (MLP 5077); unnamed brook, national road 258, 13 km before Cholila (MLP 5079); unnamed brook 3 km from Trevelín at the road to Futaleufú Lake Dam, Esquel (MLP 5078). Neuquen province: Laguna Negra (975 m elevation) between Lago Hermoso and San Martín de los Andes, province of Neuquen (MLP 5080).

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LITERATURE CITED

BONETTO, A. A. & M. P. TASSARA. 1987. Contribución al conocimiento limnológico de moluscos pelecípodos en la cuenca del plata, con particular referencia a sus relaciones tróficas. Ecosur 14–15 (25–26):17–54.

CLESSIN, S. 1871. Zur Kenntnis unserer Pisidien. Malakozoologische Blatter p. 184.

CLESSIN, S. 1879. Die Familie der Cycladen. Martini & Chemnitz in Systematisches Conchylien Cabinet 9(3). 282 pp, 46 pls.

CARCELLES, A. & S. I. WILLIAMSON. 1951. Catálogo de los moluscos marinos de la Provincia Magallánica. Revista del Instituto de Investigaciones de las Ciencias Naturales, Zoología 2(5):225–383.

DALL, W. H. 1908. Report of the scientific results of the expedition "Albatross." Mollusca and Brachiopoda. Bulletin of the Museum of Comparative Zoology 43:205–487.

DELL, R. K. 1972. Notes on nomenclature of some Mollusca from Antarctica and southern South America. Records of the Dominion Museum 8(3):21–42.

D'ORBIGNY, A. D. 1835. Synopsis terrestrium et fluviatilium molluscorum, in suo per American meridionalem itinere, ab A. d'Orbigny, collectorum. Magasin de Zoologie 6(61–62): 1–44.

D'ORBIGNY, A. D. 1835–1847. Voyage dans l'Amerique méridionale. 5, part. 3, Mollusques. ed. P. Bertrand. Paris.

FERNÁNDEZ, L. & J. A. SCHNACK. 1977. Estudio preliminar de la meiofauna bentónica en tramos poluidos de los arroyos Rodriguez y Carnaval (provincia de Buenos Aires). Ecosur 4(8):103–115.

FIGUEIRAS, A. 1965. La malacofauna dulceacuícola del Uruguay. Parte II: Pelecypoda. Comunicaciones Sociedad Malacológica del Uruguay 1(8):223–270.

FORMICA CORSI, A. 1900. Moluscos de la República Oriental del Uruguay. Anales del Museo Nacional, Uruguay 2(15–17):1–237.

HOLOPAINEN, I. J. & J. G. J. KUIPER. 1982. Notes on the morphometry and anatomy of some *Pisidium* and *Sphaerium* species (Bivalvia, Sphaeriidae). Annales Zoologici Fennici 19:93–107.

ITUARTE, C. F. & S. GORDILLO. 1991. Nuevas citas de pelecípodos dulciacuícolas de Isla Gable, Tierra del Fuego, Argentina. Neotropica 37(97):29–30.

KUIPER, J. G. J. 1962. Note sur la systématique des Pisidies. Jounal de Conchyliologie 102(2):53–57.

KUIPER, J. G. J. 1983. The Sphaeriidae of Australia. Basteria 47:3–52.

KUIPER, J. G. J. 1991. De Atlantische verspreidingsbarrière, een niet-meetbare parameter in de systematiek der Sphaeriidae. Correspondentieblad van de Nederlandse Malacologische Vereniging 263:917–924.

LANDONI, N. A. 1992. Inventario de los moluscos de agua dulce de la Provincia de Buenos Aires. Situación ambiental de la Provincia de Buenos Aires. A. Recursos y rasgos naturales en la evaluación ambiental n°17, C.I.C. provincia Buenos Aires. 57 pp.

MANSUR, M. C., C. SCHULZ, M. G. OLIVEIRA DA SILVA & N. M. R. CAMPOS-VELHO. 1991. Moluscos Bivalves limnicos da estaçao ecológica do Taim e áreas adjacentes, Rio Grande, Brasil. Iheringia, Sér. Zoologica 71:43–58.

MEIER-BROOK, C. 1967. *Pisidium forense,* a new species from Brazil (Mollusca, Eulamellibranchiata, Sphaeriidae). Archiv für Hydrobiologie 64(1):63–68.

MELVILL, J. C. & R. STANDEN. 1907. The marine Mollusca of the Scottish National Antarctic Expedition. Transactions of the Royal Society of Edinburgh 46(5):119–157, 1 pl.

MELVILL, J. C. & R. STANDEN. 1914. Notes on Mollusca collected in the North West Falklands by Mr. Rupert Vallentin, F. L. S., with descriptions of six new species. Annals and Magazine of Natural History 8(13):109–136, 7 pla.

ODHNER, N. H. 1921. On somes species of *Pisidium* in the Swedish State Museum. Journal of Conchology 16(7):218–223.

OLAZARRI, J. 1983. *Biomphalaria tenagophila* (d'Orbigny, 1835) (Moll. Gastr.) en la zona de Salto Grande. IV. Fauna de posible relación con sus poblaciones. Comunicaciones de la Sociedad Malacológica del Uruguay 6(45):131–163.

PARODIZ, J. J. & L. HENNINGS. 1965. The *Neocorbicula* (Mollusca: Pelecypoda) of the Paraná-Uruguay basin. Annals of the Carnegie Museum 38(3):69–96.

PILSBRY, H. A. 1897. New species of mollusks from Uruguay. Proceedings of the Academy of Natural Sciences of Philadelphia, May 1897:290–298, 2 pla.

PILSBRY, H. A. 1911. Non-marine Mollusca of Patagonia. Reports of the Princeton University Expedition to Patagonia (1896–1899) 3(5):513–633.

PILSBRY, H. A. 1924. South American land and freshwater mollusks. Proceedings of the Academy of Natural Sciences of Philadelphia 76:49–66, 4 pla.

STROBEL, P. 1874. Materiali per una Malacostatica de terra e di acqua dolce dell' Argentina. Biblioteca malacologica, Vol. 4. Pisa.

The Veliger 39(3):204–212 (July 1, 1996)

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The Fossil Land Snail *Micrarionta* (*Micrarionta*) *intermedia* Pilsbry (Gastropoda: Pulmonata): Insular Phylogeny Revisited

by

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Abstract. The helminthoglyptid land snail *Micrarionta* (*Micrarionta*) *intermedia* Pilsbry, 1939, found on Santa Barbara Island, California, is an extinct taxon, specifically distinct from *Micrarionta* (*M.*) *facta* (Newcomb, 1864). A prior phylogenetic hypothesis for *Micrarionta* (*Micrarionta*) is re-evaluated on the basis of characters other than shell size. A small shell is homoplastic, independently originating two or three times. The present deployment of species on the various California Channel Islands can be accounted for by a vicariance model with a single dispersal event, over a time-span beginning < 950 ka before present. No autapomorphies of *M. intermedia* falsify the concept that it represents the ancestor from which other species of *Micrarionta* (*Micrarionta*) descended.

INTRODUCTION

In his revision of the helminthoglyptid genus *Micrarionta* Ancey, 1880, Pilsbry (1939) proposed the new taxon *Micrarionta facta* form *intermedia* from Santa Barbara Island, California, as follows:

> Typical *facta* seems to be abundant as a fossil, but there is also an extinct form which reached a larger size than any recent shells, though the smallest do not excel the largest of the living form. This is form *intermedia* Hemphill. . . . It usually has the umbilicus only half covered. One measures: height 9.5 mm., diameter 14.8 mm.; 6 whorls. Some examples have the lip rather wide (Pilsbry 1939:209).

The form was illustrated by a single basal view. The name is absent from Clench & Turner's (1962) list of names introduced by Pilsbry; the holotype (ANSP 86840a) was not mentioned in Baker's (1962) list of type specimens at the Academy of Natural Sciences, Philadelphia. Coan & Roth (1987) and Pearce (1990) treated *Micrarionta intermedia* as a distinct species. Almost everything written about *M. intermedia* has been based on type and other historical material that may have been selected by conchologists for uniform size or other features (cf. Coan & Roth, 1987: 322, regarding Henry Hemphill).

On Santa Barbara Island in 1974, I examined fossil occurrences of *Micrarionta intermedia* and living colonies of *Micrarionta facta* (Newcomb, 1864). The purpose of this paper is to record additional information about the morphology of these two taxa based on unbiased samples and to examine the basis on which the two are regarded as separate species.

Roth (1984) remarked on a pattern of pairs of large- and small-shelled species of *Micrarionta* on each of the California Channel Islands.[1] From cladistic analysis, Pearce (1990) concluded that larger-shelled species—*M. feralis* (Hemphill, 1901), *M. rufocincta* (Newcomb, 1864), *M. maxima* Pilsbry, 1939, and *M. intermedia*—constitute a clade distinct from smaller-shelled species—*M. facta, M. gabbi* (Newcomb, 1864), and *M. beatula* Cockerell, 1929. That assertion is re-examined here on the basis of non-linear-dimensional characters from Pearce's (1990) data set. An alternative phylogenetic hypothesis and biogeographic history are proposed.

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[1] The same observation was also contained in an earlier, unpublished report: Hochberg, F. G., 1979. Invertebrate zoology: land molluscs. Pp. 6.1–6.119 in D. M. Power (ed.), Natural Resources Study of the Channel Islands National Monument, California. Report submitted to National Park Service, Denver, Colorado, Contract No. CX-2000-8-0040.

Table 1

Phylogenetic taxonomy of the Helminthoglyptidae, after Roth (1996).

- Helminthoglyptidae
  - Sonorellamorpha
    - *Maricopella allynsmithi* (Gregg & Miller, 1969)
    - Sonorellales
      - *Myotophallus* Pilsbry, 1939
      - "*Sonorella binneyi* group"
      - *Sonorella* Pilsbry, 1900
        - *Sonoranax* Pilsbry, 1939 (*Sonorella granulatissima* group)
        - "*Sonorella, sensu stricto*"
  - Helminthoglyptamorpha
    - *Sonorelix* Berry, 1943
      - *Mohavelix micrometalleus* (Berry, 1930)
      - *Sonorelix, sensu stricto*
    - Helminthoglyptaina
      - *Micrarionta* Ancey, 1880
        - *Nicolenea* Roth, 1996
        - *Micrarionta, sensu stricto*
      - Helminthoglyptotes
        - Chamaeariontales
          - *Chamaearionta aquaealbae* (Berry, 1992)
          - *Herpeteros* Berry, 1947
        - Xerariontales
          - *Greggelix* Miller, 1972
            - *Martirelix* Miller, 1982
            - "*Greggelix, sensu stricto*"
          - *Xerarionta* Pilsbry, 1913
            - *Xerarionta, sensu stricto*
            - "*Plesarionta*"
        - Helminthoglyptales
          - Eremariontaphim
            - *Cahuillus* Roth, 1996
            - *Eremarionta* Pilsbry, 1913
              - *Eremariontoides argus* (Edson, 1912)
              - *Eremarionta, sensu stricto*
          - Helminthoglyptaphim
            - *Noyo intersessa* (Roth, 1987)
            - Helminthoglyptaniki
              - *Rothelix* Miller, 1985
              - *Helminthoglypta* Ancey, 1887
                - *Helminthoglypta, sensu stricto*
                - *Coyote* Reeder & Roth, 1988
                - "*Charodotes*" Pilsbry, 1939

The systematics follows the rank-free, phylogeny-based taxonomy of Roth (1996), reprinted here for ready reference (Table 1). Abbreviations are as follows: ANSP, Academy of Natural Sciences, Philadelphia; BR, author's locality register, San Francisco, California; CAS, California Academy of Sciences; ka, years × 10^3. Abbreviations for the taxa of *Micrarionta* are defined in the legend of Table 2.

SYSTEMATICS

HELMINTHOGLYPTIDAE Pilsbry, 1939

Helminthoglyptamorpha

Table 2

Distribution of character states among *Micrarionta* (*Nicolenea*) and species of *Micrarionta* (*Micrarionta*). For definitions of character states see Appendix. Taxon abbreviations: NIC, *Nicolenea*; BEA, *M. beatula*; FAC, *M. facta*; FER, *M. feralis*; GAB, *M. gabbi*; INT, *M. intermedia*; MAX, *M. maxima*; RUF, *M. rufocincta*. 0 = plesiomorphic state; 1 = apomorphic state.

	Taxon							
Character	NIC	BEA	FAC	FER	GAB	INT	MAX	RUF
Non-dimensional								
ApAreaRel	0	0	0	0	1	0	0	0
ApHtFrRel-1	0	0	1	1	0	0	0	0
ApHtRel	0	1	1	1	0	0	0	0
ApShape	0	1	1	0, 1	1	0	1	1
HeightRel	0	0	0	0	1	0	0	0
LipBotWidProp	0	1	1	1	0	0	0	1
LipBotWidRel	0	1	1	1	1	1	1	0
LipConvex	0	1	1	1	1	0	1	1
LipTopRecurv	0	1	0	0	1	0	1	1
TranslRate	0	1	0	0, 1	0	1	1	1
Umbilicate	0	0, 1	0	1	0	0	0	0
Varices	0	1	0	1	0	0	0	1
Whorls-1	0	0	1	1	0	1	1	1
Whorls-2	0	0	0	1	0	0	0	1
Dimensional								
DiamWh4	0, 1	1	1	0	1	0	0	0

Helminthoglyptaina

Micrarionta Ancey, 1880

Type species: *Helix facta* Newcomb, 1864.

(*Micrarionta, sensu stricto*)

Micrarionta (*Micrarionta*) *intermedia* Pilsbry, 1939, *ex* Hemphill MS

(Figure 1)

Helix var. *feralis* Hemphill, 1901:121, in part (specimens from Santa Barbara Island); *non Micrarionta feralis* (Hemphill, 1901).

Micrarionta facta form *intermedia* Hemphill, Pilsbry, 1939: 209, fig. 104e.

Micrarionta intermedia Pilsbry, Coan & Roth, 1987:330.—Pearce, 1990:5, 7, 15, 16, 26, 30–33.

Type material: Holotype: ANSP 86840a. Paratype: ANSP 86840. Pilsbry's (1939) dimensions of the holotype include the expanded apertural lip; exclusive of the lip, the holotype measures 14.0 mm in diameter and 8.4 mm in height. The base is tumid and the umbilicus is slightly less than half covered by the inner lip. With the holotype is a

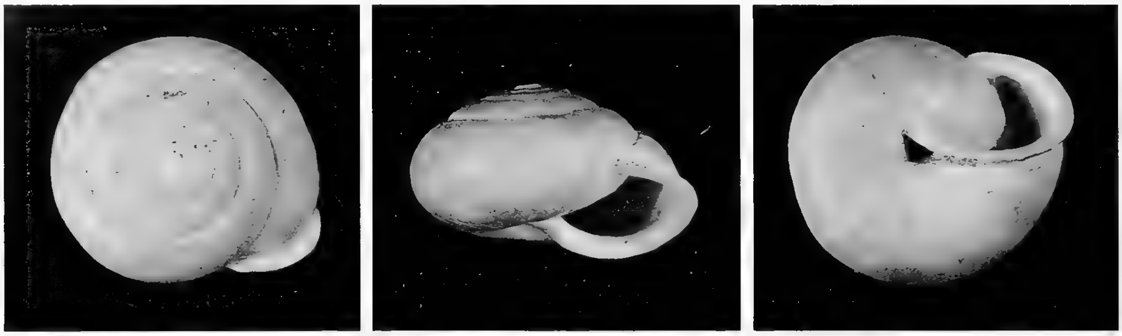

Figure 1

Micrarionta (*Micrarionta*) *intermedia* Pilsbry. Holotype, ANSP 86840a; top, lateral, and basal views. Diameter exclusive of outer lip 14.0 mm.

printed label typical of those used by Henry Hemphill around the turn of the century: "Helix ruficincta, Newc./Var. intermedia, Hemph./Santa Barbara Island. California./Collected by Henry Hemphill."

Other historical material: Six other ANSP lots of two specimens each (ANSP 10790, 86824, 86825, 86831, 86832, 86841), collected by Hemphill on Santa Barbara Island, are also *M. intermedia.* Four lots from San Clemente Island, labeled *intermedia* by Hemphill (ANSP 86638, ANSP 86639, ANSP 86641, ANSP 86642); lots are strongly spirally striate and differ in umbilical characters; they represent a different taxon or taxa. Coan & Roth (1987) listed the first three (ANSP 86638, ANSP 86639, and ANSP 86641) as paratypes of *M. intermedia.*

CAS 105974 is a lot of 201 specimens collected by Hemphill on Santa Barbara Island. It is presumably his dealer's stock, from which the preceding lots of *M. intermedia* were selected.

MICRARIONTA ON SANTA BARBARA ISLAND

Santa Barbara Island consists mainly of volcanic rocks with interbedded marine sediments. Terrace deposits of Quaternary age are widespread (Lipps et al., 1968) and contain marine and nonmarine molluscan fossils. Sandy alluvium mantles much of the island and in places contains abundant land snail shells. Samples were collected at two localities:

BR 462. Whitish (caliche-cemented?) beds on east side of Signal Peak, elevation 160–168 m. Lipps et al. (1968) considered this deposit of nonmarine origin and probable Pleistocene age, with provenance a former high area to the west of the present shoreline. The most abundant mollusk in this deposit is a form of *Xerarionta tryoni* (Newcomb, 1864) differing morphometrically from Recent populations of that species (Roth, unpublished data). Shells of *X. tryoni* and *Micrarionta* weather out readily.

BR 475. Alluvial fill in the bottom of a north-northwest-trending canyon, informally known as Cat Canyon, at the southern end of the island, elevation ~60 m. Two distinct strata of alluvium are exposed in a runoff gully down the center of the fill. The upper stratum is friable, light tan, sandy, and unconsolidated, 0.6–1.5 m thick. It is truncated above by the present soil surface and conformably overlies the lower stratum, which is less friable, darker tan, sandy to silty, and more than 1.2 m thick (base not exposed). It is apparent from the local drainage pattern that shells in the alluvium are potentially a chronologic mixture of empty shells from snail populations inhabiting the local land surface and reworked fossils transported downslope from deposits such as the beds at locality BR 462.

Lipps et al. (1968) reported *Micrarionta* (*Nicolenea*) *sodalis* (Hemphill, 1901) from a marine deposit of probable Sangamon age on the 25–30 ft (40–48 m) terrace. That species is otherwise known only as a fossil on San Nicolas Island. The record is based on one specimen (University of California at Davis, Museum of Geology), 11.2 × 6.4 mm with spire slightly crushed and 4.85 whorls. Pearce (1990) allocated the specimen to *Micrarionta intermedia* based on discriminant function analysis.

Micrarionta facta lives gregariously under stones and in crevices in the top few cm of soil in the small, rocky canyons that cut the terraces of the island. It is sympatric with *Xerarionta tryoni, Haplotrema duranti* (Newcomb, 1864), and *Binneya notabilis* Cooper, 1863. I found no living specimens resembling *Micrarionta intermedia* in this setting. Deer mice (*Peromyscus maniculatus elusus*) prey on *M. facta,* leaving the shells with the spires cracked away in "mouse middens." I found no *M. intermedia* in any of these accumulations.

MORPHOMETRIC ANALYSIS

On 148 fossil and living specimens of Santa Barbara Island *Micrarionta,* from nine well-localized lots, the following measurements were taken: maximum diameter (exclusive of the expanded outer lip (D); height parallel to the axis of coiling (H); and number of whorls, counted by the method of Pilsbry (1939:xi, fig. B). Relative height of shell (H/D) and a measure of overall size, height plus diameter (H + D), were calculated. Ranges, means, and standard

Table 3

Shell dimensions (in mm) and ratios in fossil and living *Micrarionta* from Santa Barbara Island. Statistics are range, with mean ± one SD in parentheses. Only adult shells included.

Provenance	n	D	H	W	H/D	H+D
Living	92	8.8 − 10.9 (9.71 ± 0.45)	5.5 − 7.5 (6.30 ± 0.40)	4.4 − 5.9 (5.36 ± 0.21)	0.589 − 0.756 (0.650 ± 0.036)	14.5 ± 18.4 (16.01 ± 0.74)
Fossil	56	8.0 − 14.2 (12.02 ± 1.43)	4.8 − 9.5 (7.60 ± 0.91)	5.0 − 6.2 (5.56 ± 0.24)	0.542 − 0.743 (0.633 ± 0.034)	12.8 − 23.6 (19.62 ± 2.29)

deviations of these variables were calculated for fossil and living material (Table 3). The same measurements and calculations were performed on the holotype and paratype of *M. intermedia.* The complete data are archived at ucmp1.berkeley.edu as file /pub/mollusca/veliger/intermed. The variation was examined by principal components analysis using the program SYSTAT (Systat, Inc., 1992).

Four principal components were computed; the first three cumulatively account for more than 99% of the total variance (63.082%, 26.996%, and 9.896% respectively). Table 4 shows loadings of the entered variables. The first principal component is largely an expression of size, and to a lesser extent of whorl number; a high score on this factor indicates a large shell with a high whorl count. The second principal component expresses mainly relative height; a high score indicates a shell that is high in proportion to diameter. Diameter loads negatively on this factor. Figure 2 plots the scores of measured specimens on the first two principal components. Fossil and living *Micrarionta* are well discriminated. Although individual fossil shells extend into the field occupied by living specimens, there is a large field of specimens tending to score high on component 1 and low on component 2 that consists entirely of fossils. The holotype and paratype of *M. intermedia* plot within this field.

Discussion: The morphometric analysis indicates two morphologically distinct entities, *Micrarionta intermedia* and *M. facta.* There is no stratigraphic evidence that the two lived synchronously. The only fossil deposit containing shells of both taxa probably represents a chronologic mixture of reworked *M. intermedia* and younger *M. facta.*

Table 4

Factor loadings of variables and eigenvalues of factors in principal components analysis of shells of *Micrarionta* from Santa Barbara Island.

Variable	Factor 1	Factor 2	Factor 3	Factor 4
D	0.956	−0.195	0.217	0.023
H	0.944	0.206	0.257	−0.022
W	0.837	0.143	−0.528	0.000
H/D	−0.129	0.989	0.066	0.009
Eigenvalue	2.523	1.080	0.396	0.001

Size alone would not be a sound basis for taxonomic separation of *Micrarionta intermedia* and *M. facta.* Equal or greater intraspecific size differences exist among other helminthoglyptid snails, for example: *Helminthoglypta reediana* Willett, 1932, diameter 15.5–27.8 mm; *Helminthoglypta cypreophila* (Binney & Bland, 1869), diameter 22.8–42.6 mm; *Eremarionta rowelli* (Newcomb, 1865), diameter 11.4–17.0 mm; *Sonorelix borregoensis* (Berry, 1929), diameter 16.9–23.5 mm (Roth, unpublished data). Goodfriend (1986) reviewed environmental influences on shell size within species, including moisture, temperature and insolation, calcium carbonate content of the substrate, and population density. Any of these could be argued (and tested) as having an effect on size in *Micrarionta.*

Taxonomic separation of *Micrarionta intermedia* and *M. facta* is supported by the following non-dimensional char-

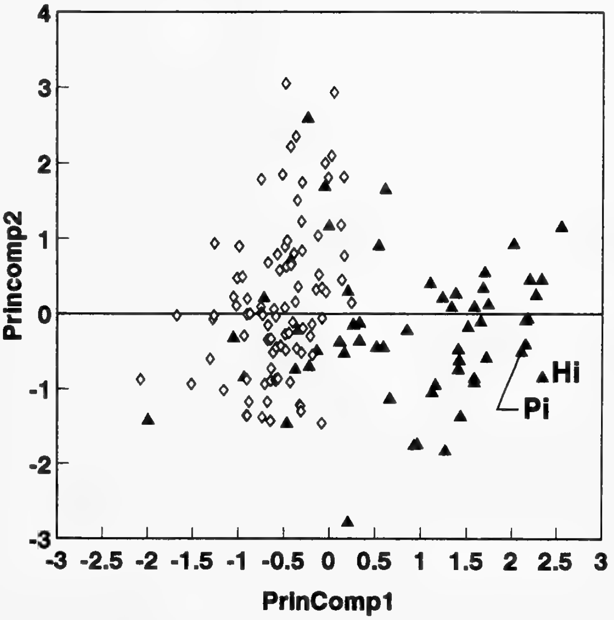

Figure 2

Plot of scores on first two principal components of 148 adult specimens of fossil and living *Micrarionta* from Santa Barbara Island. Open diamonds, living; solid triangles, fossil. Hi, holotype, and Pi, paratype, of *M. intermedia.*

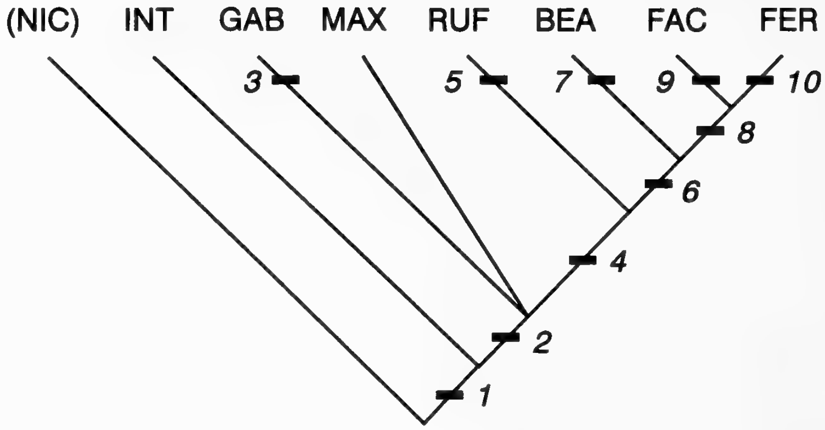

Figure 3

Phylogenetic hypothesis for *Micrarionta* (*Nicolenea*) and the species of *Micrarionta* (*Micrarionta*). Taxon abbreviations as in Table 2. Apomorphies identified by number, as follows (r = reversal; h = homoplasy): 1, LipBotWidRel, TranslRate, Whorls-1; 2, ApShape, LipConvex, LipTopRecurv; 3, ApAreaRel, HeightRel, TranslRate (r,h), Whorls-1 (r,h); 4, LipBotWidProp, Varices; 5, LipBotWidRel (r), Whorls-2 (h); 6, ApHtRel; 7, Umbilicate (h), Whorls-1 (r,h); 8, ApHtFrRel-1, LipTopRecurv (r), TranslRate (r,h); 9, Varices (r); 10, ApShape (partial r), TranslRate (partial r,h), Umbilicate (h), Whorls-2 (h).

acters from the Pearce (1990) analysis (see Appendix): aperture height in front view relative to shell height (ApHtFrRel-1), <0.38 in *M. facta,* >0.38 in *M. intermedia*; aperture height in the plane of the peristome relative to shell height (ApHtRel), <0.65 in *M. facta,* >0.65 in *M. intermedia*; aperture shape calculated as aperture height divided by aperture width (ApShape), <0.98 in *M. facta,* >0.98 in *M. intermedia*; lip bottom width relative to lip widths at top and side of aperture (LipBotWidProp), >0.35 in *M. facta,* <0.35 in *M. intermedia*; lip face convex (LipConvex) in >30% of shells in *M. facta,* <30% in *M. intermedia*; translation rate (TranslRate) <0.05 in *M. facta,* >0.05 in *M. intermedia.*

The place of these characters in evaluating the phylogenetic relations between *Micrarionta intermedia* and *M. facta* is discussed in the next section.

PHYLOGENY OF THE SPECIES OF *MICRARIONTA* (*MICRARIONTA*)

Pearce (1990:15) stated, on the basis of cladistic analysis, that the smaller and larger species of *Micrarionta* are separate clades; he suggested separate colonizations of each island where large and small species co-occur. However, the Pearce data set is heavily weighted toward shell size. Nineteen (38.8%) of the 49 characters in his analysis are raw linear measurements of shell size, introducing an element of circularity into the argument.

I performed maximum-parsimony phylogenetic analysis of the taxa of the clade from Pearce's (1990:fig. 7) consensus tree that represents *Micrarionta* (*Micrarionta*) (i.e., excluding the three taxa assigned by Roth (1996) to the subgenus *Nicolenea,* and "*Micrarionta*" *guadalupiana* Pilsbry & Vanatta, 1898), using the characters from Pearce's data set that are not linear shell dimensions and not uniform throughout the clade (Table 2). I used the implicit enumeration algorithm of HENNIG86 (Farris, 1988) with the branch-breaking and successive approximations weighting procedures. Roth's (1996) phylogenetic analysis of the taxa of Helminthoglyptidae agrees with that of Pearce (1990) in accepting *Micrarionta* as a holophyletic group. Character-state transformations were polarized by the method of outgroup comparison (Watrous & Wheeler, 1981; Brooks & McLennan, 1991), using *Micrarionta* (*Nicolenea*) as the outgroup.

A single minimum length cladogram was generated (Figure 3) and is presented as the preferred phylogenetic hypothesis for the species of *Micrarionta* (*Micrarionta*). Weighted by the successive approximations method, the tree is 90 steps in length, with consistency index 0.94 and retention index (Farris, 1989) 0.94. With each character's weight set at unity, this tree is 22 steps in length, with consistency index 0.63 and retention index 0.57. By comparison, HENNIG86 evaluates the Pearce (1990) tree for the same character/taxon matrix (character weights set at unity)—(NIC, ((GAB, (BEA, FAC)), (INT, MAX, (FER, RUF))))—as 26 steps in length, with consistency index 0.53 and retention index 0.36.

Because this phylogenetic hypothesis is based solely on shell characters, I regard it as tentative. In the future it should be tested by the addition of anatomic characters from the living species. A further limitation is that Pearce's (1990) data on *Micrarionta* (*Micrarionta*) are based on relatively few specimens (mostly $n \approx 20$ per species). In some cases they are from older museum lots that may have been selected for size or other featues by their collectors.

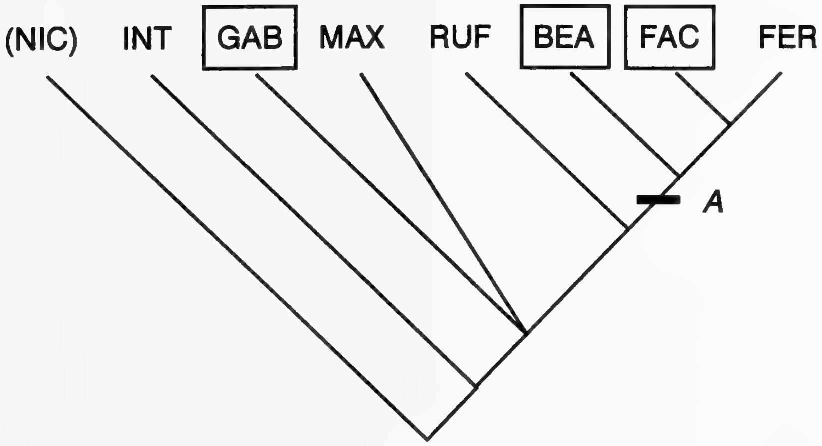

Figure 4

Small shell size mapped (boxes) on cladogram for *Micrarionta*. Abbreviations as in Table 2. A = alternative site of apomorphy in DiamWh4; see text.

Use of unbiased population samples would further test this hypothesis.

Small shell size is regarded as a derived state in *Micrarionta,* based on outgroup comparison with the rest of the Helminthoglyptaina. In the phylogenetic hypothesis for *Micrarionta* (*Micrarionta*), a small shell—expressed as suture-to-suture diameter at whorl 4 of less than 6.6 mm (Pearce's [1990] character DiamWh4, a synapomorphy of his "small" group of *Micrarionta*)—is homoplastic (Figure 4). It may have arisen twice (in *M. gabbi* and at A in Figure 4), with a reversal in *M. feralis*; or three times, once each in *M. gabbi, M. facta,* and *M. beatula.* The number of transformations (three) is the same in both scenarios. DiamWh4 <6.6 mm in *Micrarionta* (*Nicolenea*) *opuntia* Roth, 1975, is homoplastic with DiamWh4 <6.6 mm in *M.* (*Micrarionta*) in any case.

When the species of *Micrarionta* are sorted by size (Figure 5), it is apparent that there is no sharp discontinuity between "large" and "small" shells. Roth's (1984) observation about large and small pairs was correct in the sense that where two species occur on an island, one is a member of the upper and one a member of the lower half of the continuum. In Roth's (1996) phylogenetic hypothesis for the taxa of Helminthoglyptidae, the sister group of *Micrarionta* is Helminthoglyptotes. Most species of Helminthoglyptotes are larger-shelled than the largest *Micrarionta.* At the next more inclusive level, Helminthoglyptaina (i.e., *Micrarionta* plus Helminthoglyptotes) is the sister group of *Sonorelix.* Two of the three component clades of Helminthoglyptotes and the clade *Sonorelix* contain diminutive members—*Eremariontoides argus* in Helminthoglyptales, *Chamaearionta aquaealbae* in Chamaeariontales, *Mohavelix micrometalleus* in *Sonorelix*—but these are special cases of neoteny (Roth, 1996). The plesiomorphic character state in each clade is a larger shell. Size reduction is therefore a characteristic trend of the entire *Micrarionta* clade. The choice of coding one gap rather than another as apomorphic is arbitrary.

In Figure 6, contours based on the phylogenetic hypothesis are plotted on a map of the California Channel Islands. Successively more inclusive contours represent successively more inclusive clades. From this map it is evident that the present deployment of species by island could have come about almost entirely through successive episodes of vicariance within an originally pan-insular species. Only one dispersal event, of the common ancestor

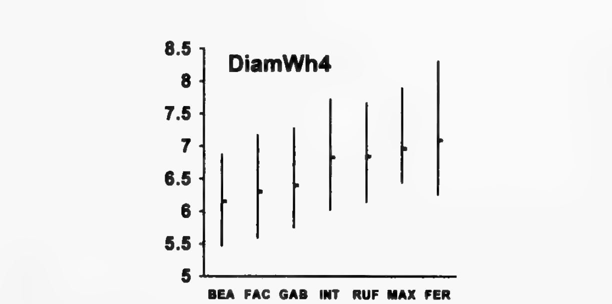

Figure 5

Maxima, minima, and means for Diameter, Height, and DiamWh4 of the species of *Micrarionta* (*Micrarionta*); data from Pearce (1990). Abbreviations as in Table 1.

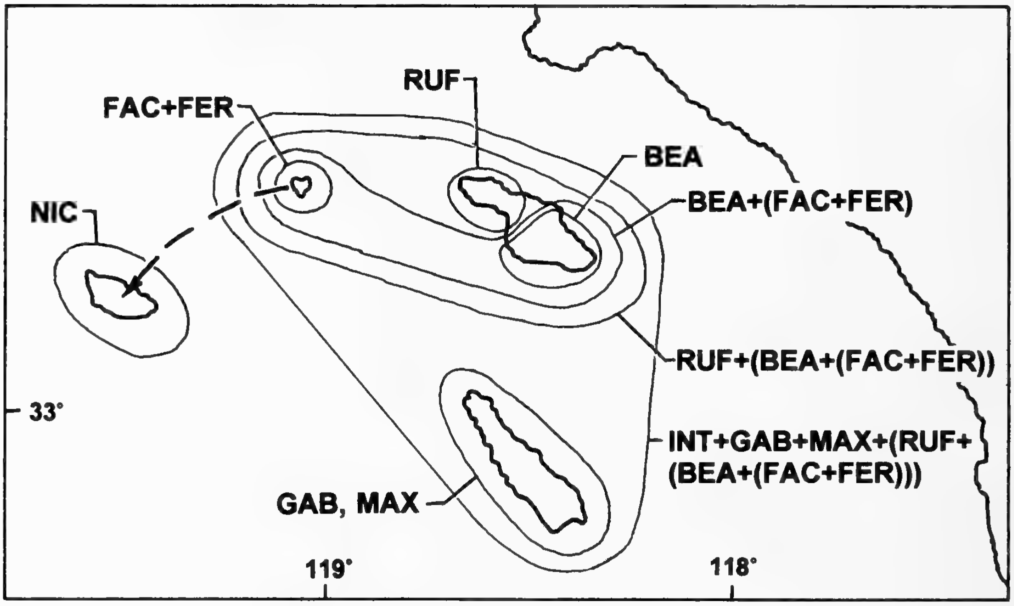

Figure 6

Phylogenetic hypothesis for *Micrarionta* mapped on California Channel Islands. Contours surround ranges of progressively more inclusive holophyletic groups of taxa from minimum length cladogram of Figure 3. Abbreviations as in Table 2. Dashed line represents dispersal of common ancestor of *M. facta* and *M. feralis* from Santa Barbara Island to San Nicolas Island.

of *Micrarionta feralis* and *M. facta* from Santa Barbara Island to San Nicolas Island, is necessary. Outgroup comparison with *M. beatula* establishes the eastern islands (i.e., not San Nicolas) as the plesiotypic distribution of the clade (FER, FAC).

Marine terrace dating and estimates of rates of tectonic uplift provide a time framework for the events of this evolutionary/biogeographic scenario and support the hypothesized order of events. Age estimates based on amino acid racemization for marine terrace 10 at 238 m elevation on San Nicolas Island range from ≥600 ka (Muhs, 1985) to 700 ± 100 ka (Lajoie et al., 1980). A 530 ± 60 ka age from uranium-trend dating is regarded as problematic and too low (Muhs et al. 1989). Calculations based on the 0.2–0.3 m/ka uplift rate suggested for San Nicolas Island by Muhs (1985) give age estimates of 920–1380 ka for the summit of the island (Pearce 1993). Pearce (1993), extrapolating from correlation between terrace heights and the Pleistocene sea level curve of Shackleton & Opdyke (1973), inferred that the highest terrace (14) on San Nicolas Island was carved about 950 ka before present. Only since that time has the island been continuously subaerial and available for colonization by the ancestor of *Micrarionta* (*Nicolenea*).

The oldest fossil occurrence of *Micrarionta feralis* is in terrestrial sediments on San Nicolas Island overlying terrace 2 at 23–33 m elevation [correlating with marine oxygen isotope stage 5e of Shackleton & Opdyke (1973) and radiometrically estimated at approximately 120 ka (Valentine & Veeh, 1969; Szabo & Vedder, 1971; Muhs et al., 1987, 1988, 1989)] and below a stratum radiocarbon dated at ca. 18 ka (Pearce, 1990; 1993). It is present in younger sediments at numerous localities (Pearce, 1993; T. A. Pearce and Roth, unpublished data). This is consistent with the origin of *M. feralis* higher on the consensus tree, i.e., later in time than the dichotomy between *M.* (*Nicolenea*) and *M.* (*Micrarionta*).

Micrarionta (*Micrarionta*) *feralis* and *M.* (*Nicolenea*) *opuntia* are the only two species of *Micrarionta* known to live microsympatrically. Timothy A. Pearce, F. G. Hochberg (personal communication), and I have observed them under the same stems of *Opuntia* cactus on San Nicolas Island. More than six nodes separate the two taxa in the present phylogenetic hypothesis. In contrast, the more closely related *Micrarionta* (*Micrarionta*) *beatula* and *M.* (*M.*) *rufocincta* are allopatric on Santa Catalina Island. They occur within 350 m of each other in Ben Weston Canyon (Pearce, 1990; Roth, personal observation) but have not yet been found together. The field relations of *Micrarionta gabbi* and *M. maxima* are not known. On San Clemente Island in 1974, I observed only *M. gabbi* living. *Micrarionta maxima* is reported to be extant; the holotype (ANSP 86616a) apparently is a Recent shell, but whether characteristic of a living taxon or merely selected by the collector Hemphill from the large end of his material of *M. gabbi* is not known. Some published records of *M. maxima* (e.g., Kanakoff, 1950) pertain to fossil material, not yet evaluated in terms of the characters discussed here.

No autapomorphies in the present data set distinguish *M. maxima*; its branch is zero steps in length.

Similarly, no autapomorphies in the present data set lift *Micrarionta intermedia* off the branch segment leading to all other *Micrarionta* (*Micrarionta*) species—in other words, no autapomorphies of *M. intermedia* falsify the concept that it represents the ancestor from which other species of *Micrarionta* (*Micrarionta*) descended. This observation leads to the prediction that fossil shells from other islands, deposited contemporaneously with Santa Barbara Island *M. intermedia,* may be found to be conspecific with it when examined in detail.

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LITERATURE CITED

BAKER, H. B. 1962. Type land snails in the Academy of Natural Sciences of Philadelphia. I. North America, north of Mexico. Proceedings of the Academy of Natural Sciences of Philadelphia 114(1):1–21.

BROOKS, D. R. & D. A. MCLENNAN. 1991. Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology. University of Chicago Press: Chicago. 434 pp.

CLENCH, W. J. & R. D. TURNER. 1962. New Names Introduced by H. A. Pilsbry in the Mollusca and Crustacea. Academy of Natural Sciences of Philadelphia Special Publication 4. 218 pp.

COAN, E. V. & B. ROTH. 1987. The malacological taxa of Henry Hemphill. The Veliger 29(3):322–339.

FARRIS, J. S. 1988. HENNIG86, Version 1.5. Computer program distributed by author. Port Jefferson Station, New York.

FARRIS, J. S. 1989. The retention index and the rescaled consistency index. Cladistics 5:417–419.

GOODFRIEND, G. A. 1986. Variations in land-snail shell form and size and its causes: a review. Systematic Zoology 35(2): 204–223.

HEMPHILL, H. 1901. A contribution to west coast conchology. The Nautilus 14(11):121–125; (12):136–140, pl. 1.

KANAKOFF, G. P. 1950. Contributions from the Los Angeles County Museum-Channel Islands Biological Survey, No. 34. Some observations on the land snails of San Clemente Island. Bulletin of the Southern California Academy of Sciences 49(3):79–89.

LAJOIE, K. R., J. F. WEHMILLER & G. L. KENNEDY. 1980. Inter- and intrageneric trends in apparent racemization kinetics of amino acids in Quaternary mollusks. Pp. 305–340 in P. E. Hare, T. C. Hoering, & K. Kinds (eds.), Biogeochemistry of Amino Acids. John Wiley & Sons: New York.

LIPPS, J. H., J. W. VALENTINE & E. MITCHELL. 1968. Pleistocene paleoecology and biostratigraphy, Santa Barbara Island, California. Journal of Paleontology 42(2):291–307.

MUHS, D. R. 1985. Amino acid age estimates of marine terraces and sea levels on San Nicolas Island, California. Geology 13(1):58–61.

MUHS, D. R., G. L. KENNEDY & G. H. MILLER. 1987. New uranium-series ages of marine terraces and late Quaternary sea level history, San Nicolas Island, CA. Geological Society of America Abstracts with Programs 19:780–781.

MUHS, D. R., G. L. KENNEDY & T. K. ROCKWELL. 1988. Uranium-series ages of corals from marine terraces, Pacific coast of North America: implications for the timing and magnitude of late Pleistocene sea level changes. American Quaternary Association Program and Abstracts of the Tenth Biennial Meeting: 140.

MUHS, D. R., J. N. ROSHOLT & C. A. BUSH. 1989. The uranium-trend dating method: principles and application for southern California marine terrace deposits. Quaternary International 1:19–34.

PEARCE, T. A. 1990. Phylogenetic relationships of *Micrarionta* (Gastropoda: Pulmonata) and distinctness of the species on San Nicolas Island, California. Malacological Review 23:1–37.

PEARCE, T. A. 1993. *Micrarionta* (Gastropoda: Pulmonata) on San Nicolas Island, California. Evolutionary relationships among the species. Malacological Review 26:15–50.

PILSBRY, H. A. 1939. Land Mollusca of North America (north of Mexico). Academy of Natural Sciences of Philadelphia Monograph 3, 1(1):i–xvii, 1–573, i–ix.

RAUP, D. M. 1966. Geometric analysis of shell coiling: general problems. Journal of Paleontology 40(5):1178–1190.

ROTH, B. 1984. Ecology and evolutionary history of land snails on San Nicolas Island. Pp. 98–101 in Third Biennial Mugu Lagoon/San Nicolas Island Ecological Research Symposium. Pacific Missile Test Center. Point Mugu, California.

ROTH, B. 1987. Structure of internal varices in the shell of *Micrarionta rufocincta* and other Helminthoglyptidae (Gastropoda: Pulmonata). Bulletin of the Southern California Academy of Sciences 86(3):145–152.

ROTH, B. 1996. Homoplastic loss of dart apparatus, phylogeny of the genera, and a phylogenetic taxonomy of the Helminthoglyptidae (Gastropoda:Pulmonata). The Veliger 39(1): 18–42.

SHACKLETON, N. J. & N. D. OPDYKE. 1973. Oxygen isotope and paleomagnetic stratigraphy of equatorial Pacific core V28-238: oxygen isotope temperatures and ice volumes on a 10^5 year and 10^6 year time scale. Quaternary Research 3:39–55.

SYSTAT, INC. 1992. SYSTAT for Windows, Version 5. Evanston, Illinois.

SZABO, B. J. & J. G. VEDDER. 1971. Uranium series dating of some Pleistocene marine deposits in southern California. Earth and Planetary Science Letters 11:283–290.

VALENTINE, J. W. & H. H. VEEH. 1969. Radiometric ages of Pleistocene terraces from San Nicolas Island, California. Geological Society of America Bulletin 80:1415–1418.

WATROUS, L. E. & Q. D. WHEELER. 1981. The out-group comparison method of character analysis. Systematic Zoology 30(1):1–11.

APPENDIX: CHARACTERS AND CHARACTER STATES

The following descriptions of characters are taken (slightly modified) from Pearce (1990:27–28). Author's comments in brackets.

ApAreaRel: relative aperture area, calculated by dividing the square root of the aperture area by shell diameter; character state <0.38 scored as apomorphic.

ApHtFrRel-1: relative aperture height in front view, calculated relative to shell height. Aperture height measurement is inside dimension, excluding thickness of the lip; character state <0.38 scored as apomorphic.

ApHtRel: relative aperture height, calculated relative to shell height; character state <0.65 scored as apomorphic. [Probably some redundancy with ApHtFrRel-1.]

ApShape: aperture shape calculated as aperture height divided by aperture width; character state <0.98 scored as apomorphic.

DiamWh4: diameter from suture to suture at whorl 4.0; character state <6.6 mm scored as apomorphic.

HeightRel: relative height, calculated as ratio of height to diameter; character state <0.65 scored as apomorphic.

LipBotWidProp: lip bottom width proportion, calculated relative to lip widths at top and side of aperture; character state >0.35 scored as apomorphic.

LipBotWidRel: relative lip width at bottom of aperture, calculated relative to shell diameter; character state >0.077 scored as apomorphic. [Probably some redundancy with LipBotWidProp.]

LipConvex: whether face of lip is convex or flattened; scored as apomorphic if $>30\%$ of shells have convex lip faces.

LipTopRecurv: whether top part of lip is recurved; scored as apomorphic if $>5\%$ of shells have recurved top lips. [Questionable whether samples of ≈ 20 are adequate to resolve character state at 5% level in a species.]

TranslRate: Raup's (1966) translation rate; character state >0.05 scored as apomorphic.

Umbilicate: whether shell has open umbilicus or not; not umbilicate scored as apomorphic.

Varices: whether shell has internal varices or not; varices present scored as apomorphic. [In *Micrarionta beatula* (scored as having varices) varices are present in 23 of a sample of 261 shells (Roth, 1987). Random draws of 20 shells from a pool with this composition will show no varices with a probability between 0.25 and 0.50 ($\chi^2 = 0.926$). Larger sample sizes are needed for reliable scoring.]

Whorls-1: number of whorls, counted by the method of Pilsbry (1939:xi); >5.3 whorls scored as apomorphic.

Whorls-2: as Whorls-1, >5.7 whorls scored as apomorphic.

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Additional Data on Morphology and Geographic Distribution of *Adontorhina cyclia* Berry, 1947 (Bivalvia: Thyasiridae), Newly Reported from the Northwestern Pacific

by

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Abstract. The Asian species *Axinopsida filatovae* (Ivanova & Moskaletz, 1984), originally described as *Genaxinus filatovae* from the Sea of Japan (depth 74 m, Bolshoi Pelis Island, Peter the Great Bay), is a synonym of *Adontorhina cyclia* Berry, 1947, previously reported only on the Pacific coast of North America. The results of a comparative analysis and an additional description of *A. cyclia* are presented.

INTRODUCTION

In 1972–1973 large numbers of samples of the shelf macrobenthos of the Commander Islands (Figure 1) were taken by joint expeditions of the Institute of Marine Biology (IMB) and the Pacific Research Institute of Fisheries and Oceanography (PRIFO) in order to investigate the composition and structure of bottom communities. During the examination of the bivalves, a species was found similar to *Adontorhina cyclia* Berry, 1947, which is widely distributed off the Pacific coast of North America and previously not recorded in the fauna of the northwestern Pacific (Scott, 1986; Kamenev, 1995).

Subsequent, more detailed studies showed that the species found on the shelf of the Commander Islands is also similar to *Axinopsida filatovae* (Ivanova & Moskaletz, 1984), described as *Genaxinus filatovae* from the Sea of Japan (Ivanova & Moskaletz, 1984); (Figure 1). The genus *Genaxinus* was designated by Iredale (1930). Its type species is *Thyasira albigena* Hedley, 1907, which Hedley (1907) presumably included in the subgenus *Axinulus.* The Recent representatives of the genus *Genaxinus,* however, inhabit the coastal zone of Australia and New Zealand (Hedley, 1907; Fleming, 1950; Powell, 1979), and the allocation of the new species from the Sea of Japan to this genus was an extraordinary fact. It attracted the attention of other Russian malacologists, and after additional studies, it was placed by Scarlato & Kafanov (1988) in the genus *Axinopsida.*

A comparative analysis of morphology and inner shell structure of *A. filatovae* from the Sea of Japan and the species from the shelf of the Commander Islands has shown that they are identical. Comparison of this species with the descriptions, drawings, and photographs of *A. cyclia* (Berry, 1947; Jones & Thompson, 1986; Scott, 1986) and some species of the genus *Genaxinus* (Hedley, 1907; Fleming, 1950; Powell, 1979) has shown that it is conspecific with *A. cyclia.*

In this paper, the results of the comparative analysis and additional data on the shell morphology, ecology, and geographic distribution of *A. cyclia* are presented. This species is new for the fauna of the northwestern Pacific and Russia.

MATERIALS AND METHODS

In this study, type material (holotype No. 1/31328 and paratypes No. 2/31329 [60 specimens] of *G. filatovae* Ivanova & Moskaletz, 1984), and material of *A. filatovae* obtained by the expeditions of PRIFO (1970) and IMB (1977, 1980–1981) in the Sea of Japan, as well as lots of bivalves from the shelf of the Commander Islands gathered by two joint hydrobiological expeditions of IMB and PRIFO (1972–1973), were used. All the material is stored in IMB.

Holotype and paratypes of *G. filatovae* are stored dry; the other material is in 70% ethanol.

A comparative statistical analysis was made for four lots: (1) 28 type (holotype and paratypes of *G. filatovae*) specimens of *A. filatovae,* collected near the Bolshoi Pelis

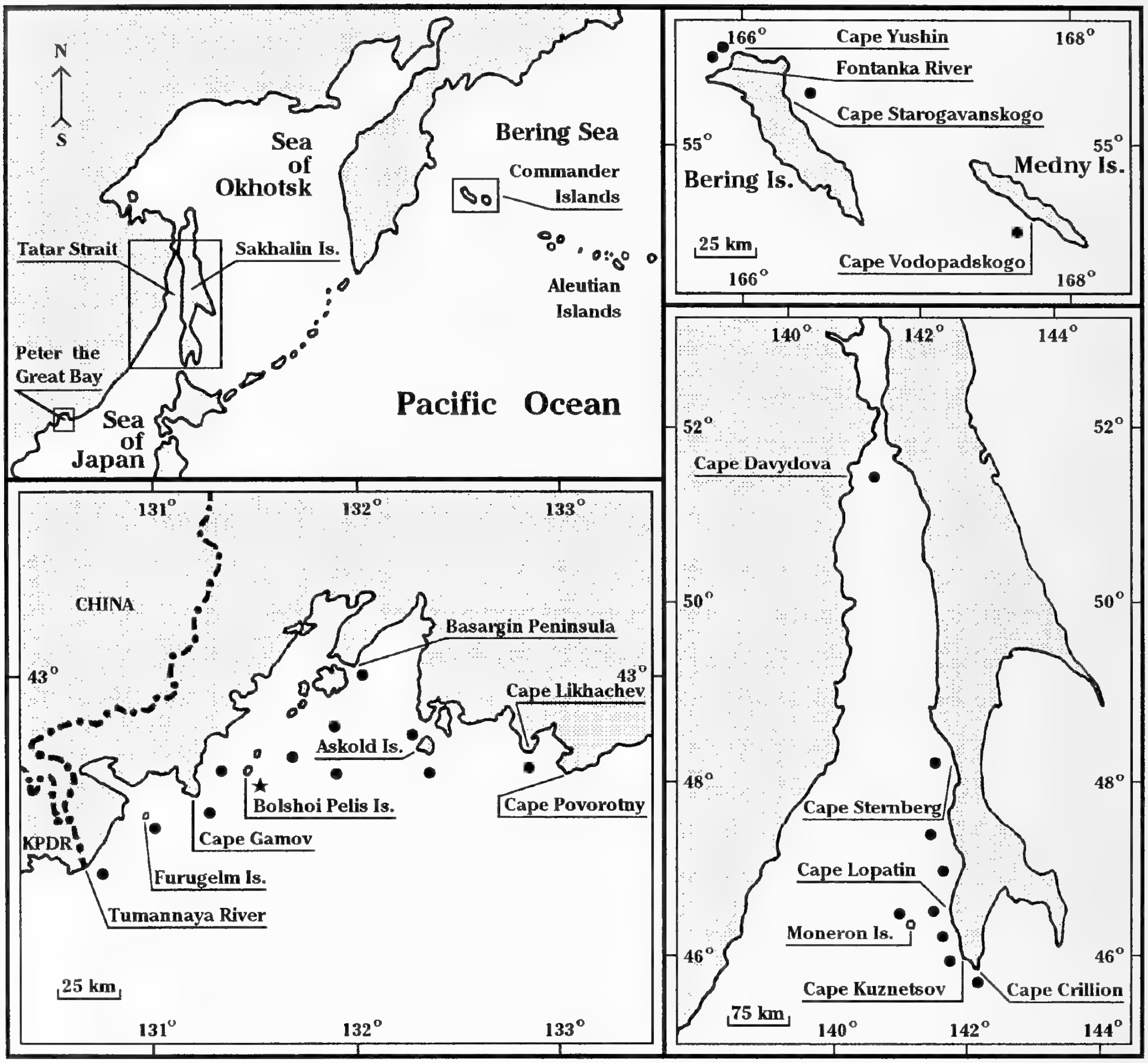

Figure 1

Distribution of *Adontorhina cyclia* in the northwestern Pacific (*—sampling sites of holotype and paratypes of *Genaxinus filatovae*).

Island (Figure 1) in Peter the Great Bay (Sea of Japan) at a depth of 74 m on the silty sand; (2) 64 specimens of *A. filatovae* from other parts of Peter the Great Bay (Sea of Japan); (3) 42 specimens of *A. filatovae* from the western coast of Sakhalin Island (Sea of Japan); (4) 17 specimens of the species from the shelf of the Commander Islands. Shell length (L), height (H), and width (W) of all the specimens were measured, and also shell length-height ratio and length-width ratio (L/H and L/W, correspondingly) were determined.

Shell measurements were made using an ocular micrometer with an accuracy of 0.1 mm. Statistical analysis of material was conducted by use of a package of statistical programs SYSTAT.

The L/H and L/W ratios are determined by shell proportions and are less susceptible to change as compared with other measured parameters, so comparison of the samples was conducted using only these characteristics. Their distributional pattern was different from the norm. Fifteen transformations were used to bring the obtained data to the norm. However, none of these transformations brought them closer to the norm. Therefore, in the comparative analysis of the samples, the nonparametric criterion of Kruskal-Wallis for comparison of several independent samples and that of Kolmogorov-Smirnov (two sample test) were used (Sachs, 1976).

RESULTS

Comparative Analysis

In Figures 2–11 the photographs of four type specimens of *A. filatovae* (paratypes, *G. filatovae*) and four specimens of the species found on the shelf zone of the Commander Islands are presented. The photographs show that by the structure of the hinge, the specimens of the species from the Commander Islands are similar to the type specimens of *A. filatovae* from the Sea of Japan. However, there are some distinctions in the form of the shell. The shell of the type specimens is slightly more angular. The posterior margin of the dorsal edge extends downward more steeply, and the anteroventral edge is bent more downward.

The results of the shell measurements of *A. filatovae* from the type locality and other parts of the Sea of Japan, as well as specimens from the Commander Islands, are shown in Table 1. From the table it can be seen that the shell L/H ratio of the specimen from the Commander Islands differs only slightly from that of the type specimens of *A. filatovae*. The shell of *A. filatovae* from other parts of Peter the Great Bay and the shelf of Sakhalin Island is slightly shorter. The shell L/H ratio of the specimens from these two lots (especially from Sakyalin Island) is smaller than that of the specimens of the species from the Commander Islands. However, the differences found are not significant. All the four lots compared belong to one general totality (Kruskal-Wallis test statistic = 6.523; $P = 0.089$).

The smallest differences in the shell L/W ratio were also found between the specimens of the species from the Commander Islands and the type specimens. The shell L/W ratio of *A. filatovae* from Peter the Great Bay significantly distinguishes this lot from the other lots. The specimens of *A. filatovae* from this area have a more convex shell. By the shell L/W ratio, the studied lots at the 95% significance level cannot be included into one general totality (Kruskal-Wallis test statistic = 8.857; $P = 0.031$). The results of the comparison of lots by pairs using the Kolmogorov-Smirnov criterion (Table 2) show that the lots of *A. filatovae* from Peter the Great Bay and the coast of Sakhalin Island differ significantly in this characteristic (99% level). Probably, the differences found are indicative of the intraspecific changeability of the shell ratio of mollusks with age (Zolotarev, 1989). The smaller specimens have a more angular and shorter shell than the large ones.

Thus, I consider that one and the same species inhabits both the Commander Islands area and the Sea of Japan, and differs significantly by the structure of the hinge from the representatives of the genera *Axinopsida* and *Genaxinus*. In the bivalve mollusks of the genus *Axinopsida*, the hinge has a distinct pseudocardinal tooth in the right valve and a corresponding pit in the left valve. In the representatives of the genus *Genaxinus*, the hinge is edentulous with subhorizontally elongate, toothlike tuberosities in each valve. The hinge plate is thin, flexed, and thickened in front of beaks, rapidly narrowing behind and passing beneath the posterior dorsal margin (Fleming, 1950; Moore, 1969). The study of other genera of the family Thyasiridae showed that by the hinge structure and shell form, the studied species should be placed into the genus *Adontorhina* described by Berry (1947) from the Lower Pleistocene ("Hilltop Quarry," San Pedro, California). Unlike the genera *Axinopsida* and *Genaxinus*, the hinge plate of the bivalve mollusks of the genus *Adontorhina* is composed of two sections, one section extending anterior to the beaks, the other section located centrally along the posterodorsal margin. The hinge is without true teeth. The hinge plate has irregular, minute granules, weakly to strongly expressed (Berry, 1947; Scott, 1986).

The genus *Adontorhina* is represented by two Recent species, *A. cyclia* and *A. sphaericosa* Scott, 1986, both inhabiting the coast of North America (Scott, 1986). The comparison of the species studied with the descriptions, drawings, and photographs of *A. cyclia* (Berry, 1947; Jones & Thompson, 1986; Scott, 1986) and *A. sphaericosa* (Scott, 1986) showed its identity with *A. cyclia* described in detail by Berry (1947) and Scott (1986). The discovery of *A. cyclia* near the Asian coast makes it possible to supplement its description by new data on shell morphology, ecology, and geographical distribution.

SYSTEMATICS

Adontorhina cyclia Berry, 1947

(Figures 1–11, Table 1)

Adontorhina cyclia Berry, 1947:260–261, pl. 1, figs. 1–2; Scott, 1986:149–156, figs. 1A, 9B, 6–11, synonymy; Jones & Thompson, 1986:687–700, fig. 1; Baxter, 1987:18; Scott et al., 1990:12; Kafanov, 1991:53; Kamenev, 1995:5, 10.

Genaxinus filatovae Ivanova & Moskaletz, 1984:48–49, fig. 3; Moskaletz, 1984:37; Romejko & Kamenev, 1985:92; Moskaletz, 1990:128.

Axinopsida filatovae (Ivanova & Moskaletz, 1984), Scarlato & Kafanov, 1988:939, 941; Kafanov, 1991:53.

Supplementary description: Shell small, length in general up to 3 mm. Maximum shell size (length 3.1 mm; height 3.2 mm; width 2.0 mm) recorded in the specimen from the shelf of the Commander Islands (Bering Island, depth 100 m), angular in upper part; length less than height or equal to it. Form of shell varying from more rounded to more angular. Transition of anterior branch of dorsal margin to anterior margin sharp. Posterior branch of dorsal margin making obtuse smooth angle with posterior margin. Anteroventral margin bent downward (this peculiarity more distinct in young specimens).

Material examined: Holotype *G. filatovae* and 1 paratype lot; 55 lots from Peter the Great Bay (Sea of Japan); 1 lot from Tatar Strait (Sea of Japan); 2 lots from Moneron Island (Sea of Japan); 19 lots from Sakhalin Island; 4 lots

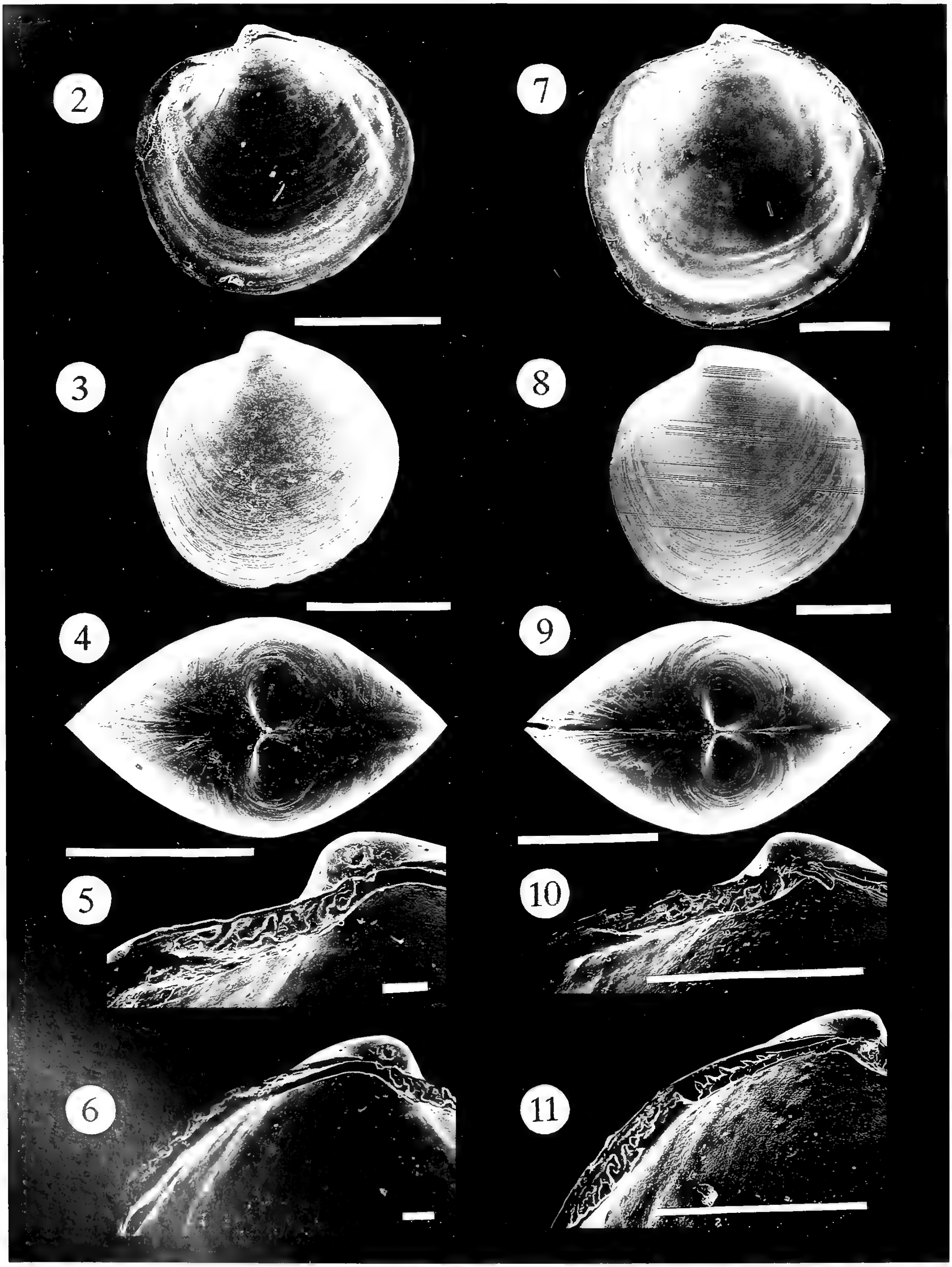
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Table 1

Results of morphological characteristics comparison of the shell of *A. cyclia* from different sites of the northwestern Pacific (L—shell length; H—height; W—width; L/H—length-height ratio; L/W—length-width ratio).

Area	Parameters	Mean	SD	SE	Min	Max	*n*
Commander Islands	L	2.441	0.298	0.072	2.0	3.1	17
	H	2.488	0.302	0.073	2.1	3.2	17
	W	1.471	0.252	0.061	1.2	2.0	17
	L/H	0.981	0.021	0.005	0.952	1.000	17
	L/W	1.674	0.115	0.028	1.389	1.846	17
Bolshoi Pelis Island, Peter the Great Bay, Sea of Japan (Holotype and paratypes *G. filatovae*)	L	1.936	0.263	0.050	1.4	2.5	28
	H	1.986	0.308	0.058	1.5	2.5	28
	W	1.179	0.225	0.043	0.8	1.5	28
	L/H	0.979	0.048	0.009	0.875	1.130	28
	L/W	1.662	0.125	0.024	1.429	1.889	28
Peter the Great Bay, Sea of Japan (*A. filatovae* from Scarlato & Kafanov, 1988)	L	2.133	0.331	0.041	1.5	3.0	64
	H	2.189	0.345	0.043	1.5	3.1	64
	W	1.331	0.273	0.034	0.8	2.2	64
	L/H	0.975	0.027	0.003	0.903	1.000	64
	L/W	1.621	0.126	0.016	1.273	1.875	64
Sakhalin Island, Sea of Japan (*A. filatovae* from Scarlato & Kafanov, 1988)	L	1.907	0.144	0.022	1.6	2.2	42
	H	1.969	0.141	0.022	1.6	2.3	42
	W	1.131	0.102	0.016	0.8	1.4	42
	L/H	0.969	0.027	0.004	0.900	1.000	42
	L/W	1.691	0.088	0.014	1.500	2.000	42

from the Commander Islands (3 lots from Bering Island; 1 lot from Medny Island); approx. 570 specimens.

Supplementary distribution and habitat: Bering Island, Commander Islands (from 55°25′3″N, 165°58′0″E to 55°15′2″N, 166°29′5″E) (Figure 1); Medny Island, Commander Islands (54°29′3″N, 167°34′1″E); Peter the Great Bay from Tumannaya River in the southwest (42°15′4″N, 130°44′6″E) to Likhachev Cape in the east (42°38′3″N, 132°43′2″E); Davydov Cape, Tatar Strait, Sea of Japan (51°31′0″N, 141°03′5″E); Moneron Island, Sea of Japan (46°13′1″N, 141°02′9″E); western coast of Sakhalin Island from Kriljon Cape in the south (45°53′0″N, 141°20′5″E) to Sternberg Cape in the north (48°15′3″N, 141°35′4″E), Sea of Japan.

In Peter the Great Bay, this species was recorded at depths of 31–241 m, in Tatar Strait (Davydov Cape)—31 m, near Moneron Island—260–300 m, Sakhalin Island—60–200 m, Bering Island—100–300 m, and Medny Island—150–200 m. In the Sea of Japan, *A. cyclia* was

Table 2

Results of comparison of shell length-width ratio (L/W) of *A. cyclia* from different sites of the northwestern Pacific using nonparametric Kolmogorov-Smirnov criterion (two sample test). Areas: 1—Bolshoi Pelis Island, Peter the Great Bay, Sea of Japan (holotype and paratypes *G. filatovae*); 2—Peter the Great Bay, Sea of Japan (*A. filatovae* from Scarlato & Kafanov, 1988); 3—Sakhalin Island (*A. filatovae* from Scarlato & Kafanov, 1988); 4—Commander Islands (*—significant 99%).

Areas	Max diff. for pairs groups	Two-sided probabilities
1 and 2	0.239	0.194
1 and 3	0.298	0.094
1 and 4	0.227	0.605
2 and 3	0.333	0.006*
2 and 4	0.284	0.202
3 and 4	0.151	0.909

←

Explanation of Figures 2 to 11

Figures 2–6. *Adontorhina cyclia* Berry, 1947 (paratypes *Genaxinus filatovae* Ivanova & Moskaletz, 1984, No. 2/313229, from Bolshoi Pelis Island, Peter the Great Bay, Sea of Japan). Figure 2. Interior of right valve. Scale bar = 1 mm. Figure 3. Exterior of left valve. Scale bar = 1 mm. Figure 4. Dorsal view of both valves. Scale bar = 1 mm. Figure 5. Anterior hinge plate of right valve. Scale bar = 100 μm. Figure 6. Posterior hinge plate of left valve. Scale bar = 100 μm.

Figures 7–11. *Adontorhina cyclia* Berry, 1947, from Bering Island, Commander Islands. Figure 7. Interior of right valve. Scale bar = 1 mm. Figure 8. Exterior of left valve. Scale bar = 1 mm. Figure 9. Dorsal view of both valves. Scale bar = 1 mm. Figure 10. Anterior hinge plate of right valve. Scale bar = 1 mm. Figure 11. Posterior hinge plate of left valve. Scale bar = 1 mm.

recorded on sand, silty sand, and silt, sometimes with some admixture of gravel and debris; on the shelf of the Commander Islands, on silty sand and silt. Bottom temperature in the sampling areas near Moneron Island was 8.0°C (Sakharnaya Golova Cape, 46°13′2″N, 141°03′7″E, depth 260 m); on the western coast of Sakhalin Island, bottom temperature varied from 1.5°C (Kuznetsov Cape, 46°02′6″N, 141°23′1″E, depth 170 m) to 6.0°C (Sternberg Cape, 48°15′3″N, 141°35′0″E, depth 100 m), in Peter the Great Bay, bottom temperature varied from 0.7°C (Askold Island, 42°27′7″N, 132°19′2″E, depth 90 m) to 14.0°C (Basargin Peninsula, depth 31 m).

DISCUSSION

Adontorhina cyclia is a common component of infauna at continental shelf and slope depths from Oregon to Alaska and the Central Bering Sea shelf (Scott, 1986). Along the Asian coast of the Pacific Ocean, this species was recorded only in the Sea of Japan and near the Commander Islands. However, *A. cyclia* is probably also a widely distributed species in the northwestern Pacific. Scott (1986) mentioned that it is probable that near the North American coast *A. cyclia* had been confused with the juveniles of the numerically dominant *Axinopsida serricata* (Carpenter, 1864). In the Sea of Japan, this species often occurs together with the common *Axinopsida subquadrata* (Adams, 1862) (Ivanova & Moskaletz, 1984). Therefore, it had for a long time been identified as *A. subquadrata.* During special studies of the changeability of *A. subquadrata,* Ivanova & Moskaletz (1984) established that some other species was present in the material on *A. subquadrata,* which they described as new. Externally, *A. cyclia* differs in appearance from *A. subquadrata* by a more angular, more convex, and more dorso-ventrally extended shell. Internally, the hinge structure is completely different.

Adontorhina cyclia was found together with *Axinospida subquadrata* in samples collected near the Commander Islands. It is possible that more thorough study of *A. subquadrata* and *A. orbiculata* (G. Sars, 1878) material from the Okhotsk and Bering seas, stored in the collections of different institutes and museums of Russia, will reveal more specimens of *A. cyclia* or *A. sphaericosa.* The two species occur together in samples from southeastern Alaska (Scott, 1986). There is a possibility that *A. cyclia* also inhabits the coastal zone of Korea and Japan.

On the coast of North America, the maximum population density of *A. cyclia* (384 ind/m^2) was registered near Santa Catalina Island (Southern California). The average population density of this species on the coast of Southern California in different years of study varied and reached up to 60.5 ind/m^2 (Jones & Thompson, 1986). In Boca de Quadra, southeastern Alaska, the density was approximately 20 ind/m^2 (Scott, 1986). In the Sea of Japan, the maximum density of this species 480 ind/m^2 was registered in Peter the Great Bay (in the site of Tumannaya River, depth 140 m). The average population density was 63.7 ± 15.1 ind/m^2. Near Sakhalin Island, the maximum density of *A. cyclia* (104 ind/m^2) was registered near Lopatin Cape (depth 100 m), with the average population density in this region 14.6 ± 4.9 ind/m^2.

Thus, *A. cyclia* on the coast of America, and Asia as well, forms rather dense settlements with similar abundance indices.

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LITERATURE CITED

Baxter, R. 1987. Mollusks of Alaska: A Listing of all Mollusks, Freshwater, Terrestrial, and Marine Reported from the State of Alaska, with Locations of the Species Types, Maximum Sizes and Marine Depths Inhabited. Shells and Sea Life: Bayside, California. 161 pp.

Berry, S. S. 1947. New Mollusca from the Pleistocene of San Pedro, California—III. Bulletins of American Paleontology 31:260–272.

Fleming, C. A. 1950. New Zealand recent Thyasiridae (Mollusca). Transactions of the Royal Society of New Zealand 78:251–254.

Hedly, C. 1907. The results of deep sea investigation in the Tasman Sea. II.—The expedition of the "Woy Woy." 2.—Mollusca from eight hundred fathoms, thirty-five miles east of Sydney. Records of the Australian Museum 6:356–364, pl. LXVI, LXVII.

Iredale, T. 1930. More notes on the marine Mollusca of new South Wales. Records of the Australian Museum 27:384–407.

Ivanova, M. B. & I. P. Moskaletz. 1984. Two new species of bivalves of the family Thyasiridae from the aquatoria of the Far Eastern State Marine Nature Reserve. Pp. 45–50 in V. S. Levin (ed.), Animal World of the Far Eastern Marine Nature Reserve. Far Eastern Science Center of the USSR Academy of Sciences Press: Vladivostok [in Russian].

Jones, G. F. & B. E. Thompson. 1986. The ecology of *Adontorhina cyclia* Berry (1947) (Bivalvia: Thyasiridae) on the Southern California Borderland. Internationale Revue der gesamten Hydrobiologie 71:687–700.

Kafanov, A. I. 1991. Shelf and Continental Slope Bivalve Molluscs of the Northern Pacific Ocean: A Check-List. Far

Eastern Branch of the USSR Academy of Sciences Press: Vladivostok. 200 pp. [in Russian, with English summary].

KAMENEV, G. M. 1995. Species composition and distribution of bivalve mollusks on the Commander Islands shelf. Malacological Review 28:1–22.

MOORE, R. C. (ed.). 1969. Treatise on Invertebrate Paleontology. Part N. Mollusca 6 (Bivalvia). The Geological Society of America, Inc. and The University of Kansas. XXXViii + 952 pp.

MOSKALETZ, I. P. 1984. Contribution to the fauna of bivalve molluscs of the Far Eastern State Marine Nature Reserve. Pp. 30–44 in V. S. Levin (ed.), Animal World of the Far Eastern Marine Nature Reserve. Far Eastern Science Center of the USSR Academy of Sciences Press: Vladivostok [in Russian].

MOSKALETZ, I. P. 1990. Zone-geographic composition and distribution of bivalve molluscs on soft bottom in the sublittoral zone of Far Eastern Marine Nature Reserve. Pp. 124–130 in V. V. Gulbin (ed.), Systematics and Ecology of Hydrobionts of the Far Eastern Marine Nature Reserve. Far Eastern Branch of the USSR Academy of Sciences Press: Vladivostok [in Russian].

POWELL, A. W. B. 1979. New Zealand Mollusca. Marine, Land and Freshwater Shells. Collins Press: Auckland, Sydney, London. 500 pp.

ROMEJKO, L. V. & G. M. KAMENEV. 1985. Bivalve molluscs of the sublittoral zone of Moneron Island. Pp. 85–101 in O. G. Kussakin (ed.), Benthos of the Shelf of Moneron Island. Far Eastern Science Center of the USSR Academy of Sciences Press: Vladivostok [in Russian].

SACHS, L. 1976. Statistical Evaluation. Statistika Press: Moscow. 598 pp. [in Russian].

SCARLATO, O. A. & A. I. KAFANOV. 1988. Contribution to the fauna of bivalve mollusks in the USSR Far East Seas. Zoologicheskiy Zhurnal 67:937–942 [in Russian, with English summary].

SCOTT, P. H. 1986. A new species of *Adontorhina* (Bivalvia: Thyasiridae) from the northeast Pacific, with notes on *Adontorhina cyclia* Berry, 1947. The Veliger 29:149–156.

SCOTT, P. H., F. G. HOCHBERG & B. ROTH. 1990. Catalog of Recent and fossil molluscan types in the Santa Barbara Museum of Natural History. I. Caudofoveata, Polyplacophora, Bivalvia, Scaphoda, and Cephalopoda. The Veliger (Supplement 1) 33:1–27.

ZOLOTAREV, V. N. 1989. Sclerochronology of the Sea Bivalve Molluscs. Naukova Dumka: Kiev. 112 pp. [in Russian].

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THE VELIGER

On Sinistral Coiling among Fossil North American Lymnaeidae

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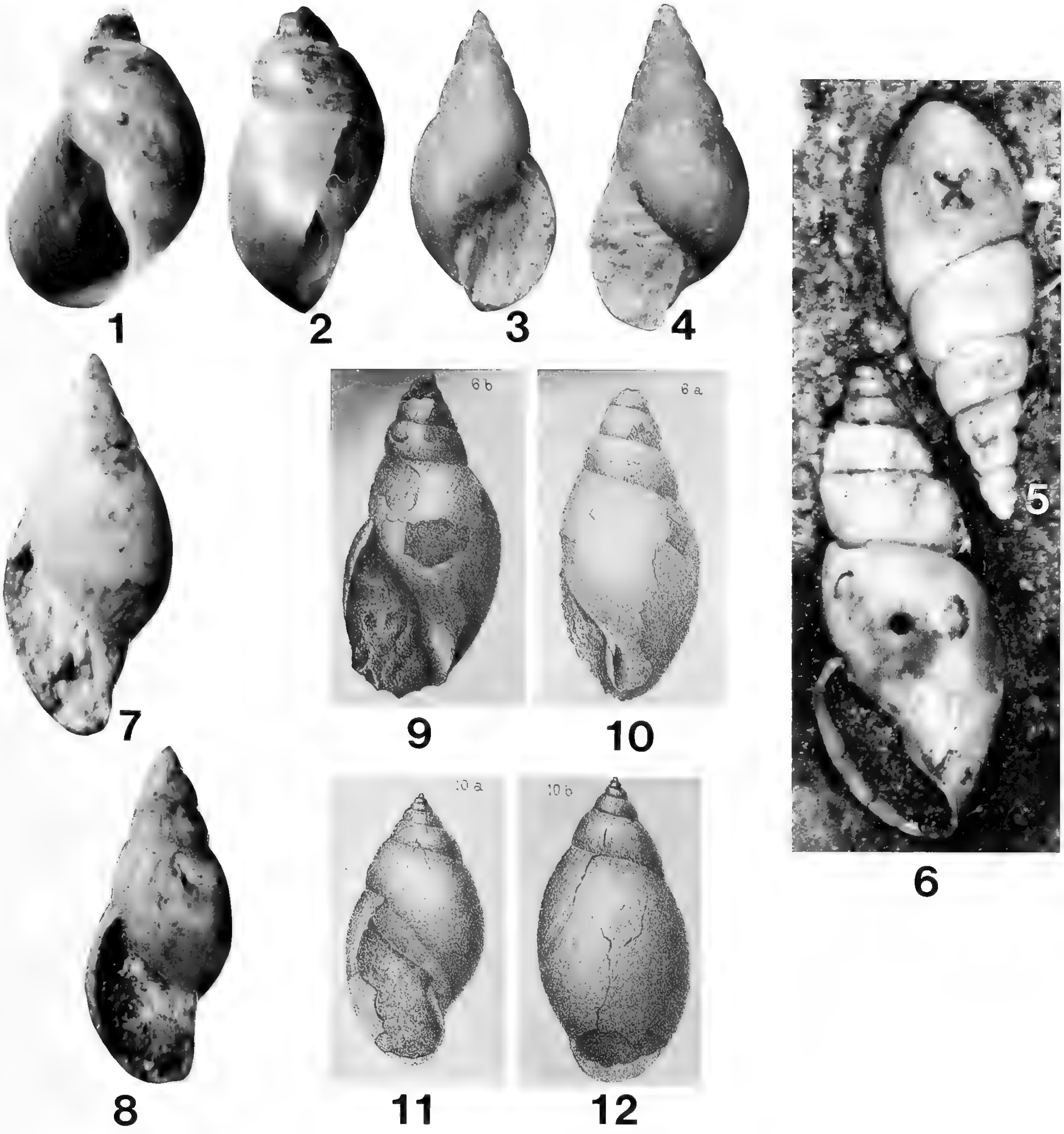
Abstract. A study of sinistral coiling among fossil members of the genus *Lymnaea* in North America shows that such coiling exists, but is uncommon. *Lymnaea* ***ambiguspira*** nom. nov. and *L. tulameenensis,* with its sinistral morph "*Aplexa ricei,*" are ambidextrous species in which both sinistrally and dextrally coiled individuals are known to exist. *Lymnaea saxarubrensis, L. disjuncta,* and *L. bridgerensis* are apparently consistent sinistral species. These species range from Paleocene (or latest Cretaceous?) to early Miocene in age. A new name, *Lymnaea* ***ambiguspira,*** is proposed for the preoccupied *Lymnaea vetusta ambigua* Pierce, 1993.

INTRODUCTION

Among Recent species of *Lymnaea* Lamarck, 1799 (*sensu* Hubendick, 1951), only the Hawaiian species *Lymnaea reticulata* (Gould, 1848) (Figures 1, 2) is distinguished by apparent consistent normal orthostrophic sinistrality (*sensu* Robertson, 1993). Among Recent normally dextral species, individual examples of sinistrality are rare. Baker (1911:1) acknowledged having seen only two specimens of normally dextral species with sinistral coiling of the shell. Populations of the widely distributed Old World *Lymnaea peregra* (Müller, 1774), an ambidextrous species (Robertson, 1993:112, 113), frequently include a small percentage (~3%) of sinistrally coiled individuals (Boycott et al., 1930). Recent work by Pierce (1993:985, 986) has presented evidence that ambidextrous sinistral coiling can also be found among fossil Lymnaeids. *Lymnaea* ***ambiguspira*** nom. nov. (formerly *L. vetusta ambigua* Pierce, 1993) from the Oligocene-Miocene of southwestern Montana, is one of two fossil ambidextrous species in which both sinistrally and dextrally coiled individuals are known to occur. The second species is *Lymnaea tulameenensis* (Russell, 1958), from the Oligocene of southern British Columbia. Search of the literature of North American paleontology failed to locate additional ambidextrous taxa. However, it appeared possible that consistent, or normally sinistral lymnaeid taxa, such as *L. reticulata,* might exist in the fossil record. Study and evaluation of these two ambidextrous species showed they are conchologically most similar to Recent *Lymnaea palustris* (Müller, 1774), which is known to very rarely produce a sinistrally coiled individual (Baker, 1911:1), and should be considered related (ancestral?) to this Recent species. *Lymnaea reticulata* can also be considered closely related to *L. palustris.* Hubendick (1951:174) stated: "Disregarding this backward torsion the shell of *L. reticulata* is somewhat similar to the general shape of the shell of *L. palustris.*"

MATERIALS AND METHODS

Paratypes of *Lymnaea ambigua* from the personal collection of Pierce, type specimens of *L. tulameenensis* and "*Aplexa ricei*" Russell, 1958, and of "*Physa*" *saxarubrensis* Russell, 1958, loaned by the Geological Survey of Canada (GSC), and Recent specimens of *L. reticulata* from Nuuanu, Island of Oahu, loaned by The Bishop Museum, were available for study. All measurements taken paralleled those used and defined by Hubendick (1951:fig. 2), with some change in nomenclature. Height, H, equates to 1 of Hubendick; Width, Wid., equates to b; and Height of aperture, Ha, equates to ml. Width of aperture was not measured. W/H and Ha/H are, respectively, ratios of the width to height of the shell, and height of the aperture to the overall height of the shell. Measurements of these parameters were made of large, apparently reproductively mature, specimens by ocular reticule with results in Table 1. Careful evaluation and measurements of these three species and comparison with the conchological characteristics of *L. palustris,* as defined by Hubendick (1951:119, 120), led to a set of criteria to be used in recognizing normally sinistral fossil Lymnaeids. These criteria are:



Explanation of Figures 1 to 12

Figures 1–8, ×5; Figures 9–12, "natural size" (White, 1880). Figures 1–2. *Lymnaea reticulata* (Gould, 1848), Bishop Museum, BPBM, Lot 15014, Nuuanu, Oahu, Hawaii, 1. apertural view; 2. left lateral view. Figures 3–4. *Lymnaea* ***ambiguspira*** Pierce, nom. nov., 3. dextral holotype, Kansas University Museum of Invertebrate Paleontology (KUMIP) 236377, apertural view; 4. sinistral paratype, KUMIP 236378, apertural view. Figures 5–6 on one slab. *Lymnaea tulameenensis* Russell, 1958, 5. dextral paratype, Geological Survey of Canada (GSC) 11617, abapertural; 6. sinistral paratype, GSC 13283, apertural view (holotype of "*Aplexa ricei*"). Figures 7–8. *Lymnaea saxarubrensis* (Russell, 1958), 7. sinistral holotype GSC 13280, apertural view; 8. sinistral paratype GSC 13281, apertural. Figures 9–10. *Lymnaea disjuncta* (White, 1879), copies of plate 24, fig. 6a, b, of White (1880). 9. apertural view; 10. right lateral view. Figures 11–12. *Lymnaea bridgerensis* (Meek, 1873), copies of plate 19, fig. 10a, b, of White (1880), 11. apertural view; 12. abapertural view.

(1) Whorls 5 or more, usually 6. (*L. reticulata* has 4 to 4.5).
(2) Suture slightly impressed, whorls slightly rounded.
(3) Apex usually acutely pointed.
(4) Columella twisted, usually with plait or fold.
(5) Ha/H usually < 0.50. (−0.60 or less for *L. reticulata*).

Based on these criteria, a review of the literature suggests that although there are examples of normally sinistral fossil lymnaeids, such are not common. These sinistral taxa range in age from Paleocene (questionably Cretaceous) to Miocene age and have been incorrectly assigned to either the genus *Physa* Draparnaud, 1801, or to the planorbid genus *Bulinus* Müller, 1781, which is not found in the Western Hemisphere. "*Bulinus*" *disjunctus* (White, 1879) is certainly a lymnaeid. "*Physa*" *saxarubrensis* (Russell, 1958) and "*P.*" *bridgerensis* (Meek, 1873) fit the criteria above and are almost certainly lymnaeids. Measurements, evaluation, and comparisons of "*B.*" *disjunctus* and "*P.*" *bridgerensis* were made using the excellent plates of White (1880: pl. 19, fig. 10, pl. 24, fig. 6; 1883:pl. 25, figs. 4, 5, pl. 30, figs. 9, 10).

SYSTEMATICS OF SINISTRAL LYMNAEIDAE

Family LYMNAEIDAE Rafinesque, 1815

Genus *Lymnaea* Lamarck, 1799

Type species: *Helix stagnalis* Linnaeus, 1758, by subsequent designation (Fleming, 1828).

Lymnaea palustris (Müller, 1774)

Description: Hubendick's (1951:119, 120) description of the shell of *Lymnaea palustris* follows: "The shell is ordinarily made up of six to seven gradually increasing whorls (fig. 302–303). The height of the aperture is between one third and one half of the total shell height. In *L. palustris* more than in any other Lymnaeid, the body whorl and even the whole shell has a tendency to become malleated. The apex is usually pointed but is sometimes obtuse. The suture is slightly impressed and the whorls slightly rounded. The aperture varies from roundly-ovate to long-ovate, usually not very expanded, and has very often a brownish or purplish line on the inner side of the peristome. A columellar fold generally occurs."

Remarks: The highly variable shell morphology for a given anatomical species of Lymnaea, resulting from the normal plasticity of the shell under varying environmental conditions, has led to a great number of named "species." Hubendick (1951) illustrated clearly the range of shell morphology for each species he recognized as valid based on anatomical criteria. Hubendick's *L. palustris,* through his synonymy, is approximated closely by the "group of *palustris*" of Baker (1911:298), and the *Stagnicola elodes* (Say, 1821) group of Burch (1989:176). From a paleontological standpoint, since only the shell is preserved, it is most practicable to follow the classification of Hubendick. For further comments on this concept, see Pierce, 1993: 984–985.

Lymnaea ***ambiguspira*** Pierce, nom. nov.

(Figures 3, 4)

Lymnaea vetusta ambigua Pierce, 1993:985, 986, figs. 1.16–1.20, tables 4, 5.

Non *Lymnaea ambigua* Westerlund, 1881, Övers. Sv. Vet.-Ak. Förh. Stockholm 4:60

Non *Lymnaea ambigua* Pease, 1870, Amer. Jour. Conch. 6:6.

Lymnaea vetusta ambigua Pierce, 1993, is a primary homonym of *Lymnaea ambigua* Pease, 1870, and *L. ambigua* Westerlund, 1881, under the International Code of Zoological Nomenclature. The new name, *Lymnaea* ***ambiguspira*** is proposed as a replacement for the preoccupied *L. v. ambigua* Pierce, 1993; the type material remains the same.

Description: Shell of moderate size, usually dextral, occasionally sinistral, elongate conic; spire medium to high, acute, angle about 55°; width/height (W/H) about 0.50; whorls 6 to 6½, rounded to slightly flattened, suture shallowly impressed, near abutting; nuclear whorls about 1½, finely punctate, shining; subsequent whorls initially with weak, regular, slightly wavy, orthocline growth striae, becoming regularly costellate on last 1½ to 2 whorls, rarely malleated. Aperture D-shaped, modestly inflated, about one-half height of shell; outer lip thin, slightly curved, occasionally with internal varix shortly behind lip; inner lip broad, closely appressed, with distinct columellar plait. Umbilicus a narrow chink or closed (Pierce, 1993).

Remarks: Further study and comparison since initial publication of this taxon as a subspecies of *L. vetusta* Meek, 1860 has shown that, although *L.* ***ambiguspira*** and *L. vetusta* are closely related, *L.* ***ambiguspira*** differs sufficiently in shell morphology from the much older *L. vetusta* to preclude being considered conspecific. *Lymnaea* ***ambiguspira*** tends to be shorter, 7–10 mm in mature specimens compared to about 14 mm for *Lymnaea vetusta,* with more whorls (6–6.5), less acute apex, 55° compared to 45°, and greater W/H, 0.50 compared to 0.46. *Lymnaea* ***ambiguspira*** is regular costellate on last 1.5 to 2 whorls, occasionally becoming malleated on very large specimens. Its aperture is more inflated with a less angular basal margin, and a curving columellar plait when compared to *L. vetusta.* The tendency to ambidextrosity observed in *L. ambigua* is highly variable. Sinistral individuals represented less than 1% at one locality and 55% at the second locality (Pierce, 1993:985, 986, tables 4, 5).

Material: More than 600 specimens were found at eight localities in southwestern Montana, ranging in age from middle Oligocene (Whitneyan?) through early Miocene (late Arikareean). Sinistral individuals were restricted to only two of the localities, both late Oligocene (early Arikareean).

Table 1

Measurements (in mm) of sinistral Lymnaeidae. E = estimated from measurements of White's (1880, 1883) plates; Max. = largest specimen available; [1] = LaRocque, 1960, p. 40; [2] = Meek, 1870, p. 517.

		Ht.	Wid.	W/H	Wh.	Ha	Ha/H
Lymnaea reticulata (n = 6) (Recent BPBM Lot #'s 15014 & 17365)							
Sinistral only	Max.	9.0	5.2	0.58	4.25	5.4	0.60
	Min.	6.0	3.6	0.60	3.33	3.7	0.62
	Ave.	7.68	4.50	0.59	3.97	4.58	0.60
Lymnaea ***ambiguspira*** (late Oligocene to early Miocene)							
Dextral	Max.	10.2	5.0	0.49	6.2	5.2	0.51
Sinistral	Max.	10.3	5.15	0.50	6.25	4.85	0.47
Lymnaea tulameenensis (middle to late Oligocene)							
Dextral	Max.	12.0	4.4	0.37	8.25	4.0	0.33
Sinistral	Max.	13.6	5.4	0.40	7.0	5.3	0.39
Lymnaea saxarubrensis (middle to late Oligocene)							
Sinistral only	Max.	11.4	5.4	0.47	5.5	6.3	0.55
Lymnaea disjuncta (?Cretaceous to early Eocene)							
Sinistral only		E44.0	E20.0	0.45	6	E21.0	0.48
Lymnaea bridgerensis (Paleocene, Oligocene)							
Sinistral only		E39.0 (29.2)[2]	E21.0 (16.8)[2]	0.54 (0.57)[2]	5–6[1]	E21.0	0.54

Lymnaea tulameenensis Russell, 1958

(Figures 5, 6)

Stagnicola tulameenensis Russell, 1958:88, pl. I, figs. 2–4.
Aplexa ricei Russell, 1958:90, pl. II, fig. 6.

Description: Russell's (1958:88) original description of the holotype, GSC 11616, follows: "Shell small, slender, volutions about six. Spire slender, whorls gently convex, apex rounded. Aperture about two-fifths total length of shell, narrowly ovoid, inner lip thickened. Surface with fine growth lines. Length of type, 6.9 mm; width, 2.9 mm; length of aperture, 2.5 mm." (Russell 1958:88). Emendation: inner margin of basal lip of aperture reflected slightly; columella twisted and with columellar fold at about mid-height; apex roundly pointed; with faint collabral costae on last three whorls. Ambidextrous; both sinistral and dextral morphs occur. Height of paratype, GSC 11617, 12.0 mm; width 4.4 mm; height of aperture 4.0 mm; W/H 0.37; Ha/H 0.33; whorls 8.25.

Remarks: *Lymnaea tulameenensis* was recognized as a species with both dextral and sinistral morphs when *L.* ***ambiguspira*** was first being studied. Russell selected a small, perhaps not reproductively mature, individual of only 6.25 whorls for his holotype, GSC 11616. He only provisionally referred a larger individual, GSC 11617, to the species. Examination of both holotype and paratype resulted in emendations to the description above. Russell's (1958:90) description of "*Aplexa ricei,*" the sinistral morph of *L. tulameenensis,* is as follows: "Shell rather small, delicate, slender; spire long and tapering; volutions five, gently convex. Aperture narrowly ovoid; distinctly less than half length of shell; inner lip thin, but with distinct columellar fold about mid-length. Surface with very faint but regular growth lines. Length of type, 13.2 mm; width, 5.4 mm; length of aperture 5.6 mm." Examination of the holotype, GSC 13283, disclosed several differences from the description above. The most significant are that the whorls are about seven rather than five as reported, and the description fails to mention that the inner margin of the basal lip is reflected, the columella is twisted, and weak collabral costellae are present on the last two to three whorls. When both amplified descriptions are compared, it becomes apparent that "*Aplexa ricei*" is an orthostrophic sinistral morph of *Lymnaea tulameenensis.* Viewing the two specimens, the paratype of *L. tulameenensis* and the holotype of "*A. ricei,*" lying almost apex to apex on the same rock slab, leaves no doubt. Russell (1958:86) was somewhat ambiguous as to the age of the Princeton fauna. Although the associated flora, insects, and fish are typical of the middle Oligocene to Miocene, he stated that at least part of the unit had to be of middle Eocene age based upon two mammal teeth found nearby. Such teeth, at least in younger sediments, may be reworked. Based on the preponderance of evidence, this fauna is considered middle to late Oligocene herein.

Material: Unfortunately, the number of individuals available for study is quite small, only two dextral specimens (GSC 11616, holotype and GSC 11617, paratype) and one sinistral specimen (GSC 13283, holotype of "*A. ricei*").

Lymnaea saxarubrensis (Russell, 1958)
(Figures 7, 8)

Physa saxarubrensis Russell, 1958:89–90, pl.II, figs. 1–4.

Description: Russell's (1958:89) original description follows: "Shell small, robust, moderately elongated; volutions five, convex; spire rather long, apex rounded. Aperture ovoid, not expanded, length a little more than half that of shell; inner lip with slight columellar fold. Surface marked by well-defined growth lines and on some specimens by a resting varix on the body whorl. Length of type, 9.7 mm; width, 4.9 mm; length of aperture, 5.2 mm." Emendation: columella twisted; apex roundly pointed; with collabral costae on last whorl, about 3 per millimeter. Measurements of holotype, GSC 13280: height 11.4 mm; width 5.4 mm; apertural height 6.3 mm; whorls 5.5. Measurements of paratype, GSC 13281: height 9.9 mm; width 5.0 mm; apertural height 4.7 mm; whorls 5, estimated.

Remarks: Since all type specimens from the Russell's (1958) Princeton fauna, southern British Columbia, were at hand, direct measurements of the holotype and paratype of *L. saxarubrensis* could be made. The discrepancy in measurements of the holotype is not understood. Russell (1958: 89–90 commented that "the present species is in contrast to most of those in the Recent fauna in having a spire almost as long as the aperture, and in lacking any inflation of the body whorl," and compared "*P.*" *saxarubrensis* to "Cretaceous and early Tertiary species such as *P. canadensis* Whiteaves, '*P.*' *disjunctus* (White), and '*P.*' *bridgerensis* Meek." The first, *P. canadensis,* does appear to be a physid. The last two are shown to be sinistrally coiled lymnaeids herein.

Material. Only two specimens were available, the holotype, GSC 13280, and a paratype, GSC 13281. Age is considered to be middle to late Oligocene.

Lymnaea disjuncta (White, 1879)
(Figures 9, 10)

Bulinus disjunctus White, 1879:165, 170, 241, 255; 1880:55, 86, pl. 24, fig. 6; 1883:451, pl. 25, figs. 4, 5.
Aplexa disjuncta (White), Henderson, 1935:263.

Description: White's (1880:86, 87) original description follows: "Shell rather large and moderately elongated; volutions about six, those of the spire increasing gradually in size, but the body volution is proportionally more inflated than those of the spire; suture distinct, but not very deep, and not conspicuous, because of the moderate convexity of the volutions; length of the spire a little more than half that of the whole shell; callus of the inner lip broad, its posterior half closely appressed against and adherent to the body; its anterior half deflected or disjoined from the body, so as to leave a kind of umbilical space between it and the body of the shell. This condition of the inner lip is evidently not accidental, as it is present on all the examples, young and old, that have yet been found; aperture moderately large, its length a little more than half the full length of the shell. Surface marked only by the fine lines of growth peculiar to the Physidae.

"Length, about 43 millimeters; breadth of body volution, 20 millimeters."

Remarks: The last sentence in the description, before the measurements, is misleading. Fine lines of growth are not peculiar to the Physidae. No mention of spiral sculpture, found on so many physids, is found. White's description is confused as to the relative length of the spire and of the aperture. Measurements from his plates result in an Ha/H of 0.48. The age of this species is not clear; it could range from very latest Cretaceous to early Eocene. Comparisons were made using published descriptions and illustrations.

Lymnaea bridgerensis (Meek, 1873)
(Figures 11, 12)

Physa bridgerensis Meek, 1873:516; White, 1880:45, pl. 19, fig. 10; 1883:450, pl. 30, figs. 9, 10; Henderson, 1935: 258; LaRocque, 1960:40, pl. 3, fig. 27, *non* figs. 28, 29.

Description: Meek's (1873:516) original description follows: "Shell attaining a large size, subovate in form; spire prominent, conical; volutions four and a half to five, moderately convex, last one large but not very ventricose; suture well defined; aperture narrow-subovate, arcuate, acutely angular above, about twice as long as the spire; columella twisted into a rather prominent fold. Surface with fine, sharp lines of growth.

"Length about 1.15 inches; breadth, 0.66 inch."

Remarks: LaRocque (1960:40, pl. 3, fig. 27) illustrated and described this species from the Paleocene Flagstaff Formation of Utah. His figure 27 is certainly *L. bridgerensis*: however, his figures 28 and 29, also identified as this species, are of a short-spired, inflated physid. His measurements correspond closely with those given in the type description, and taken from White's plate (1880:pl. 19, fig. 10), except that LaRocque counted six whorls on his illustrated hypotype, Ohio State University 20064. Age of the type locality is middle to upper Eocene.

CONCLUSIONS

The search for fossil sinistral lymnaeids in North America disclosed two ambidextrous species, *L.* ***ambiguspira*** and *L. tulameenensis,* in which both orthostrophic sinistral and dextral morphs are found in the same population. These taxa are of middle Oligocene to early Miocene age. Three species, *L. saxarubrensis, L. disjuncta,* and *L. bridgerensis,* were found that exhibit apparent normal orthostrophic sinistrality. These taxa range in age from early Eocene (questionably late Cretaceous) to late Oligocene. It appears that sinistral coiling among the Lymnaeidae has always been a rare occurrence, being most common in the middle to late Oligocene when three species displayed this tendency. It is tempting to speculate that the Recent Hawaiian *Lymnaea reticulata* is the result of adventitious avian dispersal of one of these mid-Tertiary species to a newly emergent and isolated island environment.

ACKNOWLEDGMENTS

The Geological Survey of Canada provided all type material from Russell's (1958) Princeton fauna for study. The Bernice P. Bishop Museum provided comparative specimens of Recent *L. reticulata.* This paper has benefited to a great degree from the constructive comments of R. Robertson and B. Roth.

LITERATURE CITED

Baker, F. C. 1911. The Lymnaeidae of North and Middle America, Recent and Fossil. Chicago Academy of Science Special Publication 3. 539 pp., 58 pl.

Boycott, A. E., C. **Diver**, S. L. **Garstang** & F. M. **Turner**. 1930. The inheritance of sinistrality in *Limnaea peregra* (Mollusca, Pulmonata). Philosophical Transactions of the Royal Society of London B219:51–130.

Burch, J. B. 1989. North American Freshwater Snails. Malacological Publications: Hamburg, Michigan. 365 pp.

Draparnaud, J. P. R. 1801. Tableau des Mollusques terrestres et fluviatiles de la France. Paris. viii + 164 pp., 13 pls.

Fleming, J. 1828. A History of British Animals, etc. 8 vols. Edinburg and London. 565 pp.

Gould A. A. 1848. Descriptions of new species of *Physa* from collection of the Exploring Expedition. Proceedings of the Boston Society of Natural History 2:214–215.

Henderson, J. 1935. Fossil Non-Marine Mollusca of North America. Geological Society of America Special Publication 3. 313 pp.

Hubendick, B. 1951. Recent Lymnaeidae. Their Variation, Morphology, Taxonomy, Nomenclature, and Distribution. Kungl Svenska Vetenskapsakademiens Handlingar Fjärde Serien. Band 3. No. 1. 223 pp., 5 pls.

Lamarck, J. B. P. **de**. 1799. Prodrome d'une nouvelle Classification des Coquilles, etc. Mémoire de Société Histoire Naturel, Paris i, Prairial, An vii (May 1799), pp. 63–91.

LaRocque, A. 1960. Molluscan faunas of the Flagstaff Formation of central Utah. Geological Society of America Memoir 78. 100 pp.

Linnaeus, C. A. 1758. Systema Naturae, per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentüs, synonymis, locis. 10th ed. Laurentii Salvii: Holmiae. 824 pp.

Meek, F. B. 1860. Description of new fossil remains collected in Nebraska and Utah by the exploring expedition under the command of Capt. J. H. Simpson. Tertiary species. Proceedings Academy of Natural Sciences Philadelphia 12(July 1860):312–315.

Meek, F. B. 1873. Preliminary paleontological report, consisting of lists and descriptions of fossils, with remarks on the ages of the rocks in which they are found. Pp. 429–518 in U.S. Geological and Geographical Survey of the Territories (Hayden Survey), Sixth Annual Report. U.S. Government Printing Office: Washington.

Müller, O. F. 1774. Vermium terrestrium et fluviatilum, seu animalium Infusorium, Helminthicorum et Testaceorum non marinorum succinta historia. Volumen Alterum. Heineck et Faber: Haviniae et Lipsiae. xxxv + 214 pp.

Müller, O. F. 1781. Des . . . O. F. Müller Geschichte der Perlen-Blasen. Naturforscher 15:1–20, 1 pl.

Pierce, H. G. 1993. The nonmarine mollusks of the late Oligocene-early Miocene Cabbage Patch Fauna of western Montana. III. Aquatic mollusks and conclusions. Journal of Paleontology 67:980–993.

Rafinesque Schmaltz, C. S. 1815. Analyse de la Nature, ou tableau de l'univers et des corps organises. Palerme. 224 pp.

Robertson, R. 1993. Snail handedness. National Geographic Research & Exploration 9:104–119.

Russell, L. S. 1958. Mollusca from the Tertiary of Princeton, British Columbia. National Museum of Canada Bulletin 147:84–95.

Say, T. 1821. Descriptions of univalve shells of the United States. Journal Academy of Natural Sciences Philadelphia 2:149–179.

White, C. A. 1879. Report on the paleontological field-work for the season of 1877. Pp. 161–272 in F. V. Hayden (ed.), Eleventh Annual Report of the United States Geological and Geographical Survey of the Territories embracing Idaho and Wyoming. U.S. Government Printing Office: Washington.

White, C. A. 1880. Contributions to Paleontology, Nos. 2–8. [extracted from the Twelfth Annual Report of the Survey for the year 1878], Author's Edition. U.S. Government Printing Office: Washington. 171 pp., pls. 11–42.

White, C. A. 1883. A review of the non-marine fossil Mollusca of North America. Pp. 405–550 in Third Annual Report of the United States Geological Survey, 1881–1992. U.S. Government Printing Office: Washington.

Whiteaves, J. F. 1885. Report on the Invertebrata of the Laramie and Cretaceous rocks of the vicinity of the Bow and Belly Rivers and adjacent localities in the Northwest Territory. Contributions to Canadian Paleontology, Canadian Geological and Natural History Survey, Volume 1, Part 1:1–89.

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THE VELIGER

New Species of Small to Minute Gastropods of Early Eocene Age from the Crescent Formation, Black Hills, Southwest Washington

by

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Abstract. Six new species of small to minute gastropods are part of a diverse shallow-water marine assemblage in the upper part of the Crescent Formation at Larch Mountain in the Black Hills west of Olympia, Washington.

The scissurellid *Scissurella* (*Scissurella*) ***malloryi*** is the earliest record of *Scissurella sensu stricto* and its first record from the Pacific coast of North America. The orbitestellid *Orbitestella* ***palaiopacifica*** and the omalogyrid *Ammonicera* ***benhami*** are the earliest records of these genera. In regards to the Pacific coast of North America, *O.* ***palaiopacifica*** is the first fossil record of this genus, and *A.* ***benhami*** is the first record of this genus. The fissurellid *Puncturella* (*Altrix*) ***pacifica*** is the first record of this subgenus from the Pacific coast of North America. The liotiid *Arene* ***olympiata*** is the second Paleogene record of this genus from the Pacific coast of North America. The volutomitrid *Conomitra* ***capitolina*** is the second record for this genus from the Pacific coast of North America.

New information on associated benthic foraminifera confirms a middle early Eocene age that was previously based only on molluscan data.

INTRODUCTION

This study is an outgrowth of our continuing investigation of little-studied molluscan faunas of the upper part of the Crescent Formation in southwestern Washington. The Crescent Formation ranges in age from late Paleocene to early middle Eocene (Snavely, 1987) and is the basement rock in this area. It consists predominantly of oceanic tholeiitic basalt flows, but the original tectonic setting of the Crescent Formation remains uncertain (Suczek et al., 1994). One hypothesis is that the basalts formed seamounts that later accreted to North America (Duncan, 1982), but an alternative hypothesis proposes that the basalts formed in a rift-basin environment along the continental margin (Wells et al., 1984; Babcock et al., 1992, 1994).

The upper third of the Crescent Formation contains mollusk-bearing, shallow-marine deposits and, locally, terrestrial deposits. Prior to 1992, studies of the mollusks (Weaver & Palmer, 1922) dealt with only a few new species from exposures along the north shore of the Olympic Peninsula. Although Weaver (1942) monographed Tertiary marine megafossils from Washington and Oregon, his coverage of species from the Crescent Formation was essentially a review of the species described by Weaver & Palmer (1922). The first detailed analysis of a megafossil assemblage in the Crescent Formation was made by Squires et al. (1992) and dealt with the shallow-marine upper part of the formation at Pulali Point (Figure 1), west of Seattle. That study spawned two additional articles (Squires, 1992, 1993) on certain bivalves from the Pulali Point area. Squires & Goedert (1994a) made a detailed study of another megafossil assemblage in the upper part of the Crescent Formation in the Little River area in the southern Olympic Peninsula (Figure 1). Squires & Goedert (1994b) reported new species (some minute in size) of mollusks in the upper part of the Crescent Formation in the Black Hills, west of Olympia, at the same localities (CSUN locs. 1563 and 1564) that are the focus of this paper (Figure 1). Squires & Goedert (1995) also reported additional new species of gastropods in the transition zone between the upper part of the Crescent Formation and the overlying lower member of the McIntosh Formation in the northern Doty Hills, approximately 30 km to the southwest of the Black Hills.

Additional work by us in the Black Hills has revealed six more new species of gastropods. The purpose of this paper is to describe and name the new species, all of which were found in the upper part of the Crescent Formation in richly fossiliferous and conglomeratic silty mudstone interbedded with basalt. The extrusion of the basalt caused shoaling and the establishment of a rocky shoreline/shallow-water community where gastropods and bivalves lived alongside colonial corals and coralline algae. The mollusk shells were transported a short distance and deposited in muddy matrix coquina that filled cracks between boulders of basalt. Most of the shells in the coquina are small to minute, and their size prevented them from being pulverized during transport (Squires & Goedert, 1994b; Nesbitt et al., 1994). Extraction of the fossils is possible because the muddy matrix is only poorly indurated and, upon soaking in water, the rock can be broken apart with a strong needle. If care is exercised, intact small to minute fossils can be obtained. Our studies of the minute mollusks would have been impossible without the scanning electron microscopy work by Steven R. Benham (Pacific Lutheran University, Tacoma, Washington). Benham's work also enhanced our knowledge of protoconch morphology and shell microstructure on the small mollusks.

The molluscan stages used in this report stem mainly from Clark & Vokes (1936), who proposed five mollusk-based provincial Eocene stages, namely, "Meganos" (lowermost Eocene), "Capay" (middle lower Eocene), "Domengine" (upper lower to lower middle Eocene), "Transition" (lower middle Eocene), and "Tejon" (middle middle Eocene to upper Eocene). These stage names are in quotes because they are informal terms. Givens (1974) modified the use of the "Capay Stage," and it is in this modified sense that the "Capay Stage" is used herein. The upper Eocene to lower Oligocene Galvinian Stage of Armentrout (1975) is also used in this report. This stage is used in the Pacific Northwest and is correlative to the upper part of the "Tejon Stage" in California.

The classification systems used for taxonomic categories higher than the family level generally follow that of Haszprunar (1988) for the vetigastropods and that of Ponder & Warén (1988) for the caenogastropods and heterobranch gastropods.

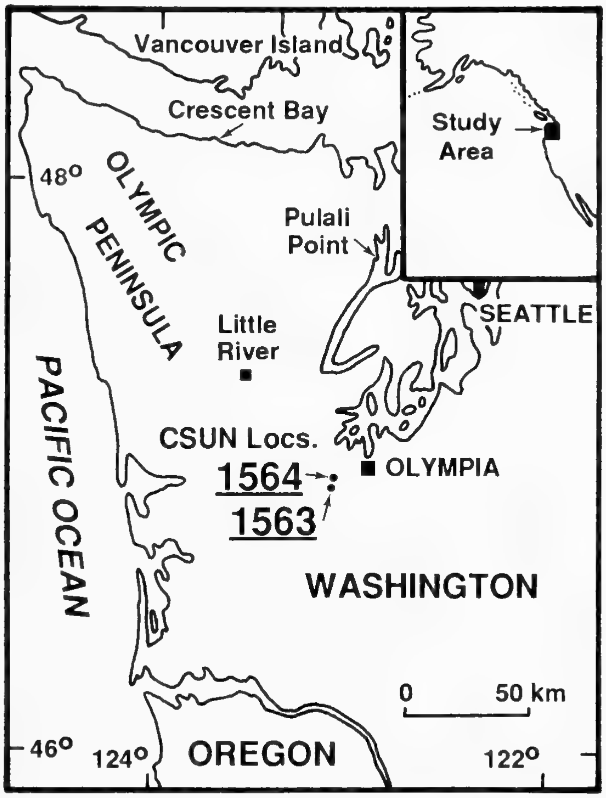

Figure 1

Index map to CSUN locs. 1563 and 1564, upper part of Crescent Formation, Larch Mountain, Black Hills, west of Olympia, Washington.

Abbreviations used for catalog and/or locality numbers are: CSUN, California State University, Northridge; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section.

AGE

Squires & Goedert (1994b) assigned the upper part of the Crescent Formation at CSUN locs. 1563 and 1564 to the middle lower Eocene ("Capay Stage") based on molluscan fossil evidence. Benthic foraminiferal analyses done during the course of the present investigation confirm this age. Two microfossil samples from CSUN loc. 1563 contained a littoral to inner sublittoral fauna and the following key species diagnostic of Mallory's (1959) Penutian Stage: *Anomalina dorri aragonensis, Quinqueloculina yeguaensis, Alabamina wilcoxensis, Cibicides martinezensis, Cibicides whitei,* and *Nonion wilcoxensis* (S. Downs, personal communication). The Penutian Stage, as used in emended sense of Almgren et al. (1988) for shallow-marine strata, is indicative of the middle lower Eocene and correlative to the molluscan "Capay Stage" (Squires et al., 1992). This corresponds well with the average age of 53.1 (± 2.0) Ma reported by Globerman et al. (1982) for basalts in the Black Hills.

The same two microfossil samples studied for benthic foraminifera were also processed for planktonic foraminifera and calcareous nannofossils, but none were found (M. V. Filewicz & S. Downs, personal communication).

SYSTEMATIC PALEONTOLOGY

Class Gastropoda Cuvier, 1797

Subclass Prosobranchia Milne-Edwards, 1848

Order Vetigastropoda Salvini-Plawén, 1980

Family SCISSURELLIDAE Gray, 1847

Subfamily SCISSURELLINAE Gray, 1847

Genus *Scissurella* d'Orbigny, 1824

Type species: *Scissurella laevigata* d'Orbigny, 1824, by subsequent designation (Gray, 1847), Recent, Mediterranean Sea.

Subgenus *Scissurella sensu stricto*

Scissurella (*Scissurella*) ***malloryi*** Squires & Goedert, sp. nov.

(Figures 2–7)

Diagnosis: A *Scissurella sensu stricto* with a nearly flat spire, sculpture beyond the first teleoconch whorl and posterior to the selenizone comprised of about 28 axial ribs and three to five spiral ribs, and sculpture on body whorl anterior to the selenizone comprised of about 28 axial ribs and 15 weaker spiral ribs.

Description: Shell minute, diameter up to 1 mm, thin and fragile, consisting of slightly more than two post-protoconch whorls. Spire small, very slightly elevated (nearly flat), rapidly expanding. Suture incised. Protoconch just less than one whorl (about 70 microns in diameter), convex, with about 10 weak axial riblets; set off from post-protoconch whorls by a prominent varix. Selenizone on upper half of body whorl, starting after the first one-half whorl of teleoconch. Selenizone on shoulder of body whorl, keel-like and bordered by produced edges; slit long. Selenizone regularly lined with prominent, widely spaced axial ribs. First whorl of teleoconch with 17 axial ribs. Beyond first teleoconch whorl and posterior to the selenizone, about 28 arcuately prosocline axial ribs and three to five, less prominent spiral ribs. Body whorl anterior to selenizone with about 28 axial ribs and 15 less prominent spiral riblets, becoming closer spaced toward the umbilicus. Prominent and deep, smooth spiral sulcus present just anterior to selenizone. Base of body whorl rounded. Umbilicus open, deep, funnel-shaped, semilunar, set off from base by spiral cord; lined within by axial growth lines. Aperture circular. Outer lip incised with slit. Columella smooth.

Dimensions of holotype: Height 1 mm, width 1 mm.

Holotype: LACMIP 11354.

Type locality: CSUN loc. 1563, Larch Mountain, Washington, 47°59′03″N, 123°8′2″W.

Paratypes: LACMIP 11355–11357, CSUN loc. 1563.

Discussion: Fifteen specimens were found, all about 1 mm in height. Thirteen of the specimens were found at CSUN loc. 1563; two were found at locality 1564.

The new species is most similar to the living species *Scissurella* (*S.*) *rota* Yaron (1983:268–270, pl. 3; Herbert, 1986:622–623, figs. 25–27) from the Red Sea and Persian Gulf to eastern Cape Province, southern Africa (Herbert, 1986). The new species differs by having stronger and more (three to five rather than one to two) spiral ribs posterior to the selenizone, more axial ribs (28 rather than 20) on the body whorl anterior to the selenizone, sculpture that is not nodulose on the body whorl at the junction of the axial and spiral ribs, and spiral ribs that do not become coarser near the umbilicus.

The new species is also similar to *S.* (*S.*) *costata* d'Orbigny, 1824, from the Canary Islands, Bermuda, and the Mediterranean Sea (Yaron, 1983). Wenz (1938:173, fig. 269) and Batten (1975:figs. 4, 11, 12) also illustrated this species. The new species differs by having spiral ribbing, much weaker axial ribbing, and a deep spiral sulcus anterior to the selenizone.

The new species resembles *Scissurella parisiensis* Deshayes (1866:5, pl. 65, figs. 8–10; Cossmann & Pissarro, 1910–1913:pl. 2, fig. 12-2) from middle Eocene (Lutetian Stage) rocks of the Paris Basin, France, but the new species has a lower spire and a deep spiral sulcus just anterior to the selenizone.

As discussed by Sohl (1992), current workers believe that family Scissurellidae may have originated during the

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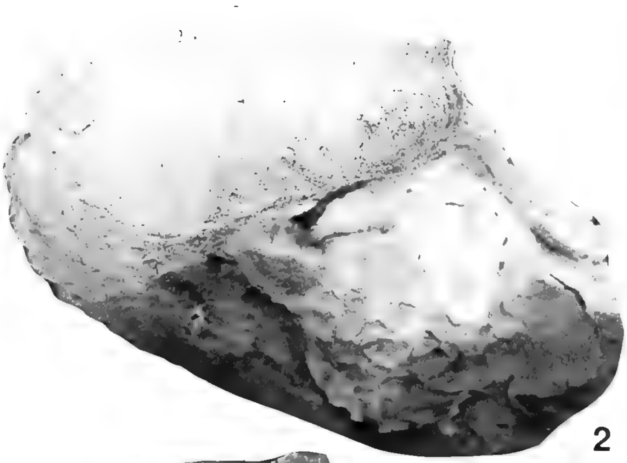
Explanation of Figures 2 to 7

All specimens from CSUN loc. 1563, and all figures = SEM micrographs. Figures 2–7. *Scissurella* (*Scissurella*) ***malloryi*** Squires & Goedert, sp. nov. Figures 2–3. Holotype LACMIP 11354. Figure 2. Apertural view, ×60, height 1.1 mm. Figure 3. Apical view, ×60, maximum diameter 1.45 mm. Figure 4. Paratype LACMIP 11355, abapertural view, ×60, height 1 mm. Figure 5. Paratype LACMIP 11356, umbilical view; ×60, maximum diameter 1.46 mm. Figures 6–7. Paratype LACMIP 11357. Figure 6. Oblique apical view, ×60, maximum diameter 1.2 mm. Figure 7. Apical view of protoconch shown in Figure 6, ×200, maximum length 0.475 mm.



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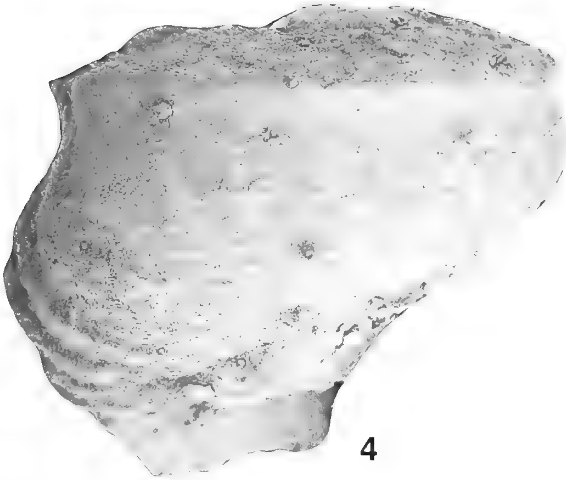

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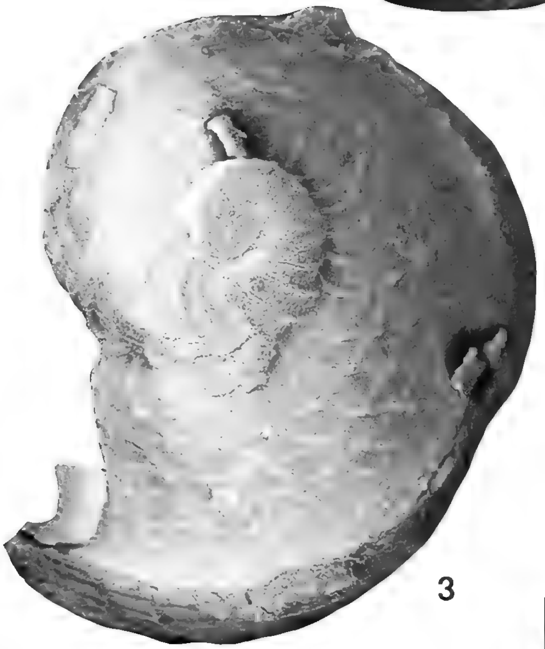

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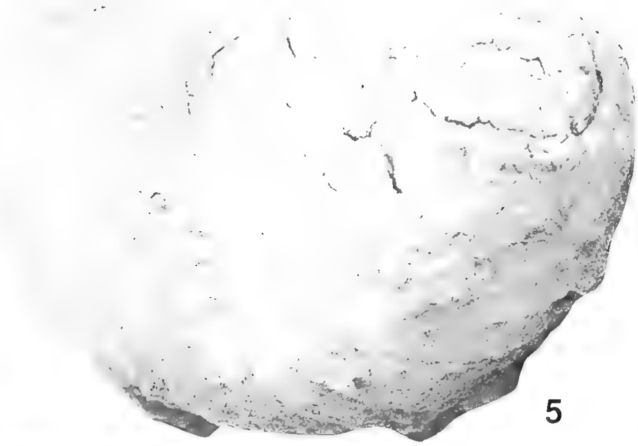

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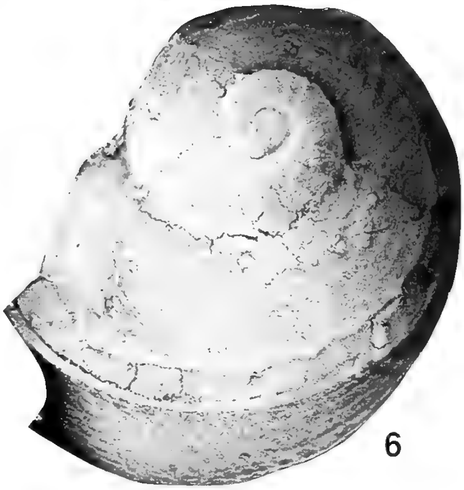

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7

Triassic. Only a single Cretaceous species is known, *Scissurella marchmontensis* Sohl, 1992 from deposits of Late Cretaceous age (Maastrichtian Stage) in Puerto Rico and Jamaica (Sohl, 1992). Sohl's species is similar to *Scissurella sensu stricto,* a taxon that is characterized (McLean, 1967) by a flattened spire, with the selenizone on the upper half of the whorl. The genus is placed in subfamily Scissurellinae because it has a protoconch with distinct axial ribs (Marshall, 1993). The new species has the characteristics of *Scissurella sensu stricto* and, to our knowledge, is the earliest representative of *Scissurella sensu stricto* anywhere. The new species is the first record of *Scissurella sensu stricto* from the Pacific coast of North America. Today, only four cool- to cold-water species of *Scissurella (Anatoma)* are found in northeastern Pacific (McLean, 1967).

Etymology: The new species is named for V. Standish Mallory for his important contributions to the study of Pacific coast of North America benthic foraminiferal biostratigraphy.

Family FISSURELLIDAE Fleming, 1822

Genus *Puncturella* Lowe, 1827

Type species: *Patella noachina* Linnaeus, 1758, by original designation.

Subgenus *Altrix* Palmer, 1942

Type species: *Fissurella altior* Meyer & Aldrich, 1886, by original designation, Eocene, Alabama.

Puncturella (*Altrix*) ***pacifica*** Squires & Goedert sp. nov.

(Figures 8–9)

Diagnosis: A conical *Puncturella* (*Altrix*) with a nearly circular apical perforation and 28 radial ribs crossed by equally strong concentric ribs.

Description: Shell small, up to 2.8 mm height, conical, slightly longer than high. Apex punctate, at summit and slightly forward of center of shell. Apical perforation nearly circular, with four, very minute constrictions. Posterior slope broadly convex, anterior slope very slightly concave and almost straight in profile. Sculpture of 28 strong, raised radial ribs approximately same width as interspaces. Concentric sculpture of equally strong raised ribs. Intersection of two sculpture components producing a rectangularly cancellate pattern. Aperture broadly circular.

Dimensions of holotype: Length 3 mm, width 3 mm, height 2.8.

Holotype: LACMIP 11358.

Type locality: CSUN loc. 1563, Larch Mountain, Washington, 47°59′03″N, 123°8′12″W.

Discussion: Only two specimens were found, both from CSUN loc. 1563. The holotype is moderately well preserved, but the other specimen is poorly preserved. The nomenclatural history of the name *Altrix* is discussed by Sohl (1992).

The new species is most similar to *Puncturella* (*Altrix*) *leesi* Sohl (1992:420, figs. 6.1–6.7), the earliest known species of this genus and known from Upper Cretaceous (Maastrichtian Stage) rocks of Puerto Rico. The new species differs in the following features: smaller shell, more conical shape, 28 rather than 16–17 radial ribs, and finer radial ribs.

The new species is similar to the type species of *Altrix, Puncturella* (*Altrix*) *altior* (Meyer & Aldrich, 1886:41, pl. 1, figs. 16a–16c; Palmer, 1937:30–31, pl. 3, figs. 1, 3, 6, 8) from middle Eocene rocks in Alabama. The new species differs in the following features: smaller, a more centrally located apex, perforation at summit, sculpture not as strong and there is no tendency for it to become nodular or scaly, and the radial ribs show much less tendency to alternate with any secondary radial ribs.

The geologic range of *Altrix* is Late Cretaceous to Recent, and only a few species are known (Sohl, 1992). The new species is the first record of the subgenus *Altrix* from the Pacific coast of North America.

Etymology: The new species is named for the Pacific Ocean.

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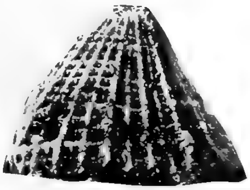
Explanation of Figures 8–21

All specimens from CSUN loc. 1563, and SEM micrographs = Figures 17, 20, 21. Other figures done by the senior author. All non-SEM specimens coated with ammonium chloride. Figures 8–9. *Puncturella* (*Altrix*) ***pacifica*** Squires & Goedert, sp. nov., holotype LACMIP 11358. Figure 8. Left-lateral view, ×8.6, height 2.8 mm. Figure 9. Apical view, ×11, length 3 mm. Figures 10–17. *Arene* ***olympiata*** Squires & Goedert, sp. nov. Figures 10–12. Holotype LACMIP 11359, ×4.9. Figure 10. Apertural view, some shell missing, ×4.9, height 5.7 mm. Figure 11. Abapertural view, ×4.5, height 5.7 mm. Figure 12. Umbilical view, ×4.5, maximum diameter 7.5 mm. Figure 13. Paratype LACMIP 11360, abapertural view, ×2.9, height 8.5 mm. Figures 14–16. Paratype LACMIP 11361, ×11. Figure 14. Apertural view, height 2 mm. Figure 15. Abapertural view, height 2 mm. Figure 16. Umbilical view, maximum diameter 3.1 mm. Figure 17. Paratype LACMIP 11362, apical view, ×60, maximum diameter 1.5 mm. Figures 18–21. *Conomitra* ***capitolina*** Squires & Goedert, sp. nov. Figures 18–19. Holotype LACMIP 11363, ×6.5, height 6.8 mm. Figure 18. Apertural view. Figure 19. Abapertural view. Figures 20–21. Paratype LACMIP 11364, ×40. Figure 20. Apical view, maximum diameter 1.4 mm. Figure 21. Apertural view, height 2.6 mm.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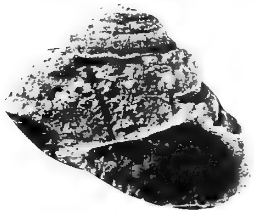
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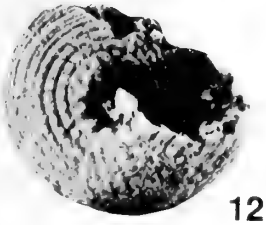
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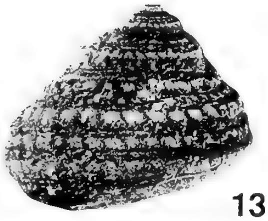
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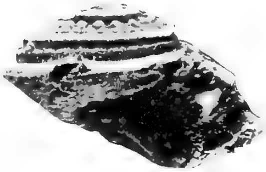
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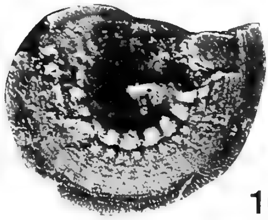
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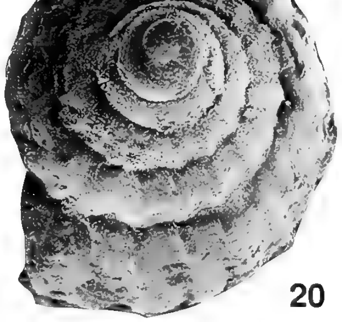
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Family TURBINIDAE Rafinesque, 1815

Subfamily LIOTIINAE Adams & Adams, 1854

Genus *Arene* Adams & Adams, 1854

Type species: *Turbo cruentatus* Megerle von Mühlfeld, 1829, by subsequent designation (Woodring, 1928), Recent, West Indies.

Arene ***olympiata*** Squires & Goedert, sp. nov.

(Figures 10–17)

Diagnosis: An *Arene* having a bicostate juvenile body whorl with the anteriormost carina keel-like, and a noded, tricostate adult body whorl; base of body whorl with about 10 spiral ribs, anteriormost ones stronger and noded.

Description: Shell small, conical-turbiniform, of five angulate whorls with tabulate shoulders. Spire moderately elevated. Protoconch, of about two whorls, very low, covered with very closely spaced growth lines. Keel on periphery of spire whorls beginning after 1½ whorls. Noded spiral ribbing on ramp area of spire whorls beginning after two whorls, with rib nearest the suture the first developed. Spire whorls with four beaded spiral ribs (two on the ramp, one on the periphery, and one anterior to the periphery). Spiral rib on tabulate shoulder the strongest, forming a carina. On specimens less than 5 mm height, body-whorl ramp area with two, equal-sized and noded spiral ribs (interspaces with or without a spiral riblet) and three carinae on the periphery. Anteriormost carina on periphery forming a keel; the other two carinae weaker and noded, with the posteriormost one strongest. On specimens greater than 5 mm height, the three carinae on the periphery approaching each other in strength, all having nodes. Interspaces between carinae with one to two spiral riblets. Anteriormost keeled carina strongly delimiting boundary of base of body whorl. Base moderately convex, covered with about 10 spiral ribs that become stronger and more noded toward the umbilicus. Umbilicus deep, bordered by strongly noded spiral funicular cord. Peristome circular. Inner lip narrow and crenulate. Outer lip moderately thick. Growth lines prosocline.

Dimensions of holotype: Height 5.7 mm, width 7.3 mm.

Holotype: LACMIP 11359.

Type locality: CSUN loc. 1563, Larch Mountain, Washington, 47°59′03″N, 123°8′12″W.

Paratypes: LACMIP 11360–11362, CSUN loc. 1563.

Discussion: Forty-four specimens were found, all from CSUN loc. 1563. Preservation is generally good, although about one-half of the specimens are fragments. There is a growth series, with specimens ranging in height from 0.25 to 12.5 mm. The largest specimen is abraded.

The progressive change on the periphery from three unequal-strength carinae in the juvenile to three equal-strength carinae in the adult is important to note for any future identifications of this species. If it were not for the presence of a growth series of the new species at the type locality, it is likely that two species would have been recognized.

The new species is similar to *Arene mcleani* Squires (1988:9–10, figs. 9–11), the only other species of *Arene* from Paleogene rocks of the Pacific coast of North America. *Arene mcleani* is from "Capay Stage" strata in Lockwood Valley and the Orocopia Mountains, southern California, and from "Capay Stage" strata in Baja California Sur, Mexico (Squires, 1988, 1991; Squires & Demetrion, 1992). The new species differs in the following features: always two spiral ribs on ramp area, three spiral carinae on periphery of the body whorl, carinae thinner and not as strongly noded, carinae interspaces can have a single spiral riblet, anteriormost carina on periphery keel-strength in juveniles and somewhat keel-like in early adults, base more convex and with many more spiral ribs (10 rather than three) that are weaker and less noded.

Etymology: The species is named for the city of Olympia, Washington, which is near the type locality of the new species.

Order Caenogastropoda Cox, 1960

Family VOLUTOMITRIDAE Gray, 1854

Genus *Conomitra* Conrad, 1865

Type species: *Mitra fusoides* Lea, 1833, by subsequent designation (Fischer, 1884), middle Eocene, Alabama.

Conomitra ***capitolina*** Squires & Goedert, sp. nov.

(Figures 18–21)

Diagnosis: A *Conomitra* with 23 axial ribs on body whorl, subangulate shoulder, weak spiral ribs on teleoconch, and four teeth on inner lip.

Description: Shell small, fusiform. Protoconch conical, multispiral, of about three whorls, smooth. Teleoconch of about five whorls. Suture deeply incised. Spire elevated with numerous axial ribs, extending from suture to suture. Shoulder subangulate on all teleoconch whorls. Body whorl with 23 axial ribs, becoming much weaker to obsolete on neck. Teleoconch with spiral striae, not noded where they cross axial ribs. Spiral striae most prominent on neck and siphonal fasciole. Aperture elongate, narrow. Anterior siphonal canal short. Inner lip with four teeth, extending deep into aperture; anteriormost tooth weakest.

Dimensions of holotype: Height 6.8 mm, width 3.5 mm.

Holotype: LACMIP 11363.

Paratype: LACMIP 11364.

Type locality: CSUN loc. 1563, Larch Mountain, Washington, 47°59′03″N, 123°8′12″W.

Discussion: Eight specimens were found; they range in height from 4 to 6.8 mm. Seven of the specimens are from CSUN loc. 1563; one is from CSUN loc. 1564.

The new species resembles certain specimens of *Conomitra fusoides* (Lea, 1833:169, pl. 6, fig. 176) from the middle Eocene Gosport Sand in Alabama. *Conomitra fusoides* has considerable variation, and the specimens that resemble the new species are illustrated in Palmer (1937: pl. 66, figs. 24, 26). The new species differs in the following features: shell less tumid, neck more constricted, and axial ribs less prominent on neck of body whorl.

The new species also resembles LACMIP collection specimens of *Conomitra graniformis* (Lamarck, 1803:59–60; Cossmann & Pissarro, 1910–1913:pl. 42, fig. 202 bis 3) from middle Eocene (Lutetian Stage) rocks of the Paris Basin, France. The new species differs in the following features: axial ribs stronger except on the neck and siphonal fasicole and axial ribs not noded anteriorly near the suture.

The only other species of *Conomitra* from the Pacific coast of North America is *Conomitra washingtoniana* (Weaver, 1912:52–53, pl. 2, fig. 16; 1942:497–498, pl. 95, figs. 8, 9, 16; Dickerson, 1915:pl. 11, figs. 11a, 11b) from the upper middle Eocene Cowlitz Formation, southwestern Washington. Turner (1938) reported that Weaver's species may also be in the upper "Umpqua Formation" of southwestern Oregon. Cernohorsky (1970) assigned Weaver's species to genus *Conomitra.* The new species differs from *C. washingtoniana* in the following features: a slightly narrower shell, well-developed axial ribbing rather than a nearly smooth shell with microscopic spiral lines and faint axial ribs on the shoulder, and a subangulate shoulder.

Conomitra ranges from the Paleocene to the Pliocene (Wenz, 1943). Although the genus has been found in the Old World, it was most common in Paleocene to upper Eocene rocks of the Gulf Coast (Palmer, 1937; Palmer & Brann, 1965–1966).

Etymology: The species is named in reference to the proximity of the type locality to both Capitol Peak, in the Capitol Forest, and to the capitol of Washington State.

Subclass Heterobranchia Gray, 1840

Order Heterostropha Fischer, 1885

Family ORBITESTELLIDAE Iredale, 1917

Genus *Orbitestella* Iredale, 1917

Type species: *Cyclostrema bastowi* Gatliff, 1906, by monotypy, Recent, Victoria, southeast Australia.

Orbitestella **palaiopacifica** Squires & Goedert, sp. nov.

(Figures 22–26)

Diagnosis: An *Orbitestella* with an upper whorl surface crossed by narrow axial ribs, a keel-like carina on the shoulder, axial ribs in the interspace between the carina on the basal margin and the carina on the edge of the umbilicus, and a wide but deep umbilicus showing overlapping whorls in its interior.

Description: Shell minute, discoidal, with a flat spire and a sunken apex. Protoconch about 1½ whorls, apparently smooth. Teleoconch 2 to 2½ whorls with a hump (ridgelike swollen area) in middle of whorl on first teleoconch whorl but near the deep suture on subsequent whorls. Teleoconch whorls crossed with about 70 axial ribs, tending to become obsolete near outer lip. A well-developed keel-like carina on the shoulder just anterior of the hump; keel-like carina beginning at about 2¾ whorl, very wide for one-half of whorl, then narrower. Another carina on the basal margin. Area between these two carinae smooth and sloping inward. A third carina on the prominent edge of the umbilicus. Interspace between carina on the basal margin and carina on the edge of the umbilicus concave with numerous axial ribs. Umbilicus wide and deep. Interior of umbilicus showing overlapping whorls. Area between carina on edge of umbilicus and the suture smooth and steep. Aperture quadratelike with sinuations corresponding to the hump, to the keeplike carina, and to the carina on the basal margin.

Dimensions of holotype: Height 0.30 mm, diameter 0.53 mm.

Holotype: LACMIP 11365.

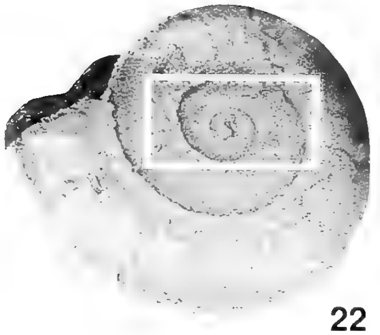
Type locality: CSUN loc. 1563, Larch Mountain, Washington, 47°59′03″N, 123°8′12″W.

Paratypes: LACMIP 11366–11367.

Discussion: Fourteen specimens were found, all about 0.3 mm in height. Ten of the specimens were found at CSUN loc. 1563; two were found at locality 1564.

The new species is most similar to *Orbitestella plicatella* (Cossmann, 1888:225, pl. 11, figs. 43–45; Cossmann & Pissarro, 1910–1913:pl. 6, fig. 105-2; Gougerot & Le Renard, 1977:14–15, fig. 16; Dolin et al., 1980:pl. 3, figs. 34a, 34b) from middle Eocene through lower Oligocene (middle Lutetian through lower Stampien) strata in the Paris Basin, France (Gougerot & Le Renard, 1977). Lozouet & Maestrati (1982) gave a synonymy of this species. Although the new species and *O. plicatella* have essentially identical basal faces, the new species differs in the following features: many more and stronger axial ribs, axial ribbing on dorsal side stronger, suture deeper, and hump on dorsal surface of whorl located closer to the suture.

The new species is also similar to the only other described Eocene species of *Orbitestella,* which is *O. planibasis* (Gougerot & Le Renard, 1977:14–15, figs. 15a–15c) from middle Eocene through upper middle Eocene (middle Lutetian through lower Bartonian) strata in the Paris Basin, France. The new species differs in the following features: axial ribs narrower and not knoblike, a more



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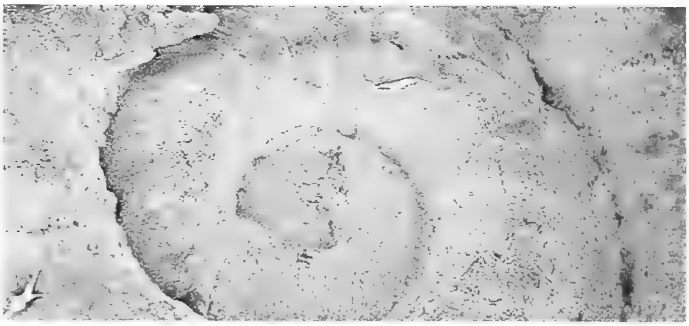

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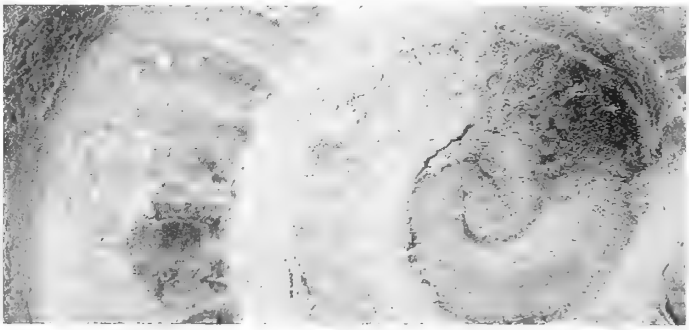

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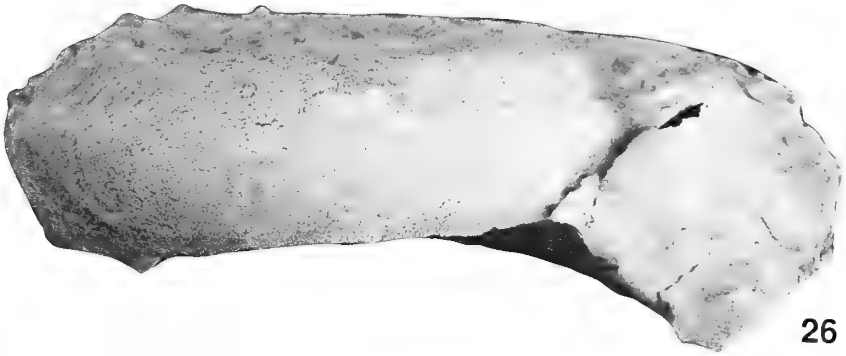

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Explanation of Figures 22–26

All specimens from CSUN loc. 1563, and all figures = SEM micrographs. Figures 22–26. *Orbitestella* ***palaiopacifica*** Squires & Goedert, sp. nov. Figures 22–23. Holotype LACMIP 11365. Figure 22. Apical view, ×60, maximum diameter 0.82 mm. Figure 23. Close-up of apex, box on Figure 22 shows area of coverage ×240, maximum length 0.38 mm. Figures 24–25. Paratype LACMIP 11366. Figure 24. Umbilical view, ×60, maximum diameter 0.65 mm. Figure 25. Close-up of umbilicus, box on Figure 24 shows area of coverage, ×240, maximum length 3.8 mm. Figure 26. Paratype LACMIP 11367, apertural view, ×90, diameter 1.2mm.

prominent keel, and a sloping smooth area in the umbilicus just anterior to suture rather than a vertical area.

The new species is also similar to *Orbitestella diegensis* (Bartsch, 1907:172–173, figs. 7a–c), which is the only species of *Orbitestella* living along the Pacific coast of North America. It is found from Monterey Bay, central California, to northern Baja California, and is common in coarse sand near kelp (McLean, 1978). The new species differs in the following features: the hump on the dorsal surface is lower, the keel is weaker and not noded, there are no spiral ribs between the keel and the basal margin, the border along the umbilicus is stronger, and fewer and coarser spiral ribs are present on the base.

The new species superficially resembles certain Cretaceous species of genus *Neamphitomaria* Bandel, 1988, that Bandel (1988) assigned to family Omalogyridae. Although *Neamphitomaria stantoni* (Sohl, 1960:67, pl. 6, figs. 29, 39, 43, 44; Dockery, 1993:92, pl. 35, figs. 1–3) and *N. planospira* Dockery (1993:93, pl. 35, figs. 4–8), both from Upper Cretaceous (Campanian Stage) strata in Mississippi, superficially resemble the new species, the new species differs by having a smooth protoconch, overlapping whorls within the umbilicus, a carina bordering the umbilicus, and fewer, much more widely spaced axial ribs.

The geologic range of genus *Neamphitomaria* is Late Cretaceous (Campanian Stage) to Eocene (Dockery, 1993). Bandel (1988) placed only one Eocene species, *Neamphitomaria rotella* (Lea, 1833:123, pl. 4, fig. 112; Palmer, 1937: 176, pl. 21, figs. 8, 13; Bandel, 1988:pl. 3, fig. 5; pl. 4, figs. 7, 8, text fig. 3) from the middle Eocene Gosport Sand, Alabama, in his genus. The new species differs from *Neamphitomaria rotella* in the following features: there is a hump on the dorsal surface, there are axial ribs, and the umbilicus is deeper.

The Orbitestellidae are minute, mainly southern hemisphere gastropods. Most species live beneath rocks and among coralline algae in the low intertidal zone (Ponder, 1990). The familial taxonomic position of the orbitestellids was unclear until anatomical work by Ponder (1990) showed them to be primitive heterobranchs, even though their protoconchs are not heterotrophic. Orbitestellids may have originated during the Middle Jurassic in New Zealand, and undescribed species are known from Eocene and Miocene rocks in southern Australia (Ponder, 1990; Beu & Maxwell, 1990).

The genus *Orbitestella* ranges with certainty from the middle early Eocene to Recent. The only described Eocene and Oligocene species are reported from the Paris Basin, France (Cossmann, 1888; Gougerot & Le Renard, 1977; Lozouet & Maestrati, 1982) and from Washington (herein). The Washington occurrence is the earliest record of *Orbitestella* anywhere and is the first fossil record of this genus from the Pacific coast of North America.

Etymology: The new species is named for the ancient Pacific Ocean, and the name is derived from *palaios,* Greek, meaning ancient.

Family OMALOGYRIDAE Sars, 1878

Genus *Ammonicera* Vayssière, 1893

Type species: *Homalogyra fischeriana* Monterosato, 1869, by monotypy, Recent, Atlantic Ocean.

Ammonicera **benhami** Squires & Goedert, sp. nov.

(Figures 27–32)

Diagnosis: An *Ammonicera* whose protoconch has a spiral cord and whose teleoconch has broad axial tubercules.

Description: Shell minute, planispiral. Protoconch ¾ whorl, with a low hump. Sutural area of protoconch bearing a spiral cord, bordered by a narrow groove on its inside. Suture deeply incised. Teleoconch almost two whorls with identical sculpture on both sides of whorls. Sculpture of about 27 axial ribs, nodelike and medially located for the first one-half whorl, flattened and extending as broad tubercles across the whorl for remaining whorls. Nine tubercles on first whorl of teleoconch. Upper and lower periphery of body whorl showing a spiral cord, interspace smooth and vertical on early part of teleoconch but bulging on latter part. Aperture quadrate, continuous.

Dimensions of holotype: Height 0.20 mm, diameter 0.59 mm.

Holotype: LACMIP 11368.

Type locality: CSUN loc. 1563, Larch Mountain, Washington, 47°59′03″N, 123°8′12°W.

Paratypes: LACMIP 11369–11371.

Discussion: Seven specimens were found, all are from CSUN loc. 1563. They range from 0.4 to 0.59 mm in diameter.

Due to the small size of the species of the family Omalogyridae, there have not been many systematic studies of living species, and the fossil record of this family is very poorly known. In recent years, the genera *Ammonicera* Vayssière, 1893, and *Omalogyra* Jeffreys, 1860, have been the most recognized by workers. There has not been consistency, however, in their usage, with some species assigned to one genus for awhile and then assigned to the other one. The work of Sleurs (1984) and Rolán (1992) has helped to refine the current thinking on diagnostic characters of each genus. Ammonicera has a groove on the protoconch, and the teleoconch has strong axial ribs (Sleurs, 1984). *Omalogyra* has a smooth protoconch or one covered with small tubercles, and the teleoconch is smooth but with a few undulated axial ribs more evident near the suture (Rolán, 1992). The new species is placed in genus *Ammonicera* because the protoconch has a shallow groove and the teleoconch has well-developed axial ribs.

The sculpture of the teleoconch of the new species is most similar to *Ammonicera sculpturata* Rolán (1992:40, figs. 9, 12, 14), which lives in the waters surrounding Cuba. The new species differs by not having three spiral cords on the protoconch and by not having any undulated spiral striae between the periphery and the row of axial tubercles on the teleoconch.

The new species is one of the two earliest known, named species of *Ammonicera.* The other species is *Ammonicera rota* (Forbes & Hanley, 1850:160, pl. 73, fig. 10; pl. 88, figs. 1, 2; Fretter & Graham, 1978:223–224, fig. 187) that ranges in age from the middle Eocene (Lutetian Stage) in the Paris Basin, France, to the Recent in Norway and the Mediterranean (Fretter & Graham, 1978; Lozouet & Maestrati, 1982; Sleurs, 1984). It lives among seaweeds, in rock pools, and also on sandy bottoms in depths of up to 25 m (Fretter & Graham, 1978). Fretter & Graham (1978) included only Recent taxa in their synonymy of *A. rota.* The new species differs from *A. rota* in the following features: fewer axial ribs and more widely spaced, axial ribs on the first one-half of the teleoconch nodelike rather than narrow and long, and axial ribs on the remaining


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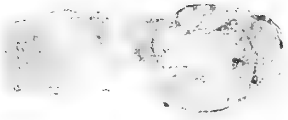
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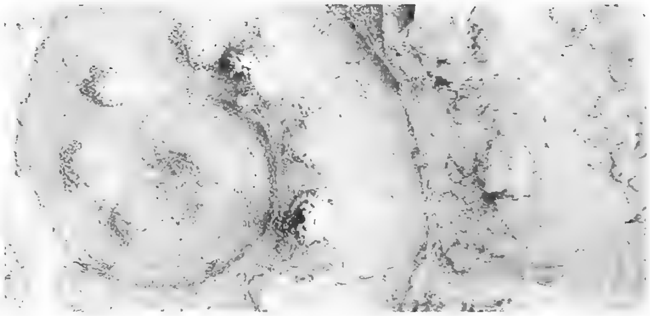
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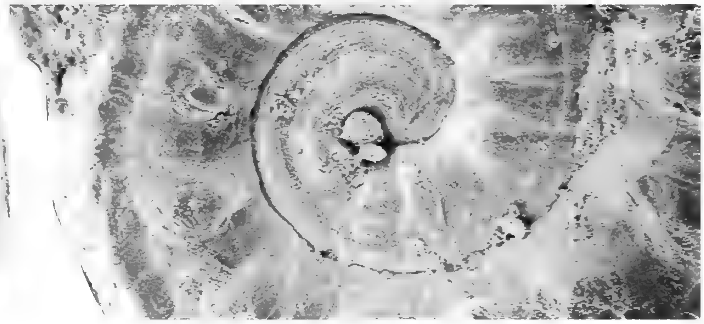
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Explanation of Figures 27 to 32

All specimens from CSUN loc. 1563, and all figures = SEM micrographs. Figures 27–32. *Ammonicera* ***benhami*** Squires & Goedert, sp. nov. Figure 27. Holotype LACMIP 11368, apical view, ×150, maximum diameter 0.55 mm. Figures 28–29. Paratype LACMIP 11369. Figure 28. Apical view, ×60, maximum diameter 0.59 mm. Figure 29. Close-up of apex, box on Figure 28 shows area of coverage, ×240, maximum length 0.36 mm. Figure 30. Paratype LACMIP 11370, apertural view, ×100, diameter 0.4 mm. Figures 31–32. Paratype LACMIP 11371. Figure 31. Umbilical view, ×150, maximum diameter 0.55 mm. Figure 32. Close-up of umbilicus shown in Figure 31, ×240, maximum length 0.38 mm.

part of the teleoconch broad and flattened rather than narrow.

Lozouet & Maestrati (1982) included a fossil species in their synonymy of *A. rota*. They reported that *Homalogyra eocaenica* Allix (1923:19–20, pl. 1, figs. 4, 4a–c) from middle Eocene (Lutetian Stage) rocks of the Paris Basin, France is conspecific with *A. rota*. Gougerot & Le Renard (1977), furthermore, reported that *H. eocaenica* Allix is also conspecific with *Homalogyra praecursor* Gougerot (1965:296–297, pl. 5, fig. 1) from middle Eocene (Lutetian Stage) rocks of the Paris Basin, France. Another species, *Homalogyra cavelieri* Gougerot (1968:222–223, pl. 1, fig. 7) from upper middle Eocene (lower Bartonian Stage) rocks of the Paris Basin, France, was regarded by Dolin et al. (1980) to be a subspecies of *H. eocaenica* Allix. The new species differs from *H. eocaenica cavelieri* by having wider and more elongate ribs and by not having a smooth body whorl.

Bandel (1988:pl. 1, fig. 7; pl. 3, fig. 6) illustrated an *Ammonicera* sp. from middle Eocene (Lutetian Stage) rocks of the Paris, France area. The new species differs in the following features: shoulder area nearly vertical rather than broadly rounded, axial ribs noded to broadly elliptical rather than narrow, and fewer axial ribs.

The shells of *Ammonicera,* as well as of *Omalogyra,* resemble minute ammonites in that each side is a mirror image of the other. The ammonite shape reflects how the shell is carried; namely, with the aperture directed forward, rather than being carried (as in most gastropods) with the under surface resting on the foot. Thus, the entire animal appears to be bilaterally symmetrical when crawling (Moore, 1971).

Few fossil or modern-day species of *Ammonicera* are known. They have been inadequately studied because of their small size. Only five modern-day species of *Ammonicera* are known from the Indo-Pacific region where they are found associated with coral rubble, covered by *Halimeda* algae, in depths of 1 to 7 m (Sleurs, 1985a, b). About the same number of modern-day species of *Ammonicera* are known from Cuba where they are usually found in depths of 2 to 5 m and no deeper than 20 m (Rolán, 1992). Rios (1985) reported a single species of *Ammonicera* living from Labrador to Florida and in Brazil. As mentioned above, *Ammonicera rota* is found along the North Atlantic coast off of Europe and also in the Mediterranean.

The geologic range of genus *Ammonicera* is middle early Eocene to Recent, and *A. benhami* is the earliest record of this genus. The new species is the first record of genus *Ammonicera* from the Pacific coast of North America.

Etymology: The new species is named for geologist Steven R. Benham (Pacific Lutheran University, Tacoma, Washington).

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LOCALITIES CITED

CSUN 1563. At elevation of 2230 ft. (680 m), exposed in roadcut on NE side of logging road, latitude 47°59'03"N, longitude 123°8'12"W, 300 m N and 50 m E of SW corner of section 1, T. 17 N, R. 4 W, and 500 m S32 E of Larch Mountain, U.S. Geological Survey, 7.5-minute, Capitol Peak Quadrangle, provisional edition 1986, Black Hills, Thurston County, Washington. Upper part of the Crescent Formation. Age: Middle early Eocene ("Capay Stage"). Collectors: J. L. & G. H. Goedert, July, 1992.

CSUN 1564. At elevation of 1738 feet (530 m), on N side of logging road, 800 m N and 50 m W of SE corner of section 25, T. 18 N, R. 3 W, and 950 m N25 W of Rock Candy Mountain, U.S. Geological Survey, 7.5-minute Summit Lake Quadrangle, 1981, Black Hills, Thurston County, Washington. Upper part of the Crescent Formation. Age: Middle early Eocene ("Capay Stage"). Collectors: J. L. & G. H. Goedert, August, 1992.

LITERATURE CITED

ADAMS, H. & A. ADAMS. 1853–1858. The Genera of Recent Mollusca; Arranged According to their Organization. 3 Vols. John Van Voorst: London. 1145 pp., 138 pls.

ALLIX, M. 1923. Sur les *Homalogyra* fossiles spécialement dans le Tertiaire de Bretagne. Bulletin Société Géologique et Mineralogique de Bretagne 4(1):18–21, pl. 1.

ALMGREN, A. A., M. V. FILEWICZ & H. L. HEITMAN. 1988. Lower Tertiary foraminiferal and calcareous nannofossil zonation of California: an overview and recommendation. Pp. 83–105 in M. V. Filewicz & R. L. Squires (eds.), Paleogene Stratigraphy, West Coast of North America. Pacific Section, Society of Economic Paleontologists and Mineralogists, West Coast Paleogene Symposium Vol. 58: Los Angeles, California.

ARMENTROUT, J. M. 1975. Molluscan biostratigraphy of the Lincoln Creek Formation, southwest Washington. Pp. 14–48 in D. W. Weaver, G. R. Hornaday & A. Tipton (eds.), Paleogene Symposium & Selected Technical Papers, Conference on Future Energy Horizons of the Pacific Coast. Pacific Sections, American Association of Petroleum Geologists, Society of Economic Paleontologists and Mineralogists, and Society of Economic Geologists: Los Angeles, California.

BABCOCK, R. S., R. F. BURMESTER, D. C. ENGEBRETSON & A. WARNOCK. 1992. A rifted margin origin for the Crescent basalts and related rocks in the northern Coast Range volcanic province, Washington and British Columbia. Journal of Geophysical Research 97(B5):6799–6821.

BABCOCK, R. S., C. A. SUCZEK & D. C. ENGREBRETSON. 1994. The Crescent "terrane," Olympic Peninsula and southern Vancouver Island. Pp. 141–147 in R. Lasmanis & E. S. Cheney (convenors), Regional Geology of Washington State. Washington Division of Geology and Earth Resources Bulletin 80: Olympia, Washington.

Bandel, K. 1988. Reprasentieren die Euomphaloidea eine naturliche einheit der gastropoden. Mitteilungen Geologisch-Paläontologisches Institut, Universitat Hamburg, Germany 67:1–33, 7 pls.

Bartsch, P. 1907. New mollusks of the family Vitrinellidae from the west coast of America. Proceedings of the United States National Museum 32:167–176, figs. 1–11.

Batten, R. L. 1975. The Scissurellidae—are they neotenously derived fissurellids? (Archaeogastropoda). American Museum Novitates 2567:1–29, figs. 1–37.

Beu, A. G. & P. A. Maxwell. 1990. Cenozoic Mollusca of New Zealand. New Zealand Geological Survey Paleontological Bulletin 58:1–518, pls. 1–57.

Cernohorsky, W. O. 1970. Systematics of the families Mitridae & Volutomitridae (Mollusca: Gastropoda). Bulletin of the Auckland Institute and Museum 8:1–190, pls. 1–18.

Clark, B. L. & H. E. Vokes. 1936. Summary of marine Eocene sequence of western North America. Bulletin of the Geological Society of America 47:851–878, pls. 1–2.

Conrad, T. A. 1865. Descriptions of new Eocene shells from Enterprise, Mississippi. American Journal of Conchology 1(2):137–141, pls. 10–11.

Cossmann, M. 1888. Catalogue illustré des coquilles fossiles de l'Éocène des environs de Paris. Fascicule 3. Annales de Société Royale Malacologique de Belgique 23:3–324, pls. 1–13.

Cossmann, M. & G. Pissarro. 1910–1913. Iconographie complète des coquilles fossiles de l'Éocène des environs de Paris. Vol. 2 (Scaphopodes, Gastropodes, Céphalopodes, Brachiopodes et Supplément). H. Bouillant: Paris. 65 pls.

d'Orbigny, A. D. 1824. Monographie d'un nouveau genre de mollusque gastéropode de la famille des trochoides. Mémoire Société d'Histoire Naturelle Paris 1:340–345, pl. 23.

d'Orbigny, A. D. 1839. Mollusques, . . . 152 pp., 15 pls. in P. B. Webb & S. Berthelt, Histoire Naturelle des Iles Canaries. Vol. 2.

Deshayes, G.-P. 1866. Description des animaux sans vertèbres découverts dans le bassin de Paris. Vol. 3 (Texte):1–667. Atlas (Part2):pls. 1–107. J.-B. Baillière et Fils: Paris.

Dickerson, R. E. 1915. Fauna of the type Tejon: its relation to the Cowlitz phase of the Tejon Group of Washington. Proceedings of the California Academy of Sciences, fourth series, 5(3):33–98, pls. 1–11.

Dockery, D. T. III. 1993. The streptoneuran gastropods, exclusive of the Stenoglossa, of the Coffee Sand (Campanian) of northeastern Mississippi. Mississippi Department of Environmental Quality Office of Geology Bulletin 129:191 pp., 42 pls.

Dolin, C., L. Dolin & J. Le Renard. 1980. Inventaire systématique des mollusques de l'Auversien a "faciès Charrié" de Baron (Oise), et remarques paléontologiques. Bulletin d'Information des Géologues du Bassin de Paris 17(2):26–28, pls. 1–3.

Duncan, R. A. 1982. A captured island chain in the Coast Range of Oregon and Washington. Journal of Geophysical Research 7:10,827–10,837.

Fischer, P. H. 1880–1887. Manuel de conchyliologie et de paléontologie conchyliologique ou histoire naturelle des mollusques vivants et fossiles. F. Savy: Paris. 1369 pp., 23 pls. [1884, fascicule 7:609–688].

Forbes, E. & S. Hanley. 1849–1853. A History of British Mollusca and Their Shells. Vol. 3. John Van Voorst: London. 616 pp.

Fretter, V. & A. Graham. 1978. The prosobranch molluscs of Britain and Denmark. Journal of Molluscan Studies, Supplement 6:153–241, figs. 131–195.

Gatliff, J. H. 1906. On some Victorian marine Mollusca, new species and other little-known. Proceedings of the Royal Society of Victoria, new series, 19:1–4.

Givens, C. R. 1974. Eocene molluscan biostratigraphy of the Pine Mountain area, Ventura County, California. University of California Publications in Geological Sciences 109: 1–107, pls. 1–11.

Globerman, B. R., M. E. Beck, Jr. & R. A. Duncan. 1982. Paleomagnetism and tectonic significance of Eocene basalts from the Black Hills, Washington Coast Range. Geological Society of America Bulletin 93:1151–1159.

Gougerot, L. 1965. Présentation de cinq espèces nouvelles et de nouveaux représentants de gastéropodes dans le Lutétian et le Bartonien du bassin de Paris. Bulletin de la Société Geologique de France, série 7, 7:296–301, pl. 5.

Gougerot, L. 1968. Quelques espèces nouvelles de mollusques de l'Éocène du Bassin de Paris. Bureau de Recherches Géologiques et Minières. Memoire 58 (Colloque sur l'Éocène), pp. 221–243, pl. 1.

Gougerot, L. & J. Le Renard. 1977. Nouvelle espèces de petits gastéropodes marins de l'Éocène des bassins de Paris, de Nantes et du Cotentin. Bulletin d'Information des Geologues du Bassin de Paris 14(4):3–33, figs. 1–38.

Gray, J. E. 1847. A list of the genera of recent Mollusca. Zoological Society of London Proceedings 179(pt. 15):129–219.

Haszprunar, G. 1988. On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. Journal of Molluscan Studies 54:367–441.

Herbert, D. G. 1986. A revision of the southern African Scissurellidae (Mollusca: Gastropoda: Prosobranchia). Annals of the Natal Museum 27(2):601–632, figs. 1–39.

Iredale, T. 1917. More molluscan name-changes, generic and specific. Proceedings of the Malacological Society 12(6):322–330.

Jeffreys, G. 1860. Sur le mollussque désigné par MM. Forbes et Hanley sous le nom de *Skenea nitidissima.* Journal de Conchyliologie 8:108–111.

Lamarck, J. B. 1802–1809. Mémoires sur les fossiles des environs de Paris. Annales du Muséum National d'Histoire: Paris. Variously paged.

Lea, I. 1833. Contributions to Geology. Philadelphia. 227 pp., 6 pls.

Linnaeus, C. 1758. Systema naturae per regna tria naturae. Editio 10, reformata, Regnum animale. Vol. 1. Holmiae. 1327 pp.

Lowe, R. T. 1827. On *Balanus punctatus, Puncturella flemingii.* etc., together with some corrections relative to *Turbo carneus,* and some of the Chitones before described. Zoological Journal 3:76–80.

Louzouet, P. & P. Maestrati. 1982. Nouvelles espèces de mollusques de l'Oligocène (Stampien) pour les bassins de Paris et d'Aquitaine. Archiv für Molluskenkunde 112:165–189, pl. 6.

McLean, J. H. 1967. West American Scissurellidae. The Veliger 9(4):404–410, pl. 56.

McLean, J. H. 1978. Marine shells of southern California, revised edition. Natural History Museum Los Angeles County, Science Series 24:1–104, figs. 1–54.

Mallory, V. S. 1959. Lower Tertiary Biostratigraphy of the California Coast Ranges. The American Association of Petroleum Geologists: Tulsa, Oklahoma. 416 pp.

Marshall, B. A. 1993. The systematic position of *Larochea* Finlay, 1927, and introduction of new genus and two new species (Gastropoda: Scissurellidae). Journal of Molluscan Studies 59:285–294, figs. 1–4.

MEGERLE VON MÜHLFELD, J. K. 1829. Fortsetzung von Johann Karl Megerle von Mühlfeld's Beschreibung einiger neuen Conchylien. Magazin der Gesellschaft Naturforschung Freunde zu Berlin 1(pt. 4):205–221, 3 pls.

MEYER, O. & T. H. ALDRICH. 1886. The Tertiary fauna of Newton and Wautubee, Mississippi. Cincinnati Society of Natural History Journal 9(2):40–50, 64, pl. 2.

MONTEROSATO, T. A. DI. 1869. Description d'espèces nouvelles de la Méditerranée. Journal de Conchyliologie 42: 274–277.

MOORE, D. R. 1971. A deep water *Omalogyra* in the western Atlantic. The Nautilus 84(4):113–117, fig. 1.

NESBITT, E. A., K. A. CAMPBELL & J. L. GOEDERT. 1994. Paleogene cold seeps and macroinvertebrate faunas in a forearc sequence of Oregon and Washington. Pp. 1D-1–1D-11 in D. A. Swanson & R. A. Haugerud (eds.), Geologic Field Trips in the Pacific Northwest. Geological Society of America Annual Meeting, Seattle, Washington.

PALMER, K. V. W. 1937. The Claibornian Scaphopoda, Gastropoda and dibranchiate Cephalopoda of the southern United States. Bulletins of American Paleontology 7(32):1–730, 1–90.

PALMER, K. V. W. 1942. Substitutes for molluscan homonyms. Journal of Paleontology 16:674.

PALMER K. V. W. & D. C. BRANN. 1956–1966. Catalogue of the Paleocene and Eocene Mollusca of the southern and eastern United States. Bulletins of American Paleontology 48(218):1–1057, pls. 1–5.

PONDER, W. F. 1990. The anatomy and relationships of the Orbitestellidae (Gastropoda: Heterobranchia). Journal of Molluscan Studies 56:515–532, figs. 1–3.

PONDER, W. F. & A. WARÉN. 1988. Classification of the Caenogastropoda and Heterostropha—a list of the family-group names and higher taxa. Malacological Review, Supplement 4:288–326.

RIOS, E. C. 1985. Seashells of Brazil. Empresas Ipiranga: Rio Grande, Brazil. 351 pp., pls. 1–32.

ROLÁN, E. 1992. The family Omalogyridae G. O. Sara, 1878 (Mollusca, Gastropoda) in Cuba. Apex 7(2):35–46, figs. 1–28.

SLEURS, W. 1984. The marine microgastropods from the northern coast of Papua New Guinea (Mollusca: Gastropoda). 1. Family: Omalogyridae (with description of two new species). Bulletin Institut Royal des Sciences Naturelles de Belgique, Biologie 55(2):1–11, pl. 1.

SLEURS, W. 1985a. Marine microgastropods from the Republic of Maldives. 1. Genus *Ammonicera* Vayssière, 1893, with description of four new species (Prosobranchia: Omalogyridae). Basteria 49:19–27, figs. 1–18.

SLEURS, W. 1985b. *Ammonicera angulata* sp. nov. from Laing Island, Papua New Guinea, with comments on the genus *Ammonicera* Vayssiere, 1893 (Mollusca: Gastropoda). Annales Société Royale Zoologique de Belgique 115(2):177–181, pl. 1.

SNAVELY, P. D., JR. 1987. Tertiary geologic framework, neotectonics, and petroleum potential of the Oregon–Washington continental margin. Pp. 305–335 in D. W. Scholl, A. Grantz & J. G. Vedder (eds.), Geology and Resources Potential of the Continental Margin of Western North America and Adjacent Ocean Basins—Beaufort Sea to Baja California. Circum-Pacific Council for Energy and Mineral Resources, Earth Science Series, Vol. 6: Houston, Texas.

SOHL, N. F. 1960. Archeogastropoda, Mesogastropoda and stratigraphy of the Ripley, Owl Creek, and Prairie Bluff Formations. U.S. Geological Survey Professional Paper 331-A:1–151, pls. 1–18.

SOHL, N. F. 1992. Upper Cretaceous gastropods (Fissurellidae, Haliotidae, Scissurellidae) from Puerto Rico and Jamaica. Journal of Paleontology 66(3):414–434, figs. 1–10.

SQUIRES, R. L. 1988. Eocene macropaleontology of northern Lockwood Valley, Ventura County, California. Natural History Museum of Los Angeles County, Contributions in Science 398:1–23, figs. 1–55.

SQUIRES, R. L. 1991. Molluscan paleontology of the lower Eocene Maniobra Formation, Orocopia Mountains, southern California. Pp. 217-226, pls. 1–2 in P. L. Abbott & J. A. May (eds.), Eocene Geologic History San Diego Region. Pacific Section, Society of Economic Paleontologists and Mineralogists, Vol. 68: Los Angeles.

SQUIRES, R. L. 1992. New occurrences of the malleid bivalve *Nayadina* (*Exputens*) from the Eocene of Jamaica, Mexico, and Washington. The Veliger 35(2):133–136, figs. 1–6.

SQUIRES, R. L. 1993. Earliest record of the anomiid bivalve *Pododesmus*: a new species from the lower Eocene of western Washington. The Veliger 36(3):270–275, figs. 1–9.

SQUIRES, R. L. & R. A. DEMETRION. 1992. Paleontology of the Eocene Bateque Formation, Baja California Sur, Mexico. Natural History Museum of Los Angeles County, Contributions in Science 434:1–55, figs. 1–144.

SQUIRES, R. L. & J. L. GOEDERT. 1994a. Macropaleontology of the Eocene Crescent Formation in the Little River area, southern Olympic Peninsula, Washington. Natural History Museum of Los Angeles County, Contributions in Science 444:32, 62 figs.

SQUIRES, R. L. & J. L. GOEDERT. 1994b. New species of early Eocene small to minute mollusks from the Crescent Formation, Black Hills, southwestern Washington. The Veliger 37(3):253–366, figs. 1–29.

SQUIRES, R. L. & J. L. GOEDERT. 1995. New species of middle Eocene gastropods from the northern Doty Hills, southwestern Washington. The Veliger 38(3):254-269, figs. 1–18.

SQUIRES, R. L., J. L. GOEDERT & K. L. KALER. 1992. Paleontology and stratigraphy of Eocene rocks at Pulali Point, Jefferson County, eastern Olympic Peninsula, Washington. Washington Division of Geology and Earth Resources, Report of Investigations 31:1–27, pls. 1–3.

SUCZEK, C. A., R. S. BABCOCK & D. C. ENGEBRETSON. 1994. Tectonostratigraphy of the Crescent terrane and related rocks, Olympic Peninsula, Washington. Pp. 1H-1–1H-10 in D. A. Swanson & R. A. Haugerud (eds.), Geologic Field Trips in the Pacific Northwest. Geological Society of America Annual Meeting: Seattle, Washington.

TURNER, F. E. 1938. Stratigraphy and Mollusca of the Eocene of western Oregon. Geological Society of America Special Papers 10:1–130, pls. 1–22.

VAYSSIÈRE, A. 1893. Observations zoologiques et anatomiques sur l'Ammonicera, nouveau genre de gastéropodes prosobranche. Annales des Faculté Science de Marseille 3:15–28.

WEAVER, C. E. 1912. A preliminary report on the Tertiary paleontology of western Washington. Washington Geological Survey Bulletin 15:1–80, pls. 1–15.

WEAVER, C. E. 1942. Paleontology of the marine Tertiary formations of Oregon and Washington. University of Washington, Publications in Geology 5 (Parts 1–3):1–789, pls. 1–104 [reprinted, 1958].

WEAVER, C. E. & K. V. W. PALMER. 1922. Fauna from the Eocene of Washington. University of Washington Publications in Geology 1(3):1–56, pls. 8–12.

WELLS, R. E., D. C. ENGEBRETSON, P. D. SNAVELY, JR. & R. S. COE. 1984. Cenozoic plate motions and the volcanotectonic evolution of western Oregon and Washington. Tectonics 3:275–294.

Wenz, W. 1938. Familia Scissurellidae. Pp. 172–174, figs. 269–274 in O. H. Schindewolf (ed.), Handbuch de Paläozoologie, Band 6, Prosobranchia, Teil 6. Gebrüder Borntraeger: Berlin [reprinted 1960–1961].

Wenz, W. 1943. Subfamilia Vexillinae. Pp. 1284–1290, figs. 3657–3676 in O. H. Schindewolf (ed.), Handbuch de Paläozoologie, Band 6, Prosobranchia, Teil 6. Gebrüder Borntraeger: Berlin [reprinted 1960–1961].

Woodring, W. P. 1928. Miocene mollusks from Bowden, Jamaica. Part 2. Gastropods and discussion of results. Carnegie Institute of Washington Publication 385:1–564, pls. 1–40.

Yaron, I. 1983. A review of the Scissurellidae (Mollusca: Gastropoda) of the Red Sea. Annalen der Naturhistorisches Museum in Wien 84(B):263–279, pls. 1–8.

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Spawning and Larval Development of the Ribbed Limpet, *Lottia digitalis* (Rathke, 1833)

by

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Abstract. We observed spawning and larval development of *Lottia digitalis* in the San Juan Islands, Washington, USA, during January 1995. Between 5000 and 8000 opaque greenish-brown eggs, each about 200 μm in diameter, were released singly by each spawning female. Sperm was extruded as a continuous pasty white "stringlike" stream that did not dissipate immediately upon release. Developing embryos exhibited spiral cleavage and became swimming trochophores 24 hours after fertilization, and larvae attained the pre-torsional veliger stage within 3 days of fertilization. We found that at least part of the San Juan Island population of *L. digitalis* is capable of spawning during winter. Our observations also showed that the egg size, spawning, and pattern of *L. digitalis* larval development are similar to those of other pattelogastropods.

INTRODUCTION

The ribbed limpet, *Lottia digitalis* (Rathke, 1833) is a common member of rocky intertidal communities along the west coast of North America. Though some aspects of its biology are fairly well known, published information about the reproductive biology of *L. digitalis* is limited to Fritchmann's (1961) findings that this limpet spawns along the California coast during winter, spring, and summer months when water temperatures exceed 10°C; Breen's (1972) paper stating that recruitment occurs on Vancouver Island in the spring and fall; and Kessel's (1962) work on *L. digitalis* oocyte differentiation.

In this paper, we describe the spawning behavior, eggs, and pattern and timing of larval development for *Lottia digitalis,* based on observations made during January 1995 at the Friday Harbor Laboratories, San Juan Island, Washington, USA. Results of our study show that *L. digitalis* can spawn (in the laboratory) during the winter in the San Juan Islands, Washington, and that egg size and the pattern and timing of *L. digitalis* development are similar to those of other pattelogastropods.

MATERIALS AND METHODS

Lottia digitalis ($n = 140$) were held in a running seawater table at the Friday Harbor Laboratories to conduct a short-term behavioral study. During the course of that work, some of the specimens spawned. We then decided to describe the spawning, eggs, and larval development of this common limpet.

The first observed spawning event occurred on 13 January 1995, about 2 days after limpets were placed in the seawater table. Other individuals also spawned in the seawater table between 13 January and 17 January. Ambient conditions in the laboratory included a light:dark regime of at least 16 h light to 8 h of darkness. At the same time, field conditions had a light:dark regime of about 8 h light to 16 h darkness, and full moon low tides of −0.06 m to −0.22 m MLLW (mean lower low water).

Spawning limpets were rinsed and placed in beakers of filtered seawater where gamete release usually continued. We measured the maximum shell aperture diameters of some of the spawning limpets.

Eggs were collected via pipette from the bottom of the seawater table or beaker holding a spawning female. Eggs were stored in filtered seawater, one beaker per spawn. We counted the total number of eggs released by each of four females that spawned during our study. Egg diameters were measured with an ocular micrometer.

Sperm was collected from males that spawned in the seawater table. A drop of sperm was diluted with 100 mL filtered seawater. We used the sperm solution to fertilize previously collected eggs.

Spawning limpets, gametes, fertilized eggs, and batches of developing embryos and larvae were all maintained at 9°C, ambient water temperature in our seawater table, by placing them in beakers that were partially submerged in the seawater table. We changed each culture's water every 2 hours for the first day, and once a day thereafter.

Developmental stages of embryos and larvae were de-

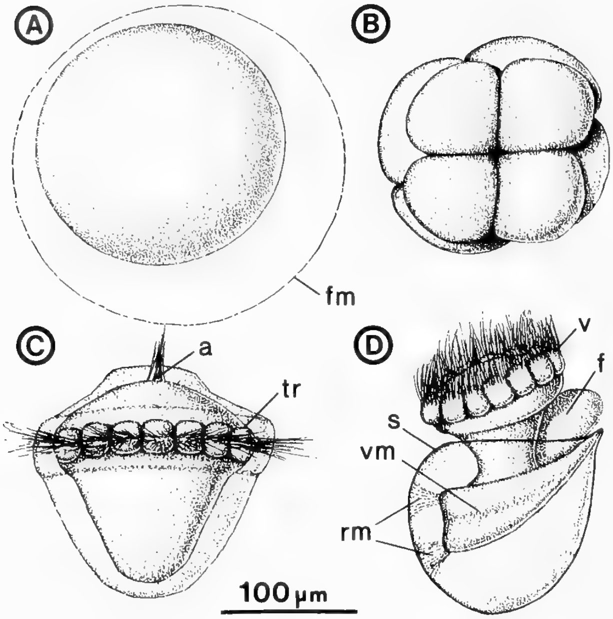

Figure 1

Developmental stages of *Lottia digitalis*. (A) Fertilized egg: fm-fertilization membrane. (B) 8-cell stage showing spiral cleavage. (C) Trochophore larva: a, apical tuft of cilia; tr, trochal band of cilia. (D) Pre-torsional veliger larva: f, foot; rm, retractor muscles; s, larval shell; v, velum; vm, visceral mass.

scribed by bright field microscopy every hour for the first day and periodically thereafter. In addition, we observed vitally stained (with nile red) eight-cell and morula stages via epifluorescence microscopy to confirm the cleavage pattern of *Lottia digitalis* embryos.

RESULTS

Nine female and seven male *Lottia digitalis* spawned in a seawater table at the Friday Harbor Laboratories between 13 and 17 January 1995. The first observed spawning was by a female on 13 January. In the afternoon of 14 January, a male spawned.

Both female and male *Lottia digitalis* exhibited mushrooming—raising the shell off the substrate—in conjunction with gamete release. During female spawning, eggs fell from under the anterior region of the shell. Eggs fell singly to the bottom of the seawater table or beaker; eggs were not connected to each other by a mucous string, nor did they form an egg mass. Sperm was released from the anterior right side of male limpets. It was extruded as a pasty white stringlike stream, about 5 mm in diameter and about 5 cm in length. The sperm did not appear to disperse immediately.

The smallest measured spawning female was 1.4 cm (maximum shell aperture diameter), and the largest was 1.8 cm ($\bar{x}$ = 1.62 cm; SD = 0.16 cm; n = 5 measured limpets). The smallest measured spawning male was 1.0 cm, and the largest was 1.7 cm ($\bar{x}$ = 1.43 cm; SD = 0.26 cm; n = 6 measured limpets).

Individual females released between 5523 and 7782 eggs per spawn ($\bar{x}$ = 6453; SD = 1069.5; n = 4 spawns in which the number of eggs released were counted). Eggs were spherical, opaque, and greenish-brown in color, with a mean diameter of 197.5 μm ± 56.6 μm (±SD; n = 51 eggs).

Zygotes were readily produced by mixing eggs and sperm. The fertilization membrane lifted 29.1 μm ± 16.5 μm (±SD; n = 6 zygotes) above the surface of a newly formed zygote. The fertilization membrane was not always a uniform distance above all parts of a zygote, as shown by the non-concentric location of the zygote with respect to its fertilization membrane in Figure 1A. The first two cleavages were equal and meridional, and the third cleavage was unequal and equatorial. Vitally stained 8-cell and morula stage embryos examined via epifluorescence microscopy confirmed observations made by bright field microscopy, that embryonic development of *L. digitalis* proceeds by spiral cleavage (Figure 1B). Subsequent embryonic and larval stages of development included morula, ciliated blastula, trochophore, and pre-torsional veliger stages (Figure 1C, D).

Table 1

Timing of *Lottia digitalis* development.

Elapsed time	Developmental stage
0 hrs	Introduction of sperm
0–0.5 hrs	Fertilization membrane
1–1.5 hrs	First cleavage
2–3 hrs	Second cleavage
3–4 hrs	Third cleavage
14 hrs	Ciliated blastula/gastrula
24 hrs	Trochophore
48–72 hrs	Pre-torsional veliger*

* The only embryos in our study to develop to the veliger stage were fertilized on 14 January 1995, but the timing of all other developmental stages indicated in this table is based on a culture fertilized on 16 January 1995.

Timing of *Lottia digitalis* larval development is shown in Table 1. Fertilization membranes were evident on eggs within 30 minutes of the introduction of sperm. Cleavage events occurred every 1–2 hours thereafter. Larvae became swimming trochophores after 1 day, and pre-torsional veligers within 3 days. We were, unfortunately, unable to determine the length of time larvae spend in the water column, or to observe settlement and metamorphosis, because our time at the laboratories ended before larvae in our cultures completed their development.

DISCUSSION

Lottia digitalis is known to recruit to intertidal communities on Vancouver Island (just north and east of the San Juan Islands) in the spring and fall. (Breen, 1972) and Nicotri

(1974) reported that they can also recruit into communities on San Juan Island during winter months. Our January 1995 observations of San Juan Island female and male *L. digitalis* spawning support Nicotri's (1974) observations. The most likely explanation for a winter spawn is that at least some *L. digitalis* individuals were already reproductively ripe, as suggested by Fritchmann's (1961) findings for California *L. digitalis.*

The duration of our study was, unfortunately, too short to include a search for environmental signals that triggered spawning among the limpets in our study. Some environmental variables that bear investigation as possible triggers for *Lottia digitalis* spawning include water temperature (Fritchmann, 1961), shifts in photoperiod (Pearse et al., 1986; Bay-Schmith & Pearse, 1987; Fong & Pearse, 1992), lunar phases, tides, and localized high population densities (Hyman, 1967). Although many stimuli could have induced spawning, further research is needed to identify the proximal triggering stimulus for spawning in *L. digitalis.*

The mean diameter of eggs released by *Lottia digitalis* during our study was 197.5 μm, a size similar to eggs produced by other patellogastropods (150 μm–230 μm diameter; see Strathmann, 1987).

Sperm was released in a single pasty white, stringlike stream that did not immediately disperse. Picken & Allan (1983) described similar sperm release by *Nacella concinna,* an Antarctic limpet. This type of sperm release may limit sperm dispersal, and thereby benefit *Lottia digitalis,* because this limpet tends to have a clumped distribution around cracks and depressions in rocks (unpublished data collected by CLK and JRG; Millard, 1968). However, realized benefits of this type of sperm release to *L. digitalis* have yet to be investigated.

The pattern and timing of *Lottia digitalis* development is similar to that of another common patellogastropod of the San Juan Islands, *Tectura scutum.* Larvae of *T. scutum* become trochophores after 20–30 h, and veligers in 40–100 h (Strathmann, 1987); larvae of *L. digitalis* become trochophores in 24 h, and pre-torsional veligers in 48–72 h (see Table 1).

In conclusion, spawning, eggs, and the timing and pattern of development of *Lottia digitalis* are similar to those of other patellogastropod species. Our results also show that San Juan Island *L. digitalis* can spawn in the winter, thereby supporting Nicotri's (1974) observations of *L. digitalis* recruitment into San Juan Island intertidal communities during winter months.

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LITERATURE CITED

Bay-Schmith, E. & J. S. Pearse. 1987. Effect of mixed day-lengths on the photoperiodic regulation of gametogenesis in the sea urchin *Strongylocentrotus purpuratus.* International Journal of Invertebrate Reproduction and Development 11: 287–294.

Breen, P. A. 1972. Seasonal migration and population regulation in the limpet *Acmaea (Collisella) digitalis.* The Veliger 15:133–141.

Fong, P. P. & J. S. Pearse. 1992. Photoperiodic regulation of parturition in the self-fertilizing viviparous polychaete *Neanthes limnicola* from central California. Marine Biology 112:81–89.

Fritchmann, H. K. II. 1961. A study of the reproductive cycle in California Acmaeidae (Gastropoda). Part III. The Veliger 4:41–47.

Hyman, L. H. 1967. The Invertebrates: Mollusca I. Volume VI. McGraw-Hill Book Company: New York.

Kessel, R. G. 1962. Differentiation of *Acmaea digitalis* oocytes with special reference to lipid endoplasmic reticulum annulate lammellae-polyribosome relationships. Journal of Morphology 171:225–243.

Millard, C. S. 1968. The clustering behavior of *Acmaea digitalis.* The Veliger 11 (Supplement):45–51.

Nicotri, M. E. 1974. Resource partitioning, grazing activities, and influence on the microflora by intertidal limpets. Ph.D. dissertation, University of Washington. 247 pp.

Pearse, J. S., V. B. Pearse & K. K. Davis. 1986. Photoperiodic regulation of gametogenesis and growth in the sea urchin *Strongylocentrotus purpuratus.* Journal of Experimental Zoology 237:107–118.

Picken, G. B. & D. Allan. 1983. Unique spawning behavior by the Antarctic limpet *Nacella concinna.* Journal of Experimental Marine Biology and Ecology 71:283–288.

Strathmann, M. F. 1987. Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast. University of Washington Press: Seattle. 670 pp.

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THE VELIGER

Seasonal Changes in Size Structure and Reproduction of the Minute Galeommatacean Bivalve *Lasaea undulata* (Gould) within Intertidal Mussel Beds

by

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Abstract. Seasonal changes in size structure and reproduction of *Lasaea undulata* (Gould) inhabiting intertidal mussel beds were studied at Shirahama, Wakayama Prefecture, central Japan. At the study site, two mytilids, *Septifer virgatus* (Wiegmann) and *Hormomya mutabilis* (Gould), formed vertically contiguous mussel beds. Abundance of *L. undulata* was much greater in the upper *S. virgatus* bed than in the lower *H. mutabilis* bed throughout the year. No marked seasonal change in density was detected either in the *S. virgatus* or the *H. mutabilis* beds. Percentage of brooding clams changed seasonally, increasing in spring and summer, and decreasing in autumn and winter, with two peaks in March and June. Recruits of juvenile clams were found abundantly in April, June–July, and September–November. The monthly change in size structure suggests that the spring and summer cohorts grew quickly during spring and summer, and many of them died after autumn reproduction, with others surviving until the next spring or summer. An autumn cohort persisted until next summer with slow growth rate during winter. Prodissoconch length of clams and number of juveniles (including eggs and embryos) within parents indicated that this species brood their young as non-planktotrophic, crawl-away juveniles.

INTRODUCTION

The minute, galeommatacean bivalves of the genus *Lasaea* Brown, 1827, have a cosmopolitan distribution (Keen, 1938; Ponder, 1971; Ó Foighil, 1989) and inhabit crevices, empty barnacle shells, tufts of lichens, and mussel beds of rocky intertidal shores (Morton, 1954; Morton et al., 1957; Kensler & Crisp, 1965; Ponder, 1971; Tsuchiya, 1979; Seed & O'Connor, 1980; Ong Che & Morton, 1992; Lintas & Seed, 1994; Iwasaki, 1995). Although classification has not yet been settled (Ponder, 1971; Ó Foighil & Eernisse, 1988), their biology has been intensively studied because their small size is of advantage in laboratory experiments to inspect reproduction, ingestion, digestion, movement, orientation, and desiccation resistance (Oldfield, 1955; Morton, 1956a, b, 1960; Ballantine & Morton, 1956; Morton et al., 1957; Kensler, 1967; Crisp, et al., 1983; Ó Foighil, 1986; Crisp & Standen, 1988; Davenport & Beard, 1988; Tyler-Walters & Davenport, 1990). All species investigated to date have been considered simultaneously hermaphroditic (summarized by McGrath & Ó Foighil, 1986 and Morton, 1992), and most of them, except *L. australis* (Lamarck), brood their young until they are released as non-planktotrophic, crawl-away juveniles (summarized by McGrath & Ó Foighil, 1986; and afterwards, Beauchamp, 1986; Ó Foighil, 1987, 1988, 1989; Morton 1992). Moreover, apomictic reproduction by *L. rubra* (Montagu) was reported by Crisp et al. (1983), Crisp & Standen (1988), and Tyler-Walters & Crisp (1989); and parthenogenetic reproduction triggered by autosperm was demonstrated in northeastern Pacific *Lasaea* clones by Ó Foighil & Thiriot-Quievreux (1991). However, field studies on population structure of this genus have been relatively much fewer than laboratory experiments presumably because of their small size and patchy distribution (Seed & O'Connor, 1980; McGrath & Ó Foighil, 1986).

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There have also been a few studies which elucidate reproductive period quantitatively in natural populations (Glynn, 1965; Roberts, 1984; Beauchamp, 1986; McGrath & Ó Foighil, 1986; Morton, 1992), though a few workers have given qualitative descriptions (Oldfield, 1955, 1961; Booth, 1979; Seed & O'Connor, 1980).

In Japan, two species of this genus were formerly reported (*L.* [originally *Kellia*] *undulata* by Gould, 1861; *L. nipponica* by Keen, 1938), and currently the latter is believed to be a synonym of the former (Habe, 1960, 1977; Kuroda & Habe, 1965). This species inhabits mussel beds of *Septifer virgatus* (Wiegmann) and rock cracks in the upper to mid intertidal zones (Tsuchiya, 1979; Mori et al., 1985a, b; Iwasaki, 1995, in press). There has been, however, no quantitative study concerning its reproduction. Ó Foighil (1989) reported recently that both direct and indirect developing *Lasaea* were found in museum collections sampled at six localities in Japan, the former at all the localities, and the latter only at Kagoshima Prefecture, southwest Japan. Morton (1992) argued from the comparison of *L.* cf. *nipponica* collected in Hong Kong that *L. undulata* in Japan might produce planktotrophic larvae and be distinct from *L. nipponica.* The aim of this paper is to examine seasonal changes in density, size structure, and proportion of brooding adults of *L. undulata* within mussel beds of two mytilid bivalves *S. virgatus* and *Hormomya mutabilis* (Gould). In comparison with *L.* cf. *nipponica* in Hong Kong reported by Morton (1992), this paper presents also the number of brooded juveniles within parent clams.

MATERIALS AND METHODS

The study site was a sandstone rocky reef on a moderately wave-exposed shore near the Seto Marine Biological Laboratory, Kyoto University, Wakayama Prefecture, central Japan (33°42′N, 135°21′E). The rocky reef sloped gently from the upper (80 cm above mean tide level) to subtidal zones with approx. 5° inclination. Shore height is hereafter expressed in cm preceded by + or −, which indicates distance above or below mean tide level. Tidal range at this site extends from +110 to −110 cm. The mussel *Septifer virgatus* formed an extensive bed from the upper to mid intertidal zone, and *Hormomya mutabilis* in the lower intertidal zone. The two mussel beds were vertically contiguous with a very narrow zone of overlap. A detailed map of this study site and the zonal distribution of both species and other sessile organisms are given in Iwasaki (1994, as the site B).

Sampling was carried out at about the mid level of the respective mussel beds (+35 cm for the *S. virgatus* bed, −35 cm for the *H. mutabilis* bed) monthly from April 1982 to April 1983. A 50 cm^2 quadrat was haphazardly tossed onto the mussel bed, and all invertebrate animals and sediment accumulated within the bed were collected using a small shovel and tweezers. Duplicate samples were taken in each mussel bed. In the laboratory, mussels, *Lasaea undulata,* other invertebrates, and the sediment were separated from one another, and all animals were counted. Sediment was dried and weighed after sifting out small shell pieces by a sieve with 1 mm mesh openings. All animals were preserved in 5% seawater formalin. Shell lengths of all *L. undulata* were measured down to 0.001 mm using micrometer under dissecting microscope at ×40–60 magnification. When the clams had distinctive prodissoconchs, their lengths were also measured. According to Ó Foighil (1988, 1989), shape and length of prodissoconch reflect developmental modes: *Lasaea* species with planktotrophic larvae have umbonate, smaller prodissoconchs (0.15–0.25 mm in length), which indicate the sizes at metamorphosis, whereas those with crawl-away juveniles have non-umbonate, D-shaped larger prodissoconchs (0.40–0.60 mm), which indicate the sizes at release from parents. A frequency histogram of shell lengths for each month was divided into distinctive cohorts, and mean shell length for each cohort was calculated by Cassie's method (1954).

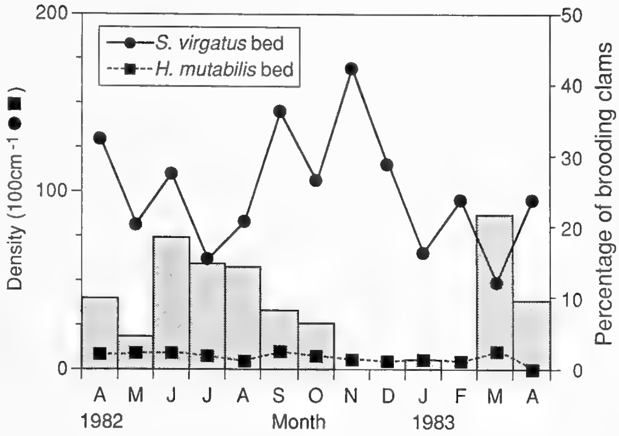

Figure 1

Monthly changes in the density of *Lasaea undulata* collected at the mid levels of the *Septifer virgatus* and *Hormomya mutabilis* beds and in the percentage of brooding clams (>1.5 mm in length) within the *S. virgatus* bed.

Reproductive period was inspected by detecting the presence of parents brooding juvenile clams under a dissecting microscope with transmitted light. Number of eggs, embryos, and shelled juveniles brooded within adult clams were also noted.

RESULTS

Changes in Density, Percentage of Brooding Clams, and Size Structure

Density (100 cm^{-2}) of *Lasaea undulata* at the mid level of the *Septifer virgatus* bed ranged from 49 to 169 over the study period, but no marked seasonal change was observed (Figure 1). Density at the mid level of the *Hormomya*

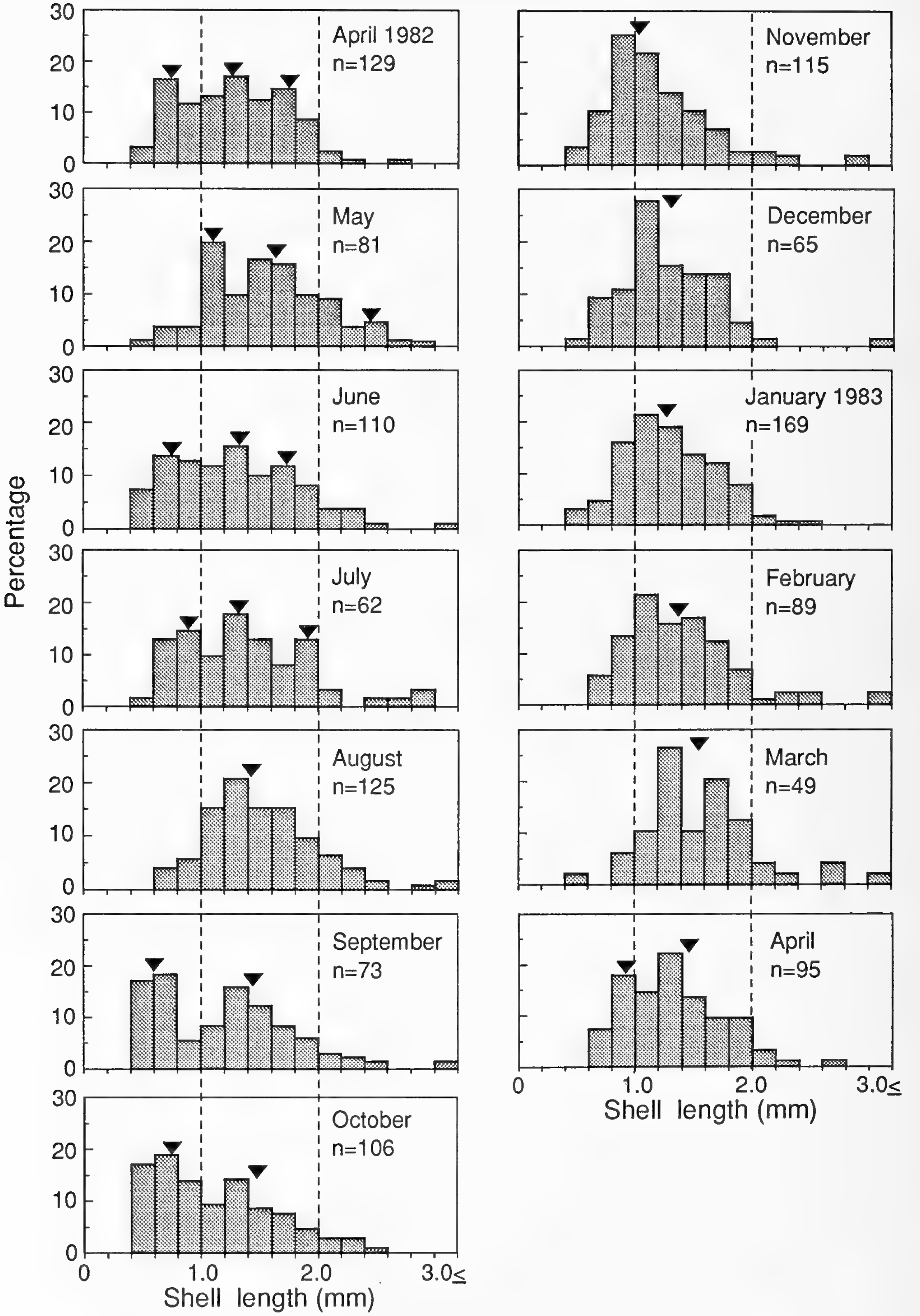

Figure 2

Monthly change in shell length structure of *Lasaea undulata* collected at the mid level of the *Septifer virgatus* bed. n: number of individuals. Closed triangles indicate the mean shell lengths of cohorts recognized by Cassie's method (1954).

mutabilis bed was very low, from 0 to 12, throughout the year. In the *S. virgatus* bed, only large clams over 1.5 mm in length brooded their young (see Figures 4, 5). The percentage of clams larger than 1.5 mm that were brooding exhibited a seasonal change with two peaks in June 1982 and March 1983 (Figure 1). From November 1982 to February 1983, only one brooding clam was found. This indicates that *L. undulata* had a restricted reproductive period from spring to autumn in which two peaks of reproductive activity were involved.

In April 1982, three distinctive cohorts were recognized in size-frequency distribution (Figure 2). The largest cohort disappeared in June 1982, but identification of the largest cohort by Cassie's method may be unreliable because this cohort is interpreted as having grown 0.8 mm in 1 month until May 1982. A new cohort of the smallest size appeared in June 1982. In August, there was only one cohort, which was presumably composed of all three cohorts recognized in the preceding month. The cohort decreased toward October, and in November onward, it incorporated with a new cohort appearing in September. Mean shell length of this compound cohort increased slowly toward March 1983. Juveniles smaller than 1 mm in length were found abundantly in April, June, July, September, October, November 1982, and April 1983 (Figure 2), indicating that there were three peaks of juvenile recruitment in a year. There were very few clams larger than 3.0 mm throughout the year.

Mean prodissoconch length of clams collected in each month ranged from 0.44 to 0.49 mm throughout the year, and no marked seasonal change in the size was recognized. The maximum prodissoconch length amounted to 0.762 mm in June 1982, while the minimum one was 0.272 mm in January 1983.

Number and Size of Brooded Juveniles

Seventeen and 27 parents brooding their young were collected from March to May and from June to October, respectively (Figure 3). No veliger larvae were found within the parents. Number of brooded juveniles (including eggs, embryos, and shelled larvae) within a parent ranged from one to 133 and increased with increasing parental shell length for both periods (March–May: $r = 0.752$, df $= 15$, $P < 0.01$; June–October: $r = 0.828$, df $= 25$, $P < 0.01$). No significant difference in the slope and elevation of regression lines in Figure 3 was detected between the two periods (ANOVA for slope: $F_{(1, 40)} = 1.45$, $P > 0.05$, ANCOVA for elevation: $F_{(1, 41)} = 0.03$, $P > 0.05$), indicating that no marked difference in brood size was found between parents of similar sizes collected in the two reproductive periods.

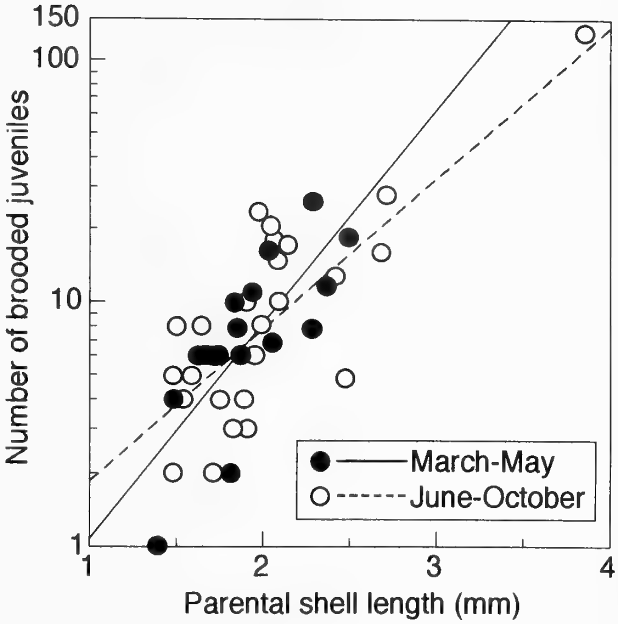

Figure 3

Number of brooded juveniles (including eggs and embryos) per parent expressed as a function of parental shell length of *Lasaea undulata* collected at the mid level of the *Septifer virgatus* bed from April 1982 to April 1983. Solid line: log(no. juveniles) = $0.893x - 0.868$, $r = 0.770$, $P < 0.001$, broken line: log(no. juveniles) = $0.620x - 0.326$, $r = 0.782$, $P < 0.001$.

DISCUSSION

Seasonal Change in Reproductive Period

Reproductive seasons of *Lasaea* spp. are summarized by McGrath & Ó Foighil (1986) and Morton (1992). *Lasaea subviridis* in the Pacific coast of USA and Canada (Glynn, 1965; Beauchamp, 1986), *L. australis* in Australia (Roberts, 1984), and *L. rubra hinemoa* in New Zealand (Booth, 1979) brood their young all year round with one or two peaks in spring and/or summer. *Lasaea rubra* in the United Kingdom and *L.* cf. *nipponica* in Hong Kong have one or two restricted reproductive periods, from late spring to early autumn in the former, with juvenile recruitment occurring during summer (June–August) (Oldfield, 1955, 1961; Seed & O'Connor, 1980; McGrath & Ó Foighil, 1986), and in May and from October to December in the latter (Morton, 1992). Morton (1992) showed for the latter species that the number and size of brooded juveniles differed between two reproductive periods in a year. The present study revealed that *Lasaea undulata* in central Japan also restricts its reproduction, from March to October, with two activity peaks in March and June (Figure 1). The number of brooded juveniles showed no variation during the reproductive period (Figure 3). However, juvenile recruitment seemed to occur three times a year, April, June–July, and September–November (Figure 2); and there was no peak of reproductive activity corresponding to the last recruitment peak (see Figure 1). This may be ascribed to the small number of quadrats or sample sizes in monthly samplings, which could not cover spatial heterogeneity of distribution and population process in this species.

Crisp et al. (1983) reported that *L. rubra* reared in the laboratory at 16°C released juveniles and died after 40 and 65 weeks, respectively, from birth. However, Seed & O'Connor (1980) and McGrath & Ó Foighil (1986) showed more than 1 year longevity of a generation in the natural populations of the same species. The present study could reveal neither the longevity nor growth rate of *L. undulata* because three cohorts resulting from discrete recruitment pulses could not always be discriminated throughout the year. Seasonal change in size structure suggests that spring and summer cohorts grew quickly during spring and summer, and many of them died after autumn reproduction, with others surviving until the next spring or summer. An autumn cohort persisted until next spring or summer with its growth slowing during winter (Figure 2). Further experimental study is essential to clarify the differences in longevity and growth rate among the cohorts.

Mode of Larval Development

Ó Foighil (1988, 1989) stated that *L. australis,* which undergoes a planktotrophic larval development, has a prodissoconch ranging in size from 0.22 to 0.30 mm, while an undescribed *Lasaea* species releasing young as crawl-away juveniles has a D-shaped prodissoconch ranging in size from 0.39 to 0.68 mm in length. Prodissoconch length of *L. undulata* ranged from 0.27 to 0.76 mm with averages of 0.44 to 0.49 mm, and mean lengths of shelled juveniles brooded within parents were within 0.3 to 0.55 mm. The sizes were among the smallest recorded for *Lasaea* species which lack veliger larvae (Ó Foighil, 1989; Morton, 1992), and there were several individuals with their prodissoconchs smaller than 0.30 mm. Accordingly, presence of clams with planktotrophic larval development cannot thoroughly be denied in the present study. However, no veliger larvae were found within parents throughout a year (the present study) and throughout the intertidal zones of this study site (Iwasaki, in press). Moreover, recruits into artificial mussel clumps within mussel-enclosure cages had prodissoconches of 0.30–0.60 mm in length (Iwasaki, in press). Therefore, it may be concluded that most clams examined have undergone non-planktotrophic larval development.

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LITERATURE CITED

Ballantine, D. & J. E. **Morton**. 1956. Filtering, feeding and digestion in the lamellibranch *Lasaea rubra.* Journal of the Marine Biological Association of the United Kingdom 35:241–274.

Beauchamp, K. A. 1986. Reproductive ecology of the brooding, hermaphroditic clam *Lasaea subviridis.* Marine Biology 93: 225–235.

Booth, J. D. 1979. Common bivalve larvae from New Zealand: Leptonacea. New Zealand Journal of Marine and Freshwater Research 13:241–254.

Cassie, R. M. 1954. Some use of probability paper in the analysis of size frequency distributions. Australian Journal of Marine and Freshwater Research 5:513–522.

Crisp, D. J., A. **Burfitt**, K. **Rodrigues** & M. D. **Budd**. 1983. *Lasaea rubra*: an apomictic bivalve. Marine Biology Letters 4:127–136.

Crisp, D. J. & A. **Standen**. 1988. *Lasaea rubra* (Montagu) (Bivalvia: Erycinacea), an apomictic crevice-living bivalve with clones separated by tidal level preference. Journal of Experimental Marine Biology and Ecology 117:27–45.

Davenport, J. & J. B. **Beard**. 1988. Observations on the temperature and salinity relations of *Lasaea rubra.* Journal of the Marine Biological Association of the United Kingdom 68:15–23.

Glynn, P. W. 1965. Community composition, structure and interrelationships in the marine intertidal *Endocladia muricata–Balanus glandula* association in Monterey Bay, California. Beaufortia 12:1–198.

Gould, A. A. 1861. Descriptions of shells collected by the North Pacific Exploring Expedition. Proceedings of the Boston Society of Natural History 8:14–40.

Habe, T. 1960. Notes on the species of Japanese shells described by A. A. Gould. Venus 21:10–31 [in Japanese].

Habe, T. 1977. Systematics of Mollusca in Japan: Bivalvia and Scaphopoda. Hokuryukan: Tokyo. 372 pp. [in Japanese].

Iwasaki, K. 1994. Distribution and bed structure of the two intertidal mussels, *Septifer virgatus* (Wiegmann) and *Hormomya mutabilis* (Gould). Publications of the Seto Marine Biological Laboratory 36:223–247.

Iwasaki, K. 1995. Comparison of mussel bed communities between two intertidal mytilids *Septifer virgatus* (Wiegmann) and *Hormomya mutabilis* (Gould). Marine Biology 123:109–120.

Iwasaki, K. In press. Vertical changes in density, size structure and shell shape of the bivalve *Lasaea undulata* within intertidal mussel beds. Journal of the Marine Biological Association of the United Kingdom.

Keen, A. M. 1938. New pelecypod species of the genera *Lasaea* and *Crassinella.* Proceedings of the Malacological Society of London 23:18–32.

Kensler, C. B. & D. J. **Crisp**. 1965. The colonization of artificial crevices by marine invertebrates. Journal of Animal Ecology 34:507–516.

Kensler, C. B. 1967. Desiccation resistance of intertidal crevice species as a factor in their zonation. Journal of Animal Ecology 36:391–406.

Kuroda, T. & T. **Habe**. 1965. Chirihagigai. P. 258 in K. Okada, S. Uchida & R. Uchida (eds.), New Illustrated Encyclopedia of the Fauna of Japan II. Hokuryukan: Tokyo [in Japanese].

Lintas, C. & R. **Seed**. 1994. Spatial variation in the fauna associated with *Mytilus edulis* on a wave-exposed rocky shore. Journal of Molluscan Studies 60:165–174.

McGrath, D. & D. Ó **Foighil**. 1986. Population dynamics and reproduction of hermaphroditic *Lasaea rubra* (Montagu) (Bivalvia, Galeommatacea). Ophelia 25:209–219.

Mori, K., M. **Tanaka** & S. **Nishihama**. 1985a. Community structure of a rocky shore in Tsuji-shima Island, Amakusa. II. Vertical distribution of dominant species and its zonation pattern. Publications from the Amakusa Marine Biological Laboratory, Kyusyu University 8:27–41.

Mori, K., S. Nishihama & M. Tanaka. 1985b. Community structure of a rocky shore in Tsuji-shima Island, Amakusa. III. The analysis of relationships between distribution of organisms and micro-topographical conditions using small quadrat. Publications from the Amakusa Marine Biological Laboratory, Kyusyu University 8:43–63.

Morton, B. 1992. Seasonal variation in brood size of *Lasaea* cf. *nipponica* (Bivalvia: Galeommatoidea) in Hong Kong. American Malacological Bulletin 9:165–171.

Morton, J. E. 1954. The crevice faunas of the upper intertidal zone at Wembury. Journal of the Marine Biological Association of the United Kingdom 33:187–224.

Morton, J. E. 1956a. Filtering, feeding, and digestion in the lamellibranch *Lasaea rubra*. Journal of the Marine Biological Association of the United Kingdom 35:241–274.

Morton, J. E. 1956b. The tidal rhythm and action of the digestive system of the Lamellibranch *Lasaea rubra*. Journal of the Marine Biological Association of the United Kingdom 35:563–586.

Morton, J. E. 1960. The responses and orientation of the bivalve *Lasaea rubra* Montagu. Journal of the Marine Biological Association of the United Kingdom 39:5–26.

Morton, J. E., A. D. Boney & E. D. S. Corner. 1957. The adaptations of *Lasaea rubra* (Montagu), a small intertidal lamellibranch. Journal of the Marine Biological Association of the United Kingdom 36:383–405.

Ó Foighil, D. 1986. Prodissoconch morphology is environmentally modified in the brooding bivalve *Lasaea subviridis*. Marine Biology 92:517–524.

Ó Foighil, D. 1987. Cytological evidence for self-fertilization in the brooding bivalve *Lasaea subviridis*. International Journal of Invertebrate Reproduction and Development (Amsterdam) 12:83–90.

Ó Foighil, D. 1988. Random mating and planktotrophic larval development in the brooding hermaphroditic clam *Lasaea australis* (Lamarck, 1818). The Veliger 31:214–221.

Ó Foighil, D. 1989. Planktotrophic development is associated with a restricted geographic range in *Lasaea*, a genus of brooding, hermaphroditic bivalves. Marine Biology 103:349–358.

Ó Foighil, D. & D. J. Eernisse. 1988. Geographically widespread, non-hybridizing, sympatric strains of the hermaphroditic, brooding clam *Lasaea* in the Northeastern Pacific Ocean. Biological Bulletin 175:218–229.

Ó Foighil, D. & C. Thiriot-Quievreux. 1991. Ploidy and pronuclear interaction in northeastern Pacific *Lasaea* clones (Mollusca: Bivalvia). Biological Bulletin 181:222–231.

Oldfield, E. 1955. Observations on the anatomy and mode of life of *Lasaea rubra* (Montagu) and *Turtonia minuta* (Fabricius). Proceedings of the Malacological Society of London 31:226–249.

Oldfield, E. 1961. The functional morphology of *Kellia suborbicularis* (Montagu), *Montacuta ferruginosa* (Montagu) and *M. substriata* (Montagu), (Mollusca, Lamellibranchiata). Proceedings of the Malacological Society of London 34:255–295.

Ong Che, R. G. & B. Morton. 1992. Structure and seasonal variations in abundance of the macro-invertebrate community associated with *Septifer virgatus* (Bivalvia: Mytilidae) at Cape D'aguilar, Hong Kong. Asian Marine Biology 9:217–233.

Ponder, W. F. 1971. Some New Zealand and subantarctic bivalves of the Cyamiacea and Leptonacea with descriptions of new taxa. Records of Domminion Museum, Wellington 7:119–141.

Roberts, D. 1984. A comparative study of *Lasaea australis, Vulsella spongarium, Pinna bicolor* and *Donacilla cuneata* (Mollusca: Bivalvia) from Princess Royal Harbor, Western Australia. Journal of Molluscan Studies 50:129–136.

Seed, R. & R. J. O'Connor. 1980. Shell shape and seasonal changes in population structure in *Lasaea rubra* (Bivalvia: Erycinidae). Journal of Molluscan Studies 46:66–73.

Tsuchiya, M. 1979. Quantitative survey of intertidal organisms on rocky shores in Mutsu Bay, with special reference to the influence of wave action. Bulletin of Marine Biological Station, Asamushi, Tohoku University 16:69–86.

Tyler-Walters, H & D. J. Crisp. 1989. The modes of reproduction in *Lasaea rubra* (Montagu) and *L. australis* (Lamarck) (Erycinidae; Bivalvia). Pp. 299–308 in J. S. Ryland & P. A. Tyler (eds.), Reproduction, Genetics and Distribution of Marine Organisms: Proceedings of the 23rd European Marine Biological Symposium, Swansea, 1988. Olsen and Olsen: Denmark.

Tyler-Walters, H. & J. Davenport. 1990. The relationship between the distribution of genetically distinct inbred lines and upper lethal temperature in *Lasaea rubra*. Journal of the Marine Biological Association of the United Kingdom 70:557–570.

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THE VELIGER

A New Subfamily of the Addisoniidae Associated with Cephalopod Beaks from the Tropical Southwest Pacific, and a New Pseudococculinid Associated with Chondrichthyan Egg Cases from New Zealand (Mollusca: Lepetelloidea)

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Abstract. **Helicopeltinae**, a new subfamily of the Addisoniidae, is proposed for a group of minute deep-sea gastropods found living and feeding on detrital cephalopod beaks from the Chesterfield Plateau and southern New Caledonia. The type species of ***Helicopelta*** gen. nov., ***H. rostricola*** sp. nov., uniquely combines an operculate, coiled shell similar to that in *Choristella* Bush, 1987 (Choristellidae), a horseshoe-shaped shell muscle characteristic of a limpet, a radula similar to that in Addisoniidae but with more numerous marginal teeth and non-homologous primary rasping teeth, a large left-centered gill, and a copulatory organ that is situated on the left side instead of the right as in all other members of the Lepetelloidea. A second (unnamed) species of ***Helicopelta*** is recorded from off southern New Caledonia. The opportunity is taken to describe a new limpet of the genus *Tentaoculus* Moskalev, 1976, from New Zealand that lives and feeds within spent chondrichthyan egg cases, the first record of a pseudococculinid from this habitat. Radulae of *Teuthirostria cancellata* Moskalev, 1976, and of species of *Addisonia, Choristella,* and *Bathysciadium* are illustrated and discussed.

INTRODUCTION

During the last 25 years, there has been a dramatic increase in knowledge of the systematics and anatomy of the Cocculinoidea and Lepetelloidea (reviewed by Haszprunar, 1988b). In this period the number of families has swelled to 10, and the number of genera and subgenera to 37, while the number of known species has substantially increased. These animals live and feed on a variety of exotic substrata, including empty polychaete (*Hyalinoecia*) tubes, the carapaces of living deep-sea Lithodidae (Crustacea), egg cases of sharks and skates (Chondrichthys), detrital cephalopod beaks, and decaying whale and fish bones, as well as terrestrial and littoral plant remains that have sunk to the deep-sea floor, such as wood, algal holdfasts and seagrass (reviewed by Haszprunar, 1988b). The Pyropeltidae (McLean & Haszprunar, 1987) and a pseudococculinid (McLean, 1991) have been recorded from sulphide crusts at hydrothermal vents on the East Pacific Rise. Warén (1993) has recently recorded a bathysciadiidlike limpet that lives and feeds on the periostracum of a species of *Capulus* (Gastropoda, Capulidae). Most species are restricted to a particular substratum type.

In this paper I introduce a new subfamily of the Addisoniidae for coiled species that live on detrital cephalopod beaks, and a pseudococculinid that lives and feeds within spent skate egg cases.

Abbreviations: AMS, Australian Museum, Sydney; MNHN, Muséum National d'Histoire Naturelle, Paris; NMNZ, Museum of New Zealand, Wellington.

SYSTEMATICS

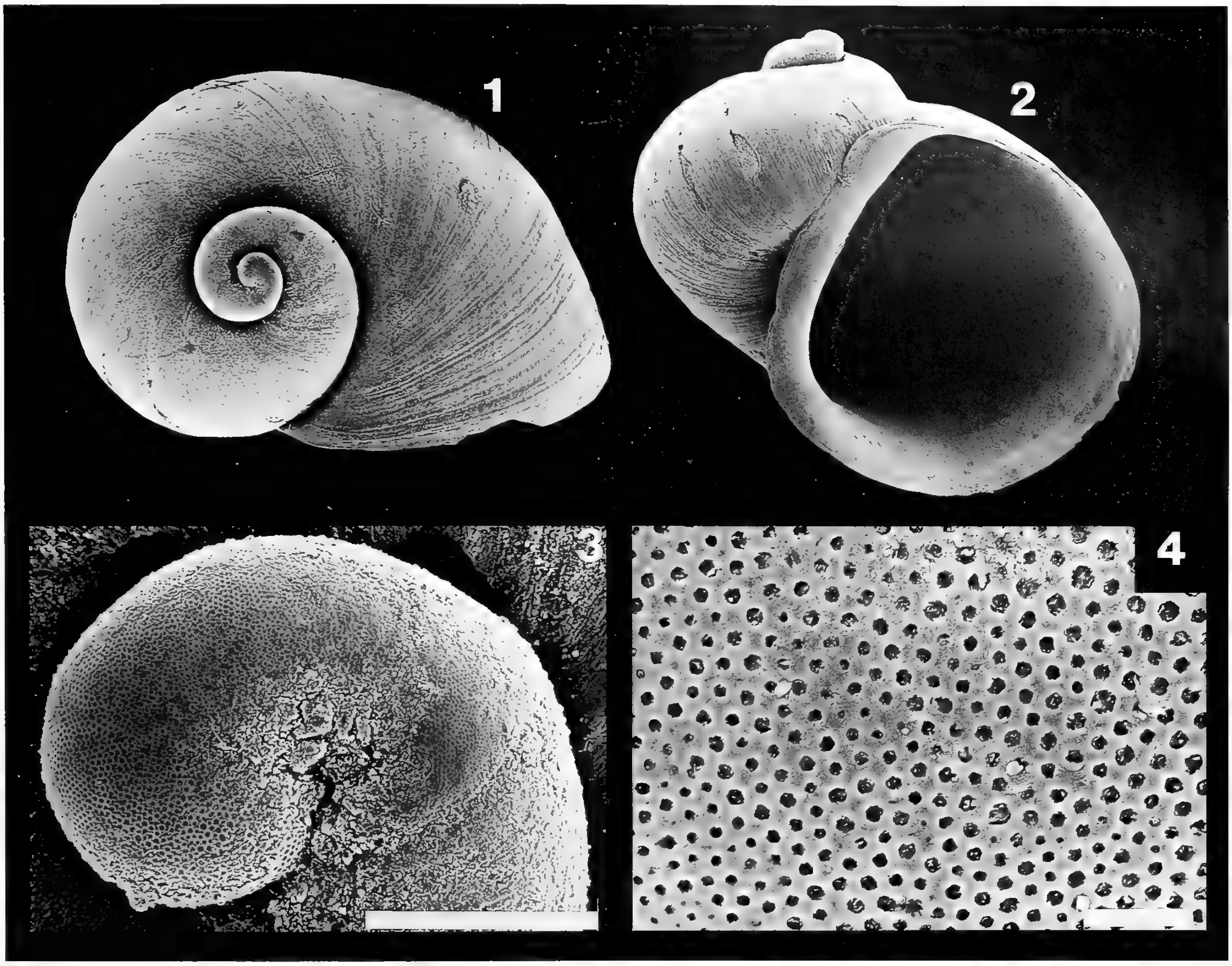
Order Archaeogastropoda Thiele, 1925

Superfamily LEPETELLOIDEA Dall, 1892

Family ADDISONIIDAE Dall, 1882

HELICOPELTINAE subfam. nov.

Diagnosis: Shell up to 1.90 mm wide, turbiniform, operculate; protoconch densely and minutely pitted, slightly



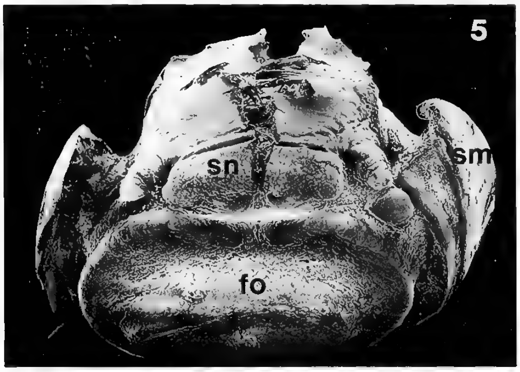
Explanation of Figures 1 to 4

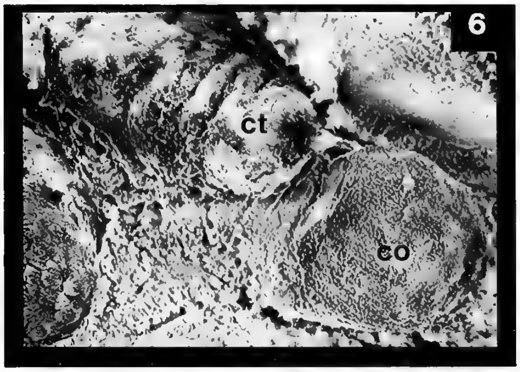
Shell of holotype of ***Helicopelta rostricola*** Marshall, gen. nov., sp. nov., Chesterfield Plateau, Coral Sea, 700–685 m. Figures 1, 2. Whole shell (width 1.90 mm). Figure 3. Protoconch. Figure 4. Enlargement of protoconch sculpture. Scale bar 3 = 100 μm, 4 = 10 μm.

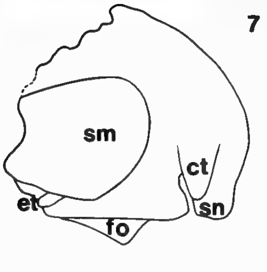
tilted; teleoconch essentially smooth. Copulatory organ beside left cephalic tentacle, hemispherical (opening not detected); large gill comprising a row of leaflets centered left of body midline; cephalic tentacles without papillae; two posterior epipodial tentacles; shell muscle horseshoe-shaped, uninterrupted, very wide. Operculum thin, chitinous. Radula 11 + 5 + 1 + 5 + 11, central tooth scalelike, laterals 1–3 tilelike, lateral 4 small, lateral 5 and marginal 1 broadest, marginal 1 longest; lateral 5 with small cusp at inner end, broad outer part tightly interlocked with base of marginal 1. Marginal 1 with bluntly angulate or rounded cusps, marginal basal plates scalelike, outer marginal teeth (10 pairs) relatively very small, slender, cutting areas finely serrate. Internal anatomy unknown.

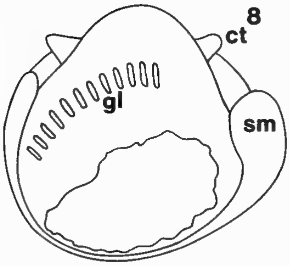
Remarks: The type species of ***Helicopelta*** gen. nov. (Figures 1–8, 13–18) differs from all hitherto known members of the Cocculinoidea and Lepetelloidea in having an operculate coiled shell (as in Choristellidae) coupled with a shell muscle characteristic of a limpet, and in having the copulatory organ on the left side instead of the right. The radula (Figures 13–18) uniquely combines central and lateral teeth similar to those of Addisoniidae (Figures 19–21) with multiple marginal teeth as in Cocculinoidea and Lepetelloidea with fully rhipidoglossate dentition (Cocculinidae, Pyropeltidae, Pseudococculinidae, Osteopeltidae), though the marginals are reduced in size and number and are evidently vestigial. The gill is large and most closely resembles those in *Addisonia* Dall, 1882, and Choristellidae, particularly the latter in being left rather than right-centered.

Helicopelta is clearly referable to the Lepetelloidea rather than the Cocculinoidea because (1) the gill comprises a row of leaflets rather than a simple fold, (2) the









Explanation of Figures 5 to 8

Animal of holotype of ***Helicopelta rostricola*** Marshall, gen. nov., sp. nov. Figures 5, 6. Critical point dried animal after extraction of radula. Figures 7, 8. Profile (7) and dorsal view (8) (posterior part of animal torn away); ct, cephalic tentacle; co, copulatory organ; et, epipodial tentacle; fo, foot; gl, gill leaflets; sm, shell muscle; sn, snout. Specimen width (Figures 5, 6) 1.20 mm.

shell muscle is not divided into discrete bundles, and (3) the radula is somewhat similar to that in Addisoniidae. The only other members of the Lepetelloidea (or Cocculinoidea) with a coiled shell and that have an operculum in the adult stage are the choristellids (McLean, 1992). No weight is assigned to the presence of an operculum in the adult, because one is present in larval Patellogastropoda (Lindberg, 1981) and has been observed in larval *Lepetella* Verrill, 1880 (A. Warén, personal communication). Choristellids differ in having jaws, a relatively small (left) shell muscle attached to the columella, and an essentially smooth protoconch, while a grooved right cephalic tentacle functions as the copulatory organ. Their radulae, moreover, are entirely different (compare Figures 13–18 with Figure 22), though both types are evidently derived by arrested development of and differential modification from a common, fully rhipidoglossate radular plan similar to that in Pseudococculinidae (Figures 27, 28), which is considered to be the primitive condition among Cocculinoidea and Lepetelloidea (Haszprunar, 1988a, b). Regrettably no complete animal of ***Helicopelta*** is yet available for sectioning and anatomical comparison with other members of the Lepetelloidea. It remains to be determined, for example, on what side the gonads are and how they are collected to the copulatory organ.

The central and inner five lateral radular teeth in *Addisonia* and ***Helicopelta*** are more similar to each other than to those of any other family of the Lepetelloidea, and suggest that the two groups have a common stem group. *Addisonia* species differ, however, in having a patelliform shell and the gill on the right side, and in that the right cephalic tentacle functions as the copulatory organ. Apart from the presence of more numerous marginal teeth, the radula in ***Helicopelta*** differs from that in *Addisonia* in the shapes and homologies of the largest teeth (Figures 16, 19, 21). Unlike ***Helicopelta***, in which the sixth tooth outward from the central tooth (here interpreted as marginal 1) is by far the largest and is thus clearly the primary rasper, tooth 6 (marginal 1) in *Addisonia* is situated beneath the large seventh and eighth elements (marginals 2 and 3), which are obviously the primary raspers in this genus. Note that McLean (1985) and Dantart & Luque (1994) recorded only 15 teeth per transverse row in the *Addisonia* species they examined, whereas Anders Warén (personal communication) has found that these same species actually have 19 teeth (9 + 1 + 9) as in the one illustrated here (Figures 19–21) (teeth 7 and 8 are typically obscured by the adjacent inner teeth through shrinkage of the basement membrane). The protoconch in *Addisonia,* as interpreted by Dantart & Luque (1994, figs. 73–76), differs markedly from that in ***Helicopelta*** in being reticulately sculptured, and in having a fused, narrowly tapered instead of broadly rounded tip. The *Addisonia* protoconch is very similar in both shape and sculpture to those in the pseudococculinid genera *Kurilabyssia* Moskalev, 1976, and *Mesoplex* Marshall, 1986, while that in ***Helicopelta*** is similar to those in Choristellidae and Cocculinoidea in shape (Marshall, 1986; McLean, 1992).

On aggregate character states ***Helicopelta*** is as different from all families and subfamilies of Lepetelloidea as they are from each other, which suggests that it may represent a family in its own right. Without a thorough re-evaluation of phylogenetic relationships within the superfamily, however, particularly in the light of knowledge of the anatomy of ***Helicopelta*** (unknowns), I favor a conservative approach and allocate it subfamilial rank within Addisoniidae, associating it there solely on the basis of similarity of the radula to that of *Addisonia.* The existence of a group of operculate, coiled species related to *Addisonia* is scarcely surprising, since Haszprunar (1988b, 1992) has already provided compelling evidence that Addisoniidae and Choristellidae are probably sister groups.

Etymology: Greek *helikos* (spiral) and *pelte* (shield)—feminine.

Helicopelta Marshall, gen. nov.

Type species: ***Helicopelta rostricola*** Marshall, sp. nov.

Diagnosis: As for **Helicopeltinae** (above).

Helicopleta rostricola Marshall, sp. nov.

(Figures 1–8, 13–18)

Description: Shell (holotype) 1.90 mm wide, turbiniform, slightly wider than high, thin, spire 0.2× as high as aperture, umbilicus small, translucent; periostracum thin, smooth, pale buff.

Protoconch 200 μm wide, sharply delineated, slightly tilted, entire surface with minute, densely crowded, sharp-edged pits.

Teleoconch of two rapidly expanding convex whorls, suture narrowly channelled, smooth apart from collabral growth lines, and a few obscure spiral lines on last quarter whorl. Aperture very large, roundly "D"-shaped, peristome continuous, inner lip flared and obscuring umbilical chink from basal view.

Animal (Figures 5–8) white, eyeless. Head broad, broadly rounded; snout broad, bluntly truncated; oral shield broad, mouth "Y"-shaped, no oral lappets. Cephalic tentacles similar, short, bluntly tapered. Copulatory organ hemispherical, set close below left cephalic tentacle, opening not detected. Gill attached to pallial roof, comprising 12 leaflets, long, arcuate, curving anterolaterally from left side to right of body midline. One slender posterior epipodial tentacle on each side beside opercular lobe. Foot large, spongy, oval, wider than long; with a narrow, laterally elongate projecting subcentral area. Shell muscle horseshoe-shaped, uninterrupted, broad, ends very broad. Jaws lacking.

Operculum extremely thin, fragile, firmly attached, colorless, transparent, nucleus slightly eccentric, similar to that in *Choristella.*

Radula (Figures 13–18) with the formula 11 + 5 + 1 + 5 + 11. Central and lateral teeth short, topographically complex, complexly interlocking, central and inner four laterals without defined cutting areas or cusps. Central tooth low, scalelike, subquadrate, medially thickened, sides thin and laterally flanged. Laterals 1–3 trapezoidal, tilelike, enlarging outward. Lateral 4 small, shorter than flanking teeth, inconspicuous, tip subangulate. Lateral 5 broad, a narrow hooked cusp on narrow inner part, broad; low outer part completely obscured by marginal 1, base strongly flanged and deeply socketed to interlock with marginal 1. Marginal 1 very large, base tightly locked between lateral 5 in its own row and the row in front, about as broad as lateral 5, with four strong, bluntly angulate or rounded, similar cusps. Marginal basal plates thin, scalelike. Outer marginal teeth small, slender, no longer than marginal 1, 10 per half transverse row, tips finely serrate.

Type data: Holotype MNHN (height 1.80 mm, width 1.90 mm, 2 teleoconch whorls); MUSORSTOM 5 station 363, 19°48′S, 158°44′E, Chesterfield Plateau, Coral Sea, alive on inner side of a detrital cephalopod beak pitted by bathysciadiids, 700–685 m, 19 October 1986, n.o. *Coriolis* (according to the label, two specimens were originally present, but the second specimen could not be located).

Distribution: Chesterfield Plateau, Coral Sea, 700–685 m.

Remarks: ***Helicopelta rostricola*** is strongly characterized by its small, coiled, operculate shell, external anatomy, radula, and association with cephalopod beaks. It remains to be determined whether or not the protoconch naturally has an external organic layer (as in the species described below) that has been abraded away in the holotype.

Etymology: Latin *rostrum* (beak) and *cola* (dweller).

Helicopelta sp. nov.

(Figures 9–12)

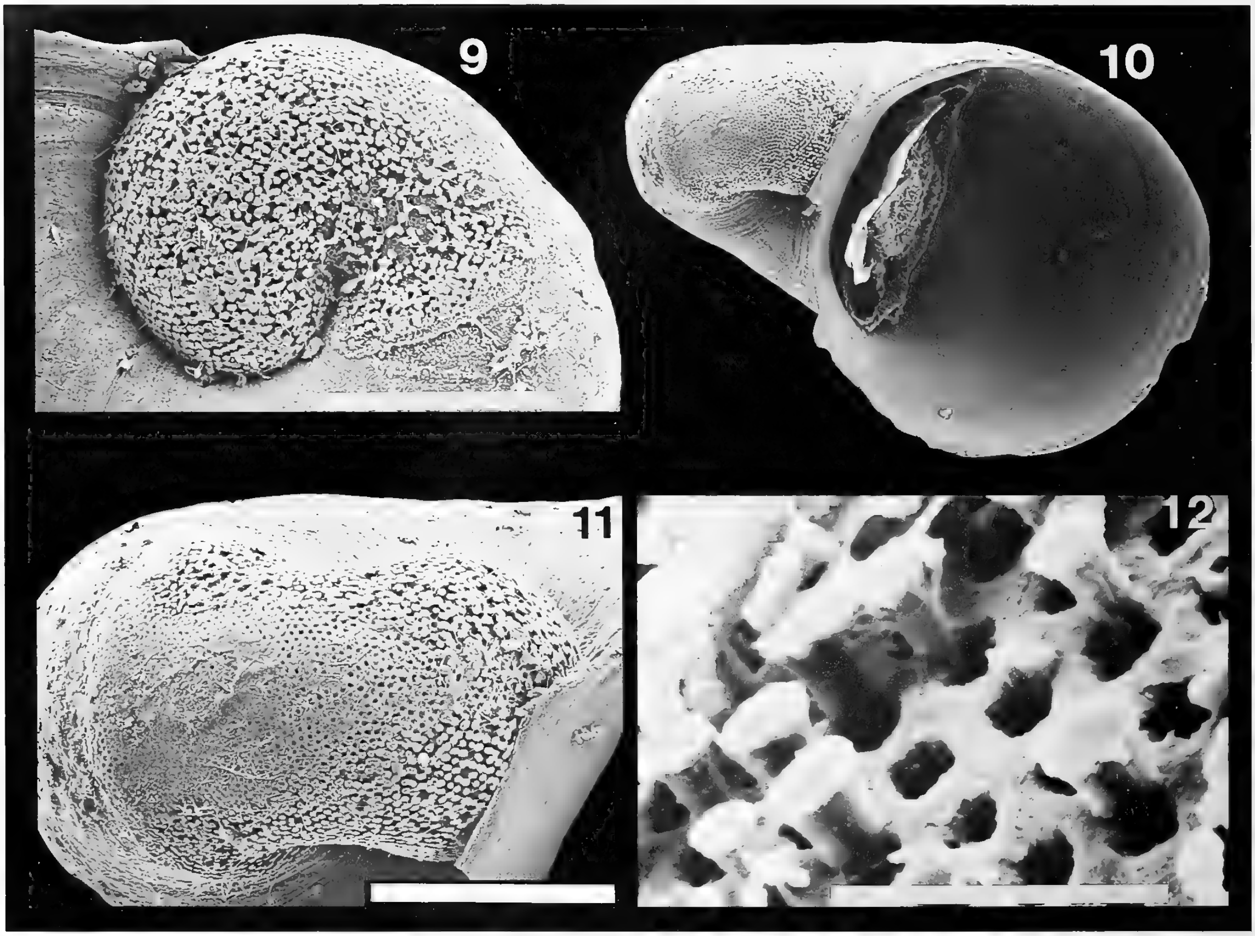
Description: Shell (immature) up to 0.60 mm wide, wider than high, almost planispiral, thin, brittle, colorless, translucent, narrowly umbilicate; periostracum pale buff, translucent, essentially smooth.

Protoconch 200 μm wide, sharply delineated, orthostrophic, covered with minute, crowded, sharp-edged pits; where unabraded, each pit with a stout column with a broader, flattened top that projects above surface (apparently dried, shrunken outer organic layer).

Teleoconch of about half a whorl, suture deeply impressed, smooth apart from growth lines, rapidly expanding, summit above tip of protoconch; aperture circular.

Animal unknown (dried). Operculum very thin, chitinous, colorless, spiral.

Material examined: CHALCAL 2 station CP22, 24°40′S,



Explanation of Figures 9 to 12

Shell of ?***Helicopelta*** sp. nov. (immature), off southern New Caledonia, 750 m. Figures 9, 11. Protoconch. Figure 10. Whole shell (width 0.60 mm), note operculum in place. Figure 12. Enlargement of protoconch sculpture. Scale bars 5, 7 = 100 μm, 8 = 10 μm.

168°39′E, southeast of New Caledonia, alive on inner side of a pitted detrital cephalopod beak with *Bathysciadium* sp., 750 m, 29 October 1986, n.o. *Coriolis* (2 juveniles MNHN).

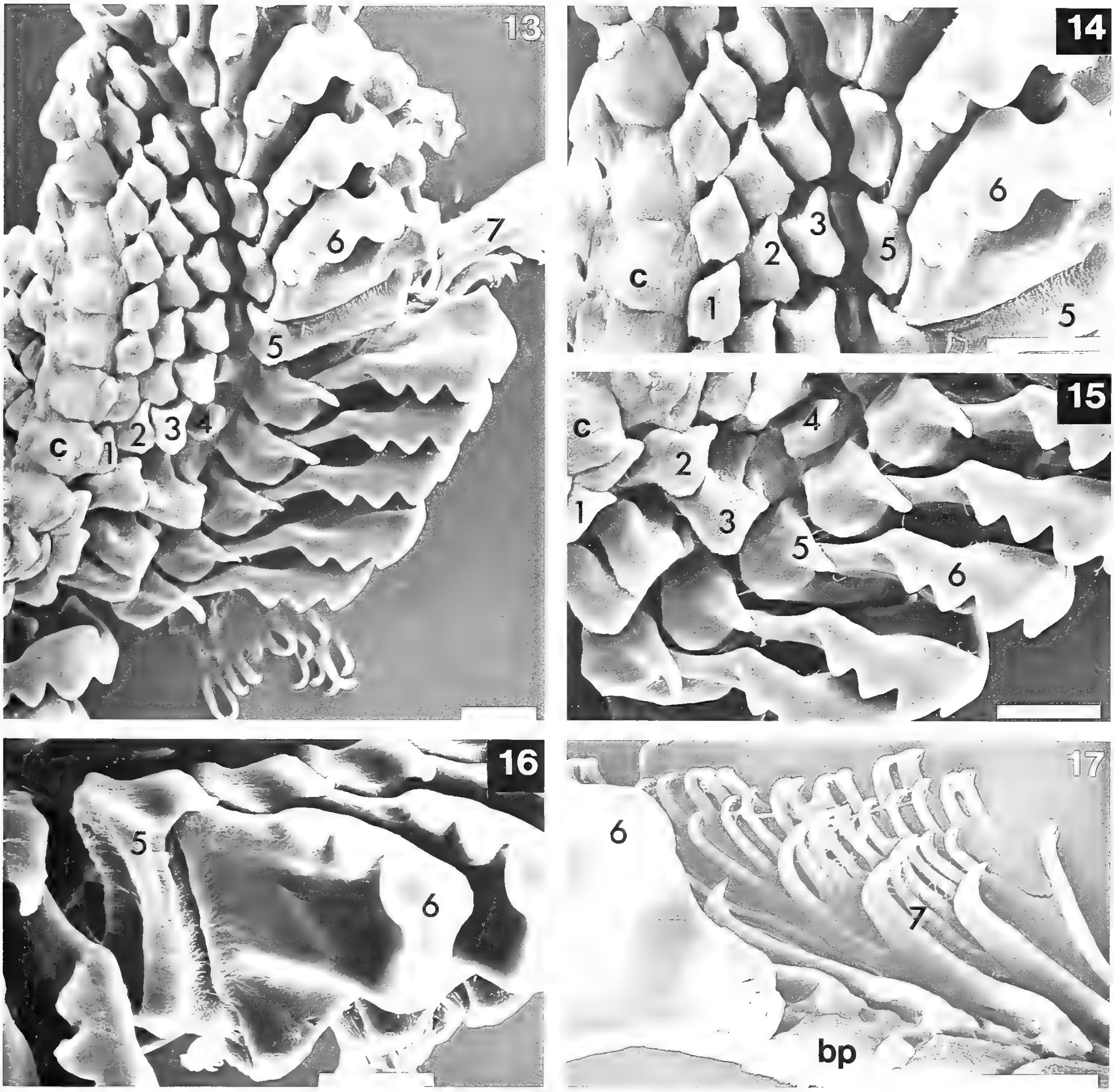
Remarks: The two available specimens are clearly immature (largest shell 0.60 mm wide). They resemble ***H. rostricola*** in protoconch size, in gross teleoconch facies, and in opercular morphology, but differ in having a strongly flattened spire. The protoconch surface is pitted exactly as in ***H. rostricola,*** but differs in that stout, nail-like columns project from the pits. Nothing like them has been previously recorded from Cocculinoidea or Lepetelloidea. Judging from the fact that the columns are narrower than the pits and stuck to their sides, they seem likely to represent the dried, shrunken remains of an organic layer that is impervious to salts secreted during mineralization of the protoconch. The columns are clearly fragile and easily removed by abrasion (Figures 5, 7, 8). There is no trace of them on the protoconch of ***H. rostricola,*** and it is yet impossible to tell whether or not they were present and have since worn away. The similarities and the association with a cephalopod beak suggest that it is a species of ***Helicopelta,*** naming of which is withheld until better material is available.

Family PSEUDOCOCCULINIDAE Hickman, 1983

Genus *Tentaoculus* Moskalev, 1976

Tentaoculus Moskalev, 1976:67. Type species (by monotypy): *Tentaoculus perlucida* Moskalev, 1976; Recent, New Guinea.

Remarks: Since the discovery of *Tentaoculus perlucida* Moskalev, 1976, off New Guinea (substratum unknown), three species have been described from off New Zealand (Marshall, 1986): *T. lithodicola* and *T. neolithodicola* from the carapaces of living stone crabs (Crustacea: Lithodidae),



Explanation of Figures 13 to 17

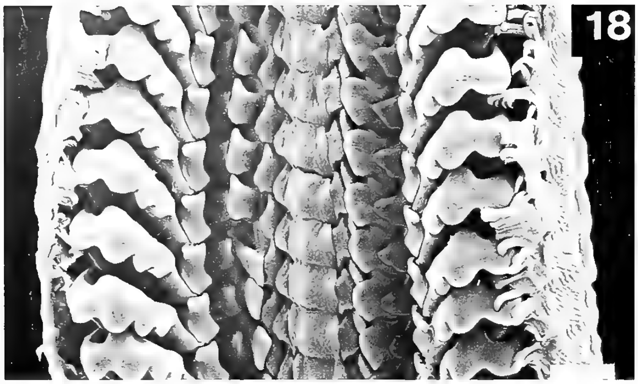
Radula of holotype of ***Helicopelta rostricola*** Marshall, gen. nov., sp. nov. Figures 13–17. Central tooth (c), lateral teeth (1–5), and marginal teeth (6, 7) of right side of radular ribbon. Figure 16. Lateral 5 (5) and marginal 1(6). Figure 17. Marginal 1 (6), marginal basal plates (bp), and slender outer marginal teeth (7). Scale bars = 10 μm.

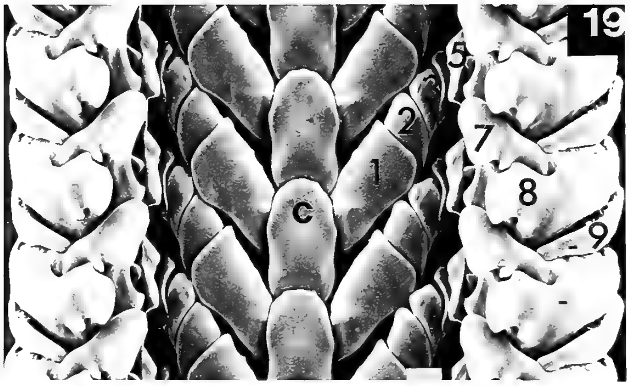
and *T. haptricola* from decaying algal holdfasts at bathyal depths. The North American species *Puncturella (Fissurisepta) eritmeta* Verrill, 1884, *Cocculina georgiana* Dall, 1927 have been referred to the genus by McLean & Harasewych (1995) on the basis of shell morphology. The new species described below is the first record of a pseudococculinid living in association with chondrichthyan egg cases.

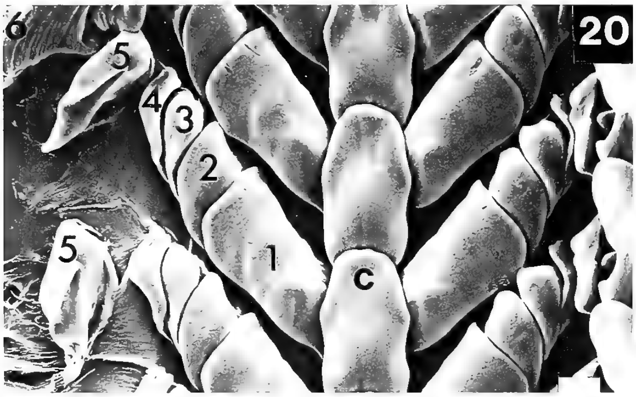
Tentaoculus ***balantiophaga*** Marshall, sp. nov.

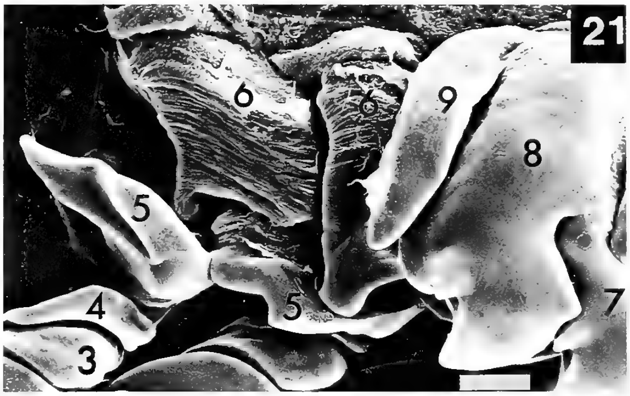
(Figures 26–28)

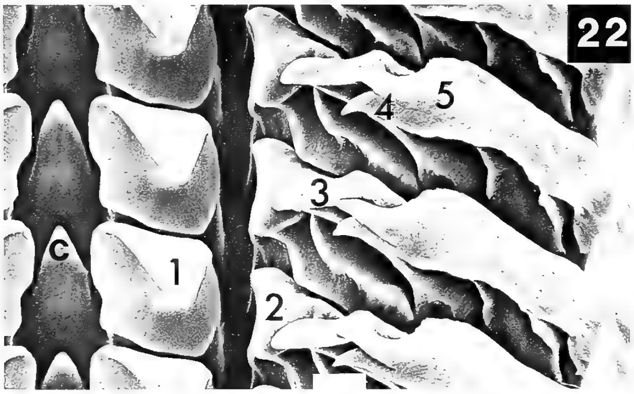
Description: Shell up to 3.25 mm long, thin, translucent, white, moderately arched, anterior end occupying 82–88% of shell length. Aperture elliptical, broadest at about anterior third, more or less flat. Anterior end more broadly

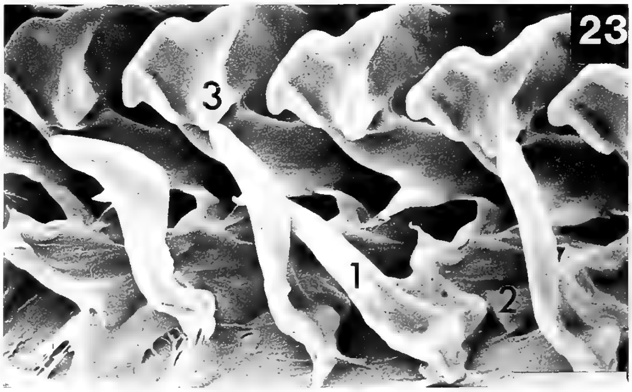


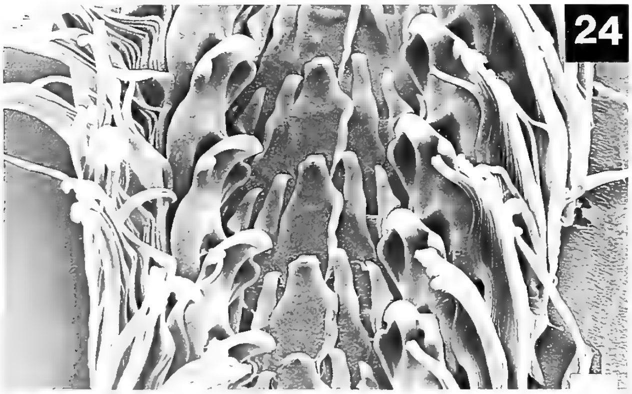


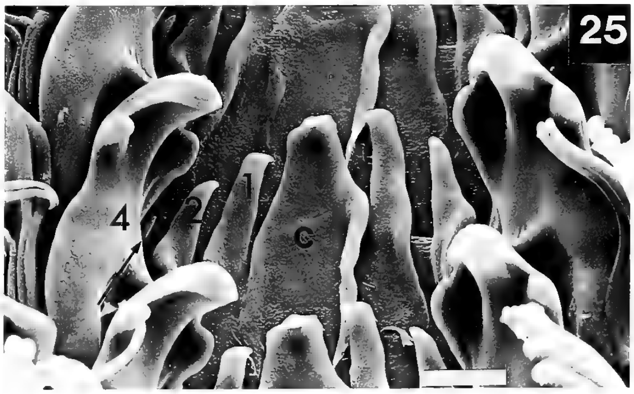












Explanation of Figures 18 to 25

Figure 18. Full width of radula of holotype of ***Helicopelta rostricola*** Marshall, gen. nov., sp. nov. Figures 19–21. Radula of *Addisonia* sp. nov., off Shoalhaven Heads, New South Wales, 494–585 m, AMS C. 200901, showing central tooth (c), lateral teeth (1–5) and marginal teeth (6–9). Figure 19. Full width. Figures 20, 21. Details. Figure

rounded than posterior, sides broadly rounded. Anterior slope broadly convex, posterior slope concave, lateral slopes more or less flat. No internal septum.

Protoconch sculpture unknown (surface etched away).

Teleoconch sculptured with fine collabral growth lines.

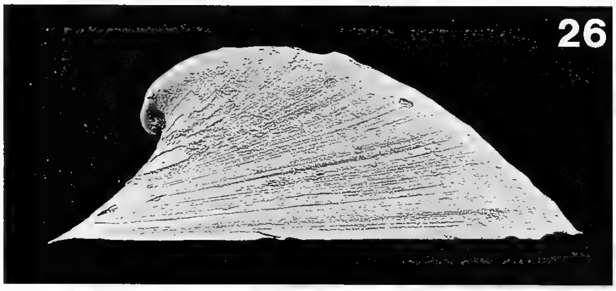
Animal translucent white, eyes unpigmented, snout broadly rounded, cephalic tentacles gently tapered and similar, oral disc broad, two posterior epipodial tentacles; narrow seminal groove entering base of right cephalic tentacle.

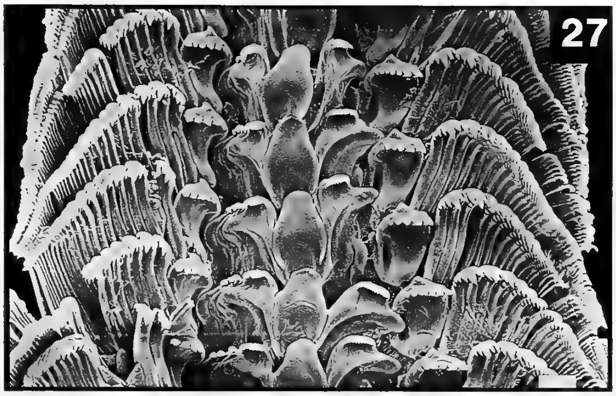
Radula (Figures 27, 28). Radular formula ∞ + 5 + 1 + 5 + ∞. Central tooth with broad, rounded, obscurely serrate cutting area. Lateral 1 large, cutting area broad, straight, outermost cusp large, inner edge with six to nine small conical cusps. Lateral 2–4 small, each with strong, hooked terminal cusp, and one to three small secondary cusps. Lateral 5 largest, broad, straight cutting area with four to seven strong conical cusps. Marginal teeth numerous, slender, tips finely serrate.

Type data: Holotype NMNZ M.118318, and 6 paratypes (1 AMS, 5 NMNZ M.117577): 41°07.61′S, 176°46.91′E, off Castlepoint, New Zealand, alive within spent skate egg case, 1335 m, 2 April 1993, f.r.v. *Tangaroa* sta. 9303/149, coll. P. Grimes. Paratypes (13 NMNZ M.117836, 1 AMS, 1 MNHN): 44°13.47′S, 178°41.87′E, western Chatham Rise, New Zealand, alive within spent skate egg case, 1065–1072 m, 8 November 1993, f.r.v. *Tangaroa* sta. 9309/197, coll. A. Hart.

Distribution: Off Castlepoint, and western Chatham Rise, New Zealand, living within and feeding on spent skate egg cases, 1065–1335 m.

Remarks: The shell, radula and external anatomy of *Tentaoculus* ***balantiophaga*** are typical of the genus *Tentaoculus* as defined by Marshall (1986) and Haszprunar (1988a). *T.* ***balantiophaga*** differs from *T. perlucida* in lacking eye pigment, and in having a more strongly developed central tooth. It differs from *T. haptricola* in lacking an internal shell septum, and from both *T. lithodicola* and *T. neolithodicola* in having finer cusps on lateral 1, and fewer and shorter cusps on laterals 2–4. *T.* ***balantiophaga*** is unique among Cocculiniformia associated with cephalopod beaks and chondrichthyan egg cases in that the radula exhibits no obvious derived character states (see below). Other egg cases from the vicinity contained *Choristella marshalli* McLean, 1992, and the two species have not been found living





Explanation of Figures 26 to 28

Holotype of *Tentaoculus* ***belantiophaga*** Marshall, sp. nov., off Castlepoint, New Zealand, 1335 m. Figure 26. Shell, length 2.55 mm. Figure 27. Full width of radula. Figure 28. Detail of radula showing central tooth (c) and lateral teeth (1–5). Scale bars = 10 μm.

←

22. Detail of radula of paratype of *Choristella marshalli* McLean, 1992, off Banks Peninsula, New Zealand, 1097–1116 m, NMNZ M.75210, showing central tooth (c) and lateral-marginal teeth (1–5). Figure 23. Oblique lateral view of right side of radula of syntype of *Bathysciadium costulatum* (Locard, 1898), MNHN, showing innermost three lateral teeth (1, 2, 3). Note that the tip of (numbered) lateral 1 locks into the socket on the inner side of (numbered) lateral 3 in the row in front. Figures 24, 25. Radula of paratype of *Teuthirostria cancellata* Moskalev, 1976, off northern Peru, 5540–5200 m, Academy of Sciences, Moscow. Figure 24. Full width, note low number of marginal teeth. Figure 25. Detail showing central tooth (c) and lateral teeth (1–4; tooth 3 obscured, tip arrowed). Scale bars = 10 μm.

together within the same egg case. *T.* ***balantiophaga*** forms grazing scars on the inner surface of the egg cases similar to those produced by *Choristella* and *Addisonia* species.

Etymology: From the Greek *balantion* (purse) and *phagos* (to eat), the word *balantion* alluding to "mermaid's purse," a common name for chondrichthyan egg cases.

DISCUSSION

There is compelling evidence that gastropod limpets are derived from coiled forms (Yonge, 1947; Eales, 1950; Fretter & Graham, 1962; McLean, 1981, 1984; Lindberg, 1988), though Haszprunar (1988b, c, 1992) considered the uncoiled limpet form to be primary and coiled forms secondary in gastropod evolution. On the basis of outgroup comparison (Pseudococculinidae and/or Osteopeltidae), Haszprunar (1988b, c, 1992) concluded that Choristellidae were not phylogenetically primitive among Cocculinoidea and Lepetelloidea, and that coiling in this particular family must thus be a derived condition. The presence of a relatively huge, horseshoe-shaped shell muscle in ***Helicopelta*** suggests derivation from a limpet ancestor and lends support to this contention. It is unclear, however, whether the shells in Choristellidae and **Helicopeltinae** have become coiled independently.

It is difficult to imagine an advantage that might be conferred through reacquisition of a coiled shell other than increased mobility. Why secondary coiling should have occurred in Choristellidae and **Helicopeltinae** alone among Lepetelloidea is unclear, though it is perhaps no coincidence that these groups are the only ones to be entirely dependent on chondrichthyan egg cases and cephalopod beaks for food other than Bathysciadiidae, *Teuthirostria cancellata* Moskalev, 1976 (Cocculinidae), and *Tentaoculus* ***balantiophaga*** sp. nov. (Pseudococculinidae) (see below), all of which have patelliform shells. Judging from firsthand sorting of more than 1000 dredge and trawl samples from depths greater than 500 meters (personal observation; P. Bouchet & A. Warén personal communication), beaks, egg cases, bones, wood and algal holdfasts are generally rare, and must be so thinly distributed over most of the seafloor that these animals probably do not depend on an ability to crawl from one substratum to another. ***Helicopelta*** species presumably utilize the substratum between more sedentary (scar-forming) bathysciadiids, or perhaps areas formerly occupied by the limpets. A coiled shell may enhance reproductive fitness by enabling animals to seek parts of the original substratum following its ultimate disintegration and scattering of the parts or, for the choristellids, perhaps other egg cases deposited in the immediate vicinity.

Helicopelta rostricola joins the limpets of the Bathysciadiidae (= Bathypeltidae) (Moskalev, 1973; Hickman, 1983; Haszprunar, 1987b), and the cocculinid limpet *Teuthirostria cancellata* Moskalev, 1976 (Moskalev, 1976) as the only gastropods known to live and feed on the beaks of cephalopods, while *Tentaoculus* ***balantiophaga*** joins Addisoniidae and Choristellidae as the only gastropods known to live and feed within the egg cases of sharks and skates (Verrill, 1882, 1884; Villa, 1985; McLean, 1985, 1992; Gubbioli & Nofroni, 1986).

Warén (1993) has recently introduced a new limpet genus, *Xenodonta,* which he tentatively referred to Bathysciadiidae. Whereas he could not record the diet of the North Atlantic type species (*X. bogasoni* Warén, 1993), an undescribed species from the Galapagos Islands was reported to live and feed on the periostracum of a species of *Capulus.* Compared with *Bathysciadium,* the radula in *Xenodonta* differs in lacking the low articulatory tooth (tooth 2, Figure 23) between the bases of laterals 1 and 3, in that lateral 2 (Warén's tooth 3) is more like that in *Lepetella* Verrill, 1880 (Lepetellidae), and in having an extra pair of outer lateral teeth.

The external anatomy and radula of *Teuthirostria cancellata* (paratype, off northern Peru, 5540–5200 m) (Figures 24, 25) are accordant with Cocculinidae, though serial sections reveal some deviations from the standard cocculinid plan (G. Haszprunar, personal communication). Moreover, the radula has substantially fewer marginal teeth per transverse row (about 23 pairs) than any other known cocculinid. The lower number of marginal teeth suggests that the radula has undergone or is undergoing a progressive morphological transformation, presumably through retardation of radular ontogenesis. Regrettably, the shell of the only specimen available to me had dissolved in its preservative, so it was not possible to check the protoconch, which was described as being smooth (this requires confirmation as the protoconch surface is not in fact shown in the original illustration—Moskalev, 1976: fig. 3).

Cephalopod beaks are composed of chitin, a polysaccharide with long fibrous molecules. By contrast the egg cases of sharks and skates are composed primarily of layers of the structural protein collagen (Wourms, 1977; McLean, 1985). Gastropod periostracum comprises largely sclerotized fibrous protein (Hochachka, 1983; Saleuddin & Petit, 1983). How these tough, almost inert substances are metabolized is unknown, though it is possible that endosymbiotic bacteria are involved. All that can be said at present is that the animals exhibit certain derived features in their alimentary tracts: bathysciadiids have a large stomach and have lost the midgut gland, which has been functionally replaced by a greatly enlarged esophageal gland; choristellids lack a gastric shield and have a specific gland at the posterior esophagus, large "cul-de-sacs" (probably the midgut gland), and a short intestine; *Addisonia* species have entirely lost the stomach and have it replaced by a greatly enlarged intestinal sac (Haszprunar, 1987a, 1988b, 1992).

Aside from the strong probability that larvae in Cocculinoidea and Lepetelloidea are non-planktotrophic (as in all known archaeogastropods other than Neritimorpha), nothing is known of the development of these animals. Given the *fact* of their ability to colonize static, widely scattered, ephemeral substrata, it seems obvious that this is accomplished by transportation of eggs or larvae in currents close to the seafloor, settlement occurring when the presence of food is detected, probably by chemoreception. Brood protection of yolk-rich eggs has been reported for a number of families (Haszprunar, 1988b). Retention of eggs to a late stage of development would maximize exploitation of the substratum, whereas yolk-richness would enhance long-term survival during larval dispersal.

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LITERATURE CITED

DANTART, L. & A. LUQUE. 1994. Cocculiniformia and Lepetidae (Gastropoda: Archaeogastropoda) from Iberian waters. Journal of Molluscan Studies 60:277–313.

EALES, N. B. 1950. Torsion in gastropods. Proceedings of the Malacological Society of London 28:53–61.

FRETTER, V. & A. GRAHAM. 1962. British Prosobranch Molluscs. Ray Society: London. 755 pp.

GUBBIOLI, F. & I. NOFRONI. 1986. First record of "*Cithna*" *naticiformis* Jeffreys, 1883 in the Mediterranean. La Conchiglia (Roman) 18 (204–205):6–7.

HASZPRUNAR, G. 1987a. The anatomy of *Addisonia* (Mollusca, Gastropoda). Zoomorphology 106:269–278.

HASZPRUNAR, G. 1987b. Anatomy and affinities of cocculinid limpets (Mollusca, Archaeogastropoda). Zoologica Scripta 16:305–324.

HASZPRUNAR, G. 1988a. Anatomy and affinities of pseudococculinid limpets (Mollusca, Archaeogastropoda). Zoologica Scripta 17:161–179.

HASZPRUNAR, G. 1988b. Comparative anatomy of cocculiniform gastropods and its bearing on archaeogastropod systematics. Malacological Review, Supplement 4:64–84.

HASZPRUNAR, G. 1988c. On the origin and evolution of major gastropod groups with special reference to the Streptoneura. Journal of Molluscan Studies 54:367–441.

HASZPRUNAR, G. 1992. On the anatomy and relationships of the Choristellidae (Archaeogastropoda: Lepetelloidea). The Veliger 35:295–307.

HICKMAN, C. S. 1983. Radular patterns, systematics, diversity, and ecology of deep-sea limpets. The Veliger 26:73–92.

HOCHACHKA, P. W. 1983. Quinone-tanned scleroproteins. Pp. 467–504 in P. W. Hochachka (ed.), The Mollusca 1. Academic Press: New York.

LINDBERG, D. R. 1981. Is there a coiled ancestor in the docoglossan phylogeny? The Western Society of Malacologists Annual Report 13:15.

LINDBERG, D. R. 1988. The Patellogastropoda. Malacological Review, Supplement 4:35–63.

MCLEAN, J. H. 1981. The Galapagos Rift limpet *Neomphalus*: relevance to understanding the evolution of a major Paleozoic—Mesozoic radiation. Malacologia 21:291–336.

MCLEAN, J. H. 1984. A case for derivation of the Fissurellidae from the Bellerophontacea. Malacologia 25:3–20.

MCLEAN, J. H. 1985. The archaeogastropod family Addisoniidae Dall, 1882: life habit and review of species. The Veliger 28:99–108.

MCLEAN, J. H. 1991. Four new pseudococculinid limpets collected by the deep-submersible *Alvin* in the Eastern Pacific. The Veliger 34:38–47.

MCLEAN, J. H. 1992. Systematic review of the family Choristellidae (Archaeogastropoda: Lepetellacea) with descriptions of new species. The Veliger 35:273–294.

MCLEAN, J. H. & M. G. HARASEWYCH. 1995. Review of Western Atlantic species of cocculinid and pseudococculinid limpets, with descriptions of new species (Gastropoda: Cocculiniformia). Natural History Museum of Los Angeles, Contributions in Science 453:1–33.

MCLEAN, J. H. & G. HASZPRUNAR. 1987. Pyropeltidae, a new family of cocculiniform limpets from hydrothermal vents. The Veliger 30:196–205.

MARSHALL, B. A. 1986. Recent and Tertiary Cocculinidae and Pseudococculinidae (Mollusca: Gastropoda) from New Zealand and New South Wales. New Zealand Journal of Zoology 12:505–546.

MOSKALEV, L. I. 1973. Pacific Ocean Bathysciadiidae (Gastropoda) and forms similar to them. Zoologicheskyi Zhournal 52:1297–1303 [in Russian].

MOSKALEV, L. I. 1976. Concerning the generic diagnostics of the Cocculinidae (Gastropoda, Prosobranchia). Works of the P. P. Shirshov Institute of Oceanology, Academy of Sciences of the USSR 99:59–70 [in Russian].

SALEUDDIN, A. S. M. & H. P. PETIT. 1983. The mode of formation and the structure of the periostracum. Pp. 199–234 in A. S. M. Saleuddin & K. M. Wilbur (eds.), The Mollusca 4 (1). Academic Press: New York.

VERRILL, A. E. 1882. Catalogue of marine Mollusca added to the fauna of New England during the past ten years. Transactions of the Connecticut Academy of Sciences 5:447–587.

VERRILL, A. E. 1884. Second catalogue of Mollusca recently added to the fauna of the New England Coast and adjacent parts of the Atlantic, consisting mostly of deep-sea species, with notes on others previously recorded. Transactions of the Connecticut Academy of Sciences 6:139–294.

VILLA, R. 1985. Note su habitat ed ecologia di *Addisonia lateralis* (Réquien, 1848). Notiziario Centro Italiano Studi Malacologici (Roma) 5(1–2):9–12.

WARÉN, A. 1993. New and little known Mollusca from Iceland and Scandinavia. Part 2. Sarsia 78:159–201.

WOURMS, J. P. 1977. Reproduction and development in chondrichthyan fishes. American Zoologist 17:379–410.

YONGE, C. M. 1947. The pallial organs in the aspidobranch gastropods and their evolution throughout the Mollusca. Philosophical Transactions of the Royal Society of London, B 232:443–518.

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Comparative Karyology of Four American Oyster Species

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Abstract. Karyotypic relationships among the tropical congeneric oyster species *Crassostrea virginica* (Gmelin, 1791), *Crassostrea rhizophorae* (Guilding, 1827), and *Crassostrea corteziensis* (Hertlein, 1951) were studied. Chromosome similarities among species were determined using a one way ANOVA and Student-Newman-Keuls (SNK) test, in order to minimize subjective appraisal from the researcher. *Tiostrea chilensis* (Philippi, 1845) was used as an outgroup.

The use of standard statistical procedures enabled us to recognize quantitative differences of chromosome morphology among these oyster species. The three *Crassostrea* species are karyologically more closely related to each other than they are to *T. chilensis.* Two different patterns of karyological similitude were found among *Crassostrea* species. In the first, *C. virginica* and *C. corteziensis* are more similar to each other than either of them is to *C. rhizophorae.* In the second, *C. virginica* and *C. rhizophorae* are more similar to each other than either of them is to *C. corteziensis. Crassostrea rhizophorae* and *C. corteziensis* seem to arise by pericentric inversions from a primitive *C. virginica*-like karyotype.

INTRODUCTION

Crassostrea virginica (Gmelin, 1791), *Crassostrea rhizophorae* (Guilding, 1827), and *Crassostrea corteziensis* (Hertlein, 1951) are a closely related group of oviparous oyster species from coastal waters of Central America. *C. virginica* ranges in the Atlantic from Nova Scotia to the Yucatán Peninsula, Mexico. *C. rhizophorae* is distributed from the Florida Peninsula to Brazil and the Caribbean islands. *C. corteziensis* occurs in the Pacific, from Panama to the Gulf of California. Based on studies of shell morphology and soft tissue, Castillo (1986) concluded that these three species are closely related. Menzel (1973) and Harry (1985) proposed that *C. rhizophorae* is a subspecies of *C. virginica.* On the other hand, Hedgecock & Okazaki (1984), who reviewed the literature on evolutionary divergence in this group and also provided biochemical data on genetic diversity within and between these taxa, observed strong genetic differences between species and concluded that *C. virginica* and *C. rhizophorae* are two distinct species.

Stenzel (1971) suggested that *C. virginica* and *C. corteziensis* were two species derived from a common ancestor which divided after the emergence of the Isthmus of Panama. Allozyme (Hedgecock & Okazaki, 1984) and paleontological (Hertlein, 1951) data indicate that this group of species probably evolved much before the Isthmus of Panama geographically isolated *C. corteziensis* from the Atlantic populations of the species group.

The study of chromosome morphology of related species usually allows one to detect the changes which modified the ancestral karyotype and stayed in the newly generated lines. Also, the relative morphological invariability of chromosomes with respect to environmental conditions makes their study useful in investigating the phylogeny of a group of species (White, 1973), the taxonomic status of the species involved, and their most likely pattern of speciation.

The karyotypes of these three species have been described. All of them have a $2n = 20$ complement. No karyological differences have been found among populations of *C. virginica* from Connecticut (Longwell et al., 1967), northwest Florida (Menzel, 1968), and Tabasco, Mexico (Rodríguez-Romero et al., 1978). *C. corteziensis* has a metacentric pair nine rather than the submetacentric one shared by *C. virginica* and *C. rhizophorae*. *C. rhizophorae* has a submetacentric chromosome pair six rather than a metacentric one shared by *C. virginica* and *C. corteziensis* (Rodríguez-Romero et al., 1978, 1979a, b).

In a classical karyological analysis, the chromosome morphology is defined based on the Centromeric Index (Levan et al., 1964). This index separates a continuous variation of centromere position into discrete classes not considering the total relative length of each chromosome. When these categories are used to make comparisons among species, a bias can arise because small differences of centromere position that change the qualitative classification of a chromosome are scored as differences. In turn, large changes not affecting the qualitative classification are neglected. It is necessary, then, to base comparisons of chromosome morphology on a more objective quantitative method that uses most of the available information. In this work, the use of a quantitative method is proposed.

The larviparous species *Tiostrea chilensis* (Philippi, 1845) (*Ostrea* (*Eostrea*) *puelchana sensu* Harry (1985)) is used as outgroup of the karyological analysis. This is a species distributed in southern Chile and New Zealand (Solís, 1967; Dinamani & Beau, 1981; Buroker et al., 1983).

MATERIALS AND METHODS

The procedures to obtain metaphase plates in each species are described in the papers where karyotypes were originally described: *C. virginica* (Rodríguez-Romero et al., 1978); *C corteziensis* (Rodríguez-Romero et al., 1979a); *C. rhizophorae* (Rodríguez-Romero et al., 1979b); *T. chilensis* (Ladrón de Guevara et al., 1994).

Chromosome arm lengths measured in various individuals from each species were transformed to values relative to the total length of each haploid genome. The means of their relative lengths are used to build a karyo-idiogram (Spotorno, 1985). In this graph each chromosome pair is plotted as a dot whose position is defined by the relative lengths of either arm.

To make statistical tests, relative lengths of chromosome arms were transformed to the arcsine of the square root of the proportion in order to prevent distributional restrictions (Zar, 1974). Differences in the lengths of short and long arms were tested independently for each chromosome pair among species using a one way analysis of variance (ANOVA) and the *a posteriori* test of Student-Newman-Keuls or SNK (Zar, 1974). A chromosome pair is considered not different between two species only if both arms do not show statistical differences of length ($P < 0.05$).

With the information obtained from the SNK test, a data matrix of similitude is constructed, where the number of chromosomes of equal morphology present in a given pair of species can be determined. In order to express graphically the content of this matrix, the data were grouped in a dendrogram using the Unweighted Pair Grouping Method of Averages (UPGMA).

RESULTS

The diploid chromosome number of all species studied is 20. Mean lengths and standard deviations of the chromosome arm lengths are shown in Table 1. Chromosome morphology can be easily appraised in the karyo-idiogram (Figure 1). It is possible to observe that chromosome pairs 1, 3, 5, and 8 are metacentric in all four species. All these pairs show little variation of the position of centromeres and total length among species. Pairs 4 and 7 in all species have submetacentric morphology with small variations of length and centromere position. Chromosome pair 10, despite its small size and being metacentric in all species, shows a marked variation of total length and centromere position. Chromosome pairs 2, 6, and 9, on the other hand, show little interspecific variation of total length, but show marked differences of the centromere position among species. No subtelocentric or telocentric chromosomes were found. Extreme sizes are represented by chromosome 1 of *C. rhizophorae* (total length = 13.85%) and chromosome 10 of *C. virginica* (total length = 5.79%).

Results of the SNK text are presented in Table 2. Chromosome pairs 1, 4, 5, 7, and 8 have similar morphology in all species. *T. chilensis* can be distinguished from the *Crassostrea* group mainly by chromosome pairs 2, 6, and 10. Among *Crassostrea* species, *C. corteziensis* can be distinguished from the other two species by chromosomes 2 and 9. *C. rhizophorae,* on the other hand, can be identified by its chromosomic pair 6. *C. virginica,* however, does not present exclusive karyotypic characters.

This information was summarized in a species-species matrix (Table 3) where the number of chromosomes with the same morphology in a given pair of species is shown. In this matrix, the most similar pair of species, according to the number of chromosomes of similar morphology, is *C. virginica* with *C. rhizophorae* (eight chromosomes of similar morphology), and *C. virginica* with *C. corteziensis* (eight chromosomes of similar morphology). The most dissimilar pair is *T. chilensis* with *C. corteziensis.* This information, translated into a dendrogram, is shown in Figure 2. Because in the first matrix (Table 3) there are two pairs of species sharing morphology of eight chromosomes, two dendrograms can be constructed. One of them (Figure 2A) shows the largest similitude value for *C. virginica* and *C. corteziensis* pair. A lower value relates this group with *C. rhizophorae.* Finally, with the smallest similitude, *T. chi-*

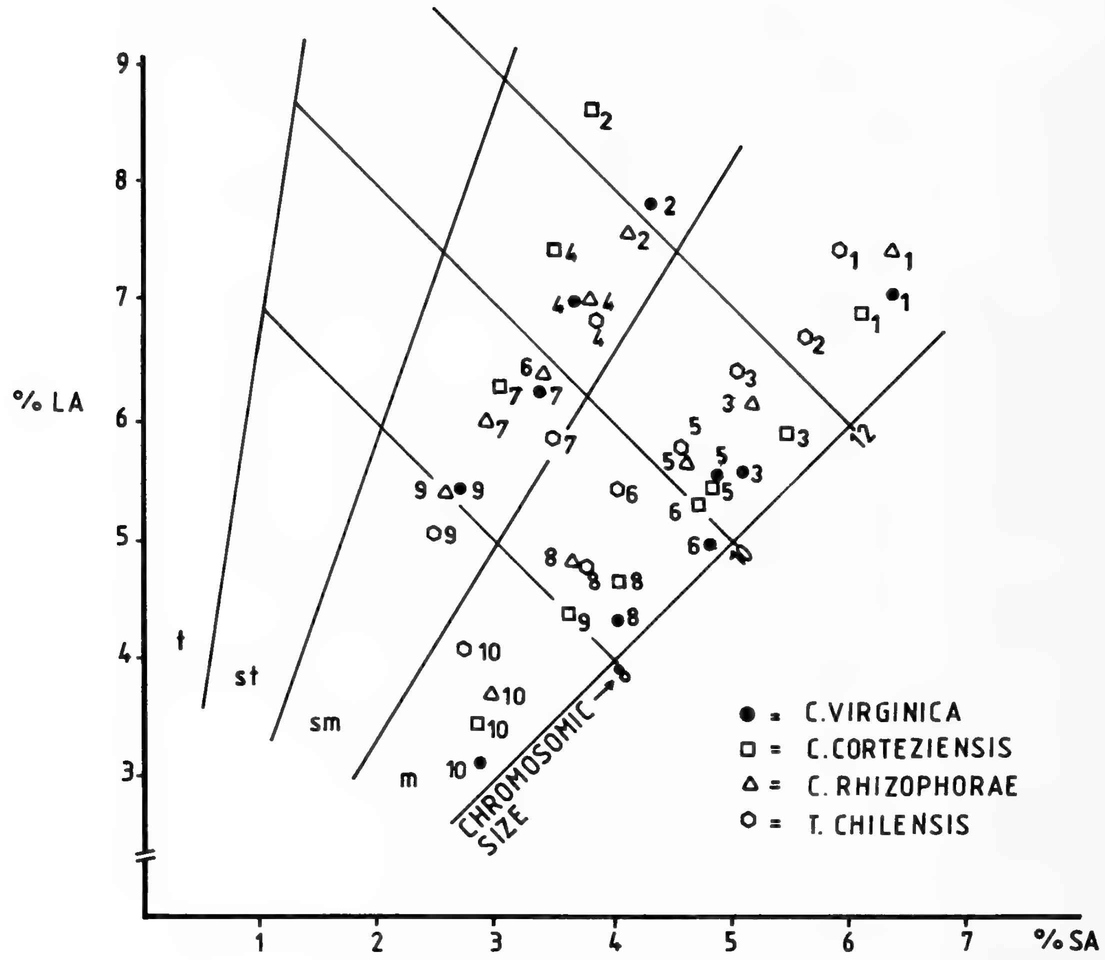

Figure 1

Karyo-idiogram showing chromosomic morphology of all studied species. Each point represents the mean value of the lengths of long (LA) and short (SA) arms of a chromosomic pair from one species. Different morphology areas, according to the Centromeric index of Levan et al. (1964), are indicated by m (metacentric), sm (submetacentric), st (subtelocentric), and t (telocentric).

lensis is associated to the main group. The other possible dendrogram (Figure 2B) forms a group with *C. virginica* and *C. rhizophorae,* and, with lower similitude, joins this group with *C. corteziensis.* Finally, in a similar way to the first proposed dendrogram, the main group is related to *T. chilensis* with the lowest similitude value.

DISCUSSION

The cytotaxonomic analysis has not been used very often in taxonomical and systematical studies of oysters because coarse chromosome characteristics such as the diploid number (2n = 20, except for *Dendrostrea folium* [Ieyama, 1990] which has a 2n = 22 chromosomes) and number of arms (Thiriot-Quiévreux, 1984) are quite constant in all studied oyster species. However, differences among species have been observed in karyotypic analysis based on diploid number, nucleolar position, and the number of chromosome pairs that share qualitative morphology among species (Rodríguez-Romero et al., 1979c; Thiriot-Quiévreux & Ayraud, 1982; Ieyama, 1990; Thiriot-Quiévreux & Insua, 1992; Insua & Thiriot-Quiévreux, 1993; Ladrón de Guevara et al., 1994).

In a classical karyotypic analysis, chromosomes are classified in qualitative morphologic categories (metacentric, submetacentric, subtelocentric, and telocentric) based on the ratio among the long and short arm lengths of each chromosome pair (Levan et al., 1964). This method separates the continuous variation of the centromere position into discrete classes and does not consider the relative length of each chromosome arm because it uses just the ratio among them. Comparisons based on that qualitative clas-

Table 1

Relative lengths of long (LA) and short (SA) arms from chromosomes of *Crassostrea virginica* (V), *C. corteziensis* (C), *C. rhizophorae* (R), and *Tiostrea chilensis* (T).

		Species			
		T (n = 26)(*)	V (n = 12)	C (n = 11)	R (n = 14)
Chrom pair	Arms	Avg ± SD(**)	Avg ± SD	Avg ± SD	Avg ± SD
1	SA	5.29 ± 0.78	6.33 ± 0.77	6.09 ± 0.51	6.35 ± 0.48
	LA	7.49 ± 1.00	7.19 ± 0.52	6.94 ± 0.54	7.50 ± 0.71
2	SA	5.29 ± 0.60	4.28 ± 0.28	3.77 ± 0.28	4.09 ± 0.39
	LA	6.78 ± 0.67	7.92 ± 0.54	8.70 ± 0.83	7.64 ± 0.47
3	SA	5.03 ± 0.62	5.09 ± 0.47	5.47 ± 0.42	5.14 ± 0.47
	LA	6.49 ± 0.62	5.83 ± 0.46	5.93 ± 0.37	6.19 ± 0.45
4	SA	3.83 ± 0.75	3.85 ± 0.39	3.46 ± 0.32	3.75 ± 0.41
	LA	6.87 ± 0.75	7.05 ± 0.38	7.29 ± 0.41	7.05 ± 0.45
5	SA	4.57 ± 0.55	4.91 ± 0.44	4.86 ± 0.37	4.61 ± 0.31
	LA	5.97 ± 0.57	5.59 ± 0.66	5.49 ± 0.43	5.66 ± 0.54
6	SA	4.02 ± 0.56	4.79 ± 0.35	4.66 ± 0.20	3.37 ± 0.24
	LA	5.46 ± 0.57	4.98 ± 0.32	5.10 ± 0.45	6.41 ± 0.60
7	SA	3.26 ± 0.58	3.38 ± 0.55	3.00 ± 0.32	2.89 ± 0.36
	LA	5.90 ± 0.66	6.26 ± 0.60	6.32 ± 0.34	6.03 ± 0.32
8	SA	3.69 ± 0.67	4.01 ± 0.24	4.02 ± 0.33	3.64 ± 0.51
	LA	4.78 ± 0.53	4.35 ± 0.31	4.61 ± 0.63	4.83 ± 0.40
9	SA	2.46 ± 0.63	2.70 ± 0.44	3.60 ± 0.39	2.57 ± 0.33
	LA	5.07 ± 0.77	5.26 ± 0.65	4.35 ± 0.51	5.43 ± 0.35
10	SA	2.75 ± 0.61	2.86 ± 0.43	2.83 ± 0.35	2.98 ± 0.38
	LA	4.05 ± 0.64	3.11 ± 0.37	3.44 ± 0.38	3.69 ± 0.35

(*) "n" number of metaphase plates measured.
(**) Means values (Avg.) ± standard deviations (SD) of arm length.

sification usually recognize differences among taxa when chromosomes of the same pair fall into different qualitative classes. In turn, chromosomes with remarkable differences in arm ratio or total length are considered of the same morphology if they fall into the same category. The ANOVA and SNK tests provide formal statistical methods for verifying statistically significant differences in the mean relative lengths of the short and/or long arms of a group

Table 2

Chromosomic morphology comparison between species pairs using the SNK test (SL: 0.05). Abbreviations as in Table 1.

		Species pairs											
		T:V		T:C		T:R		V:C		V:R		C:R	
Pair	Arm	SA	LA	SA	LA	SA	LA	SA	LA	SA	LA	SA	LA
1		=	=	=	=	=	=	=	=	=	=	=	=
2		*	*	*	*	*	*	*	*	=	=	=	*
3		=	*	=	*	=	=	=	=	=	=	=	=
4		=	=	=	=	=	=	=	=	=	=	=	=
5		=	=	=	=	=	=	=	=	=	=	=	=
6		*	*	*	=	*	*	=	=	*	*	*	*
7		=	=	=	=	=	=	=	=	=	=	=	=
8		=	=	=	=	=	=	=	=	=	=	=	=
9		=	=	*	*	=	=	*	*	=	=	*	*
10		=	*	=	*	=	*	=	=	=	*	=	=

= No significant differences ($P > 0.05$).
* Significant differences ($P < 0.05$).

Table 3

Species-species matrix showing number of chromosomes of equal morphology according to data obtained from the SNK test (Table 2). Abbreviations as in Table 1.

	T	C	V	R
T	–	5	6	7
C		–	8	7
V			–	8
R				–

of homologous chromosomes, avoiding subjective decisions about the morphological similarity of one chromosome pair between species.

Centromeric position usually changes when pericentric inversions involve different length of the chromosomal segment on each side of the centromere. This mechanism has been previously proposed to explain karyotypic differences between *C. corteziensis* and *C. virginica* (Rodríguez-Romero et al., 1979c) and could explain most of the chromosomic variation among this group of species. However, pericentric inversions can occur without changes in centromere position, when equal segments on each side of the centromere are involved or when inversions that involve unequal chromosome segments in a non-metacentric chromosome do not alter the arm ratio. The use of centromeric position alone underestimates the number of chromosomic differences among species. The use of statistical procedures improves the capacity to recognize karyological differences in the analyzed group of oyster species. Chromosome pairs 2 and 10, qualitatively similar, are statistically different among some *Crassostrea* species.

Because of the ease of hybridization, viability of the F_1 trough metamorphosis, and intergradation in the F_1 larval shell and pigmentation, Menzel (1973) concluded that *C. rhizophorae* is a subspecies of *C. virginica.* Our data show that these two species are karyologically as different from each other as *C. corteziensis* is from *C. virginica.* Our data agrees with Hedgecock & Okazaki's (1984) genetically based conclusion that *C. rhizophorae* and *C. virginica* are well separated species. *C. rhizophorae* lives over mangrove roots, in waters with temperatures ranging from 25 to 31°C and a salinity of 37 to 44 ppm (Mattox, 1949). *C. virginica* lives in a lower range of temperature (18–27°C) and sa-

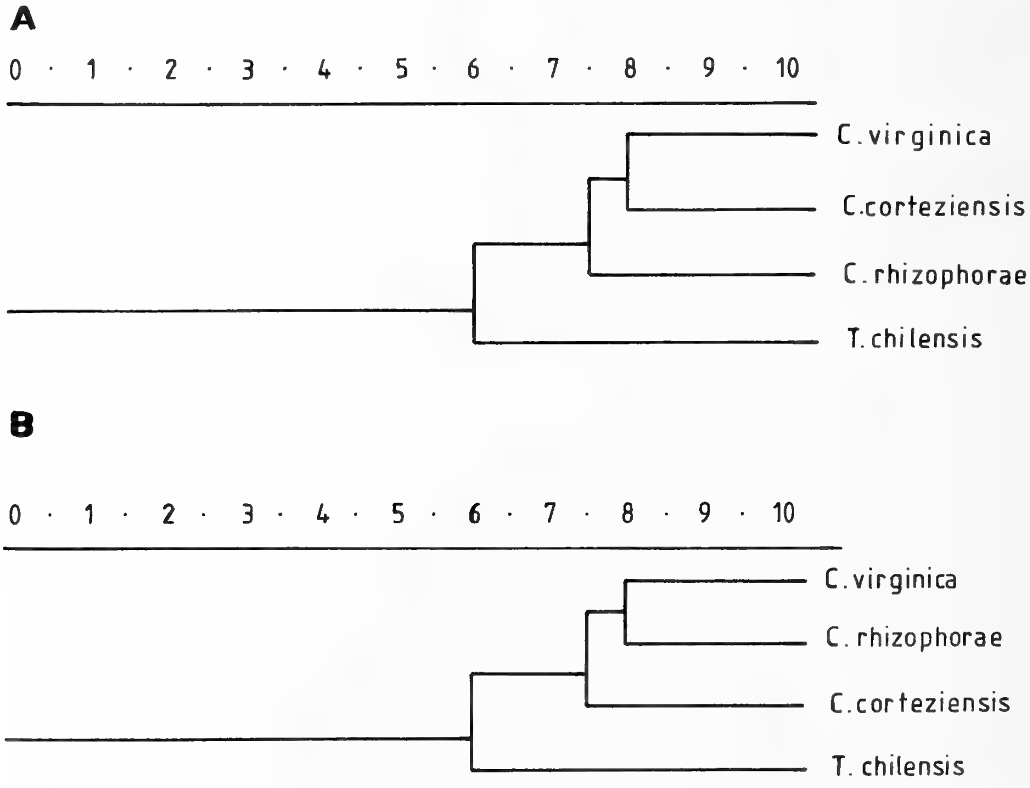

Figure 2

Dendrograms showing the association pattern given by the chromosomic morphology evaluated using the SNK test. According to the results shown in the main matrix (Table 3), there are two possible associations (A or B). Scale shows number of chromosomes of equal morphology.

linity (19–25 ppm) on the bottom of shallow waters (Castillo, 1986). Shell morphology and soft tissue anatomy show slight but clear differences between these two species (Castillo, 1986). The above data strongly support the idea that *C. rhizophorae* is specifically different from *C. virginica,* and not a subspecies as proposed by Menzel (1973) and Harry (1985).

The analysis of karyological information gives two different patterns of similitude among the three *Crassostrea* species (Figure 2). In the first one, *C. corteziensis* and *C. virginica* are more similar to each other than either is to *C. rhizophorae.* In the second one, *C. rhizophorae* and *C. virginica* are more similar to each other than either is to *C. corteziensis.* The chromosomic condition of pairs 2, 6, and 9 of both *C. corteziensis* and *C. rhizophorae* can be obtained by single independent pericentric inversions starting from *C. virginica* karyotype, giving the most parsimonious pattern of change. This agrees with Stenzel's (1971) hypothesis that all three *Crassostrea* species descended from a *C. virginica*-like ancestor and suggests that *C. virginica* shows the most primitive karyological condition among them.

Paleontological evidence dates *C. corteziensis* to the Pliocene, previous to the rising of Isthmus of Panama (Hertlein, 1951). Molecular evidence is compatible with the paleontological information and suggests that *C. rhizophorae* emerged from the ancestral lineage before the *virginica-corteziensis* clade (Hedgecock & Okazaki, 1984). On the other hand, both shell morphology and soft tissue anatomy also showed closer similitude between *C. virginica* and *C. corteziensis* than either with *C. rhizophorae* (Castillo, 1986). Based on this evidence, the first pattern of chromosomic relationship seems to be the most likely pattern of karyotypic evolution in this species. However, more detailed karyological studies, using chromosomal banding patterns and NOR regions position, are necessary to confirm the above proposed relationships.

ACKNOWLEDGMENTS

The authors are grateful to Pablo Schmiede for his review of the English version, to an anonymous referee for comments and suggestions, and to Dra. Elisabeth von Brand who encouraged us to study the Chilean oysters cytogenetically. This work was supported by the Research Project DGI-UCN N° 021.

LITERATURE CITED

Buroker, N., P. Chanley, H. Cranfield, & P. Dinamani. 1983. Systematic status of two oyster populations of the genus *Tiostrea* from New Zealand and Chile. Marine Biology 77:191–200.

Castillo, Z. 1986. Taxonomía y anatomía comparada de las ostras en la costa de México. Anuario del Instituto de Ciencias del Mar y Limnología. Universidad Nacional Autónoma de México 143:249–314.

Dinamani, P. & A. G. Beau. 1981. Description of a new species of incubatory oyster from northern New Zealand, with notes on its ecology and reproduction. New Zealand Journal of Marine and Freshwater Research 15:109–119.

Harry, H. 1985. Synopsis of the supraspecific classification of living Oysters (Bivalvia: Grypheidae and Ostreidae). The Veliger 28:121–158.

Hedgecock, D. & B. Okazaki. 1984. Genetic diversity within and between populations of American oysters (*Crassostrea*). Malacologia 25:535–549.

Hertlein, L. G. 1951. Description of two new species of marine pelecypods from West México. Bulletin of the Southern California Academy of Sciences 50:331–335.

Ieyama, H. 1990. Chromosomes of the oysters, *Hyotissa imbricata* and *Dendrostrea folium* (Bivalvia: Pteriomorphia). Venus 49:63–68.

Insua, A. & C. Thiriot-Quiévreux. 1993. Karyotype and nucleolus organizer regions in *Ostrea puelchana* (Bivalvia: Ostreinae). The Veliger 36:215–219.

Ladrón de Guevara, B., C. Palma, & F. Winkler. 1994. Karyotype description and the position of the nucleolar organizer region (NOR) in the Chilean oyster *Tiostrea chilensis.* (Philippi) Chanley and Dinamani. Pp. 399–405 in A. Beaumont (ed.), Genetic and Evolution of Aquatic Organisms. Chapman & Hall: London.

Levan, A., K. Fredga, & A. A. Sandberg. 1964. Nomenclature for centromeric position on chromosomes. Hereditas 52: 201–220.

Longwell, A. C., S. S. Stiles, & D. G. Smith. 1967. Chromosome complement of the American oyster *Crassostrea virginica* as seen in meiotic and cleaving eggs. Canadian Journal of Genetics and Cytology 9:845–856.

Mattox, N. T. 1949. Studies on the biology of the edible oyster, *Ostrea rhizophorae* (Guilding) in Puerto Rico. Ecological Monographs 19:330–356.

Menzel, R. W. 1968. Chromosome number in nine families of marine pelecypod mollusks. The Nautilus 82:45–50, 53–58.

Menzel, R. W. 1973. Some species affinities in the oyster genus *Crassostrea.* Bulletin of the American Malacological Union, Inc. 1973:38.

Rodríguez-Romero, F., M. Uribe-Alcocer & A. Laguarda-Figueras. 1978. Cytogenetic study of an oyster population of the species *Crassostrea virginica* Gmelin, from the coast of Tabasco, México. Venus 37:83–86.

Rodríguez-Romero, F., M. Alcocer-Uribe & A. Laguarda-Figueras. 1979a. The karyotype of *Crassostrea corteziensis* Hertlein (Mollusca: Ostreidae). Anales del Centro de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México 6:15–18.

Rodríguez-Romero, F., M. Uribe-Alcocer, A. Laguarda-Figueras, & M. Diupotex-Chong. 1979b. The karyotype of *Crassostrea rhizophorae* (Guilding, 1828). Venus 38:135–140.

Rodríguez-Romero, F., A. Laguarda-Figueras, & M. Uribe-Alcocer. 1979c. Comparative analysis of the caryotypes of two oyster species of the genus *Crassostrea* from México: *C. virginica* and *C. corteziensis.* Anales del Centro de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México 6:19–24.

Solís, I. 1967. Observaciones biológicas en ostras (*Ostrea chilensis*) de Pullinque. Biología Pesquera, Ministerio de Agricultura, Santiago Chile 2:51–82.

Spotorno, A. E. 1985. Conceptos y métodos en cariología comparada. Pp. 135–165 in R. Fernández-Donoso (ed.), El núcleo, los cromosomas y la evolución. UNESCO.

Stenzel, H. B. 1971. Oysters. Pp. N953-N1224 in R. C. Moore, (ed.), Treatise on Invertebrate Paleontology, Part

N, Vol. 3 (of 3), Mollusca 6. Geological Society of America Inc. and the University of Kansas: Boulder, Colorado.

THIRIOT-QUIÉVREUX, C. 1984. Les caryotypes de quelques Ostreidae et Mytilidae. Malacologia 25:465–476.

THIRIOT-QUIÉVREUX, C. & N. AYRAUD. 1982. Les caryotypes de quelques espèces de bivalves et gasèropodes marins. Marine Biology 70:165–172.

THIRIOT-QUIÉVREUX, C. & A. INSUA. 1992. Nucleolar organizer region variation in the chromosomes of three oyster species. Journal of Experimental Marine Biology and Ecology 157:33–40.

WHITE, M. J. D. 1973. Animal Cytology and Evolution. Cambridge University Press: Cambridge. 961 pp.

ZAR, J. 1974. Biostatistical Analysis. Prentice Hall Inc.: Englewood Cliffs, New Jersey. 620 pp.

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NOTES, INFORMATION & NEWS

Designation of a Neotype for the Pismo Clam, *Tivela stultorum* (Mawe, 1823), and Lectotypes for Synonymous Nominal Taxa (Bivalvia: Veneridae)

by

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In preparing an identification manual and nomenclatural revision of the northeastern Pacific Bivalvia (Coan et al., in preparation), it has been noted that the association of the large and once commercially important northeastern Pacific Pismo clam with the name *Donax stultorum* Mawe, 1823, hangs by a slender thread. The purpose of this note is to designate a neotype to clarify this identity.

This species was long known as *Tivela crassatelloides* (Conrad, 1837), originally proposed as *Cytherea* (*Trigonella*) *crassatelloides* Conrad, 1837:253–254, pl. 19, fig. 17, with localities of Santa Barbara and San Diego, California. This taxon is represented by a syntype in the Academy of Natural Sciences of Philadelphia (ANSP 53900), labeled "California, Conrad." No additional syntypes have come to light in The Natural History Museum in London or elsewhere (Keen, 1966:169). This ANSP specimen, consisting of paired valves, is here designated as **lectotype** (Figure 1); it is 127.3 mm long, 98.3 mm high, and 61.8 mm in width.

G. B. Sowerby II (1851:612, pl. 127, fig. 17) was the first to suggest that the name "*Trigona*" *stultorum* might be based on a juvenile specimen of the Pismo clam, citing the name from Wood (1828:4, pl. 2, fig. 2), Gray (1838: 304), and Hanley (1843:106 [as "105"]). Carpenter (1864: 524, 526) repeated this suggestion, referencing Mawe's original publication (1823:37, 40, pl. 9, fig. 7), as well as the subsequent treatments of Gray (1838) and Hanley (1856:202, suppl. pl. 2, fig. 2).

In Mawe's publication, there is a figure but no description, and the only locality cited is "Indian Seas." No type material has been located in The Natural History Museum in London (K. Way, in correspondence, 12 Feb. 1992). The first written description of this species is that of Hanley (1843:106), as *Cytherea stultorum.*

Mawe's name was not used for the northeastern Pacific species until Stearns (1899) noted that Carpenter had made this suggestion. Shortly thereafter, Dall (1902:386) adopted Mawe's name for the species, and then nearly all subsequent authors followed him.

Mawe's original figure is an external view of a right valve; the figure measures 38.3 mm in length and 29.7 mm in height (Figure 2). Although it is a reasonable match for small specimens of the California species, there is an Indian Ocean species, *Tivela ponderosa* (Philippi, 1844: 149, pl. 1, fig. 1, *ex* Koch ms), and Mawe might have illustrated a small specimen of this species instead. Throughout its growth, this Indian Ocean species is more trigonal and equilateral than the Pismo clam (Figure 4).

It would not be in the interest of nomenclatural stability to abandon the now-familiar name *stultorum* for the Californian species or to use *stultorum* in some other sense, but it seems prudent to clarify its status (ICZN Code Art. 75; Ride et al., 1985) by selecting the following neotype:

SBMNH 142890, **neotype (herein)** (Figure 3); Long Beach, California (33.7°N, 118.1°W); S. S. Berry. This is a small set of paired valves resembling Mawe's illustration. It is 49.9 mm in length, 37.2 mm in height, and 23.2 mm in thickness.

Mawe (1823:40) selected a vernacular name for this species, "foolish donax," a rough translation of the Latin name. The well-known present vernacular "Pismo clam" is based on the town of Pismo Beach, California, where the species was once particularly abundant.

The following color varieties were named by Stearns (1898) as trinomials under *Cytherea* (*Tivela*) *crassatelloides,* without clear indication that infrasubspecific rank was intended (ICZN Code Art. 45f, g). He named them because he wanted to demonstrate the color variation among some 1000 specimens that had been received in the United States National Museum, and he provided statistics on the frequency of each color form. The material was all subsequently labeled "California," although he stated that two varieties—*C.* (*T.*) *c. luteobrunnea* and *C.* (*T.*) *c. multiradiata*—occurred only at Santa Monica. The original material may all have come from there. Because no type material for these taxa had yet been isolated and placed in the type collection at the U.S. National Museum of Natural History, I have selected and **here designate lectotypes** for each of them, with the remaining material that had been in the lots cited recatalogued as paralectotypes. These are listed in their order in Stearns (1898), with the number of the lectotype (or holotype) given in brackets: *Cytherea* (*Tivela*) *crassatelloides pauciradiata* [USNM 150882], *multiradiata* [USNM 150888], *alternata* [USNM 150889], *eccentrica* [USNM 150874], *serialis* [USNM 150884], *interrupta* [USNM 150875, holotype], *luteobrunnea* [USNM 150878], *uniradiata* [USNM 150884], *biradiata* [USNM 150886], *triradiata* [USNM 150872], *ochracea* [USNM 150883], *purpureochocolata* [USNM 150873],

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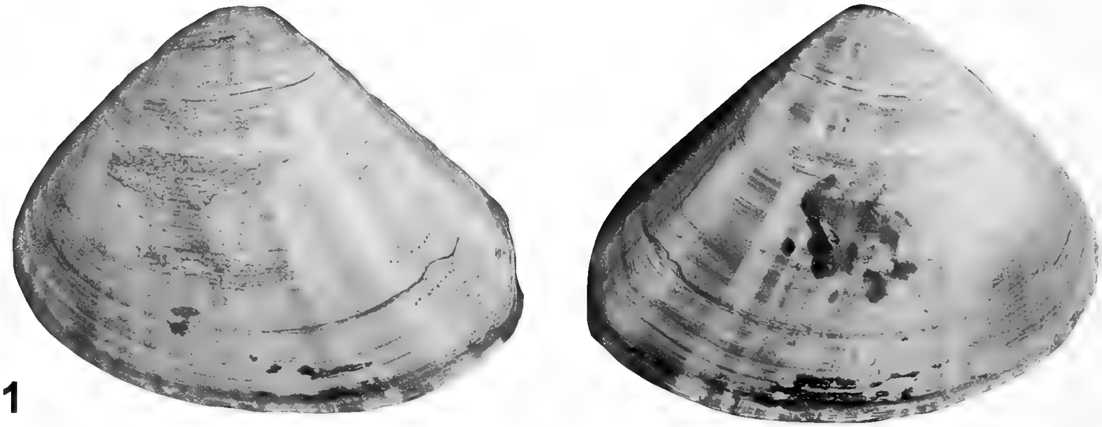

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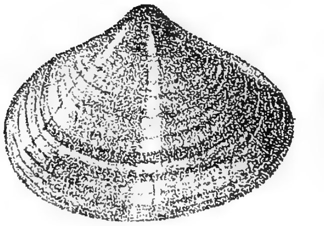

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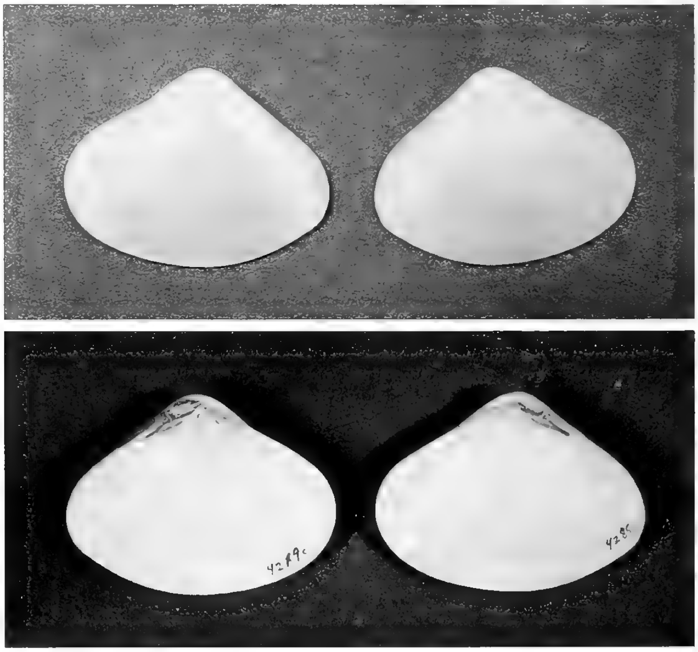

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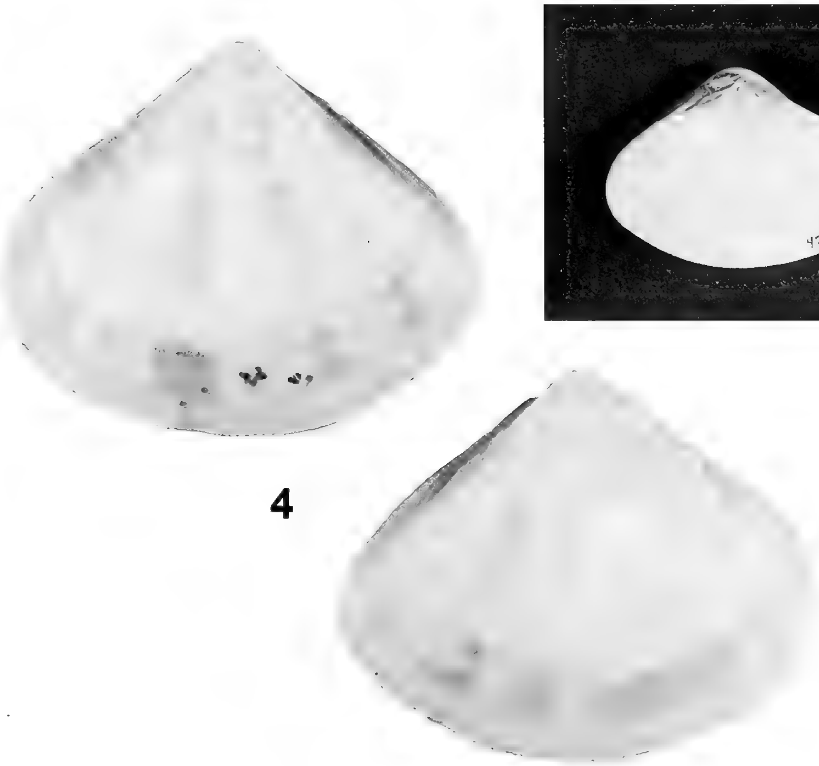

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biserialis [USNM 150890], *triserialis* [USNM 150881], *aurora* [USNM 150885], and *duplicata* [USNM 150896].

Additional synonyms that have been allocated to this species include *Cytherea virginea* A. Adams & Reeve, 1850; *C. solidissima* Philippi, 1851; and *Tivela scarificata* Berry, 1940. It is the type species of *Trigonella* Conrad, 1837, by monotypy (as *Cytherea crassatelloides*), *non* da Costa, 1778. This junior homonym was renamed *Pachydesma* Conrad, 1854, which is often used as a subgeneric name, although it is of doubtful utility. *Tivela stultorum* occurs from Stinson Beach, California (37.9°N), south to Bahía Magdalena, Baja California Sur (24.6°N), from the intertidal zone to 30 m. It attains 176 mm in length and has been recorded as early as the Pliocene in western North America.

I appreciate the help of Kathie Way of The Natural History Museum, London, in searching for Mawe's original specimen. Richard E. Petit assisted in interpreting Hanley's publications. Alan R. Kabat and Raye N. Germon helped straighten out Stearns' types. Mel Harte, Alan R. Kabat, Barry Roth, and Paul H. Scott provided useful comments on the manuscript.

Literature Cited

ADAMS, A. & L. A. REEVE. 1848–1850. Mollusca. x + 87 pp., 24 pls. in A. Adams (ed.), The Zoology of the Voyage of H. M. S. Samarang, under the Command of Captain Sir Edward Belcher, . . . during the Years 1843–1846. Reeve et al.: London.

BERRY, S. S. 1940. New Mollusca from the Pleistocene of San Pedro, California—I. Bulletins of American Paleontology 25:147–164, pls. 17, 18.

CARPENTER, P. P. 1864. Supplementary report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. British Association for the Advancement of Science, Report 33 [for 1863]: 517–686.

COAN, E. V., P. H. SCOTT & F. R. BERNARD. In preparation. Bivalve Seashells of Western North America. Santa Barbara Museum of Natural History.

CONRAD, T. A. 1837. Descriptions of new marine shells from Upper California, collected by Thomas Nuttall, Esq. Academy of Natural Sciences of Philadelphia, Journal 7:227–268, pls. 17–20.

CONRAD, T. A. 1854. Notes on shells, with descriptions of three Recent and one fossil species. Academy of Natural Sciences of Philadelphia, Proceedings 7 [for 1854]: 31–32.

DALL, W. H. 1902. Synopsis of the family Veneridae and of the North American Recent species. United States National Museum, Proceedings 26:335–412, pls. 12–16.

GRAY, J. E. 1838. Catalogue of the species of the genus *Cytherea*, of Lamarck, with the description of some new genera and species. The Analyst, London 8:302–309.

HANLEY, S. C. T. 1842–1843. Illustrated, Enlarged, and English Edition of Lamarck's Species of Shells, . . . Forming the Third Edition of the *Index Testaceologicus.* Wood: London. 224 + 8 + [3] + 8 pp., 3 pls. (pp. 1–32, pls. 1, 2, late 1842; pp. 1–32 [reissue], 33–144, early 1843; pp. 145–224 + 8 + [3] + 8 pp., pl. 3, late 1843).

HANLEY, S. C. T. 1842–1856. An Illustrated and Descriptive Catalogue of Recent Bivalve Shells. Williams & Norgate: London. xviii + 392 + 24 pp., pls. 9–24 (pp. 1–32, late 1842; pp. 1–32 [reissue], 33–144, pls. 9–13, early 1843; pp. 145–272, late 1843; pls. 14–16, late 1844; pls. 17–19, 1846; pp. 273–392 + xviii + 24 pp., pls. 20–24, 1856).

HANLEY, S. C. T. 1856. Index Testaceologicus, an Illustrated Catalogue of British and Foreign Shells, Containing about 2800 Figures Accurately Coloured after Nature, by W. Wood, F.R.S., F.L.S. A new and entirely revised edition, with ancient and modern appellations, synonyms, localities, etc. Willis & Sotheran: London. xx + 234 pp., 38 + 8 pls.

KEEN, A. M. 1966. West American mollusk types at the British Museum (Natural History), I. T. A. Conrad and the Nuttall Collection. The Veliger 8:167–172.

MAWE, J. 1823. The Linnaean System of Conchology, Describing the Orders, Genera, and Species of Shells, Arranged into Divisions and Families: with a View to Facilitate the Student's Attainment of the Science. Mawe & Longman et al.: London. xv + 207 pp., 36 pls., frontis.

PHILIPPI, R. A. 1844–1848. [Monograph of] *Cytherea.* Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien 1(6):149–150, pl. 1; (7):169–173, pl. 2 (1844); (8):197–200, pl. 3 (1845) 2(4):95–97, pl. 4 (1846); (6):179–182, pl. 5; (8):199–231, pls. 6–7: 3(1):23–25, pl. 8 (1847); (3):71–74, pl. 9 (1848).

PHILIPPI, R. A. 1849–1851. Centuria quarta testaceorum novorum. Zeitschift für Malakozoologie 6:27–32 (1849); 8:29–32, 39–48, 49–64, 65–74 (1851).

RIDE, W. D. L., C. W. SABROSKY, G. BERNARDI & R. V. MELVILLE, (eds.). 1985. International Code of Zoological Nomenclature, third ed., adopted by the XX General Assembly of the International Union of Biological Sciences. International Trust for Zoological Nomenclature: London. xx + 338 pp.

SOWERBY, G. B., II. 1851. Monograph of the genus *Cytheraea.* Pp. 611–648, pls. 127–136 in G. B. Sowerby II, (ed.), Thesaurus conchyliorum; or, Monographs of Genera of Shells.

STEARNS, R. E. C. 1898. 1898. Notes on *Cytherea* (*Tivela*) *crassatelloides* Conrad, with descriptions of many varieties. United States National Museum, Proceedings 21:371–378, pls. 23–25.

STEARNS, R. E. C. 1899. *Donax stultorum,* Mawe = Conrad's species, *Cytherea crassatelloides.* The Nautilus 13:73–75.

WOOD, W. 1828. Supplement to the Index Testaceologicus; or a Catalogue of Shells, British and Foreign. Wood: London. vi + 59 pp., 8 pls.

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Explanation of Figures 1 to 4

Figures 1–3. *Tivela* (*Pachydesma*) *stultorum* (Mawe, 1823). Figure 1. **Lectotype** (herein) of *Cytherea* (*Trigonella*) *crassatelloides* Conrad, 1837; length, 127.3 mm. Figure 2. Mawe's figure of *Donax stultorum*; length, 38.3 mm. Figure 3. **Neotype** (herein) of *Donax stultorum,* SBMNH 142890; length, 49.9 mm. Figure 4. *Tivela* (*Pachydesma*) *ponderosa* (Philippi, 1844), USNM 657341, Muscat, Oman; length, 41.5 mm.

A New Species of *Thalassonerita*? (Gastropoda: Neritidae?) from a Middle Eocene Cold-Seep Carbonate in the Humptulips Formation, Western Washington

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Introduction

A few specimens of *Thalassonerita*? ***eocenica,*** sp. nov., possibly a neritid gastropod, are present in a localized cold-seep limestone of middle Eocene age in the Humptulips Formation, Grays Harbor County, western Washington. The specimens were found at California State University, Northridge (CSUN) locality 1583, latitude 47°15′10″N, longitude 123°49′W, at an elevation of 83 m (275 ft.), in a small limestone deposit approximately 1 m thick, exposed on the east side of East Fork of Humptulips River, approximately 600 m south and 110 m west of the northeast corner of section 5, T. 20 N, R. 9 W, Burnt Hill quadrangle, 7.5-minute, 1990 provisional edition, Grays Harbor County, Washington. Goedert & Kaler (1996) studied this limestone and interpreted it to be a cold-seep deposit (Figure 1). Although they reported neritiform gastropods from this deposit, they did not describe or name them. Their neritiform gastopods are the same as the new species described in this paper. They also reported the following mollusks from this locality: the gastropod *Abyssochrysos raui* Goedert & Kaler (1996) and the bivalves *Vesicomya* sp. and an unidentified possible lucinid. Saul et al. (in press) recognized two species of this possible lucinid, which they assigned to *Cryptolucina* Saul et al. (in press). They also reported that, based on benthic foraminiferal data, the rocks at CSUN loc. 1583 are middle Eocene in age and were deposited at 1500 to 2000 m depth.

Nearly all ancient and modern species of neritids live in shallow subtidal or intertidal marine habitats or in brackish or freshwather habitats (Clarke, 1989). In 1989, however, a deep-sea neritid, *Bathynerita naticoidea* Clarke, 1989, was discovered living at archibenthal oil and gas seeps on the Louisiana slope in the Gulf of Mexico. This small gastropod was found at depths of 541 and 722 m and was videotaped crawling on live mytilid bivalves, which thrive at these cold-seep sites. Other associated mollusks include vesicomyid and lucinid bivalves. Warén & Bouchet (1993) studied the soft-part anatomy of *B. naticoidea.*

In 1966, a few specimens of a gastropod belonging to subgenus *Thalassonerita* Moroni, 1966, were found in some small isolated outcrops of limestone from the upper Miocene (Tortonian Stage) near the town of Forlì south of Bologna, in the northern Apennines, north-central Italy. Moroni (1966), who assigned these gastropods to family Neritidae, reported that the gastropod-bearing marly limestones contain a low-diversity molluscan assemblage. The fossil fauna is dominated by lucinids and articulated vesicomyids, as well as by modiolid bivalves (Taviani, 1994). Based on faunal composition and on carbon and oxygen isotope studies, Taviani (1994) interpreted these limestones to be authigenic and to have formed in association with venting of methane-rich cold seep fluids on the Miocene sea floor.

Olsson (1931:23) mentioned the presence of *Nerita*? in isolated cherty limestones of middle Eocene? or Oligocene? age in the lower Lomitos cherts, northwestern Peru. The isolated limestones contain abundant specimens of thyasirids associated with lucinids, vesicomyids, and solemyids. Goedert et al. (1995) and Squires & Gring (1996) tentatively reported that these cherty limestones are probably cold-seep deposits. Unfortunately, Olsson did not illustrate these specimens of *Nerita*?, nor did he assign any of them catalog numbers for future study.

The new species from the Humptulips Formation in Washington might belong to family Neritidae, and, if so, it would be the earliest record of neritids that lived around cold-seeps and the first record of a cold-seep neritid from the fossil record of North America.

Systematic Paleontology

Family NERITIDAE? Rafinesque, 1815

Discussion: As will be mentioned below, the new species closely resembles cold-seep gastropods that have been reported to be neritids. In order to confirm the systematic position of this new species, it will be necessary to check for the absence of internal whorl partitions on the earlier whorls, which are known (Keen, 1971) to be resorbed in, at least, shallow-marine neritids. Unfortunately, the poor preservation of the available specimens of the new species does not allow study of the earlier whorls. Until better specimens are found, we judge that the neritid assignment should be tentative.

Genus *Thalassonerita* Moroni, 1966

Discussion: *Thalassonerita* was originally considered to be a subgenus-level taxon (Moroni, 1966). Warén & Bouchet (1993) elevated subgenus *Thalassonerita* to a genus. Taviani (1994) mentioned that, based on unpublished data, he considers *Thalassonerita* to be a senior synonym of the Recent cold-seep taxon *Bathynerita.*

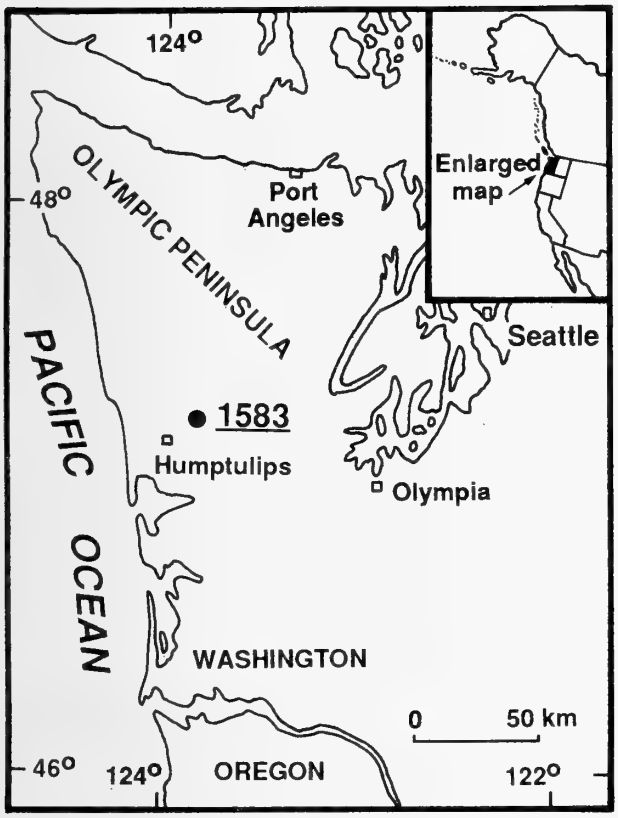


Figure 1

Index map to CSUN loc. 1583, Humptulips Formation, Grays Harbor County, Washington.

Type species: *Neritina* (*Thalassonerita*) *megastoma* Moroni, 1966, upper Miocene, near Forlìi, north-central Italy. Moroni (1966) was inconsistent as to the generic placement of this species, and she variously referred to it either as *Neritina* (*T.*) *megastoma* or *Nerita* (*T.*) *megastoma.*

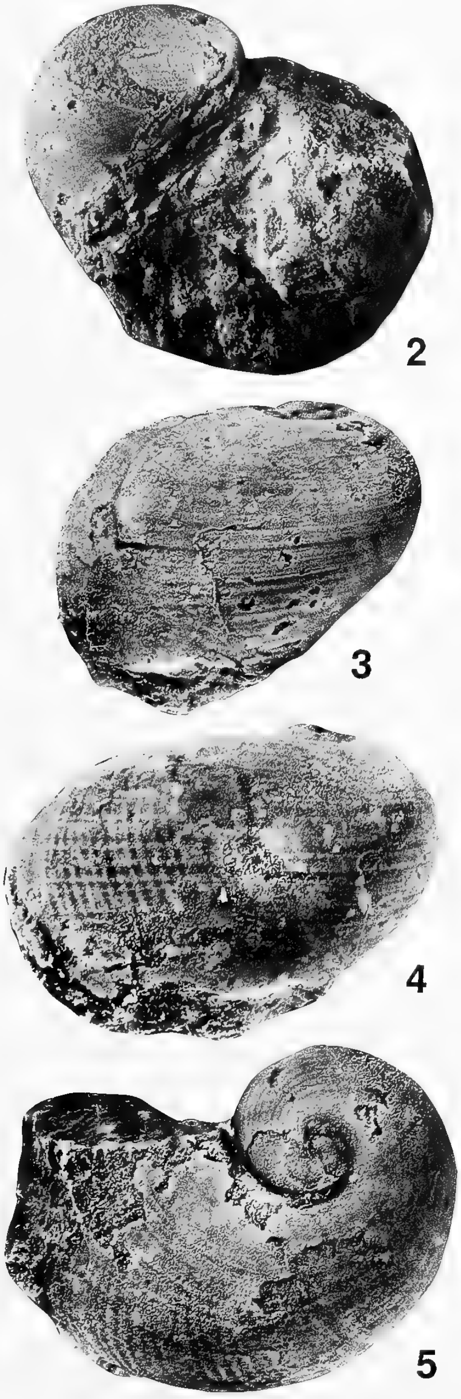
Thalassonerita? **eocenica** Squires & Goedert, sp. nov.

(Figures 2–5)

Neritiform gastropod Goedert & Kaler, 1996: 67, table 1.

Diagnosis: Small, neritiform, spire very low, body whorl with weak spiral threads grading into cancellate ornamentation, inner lip apparently smooth with no callus or deck area.

Description: Shell small, up to 6 mm height and 10 mm width; neritiform with very low spire, shell thin; protoconch missing; teleoconch 1½ whorls; suture between spire and body whorl impressed; body whorl rounded, juvenile specimens (about 3 mm height or less) with many weak spiral threads grading, on adult specimens, into slightly stronger cancellate ornamentation; periostracum very thin and with prosocline growth lines; aperture moderately large;



Explanations of Figures 2 to 5

Figures 2–5. *Thalassonerita*? **eocenica** Squires & Goedert, sp. nov., holotype LACMIP 11426, CSUN loc. 1583, height 5.8 mm, width 8.5 mm, ×6.6. Figure 2: apertural view. Figure 3: left-lateral view. Figure 4: abapertural view. Figure 5: dorsal view.

inner lip margin sharp with no evidence of teeth and no callus or deck area; outer lip not preserved.

Holotype: Natural History Museum of Los Angeles County, Invertebrate Paleontology Section (LACMIP) 11426.

Type locality: CSUN loc. 1583, latitude 47°15′10″N, longitude 123°49′W.

Paratype: LACMIP 11427, CSUN loc. 1583.

Discussion: Fourteen specimens of the new species were found at CSUN loc. 1583. All show some degree of weathering. Five of the 14 specimens are whole and have shell material, but the shell material is nearly completely gone with only a very thin remnant left. These specimens are nearly internal molds. In addition, the shell is missing on the spires of all these specimens. Five other specimens are internal molds, and four other specimens are fragments. The specimens range in height from 1 to 6 mm. Cleaning of the specimens is difficult because they are embedded in hard limestone. Only remnants of the periostracum are preserved, and they are usually only on juvenile specimens.

The new species most resembles *Thalassonerita megastoma* (Moroni, 1966:70–72, pl. 1, figs. 1–7) from the upper Miocene "Calcari a Lucine" near Forlì, north-central Italy. Moroni (1966) and Warén & Bouchet (1993) reported this species to be a neritid. The new species differs from *T. megastoma* in the following features: no callused flattened deck area along the inner lip, spiral threads on the entire body whorl rather than just on the initial (juvenile) portion, and the presence of cancellate ornamentation on the adult portion of the body whorl near the outer lip.

The new species resembles *Bathynerita naticoidea* Clarke (1989:125–129, pl. 2, figs. 3, 4, text figs.) from modern oil and gas seeps on the Louisiana slope in the Gulf of Mexico. Clarke (1989) reported this species to be a neritid as did Warén & Bouchet (1993:3–7, figs. 1, 2, 3a–c), who also illustrated and discussed it. The new species differs from *B. naticoidea* in the following features: no callused flattened deck area along the inner lip, and presence of spiral threads and cancellate ornamentation rather than being smooth.

Although both *Thalassonerita megastoma* and *Bathynerita naticoidea* have a callused flattened deck area like that found in many neritids, no information is available as to whether or not the internal whorl partitions of the earlier whorls have been resorbed. The systematic assignment of both of these species to family Neritidae would be strengthened if it could be shown that these internal whorl partitions are absent.

The lack of a callused deck area on the new species would seem to indicate assignment to a new genus that is otherwise closely related to *Thalassonerita* and *Bathynerita*. The inner lip callus of neritids, however, is especially prone to post-mortem dissolution (Squires & Saul, 1993), and cold-seep sites are commonly associated with selective dissolution of molluscan carbonate shell material (Squires & Gring, 1996). Until it can be determined whether or not the new species can have a callused deck area, we judge that the generic assignment remain tentative.

Warén & Bouchet (1993) reported that although it is difficult to conclude anything about the age of the lineage represented by neritids that live in the deep sea around cold seeps, it is probable that they evolved independently of other neritids since before the Tertiary. If the deep-sea, cold-seep gastropod *Thalassonerita*? ***eocenica*** sp. nov. does eventually prove to be a neritid, it would significantly extend the fossil record of this lineage and would thereby strengthen the hypothesis of Warén & Bouchet (1993).

Acknowledgments

Keith L. Kaler (Olympia, Washington) and Gail H. Goedert helped collect the fossils. Lindsey T. Groves (Natural History Museum of Los Angeles County, Malacology Section) helped in obtaining literature.

Literature Cited

CLARKE, A. H. 1989. New mollusks from undersea oil seep sites off Louisiana. Malacology Data Net 2:122–134, pl. 2.

GOEDERT, J. L., & K. L. KALER. 1996. A new species of *Abyssochrysos* (Gastropoda: Loxonematoidea) from a middle Eocene cold-seep carbonate in the Humptulips Formation, western Washington. The Veliger 39:65–70.

GOEDERT, J. L., R. L. SQUIRES & L. G. BARNES. 1995. Paleoecology of whale-fall habitats from deep-water Oligocene rocks, Olympic Peninsula, Washington state. Palaeogeography, Palaeoclimatology, Palaeoecology 117:151–158.

KEEN, A. M. 1971. Sea Shells of Tropical West America. Marine Mollusks from Baja California to Peru. 2nd ed. Stanford University Press: Stanford, California. 1064 pp., pls. 1–22.

MORONI, M. A. 1966. Malacofauna del "Calcare a Lucine" di S. Sofia-Forlì. Palaeontographica Italica 60:69–87, pls. 1–6.

OLSSON, A. A. 1931. Contributions to the Tertiary paleontology of northern Peru: Part 4, The Peruvian Oligocene. Bulletins of American Paleontology 17:99–264, pls. 1–21.

SAUL, L. R., R. L. SQUIRES & J. L. GOEDERT. In press. A new genus of cryptic lucinid bivalve from lower Cenozoic cold seeps of the Pacific slope of North America. Journal of Paleontology.

SQUIRES, R. L. & M. P. GRING. 1996. Late Eocene chemosynthetic? bivalves from suspect cold seeps, Wagonwheel Mountain, central California. Journal of Paleontology 70(1): 63–73, figs. 1–4.

SQUIRES, R. L. & L. R. SAUL. 1993. A new species of *Otostoma* (Gastropoda: Neritidae) from near the Cretaceous/Tertiary boundary at Dip Creek, Lake Nacimiento, California. The Veliger 36:259–264.

TAVIANI, M. 1994. The "Calcari a *Lucina*" macrofauna reconsidered: deep-sea faunal oases from Miocene-age cold vents in the Romagna Apennine, Italy. Geo-Marine Letters 14:185–191, figs. 1–4.

WARÉN, A. & P. BOUCHET. 1993. New records, species, genera, and a new family of gastropods from hydrogthermal vents and hydrocarbon seeps. Zoologica Scripta 22:1–90, pls. 1–59.

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The Veliger 39(3):273–275 (July 1, 1996)

BOOKS, PERIODICALS & PAMPHLETS

Letting Go

Origin and Evolutionary Radiation of the Mollusca edited by JOHN D. TAYLOR. 1996 [actual date of issue 30 November 1995]. Oxford University Press. xiv + 392 pp. ISBN 0 19 854980 6.

In September 1993, the Malacological Society of London met at the Natural History Museum in London to commemorate the centenary of the Society. Thirty-one papers emerging from the presentations at that meeting are here gathered in an extraordinary volume—"the London Volume," as this benchmark work is coming to be known. Many, perhaps most, of the papers were updated substantially by their authors between the date of the meeting and the date of publication, with the result that this compilation reflects the state of the art *circa* 1995. That is both the good news and the bad news about the London Volume.

Concerns reflected in many of the papers are instructive as to where systematic/evolutionary malacology now stands, and where it has yet to go: the discovery of sister-group relationships; the recognition of homoplasy (important for avoiding spurious inferences of genetic relationship); and the polarity of character-state transformations (presumably because it is now widely recognized that the only defensible taxonomic groupings are those based on shared derived character states). All of these represent the impact of phylogenetic systematics upon the discipline. Even some of the papers that do not include phylogenetic analysis within their scope address questions of apomorphy (e.g., "Molluscan sperm ultrastructure: correlation with taxonomic units within the Gastropoda, Cephalopoda and Bivalvia" by J. M. Healy) and homology (e.g., "Shell pores (caeca, aesthetes) of Mollusca: a case of polyphyly" by S. Reindl and G. Haszprunar; "Development and homologies of the anal gland in *Haminaea navicula* (Da Costa, 1778) (Opisthobranchia, Bullomorpha)" by K. Schaefer; and "Parallelism in the origin of the G-type clausilial apparatus (Gastropoda, Pulmonata, Clausiliidae)" by E. Gittenberger and M. Schilthuizen).

Where phylogenetic inference is attempted, both cladistic and non-cladistic methods come into play, with a predictable mixture of results. Fifteen of the papers include branching diagrams purporting to show phylogenetic relationships among taxa, but not all are the result of cladistic protocols. For example, "Origin of Aculifera and problems of monophyly of higher taxa in molluscs" by D. L. Ivanov represents (fig. 4.6) a "scheme of cladistic events in the origin and phylogeny of Aculifera" in which various character states characterize branch segments. But the method of the paper itself is authoritarian rather than analytical: character states are asserted to be apomorphies without explicit test (such as outgroup comparison), and criteria of parsimony are not employed. "The evolutionary history of the Bivalvia" by B. Morton presents (fig. 29.9) a totally dichotomous "proposed evolutionary tree for the Bivalia," but the method is that of functional/adaptive narrative.

"Origin and evolutionary radiation" is, of course, a broad enough subject area to take in a wide range of topics. (Only article 27, "Crab predation as a selective agent on shelled gastropods: a case study of *Calliostoma zizyphinum* (Prosobranchia: Trochidae)" by S. J. Preston, D. Roberts, and W. I. Montgomery seems to strain the boundary—not a fault of the paper, which is a well-conducted field and lab study of predator-prey relations.) In fact, only the first paper in the volume ("The Mollusca: coelomate turbellarians or mesenchymate annelids?" by G. Haszprunar) and to some extent the second ("Synapomorphies and plesiomorphies in higher classification of Mollusca" by L. v. Salvini-Plawen and G. Steiner) truly bear on the origin of Mollusca as a clade. "Phylogenetic position of Sipuncula, Mollusca and the progenetic Aplacophora" by A. H. Scheltema discusses the possibility that Sipuncula and Mollusca are sister taxa, but its discussion is couched entirely in two-taxon statements, and testing of the suspected homologies is left for future developmental studies. By contrast, the Salvini-Plawen and Steiner paper uses Turbellaria and Sipunculida effectively as outgroups in analyzing relationships among the component clades of Mollusca (e.g., fig. 2.3). "An evolutionary tree for the Mollusca: branches or roots?" by D. R. Lindberg & W. F. Ponder addresses the deep framework of the molluscan tree and the monophyly, or not, of the Conchifera.

At the other end of the scale of taxonomic scope, M. Schilthuizen and E. Gittenberger ("Allozyme variation in some Cretan *Albinaria* (Gastropoda): paraphyletic species as natural phenomena") and S. Crossland, D. Coates, J. Grahame, and P. J. Mill ("The *Littorina saxatilis* species complex—interpretation using random amplified polymorphic DNAs") investigate population-level phenomena; the phena, or units of analysis, are predominantly allopatric in *Albinaria,* sympatric in *Littorina.*

"Gastropod phylogeny—challenges for the 90s" by Ponder and Lindberg is a short version of a broad cladistic overview now in press. Beside their results (statistically compared to major competing trees in table 11.3), the authors share the lessons of their analytical experience, point out problems ranging from data sets to mind sets, and suggest directions for future study.

Brief takes on a few of the other contributions:

"The Diaphanidae as a possible sister group of the Sacoglossa (Gastropoda, Opisthobranchia)" by K. R. Jensen asks the right kind of question and amasses the data to answer it, but stops short of performing the analysis.

The answer ("The Diaphanidae does not constitute the sister group of the Sacoglossa, nor does any of the genera included in the Diaphanidae"; p. 245) seems to have been derived by visual inspection of the data matrix (table 20.3). My run of the data with HENNIG86 (Farris, 1988) leads to the same conclusion and supports it with a parsimony argument as well. One wonders why this type of analysis was not done in the paper.

"Phylogeny and patterns of evolutionary radiation in trochoidean gastropods" by C. S. Hickman presents a fully realized cladistic analysis of Trochoidea including explicit laying out of characters and character states drawn from many systems, in welcome contrast to the author's earlier work (Hickman & McLean, 1990) with its *a posteriori* "retrospective cladograms."

In "Evolutionary radiations in the Cypraeidae" by E. A. Kay, the units of analysis are traditional genera without any consideration of the nature of those nominal taxa. Are the "genera" monophyletic or paraphyletic groups? If the latter, then some of the extinctions shown in fig. 18.3 may in fact be pseudo-extinctions. Without an estimate of sister taxon relationships, we cannot tell how much further back in time some lineages actually extend (i.e., as "ghost taxa"). It would be most interesting to revisit this topic after the group has been subjected to phylogenetic analysis.

Treatment of the Bivalvia lags behind that of the other classes. The Morton paper mentioned above is virtually a homage to C. M. Yonge. It takes as its starting point the hypothetical primitive bivalve of Morton & Yonge (1964) and narrates a speculative (although not implausible) history of radiations motivated by predation pressures, interspersed with mass extinctions that affect predominantly the more specialized members. This reviewer would like to see some ambitious bivalve specialist produce a parsimony-driven phylogenetic hypothesis for the Bivalvia against which Morton's story can be evaluated.

"The early evolution of the Bivalvia" by J. C. W. Cope is predominantly a summary of the fossil record. A branching diagram (fig. 30.3) of "possible phylogenetic links of the bivalve classes" is said to employ "the most parsimonious analysis of shell microstructural types," but the procedure for arriving at that estimate is not specified.

The overwhelming message of this volume is that all is not "business as usual" in malacology. The transition is well under way to a more analytical, hypothesis-driven (that is to say, scientific) practice of molluscan systematics. Even though, as one ecologist said to me recently, the war may be over—with phylogenetic systematics having no serious competitor at providing useful, testable hypotheses of relationship—there are skirmishes still to be fought. The molluscan literature of the future will be data-rich and explicit. Tables and taxon/character matrices will fill the pages of our systematic literature; and while they won't make good bedtime reading, they will place our conclusions on a testable, replicable footing. Reiterations of the old, canonical style of malacology with authoritarian assertions, imagined phylogenies, and the like will be increasingly seen as fraudulent (not merely incompetent, because claims of ignorance of the best available methods are no longer credible) and will be marginalized—their conclusions not necessarily wrong, merely irrelevant.

While its contents are a mixed bag, the London Volume gives plenty of reason for optimism. Old data sets are being revisited, re-analyzed, and supplemented. Long-accepted homologies are being inspected for homoplasy. The honorable rubric of peaceful social change, "Question Authority," is becoming the order of the day.

The book is available from Oxford University Press, Walton Street, Oxford OX2 6DP U.K. and Oxford University Press offices in other countries, at a price of £75.

B. Roth

Literature Cited

FARRIS, J. S. 1988. HENNIG86, Version 1.5. Computer program distributed by author. Port Jefferson Station, New York.

HICKMAN, C. S. & J. H. MCLEAN. 1990. Systematic revision and suprageneric classification of trochacean gastropods. Natural History Museum of Los Angeles County Science Series 35:i–vi, 1–169.

MORTON, B. & C. M. YONGE. 1964. Classification and structure of the Mollusca. Pp. 1–58 in K. M. Wilbur & C. M. Yonge (eds.), Physiology of Mollusca. Vol. 1. Academic Press: New York.

Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel. Volume 9. The Mollusca Part 2—The Gastropoda

by JAMES H. MCLEAN & TERRENCE M. GOSLINER. 3 April 1996. Series edited by PAUL H. SCOTT, JAMES A. BLAKE & ANDREW L. LISSNER. Santa Barbara Museum of Natural History, Santa Barbara, California. viii + 228 pp. ISBN 0-93649-14-X.

This spiral-bound, quarto size volume actually contains two separate, independently-authored contributions: The Prosobranchia by McLean (pp. 1–160), and The Opisthobranchia by Gosliner (pp. 161–213). An appendix with maps and station lists relates to both articles. Both contributions are clear, well-written taxonomic/identification treatises covering the gastropods collected during US Department of the Interior Minerals Management Service (MMS) benthic monitoring in the Santa Maria Basin off Central California, from about Point Estero to Point Conception, and the western Santa Barbara Channel, southeast of Point Conception, in depths of approximately 100–600 m. The utility of both, however, extends well beyond those specific areas.

As described in his introductory text, McLean uses the opportunity to provide an illustrated identification manual for southern California prosobranchs occurring at depths beyond those treated in his *Marine Shells of Southern California* (1969, revised 1978). The treatment of species herein is more detailed than in that book, and includes synonymies, deposition of type specimens, and remarks that sometimes go to some length to explain taxonomic choices or other points of interpretation. For many species, this work contains the only significant descriptive text published since their original proposals (or Oldroyd's republications of same), and quite often the only such treatment in a modern systematic context. Seven new species and one new genus are proposed; major taxonomic innovations are introduced in the genera *Lirobittium, Boreotrophon, Scabrotrophon* (new genus), *Borsonella, Ophiodermella,* and *Crockerella.*

Gosliner's treatment of the Opisthobranchia stays more within the confines of the MMS study; every species treated is represented by specimens in the voucher collections. But again, many of the taxa range beyond central California (indeed, the handsome cover photograph of *Tritonia festiva,* a species present in the voucher collections, shows a specimen from British Columbia). Twenty-eight species are described and discussed; half of these have never before been described morphologically. Seven species appear to be undescribed, although apparently because of the lack of comprehensive material, they are not named but merely cited as "sp. 1" and so forth. The genera *Parvamplustrum* and *Holoplocamus* are newly recorded from the Pacific coast of North America.

Both articles include keys to the species; the quality of the black-and-white photographs ranges from good to adequate. These contributions provide important clarification of the systematics and identification of regional bathyal gastropods; they make the volume a "must have" for workers concerned with benthic sampling and (because much of the Neogene fossil record of California involves sediments deposited in this depth range) paleontology in this part of the world.

The volume is available from the Department of Invertebrates, Santa Barbara Museum of Natural History, 2559 Puesta Del Sol Road, Santa Barbara, California 93105-2936, USA.

B. Roth

Marine Mollusca of the Galapagos, Gastropods, A Monograph and Revision of the Families Trochidae, Skeneidae, Turbinidae and Neritidae

by Yves Finet. 1995. Monographs on Galapagos Mollusca, No. 2. L'Informatore Piceno, Ancona, Italy. Glossy hard cover, 139 pp., 27 color and 10 black and white plates. ISBN 88-86070-24-1. Approximately $70 from US distributors.

> *Recent reports state that there has already been a perceptible reduction in the richness and diversity of the populations of molluscs and other marine invertebrates in the Galápagos Islands. **** Therefore compiling an inventory and a detailed systematic description of the marine molluscs in the Galápagos is, in my view, an indispensible, valuable and even urgent task.*
>
> –from the Preface, by Prince Sadruddin Aga Khan

Yves Finet's contribution toward this urgent task continues with this volume. Like the first in the series (reviewed, *The Veliger* 38:274), covering Haliotidae, Scissurellidae, Fissurellidae, and Lottiidae, this monograph is lavishly produced in a large format with stunningly beautiful illustrations. Several color images of each taxon practically place the specimens in the reader's hand (slightly greater depth-of-field is needed for specimens in the 3–4 mm size range), and ultra-sharp SEM pictures of minute shells, protoconchs, and radulae convey these details superbly.

Emphasis is on careful presentation of essential systematic information—synonymies, statements of type localities, republications of original descriptions (with additional description as necessary), keys to the taxa, and locality lists of specimens examined—rather than taxonomic innovation. It succeeds well in this aim, and with the books of this series in hand there should be little excuse for faunal surveyors ever to misidentify the gastropods in their samples.

B. Roth

Bivalvos, Gasterópodos, Quitones

by Jean-Maurice Poutiers. 1995. Pp. 99–304 in W. Fischer, F. Krupp, W. Schneider, C. Sommer, K. E. Carpenter & V. H. Niem (eds.), Guia FAO para la Identificación de Especies para los Fines de la Pesca. Pacífico Centro-Oriental. Vol. 1. Plantas e Invertebrados. Food and Agriculture Organization of the United Nations: Rome.

This substantial work in Spanish, organized in alphabetical order by family under each class, treats species of fisheries importance: 110 bivalves, 62 gastropods, and two chitons. Each species has a brief description and a distributional map, and each is illustrated with an excellent line drawing.

Gene Coan

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References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Phillips, 1981), for two authors (Phillips & Smith, 1982), and for more than two (Phillips et al., 1983). The reference need not be cited when author and date are given only as authority for a taxonomic name.

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a) Periodicals:

Hickman, C. S. 1992. Reproduction and development of trochacean gastropods. The Veliger 35:245–272.

b) Books:

Bequaert, J. C. & W. B. Miller. 1973. The Mollusks of the Arid Southwest. University of Arizona Press: Tucson. xvi + 271 pp.

c) Composite works:

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135 in R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal Invertebrates of California. Stanford University Press: Stanford, Calif.

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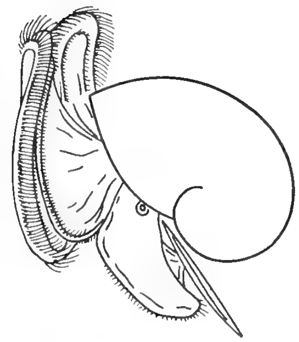

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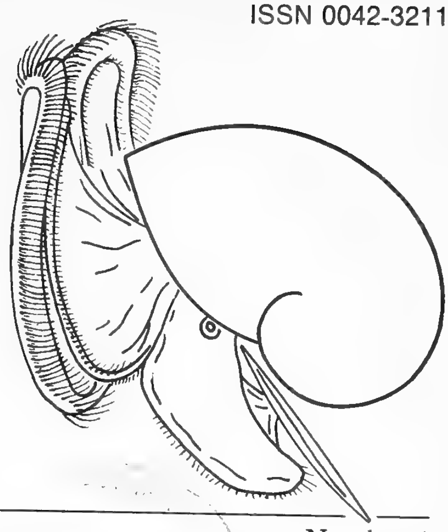

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THE VELIGER

Description of Zerotulidae fam. nov. (Littorinoidea), with Comments on an Antarctic Littorinid Gastropod

by

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Abstract. **Zerotulidae** fam. nov. is described and placed in the Littorinoidea. The family includes the genera *Zerotula* Finlay, 1926 (formerly in Architectonicidae); *Frovina* Thiele, 1912 (synonymized with *Prolacuna* Thiele, 1913, both formerly in Naticidae); ***Trilirata*** Warén & Hain, gen. nov. (type species *Prolacuna trilirata* Thiele, 1912, Antarctic); and ***Dickdellia*** Warén & Hain, gen. nov. (type species *Laevilitorina* (*Corneolitorina*) *labioflecta* Dell, 1991, Antarctic, bathyal).

The following new species are described: *Frovina* ***angularis*** Warén & Hain (New Caledonia, bathyal), *Zerotula* ***incognita*** Warén & Hain (North Atlantic, abyssal), *Z.* ***stellapolaris*** Warén & Hain (Antarctic), *Z.* ***coronata*** Warén & Hain (New Zealand, shelf), ***Trilirata sexcarinata*** Warén & Hain (Antarctic), ***T. triregis*** Warén & Hain (New Zealand, shelf), and ***T. herosae*** Warén & Hain (New Caledonia, bathyal). The anatomy is described for *Frovina soror* Thiele, 1912, *F. indecora* (Thiele, 1912), *Zerotula* ***stellapolaris***, ***Trilirata*** *macmurdensis* (Hedley, 1911), ***T. sexcarinata***, and ***D.*** *labioflecta.*

Antitrichotropis wandelensis (Lamy, 1906) (formerly in Capulidae, Neotaenioglossa) is transferred to Laevilitorininae (Littorinidae), based on examination of radula and external morphology of the head-foot. It is classified in *Laevilitorina,* subgenus *Pellilacunella.*

INTRODUCTION

The genera *Prolacuna* Thiele, 1913, *Frovina* Thiele, 1912, and *Zerotula* Finlay, 1926, have for a long time been classified in the Naticidae (*Prolacuna* and *Frovina*) and in the Architectonicidae (*Zerotula*). The only basis for this has been a misidentified naticid (*Prolacuna* and *Frovina*) and the planispiral shells of the species placed in *Zerotula.* Examination of types and additional material proved these classifications, dating from the first half of this century, to be mistakes. The genus *Zerotula* actually contained species of archaeogastropods, neotaenioglossates, and heterobranchs. When Hain obtained numerous Antarctic specimens of these groups, we decided to make a closer investigation of their systematic relationships.

We have examined the anatomies of the type species (or, in the case of *Zerotula,* a species similar to the type species) to get a more robust basis for the systematic placement of these taxa. We have also examined, in as much detail as our material allowed, several additional species about which we had accumulated information during many years of routine examination of museum collections and expedition material.

MATERIALS AND METHODS

Our work is largely based on specimens obtained during cruises of R/V *Polarstern* in the Weddell Sea and adjacent areas between 1985 and 1991. It has been supplemented by examination of type material and specimens from other sources according to our needs. Our material is listed under each species and deposited in the following museums: AMS, Australian Museum, Sydney; BMNH, Natural History Museum, London; MNHN, Muséum National d'Histoire Naturelle, Paris; MNZ, Museum of New Zealand, Wellington; NMWZ, National Museum of Wales, Cardiff; RSM, The Royal Scottish Museum, Edinburgh; SMNH, Swedish Museum of Natural History, Stockholm; USNM, National Museum of Natural History, Washington D.C.; ZMHU, Zoologisches Museum der Humboldt Universität, Berlin.

The material from the *Polarstern* cruises is referred to under each species by PS (*Polarstern*) followed by the cruise and station numbers. In order to avoid unnecessary repetition, we give a list of the station data below and repeat only depth and approximate longitude in the lists of "Material examined."

R/V *Polarstern* (PS)
Antarctic stations

Roman numbers/Arabic numbers are cruise/leg number.

III/3, sta. 345, 73°23'S, 021°37'W, 617 m, February 1985.
VII/4, sta. 224, 71°15.8'S, 013°04.2'W–71°15.8'S, 013°01.7'W, 186–187 m, 25 January 1989.
VII/4, sta. 230, 75°14.2'S, 026°59.4'W–75°12.9'S, 027°01.2'W, 270–280 m, 30 January 1989.
VII/4, sta. 250, 74°35.1'S, 029°39.9'W–75°32.4'S, 029°53.0'W, 799–810 m, 04 February 1989.
VII/4, sta. 272, 73°26.9'S, 021°33.6'W–73°25.7'S, 021°30.2'W, 409–406 m, 13 February 1989.
VII/4, sta. 274, 71°38.8'S, 012°09.4'W–71°38.3'S, 012°13.1'W, 196–212 m, 15 February 1989.
VII/4, sta. 282, 71°31.7'S, 012°27.4'W–71°30.6'S, 012°29.3'W, 609–575 m, 18 February 1989.
VII/4, sta. 284, 71°12.0'S, 013°14.0'W–71°12.2'S, 013°16.8'W, 402–412 m, 18 February 1989.
VII/4, sta. 289, 71°12.0'S, 013°27.9'W, 672 m, 19 February 1989.
VII/4, sta. 291, 71°06.1'S, 012°33.5'W–71°05.9'S, 012°34.8'W, 499–515 m, 19 February 1989.
VII/4, sta. 293, 71°06.2'S, 012°53.8'W–71°05.7'S, 012°58.4'W, 771–793 m, 20 February 1989.
VIII/5, sta. 491, 73°69'S, 022°42'W, 390–370 m, 21 February 1990.
IX/3, sta. 165, 70°18.9'S, 03°15.8'W–70°19.2'S, 03°16.8'W, 191–204 m, 17 February 1991.
IX/3, sta. 173, 70°00.5'S, 07°09.1'E–70°00.4'S, 07°07.4'E, 739–765 m, 20 February 1991.
IX/3, sta. 174, 69°43.7'S, 10°44.7'E–69°42.4'S, 10°47.5'E, 432–432 m, 21 February 1991.
IX/3, sta. 179, 69°58.9'S, 08°00.7'E–69°59.3'S, 07°59.9'E, 185–161 m, 22 February 1991.
IX/3, sta. 180, 69°57.4'S, 06°19.0'E–69°57.7'S, 06°21.0'E, 280–298 m, 23 February 1991.
IX/3, sta. 206, 69°06.9'S, 10°01.0'E–69°46.8'S, 10°01.6'E, 343–338 m, 07 March 1991.
IX/3, sta. 207, 69°57.4'S, 05°08.4'E–69°57.5'S, 05°00.4'E, 213–210 m, 07 March 1991.
IX/3, sta. 211, 69°58.9'S, 05°08.4'E–69°57.9'S, 05°00.4'E, 661–742 m, 10 March 1991.
IX/3, sta. 212, 70°00.5'S, 03°56.4'E–70°00.4'S, 03°57.3'E, 568–644 m, 11 March 1991.
IX/3, sta. 220, 70°24.1'S, 06°07.6'E–70°24.3'S, 06°08.6'E, 118–126 m, 13 March 1991.

Further data on the work during *Polarstern* VII/4–5 can be obtained in "Berichte zur Polarforschung," vol. 68 (1990); for cruise IX/3, vol. 100 (1992); and for earlier cruises in Hain (1990).

The material from the *Polarstern* Antarctic Expedition IX/3 was processed as follows. From each trawl 50 liters of sediment that passed a 4 mm sieve were subsequently sieved on a 0.5 mm sieve. The material that remained in the sieve was saved and fixed in 95% alcohol (to compensate for water in the sediment). These residues were then sorted under a stereomicroscope at SMNH and turned out to be very rich in small mollusks (Warén & Hain, 1992).

Serial sections were prepared of a range of species, as the material allowed. The sections were cut 5–7 µm thick and stained with Ehrlich's hematoxylin-eosin (EHE). Regrettably, all material available for this work had been preserved in alcohol (of varying strength since it was used for fixing sediment samples), which is not good for most histological purposes. The sections were therefore not of good quality, but have allowed a more precise systematic allocation than only external morphology would have done.

Egg capsules were identified to species by SEM examination of larvae ready to hatch and comparison with protoconchs of adult specimens.

We have divided the anatomical descriptions into two main parts: (1) what can be seen from the outside after removing the shell, including features seen only by transparency; (2) the results from serial sections.

SYSTEMATICS

Mollusca, Gastropoda,
Neotaenioglossa

Superfamily LITTORINOIDEA

The superfamily has been discussed by Ponder (1988), Haszprunar (1988), and Reid (1989); and we refer to these papers for general information about the taxon.

Family **Zerotulidae** Warén & Hain, fam. nov.

Diagnosis: Small to medium-sized neotaenioglossates with a featureless, planispiral to turbiniform shell with no or mainly spiral sculpture. Protoconch large, simple, and smooth, not distinctly demarcated (encapsulated development). Radula long, slender, with 80–200 transverse rows and more than 8-times as long as broad. Central tooth usually with a ridge projecting above cusps. Lateral tooth lacking "littorinid notch." Outer marginal very slender except basally; usually with long cusps; often with weak zone and membranous cusp at mid-length. No pallial tentacle; no metapodial tentacles. Esophagus with large esophageal gland and with lateral pouches in at least some species. Penis below and to the right of right cephalic tentacle. No paraspermatozoa. Sperm often stored in pericardium of female, sometimes also in a dorsal seminal receptacle opening between albumen and capsule gland of oviduct (***Trilirata***) or in albumen gland (***Dickdellia***). Pedal ganglia with a single accessory ganglion innervating propodium or two accessory ganglia innervating pro- and mesopodium, respectively. Osphradium long, slender; a low ridge containing osphradial ganglion between two slightly taller ciliated ridges.

Remarks: Four genera are included in this new family, *Zerotula,* ***Trilirata*** gen. nov., *Frovina,* and ***Dickdellia*** gen. nov. Warén originally recognized them as probably being related from radular characters, especially by the "hooded" (Reid, 1989) central tooth and the outer marginal teeth, which have unusually long apical cusps. Furthermore, the outer marginals, and sometimes also the inner marginals, are separated from the more central teeth by a bare zone of radular membrane. The radula is 8–20 times as long as broad, and it is usually difficult to unfold the marginal teeth. It differs drastically from the much shorter and broader (3–4 times as long as broad) type present in the Rissooidea (based on Rissoidae Gray, 1847, which name was given precedence over Truncatellidae Gray, 1840; ICZN Opinion 1664).

When additional material with preserved soft parts became available during Hain's work on Antarctic mollusks, we examined several species anatomically. This revealed similarities in the anatomy, despite the variations in shell morphology.

Systematic position of Zerotulidae: The anatomy seems highly plesiomorphic for the "rissooid-cingulopsoid-littorinoid radiation" as understood by Ponder (1988). ***Dickdellia*** differs considerably from the three other genera, and its special features are discussed under that generic heading.

The shells of zerotulids are about as featureless as gastropod shells come, but quite variable within the family (cf. Figures 1, 10A–C, 16, 19). None of the species so far included in the family has planktotrophic larvae, and the protoconch is thus of no use for classification. All species lack an "inner chitinous layer" (Ponder, 1988; Reid, 1989), known from Skeneopsidae, Cingulopsoidea, and some Rissooidea.

The cephalic tentacles are highly contractile and do not have any arrangement of conspicuous cilia and cirri, characteristic of most Rissooidea and Cingulopsoidea. This lack is shared with the other Littorinoidea, including the Eatoniellidae. This is probably a plesiomorphy, since it is shared with most neotaenioglossates.

A posterior pedal gland is present in many groups of the Neotaenioglossa, especially among the small species. It is, however, also common in veligers, also of large Neotaenioglossa and neogastropods (see, e.g., Fioroni, 1966), and may be a larval organ of general occurrence, retained only in certain taxa of small species, where a thin mucus thread helps prevent the adults from being washed away from the substrate. In such species, the gland usually opens via a well-defined pore centrally and ventrally on the sole of the foot. This seems not to be the case among zerotulids, where the gland is voluminous but lacks a defined opening. We therefore assume that there must be numerous, hardly discernable openings for the mucus. A posterior pedal gland is missing in adult Littorinidae (Reid, 1989).

The position of the penis, distinctly below the right cephalic tentacle, seems restricted to the Littorinidae and **Zerotulideae**. Reid (1989) considered this position apomorphic for littorinids. Now knowing this also in **Zerotulidae**, we find it more likely to be a plesiomorphy of Littorinoidea.

The innervation of the penis is of considerable interest, both for the understanding of the evolution of this organ and for the systematic positon, since there seems to be variation in this between the families (see Ponder, 1988; Reid, 1989). The quality of the sections did not allow any certain conclusions since it could be seen only in ***Z. stellapolaris***, and even in that species, the nerves could not be followed without interruption to their origin. It seems, however, that there are nerves both from the subesophageal and right pedal ganglia that join to a "penial ganglion," posteriorly at the base of the penis. From this "penial ganglion," there are also nerves to the pallial sperm duct and the prostate, and it is possible that the nerves to the penis are those from the pedal ganglion, and the ones to the sperm duct and prostate come from the subesophageal ganglion. The "penial ganglion" may then be a secondary fusion for coordination of the differently derived components of the male reproductive system (zygoneury). A similar zygoneury was described by Bouvier (1887) in *Littorina littorea,* but the relations to the penis were not mentioned.

This type of penial innervation is known from Annulariidae and Pomatiasidae, but we cannot exclude that it occurs elsewhere in the Rissooidea-Cingulopsoidea-Littorinoidea, since few species are known in enough detail to reveal this.

All examined species of **Zerotulidae** lack paraspermatozoa. This was also reported by Reid (1989) from the Lacuninae and Laevilittorininae, the two most "primitive" littorinid subfamilies. Absence of paraspermatozoa among almost all Rissooidea suggested to Reid that their presence is apomorphic for the higher littorinids. Healy (1990) and Warén & Ponder (1991) reported developing paraspermatozoa in the little-known family Provannidae to be "extremely similar to the 'nurse-cell' type paraspermatids of littorinids." We therefore favor the view that the production of paraspermatozoa is plesiomorphic and may be suppressed (but perhaps not lost) in these two littorinid subfamilies and the zerotulids.

Frovina indecora, ***Trilirata*** *macmurdensis*, ***T. sexcarinata***, and possibly *Zerotula* ***stellapolaris*** were found to store sperm in the pericardium. We do not know if this is natural or an artifact, and we cannot rule out the possibility that sperm from the female system was pushed through the gonopericardial duct by a violent contraction when the animal was fixed, but this seems unlikely given the large quantities found in some specimens, and in most species, the absence of sperm in other places.

Pericardial sperm storage is known from scattered occurrences in the rissooid-cingulopsoid-littorinoid radiation (Ponder, 1988:149), but in most of these examples, there are modifications involved, e.g., a receptaculum bulging into the pericardium. Such is not the case in **Zerotulidae**, where spermatozoa evidently enter the pericardium via the gonopericardial duct. Sperm storage (not described in detail) in the pericardium occurs also in *Globularia fluctuata* (Sowerby, 1825), which, however, is aphallic (Kase, 1990). No further details about this have been published. (*Globularia* is usually referred to the Naticidae, subfamily Ampullospirinae.) *Campanile symbolicum* Iredale, 1917 (Campanilidae, Cerithioidea) also stores sperm in the pericardium, but in a seminal receptaculum within the pericardium, and opening into the pallial cavity close to the pallial gonoduct (Houbrick, 1981, 1989).

Both the male and female glandular ducts are closed. This has usually been considered an advanced feature among caenogastropods, but Reid (1989) found it to be plesiomorphic in the Littorinoidea. A closed system in the **Zerotulidae** supports this conclusion.

The pedal ganglia have accessory ganglia, a single, anterior one, or two, one anteriorly, one posteriorly. The Littorinidae have two accessory pedal ganglia, one anteriorly, one posteriorly (Johansson, 1939; Fretter & Graham, 1962); the Rissoidae and Hydrobiidae also have two (Johansson, 1939; Hershler & Davis, 1980) in a similar position. We consider the single zerotulid accessory ganglion a synapomorphy of most zerotulids, but the two accessory ganglia in ***Dickdellia*** may be the plesiomorphic condition.

The osphradium differs from that of the Littorinidae in having the lateral ridges of the same height as the central ridge; in the Littorinidae they are much smaller, ciliated tracts (Johansson, 1939; Taylor & Miller, 1989; Reid, 1989). The rissoid osphradium is quite similar to that of the zerotulids (Johansson, 1939: pl. 3, figs. 3–4). Information about other possibly related taxa is insufficient to allow useful comparison.

We assume a long, slender radula to be a plesiomorphic feature for neotaenioglossates since it occurs also in the Abyssochrysidae, Provannidae, and many Cerithioidea, which are generally recognized as being old neotaenioglossate taxa (Houbrick, 1979, 1988; Warén & Ponder, 1991). A hooded rachidian tooth also occurs in the Littorinidae (Reid, 1989) and Cingulopsidae (Ponder & Yoo, 1980). The lateral tooth lacks the "littorinid notch" (Reid, 1989) in all zerotulids, which probably is the plesiomorphic condition. The gross morphology of the zerotulid radula is most similar to that of Abyssochrysidae and Littorinidae. Both these families have a "bare" zone between and no overlap of the inner and outer marginal teeth (see Houbrick, 1979:fig. 8; and Figure 3C, herein). We therefore consider the general morphology of the radula plesiomorphic, while the unusually long cusps and strange outer marginal tooth in ***Trilirata*** and *Zerotula* ***incognita*** are considered apomorphic features.

The radular sac passes through the nerve ring, centrally in the cephalopedal haemocoel and ventral to the esophageal gland, extending as far back as this. Here it may eventually make a short lateral loop. In littorinids it lies coiled in several loops over the gland.

The development of the jaw varies considerably among the zerotulids. So it does also in the whole "rissooid-cingulopsoid-littorinoid radiation" (Reid, 1989), but since a similarly shaped jaw is present in most prosobranchs, little can be concluded from this.

A well-developed esophageal gland is common among Neotaenioglossa; the combination with esophageal pouches is known from the Eatoniellidae, some Cingulopsidae and Littorinidae (Ponder, 1988; Reid, 1989). Esophageal pouches are, however, easily overlooked in serial sections, and therefore they may be more widespread than presently known.

Unusual features of the "rissooid-cingulopsoid-littorinoid radiation," present in zerotulids are:

- —Posterior pedal gland large in adult specimens but without large duct (considered an apomorphy of **Zerotulidae**; absent in adult Littorinidae).
- —Penis situated below right cephalic tentacle (as in Littorinidae, considered plesiomorphic in Neotaenioglossa).
- —Sperm storage in the pericardium (apomorphy of **Zerotulidae**?).
- —Absence of a bursa copulatrix (apomorphy of **Zerotulidae**?).
- —A long, slender radula with a bare zone between the marginals and with lateral teeth without "littorinid notch" (plesiomorphy of the Neotaenioglossa).
- —Presence of a large esophageal gland (plesiomorphy of Neotaenioglossa).
- —Presence of esophageal pouches in at least some species (apomorphy of Littorinoidea?).

From this, we conclude that the zerotulids are more closely related to the Littorinidae than to other taxa within the "rissooid-cingulopsoid-littorinoid radiation," and place them in the Littorinoidea. We refrain from comparisons with the pomatiasids and other land and freshwater radiations since we find it difficult to assess differences, which may be caused by their different environment.

We readily admit that there are few and not very clear apomorphies uniting the species included in **Zerotulidae**, and there is a possibility that what we have brought together as **Zerotulidae** actually is a series of unusually plesiomorphic littorin(o?)ids. In that case, the **Zerotulidae** would be paraphyletic and perhaps polyphyletic. We suspect this especially with ***Dickdellia** labioflecta,* which differs considerably from the other species in the anatomy of the foot. Nevertheless, if this is the case, there will still remain a need for a family level name based on *Zerotula,* as a sister group to Littorinidae.

The type species of *Skeneopsis* (Skeneopsidae, Littorinoidea), somewhat similar in shell shape to certain zerotulids, was described anatomically by Fretter (1948). Huber (1993) described the central nervous system. The Skeneopsidae includes two North Atlantic species, and shows clear affinity to the Littorinoidea and Cingulopsoidea (Ponder, 1988; Reid, 1989). The single anatomically known species does, however, have a very large penis (pedally innervated, Ponder, 1988) attached behind the right cephalic tentacle, not below, as in Littorinidae and **Zerotulidae**, and it lacks an esophageal gland. Its osphradium is not bipectinate as stated by Fretter (1948), but a low, rather broad ridge, twice as long as broad (Warén, unpublished). The nervous system is highly concentrated.

The Skeneopsidae seems to be a highly apomorphic group and is difficult to place in a superfamily, though the radula and inner chitinous layer of the shell indicate relations to Cingulopsoidea and Littorinoidea, not to Rissooidea. We consider the similarity in shell shape to some zerotulids due to convergence.

Separation of *Frovina, Trilirata, Dickdellia,* and *Zerotula*: The soft parts are of very little use in this (except for ***Dickdellia***) since they are very featureless, and we have had access to preserved material of only a single species of *Zerotula.* The radula is, however, quite characteristic in the group we have separated as ***Trilirata*** (plus *Z.* ***incognita***), with an extra cusp halfway up the shaft of the outer marginal tooth combined with a weaker zone across the shaft that causes the tooth to fold here. Also, the shell is quite similar in ***T.*** *macmurdensis* and ***T. herosae***, whereas that of ***T. sexcarinata*** has a much more depressed spire. ***Trilirata sexcarinata*** also stands out among the species of this genus in the extreme development of the periostracum. The periostracum is thin in *Z.* ***stellapolaris*** and *Z.* ***incognita***, both in alcohol and dry, but not known in the other species of *Zerotula.* It is thin and brittle in species of *Frovina.* At present we therefore consider the periostracal development of ***T. sexcarinata*** an autapomorphy.

The two species in *Frovina* which have been examined anatomically have very similar shells, which, however, may be plesiomorphic since they also resemble the shell of unmodified littorinids (Laevilittorininae and Lacuninae).

The shells of the species placed in *Zerotula* are quite similar to each other, but also simple, with a strongly depressed spire, ranging from slightly hyperstrophic via perfectly planispiral to having the larval shell level with the top of the peristome. Several species with similar shells previously classified in *Zerotula* are herein referred to other families.

Frovina Thiele, 1912

Frovina Thiele, 1912:196. Type species *F. soror* Thiele, 1912, by original designation.
Sublacuna Thiele, 1912:195 (not Pilsbry, 1895). Type species *S. indecora* Thiele, 1912, by original designation.
Prolacuna Thiele, 1913:86 (new name for *Sublacuna*).
Frigidilacuna Tomlin, 1930:23 (new name for *Sublacuna*).

Remarks: We cannot see any great differences between the type species of *Prolacuna* and *Frovina*, except the shape of the central tooth, which has only three strong, flat cusps of equal size in *F. soror,* and five conical cusps, which become gradually smaller toward the side of the tooth in *F. indecora* (Figure 3C, E). This was Thiele's only reason for separation of *Frovina* and *Prolacuna*, but we consider the similarities in other radular features, shell, and anatomy more important. Consequently, the name *Frovina* has to be used, since it is the oldest one available.

Prolacuna macmurdensis stands out by its strong spiral sculpture and the strange morphology of the outer marginal tooth, similarities to two new species, and has therfore been united with these in a new genus, ***Trilirata.***

Frovina ***angularis***, sp. nov. is classified in *Frovina* with some doubt also at family level; no soft parts were available, but the shell shows more similarities to this family and genus than to any other taxon known to us.

Frovina soror Thiele, 1912

(Figures 1D, E, 2A, B, 3E, F, 4E, F, 6B)

Frovina soror Thiele, 1912:196, pl. 11, fig. 40; pl. 15, fig. 20.
Frovina soror: Egorova, 1982:31, figs. 144, 44.
Prolacuna indecora: Dell, 1990:162 (partly, fig. 239 only).

Type locality: Antarctica, Gauss Station, 89°E, 385 m.

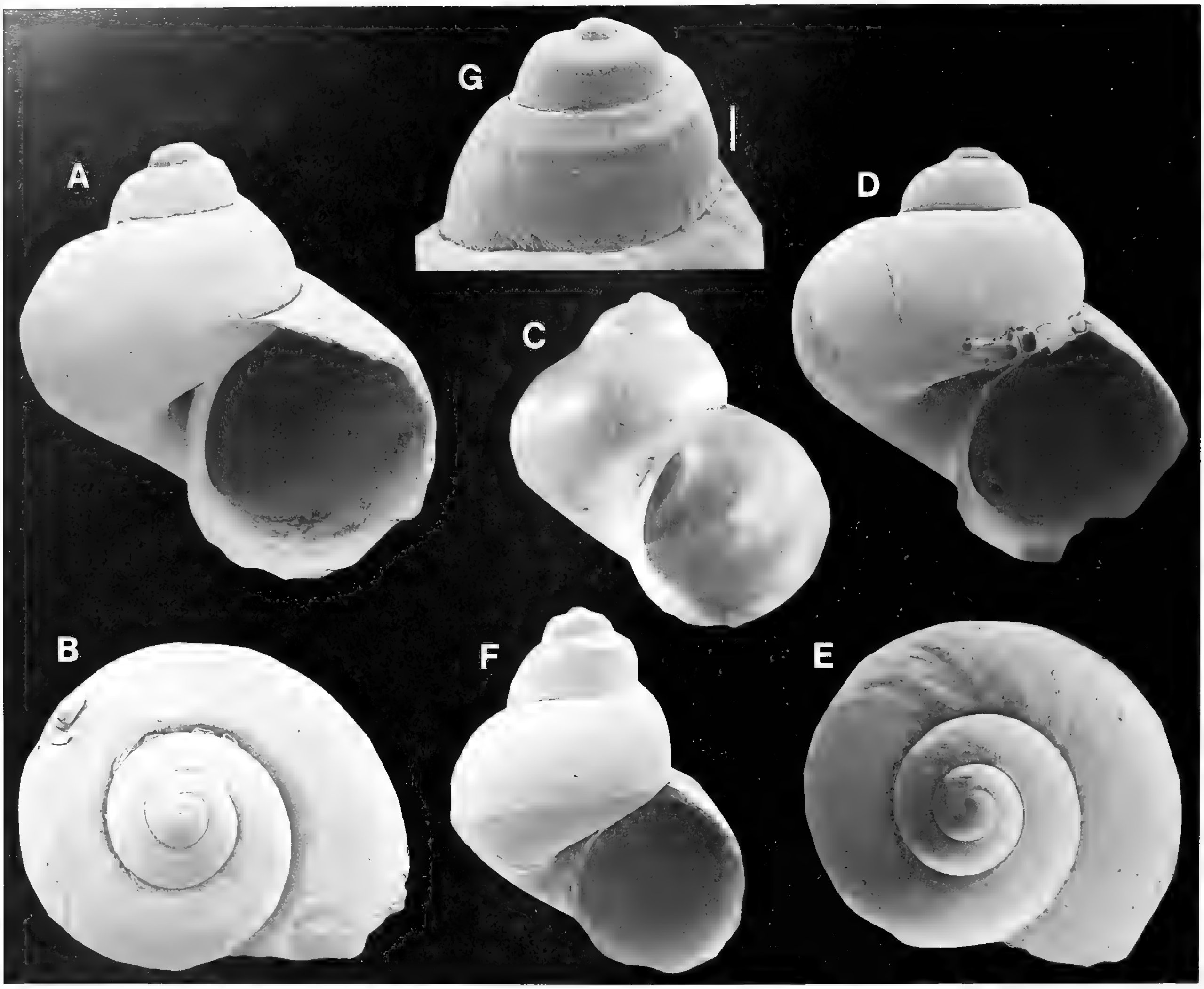
Type material: Holotype in ZMHU, not seen.

Material examined: Davis Sea, 66°33′S, 93°01′W, 80 m, 1 specimen (det. *P. indecora* by Dell, 1990), USNM 613041.—PS VII/4 sta. 224, 013°W, 186–187 m, 2 specimens.—PS VII/4 sta. 274, 012°W, 196–212 m, 5 specimens.—PS IX/3, sta. 173, 007°E, 739–765 m, 5 specimens, 2 shells.—PS IX/3, sta. 174, 011°E, 432–432 m, 10 specimens, 4 shells.—PS IX/3, sta. 179, 007°E, 185–161 m, 2 specimens, 9 shells.—PS IX/3, sta. 180, 06°E, 280–298 m, 17 specimens, 3 shells.—PS IX/3, sta. 206, 10°E, 343–338 m, 2 specimens, 10 egg capsules, 3 shells.—PS IX/3, sta. 211, 05°E, 661–742 m, 3 shells (all in SMNH).

Distribution: From the Bellinghausen Sea (93°W), eastward to the Davis Sea (98°E), in 80–765 m.

Redescription: We describe only the anatomy, based on several decalcified specimens and sections of one adult female. Shell, Figure 1D, E; protoconch, Figure 2A, B.

External morphology of soft parts: The head-foot and pallial complex comprise half a whorl in contracted spec-

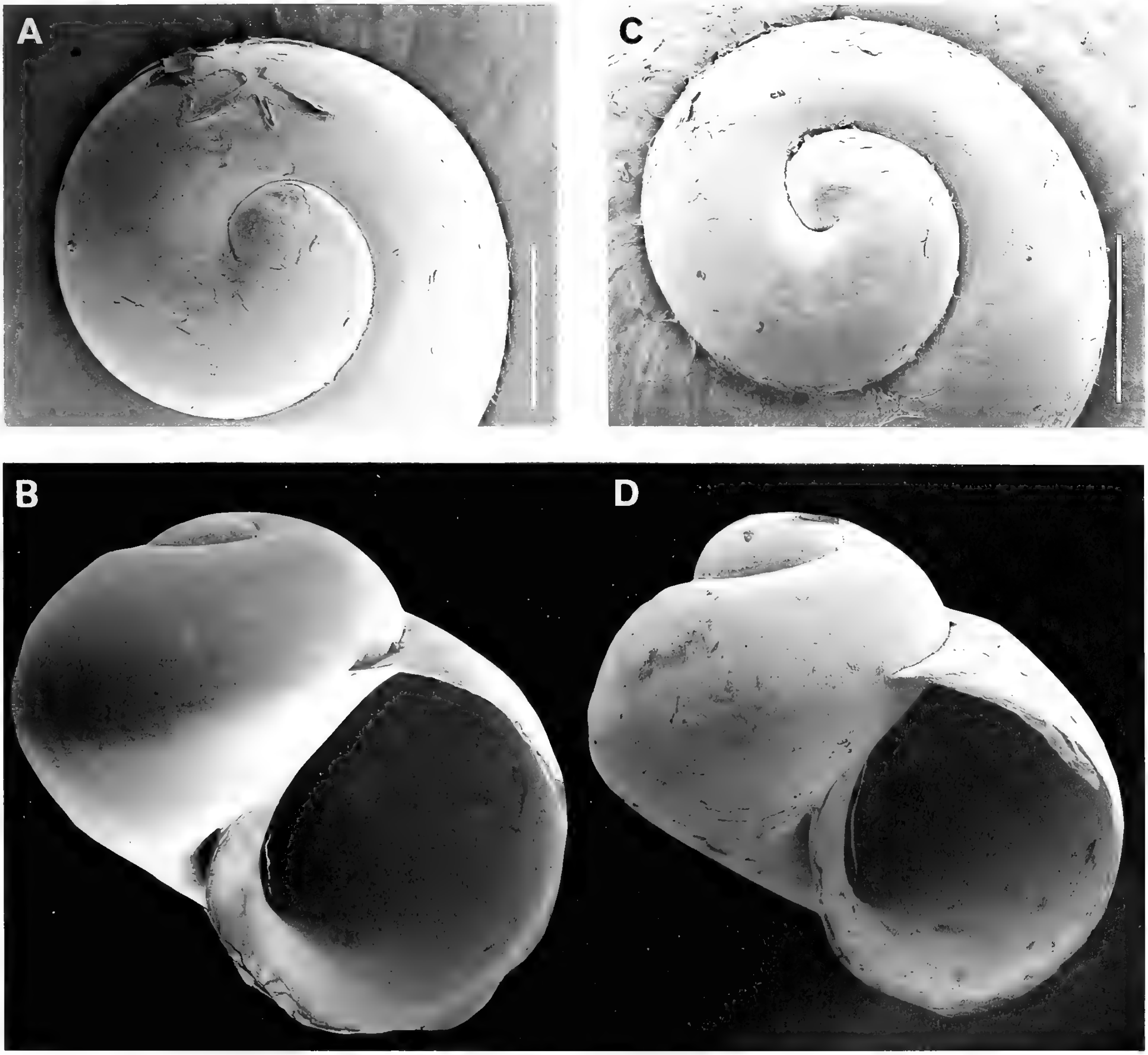


Explanation of Figure 1

Frovina spp. Figures A, B. F. *indecora,* PS IX/3 sta. 179, height 3.4 mm. Figure C. *F. indecora,* holotype, ZMHU 63025, height 2.3 mm. Figures D, E. *F. soror,* USNM 613041, height 3.3 mm and (E) PS IX/3 sta. 179, diameter 3.2 mm. Figures F, G. *F.* ***angularis*** Warén & Hain, sp. nov., holotype, height 3.2 mm. Scale line (G) = 0.2 mm.

imens, the visceral mass slightly more than two whorls. The head-foot is pale beige, the visceral mass pale orange-brown (in alcohol) and covered with small dark brown spots, diameter about 5–15 μm. The anterior $\frac{1}{10}$ whorl of the visceral mass is dominated by the still paler kidney. At the left side, the pericardium with the ventricle and auricle lies directly behind the gill and osphradium. The gonad is not easily distinguished externally, although the specimens are sexually mature. Directly behind the pericardium, the esophagus and stomach reach about a third of a whorl backward, before the esophagus enters the posteriorly situated part of the stomach. Forming a continuation of the anteriorly situated part of the stomach, the intestine very soon turns sharply to the right and disappears under the kidney.

The pallial cavity is quite deep, and the pallial skirt normally covers the whole head in preserved specimens. The pallial margin is thin and simple, without tentacles and papillae, except at the right $\frac{1}{5}$, where it is "uneven," but the details could not be worked out. The osphradium is elongate and paralleled by two ciliated ridges. It runs along the gill from its most posterior part, forward to the anterior $\frac{1}{4}$ of the gill. The gill consists of a series of about 12 triangular leaflets, drawn out to a ventral point; the gill width corresponds to $\frac{1}{4}$ of the pallial cavity. The leaflets in its central part are about twice as wide and high as the anterior ones. The columellar muscle projects at the right side of the body, 80–100° from the operculum. Its left part is much less conspicuous and narrower. The hypobranchial gland is not very conspicuous and partly covered by the



Explanation of Figure 2

Frovina spp., juveniles. Figures A, B. *F. soror,* PS IX/3 sta. 179, diameter 1.1 mm. Figures C, D. *F. indecora,* PS IX/3 sta. 179, diameter 1.1 mm. Scale lines = 250 μm.

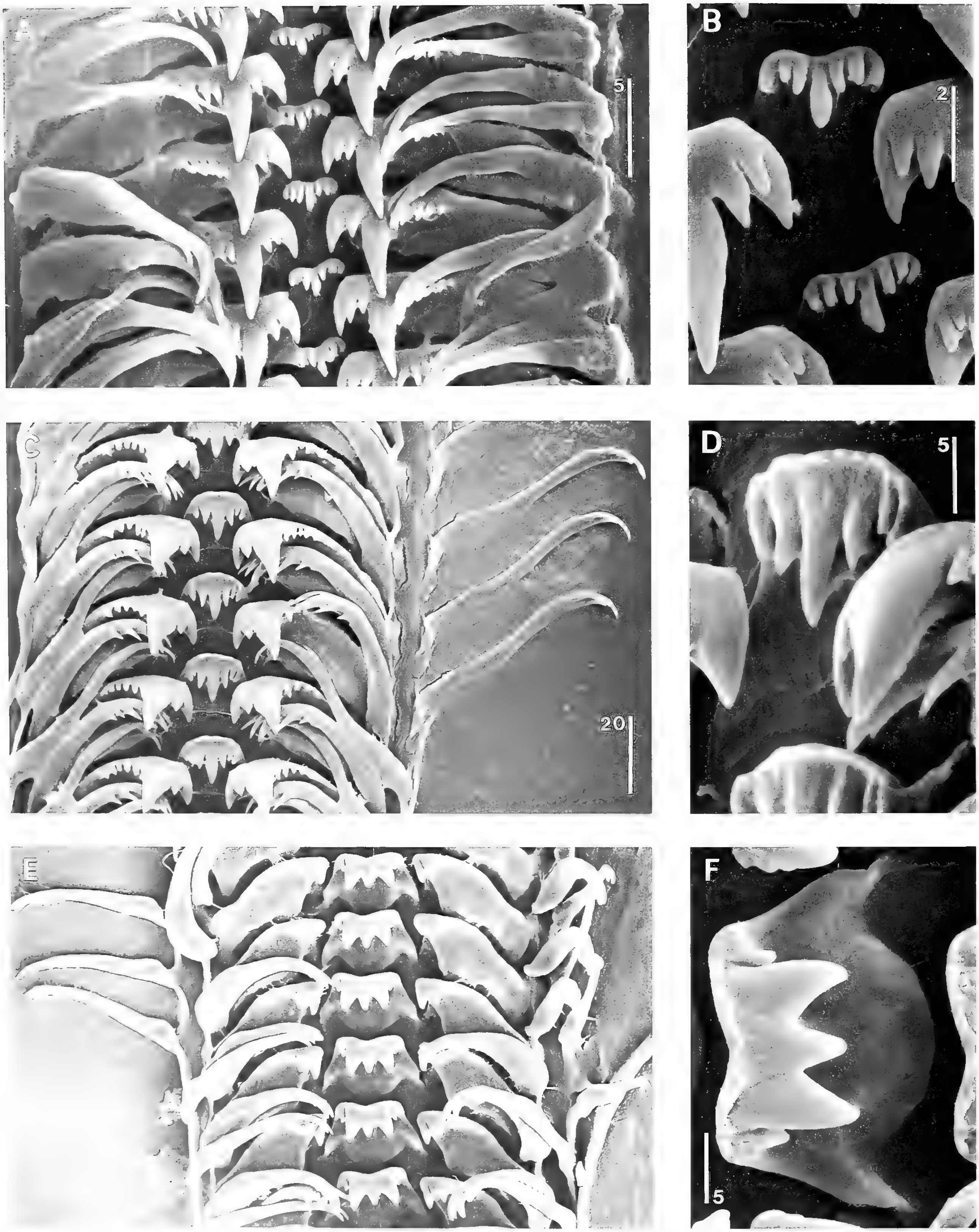
tips of the gill leaflets. The pallial oviduct is restricted to the posterior right half of the cavity, and its left side contains the rectum, which opens at the same level as the duct.

The head is medium-sized, has a pair of short (contracted), conical, flattened tentacles with large, black eyes in basal-lateral bulges. The snout is rather short, slightly tapering, and somewhat flattened with a subventral mouth.

The male has a simple, tapering, finger-shaped penis just below the right cephalic tentacle, with a seemingly open furrow along its dorsal side. The furrow continues as a duct buried in the right corner of the pallial cavity, to the prostate.

The foot is flat, large, and broad. It is strongly contracted in all specimens, but judging from the folds, its anterior edge is probably blunt, and the corners are not drawn out to small, tentaclelike extensions. Posteriorly, it seems bluntly rounded. An anterior pedal gland opens between the indistinctly set-off propodium and the mesopodium. The sides of the foot are smooth and there are no epipodial ridges or furrows.

Internal anatomy: The foot is almost filled by the large posterior pedal gland, which, together with the slightly smaller anterior pedal gland, bulges into the cephalopedal



Explanation of Figure 3

Radulae of *Zerotula* and *Frovina.* Figures A, B. *Z. hedleyi,* MNZ M.33660. Figures C, D. *F. indecora,* PS IX/3 sta. 180. Figures E, F. *F. soror,* USNM 613041. Scale lines in μm.

haemocoel, well past the nerve ring, both to the right and left of it. The posterior pedal gland stains dark bluish violet, the anterior one, a much lighter grayish violet. The posterior pedal gland seems not to have a defined opening, but this is not certain, because all the ventral surface of the foot is badly preserved, and the outer layers are peeling. The anterior one has a storage space under the propodium lined with tall epithelium, and opens via the slit between the pro- and mesopodium. The muscle layer of the foot is quite thin, 30–60 μm along the sides and ventrally, and the sole is very poor in muscle fibers.

The tentacles are solid and muscular, all the way to the base, where they have a subcutaneous eye with lens and pigment layer, in a bulge. The snout is very muscular and can probably be extended considerably when the snail is grazing.

The alimentary system consists of the mouth, a large, rather weakly muscular buccal mass, a very short anterior esophagus, a large esophageal gland, a narrow posterior esoghagus, stomach, intestine, and rectum. From the posterior esophagus and backward, the preservation was too poor to observe any detail, except that the stomach has a gastric shield but seems to lack a crystalline style.

The jaw is very thin and membranous, mainly forming a cuticular lining of the oral tube.

The radular sac is straight, long, and slender, passes backward through the nerve ring and lies ventral to the esophageal gland as far back as this. The part of the radula in use is supported by a pair of narrow cartilages.

Two salivary glands open into the buccal cavity, close to its mid-line, via short, inconspicuous ducts, which do not pass through the nerve ring. The salivary glands are large and situated in front of and above the cerebral ganglia. They consist of a short, thin duct and a longer, coiled and branching glandular tube. Their structure and staining are very similar to the dorsal part of the esophageal gland, but the nuclei are more numerous and conspicuous. The dorsal food channel is characterized by the presence of numerous mucus-producing cells, which stain dark blue. These start in the posterio-dorsal part of the buccal cavity, are displaced to the left when passing the nerve ring, and end up ventrally in the esophageal gland, where they do not reach its posterior end. A paired structure (about 0.2 mm long), which could be a pair of esophageal pouches, bulges from the esophagus, just in front of the gland.

The nervous system follows the normal pattern, with dialyneury between the left pleural and the supraesophageal ganglia. The distances between the ganglia are fairly short (contracted specimen). The left pleural and cerebral ganglia are partly fused, the right ones abutting. The supra- and subesophageal ganglia are situated less than twice their diameter from the corresponding pleural ganglion. The length of the connectives to the pedal ganglia is twice the diameter of the ganglia. The supraesophageal ganglion lies free at the left side of the cephalopedal haemocoel; the subesophageal one is well embedded in the body wall. The buccal ganglia are situated dorsally on the buccal mass, close to the exit of the esophagus, and connected by a commissure. In front of the pedal ganglia is an accessory pedal ganglion, lying in the anterior pedal gland, connected by a connective of 1.5 times the diameter of the accessory ganglion and innervating the anterior pedal gland and propodial area. The visceral ganglia were not identified.

The statocysts are situated above and behind the pedal ganglia and slightly displaced to the right. Their diameter corresponds to ⅓ of the length of the ganglion. They have a single statolith.

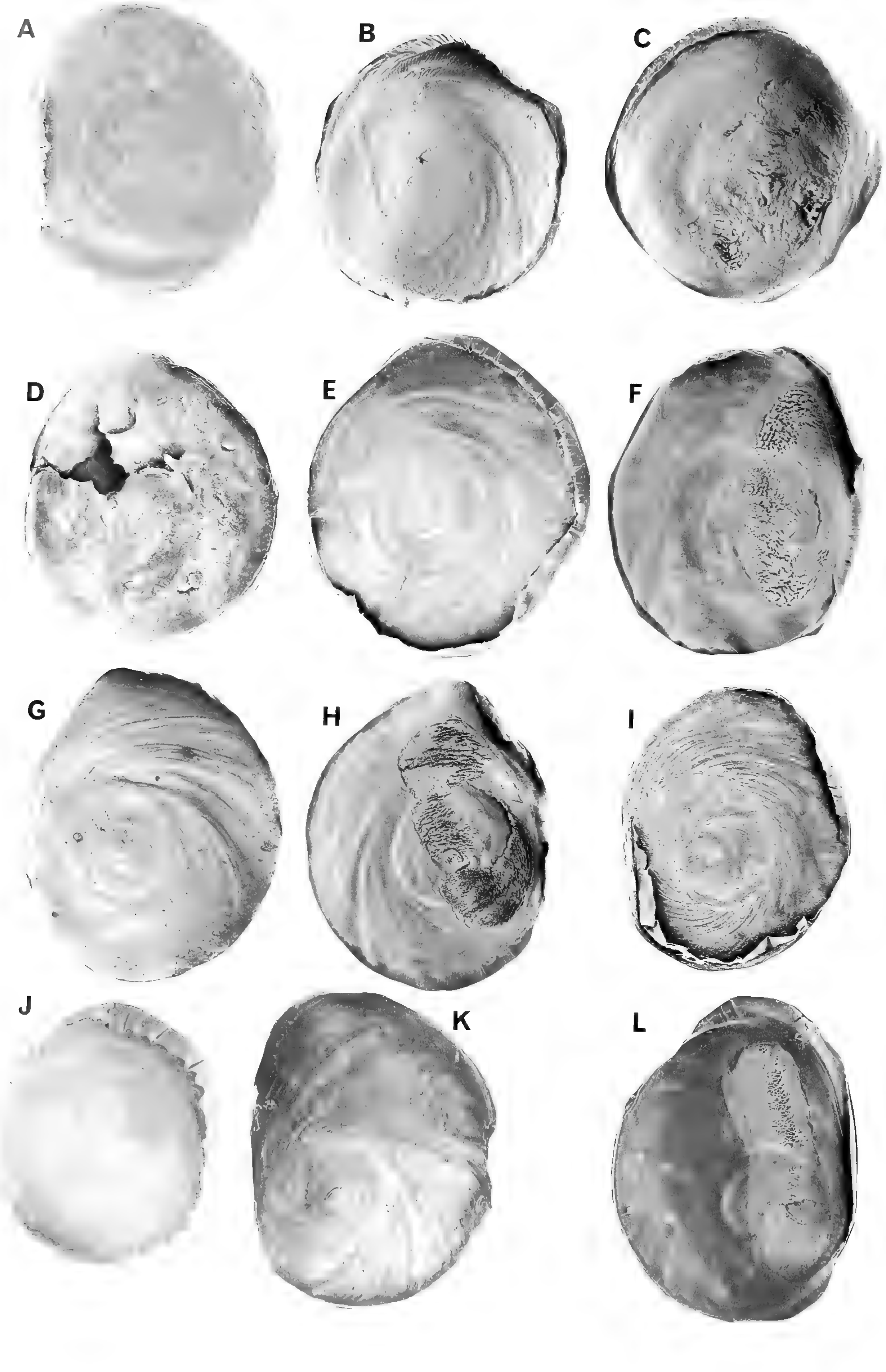
Reproductive system. The sexes are separate, or at least the males whose external morphology was examined were of the same size as the sectioned female. The fixation does not allow any detailed description of the female system. The ovary (and testis) lie along the right side of the visceral mass. An ovarian duct leads to a large albumen gland, which stains very lightly. Along the left and anterior side of this is a capsule gland (staining dark violet), but the detailed morphology of these could not be worked out due to missing and ruptured sections. No bursa copulatrix was identified. No receptaculum seminis was found, and no sperm was found in the pericardium.

The radula (Figures 3E, F, 6B) is taenioglossate, long, and slender, with about 80 transverse rows of teeth. The central tooth (Figure 3F) has a low and thin, irregularly denticulated hood along its anterior, apical margin. Below this, three large cusps form a cutting edge. Beside these, and partly concealed by them, is a much smaller denticle on each side. The "wings" are drawn out to a small denticle on each side close to the base. The front of the tooth forms a large supporting bulge at the base. The lateral tooth usually has about 10 denticles, of which numbers 2 and 4 (counted from the inner edge) are at least twice the size of the others. The littorinid notch is missing. The first marginal tooth is simple, claw-shaped, with a sturdy shaft and three to five apical cusps. The outer marginal tooth is slightly shorter, straighter, half the thickness, and has three apical cusps. Very young specimens (from egg capsules) have a proportionally shorter radula with fewer transverse rows of teeth, but the radulae are otherwise identical.

The operculum (Figure 4E, F) has a few whorls, a central nucleus, and is transparent, slightly brownish yellow, especially where it is attached to the foot. The surface is distinctly wrinkled by the growth lines.

Reproduction. The egg capsules are identical to those described for *F. indecora* below.

Remarks: *Frovina soror* was based on a small specimen, 1.5 mm high and 1.4 mm in diameter. Thiele's drawing of the shell (1912: pl. 11, fig. 40) is not much of an aid to identification, but the radula is distinctive (Thiele, 1912: pl. 15, fig. 20), even in juveniles (Figure 6B, from egg capsules) with three large cusps of equal size on the central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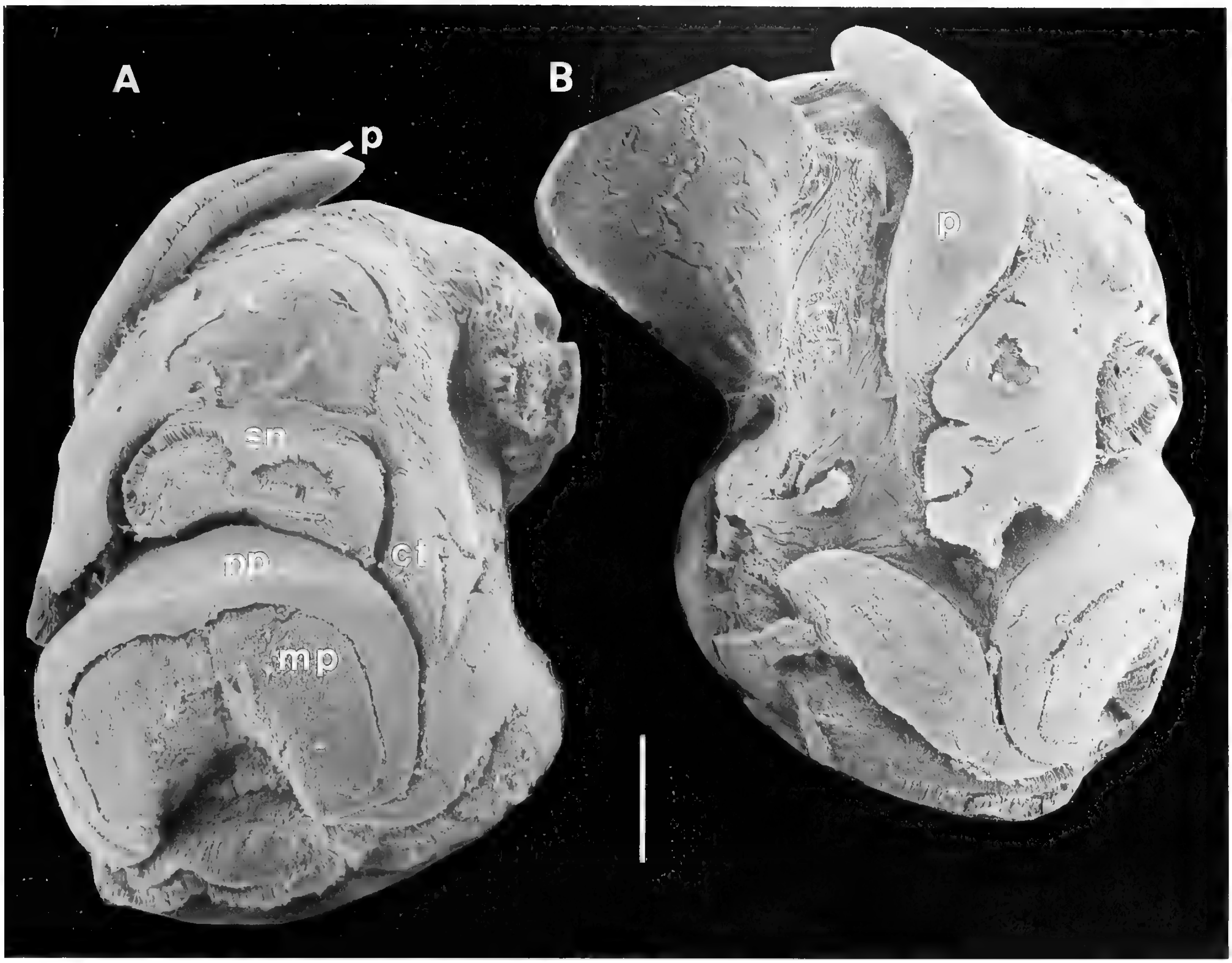

Explanation of Figure 5

Frovina indecora, critical point dried, PS IX/3 sta. 212. Figure A. front view. Figure B. right side of head-foot. **ct**—cephalic tentacle, **mp**—mesopodium; **p**—penis with sperm groove; **pp**—propodium; **sn**—snout. Scale line = 200 μm.

tooth. Our material indicates a size of a little more than 3 mm for adult specimens.

Neither sperm nor a receptaculum seminis was found in the single sectioned female. The reason is probably that it had not been fertilized, because the sections were good enough to find a filled receptaculum or sperm in the pericardium.

Frovina indecora (Thiele, 1912)
(Figures 1A–C, 2C, D, 3C, D, 4G, H, 5, 6A, 7, 8, 9, 22D)

Sublacuna indecora Thiele, 1912:195, pl. 12, fig. 4; pl. 15, fig. 19.
Prolacuna indecora: Arnaud, 1972:126.
Prolacuna indecora: Egorova, 1982:30, fig. 142–143, 42.

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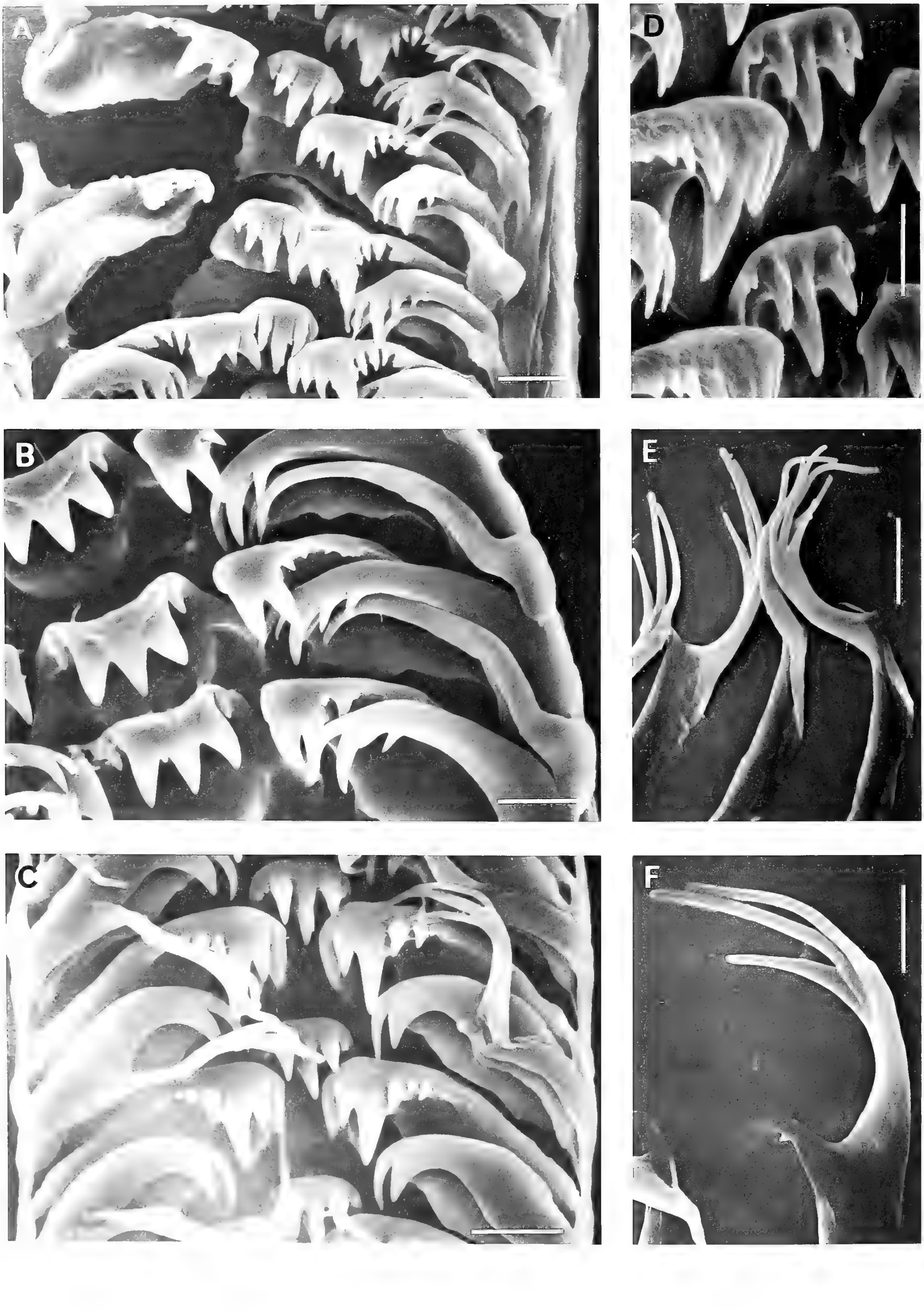
Explanation of Figure 4

Opercula. Figure A. *Zerotula hedleyi,* MNZ M.33660, diameter 0.40 mm. Figures B, C. *Z.* ***stellapolaris*** Warén & Hain, sp. nov., PS IX/3 sta. 180, diameter 0.68 mm. Figure D. *Z.* sp., Bounty Trough, diameter 0.85 mm. Figures E, F. *Frovina soror,* PS IX/3 stas. 179 and 180, diameter 1.8 and 1.9 mm. Figures G, H. *F. indecora,* PS IX/3 sta. 179 and 180, diameter 2.1 and 1.9 mm. Figure I. ***Trilirata*** *macmurdensis,* USNM 612745, diameter 1.6 mm. Figure J. ***T. herosae*** Warén & Hain, sp. nov., holotype, diameter 1.7 mm. Figures K, L. ***T. sexcarinata*** Warén & Hain, sp. nov., PS VII/4 sta. 291 and 284, 1.7 and 1.6 mm.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Explanation of Figure 7

Frovina indecora, longitudinal section. The pedal ganglion has just branched to two major tracts (indicated by arrows), to the accessory pedal ganglion and to the posterior region of the mesopodium. **cg**—cerebral ganglion; **df**—dorsal (now ventral) food channel; **f**—foot; **j**—jaw; **oe**—esophagus; **oep**—esophageal pouch; **pc**—pallia cavity; **pg**—pedal ganglion; **plg**—pleural ganglion; **pp**—propodium; **sg**—salivary gland; **sn**—snout. Scale line = 100 μm.

Prolacuna indecora: Powell, 1951:121.
Trochaclis antarctica: Powell, 1958:185, not Thiele, 1912.
Prolacuna indecora: Powell, 1958:190.
Prolacuna indecora: Dell, 1990:162 (not fig. 239, = *Frovina soror*).
NOT *Sublacuna indecora* Eales, 1923:21 (= unidentified naticid).

Type locality: Davis Sea, Gauss Station, 89°E, 385 m.

Type material: Syntype ZMHU 63025, examined.

Material examined: PS VII/4 sta. 284, 013°W, 402–412 m, 2 specimens.—PS VII/4 sta. 274, 012°W, 196–212 m, 6 shells.—PS IX/3, sta. 165, 003°W, 191–204 m, 2 shells.—PS IX/3, sta. 173, 007°E, 739–765 m, 33 specimens, 5 shells, 14 egg capsules.—PS IX/3, sta. 174, 010°E, 432–432 m, 2 specimens.—PS IX/3, sta. 179, 007°E, 185–161 m, 14 specimens, 10 egg capsules, 21 shells.—PS IX/3, sta. 180, 006°E, 280–298 m, 26 specimens, 15 egg capsules, 4 shells.—PS IX/3, sta. 206, 010°E, 343–338 m, 2 specimens, 3 shells.—PS IX/3, sta. 211, 005°E, 661–742 m, 1 specimen, 2 shells.—PS IX/3, sta. 212, 003°E, 568–644 m, 15 specimens, 5 egg capsules (all in SMNH).

Distribution: Circumpolar in 67–836 m.

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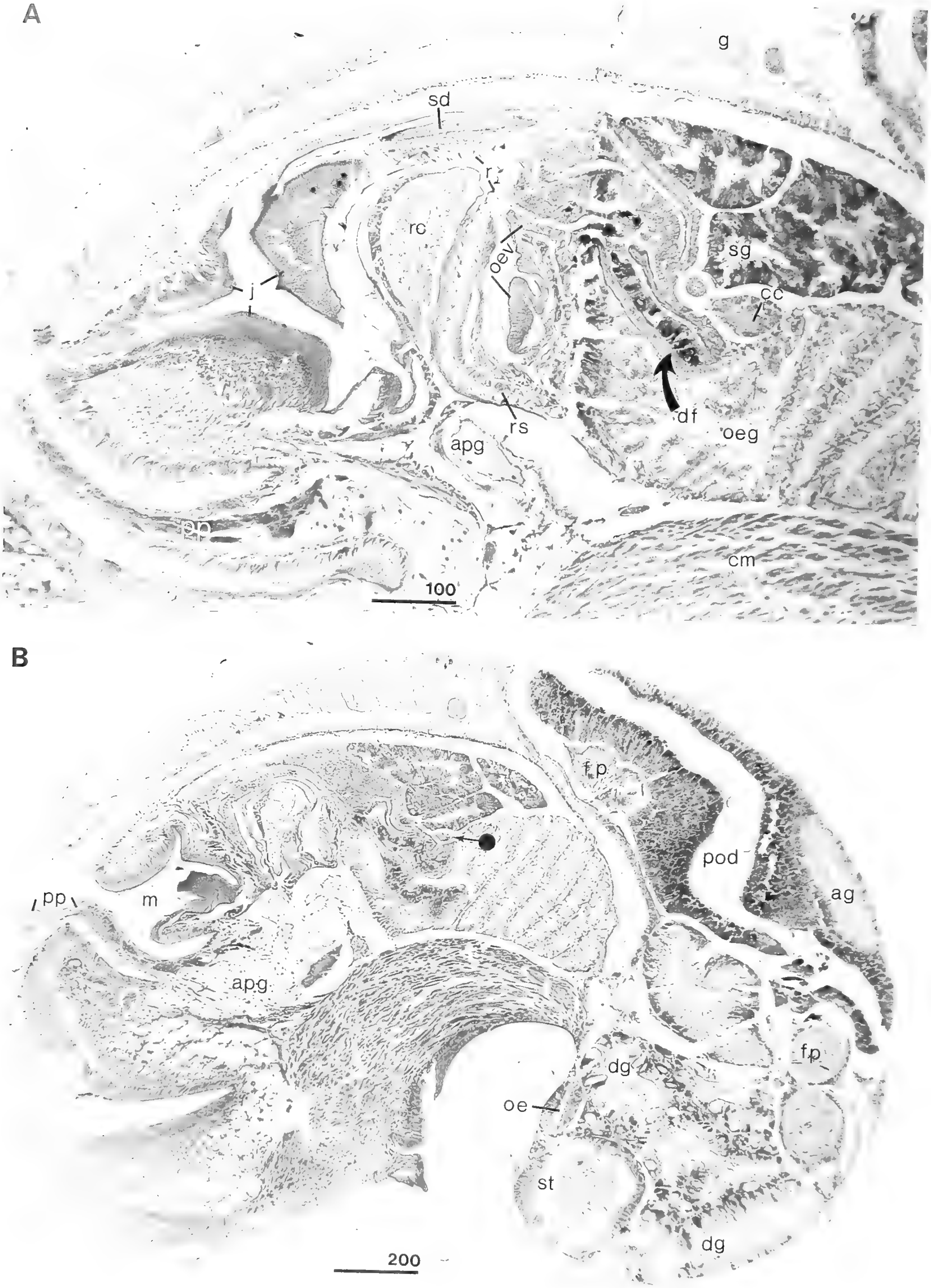
Explanation of Figure 6

Figure A. *Frovina indecora* juvenile, from Figure 2D, PS IX/3 sta. 179. Figure B. *F. sorror* juvenile, from Figure 2B, PS IX/3, sta. 179. Figures C–F. ***Trilirata*** *macmurdensis,* PS IX/3, sta. 173. C. Juvenile, from Figure 34F. D–F. Adult to show central tooth and folding of outer marginals. Scale lines = 5 μm.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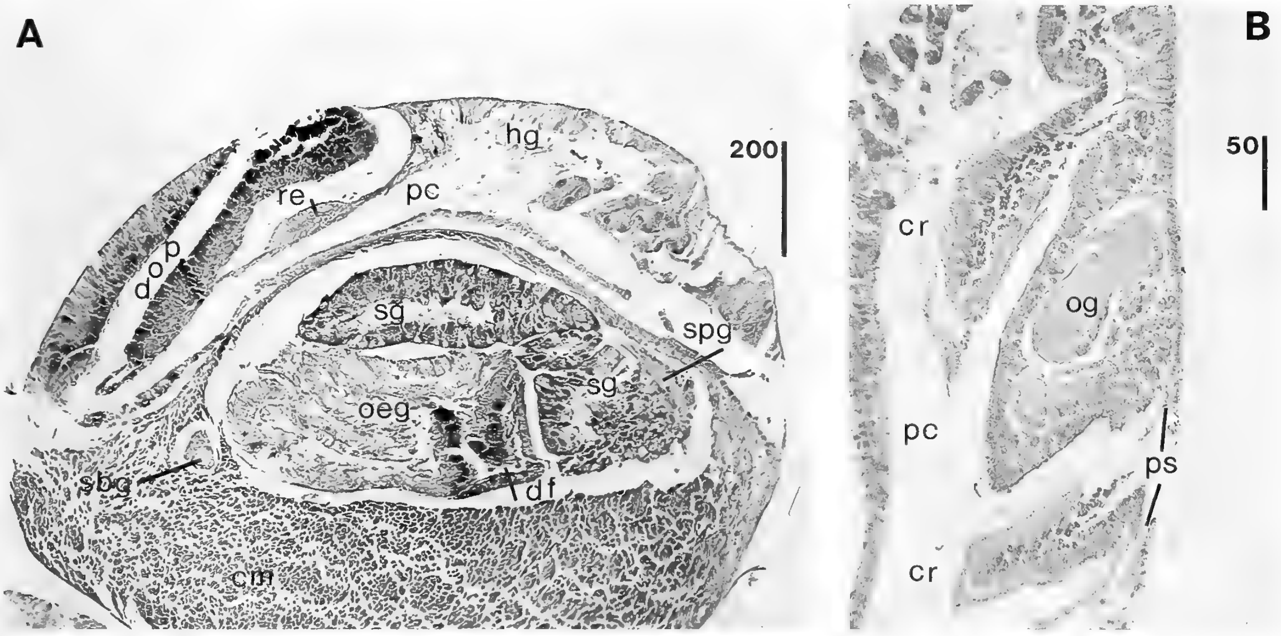

Explanation of Figure 9

Frovina indecora. Figure A. Cross section of body behind cerebral ganglia, to show position of esophageal ganglia. Figure B. Cross section of osphradium. **cm**—columellar muscle; **cr**—ciliated ridge; **df**—dorsal food channel; **hg**—hypobranchial gland; **oeg**—esophageal gland; **og**—osphradial ganglion; **pc**—pallial cavity; **pod**—pallial oviduct; **ps**—pallial skirt; **re**—rectum; **sbg**—subesophageal ganglion; **sg**—salivary gland; **spg**—suprasophageal ganglion. Scale lines in μm.

Redescription: We only describe the anatomy, based on three sectioned adult females and several decalcified males and females. Shell, Figure 1A–C; protoconch, Figure 2C, D.

External morphology of soft parts: The head-foot (Figure 5) and pallial complex comprises ⅖ of a whorl in a contracted specimen, the visceral mass slightly more than two whorls. The anterior part of the head-foot has a weak, granular, grayish pigmentation, best visible along the edges of the snout, foot, and tentacles. Behind the tentacles, including the visceral mass, it is light beige (in alcohol). The anterior ⅒ whorl of the visceral mass is yet paler and contains the kidney. At the left side, the pericardium, with the ventricle and auricle, lies directly behind the gill and osphradium. The gonad is not easily distinguished externally also in sexually mature specimens. Directly behind the pericardium, the esophagus and stomach reach about a third of a whorl backward, before the esophagus enters the posteriorly situated part of the anterior stomach. Forming a continuation of the anteriorly situated part of the stomach, the intestine very soon turns sharply to the right and disappears under the kidney.

The pallial cavity is quite deep, and the pallial skirt normally covers the whole head in preserved specimens. The pallial margin is thin and simple, without tentacles and papillae, except at the right ⅙, where it is "uneven," but the details could not be worked out. The osphradium (Figure 9B) is paralleled by two ridges; it runs along the gill from its most posterior part, forward to the anterior ¼ of the gill. The gill consists of a series of about 12 triangular leaflets, drawn out to a ventral tip; the gill width corresponds to ¼ of the pallial cavity. The leaflets in its

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Explanation of Figure 8

Frovina indecora, sagittal sections. Figure A. Longitudinal section of central anterior part of cephalopedal haemocoel. Figure B. Longitudinal section through head-foot, changing to cross section of anterior part of visceral mass. **ag**—albumen gland; **apg**—anterior pedal gland; **cc**—cerebral commissure (in B indicated by black dot and fine arrow); **cm**—columellar muscle; **df**—dorsal (now ventral) food channel (visible by its dark staining gland cells); **dg**—digestive gland; **fp**—fecal pellet (in rectum); **m**—mouth; **oe**—esophagus; **oeg**—esophageal gland; **oev**—esophageal valve; **pod**—pallial oviduct; **pp**—propodium; **rc**—radular cartilage; **rs**—radular sac; **sd**—salivary duct; **st**—stomach. Scale lines in μm.

central part are about twice as wide and high as the anterior ones. The columellar muscle projects at the right side of the body, 80–100° from the operculum. Its left part is much less conspicuous and narrower. The hypobranchial gland is rather inconspicuous and partly covered by the tips of the gill leaflets. The pallial oviduct is restricted to the posterior right half of the cavity, and its left side contains the rectum, which opens at the same level as the duct. In the male, the rectum parallels the sperm duct and prostate in the corresponding position.

The head is medium-sized and has a pair of short (contracted), conical, flattened tentacles with large black eyes in basal-lateral bulges. The snout is rather short, with parallel sides, somewhat flattened with a subventral mouth.

The male has a simple, tapering, finger-shaped penis just below the right cephalic tentacle, with a dorsal furrow containing a closed sperm duct. The duct continues in the right corner of the pallial cavity, lined by a narrow prostate gland.

The foot is flat, large, and broad. Judging from the folds, its anterior edge is probably blunt, but the corners seem not to be drawn out to small, tentaclelike extensions. Posteriorly, it seems bluntly rounded. There is no distinct opening for the posterior pedal gland. Anteriorly, between the distincly set-off propodium and the mesopodium, opens an anterior pedal gland. The sides of the foot are smooth, and there are no epipodial ridges or furrows.

Internal anatomy (Figures 7–9): The foot (Figure 8B) is almost filled by the large posterior pedal gland. The slightly smaller anterior pedal gland bulges into the cephalopedal haemocoel, but not behind the nerve ring. The posterior pedal gland stains dark bluish violet, the anterior one a much lighter grayish violet with conspicuous nuclei. The posterior pedal gland does not have a defined opening. The anterior one has a storage space under the propodium lined with tall epithelium, and opens via a broad and flat duct, which penetrates most of the gland. The muscle layer of the foot is quite thin, 75–100 μm along the sides and ventrally.

The tentacles are solid and muscular all the way to the base, where they have a subcutaneous eye with lens and pigment layer, in a bulge. The snout is very muscular and can probably be extended considerably when the snail is grazing.

The alimentary system consists of the mouth; a large, rather muscular buccal mass; a very short anterior esophagus; a large esophageal gland; a narrow posterior esophagus; stomach; intestine; and rectum. From the posterior esophagus and backward, the preservation was too poor for any detail except that the stomach has a gastric shield but seems to lack a crystalline style.

The jaw (Figure 22D) is bilobed and thin but with a prismatic structure.

The radular sac (Figure 8A) is straight, long, and slender, passes backward through the nerve ring and lies ventral to the esophageal gland, reaching as far back as this, where it curves dorsally to the right of the esophagus. The part of the radula in use is supported by a pair of large cartilages.

Two salivary glands open into the buccal cavity close to its mid-line, via short, inconspicuous ducts which do not pass through the nerve ring. The salivary glands are large and situated in front of and above the cerebral ganglia. Each consists of a short, thin duct and a voluminous gland of several lobes. With EHE they stain violet. The dorsal food channel (Figures 7, 8A) is characterized by the rich occurrence of mucus-producing cells, staining dark blue. These start in the posterior, dorsal part of the buccal cavity, get displaced toward the left side when passing the nerve ring and end up ventrally in the esophageal gland, where they do not reach its posterior end. In front of the esophageal gland is a pair of small esophageal pouches.

The nervous system follows the normal pattern of littorinids, with dialyneury between the left pleural- and the supraesophageal ganglia. The distances between the ganglia are fairly short (contracted specimen), the pleural and cerebral ganglia abutting. The supra- and subesophageal ganglia are situated less than twice their diameter from the corresponding pleural ganglion. The length of the connectives to the pedal ganglia is twice the diameter of these ganglia. The supraesophageal ganglion lies free at the left side of the cephalopedal haemocoel; the subesophageal one in a pit in the body wall (Figure 9A). The buccal ganglia are situated dorsally on the buccal mass close to the exit of the esophagus, and connected by a commissure. In front of the pedal ganglia is an accessory pedal ganglion, connected by a connective of the same length as the accessory ganglion and innervating the anterior pedal gland and propodial area.

The visceral ganglia were not identified.

The statocysts are situated above and behind the pedal ganglia and slightly displaced laterally. Their diameter corresponds to half the length of the ganglion. They have a single statolith.

Reproductive system. The sexes are separate. The fixation does not, however, allow any detailed description. The gonad lies along the right side of the visceral mass. An ovarian duct leads to a large albumen gland, which stains very lightly. Along the left and anterior side of this is a capsule gland (staining dark violet with EHE), but the detailed morphology of these could not be worked out due to missing and ruptured sections. They are, however, closed except for a short opening close to the anterior end of the capsule gland. No trace of a bursa copulatrix or a receptaculum seminis was found. A well-developed gonopericardial duct is present, opening into the ovarian duct close to the albumen gland. All three females that were sectioned had the pericardium filled with sperm.

The radula (Figures 3C, D, 6A) is taenioglossate, long, and slender, with about 100 transverse rows of teeth. The central tooth (Figure 3D) has a low and thin, irregularly crenulated hood along its apical margin. Below this, one large and two smaller cusps form a cutting edge on each side. Beside these, and partly concealed by them, is a much smaller denticle on each side. The "wings" are not drawn out to small denticles on the sides. The front of the tooth forms a large supporting bulge at the base. The lateral tooth usually has seven or eight denticles, of which numbers 1 and 3 or 4 (counted from the inner edge) are at least twice the size of the others. The littorinid notch is missing. The first marginal tooth is simple, claw-shaped, with a sturdy shaft and three to five large apical cusps. The outer marginal tooth is longer and of a fourth of the thickness of the inner one. It has two or three apical cusps. Very young specimens have a proportionally shorter radula with fewer transverse rows of teeth, otherwise identical (Figure 6A).

The operculum (Figure 6G, H) has a few whorls, a central nucleus, and is transparent, pale brownish yellow, more distinctly so where attached to the foot. The surface is distinctly wrinkled by the growth lines.

Reproduction. The egg capsules are laid singly and contain one embryo. The capsules are globular, transparent, slightly yellowish, and attached to some firm substrate along a surface corresponding to a sector of 60–90° of the sphere. The young snails have a diameter of 1 mm at hatching, and the shell consists of 1.5 whorls. The development is thus lecithotrophic and encapsulated. These may be the unidentified egg capsules reported by Hedgpeth (1964) on legs of the pycnogonid *Colossendeis megalonyx* Hoek, 1881, at the northern part of the Antarctic Peninsula.

Remarks: Eales (1923) outlined some anatomical characters of a species identified as "*Prolacuna indecora.*" The description contains details about a "partly calcareous operculum" and "coalescence of tentacles in the mid-dorsal line." She also figured a radula (fig. 26b). On the basis of this, she placed *Prolacuna* in the Naticidae, a position maintained by later authors (Dell, 1990; Kabat, 1991). The information presented, especially the presence of a calcareous layer on the operculum, makes it obvious that she had examined a young naticid, not *Prolacuna indecora,* which lacks alcareous deposits on the operculum.

Examination of one of Powell's (1958) specimens of "*Trochaclis antarctica*" (from Banzare sta. 41, off Enderby Land, the only one that still could be found) showed that it was misidentified and the record was based on *F. indecora.* Dell (1990:fig. 239) figured *Frovina soror* as *P. indecora.*

Frovina indecora is very similar to *Frovina soror,* but adult specimens can be distinguished by *F. soror* having a wider umbilicus and a slightly blunter apex. Access to specimens of both species for comparison is imperative. We recommend that identification of these species be verified by radular examination.

Frovina ***angularis*** Warén & Hain, sp. nov.

(Figure 1F, G)

Type locality: BIOCAL station DW70, off southern New Caledonia, 23°25′S, 167°53′E, 965 m.

Type material: Holotype and 1 paratype (the latter from BIOCAL DW51) in MNHN.

Material examined: The holotype and BIOCAL station DW51, off southern New Caledonia, 23°05′S, 167°45′E, 680–700 m, 1 shell.

Distribution: Only known from south of New Caledonia in 680–965 m (shells only).

Etymology: "*angularis*" (Latin) meaning angular, from the appearance of the protoconch.

Description: Shell (Figure 1F) small, rissoidlike, with an angular appearance, grayish semitransparent. The protoconch (Figure 1G) is not distinctly demarcated and has slightly more than 1.5 whorls of a diameter of 1.0 mm. Apically it is distinctly flattened with a successively stronger keel, which demarcates a subsutural shelf. The teleoconch has 1.5–2.0 whorls, demarcated from the protoconch mainly by the gradual weakening of the protoconch keel. It is sculptured by a few, very indistinct spiral lines, a stronger peripheral spiral rib, and scattered prosocline incremental lines. The umbilicus is narrow but deep. The aperture is rounded; the outer lip prosocline.

Dimensions. Height of shell 3.2 mm (paratype slightly smaller).

Remarks: *Frovina* ***angularis*** is a featureless shell, and the classification in *Frovina* is provisional in the absence of soft parts. Also, the placement in **Zerotulidae** is based more on intuition and absence of other alternatives than on actual synapomorphies.

Trilirata Warén & Hain, gen. nov.

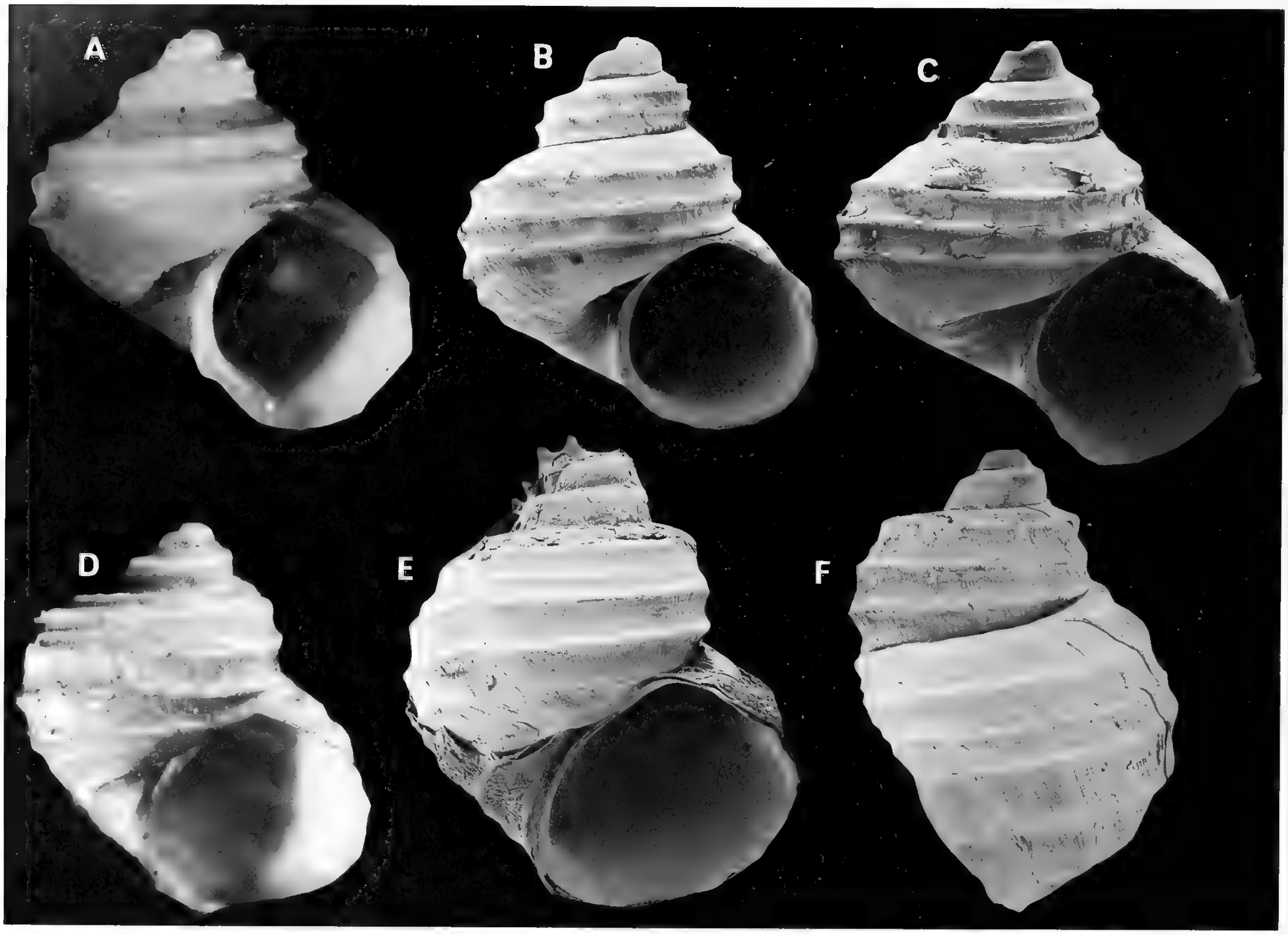
Type species: *Sublacuna trilirata* Thiele, 1912 (= *Lacuna macmurdensis* Hedley, 1911).

Diagnosis: Shell of medium to large size for family, of moderate height or planispiral, mainly sculptured by spiral keels. Protoconch poorly demarcated but indicating lecithotrophic development (known in *T. macmurdensis*). Soft parts as for family. Outer marginal tooth of radula with thin, flat cusp and weak zone halfway up the shaft.

Etymology: "*trilirata*" (Latin), with three spiral cords, also the specific name of the type species.

Remarks: Our reasons for introducing this new generic name were presented under the family heading. We have preferred to select *S. trilirata* as nominal type species since our material is more similar to Thiele's specimens than those of Hedley (although we consider them synonyms).

The four species included in ***Trilirata*** look quite different when shells only are considered and had we not had some information about anatomy and radula they would have been difficult to classify. The relationship to *Frovina* and *Zerotula* is not obvious from the shell morphology. At the same time, their shell morphology does not easily fall into other families, except ***T. sexcarinata***, which easily



Explanation of Figure 10

***Trilirata** macmurdensis* and *Laevilitorina wandelensis.* Figure A. ***T.** macmurdensis* (holotype of *T. trilirata*), ZMHU 63024, height 3.3 mm. Figure B. ***T.** macmurdensis,* USNM 612745, height 3.4 mm. Figure C. ***T.** macmurdensis,* PS IX/3 sta. 179, height 3.1 mm. Figure D. *L. wandelensis* (holotype of *Lacuna notorcadensis,* RSM 1921.143.623, height 3.0 mm. Figures E–F. *L. wandelensis* (paratype of *L. notorcadensis*) NMWZ 1955.158.157, height 3.6 mm.

could have been classified in the Capulidae from the shape of the shell and the development of the periostracum.

***Trilirata** macmurdensis* (Hedley, 1911)

(Figures 4I, 6C–F, 10A–C, 11A–C, 12, 34F, G)

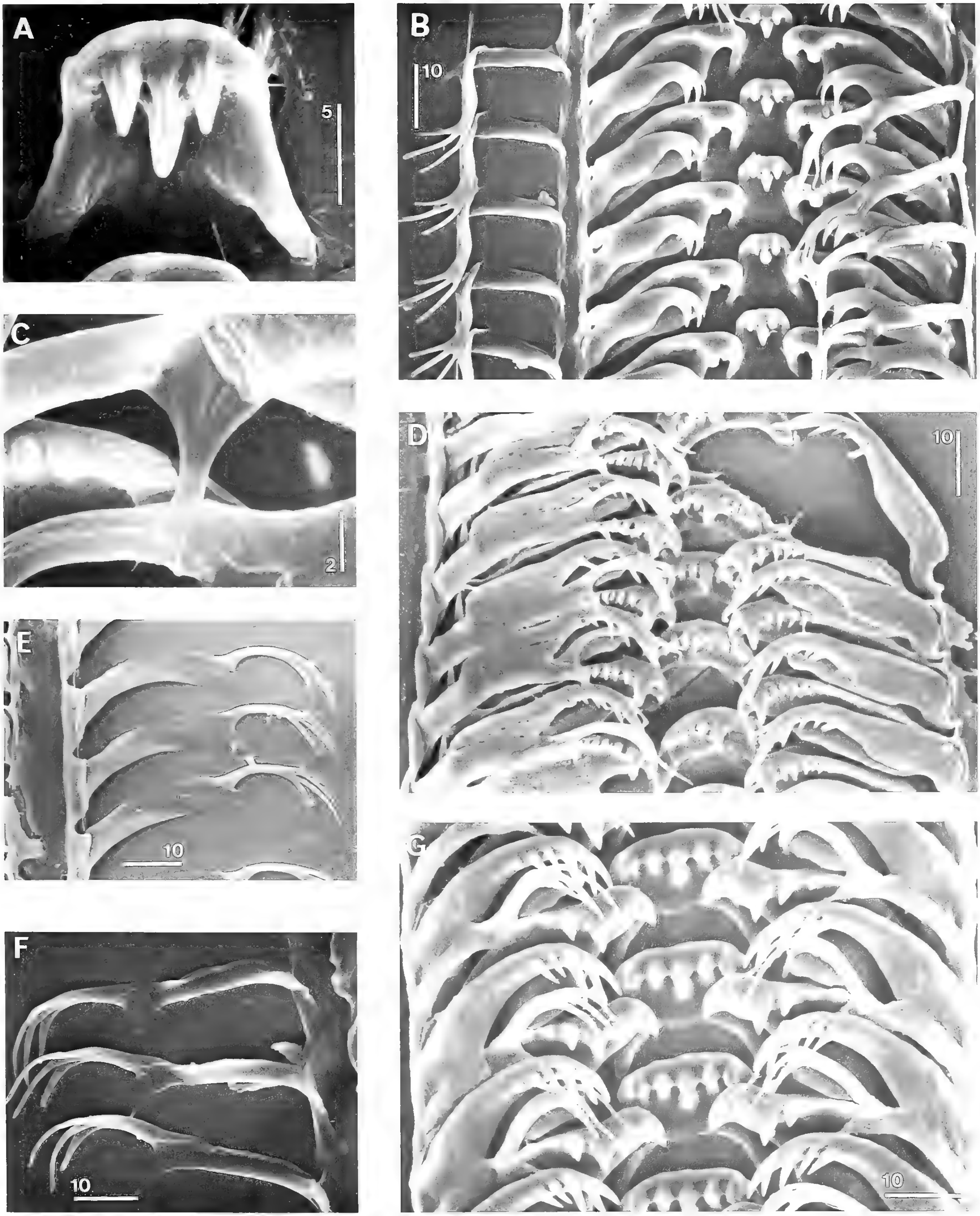
Lacuna macmurdensis Hedley, 1911:4. pl. 1, fig. 6.
Sublacuna trilirata Thiele, 1912:196, pl. 12, fig. 5.
Prolacuna macmurdensis: Arnaud, 1972:126.
Prolacuna trilirata: Egorova, 1982:30, fig. 141.
Prolacuna macmurdensis: Powell, 1951:121.
Prolacuna trilirata: Powell, 1958:190.
Prolacuna macmurdensis: Powell, 1958:191.
Prolacuna macmurdensis: Dell, 1990:163, fig. 258.

Type localities: *L. macmurdensis,* off Cape Royds, Macmurdo Sound, Ross Sea, 18–36 m: *S. trilirata,* Davis Sea, GAUSS Station, 89°E, 385 m.

→

Explanation of Figure 11

Radulae of ***Trilirata*** spp. Figures A–C. ***T.** macmurdensis.* A. Central tooth. B. Complete width of radula. C. Detail of outer marginal tooth. Figures D, E. ***T.* herosae** Warén & Hain, sp. nov., holotype. F, G. ***T. sexcarinata*** Warén & Hain, sp. nov., PS VII/4, sta. 291. Scale lines in μm.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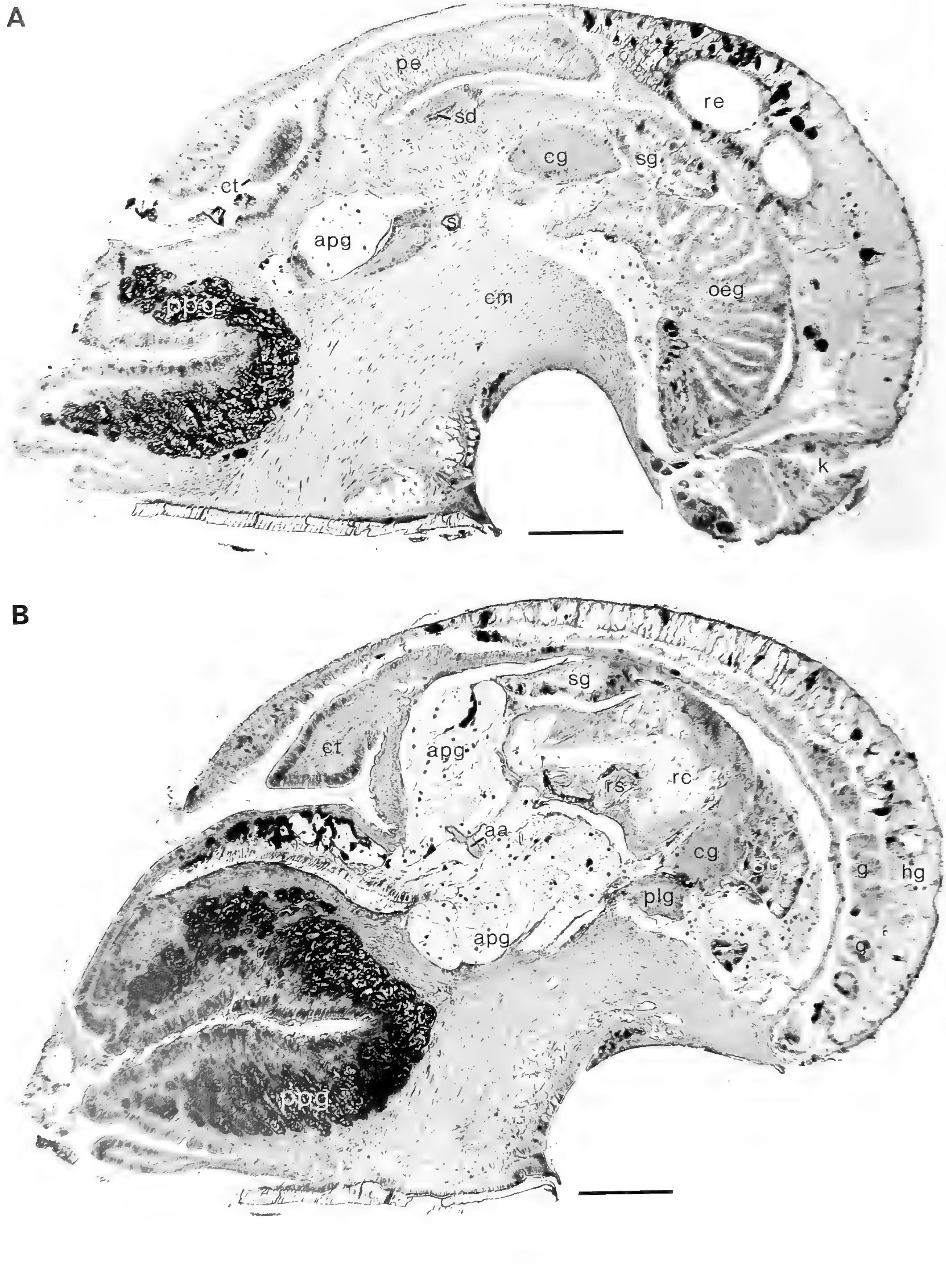
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Type materials: *L. macmurdensis,* in AMS, not examined; *S. trilirata,* syntype ZMHU 63024, examined.

Material examined: PS VII/4, sta. 224, 013°W, 186–187 m, 1 specimen, 3 shells.—PS VII/4, sta. 230, 027°W, 270–280 m, 1 shell.—PS VII/4, sta. 274, 012°W, 196–212 m, 1 shell.—PS VII/4, sta. 289, 013°W, 672 m, 1 specimen.—PS IX/3, sta. 165, 003°W, 191–204 m, 5 shells.—PS IX/3, sta. 173, 007°E, 739–765 m, 3 specimens, 12 shells.—PS IX/3, sta. 174, 010°E, 432–432 m, 6 shells.—PS IX/3, sta. 179, 007°E, 185–161 m, 5 specimens, 5 shells.—PS IX/3, sta. 180, 006°E, 280–298 m, 32 specimens, 5 shells.—PS IX/3, sta. 206, 010°E, 343–338 m, 1 specimen, 1 shell.—PS IX/3, sta. 207, 005°E, 213–210 m, 1 shell.—PS IX/3, sta. 211, 005°E, 661–742 m, 3 shells.—PS IX/3, sta. 212, 003°E, 568–644 m, 3 shells.—PS IX/3, sta. 220, 006°E, 118–126 m, 2 specimens (all in SMNH).

Distribution: Antarctic circumpolar in 36–765 m.

Redescription: We only describe the anatomy, based on three decalcified specimens of 2.5 mm diameter, and serial sections of three adult and two young males, two adult females, and one female pallial skirt. Shell, Figure 10A–C; protoconch, Figure 34F, G.

External morphology of soft parts: The head-foot and pallial complex comprises ⅗ of a whorl in contracted specimens, the visceral mass slightly more than two whorls. The anterior part of the head-foot has a weak and diffuse granular grayish pigmentation, best visible along the edges of the snout, foot, and tentacles; behind the tentacles, including the visceral mass, it is light beige (in alcohol). The anterior ⅒ whorl of the visceral mass is still paler because of the overlying kidney. At the left side, the pericardium with the ventricle and auricle lies directly behind the gill and osphradium. The gonad is not easily distinguished externally, even in sexually mature specimens. Directly behind the pericardium, the esophagus and stomach extend about a third of a whorl backward before the esophagus enters the rear part of the stomach. Forming a continuation of the anteriorly situated part of the stomach, the intestine very soon turns sharply to the right and disappears under the kidney.

The pallial cavity is quite deep, and the pallial skirt normally covers the whole head in preserved specimens. The pallial margin is thin and simple, without tentacles and papillae, except at the right ⅙, where it is "uneven," but the details could not be worked out. The osphradium is surrounded by two ridges and runs along the gill from its most posterior part, forward to the anterior ¼ of the gill. The gill consists of a series of about 12 triangular leaflets, drawn out to a ventral tip; the gill width corresponds to ¼ of the pallial cavity. The leaflets in its central part are about twice as wide and high as the anterior ones. The columellar muscle projects at the right side of the body, 80–100° from the operculum. Its left part is much less conspicuous and narrower than the right. The hypobranchial gland is rather inconspicuous and partly covered by the tips of the gill leaflets. The pallial oviduct is restricted to the posterior right half of the cavity, and its left side contains the rectum, which opens at the same level as the duct. In the male, the rectum parallels the sperm duct and prostate in the corresponding position.

The head is medium-sized and has a pair of short (contracted), conical, flattened tentacles with large, black eyes in basal-lateral bulges. The snout is rather short, with parallel sides, somewhat flattened with a subventral mouth.

The male has a simple, tapering, finger-shaped penis just below the right cephalic tentacle, with a dorsal furrow containing a closed sperm duct. The duct continues buried in the right corner of the pallial cavity where there is a rather voluminous prostate.

The foot is flat, large, and broad. Judging from the folds, its anterior edge is probably blunt, but the corners seem not to be drawn out to small, tentaclelike extensions. Posteriorly, it seems bluntly rounded. There is no distinct opening for the posterior pedal gland; anteriorly, between the distinctly set-off propodium and the mesopodium opens an anterior pedal gland. The sides of the foot are smooth, and there are no epipodial ridges or furrows.

Internal anatomy (Figure 12): The foot is almost filled by the large posterior pedal gland (Figure 12A, **ppg**). The slightly smaller anterior pedal gland bulges into the cephalopedal haemocoel, but not behind the nerve ring. The posterior pedal gland stains dark bluish violet, the anterior one, a much lighter grayish violet with conspicuous nuclei. The posterior pedal gland does not have a defined opening. The anterior one has a storage space under the propodium lined with tall epithelium and opens via a broad and flat duct, which penetrates most of the gland. The muscle layer of the foot is quite thin (height 75–100 μm) along the sides and ventrally.

The tentacles are solid and muscular all the way to the base where they have a subcutaneous eye with lens and pigment layer, in a bulge. The snout is very muscular and

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Explanation of Figure 12

***Trilirata** macmurdensis,* two sagittal sections. Figure A. Oblique longitudinal section through left part of head-foot. Figure B. Oblique longitudinal section through right part of head-foot. **aa**—anterior aorta; **apg**—anterior pedal gland; **cg**—(right and left respectively) cerebral ganglion; **cm**—columellar muscle; **ct**—cephalic tentacle; **g**—tips of gill leaflets (embedded in mucus); **hg**—hypobranchial gland; **k**—kidney; **oeg**—esophageal gland; **pe**—penis; **pg**—pedal ganglion; **plg**—pleural ganglion; **rc**—radular cartilage; **re**—bulges from rectum; **rs**—radular sac; **s**—statocyst; **sd**—seminal duct; **sg**—salivary gland; **sn**—snout. Scale lines = 200 μm.

can probably be extended considerably when the snail is grazing.

The alimentary system consists of the mouth; a large, rather muscular buccal mass; a very short anterior esophagus; a large esophageal gland; a narrow posterior esophagus; stomach; intestine; and rectum. From the posterior esophagus backward, the preservation was too poor for any detail other than that the stomach has a gastric shield but seems to lack a crystalline style.

The jaw is reduced to a thick cuticular lining of the oral tube.

The radular sac is straight, long, and slender, passes backward through the nerve ring and lies ventral to the esophageal gland, extending as far back as this where it curves dorsally to the right of the esophagus. The part of the radula in use is supported by a pair of large cartilages.

Two salivary glands (Figure 12A, B, **sg**) open into the buccal cavity close to its mid-line via short, inconspicuous ducts, which do not pass through the nerve ring. The salivary glands are large and situated in front of and above the cerebral ganglia. Each consists of a short, thin duct and a voluminous gland of several lobes. With EHE they stain violet.

The dorsal food channel is characterized by the rich occurrence of mucus-producing cells. These start in the posterior, dorsal part of the buccal cavity, get displaced toward the left side when passing the nerve ring and end up ventrally in the esophageal gland (Figure 12A, **oeg**) where they do not reach its posterior end. No structure which could be a pair of esophageal pouches was found. Most specimens had foraminiferans in various stages of digestion in the stomach, intestine, and rectum. In the rectum these consist of almost empty "husks" containing some particles, which stain blackish violet with EHE.

The nervous system follows the normal pattern of littorinids with dialyneury between the left pleural and the supraesophageal ganglia. The distances between the ganglia are fairly short (contracted specimen), the pleural and cerebral ganglia abutting. The supra- and subesophageal ganglia are situated less than twice their diameter from the corresponding pleural ganglion. The length of the connectives to the pedal ganglia are twice the diameter of these ganglia. The supraesophageal ganglion lies free at the left side of the cephalopedal haemocoel; the subesophageal one in a pit in the body wall. The buccal ganglia are situated dorsally on the buccal mass close to the exit of the esophagus, and connected by a commissure. In front of the pedal ganglia is an accessory pedal ganglion, connected by a connective of the same length as its own diameter and innervating the anterior pedal gland and propodial area.

The statocysts are situated above and behind the pedal ganglia and are slightly displaced laterally. Their diameter corresponds to half the length of the ganglion. They have a single statolith.

Reproductive system. The sexes are separate. The fixation does not, however, allow any detailed description of the systems. The gonad lies along the right side of the visceral mass.

Female. An ovarian duct leads to a large albumen gland, which stains very lightly. Along the left side and anterior half of the albumen gland is a capsule gland (staining dark violet with EHE), but the detailed morphology and connections of these could not be worked out due to histolysis and missing and ruptured sections. They are, however, closed except for a short opening close to the anterior end of the capsule gland, and there is no bursa copulatrix. Just behind the capsule gland and above the albumen gland is a receptaculum seminis, which opens to the connection between the capsule and albumen gland. It contains oriented sperm. A well-developed gonopericardial duct is present, opening into the ovarian duct close to the albumen gland. Four of the five females that were sectioned had the pericardium filled with sperm.

Male. The simple, tapering penis is situated below the right cephalic tentacle. It has a seemingly open sperm groove along its dorsal side, but this furrow contains a closed sperm duct, which turns to the right side and runs backward in the right corner of the pallial cavity. Along the most posterior part in the cavity lies a closed prostate gland, which continues backward abutting the rectum and the kidney, and eventually extends into the visceral mass at the right side of the kidney. The epithelium of the prostate is divided into the more dorsal half, which is covered by tall cylindrical epithelium, staining violet with EHE, and the more ventral half, covered by much less ordered cells of an almost cotton or wool-like structure, which stains bluish gray with EHE. The vas deferens seems to open into the prostate at its anterior ⅓. The more posterior part of the vas deferens lies coiled close to the columella, is voluminous, thin-walled, and functions for storage of sperm.

The radula (Figures 6C–F, 11A–C) is taenioglossate, long, and slender, with about 100 transverse rows of teeth. The central tooth (Figures 6D, 11A) has a low and indistinct hood with a few tubercles along its apical margin. Below this, one large central and one smaller cusp on each side form a cutting edge. Beside these, and partly concealed by them, are two much smaller denticles on each side. The "wings" are not drawn out to small denticles on the sides. The front of the tooth is concave and lacks a supporting bulge at the base. The lateral tooth usually has six denticles, of which numbers 1 and 3 (counted from the inner edge) are at least twice the size of the others. The littorinid notch is missing. The first marginal tooth is simple, claw-shaped, slightly flattened with a sturdy shaft and three large apical cusps. The outer marginal tooth is longer and a fourth the thickness of the inner one. It has three long and slender apical cusps. At mid-length, the shaft is crossed by a furrow and has a small, very thin, and membranous cusp (Figure 11C). This furrow makes the tooth pliable, and the outer part is frequently folded here (Figures 6E, 11B). Very young specimens have a proportionally shorter radula with fewer transverse rows of teeth, otherwise identical (Figure 6C).

The operculum (Figure 4I) has a few whorls and central nucleus, is transparent, slightly yellowish brown, especially where it is attached to the foot. The surface is distinctly wrinkled by the growth lines.

Reproduction. The eggs are laid singly in simple, globular capsules with a thin, transparent wall. The size of the young in capsules agrees with our smallest benthic stages, and the development is thus lecithotrophic and encapsulated.

Remarks: Powell (1958:191) suggested that *Prolacuna trilirata* is a synonym of *P. macmurdensis.* This was accepted by Arnaud (1972:126) and Dell (1990:163), and we can see no reason to question this, although there is considerable variation in the shell morphology (Figure 10A–C).

Trilirata herosae Warén & Hain, sp. nov.

(Figures 4J, 11D, E, 13E–H)

Type locality: BIOCAL DW35, New Caledonia, 23°10′S, 167°10′E, 675–680 m.

Type material: Holotype and 2 paratypes (from DW70) in MNHN.

Material examined: BIOCAL sta. DW70, New Caledonia, 23°25′S, 167°53′E, 965 m, 2 shells (paratypes), MNHN.—BIOCAL sta. DW46, New Caledonia, 22°53′S, 167°17′E, 570–610 m, 2 shells.

Distribution: Only known from the material examined, from south of New Caledonia, in 570–965 m.

Etymology: "*herosae*," after Mme. Virginie Heros, MNHN, who has sorted a large part of the sediments in which the species was found.

Description: *Shell* (Figure 13E–G) angular, low-spired, with three spiral keels and a wide umbilicus. The protoconch (Figure 13H) is not demarcated, is sculptured with some spiral ribs and keels and some indistinct bumps and dents. The proto- and teleoconch together form 2.5 whorls, sculptured by indistinct and irregular growth lines, some indistinct and low spiral striae, and three strong spiral keels, one at the edge of the shoulder, one at the periphery, and one around the umbilicus. The umbilicus is deep, penetrating shell to the protoconch, and of a diameter corresponding to 45% of the shell diameter. The parietal callus is thin. The inner lip is evenly curved, the outer lip almost straight between the suture, the spiral keels, and the lower corner of the aperture.

Dimensions. Diameter of holotype (largest specimen) 3.7 mm.

The radula (Figure 11D, E) is taenioglossate, long, and slender with about 80 transverse rows of teeth. The central tooth has a low, thin hood with no cusps. Below this, one major central and three smaller, lateral, rounded cusps form a cutting edge. The "wings" are not drawn out to small denticles. The front of the tooth is deeply excavated. The lateral tooth usually has about 10 denticles, of which numbers 1 and 3 (counted from the inner edge) are at least twice the size of the others. The littorinid notch is missing. The first marginal tooth is simple, claw-shaped, with a sturdy shaft and eight apical cusps. The apical four of these cusps are very long; the more basal four are situated along the outer edge and are less than half the size of the others. The outer marginal tooth is of about the same length, much thinner, with four long apical digits of ⅛ the length of the tooth. At mid-length, the shaft has a transverse groove where it is much thinner and equipped with a very thin, triangular cusp (Figure 11E).

The operculum (Figure 4J) has a few whorls, a distinctly subcentral nucleus, and is transparent, pale brownish yellow, more distinctly so where attached to the foot. The surface is distinctly wrinkled by the growth lines.

Remarks: The shell has some resemblance to that of *Aorotrema* Pilsbry & McGinty, 1942 (now in Vitrinellidae: Abbott, 1974). Species of that genus, however, have a rough surface, a columellar tooth, and a hyperstrophic larval shell. Their closer affinity remains unknown, since only empty shells are known, but the Pyramidellidae is probably a good guess.

Trilirata triregis Warén & Hain, sp. nov.

(Figure 13A–D)

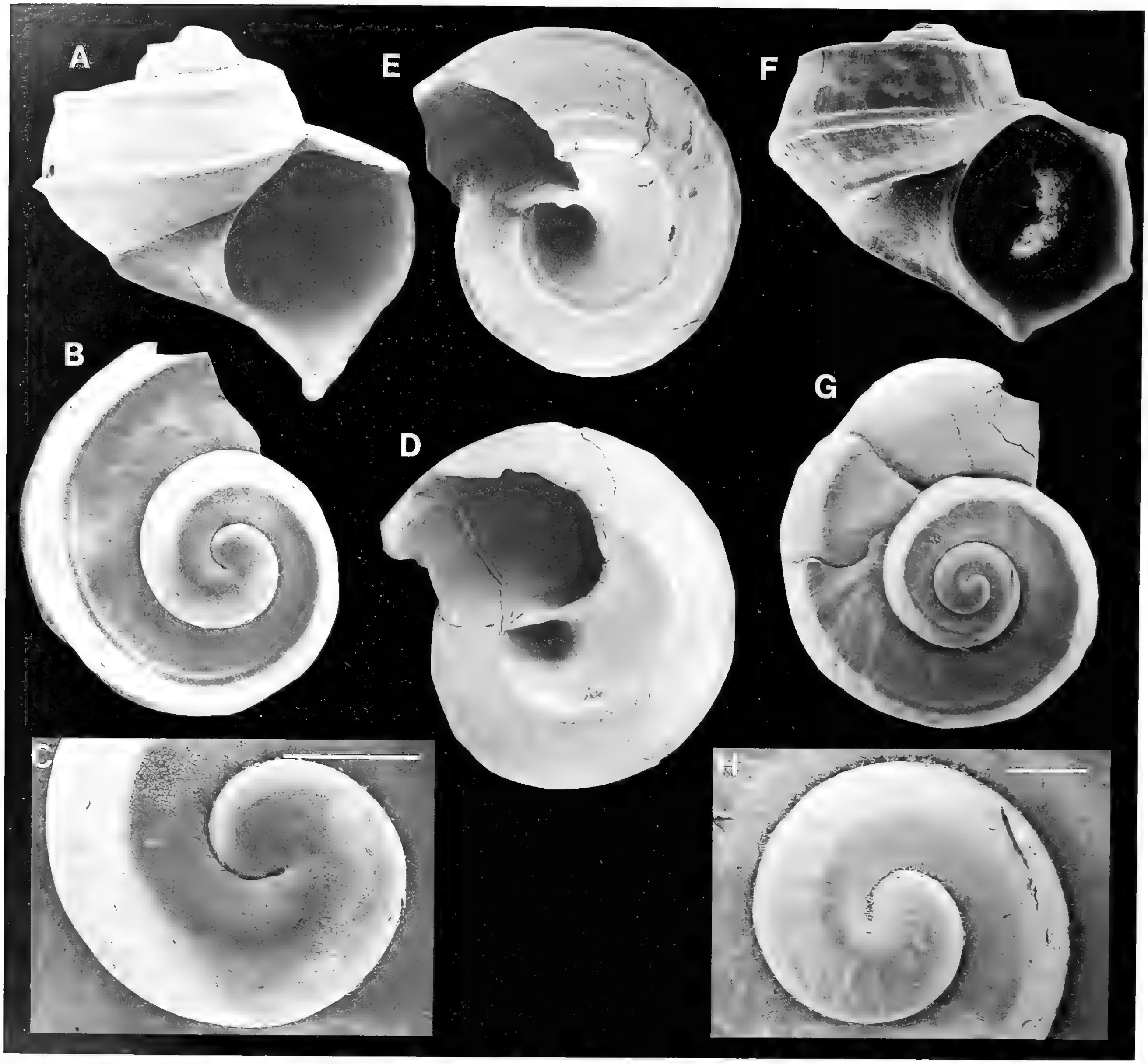
Type locality: Northern New Zealand, off Three Kings Islands, 34°00′S, 171°51′E, 800 m.

Type material: Holotype and 14 paratypes, MNZ M.49033 and 127384.

Material examined: Northwestern New Zealand, northwest of Three Kings Islands, Middlesex Bank, 34°02.0′S, 171°44.0′E, 246–291 m, 3 shells, MNZ M.118932.—Three Kings Islands, 24 km northwest of Great Island, 34°05.9′S, 171°55.1′E, 710 m, 9 shells, MNZ M.118934.—Three Kings Islands, 11 km northwest of Great Island, 34°06.5′S, 172°04.7′E, 310 m, 1 shell MNZ M.118931.—Three Kings Islands, 18 km north of Great Island, 33°59.2′S, 172°13.6′E, 155 m, 1 shell, MNZ M.118929.—Three Kings Islands, 13 km north of Great Island, 34°01.8′S, 172°12.0′E, 508 m, 1 shell, MNZ M.118928.—Northwest of Three Kings Islands, Middlesex Bank, 34°00.9′S, 171°44.7′E, 201–216 m, 1 shell, MNZ M.118935.

Distribution: Only known from the material examined from the Three Kings Islands area, 155–800 m (shells only).

Etymology: "*triregis*" (Latin) from *tri* and *rex,* meaning "of the three kings," referring to the type locality.



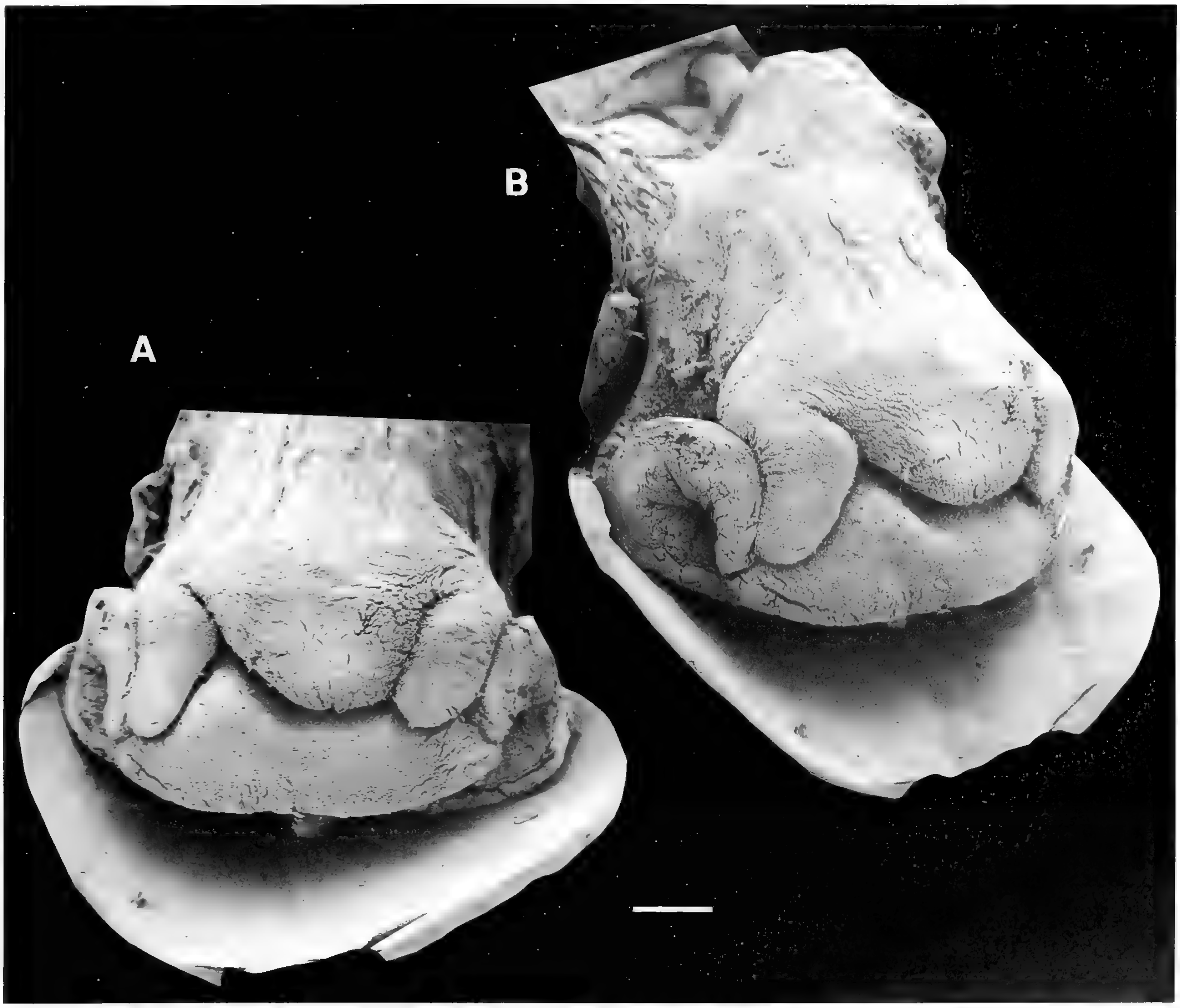
Explanation of Figure 13

Trilirata spp. Figure A. ***T. triregis*** Warén & Hain, sp. nov. Holotype, diameter 2.8 mm. Figures B–D. ***T. triregis*** Warén & Hain, sp. nov. Paratypes, diameter 1.3, and 2.25 mm. Figure E, F. ***T. herosae*** Warén & Hain, sp. nov. Holotype, diameter 3.7 mm. Figures G, H. ***T. herosae*** Warén & Hain, sp. nov. Paratype, diameter 3.2 mm. Scale lines = 200 μm.

Description: *Shell* (Figure 13A, B, D, E) angular, low-spired, with three spiral keels and a wide umbilicus. The protoconch (Figure 13C) is not demarcated and almost smooth. The proto- and teleoconch together form about 2.6 whorls, sculptured by indistinct and irregular growth lines, and three strong spiral keels, one at the edge of the shoulder, one at the periphery, and one around the umbilicus. The umbilicus is deep, penetrating the shell to the protoconch, and of a diameter corresponding to 45% of the shell diameter. The parietal callus is thin. The inner lip is evenly curved, the outer lip almost straight between the suture, the spiral keels, and the lower corner of the aperture.

Dimensions. Diameter of holotype (largest specimen) 2.8 mm, height 2.8 mm.

Remarks: ***Trilirata triregis*** resembles ***T. herosae***, and close relations between the two seem beyond doubt, despite



Explanation of Figure 14

Trilirata sexcarinata Warén & Hain, sp. nov., PS VII/4, sta. 291. Figure A. Front view of head-foot. Figure B. Slightly oblique view of right side of the foot. Scale line = 200 μm.

no soft parts being available of ***T. triregis***. The only noticeable difference is that ***T. herosae*** is slightly larger at the same number of whorls and has a more pronounced spiral sculpture on the basal surface.

The holotype of ***T. triregis*** is the largest specimen available, but its aperture is broken. Also, the smaller specimens are in rather bad condition, and it is possible that the specimens are fossil.

Trilirata sexcarinata Warén & Hain, sp. nov.

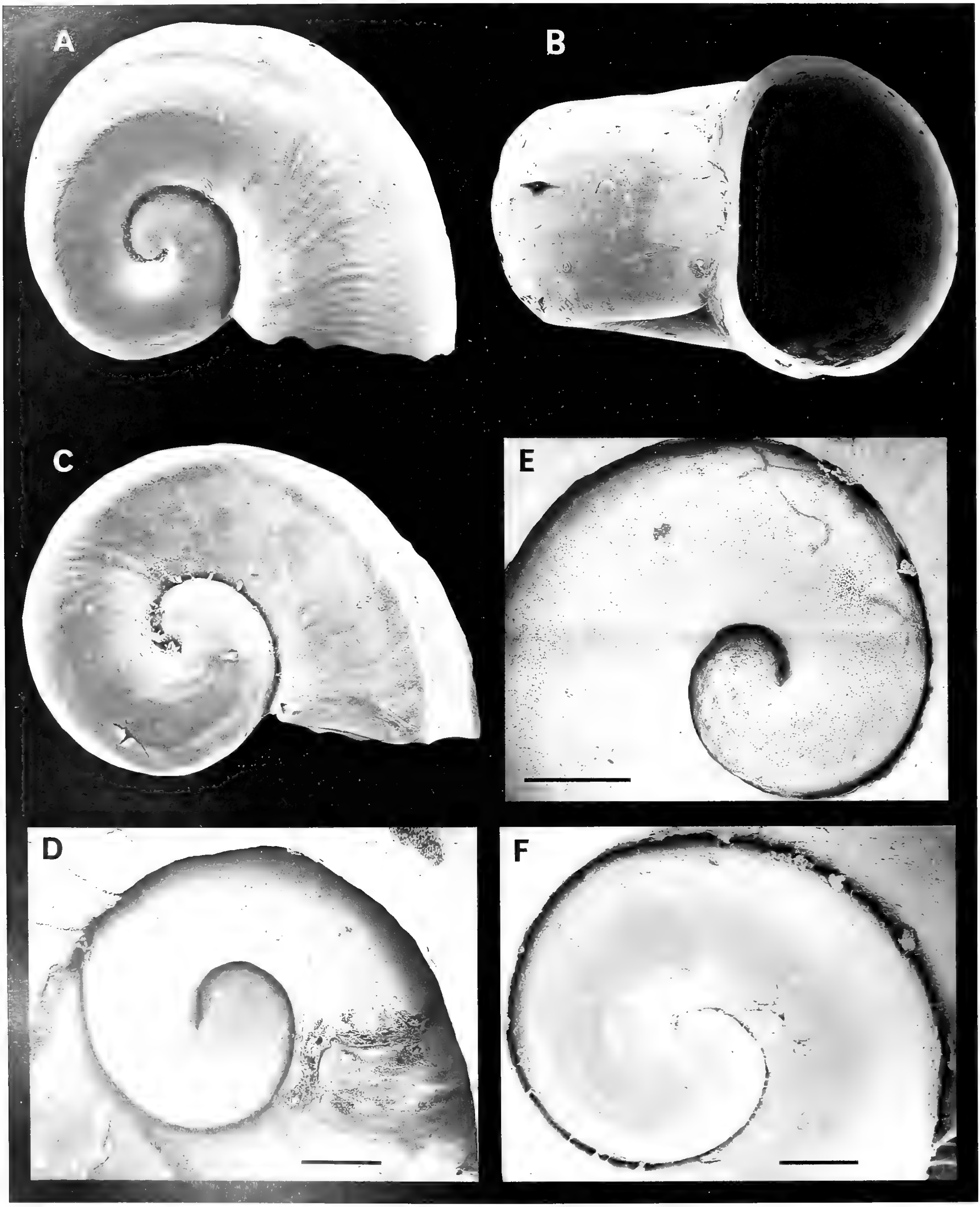
(Figures 4K, L, 11F, G, 14, 15A, B, 16–18)

Mesogastropoda sp. 1: Hain, 1990:53, pl. 3, fig. 7a–f; pl. 22; fig. 5.

Type locality: PS IX/3, sta. 220, 70°24.1′S, 06°07.6′E–70°24.3′S, 06°08.6′E, 118–126 m, 13 March 1991.

Type material: Holotype and 4 paratypes (immature, from sta. 179) in SMNH, nos. 4658 and 4659.

Material examined: PS VII/4 sta. 284, 013°W, 402–412 m, 2 specimens.—PS VII/4 sta. 291, 012°W, 499–515 m, 1 specimen.—PS VII/4 sta. 293, 012°W, 771–793 m, 1 specimen.—PS IX/3, sta. 165, 003°W, 191–204 m, 1 specimen, 1 shell.—PS IX/3, sta. 173, 007°E, 739–765 m, 2 specimens, 3 shells.—PS IX/3, sta. 179, 007°E, 185–161 m, 1 specimen, 6 shells. — PS IX/3, sta. 180, 006°E, 280–298 m, 1 specimen.—PS IX/3, sta. 212, 003°E, 568–644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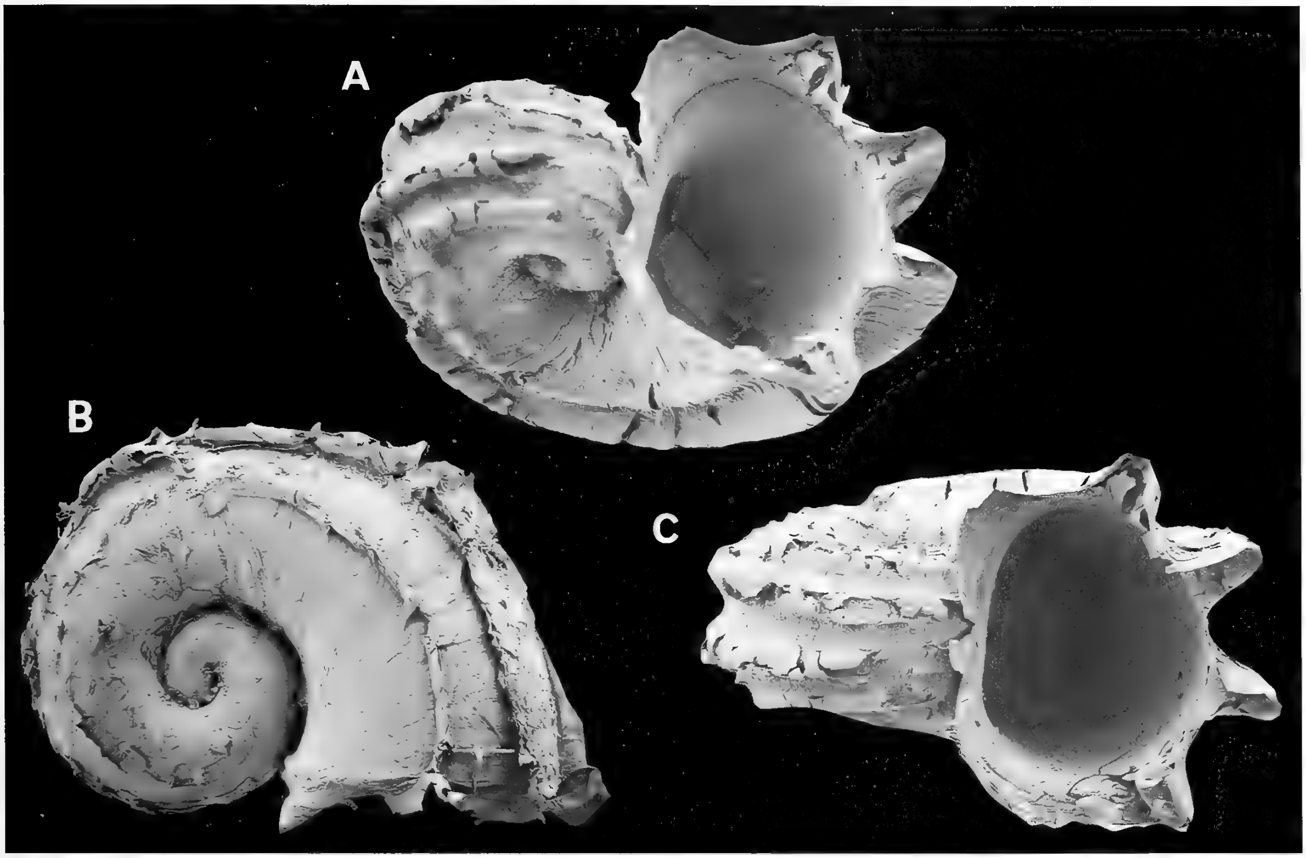

Explanation of Figure 16

Trilirata sexcarinata Warén & Hain, sp. nov., PS VII/4, sta. 284. Figures A–C. Diameter 2.5 and (B) 2.1 mm.

m, 1 shell.—PS IX/3, sta. 220, 006°E, 118–126 m, 2 specimens (all in SMNH).

Distribution: Weddell and Lazarev seas, from 13°W, eastward to 7°E, in 118–765 m.

Etymology: "*sexcarinata*" (Latin), with six keels.

Description: Based on the material above; three adult sectioned females, one critical point dried female, and two decalcified males.

Shell (Figure 16) large for the genus, corneous, planispiral with strongly convex whorls and strong spiral keels. The protoconch (Figure 15A) is poorly demarcated, smooth, consists of about 1 whorl of a diameter of 0.6 mm. Adult specimens have 2 teleoconch whorls, sculptured by uniform and distinct incremental lines. The spiral sculpture of the teleoconch starts with three spiral ribs which rapidly fade away. The aperture is higher than broad, evenly rounded, not indented by the preceding whorl. The periostracum is extremely thick, and forms six spiral keels, one keel at the most apical part of the shell, one at the basal part of shell, and four keels between these.

Dimensions. Holotype 2.6 mm, maximum diameter 6 mm.

External morphology of soft parts: The head-foot (Figure 14) and pallial complex comprise ¼ of a whorl in a contracted specimen, the visceral mass 1.5–2 whorls. The

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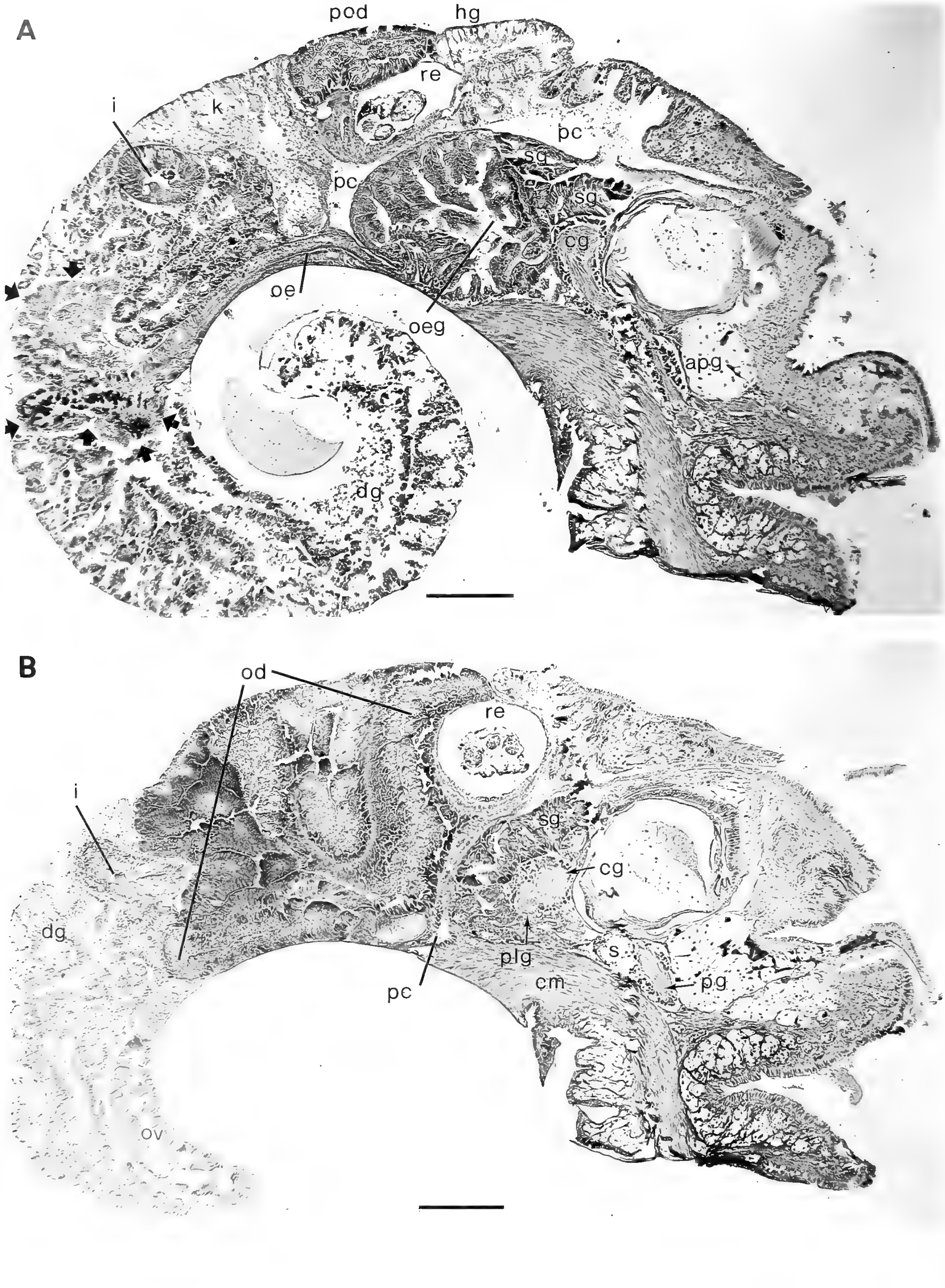
Explanation of Figure 15

Figures A, B. ***Trilirata sexcarinata*** Warén & Hain, sp. nov., young specimens, PS IX/3 sta. 179, diameter 1.33 and 1.17 mm. Figures C–E. *Zerotula* ***stellapolaris*** Warén & Hain, sp. nov., PS IX/3 sta. 179, diameter 0.45 mm. Figure F. *Zerotula* ***incognita*** Warén & Hain, sp. nov., holotype. Scale lines = 100 μm.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head-foot is pale beige. The visceral mass is brownish or greenish (in alcohol), its anterior $\frac{1}{10}$ whorl is paler and contains the kidney and most of the albumen gland of the oviduct. At the left side, the pericardium with the ventricle and auricle lies directly behind the gill and osphradium, in females strongly iridescent from its contents of sperm. The gonad is not easily distinguished externally, although the specimens are sexually mature. The esophagus and stomach cannot be discerned externally.

The columellar muscle is inconspicuous and projects at the right and left side of the body, 70–90° from the operculum; dorsally it reaches less than $\frac{1}{6}$ of the height of the whorl and is thus mainly ventral. Its left part is far less conspicuous and narrower.

The pallial cavity is quite deep, and the pallial skirt normally covers the whole head in preserved specimens. The pallial margin is thin and simple, without tentacles or papillae. The osphradium is encircled by two ridges and runs along the gill from its most posterior part, forward to the anterior $\frac{1}{4}$ of the gill. The gill consists of a series of about nine triangular leaflets, drawn out to a ventral tip; the gill width corresponds to $\frac{1}{4}$ of the pallial cavity. The leaflets in its central part are about twice as wide and high as the anterior ones. The hypobranchial gland is rather inconspicuous and partly covered by the tips of the gill leaflets. The brown pallial oviduct is restricted to the posterior right half of the cavity, and its left side contains the rectum, which opens at the same level as the duct.

The head is medium-sized and has a pair of short (contracted), conical, flattened tentacles with large, black eyes in basal-lateral bulges. The snout is rather short, slightly tapering, somewhat flattened with a subventral mouth.

The foot is flat, large, and broad. It is strongly contracted in all specimens, but judging from the folds, its anterior edge is probably blunt. Posteriorly it seems bluntly rounded. Anteriorly, between the indistinctly set-off propodium and the mesopodium opens an anterior pedal gland. The sides of the foot are smooth and there are no epipodial ridges or furrows.

Internal anatomy (Figures 17, 18): The foot (Figure 18A) is almost filled by the large posterior pedal gland (**ppg**) and the slightly smaller anterior pedal gland (**apg**). These do not bulge into the cephalopedal haemocoel. The posterior pedal gland stains dark bluish violet, the anterior one, a much lighter grayish violet. The posterior pedal gland has no defined opening. The anterior one has a storage space under the propodium lined with tall epithelium and opens via the slit between the pro- and mesopodium. The muscle layer of the foot, 75–100 μm thick along the sides and ventrally, is rich in muscle fibers.

The tentacles are solid and muscular all the way to the base where they have a subcutaneous eye with lens and pigment layer, in a bulge. The snout is very muscular and can probably be extended considerably when the snail is grazing.

The alimentary system consists of the mouth, a large, not very muscular buccal mass, a very short anterior esophagus, a large esophageal gland, a narrow posterior esophagus, a a poorly defined stomach, intestine, and rectum.

The jaw is thin and membranous, only a thick cuticule lining of the oral tube.

The radular sac (Figure 18B, **rs**) is straight, long, and slender, passes backward through the nerve ring below the esophageal gland and extends as far back as this. The part of the radula in use is supported by a pair of large cartilages.

Two salivary glands (Figure 18, **sg**) open into the buccal cavity close to its mid-line via short, inconspicuous ducts which do not pass through the nerve ring. The salivary glands are large and situated above the cerebral ganglia. Each consists of a short, thin duct and a longer, coiled glandular tube. The shallow dorsal food channel is characterized by the rich occurrence of mucus-producing cells. These start in the posterior, dorsal part of the buccal cavity, get displaced toward the left side when passing the nerve ring and end up ventrally in the esophageal gland where they do not reach its posterior end. A pair of esophageal pouches seems to be present, but this is uncertain. The interior of the esophageal gland (Figure 18B) is filled by glandular, transverse septa which leave only a small ventral lumen for the (now ventral) dorsal food channel. The posterior esophagus exits from the gland as a much narrower, internally strongly ciliated tube of $\frac{1}{6}$ of the diameter of the gland. It continues backward where it ends in a large cavity formed by the digestive gland. From this cavity a very simple stomach, without gastric shield, continues and goes over into the intestine, which is twice the diameter of the stomach. The intestine continues with a thick wall, turns to the right just behind the kidney, crosses the body, turns abruptly forward ventrally to the kidney. It continues forward surrounded by the lobes of the albumen gland

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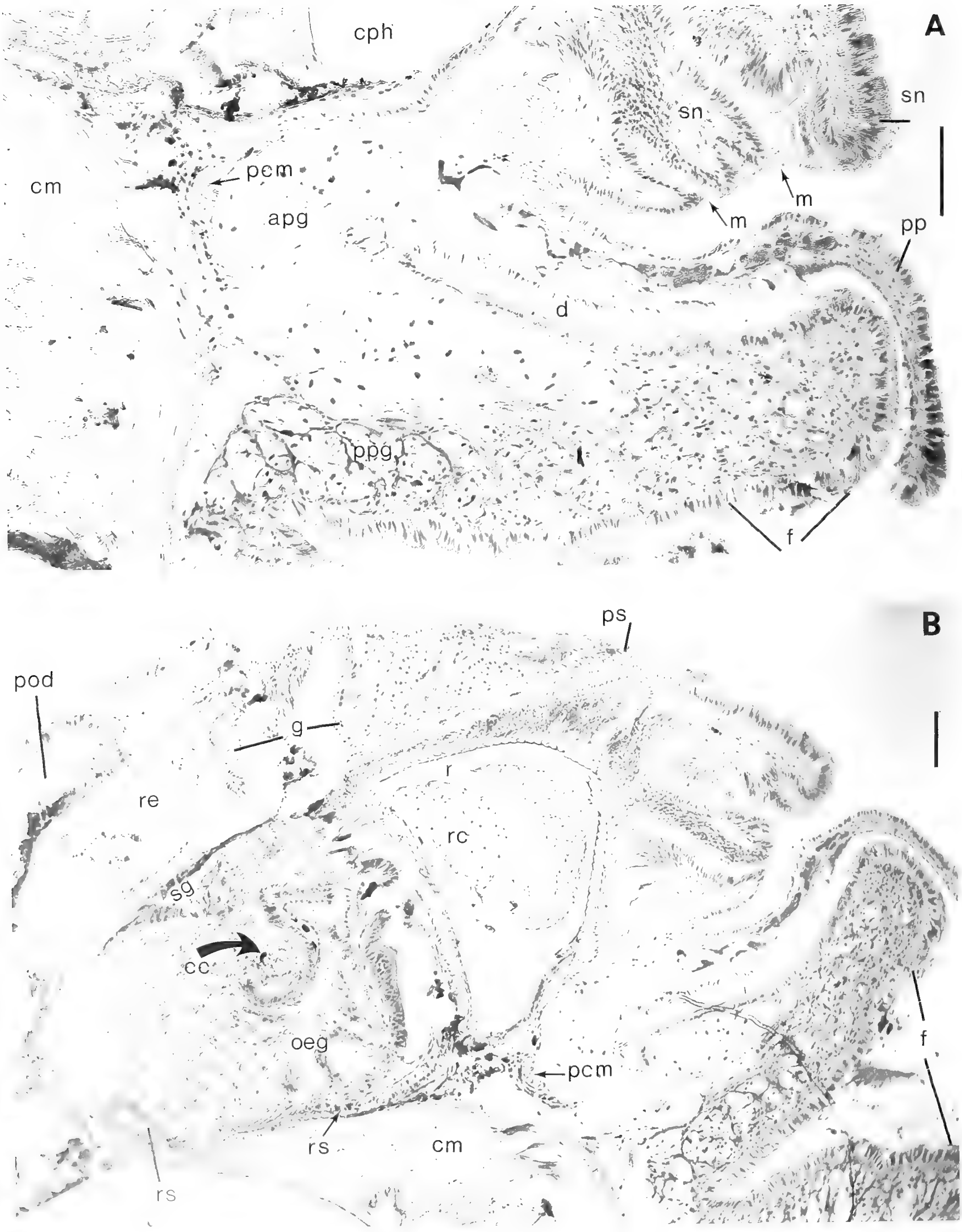
Explanation of Figure 17

Trilirata sexcarinata Warén & Hain, sp. nov. Figure A. Longitudinal section, left side of body. Stomach (histolysed) demarcated by a series of black arrows. Figure B. Longitudinal section, right side of body. **apg**—anterior pedal gland; **cg**—cerebral ganglion; **cm**—columellar muscle; **dg**—digestive gland; **hg**—hypobranchial gland (distorted and jammed with part of gill); **i**—intestine; **od**—oviduct; **oe**—esophagus; **oeg**—osophageal gland; **ov**—ovary; **pc**—pallial cavity; **pg**—pedal ganglion; **plg**—pleural ganglion; **pod**—pallial oviduct; **re**—rectum (with remains of forams); **s**—statocyst; **sg**—salivary gland. Scale lines = 250 μm.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and goes over into a much more thin-walled rectum when it enters the pallial skirt. Most specimens had remains or almost complete forams in the digestive canal.

The nervous system follows the normal pattern, with dialyneury between the left pleural and the supraesophageal ganglia. The distances between the ganglia are fairly short (contracted specimen), the left pleural and cerebral ganglia partly fused, the right ones abutting. The supra- and subesophageal ganglia are situated less than their diameter from the corresponding pleural ganglion. The length of the connectives to the pedal ganglia is twice the diameter of the ganglia. The supraesophageal ganglion lies free in the left side of the cephalopedal haemocoel beside the left cerebral ganglion; the subesophageal one is well embedded in the body wall slightly farther back. The buccal ganglia are situated dorsally on the buccal mass close to the exit of the esophagus, and connected by a commissure. In front of the pedal ganglia is an accessory pedal ganglion connected by a connective of its own length and innervating the anterior pedal gland and propodial area.

The visceral ganglia were not identified.

The statocysts (with a single statolith) are situated above and behind the pedal ganglia and slightly displaced to the right. Their diameter corresponds to the width of the ganglion.

Reproductive system. The sexes are separate, or at least the three sectioned specimens were females with no trace of male organs. The fixation does not, however, allow any detailed description. The ovary lies along the right side of the visceral mass. An inconspicuous ovarian duct close to the ventral body wall leads to a large albumen gland, which stains very lightly. Along the left and anterior side of this is a capsule gland (staining dark violet). The pallial oviduct system bulges deep into the visceral mass, occupying about 80° of the whorl and extending from the ventral to the dorsal edge of the body. The detailed morphology could not be worked out due to missing sections. There is no receptaculum seminis, but oriented sperm is stored in the pericardium (which communicates with the oviduct via the gonopericardial duct).

The radula (Figure 11F, G) is taenioglossate, long, and slender with about 80 transverse rows of teeth. The central tooth has a low and thin, slightly undulating hood with a triangular cusp at each end along its apical margin. Below this, one major central and two smaller, lateral, rounded cusps form a cutting edge. Beside these and partly concealed by them is a much smaller denticle on each side. The "wings" are drawn out to a small denticle on each side close to the base. The front of the tooth is deeply excavated. The lateral tooth usually has about seven denticles, of which number 4 (counted from the inner edge) is at least twice the size of the others. The littorinid notch is missing. The first marginal tooth is simple, claw-shaped, with a sturdy shaft and six apical cusps. The inner three of these cusps are very long, the outermost one is a mere denticle. The outer marginal tooth (Figure 11F) is of about the same length, much thinner, with three long apical digits of ⅙ the length of the tooth. Halfway to the point, the shaft has a transverse groove where it is much thinner and equipped with a very thin and triangular cusp.

The operculum (Figure 4K, L) has a few whorls, distinctly subcentral nucleus; it is transparent, slightly brownish yellow, especially where it is attached to the foot. The surface is distinctly wrinkled by the growth lines.

Remarks: The shell of this species bears some resemblance to echinospira larvae in that the periostracum to a large extent is separated from the shell by a transparent, gelatinous layer which dries to virtually nothing. It also resembles closely an unidentified gastropod larva figured by Pelseneer (1903:figs. 61–63), but that larva has a different type of radula and velar lobes, and seems to belong to a capulid, possibly a species of *Torellia,* judging from the radula.

It may seem strange to classify ***T. sexcarinata*** with a very strongly developed periostracum in the same genus as *macmurdensis* and ***herosae***, which have a very thin periostracum. Such differences in periostracal structure are, however, also known in the genus *Lacuna,* where *L. vincta* has a normal periostracum and *L. crassior* (Montagu, 1803) has a very thick periostracum, which dries to a thin skin (A. Warén, unpublished).

Trilirata sexcarinata looks very different from the other species of ***Trilirata***, especially in alcohol when the periostracum is intact. However, when the initial part of a cleaned teleoconch is compared, they are much more similar (Figures 15A and 34G). The radulae are virtually identical, especially the extra cusp halfway along the shaft of the outer marginal, and we consider these good synapomorphies for bringing the species together in a distinct genus.

Young specimens (Figure 15A, B) have a proportionally broader shell than *Zerotula* ***stellapolaris*** and lack the hypertrophied periostracum.

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Explanation of Figure 18

Trilirata sexcarinata Warén & Hain, sp. nov. Figure A. Longitudinal section through center of anterior part of foot and snout. Figure B. Longitudinal section through central part of head-foot. **apg**—anterior pedal gland; **cc**—cerebral commissure (embedded in anterior esophagus and esophageal gland); **cm**—columellar muscle; **cph**—cephalopedal haemocoel; **d**—duct from apg; **f**—foot (mesopodium); **g**—gill leaflets; **m**—mouth (between arrows); **pcm**—pedal commissure; **pp**—propodium; **ppg**—posterior pedal gland; **ps**—pallial skirt; **r**—radula; **rc**—radular cartilage; **re**—rectum; **rs**—radular sac; **sg**—salivary gland; **sn**—snout. Scale lines = 100 μm.

Zerotula Finlay, 1926

Zerotula Finlay, 1926:379. Type species *Discohelix hedleyi* Mestayer, 1916 by original designation.

Remarks: *Zerotula* was included in Architectonicidae by Finlay (1926). It has later been used almost exclusively by Powell (1979 and other references), who has kept it in the Architectonicidae without comments. Several of the species classified in *Zerotula* by Powell are here referred to other genera.

The shells of the species here included in *Zerotula* vary considerably in sculpture, but the three (four?) species of which we know the radula have a very uniform lateral tooth, which is remarkably broad and low. *Zerotula incognita* resembles the species of ***Trilirata*** in having an outer marginal tooth with a thinner zone with a cusp (Figure 22A; cf. ***T.*** *macmurdensis,* Figure 11C), which convincingly shows the genera to be related, since no similar structure is known in any other gastropod group.

We have searched museum collections and the literature for species which have been placed in the wrong genera or families, but so far there are no candidates for inclusion in *Zerotula,* except the species included below.

For the systematics of *Discohelix* (Archaeogastropoda) where *Zerotula hedleyi* originally was classified, see Warén, Gofas, & Ponder (in preparation).

Zerotula hedleyi (Mestayer, 1916)

(Figures 3A, B, 4A, 19A–C, 20F)

Discohelix hedleyi Mestayer, 1916:125, pl. 12, figs. 6–6b.
Zerotula hedleyi: Finlay, 1926:379.

Type locality: New Zealand, Three Kings Islands, 15′S of Big King, 175 m depth.

Type material: Holotype and one paratype in MNZ, one paratype in AMS, not examined.

Material examined: New Zealand. Off Three Kings Islands, 34°11′S, 172°10′E, 90 m, 14 shells, 5 specimens (dried), MNZ M.33660.—Off Three Kings Islands, 34°00′S, 171°55′E, 805 m, 2 shells, MNZ M.11847.—11 km northwest of Great Island, Three Kings Islands, 34°06.5′S, 172°04.7′E, 310 m, 30 shells, MNZ M.118153.—Middlesex Bank, Three Kings Islands, 33°59.8′S, 171°46.8′E, 143–163 m, 1 shell, MNZ M.118309.—Southeast of Great Island, Three Kings Islands, 34°14.1′S, 172°09.0′E, 192–202 m, 14 shells, MNZ M.118306.—Middlesex Bank, Three Kings Islands, 34°01.4′S, 171°45.2′E, 201–216 m, 1 shell, MNZ M.118308.—King Bank, northeast of Three Kings Islands, 33°57.4′S, 172°19.4′E, 128–123 m, 35 shells, MNZ M.118307.—Off Three Kings Islands, 34°10′S, 172°12′E, 250 m, 6 shells, MNZ M.34081.—Off Three Kings Islands, 34°00′S, 171°55′E, 805 m, 4 shells, MNZ M.118147.—Southeast of Great Island, Three Kings Islands, 34°14.8′S, 172°13.6′E, 173–178 m, 10 shells, MNZ M.118150.—Southeast Bay, Great Island, Three Kings Islands, 54 m, 1 shell, MNZ M.33904.—North of Three Kings Islands, 34°01′S, 172°07′E, 700 m, 25 shells, MNZ M.34687.

Distribution: North of New Zealand, around Three Kings Islands; depth range 54–805 m (shells), found alive only once, in 90 m, MNZ M.33660.

Redescription: We have only described the radula and operculum; no soft parts are available. Shell, Figure 19A–C; protoconch, Figure 20F.

Radula. The radula (Figure 3A, B) is long and slender with close to 100 transverse rows of teeth. The central tooth is small and has a very low and indistinct hood. Below this, one major central and three smaller, lateral, rounded cusps form a cutting edge. The "wings" are not drawn out to small denticles at the sides. The front of the tooth is not excavated. The lateral tooth usually has about 10 denticles, of which number 1 (counted from the inner edge) is twice and number 3 is three times the size of the others. The six outer ones form a rather even "comb." The littorinid notch is missing. The first marginal tooth is simple, claw-shaped, with a sturdy shaft and forked point (two or three cusps). The outer marginal tooth is the same length but much thinner and flatter, with two long apical digits of ⅕ the length of the tooth.

The operculum (Figure 4A) has a few whorls, an almost central nucleus, and is transparent. The surface is indistinctly wrinkled by the growth lines.

Remarks: *Zerotula hedleyi* (Figure 19A–C) resembles ***Z. coronata***, sp. nov. (Figure 19D–F), but lacks the tubercles on the spiral keels.

Zerotula **coronata** Warén & Hain, sp. nov.

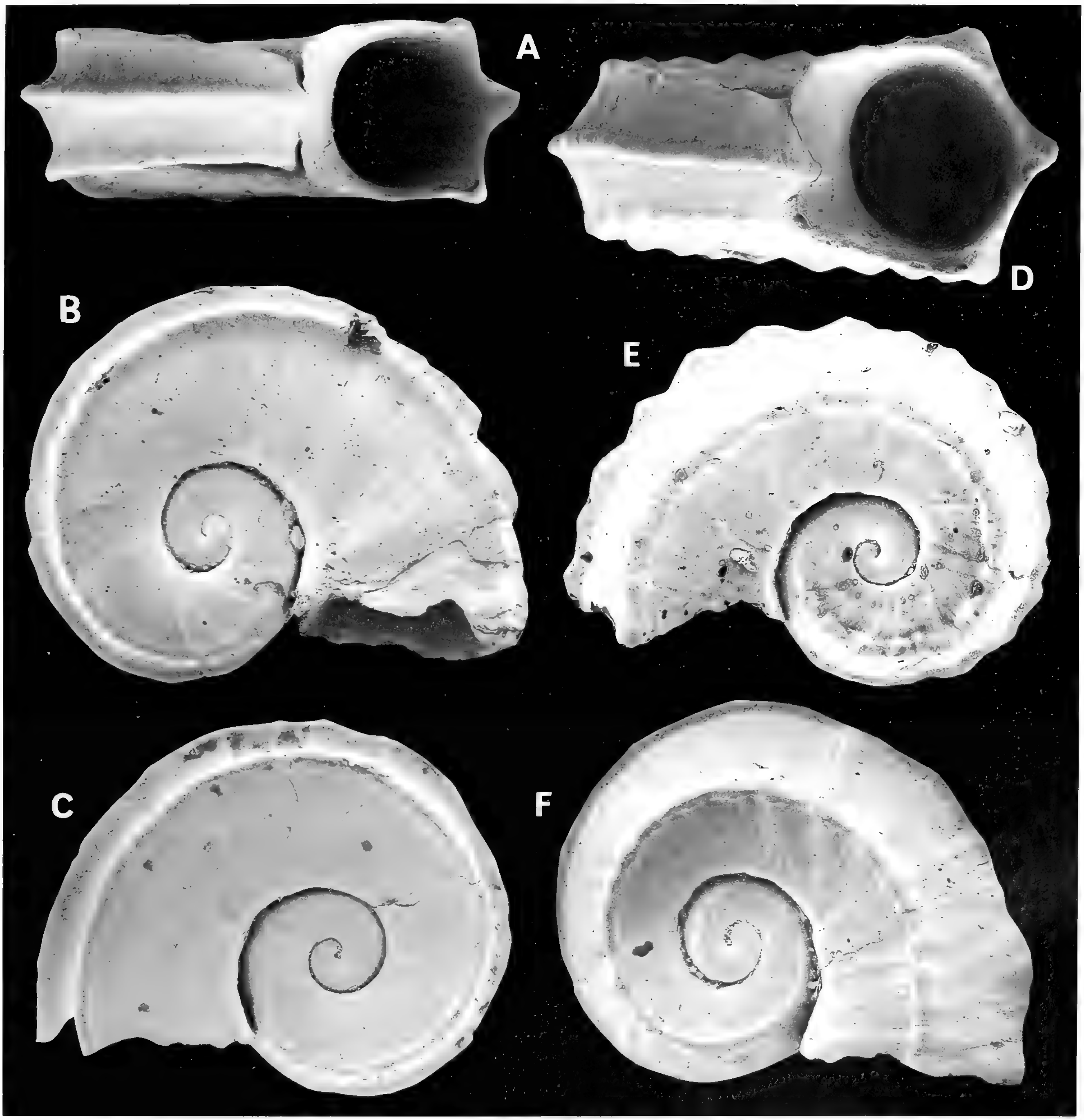
(Figures 19D–F, 20E)

Type locality: Off Three Kings Islands, 34°00′S, 171°55′E, 805 m, 40 shells.

Type material: Holo- and 39 paratypes MNZ, nos. M.49224 and 118852.

Material examined: New Zealand, Middlesex Bank, northwest of Three Kings Islands, 34°01.2′S, 171°44.4′E, 206–211 m, 4 shells, MNZ M.118312.—Southeast of Great Island, Three Kings Islands, 34°14.1′S, 172°09.0′E, 192–202 m, 7 shells, MNZ M.118311.—Off Northeast Island, Three Kings Islands, 34°08.5′S, 172°11′E, 100 m, 1 shell, MNZ M.34409.—North of Three Kings Islands, 34°01′S, 172°07′E, 700 m, 8 shells, ex MNZ M.34687.—Off Three Kings Islands, 34°10′S, 172°12′E, 250 m, 9 shells, MNZ M.34082.—11 km northwest of Great Island, Three Kings Islands, 34°06.5′S, 172°04.7′E, 310 m, 13 shells, MNZ M.118154.

Distribution: North of New Zealand, around Three Kings Islands; depth range 100–790 m (shells), living specimens not known.



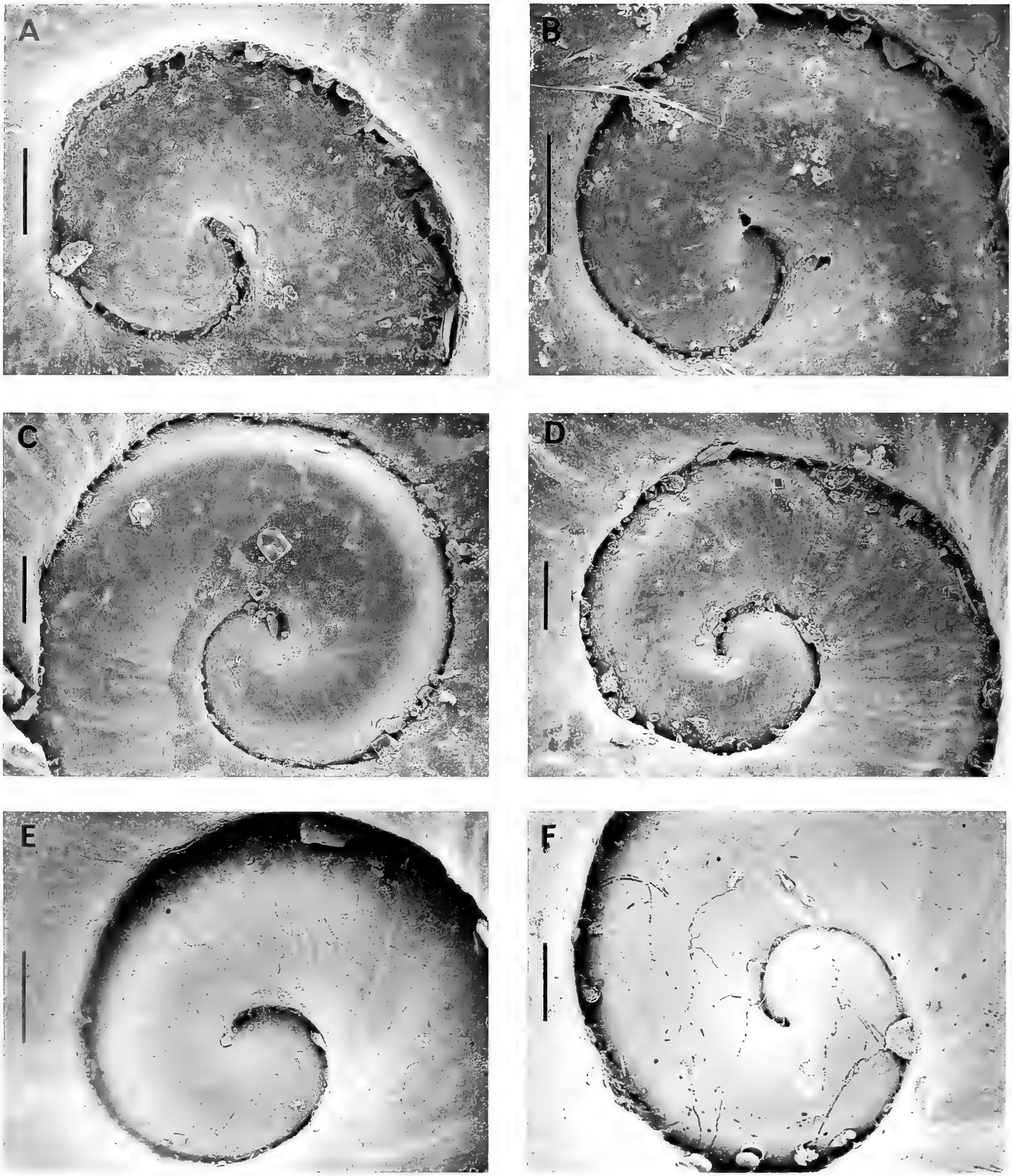
Explanation of Figure 19

Figures A–C. *Zerotula hedleyi,* MNZ M.33660. Diameters 1.3, 1.6 and 1.3 mm. Figures D–F. *Zerotula* ***coronata*** Warén & Hain, sp. nov., paratypes, MNZ M.118852. Diameters, 1.3, 1.3, and 1.4 mm.

Etymology: "*coronatus*" (Latin), with a crown.

Description: Based on shells only.

Shell (Figure 19D, E) very small, vitreous, planispiral, three-keeled, of rapidly increasing diameter. The protoconch (Figure 20E) is not clearly set off; its earlier part is smooth, later there are incremental lines, which form a gradual transition to the teleoconch sculpture. The cross section of the whorls is circular internally; their circumference is distinctly pentagonal with three peripheral, strong



Explanation of Figure 20

Zerotula spp., early whorls. Figure A. *Z. nummaria,* MNZ M.59448. Figure B. *Z. bicarinata,* MNZ M.66015. Figures C, D. *Z. triangulata* MNZ M.118148. Figure E. *Z.* ***coronata*** Warén & Hain, sp. nov., MNZ M.118852. Figure F. *Z. hedleyi* MNZ M.33660. Scale lines = 50 μm.

nodulose keels and two sharp corners beside the connection to the preceding whorl. The only additional sculpture consists of irregular growth lines of varying strength.

Dimensions. Diameter of holotype 1.30 mm, maximum diameter 1.40 mm.

Remarks: *Zerotula* ***coronata*** is most similar to *Z. hedleyi,* but differs in having distinct tubercles on the keels.

Zerotula ***stellapolaris*** Warén & Hain, sp. nov.

(Figures 4B, C, 15C–E, 21A–C, 22C, 23)

Type locality: PS IX/3, sta. 179, 69°58.9′S, 08°00.7′E to 69°59.3′S, 07°59.9′E, 185–161 m, 22 February 1991.

Type material: Holotype and 34 paratypes in SMNH, nos. 4660 and 4661.

Material examined: PS VII/4 sta. 271, 020°W, 399–352 m, 1 specimen.—PS VII/4 sta. 284, 013°W, 402–412 m, 2 specimens.—PS IX/3, sta. 165, 003°W, 191–204 m, 1 shell.—PS IX/3, sta. 173, 007°E, 739–765 m, 5 specimens, 5 shells.—PS IX/3, sta. 174, 010°E, 432–432 m, 3 specimens, 58 shells.—PS IX/3, sta. 180, 006°E, 280–298 m, 24 specimens, 6 shells.—PS IX/3, sta. 206, 010°E, 343–338 m, 1 specimen, 1 shell.—PS IX/3, sta. 207, 005°E, 213–210 m, 2 shells.—PS IX/3, sta. 211, 005°E, 661–742 m, 4 shells.—PS IX/3, sta. 212, 003°E, 568–644 m, 3 specimens, 9 shells (all in SMNH).

Distribution: Only known from the material examined, from the Weddell and Lazarev seas, 21°W eastward to 11°E, depth 190–765 m.

Etymology: "*stella polaris*" (Latin), North Star, German "Polarstern."

Description: Based on the material above; several decalcified specimens, and sections of two adult female and two adult males.

Shell (Figure 21A–C) small, transparent, planispiral, rather high with angular whorls and conspicuous periostracal keels. The protoconch (Figure 15C–E) is not demarcated from the teleoconch and lacks distinct sculpture. It is distinguishable in very young specimens and consists of about 1 whorl, diameter 0.4 mm. The proto- and teleoconch together form 2.1 whorls of rapidly increasing diameter, sculptured by irregular incremental lines and three strong spiral keels. The two lateral keels are situated close to the periphery at 75% of the radial width of the whorl. The aperture is squarish to rounded with sigmoid peristome. The periostracum is thin, straw-colored, and forms a narrow ridge on the median spiral keel.

Dimensions. Diameter of holotype 1.90 mm (maximum diameter).

External morphology of soft parts: The head-foot and pallial complex comprise almost half a whorl in a contracted specimen, the visceral mass 1.5 whorls. The head-foot is pale beige, the visceral mass more brownish (in alcohol). Its anterior $\frac{1}{10}$ whorl is paler and contains the kidney and the albumen gland of the oviduct. At the left side, the pericardium (sometimes strongly iridescent; contents of sperm?) with the ventricle and auricle lies directly behind the gill and osphradium. The gonad is not easily distinguished externally, although the specimens are sexually mature. The esophagus and stomach can be seen by transparency, a little more than half a whorl from the operculum, lying obliquely across the left side.

The columellar muscle is inconspicuous and projects slightly at the right and left side of the body, 90–100° from the operculum; dorsally it reaches less than $\frac{1}{5}$ of the height of the whorl and is thus mainly ventral. Its left part is much less conspicuous and narrower.

The pallial cavity is quite deep, and the pallial skirt normally covers the whole head-foot in preserved specimens. The pallial margin is thin and simple, without tentacles and papillae. The osphradium is paralleled by two ridges and runs along the gill from its most posterior part, forward to the anterior $\frac{1}{4}$ of the gill. The gill consists of a series of about 10 small tubercules; the gill width corresponds to $\frac{1}{10}$ of the pallial cavity. The hypobranchial gland is rather inconspicuous. The pallial oviduct is restricted to the posterior right half of the cavity, and its left side contains the rectum, which opens at the same level as the duct.

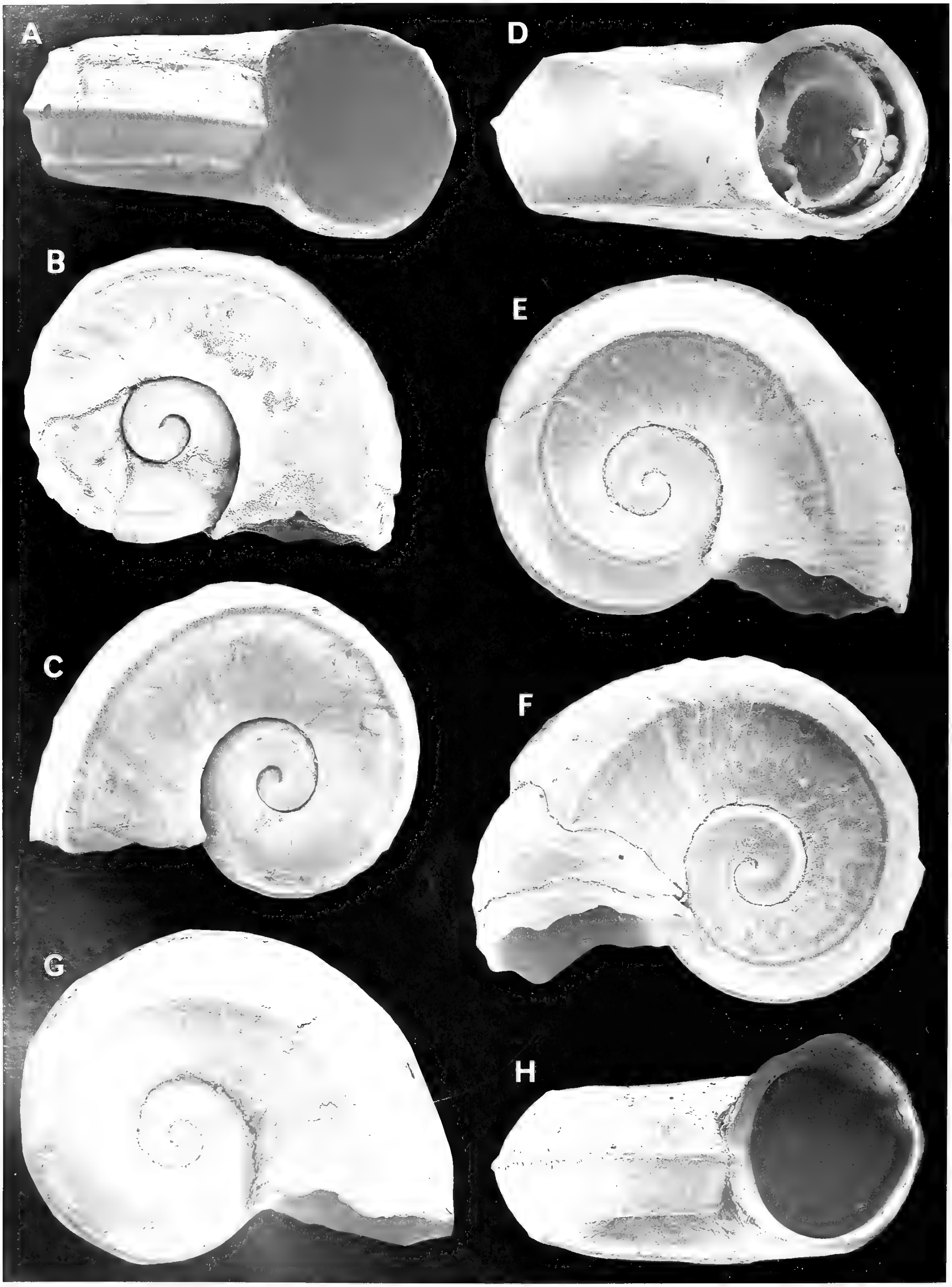
The head is medium-sized, has a pair of slender tentacles, twice as long as the snout. The eyes lack pigment and can be seen as more transparent, round structures in the base of the tentacles. The snout is rather short, slightly tapering, somewhat flattened with a subventral mouth. Males have a simple penis below the right cephalic tentacle.

The foot is strongly contracted in all specimens, and the details of its shape could not be discerned. Anteriorly, between the rather poorly demarcated propodium and mesopodium, an anterior pedal gland opens. The sides of the foot are smooth, and there are no epipodial ridges or furrows.

Internal anatomy (Figure 23): The foot (Figure 23B) is almost filled by the large posterior pedal gland and the smaller anterior pedal gland. These bulge a short distance into the cephalopedal haemocoel. The posterior pedal gland stains dark bluish violet, the anterior one, a much lighter grayish violet. The posterior pedal gland has no defined opening. The anterior one has a spacious cavity under the propodium lined with tall epithelium and opens via the slit between the pro- and mesopodium. The muscle layer of the foot is well developed, and the sole is rich in muscle fibers.

The tentacles are solid and muscular, all the way to the base where they have a subcutaneous eye with lens but no pigment layer, in a bulge. The snout is very muscular and can probably be extended considerably when the snail is grazing.

The alimentary system consists of the mouth, a large,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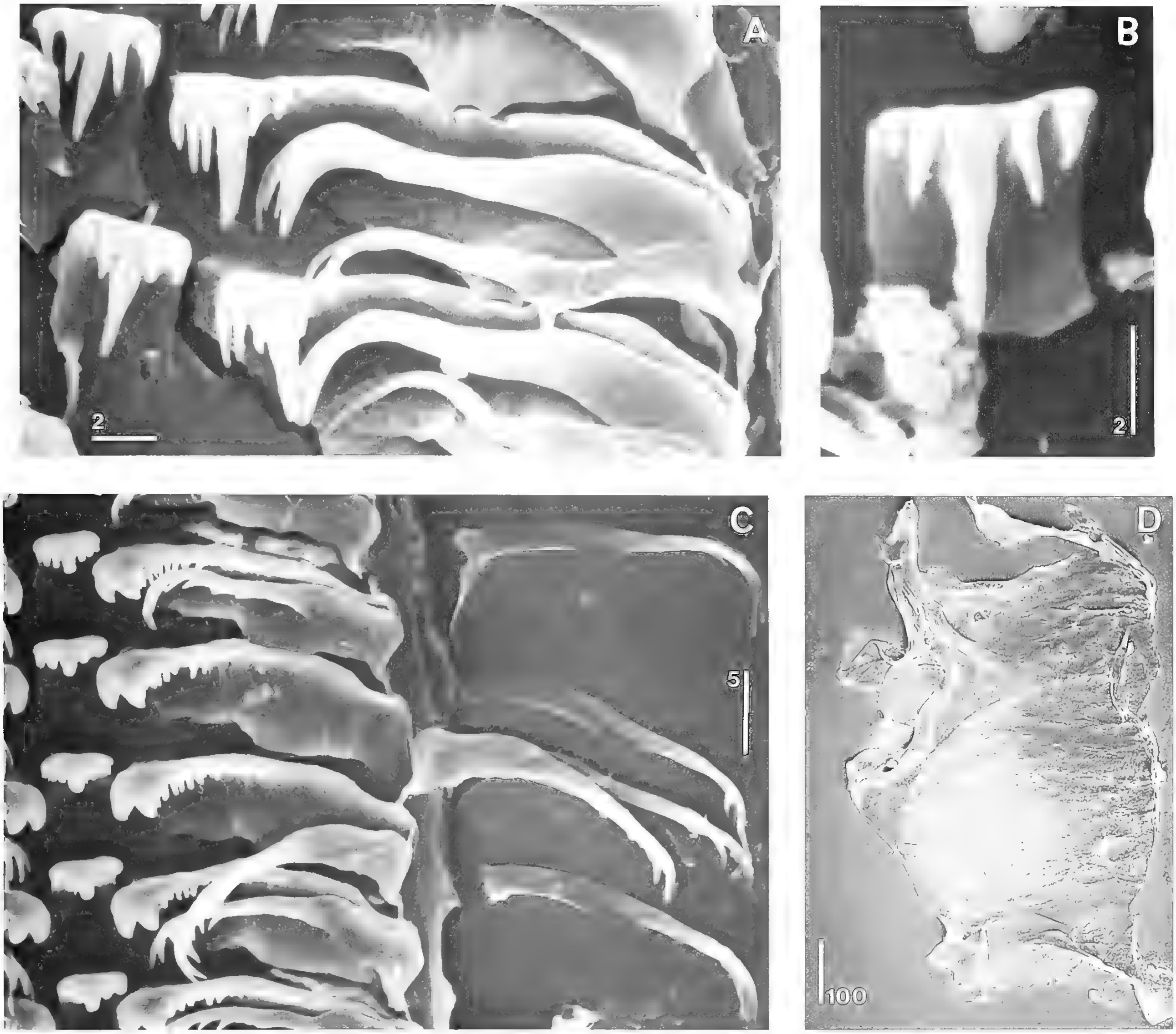

Explanation of Figure 22

Radulae and jaw. Figures A, B. *Z.* ***incognita*** Warén & Hain, sp. nov., paratype. Figure C. *Zerotula* ***stellapolaris*** Warén & Hain, sp. nov., PS IX/3 sta. 180. Figure D. *Frovina indecora,* PS IX/3 sta. 179, jaw, partly torn. Scale lines in μm.

weakly muscular buccal mass, a very short anterior esophagus, a large esophageal gland, a narrow posterior esophagus, a stomach, intestine, and rectum.

The jaw is thin and membranous.

The radular sac is straight, long, and slender, passes backward, through the nerve ring under the esophageal gland, extending as far back as this. The part of the radula in use is supported by a pair of large cartilages.

Two salivary glands open into the buccal cavity close to its mid-line via short, inconspicuous ducts which do not pass through the nerve ring. The salivary glands are large and situated above the cerebral ganglia. Each consists of

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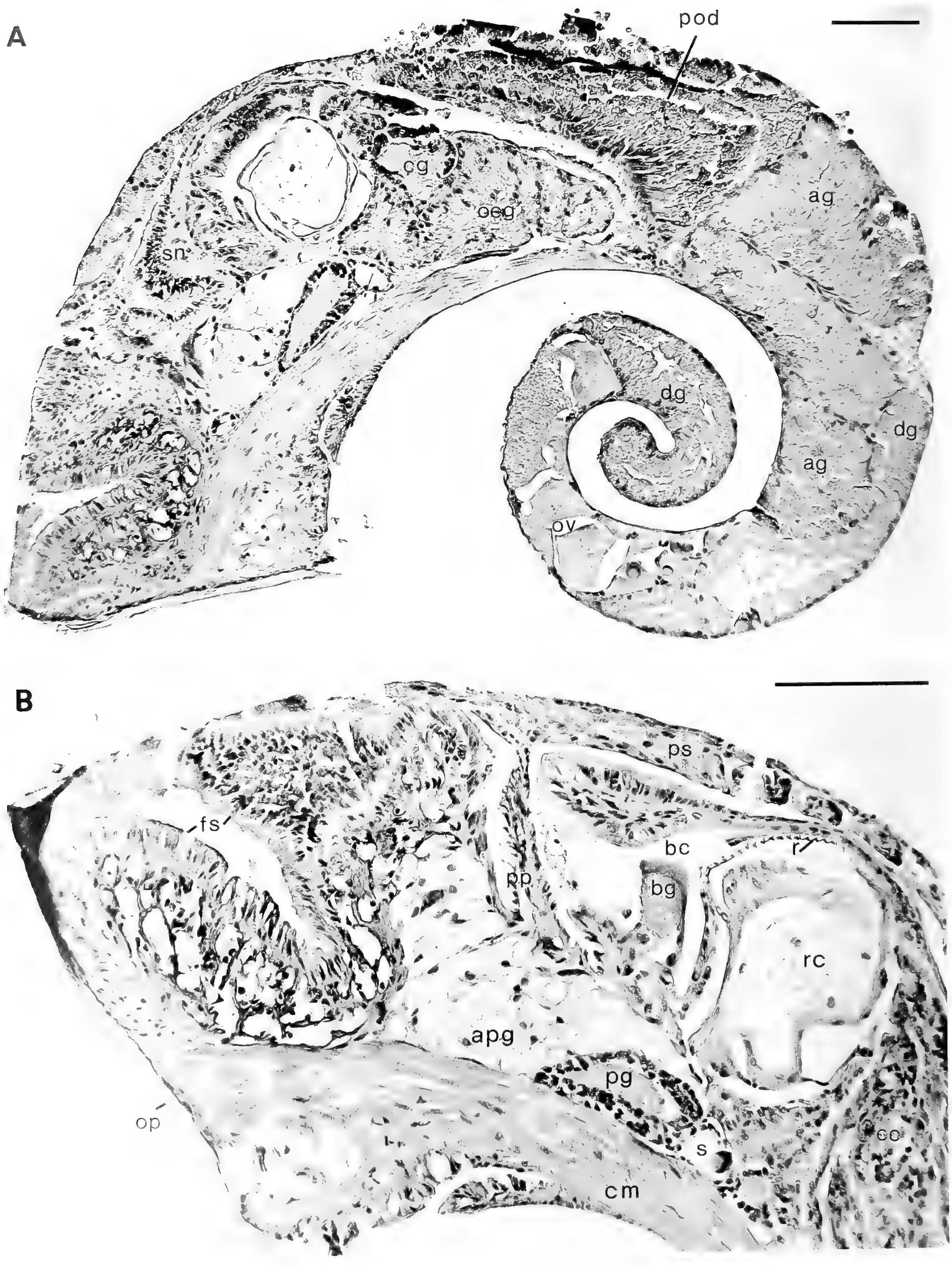
Explanation of Figure 21

Zerotula spp. Figures A–C. *Z.* ***stellapolaris*** Warén & Hain, sp. nov., PS VII/4 sta. 284, diameters 1.55, 1.58, and 1.62 mm. Figures D, E. *Z. triangulata* MNZ M.118148, diameters 1.05, 1.18, and 1.19 mm. Figures F–H. *Z.* sp., Bounty Trough, 45°48.8′S, 174°30.5′E, 1586 m, 26 October 1979, MNZ unregistered, diameter 1.77 mm.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a short, thin duct and a longer, coiled glandular tube. The shallow dorsal food channel is characterized by the rich occurrence of mucus-producing cells. These start in the posterior, dorsal part of the buccal cavity, get displaced toward the left side when passing the nerve ring and end up ventrally in the esophageal gland where they do not reach its posterior end. There seems to be present a pair of esophageal pouches. The interior of the esophageal gland is filled by glandular, transverse septa, which leave only a small ventral lumen for the (now ventral) dorsal food channel. The posterior esophagus exits from the gland as a much narrower, internally strongly ciliated tube of ⅕ of the diameter of the gland. It continues backward where it ends in a large cavity formed by the openings of the two digestive glands. This cavity opens into the left, ventral, posterior third of the stomach. The stomach measures 0.45 mm long, 0.10 mm high, and 0.15 mm broad. The intestine exits from the anterior part of the stomach, continues obliquely to the right close to the dorsal body wall and behind the kidney. Its diameter is slightly smaller than that of the stomach. Most specimens had remains of forams in the digestive canal.

The nervous system follows the normal pattern, but the dialyneury between the left pleural and the supraesophageal ganglia could not be verified. The distances between the ganglia are very small (contracted specimen), the left pleural and cerebral ganglia partly fused, the right ones abutting. The supra- and subesophageal ganglia are situated less than their diameter from the corresponding pleural ganglion. The length of the connectives to the pedal ganglia corresponds to the diameter of the cerebral ganglia. The supraesophageal ganglion lies free in the left side of the cephalopedal haemocoel behind and beside the left cerebral ganglion; the subesophageal one is well embedded in the body wall slightly farther back. The buccal ganglia are situated dorsally on the buccal mass close to the exit of the esophagus, and connected by a commissure. In front of the pedal ganglia is an accessory pedal ganglion, connected by a short connective, and innervating the anterior pedal gland and propodial area.

Posteriorly and laterally at the base of the penis is a small ganglion, which seems to receive nerves from the right pedal and the subesophageal ganglia (zygoneury).

The visceral ganglia were not identified.

The statocysts (with a single statolith) are situated above and behind the pedal ganglia and slightly displaced to the right. Their diameter corresponds to the width of the ganglion.

Reproductive system. The sexes are separate, or at least the four specimens sectioned were two males and two females with no trace of intermediate stages. The fixation does not, however, allow any detailed description of the reproductive systems.

Female. The ovary occupies most of the apical 1.5 whorls of the visceral mass. An inconspicuous ovarian duct close to the ventral body wall leads to a large albumen gland, which stains very lightly. It occupies the right third of ¼ whorl behind the pallial cavity. In front of this is a capsule gland (staining dark violet), mainly situated in the right wall of the pallial cavity along ¼ of a whorl, slightly protruding into and to the right of the anterior part of the albumen gland. The detailed morphology of these could not be worked out due to missing sections. The presence of a gonopericardial duct was confirmed. No receptaculum seminis was found, and no sperm was found in the pericardium of the sectioned females (although one decalcified specimen had a strongly iridescent pericardium as if it were filled by sperm).

Male. The testis lies in the right side of the posterior part of the visceral mass (but does not reach its apex), and is drained by a large, thin-walled duct, which also serves as a vesicula seminalis. About ¼ whorl behind the pallial cavity the duct leaves its ventral position and turns into a more laterally and dorsally situated prostate gland. This projects into the right side of the pallial skirt. It seems to be closed and there is no differentiation of cell types in the walls. The prostate is continued by a ciliated duct in the right corner of the cavity. The duct turns to the left, to a long, slender, and tapering penis with a closed sperm duct.

The radula (Figure 22C) is taenioglossate, long, and slender with about 150 transverse rows of teeth and a length corresponding to ⅔ of the diameter of the shell. The central tooth has a very low and thin, slightly undulating hood. Below this, one major central and three smaller, lateral, rounded cusps form a cutting edge. The "wings" are not drawn out to small denticles at the sides. The front of the tooth is deeply excavated. The lateral tooth usually has about 13 denticles, of which numbers 1 and 3 (counted from the inner edge) are at least three times the size of the others, which form a rather even "comb." The littorinid notch is missing. The first marginal tooth is simple, claw-shaped, with a sturdy shaft and seven apical cusps. The

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Explanation of Figure 23

Zerotula ***stellapolaris*** Warén & Hain, sp. nov. Figure A. Longitudinal section of right side of head-foot. Figure B. Longitudinal section of central part of head-foot. **ag**—albumen gland; **apg**—anterior pedal gland; **bc**—buccal cavity; **bg**—buccal ganglion; **cc**—cerebral commissure; **cg**—(right) cerebral ganglion; **cm**—columellar muscle; **dg**—digestive gland; **fs**—sole of foot; **oeg**—esophageal gland; **op**—operculum; **ov**—ovary; **pg**—pedal ganglion; **pp**—propodium; **pod**—pallial oviduct; **ps**—pallial skirt; **rc**—radular cartilage; **s**—statocyst; **sn**—snout. Scale lines = 100 μm.

inner three of these cusps are twice the length of numbers 4–7, which form a series of rapidly diminishing size. The outer marginal tooth is of about the same length, much thinner, with five long apical digits of ⅓ the length of the tooth. The shaft has an oblique, impressed, shallow furrow starting close to the base and reaching the outer edge of the shaft halfway to the point of the tooth. This probably corresponds to the "joint" in some other zerotulids.

The operculum (Figure 4B, C) has a few whorls, an almost central nucleus, and is transparent, pale brownish yellow, more distinctly so where it is attached to the foot. The surface is distinctly wrinkled by the growth lines.

Remarks: *Zerotula* ***stellapolaris*** resembles *Z. triangulata* (Figure 21D, E), from the Three Kings Islands, north of the New Zealand mainland, but that species has the lateral keels situated less close to the periphery, at 50–60% of the radial width of the whorl. That shell also has a more distinctly hyperstrophic coiling than *Z.* ***stellapolaris***.

Zerotula ***stellapolaris*** is very similar in shell and radular morphology to a single specimen of a *Zerotula* species (Figure 21F–H) from deep water in the Bounty Trough, east of New Zealand (45°48.8′S, 174°30.5′E, 1586 m, 26 October 1979, MNZ unregistered). That specimen is virtually identical, and we cannot exclude that the peaks of the Macquarie-Balleny Ridge act as stepping stones. We do not, however, have evidence from any other gastropod species that such a connection occurs, but this deep fauna off New Zealand is virtually unknown and there are no hints about such relations among gastropods with more characters in their morphology (B. Marshall, personal communication). Therefore we leave this specimen unidentified so as not to set a precedent in either direction.

Zerotula triangulata Powell, 1937

(Figures 20C, D, 21D, E)

Zerotula triangulata Powell, 1937:209, pl. 54, figs. 15, 16.

Type locality: Off Three Kings Islands, 260 m.

Type material: Holotype in BMNH, not examined.

Material examined: New Zealand, off Three Kings Islands, 34°00′S, 171°55′E, 805 m, 21 shells, MNZ M.118148.—Northwest of Great Island, Three Kings Islands, 34°06.5′S, 172°04.7′E, 310 m, 2 shells, MNZ M.118152.—Southeast of Great Island, Three Kings Islands, 34°14.8′S, 172°13.6′E, 173–178 m, 1 shell, MNZ M.118151.

Distribution: Off northern New Zealand, around Three Kings Islands, depth range 173–805 m (shells only).

Remarks: *Zerotula triangulata* has not been reported since the original description, but the material in MNZ agrees well with Powell's description and figure. As usual in this group, the shell is not very informative. The species is known from empty shells only.

Zerotula nummaria Powell, 1940

(Figures 20A, 24A–E)

Zerotula nummaria Powell, 1940:236, pl. 28, figs. 14, 15.

Type locality: New Zealand, Doubtless Bay, off Awanui, 22 m.

Type material: Holotype in Auckland Museum, not examined.

Material examined: New Zealand, Kapo Wairua, Spirits Bay, shell sand, 6 shells, MNZ M.59448.—Poor Knights Island, northern end of North Island, 32°26.5′S, 178°44′E, 40–45 m, 1 shell, Los Angeles County Museum of Natural History, locality 65-165.—Whangarei, McGregors Bay, 1 shell, MNZ M.20610.—Off Twin Rocks, Bay of Islands, 40–72 m, 1 shell, MNZ M.42208.—Spirits Bay, Kapo Wairua, 2 shells, MNZ M.59448.—Off Three Kings Islands, 34°11′S, 172°10′E, 90 m, 1 shell, MNZ M.33662.—125 m off shore from Motuwhekeke Island, Bay of Islands, 22–30 m, 1 shell, MNZ M.41898.

Distribution: New Zealand, northeastern North Island (north of 36°S) in 22–90 m (shells only).

Remarks: *Zerotula nummaria* resembles some undescribed species of the genus *Bichoristes* McLean, 1992 (Choristellidae) (McLean, 1992), but is smaller, the shell has a rougher surface, less sharp peripheral keels, and the protoconch is very indistinctly demarcated (sharply demarcated in *Bichoristes*). *Zerotula bicarinata* differs in having an indistinct central keel or at least a keel-like convexity between the two lateral keels.

Zerotula bicarinata (Suter, 1908)

(Figures 20B, 25A–E)

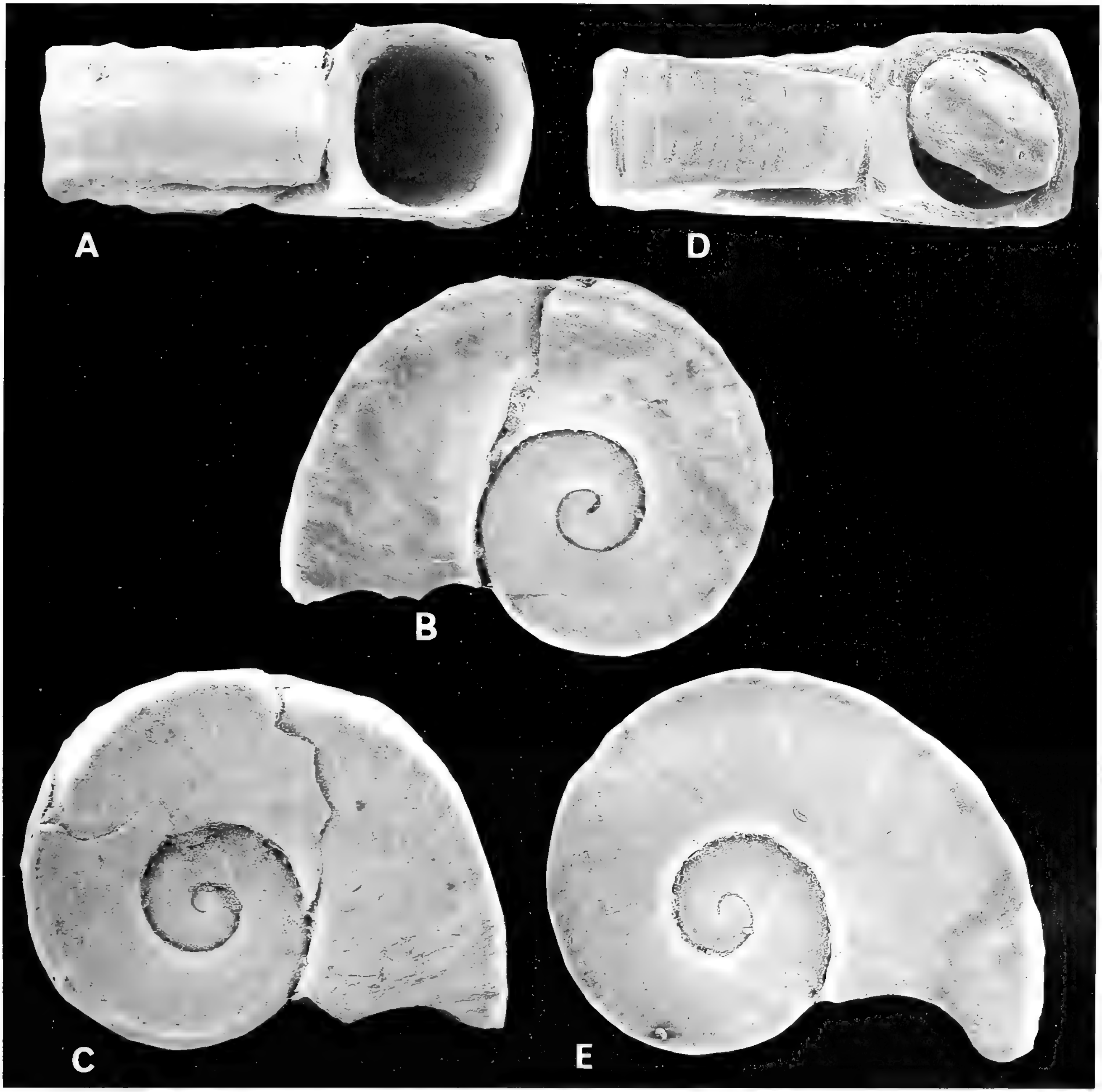
Omalogyra bicarinata Suter, 1908:33, figs. 37, 37a.
Zerotula bicarinata: Finlay, 1926:379.

Type locality: New Zealand, off Snares Island, 90 m.

Type material: Holotype in coll. Suter, Institute of Geological and Nuclear Sciences, Lower Hutt, not seen.

Material examined: New Zealand, western coast, North Island, off Ahipara, 35°02.6′S, 172°52.6′E, 48 m, 1 shell, MNZ M.118315.

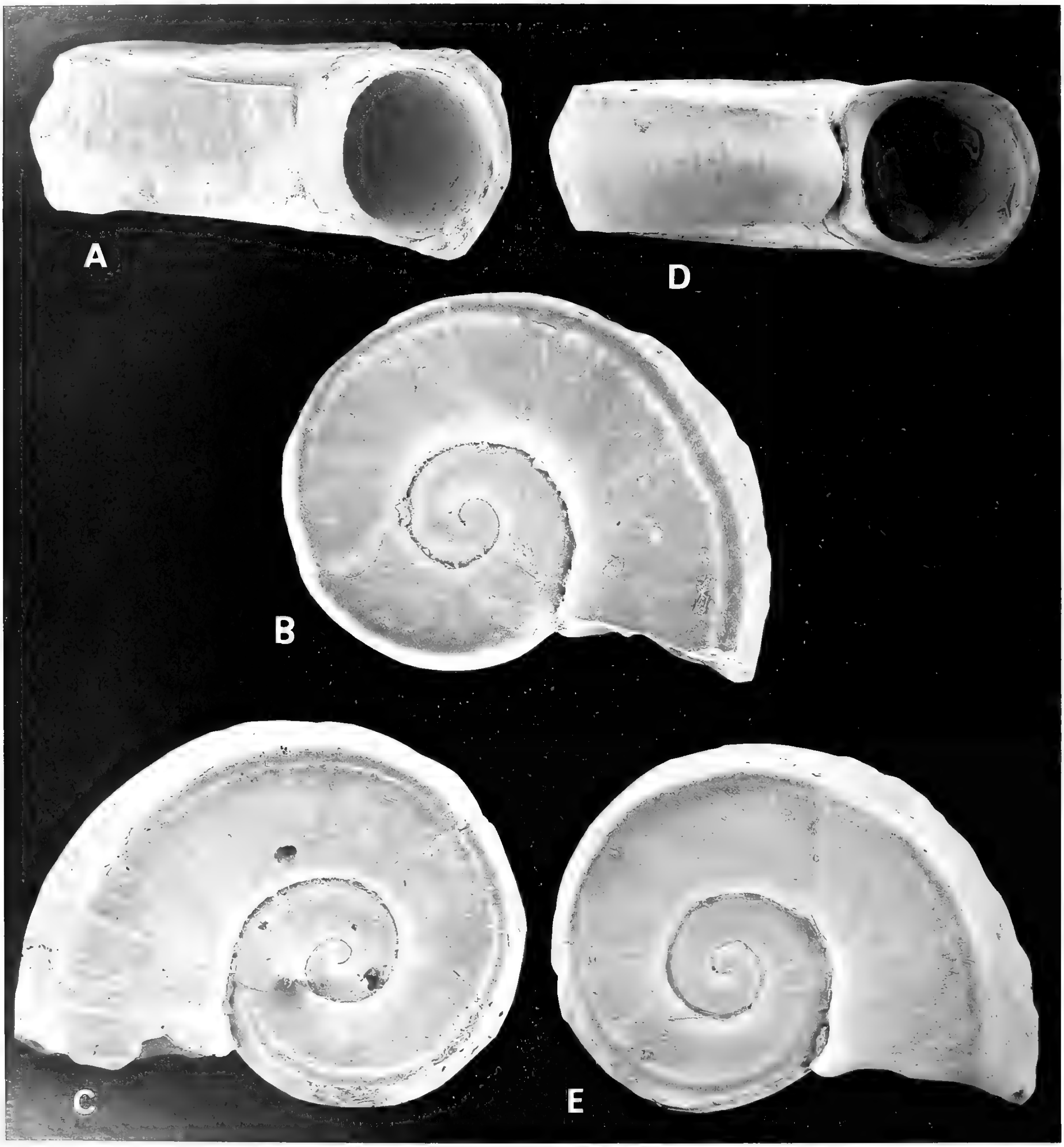
New Zealand eastern coast, East Cape, Ranfurly Bank, 37°33.1′S, 178°49.5′E, 94–89 m, 2 shells, MNZ M.74721.—East Cape, Ranfurly Bank, 37°33.2′S, 178°50.3′E, 76–71 m, 18 shells, MNZ M.72700.—East Cape, Ranfurly Bank, 37°33.4′S, 178°48.3′E, 106–103 m, 2 shells, MNZ M.74804.—Cook Strait, between Pt. Dorset and Pt. Howard, 125 m, 1 shell, MNZ M.44892.—Wellington, Island Bay, 2 shells, MNZ M.18518.—Off East Otago, 45°37.5′S, 171°03′E, 420 m, MNZ M.45582.—East Otago, northeast of Cape Saunders, 45°50′S, 170°56′E,



Explanation of Figure 24

Zerotula nummaria. Figures A–C. MNZ M.41848, diameters 1.28, 1.42, and 1.44 mm. Figures D, E. MNZ M.59448, diameters 1.24 and 1.42 mm.

105 m, 2 shells, MNZ M.45334.—Off Otago Heads, 45°50′S, 170°59′E, 220 m, 1 shell, MNZ M.66916.—Dunedin, off Taiere, 46°12′S, 170°41.5′E, 150 m, 6 shells, MNZ M.65876.—Dunedin, off Taiere, 46°09′S, 170°27′E, 60 m, 1 shell, MNZ M.67032.—Dunedin, off Taiere, 46°17′S, 170°32′E, 180 m, 1 shell, MNZ M.66401.—Dunedin, off Taiere, 46°15′S, 170°29′E, 91 m, 2 shells, MNZ M.66292.—Southeast of Nugget Point, 46°40′S, 170°00′E, 140 m, 6 shells, MNZ M.66015.—Foveaux Strait, 36 m, 1 shell, MNZ M.20606.—Foveaux Strait, 36 m, 1 shell, MNZ M.20603.—Stewart Island, South Cape, Big Ships Passage, 35–65 m, 1 shell, MNZ



Explanation of Figure 25

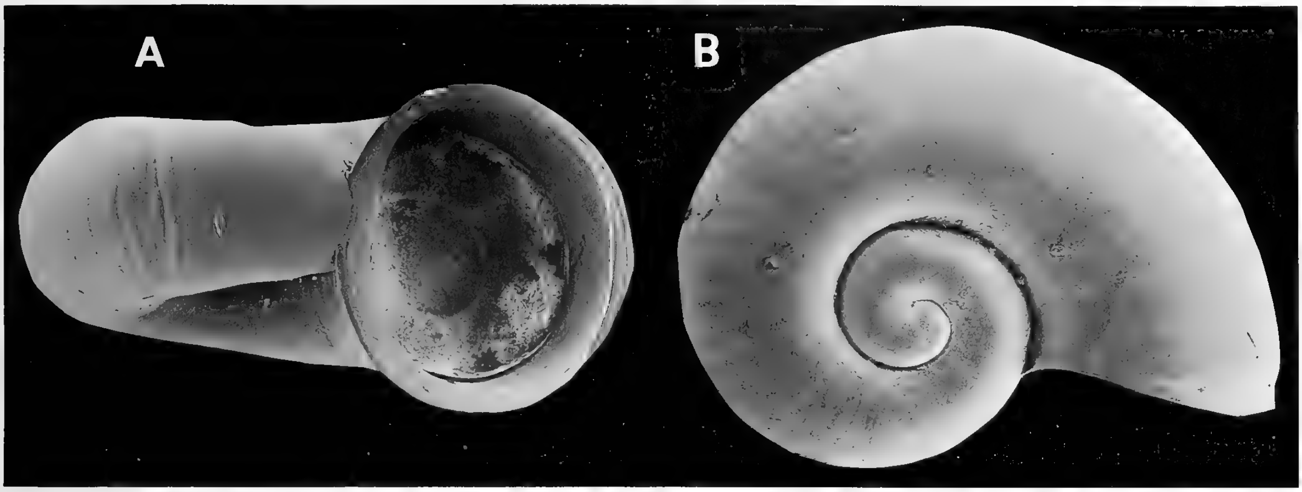
Zerotula bicarinata. Figures A–C. MNZ M.66015, diameters 1.26, 1.12, and 1.41 mm. Figures D, E. MNZ M.20609, diameters 1.6 and 1.5 mm.

M.20684.—Stewart Island, Big S. Cape Island, 90 m, 9 shells, MNZ M.20608.—Stewart Island, off Poutamu Island, 55 m, 3 shells, MNZ M.20609.

Pliocene fossil. Northern bank of Mangahao River, 1 mile south of Mangahao, northern Wairarapa, 31 shells, MNZ M.42687.

Distribution: New Zealand North and South Islands (35–47°S), 35–420 m (shells only).

Remarks: *Omalogyra bicarinata* was included in *Zerotula* by Finlay (1926:379). For differences from *Z. nummaria,* see that species.



Explanation of Figure 26

Figures A, B. *Zerotula* ***incognita*** Warén & Hain, sp. nov., holotype, diameter 1.78 mm.

Zerotula ***incognita*** Warén & Hain, sp. nov.

(Figures 15F, 22A, B, 26A, B)

Type locality: North Atlantic, off Portugal, ABYPLAINE CP 13, 40°00.0′N, 15°05.3′W, 5270 m, 8 June 1981, 3 specimens.

Type material: Holotype and one paratype in MNHN.

Distribution: Only known from the type locality, at the Iberia Abyssal Plain, west of Portugal.

Etymology: "*incognitus*" (Latin), unknown, not recognized.

Description: Based on the type series, three dried specimens of which one was sacrificed for preparation of radula and operculum.

Shell (Figure 26A, B) very small, transparent brownish yellow, smooth and planispiral, thin and fragile. The protoconch (Figure 15F) is smooth, not demarcated. The teleoconch consists of about 1.25 whorls and is sculptured by very indistinct, scattered spiral lines and just as weak and irregular growth lines. The peristome is perfectly circular, orthocline, and radial. The whorls are just barely indented by the preceding whorl.

Dimensions. Diameter of holotype 1.78 mm.

Radula (Figure 22A, B). Long and slender. The central tooth (Figure 22A) has two minor cusps on each side of the long and slender main cusp and lacks a hood. The lateral tooth is not clearly visible in our preparation, but as in all *Zerotula* species, there are two main cusps, in this case with two minor ones between them. The inner marginal is long and slender with at least two long apical denticles. The outer marginal tooth is extremely slender, bends at the middle of its length, and has at least two long apical cusps.

Operculum. Circular, thin and colorless, with subcentral nucleus and about three whorls.

Remarks: This species was recognized by the senior author some 13 years ago as being something strange, but since it could not be satisfactorily classified and was believed to be a larva, it was not treated by Bouchet & Warén (1993). It is the only zerotulid we have encountered outside the Antarctic-New Zealand-New Caledonian area.

We can not entirely disregard the possibility that this is a veliger larva, since the shell is characteristically yellowish, thin, and semitransparent. We do not, however, know any gastropod from the North Atlantic with a protoconch that fits this assumption. Moreover, if it is a larva, the presence of a radula indicates that it is ready to metamorphose, and the similarity in radular morphology is close enough to be quite certain it is related to the Zerotulidae.

Species excluded from *Zerotula*

Zerotula crenulata Powell, 1937

Zerotula crenulata Powell, 1937:209, pl. 54, figs. 6, 7.

Type locality: New Zealand, off Three Kings Islands, 260 m.

Type material: Holotype in BMNH (not examined).

Remarks: On the basis of the material examined (MNZ), this seems to be a species of *Adeuomphalus* Seguenza, 1876 (Archaeogastropoda, Family uncertain: Warén 1991:74), or (much less likely) a species of *Zerotula,* similar to *Z. nummaria.*

Zerotula ramosa Powell, 1940

Zerotula ramosa Powell, 1940:237, pl. 29, fig. 3.

Type locality: Off North Cape, New Zealand, 135 m.

Type material: In Auckland Museum, not examined.

Remarks: On the basis of the material examined (MNZ), this is certainly a species of *Palazzia* Warén, 1991 (Archaeogastropoda, systematic position uncertain, Warén 1991:75).

Zerotula ammonitoides Powell, 1940

Zerotula ammonitoides Powell 1940:236, pl. 29, figs. 1, 2.

Type locality: New Zealand, Mangonui, Doubtless Bay, 10–18 m.

Type material: Holotype in the Auckland Museum, not examined.

Remarks: From the material examined (MNZ), this is most likely an omalogyrid, possibly an orbitestellid (Heterobranchia).

Zerotula nautiliformis Powell, 1927

Zerotula nautiliformis Powell, 1927:118, pl. 21, fig. 5.

Type locality: New Zealand, SW of Otago, off Puysegur Point, 310 m.

Type material: Holotype in Canterbury Museum, Christchurch.

Remarks: From material examined, this certainly looks like a species of *Palazzia* Warén, 1991 (Archaeogastropoda, systematic position uncertain, Warén 1991:75).

Dickdellia Warén & Hain, gen. nov.

Type species. *Corneolitorina labioflecta* Dell, 1990.

Etymology: Named after Richard Kenneth Dell (MNZ), who described the only species of the genus.

Diagnosis: Large zerotulids with a poorly calcified, depressed, smooth and rounded shell. Radula long and slender with square, hooded, multicusped central tooth; lateral without "littorinid notch"; outer marginal tooth simplified. Operculum mesospiral without ridge. No metapodial tentacles. Snout small; cephalic tentacles connected by skin fold; mesopodium large and thin, anteriorly drawn out to tentaclelike corners; penis simple, situated well below the right cephalic tentacle; pallial oviduct without bursa and receptaculum.

Remarks: ***Dickdellia*** *labioflecta* was originally described in *Corneolitorina* Powell, 1951, a generic name considered a synonym of *Laevilitorina* by Reid (1989). The type species of *Corneolitorina* is *Littorina coriacea* Melvill & Standen, 1907, which has a much more normal littorinid-type radula. We agree with Reid (1989) that *L. coriacea* is similar to *Laevilitorina,* and the present resolution of that clade does not necessitate recognition of a genus level name for *L. coriacea.*

We had access to some live-taken specimens, and to give the systematic position a more stable foundation, we examined the anatomy in some detail. This work was difficult, however, since the specimens had been frozen (because of the temperature during the fieldwork) and were then "fixed" in alcohol. Therefore the whole visceral mass was in a state of disintegration. The results are presented under the species heading.

Systematic position: Several characters of ***D.*** *labioflecta* are unusual or strange, to some extent misleading, also in comparison with other zerotulids. Below we list those that have been important for our decisions.

—The shell is very simple and the reduction of the calcareous layer, apomorphic.

—The long and slender radula is consistent with a position among the Littorinoidea.

—A "hooded" radula is unusual. It is known from the Cingulopsidae (see Ponder & Yoo, 1980, fig. 14H) and the Zerotulidae (see above). Its occurrence in *Littoraria* (Littorinidae) was considered apomorphic by Reid (1989: 52).

—The foot has the anterior corners drawn out to tentaclelike protrusions. This is common among archaeogastropods, some higher Neotaenioglossa, and some Neogastropoda, but we know it from the lower neotaenioglossates only in the Litiopidae (Houbrick, 1987; A. Warén, unpublished in *Stiliferina*). In *Stiliferina,* these tentacles do not look like drawn-out corners, but more like set-off tentacles, and may not be homologous.

—The penis, situated well below the cephalic tentacles, indicates a systematic position within or in the vicinity of the Littorinoidea, unless this is a convergence. The innervation could not be examined since we had no male to section.

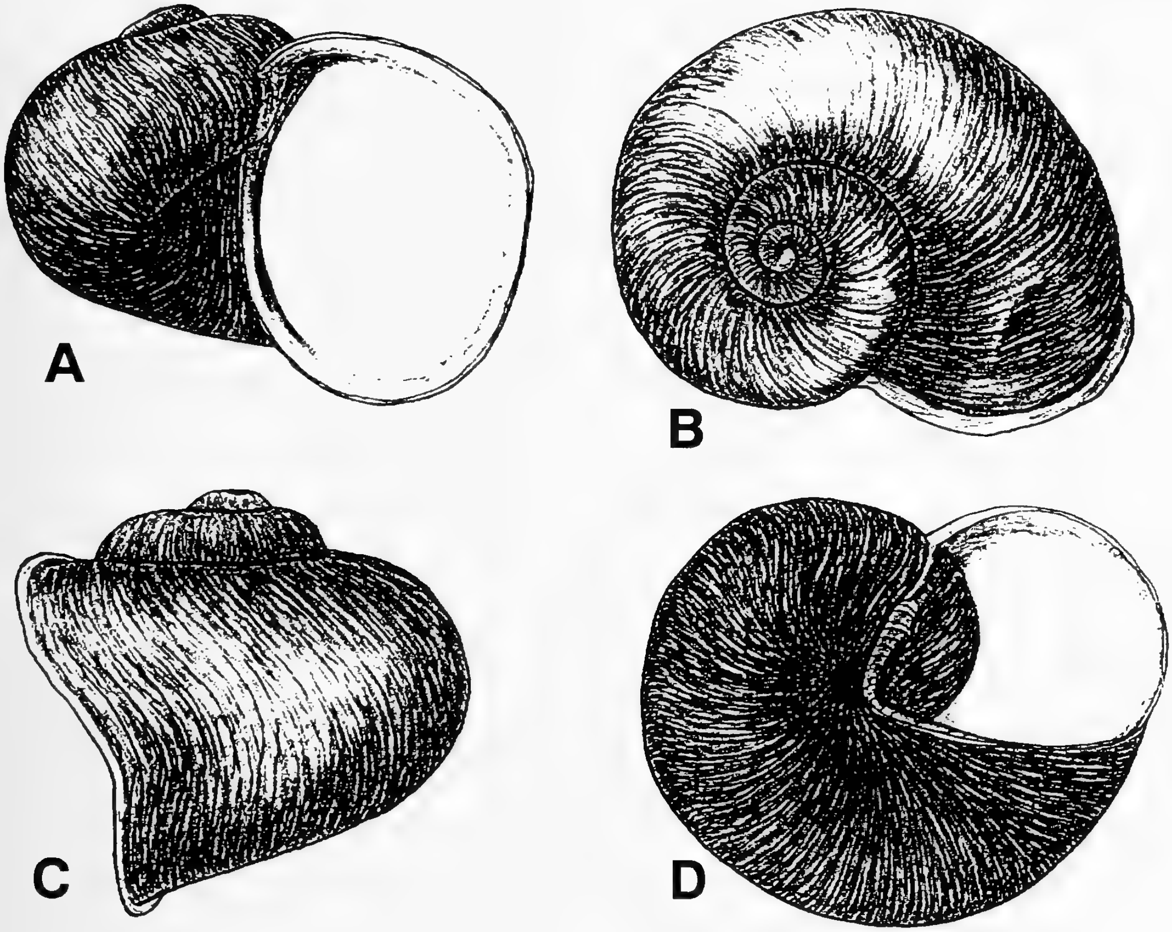
—The alimentary system with a snout, long taenioglossate radula, a pair of radular cartilages, posterior salivary glands, esophageal gland, agrees with the lower taenioglossates; absence of crystalline style with the Littorinoidea.

—A skin-fold uniting the tentacles is not common among Neotaenioglossa with a snout. It occurs among the Adeorbidae (Rissooidea), Naticidae, and Fossariidae (Cerithioidea). A similar but incomplete fold is present in *Lacuna vincta* (Figure 33A, B) and *L. pallidula.* It is, however, a simple structure and homology is uncertain.

—The nervous system follows the general littorinoid-rissooid pattern, with moderate distances between the ganglia. Presence of two accessory pedal ganglia at each main ganglion resembles Littorinidae, but is also known from the Provannidae (Warén & Ponder, 1991) and Rissoidae (Johansson, 1939) and may be plesiomorphic.

—Absence of receptaculum seminis is rare in the littorinoid-cingulopsoid-rissooid radiation, but known from *Pellilitorina, Lacuna,* and *Cremnoconchus* (sperm stored in oviduct, Reid, 1989:36) and most of the zerotulids.

—The general structure of the osphradium is shared with most Littorinoidea-Rissooidea, but the apical flexure is known only from the genus *Lacuna* (Reid, 1989).



Explanation of Figure 27A–D

***Dickdellia** labioflecta*, PS III/3, sta. 345, diameter 7.7 mm.

- —The length of the pleural sub- and supraesophageal connective is about eight times the length of the latter ganglia, which is similar to the littorinids (Reid, 1989). This length, however, seems better correlated with the size of the gastropod (both long in *Pomatias elegans* and Littorinidae; short in Zerotulidae (this study) *Skeneopsis,* Rissooidea and Cingulopsidae; one of them long, one short in Aciculidae and Eatoniellidae (Reid, 1989).
- —The habitat is considerably deeper than any littorinid (approx. 200–900 m versus 0–50 m), but the presence of eyes indicates that ***Dickdellia*** does not originate from a group with exclusive deep-water distribution, especially since it has lecithotrophic development.

Of these characters, we pay special attention to the position and shape of the penis, long and slender radula, laterals without littorinid notch, an interspace between the two marginal teeth, and place ***Dickdellia*** in the Zerotulidae (Littorinoidea).

***Dickdellia** labioflecta* (Dell, 1990)

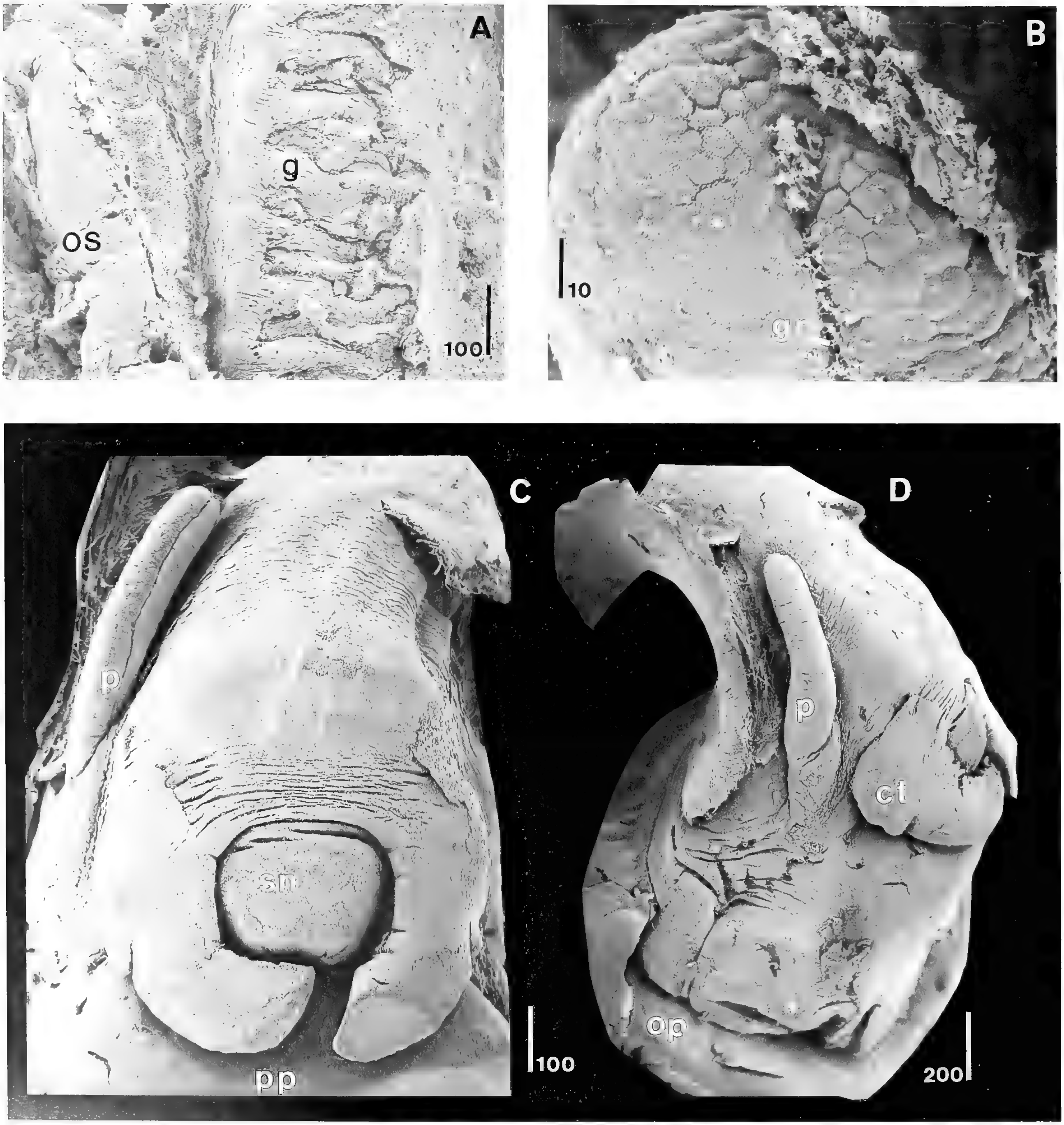
(Figures 27–29, 30A, B, 31, 32, 34E)

Corneolitorina labioflecta Dell, 1990:110, figs. 187, 188.
Mesogastropoda sp. 2: Hain 1990:54, pl. V, figs 1a–d, pl. 22, fig. 6.

Type locality: Ross Sea, off Elephant Island, *Eltanin* sta. 410, 61°18′S, 56°09′W, 220–240 m.

Type material: Holotype USNM 860099, paratypes USNM 860100 and MNZ MZ.56598, not seen.

Material examined: PS III/3, sta. 345, 021°W, 617 m, 2 specimens.—PS VII/4, sta. 282, 012°W, 609–575 m, 3 specimens.—PS VII/4, sta. 250, 030°W, 799–810 m, 2 specimens.—PS VII/4, sta. 272, 022°W, 409–406 m, 1 specimen. 3.8 mm diameter.—PS VII/4, sta. 293, 012°W, 771–793 m, 1 specimen.—PS VIII/5, sta. 491, 022°W, 390–370 m, 1 specimen. 6.8 mm diameter (all in SMNH).



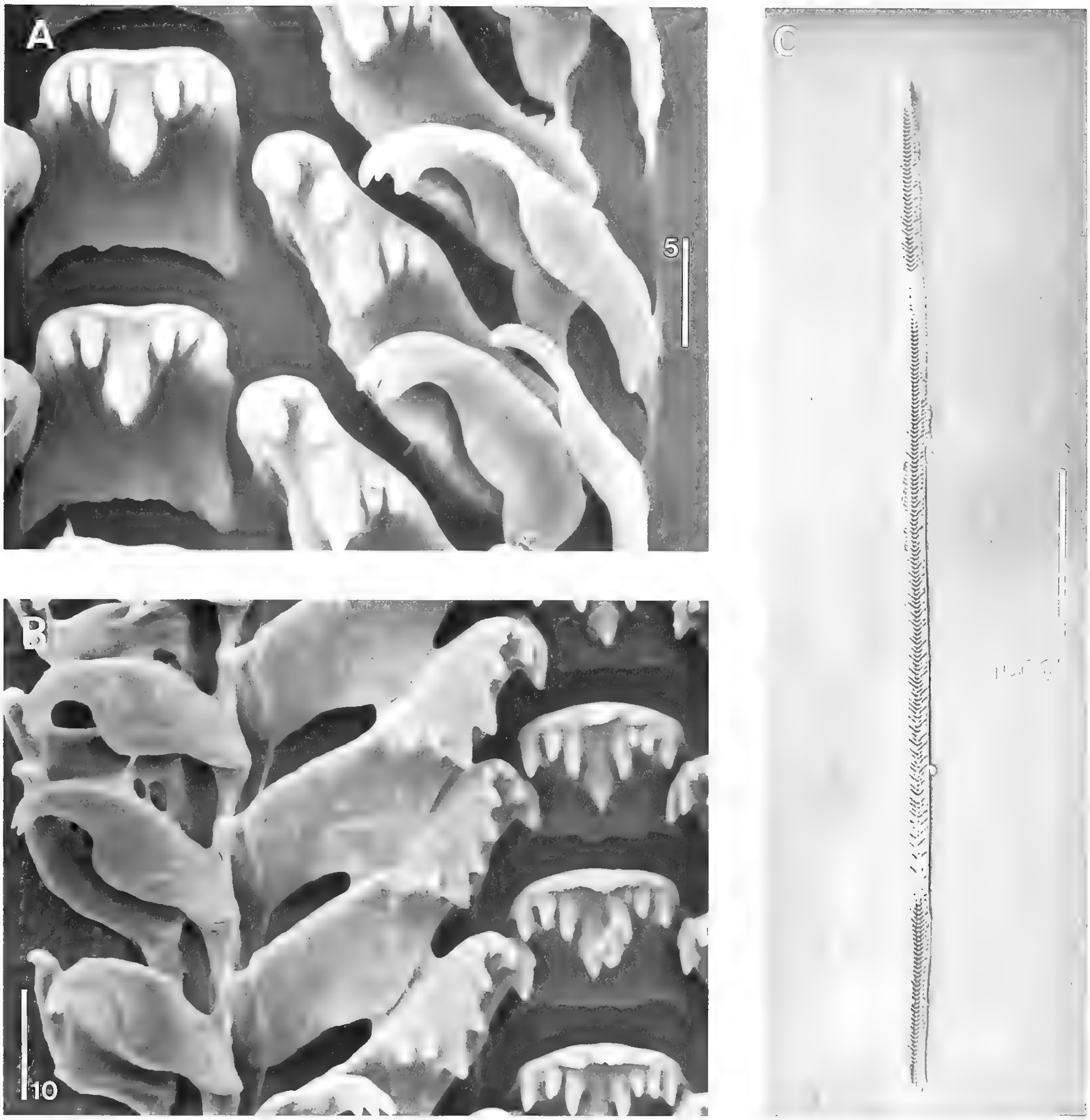
Explanation of Figure 28

Dickdellia labioflecta, PS VII/4 sta. 293, critical point dried. Figure A. Part of pallial skirt with gill and osphradium. Figure B. Tip of penis with seemingly open sperm duct. Figure C. Front view of head-foot. Figure D. Right side of head-foot. **ct**—cephalic tentacle; **g**—gill leaflet; **op**—operculum; **os**—osphradium; **p**—penis, seminal groove visible in Figure C; **pp**—propodium; **sn**—snout. Scale lines in μm.

Distribution: South Shetland Islands, Ross Sea, and the Weddell Sea in 220–891 m.

Redescription: Based on the specimens above of which four females were sectioned, one male critical point dried, and one female was dissected. The shell (Figure 27), which measures up to 8.3 mm in diameter, was adequately described by Dell (1990), and we give only some supplementary details.

Shell (Figures 27, 34E). The periostracum is thick (0.1



Explanation of Figure 29

Dickdellia *labioflecta*, PS VII/4 sta. 293, radula. Figure A. From a specimen of 2.5 mm shell diameter. Figures B, C. From a specimen of 6 mm shell height. Scale lines in μm.

mm), brown and tough, slightly brittle. The internal calcareous layer is very thin, less than 5 μm thick at the periphery of the body whorl, thicker toward the columella, and in the two, most apical whorls where it is about as thick as the periostracum.

External morphology of soft parts: The head-foot (Figure 28C, D) and pallial complex (Figure 28A) comprise $^{3}/_{10}$ of a whorl in contracted specimens, the visceral mass about two whorls. The whole animal is creamy white, also the visceral mass (in alcohol and alive). The anterior $^{1}/_{10}$ whorl of the visceral mass is still paler from the superficial part of the kidney. At the left side, the pericardium with the ventricle and auricle, lies directly behind the gill and osphradium. The gonad is not easily distinguished externally even in sexually mature specimens. The esophagus and stomach could not be discerned externally by transparency.

The pallial cavity is quite shallow, and the pallial skirt normally covers the whole head in preserved specimens. The pallial margin is thin and simple, without tentacles and papillae, except at the right and left $^{1}/_{5}$, where it is thicker and with some structure, but the details could not be worked out. The osphradium (Figure 28A) consists of a ridge containing the osphradial ganglion. It parallels the gill from the most posterior part, forward to the anterior

¼ of the gill, where it abruptly curves 180° to the left and returns ⅓ of its length. Along each side is a narrow, ciliated ridge. The gill (Figure 28A) consists of a series of about 30 narrow, triangular leaflets twice as high as broad and drawn out to a ventral tip. The width of the gill corresponds to ⅙ of the pallial cavity. The leaflets in its central part are about twice as wide and high as the anterior ones. The columellar muscle projects at the right side of the body, 60–80° from the operculum. Its left part is much less conspicuous and narrower. The hypobranchial gland is rather inconspicuous and partly covered by the tips of the gill leaflets. The pallial oviduct is restricted to the posterior right half of the cavity and its left side contains the inconspicuous rectum which opens shortly behind the oviduct.

The head is medium-sized and has a pair of short (contracted; slender and tapering when crawling), conical, flattened tentacles with large black eyes in basal-lateral bulges. The inner sides of the tentacles meet over the small snout by a simple fold of the outer part of the body wall. The male has a simple, finger-shaped penis situated well below the right cephalic tentacle, and with a dorsal furrow (Figure 28B, D). Whether this furrow forms an open or closed sperm duct could not be seen.

The foot is flat, large, and broad. The corners are drawn out to small tentaclelike extensions. Posteriorly, it is bluntly rounded. There is no distinct opening for the posterior pedal gland; anteriorly, between the distinctly set-off propodium and the mesopodium opens an anterior pedal gland. The sides of the foot are smooth and there are no epipodial ridges or furrows.

Internal anatomy (Figures 31, 32): The foot is almost filled by the large posterior pedal gland mixed with a dense three-dimensional network of muscle fibers. The slightly smaller anterior pedal gland bulges into the cephalopedal haemocoel, shortly behind the nerve ring and into the snout. The posterior pedal gland stains bluish violet, the anterior one a much lighter grayish violet, with conspicuous nuclei. The posterior pedal gland does not have a defined opening. The anterior one has a flat cavity under the propodium, lined with tall epithelium and opens via a broad and flat duct, which penetrates most of the gland.

The anterior part of the tentacles is solid and muscular, but behind the eye there are large lacunae. The large subcutaneous eyes (with lens and pigment layer) are situated in a large bulge in the latero-basal part. The snout is very muscular and can probably be extended considerably when the snail is grazing.

The alimentary system consists of the mouth, a large, thin-walled buccal mass, a very short anterior esophagus, a large esophageal gland, a narrow posterior esophagus, stomach, intestine, and rectum.

There are no jaws. Not even a noticeable cuticular lining was found in or behind the mouth.

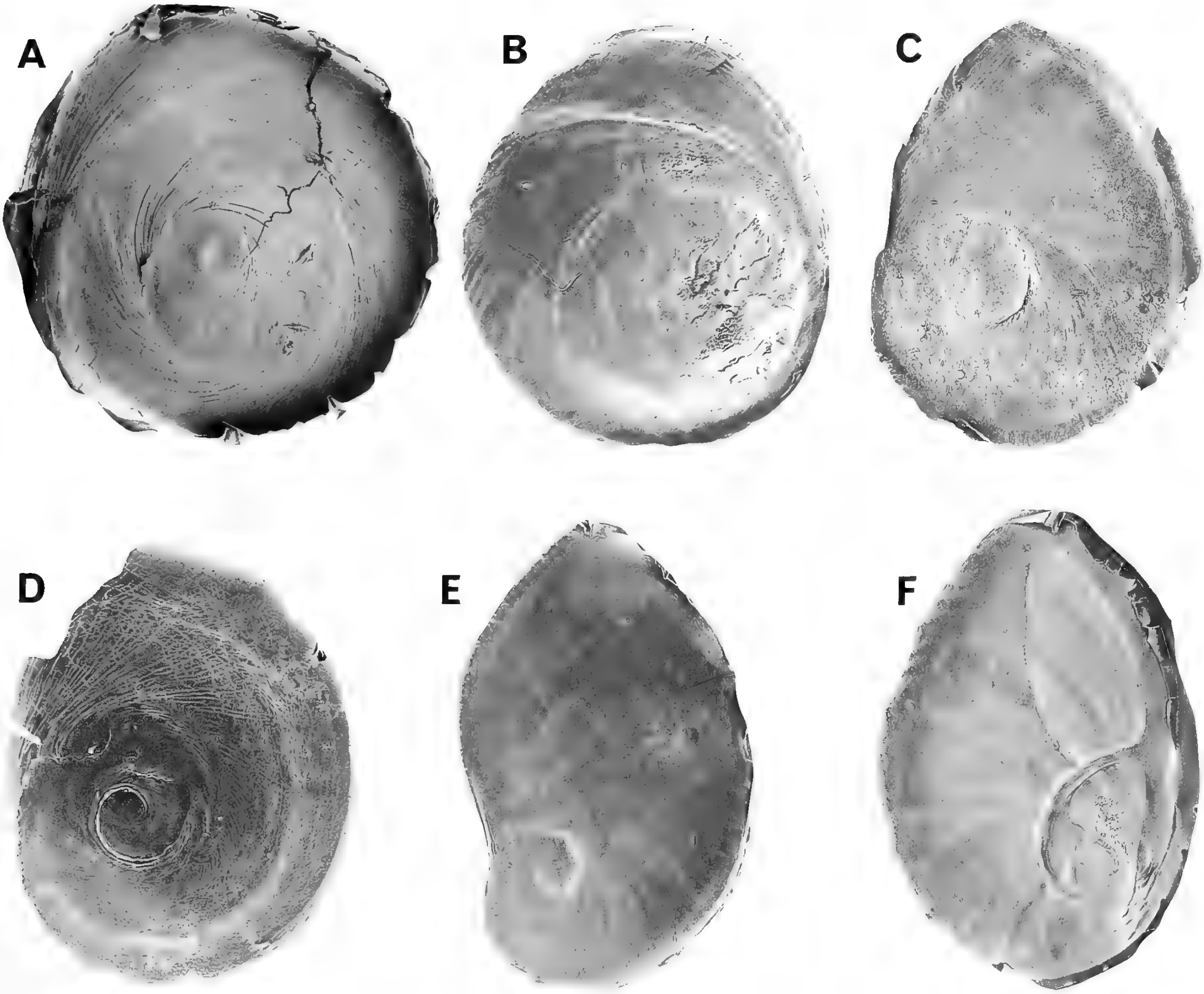
The radular sac is straight, rather long, curves to the right after the exit from the buccal mass and ends between the roof of the cephalopedal haemocoel and the buccal mass. The part of the radula in use is supported by a pair of large, anteriorly diverging cartilages.

Two salivary glands open into the buccal cavity, close to its mid-line, via short, inconspicuous ducts which do not pass through the nerve ring. The salivary glands are large and situated before and above the cerebral ganglia. Each consists of a short, thin duct and a voluminous gland of several lobes (staining violet with EHE). The dorsal food channel is characterized by the occurrence of numerous mucus-producing cells. These cells commence in the postero-dorsal part of the buccal cavity, are displaced toward the left when passing the nerve ring, and end up ventrally in the esophageal gland, where they continue until the start of the posterior esophagus. No trace of esophageal pouches was found. The esophageal gland is quite voluminous and full of transverse septa which leave only a small space for the longitudinal food channel. At the end of the cephalopedal haemocoel, the posterior esophagus exits from the gland, passes the transverse septum and enters the visceral mass. It continues backward, ventrally and close to the body wall at the left side of the body. Finally, it enters the stomach, 0.3 mm from its most posterior part. The diameter of the stomach is about 0.20 mm. The stomach continues forward 0.35 mm, turns abruptly dorsally, a loop 0.5 mm long; then another abrupt turn to the left, for a distance of 0.5 mm, after which it starts parallelling the oviduct in a rectal sinus, which thus by definition must be a rectum. It was not possible to see any distinct transition from a stomach to an intestine between the esophagus and rectum. The rectum is unusually small (Figure 31B, **re**).

The nervous system follows the normal pattern of littorinids, with dialyneury between the left pleural and the supraesophageal ganglia. The distances between the ganglia are fairly short (contracted specimen), the pleural and corresponding cerebral ganglia abutting. The supra- and subesophageal ganglia are situated about eight times their diameter from the corresponding pleural ganglion. The length of the connectives to the pedal ganglia are twice the diameter of these ganglia. The supraesophageal ganglion lies free at the left wall of the cephalopedal haemocoel, at half its height; the subesophageal one in a pit in the body wall. The buccal ganglia are situated dorsally on the buccal mass, close to the exit of the esophagus, and connected by a commissure. Ventrally and anteriorly to the pedal ganglia is an anterior accessory pedal ganglion, connected by a connective of about its own length and innervating the anterior pedal gland and propodial area. Posteriorly and ventrally there is a posterior accessory pedal ganglion, connected by a connective of half its own length and innervating the meso- and metapodium.

The visceral ganglia were not identified.

The statocysts are situated above and behind the pedal ganglia and slightly displaced laterally. Their diameter corresponds to half the length of the ganglion. They have a single statolith.



Explanation of Figure 30

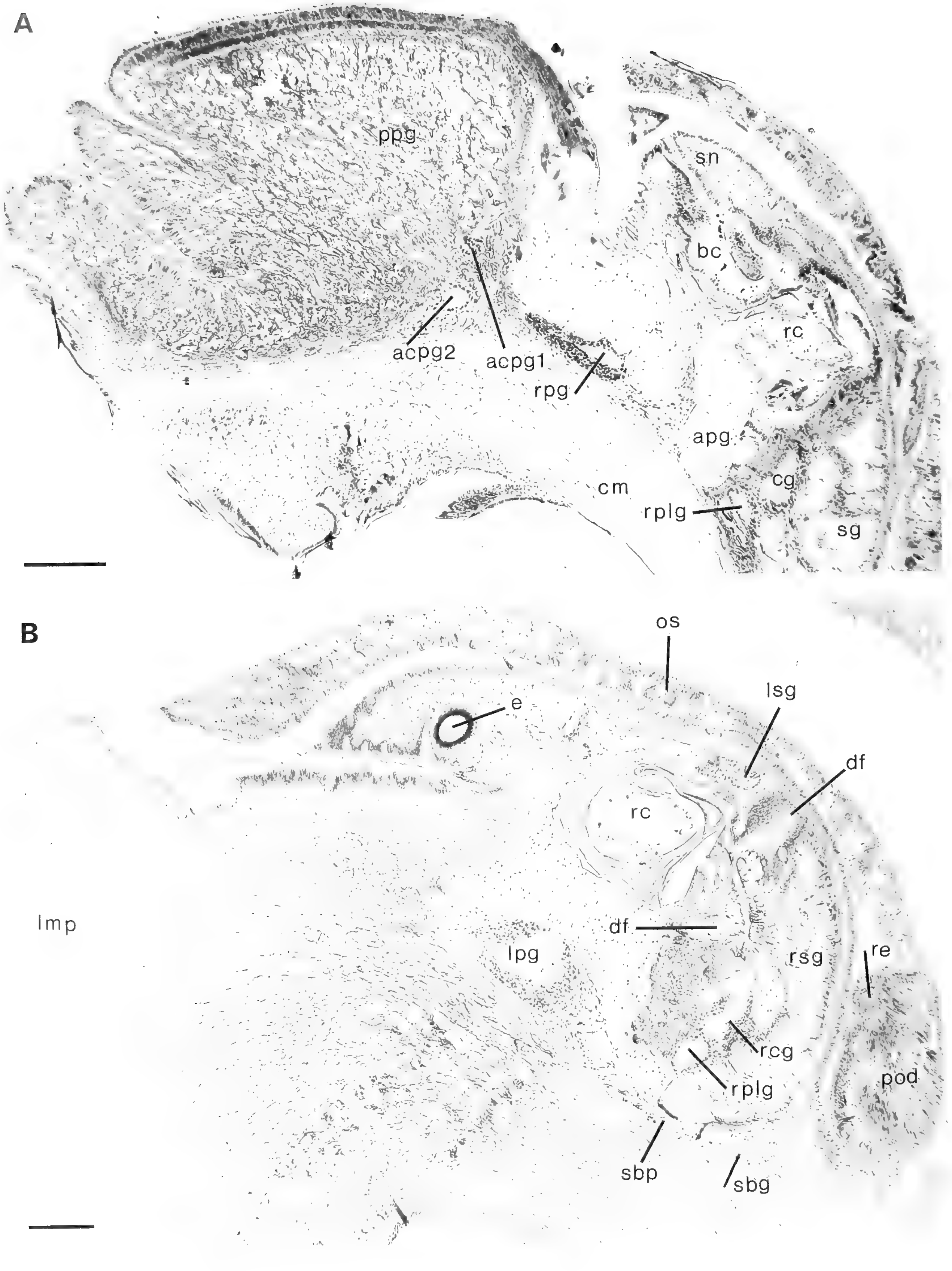
Opercula. Figures A, B. ***Dickdellia** labioflecta*, PS VII/4 sta. 293, diameters 3.6 and 3.1 mm. Figure C. *Laevilitorina notorcadensis,* paratype, diameter 2.0 mm. Figure D. *Laevilitorina antarctica,* South Georgia, Cumberland Bay, 1–2 m, on algae, SMNH 2794, diameter 3.9 mm. Figures E, F. *Lacuna vincta,* Swedish west coast, diameter 4.2 and 5.2 mm.

Circulatory system. The pericardium and kidney are unexpectedly small.

Reproductive system. The sexes are separate. One of the sectioned specimens, 3.8 mm in shell diameter, turned out to be a female without pallial oviduct, but with an early ovary and no trace of male systems, while the male used for critical point drying had a shell diameter of 3.0 mm.

The fixation does not, however, allow any detailed description of the female system, and no male was sectioned. The ovary lies along the right side of the visceral mass. A short ovarian duct leads to a large, strongly folded albumen gland, which stains very lightly. Along the anterior right side of this and continuing anteriorly is a capsule gland (Figure 32B; staining dark violet with EHE), but the detailed morphology of these could not be worked out due to missing and ruptured sections. They are, however, closed except for a short opening close to the anterior end of the capsule gland. No trace of a bursa copulatrix or a receptaculum seminis was found. A well-developed gonopericardial duct is present, opening into the albumen gland close to the ovarian duct. None of the two females that were sectioned had sperm in the pericardium, or a receptaculum seminis, but sperm was abundant in the posterior folds of the albumen gland. External features of the male were described above.

The radula (Figure 29) is long and slender, almost 50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times as long as broad, with about 200 transverse rows (Figure 29C). The central tooth is rather low, distinctly hooded, and has a large, conical main cusp and three similar cusps of half the size on each side, situated above the main cusp. The lateral tooth is long, rather slender, and oblique and lacks a "littorinid notch." The central half is strongly denticulated with about 12 strong subequal cusps. The first marginal tooth is attached slightly in front of the lateral and is quite sturdy with its proximal part twice as broad as its distal third. It has three small apical denticles. The second marginal tooth is slightly smaller than the first marginal, and separated from it by a zone of smooth radular membrane, of a width corresponding to $\frac{1}{20}$ of that of the radula. Its apical third is proportionally narrower than in the first lateral and the apical denticles are smaller. Young specimens have less sturdy and proportionally taller teeth with fewer denticles.

The operculum (Figure 30A, B) is rather sturdy and distinctly wrinkled by incremental lines. It consists of about three whorls with a subcentral nucleus, but lacks a ridge.

Remarks: The smooth, poorly calcified shell with a shallow labial sinus makes this species easily recognizable among Antarctic gastropods.

The remarkably small and slender esophagus, stomach, and intestine, containing very little remains of food, suggest an unusual type of food, not detritivory or forams. This is also suggested by a strange appearance of the digestive gland which has much smaller tubules than usual.

Family LITTORINIDAE

Subfamily LAEVILITORININAE

Reid (1989) gave an exhaustive survey of the classification of the Littorinidae and analyzed the relations within the family. We have extensively used this gold mine of information, and supplemented it with our own observations in some cases.

Laevilitorina Pfeffer, 1886

Laevilitorina Pfeffer, in von Martens & Pfeffer, 1886, type species, *Littorina caliginosa* Gould, 1849, by subsequent designation (Suter, 1913).

(*Pellilacunella*) Powell, 1951

Pellilacunella Powell, 1951, type species *Pellilitorina bennetti* Preston, 1916, by original designation.

Remarks: Reid (1989) recognized a new subfamily for *Laevilitorina* with several subgenera. Among these are *Pellilacunella,* characterized by four opercular tentacles on each side, a simple penis with short filament, numerous small cusps on the rachidian tooth, and a single small cusp on the outer marginal tooth. The shell is simple, smooth, and rounded; the operculum belongs to Reid's (1989) paucispiral type with no internal ridge.

Reid (1989) presented information on most type species of the littorinid generic names. We here add a few details on little known generic names we encountered, to complete Reid's treatment.

Lacunella reflexa Dall, 1884, and its "variety" *minor* Dall, 1919, were both described from shallow water in Alaska. The former species is the type species of *Haloconcha* Dall, 1886, usually regarded as a genus, but with some hesitation synonymized with *Lacuna* (at subgenus level) by Reid (1989). Our information comes from reconstituted type specimens in USNM. Shell, Figure 34A, B; radula, Figure 35A. The soft parts were not in good condition, but the pair of opercular tentacles are replaced by a thin, wide membrane. The operculum has an unusually low and indistinct opercular ridge, like other Lacuninae. Also, this generic name can thus safely be placed in the Lacuninae, although more information is needed to evaluate its detailed placement there.

We also examined type material of *Aquilonaria turneri* Dall, 1886, from Alaska, type species of *Aquilonaria* Dall, 1886. Two pairs of opercular tentacles, a ridge on the operculum, well-developed periostracum, and an indistinctly hooded rachidian tooth confirm a position in the Lacuninae and relations to *Lacuna* (*Lacuna*) *crassior* (Montagu, 1803).

Both *Lacuna pallidula* (Da Costa, 1778) and *L.* (*Epheria*) *vincta* (Montagu, 1803) (both north European) have a distinct skin fold across the basal part of the cephalic tentacles, continuing a short distance toward the center of the snout. Possibly this is an artifact, but it is persistently there and probably has some internal cause in the arrangement of the muscles.

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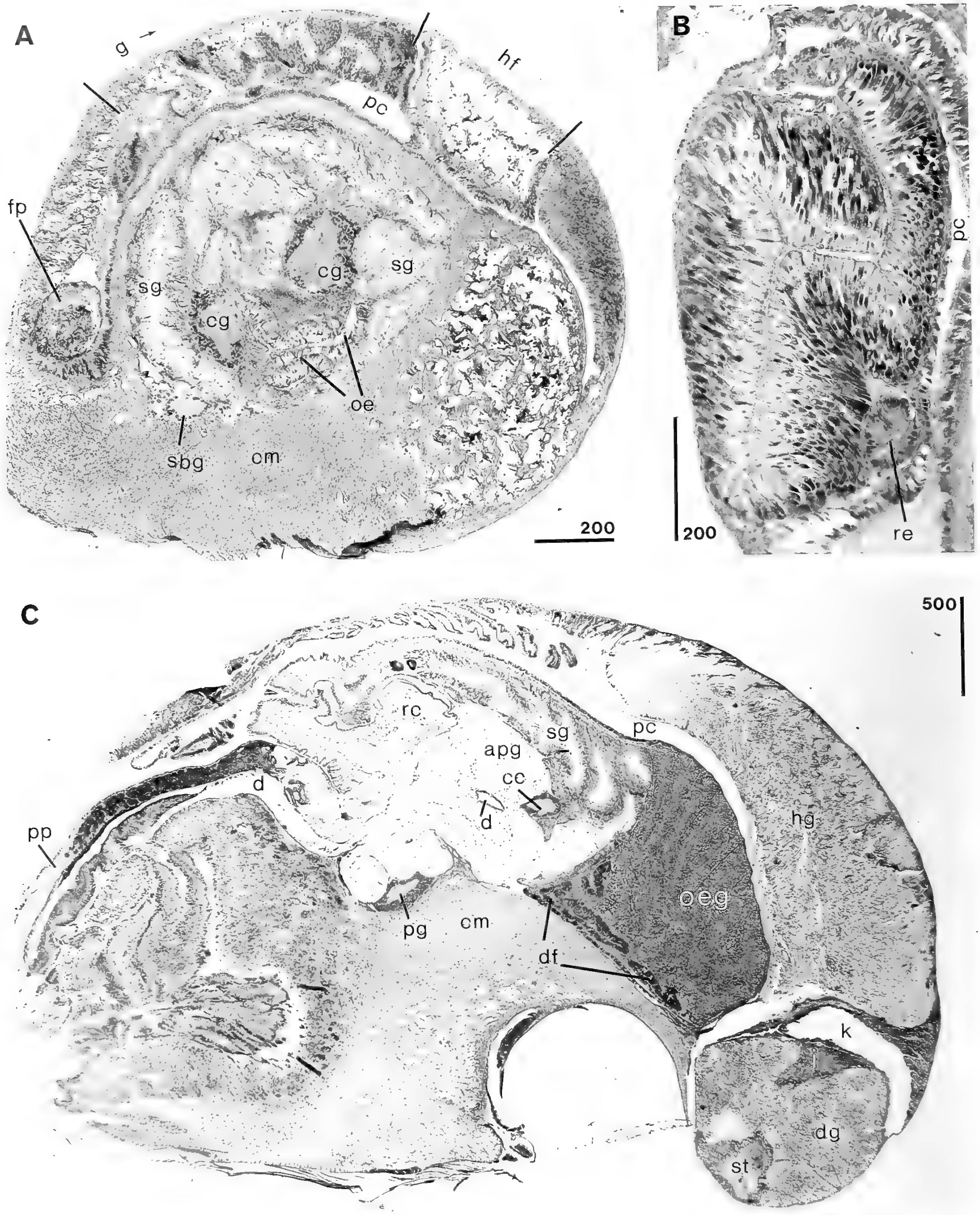
Explanation of Figure 31

***Dickdellia** labioflecta.* Figure A. Longitudinal section of head-foot to the right of mid-line. Figure B. Oblique cross sections of head-foot, through left eye, further posterior through right side. **acpg1**—propodial accessory pedal ganglion; **acpg2**—mesopodial accessory pedal ganglion; **apg**—anterior pedal gland; **bc**—buccal cavity; **df**—dorsal food channel; **e**—eye; **lmp**—left part of mesopodium; **lpg**—left pedal ganglion; **lsg**—left salivary gland; **oeg**—esophageal gland; **os**—osphradium; **pod**—pallial oviduct; **ppg**—posterior pedal gland; **rc**—radular cartilage; **rcg**—right cerebral ganglion; **re**—rectum; **rpg**—right pedal ganglion; **rrplg**—right pleural ganglion; **rsg**—right salivary gland; **sbg**—subesophageal ganglion; **sbp**—subesophageal pleural connective; **sg**—salivary gland; **sn**—snout. Scale lines = 200 μm.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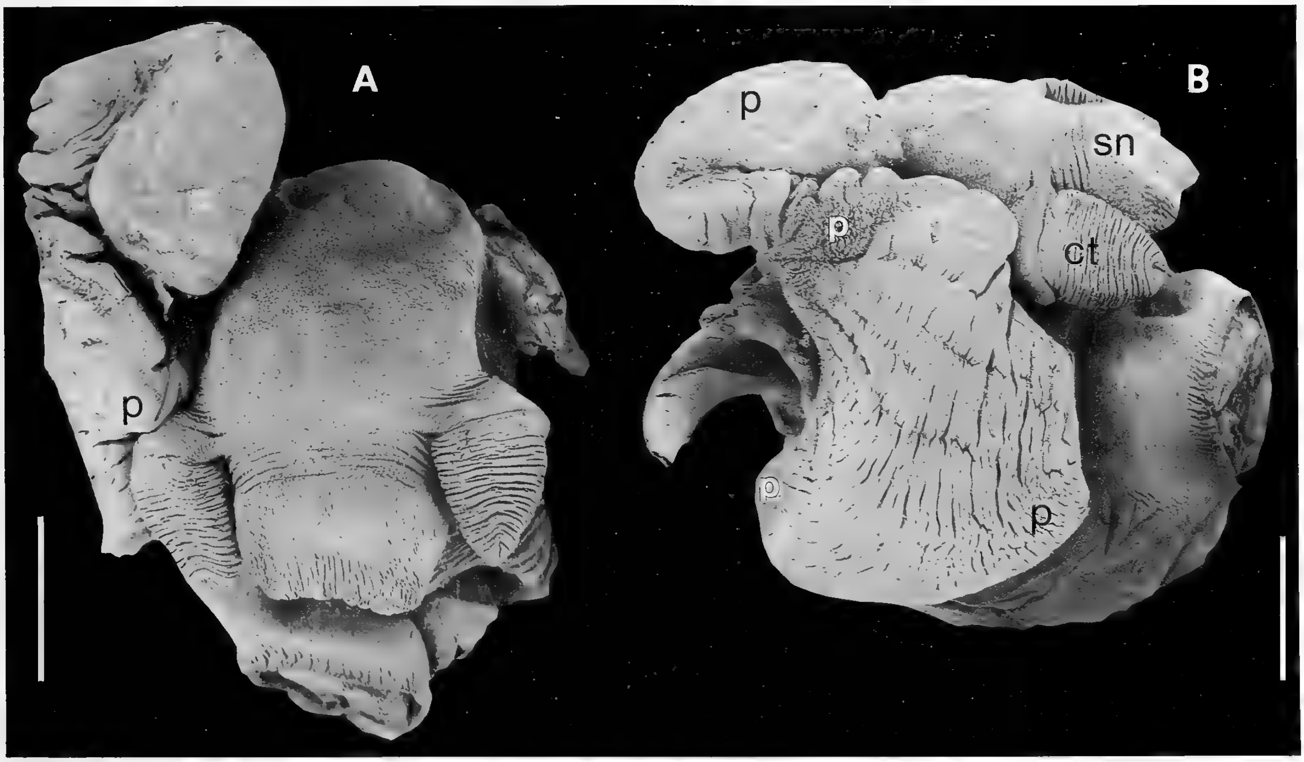


Explanation of Figure 33

Lacuna vincta, Koster Area, Swedish west coast. Figure A. Dorsal view of head-foot. Figure B. Right side of head-foot. **ct**—cephalic tentacle; **p**—penis; **sn**—snout. Scale lines = 1 mm.

The penis of *Lacuna vincta* is very large, and we give an SEM photo of a head-foot showing this and the morphology of the cephalic tentacles (Figure 33).

Systematic position of *Lacuna wandelensis*: The combination of undivided foot, presence of metapodial (opercular) tentacles on each side, and a thin, fragile shell are characters of Laevilitorininae with its single genus *Laevilitorina* Pfeffer, 1886; the Lacuninae; and *Lacuna wandelensis.*

For the choice between these two subfamilies, we pay attention to the absence of a spiral ridge on the operculum, presence of four pairs of opercular tentacles, strong resemblance in radular characters and classify *Lacuna wandelensis* in Laevilitorininae, genus *Laevilitorina,* subgenus *Pellilacunella.*

Further details which may or may not mean something are:

(1) We have noticed an apical, fine striation in *L. wandelensis* (Figure 34D), identical to that in *Laevilitorina* (*Macquariella*) *antarctica* (von Martens, 1886) (Figure 34C, H) also in size. We have scanned several true lacunines, which all have smooth apical whorls.

(2) A "hooded" radula occurs also in the Lacuninae, e.g., *Haloconcha* (Figure 35A) and *Lacuna* (*Lacuna*) *crassior* (Montagu, 1803), while the closely related *Lacuna* (*Epheria*) *vincta* Montagu, lacks a "hood" (Figure 35B). The "hood" seems therefore more widely distributed among the littorinids than previously assumed.

←

Explanation of Figure 32

***Dickdellia** labioflecta.* Figure A. Oblique cross section of body at the level of the cerebral ganglia. Figure B. Cross section of pallial oviduct. Figure C. Longitudinal section through head-foot. **apg**—anterior pedal gland; **cc**—cerebral commissure; **cg**—cerebral ganglion; **d**—duct from anterior pedal gland; **dg**—digestive gland; **fp**—fecal pellet; **g**—part of pallial skirt with gill; **hf**—pallial skirt fused to head-foot; **hg**—hypobranchial gland; **i**—intestine; **k**—kidney; **oe**—esophagus; **oeg**—esophageal gland; **pc**—pallial cavity; **pp**—propodium; **rc**—radular cartilage; **sbg**—subesophageal ganglion; **sg**—salivary gland; **st**—stomach. Scale lines in μm.

(3) The radula of *Laevilitorina* (*Pellilacunella*) *wandelensis* is more similar to that of the type species of *Pellilacunella* than what is evident from a comparison with Reid's stylized fig. 13a. We have compared with unpublished SEM photos of the radula of *L.* (*P.*) *bennetti,* kindly supplied by Reid. The two species share the unique, erect appearance of the rachidian, the lateral, and first marginal teeth. This is also the case in *Laevilitorina* (*Macquariella*) *antarctica* (Figure 35D), though to a lesser extent.

Laevilitorina (*Pellilacunella*) *wandelensis* (Lamy, 1905)

(Figures 10D–F, 30C, 34D, 35C, E, F)

Lacuna wandelensis Lamy, 1905:478, fig. 2.
Lacuna wandelensis: Lamy 1906:5, pl. 1, figs. 5–7.
Lacuna notorcadensis Melvill & Standen, 1907:131, fig. 2.
Lacuna wandelensis: Melvill & Standen 1912:349.
Antitrichotropis wandelensis: Powell 1951:124.

Type localities: *L. wandelensis,* Antarctic, Palmer Archipelago, Wandel Island, Port Charcot, 40 m; *L. notorcadensis,* South Orkneys, Scotia Bay, 15–18 m.

Type materials: *L. wandelensis,* Holotype in MNHN, examined; *L. notorcadensis,* Holotype (Figure 10D) RSM 1921.143.623, syntypes (Figure 10E, F), NMWZ 1955.158.157 (see Trew, 1987).

Material examined: Type material of *L. wandelensis* and *L. notorcadensis* and: POLISH ANTARCTIC EXPEDITION 1980, stas. N70 and N119, South Shetland Islands, King George Island, Admiralty Bay, 30–38 m, 2 specimens (from P. Arnaud).

Distribution: South Shetland, Antarctic Peninsula, and South Orkneys, about 10–40 m depth, "on *Macrocystis* and other large fuci" (Melvill & Standen, 1912).

Redescription: We only describe the external morphology of the soft parts, the radula, and the operculum. Shell, Figure 10D–F; protoconch, Figure 34D.

Soft parts. The whole head-foot is blackish green in a dried specimen, especially the snout and tentacles. The head has a large snout, about as long as broad, slightly conical, and with terminal mouth. The cephalic tentacles are about twice as long as the snout and are distinctly flattened. The eyes are situated close to the base of the tentacles in a low bulge on their outer sides. The penis is short, rounded, fingerlike, situated somewhat below the right cephalic tentacle. The foot has four flattened metapodial tentacles connected by a membrane on each side. The gill has about 20 leaflets in the roof of the unexpectedly deep pallial cavity. The osphradium consists of a low ridge running along and to the left of gill, but this may be composed of more than one ridge, now fused because of the drying. There are no pallial tentacles. The left corner of the pallial edge has two low, indistinct siphonal ridges.

The radula (Figure 35C, E, F) is colorless, about as long as the diameter of shell. The outer marginal tooth is small and narrow, with three to five apical denticles. The inner marginal, lateral, and central teeth are similar to each other, with the cutting edge forming a right angle to the narrower basal plate. At each side and below the broad, straight, weakly serrated cutting edge there is a small denticle. The inner marginal tooth is much larger than the outer one. The lateral tooth has a poorly developed outer lateral process. The central tooth has a hood (partly obscured by the fact that the whole tooth is strongly recurved), a finely serrate cutting edge, a large lateral cusp at each side, and a latero-basal point.

The operculum (Figure 30C) is paucispiral, thin, corneous, without internal ridge.

Remarks: The holotype of *L. wandelensis* is immature, about 2.4 mm high, the type specimens of *L. notorcadensis* are somewhat larger, just below 3 mm.

Two specimens were available for examination of the soft parts and radula. The radulae of two type specimens of *L. notorcadensis* were examined after rehydration and extraction of the soft parts. The soft parts of the type specimens were, however, too poorly preserved to allow examination of the external morphology.

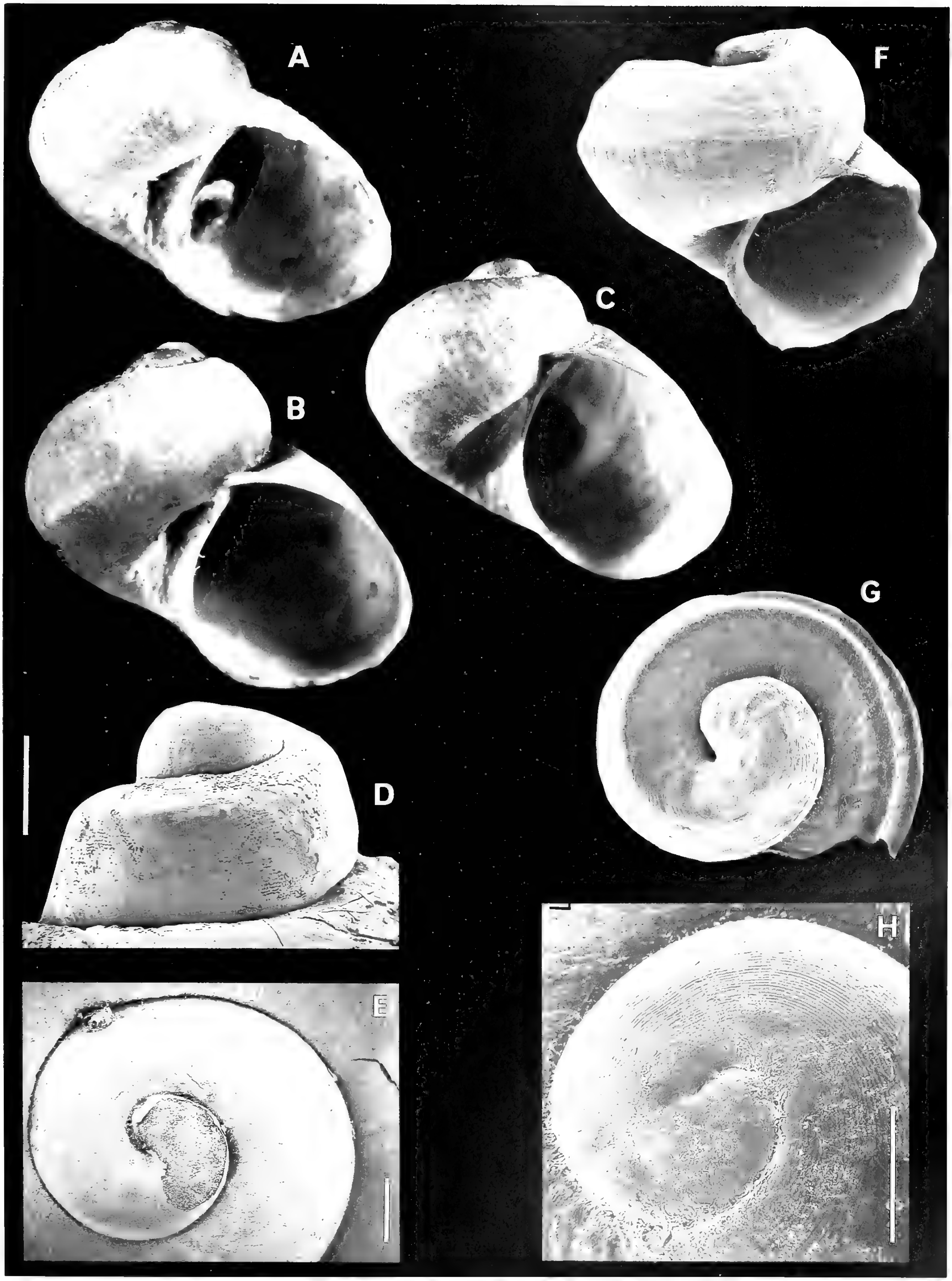
Lacuna wandelensis was referred to *Antitrichotropis* by Powell (1951:124, 1960:143). He may, however, have had a specimen of Trichotropidae, since he mentioned the presence of "odd tufts of hair-like processes disposed at regular intervals on the carinae." Such are not present in *L. wandelensis.*

Dell (1990:162) suggested that *L. notorcadensis* may be a synonym of *Lacuna wandelensis,* an opinion we share.

→

Explanation of Figure 34

Figure A. *Haloconcha reflexa reflexa,* syntype, USNM 40928, diameter 3.7 mm. Figure B. *Haloconcha minor,* syntype, USNM 215073, diameter 6.3 mm. Figures C, H. *Laevilitorina* (*Macquariella*) *antarctica,* South Georgia, Cumberland Bay, 1–2 m, on algae, SMNH 2794, diameter 4.7 mm. Figure D. *Laevilitorina wandelensis* (paratype of *Lacuna notorcadensis*), apex, NMWZ 1955.158.157. Figure E. ***Dickdellia*** *labioflecta,* apex, PS VII/4, sta. 293. Figures F, G. ***Trilirata*** *macmurdensis,* PS IX/3, sta. 173, diameter 1.0 mm. Scale lines = 200 μm.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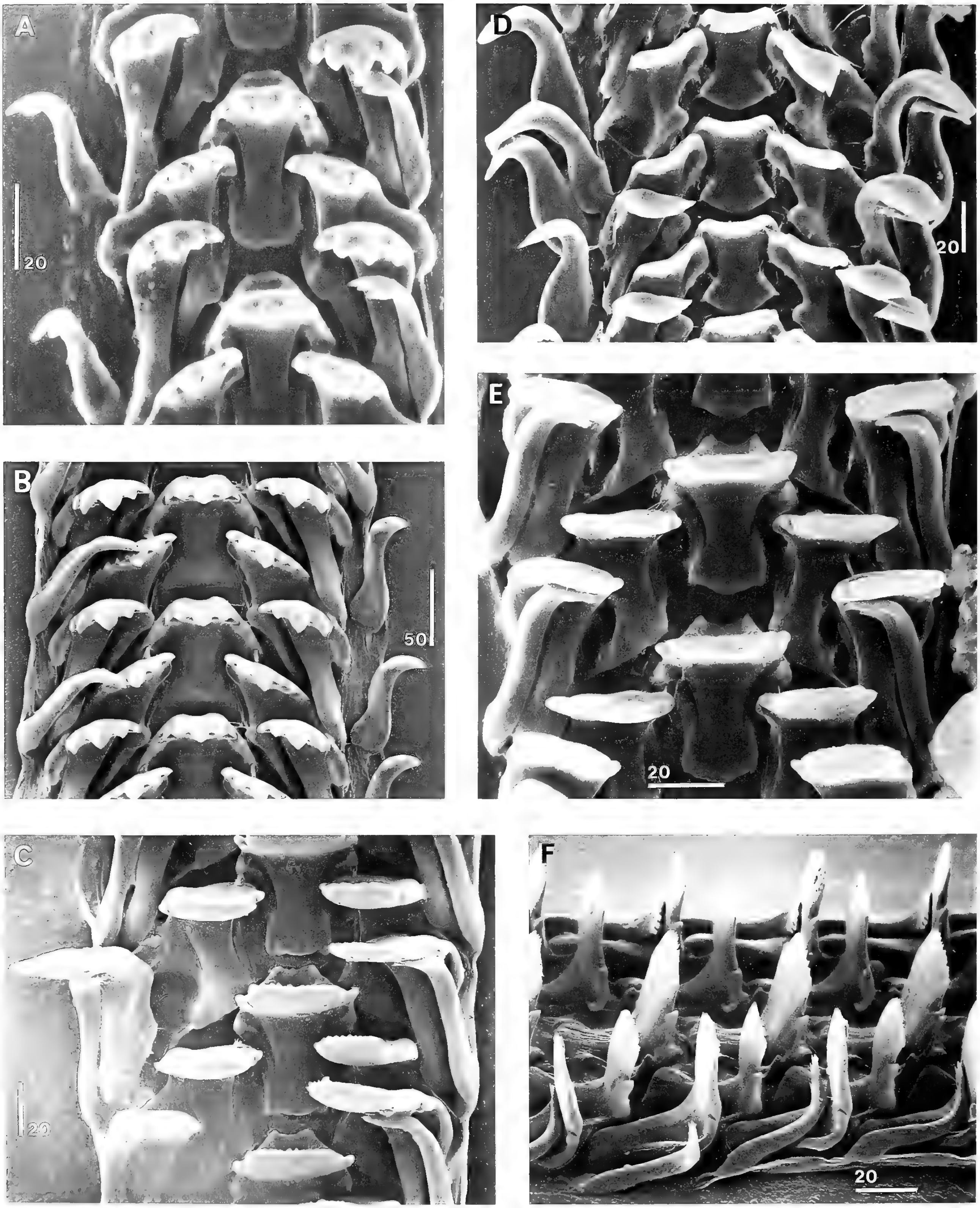
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LITERATURE CITED

Abbott, R. T. 1974. American Seashells. 2nd ed. Van Nostrand Reinhold: New York. 663 pp.

Arnaud, P. 1972. Invertébrés marins des XIIème et XVème expéditions antarctiques Françaises en Terre Adélie. Gastéropodes prosobranches. Tethys Supplement 4:105–134.

Bouchet, P. & A. Warén. 1993. Revision of the Northeast Atlantic bathyal and abyssal Mesogastropoda. Bollettino Malacologico, Supplement 3. Pp. 579–840.

Bouvier, E.-L. 1887. Système nerveux des gastéropodes prosobranches. Annales des Sciences naturelles, Zoologie et Paléontologie 3:1–510.

Dell, R. K. 1990. Antarctic Mollusca. Bulletin of the Royal Society of New Zealand 27:1–311.

Eales, N. B. 1923. Mollusca. Part V. Anatomy of Gastropoda (except the Nudibranchia). British Antarctic ("Terra Nova") Expedition 1910. Natural history report. Zoology 7(1):1–46.

Egorova, E. N. 1982. Biological results of the Soviet Antarctic Expeditions. 7. Explorations of the Fauna of the Seas 26(34): 1–143.

Finlay, H. J. 1926. A further commentary on New Zealand molluscan systematics. Transactions and Proceedings of the New Zealand Institute 57:320–485.

Fioroni, P. 1966. Zur Morphologie und Embryogenese des Darmtraktes und der transitorischen Organe bei Prosobranchiern (Mollusca, Gastropoda). Revue Suisse de Zoologie 73:621–876.

Fretter, V. 1948. The structure and life history of some minute prosobranchs of rock pools: *Skeneopsis planorbis* (Fabricius), *Omalogyra atomus* (Philippi), *Rissoella diaphana* (Alder), and *Rissoella opalina* (Jeffreys). Journal of the Marine Biological Association of the U.K. New Series 27:597–632.

Fretter, V. & A. Graham. 1962. British Prosobranch Molluscs. Ray Society: London. XVI + 755 pp.

Hain, S. 1990. Die beschalten benthischen Mollusken (Gastropoda und Bivalvia) des Weddellmeeres, Antarktis. Berichte zur Polarforschung 70:1–180.

Haszprunar, G. 1988. On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. Journal of Molluscan Studies 54:367–441.

Healy, J. M. 1990. Taxonomic affinities of the deep sea genus *Provanna* (Caenogastropoda): new evidence from sperm ultrastructure. Journal of Molluscan Studies 56:119–122.

Hedgpeth, J. W. 1964. Notes on the peculiar egg laying habit of an Antarctic prosobranch (Mollusca: Gastropoda). The Veliger 7:45–46.

Hedley, C. 1911. Mollusca. British Antarctic Expedition 1907–9. Report on the scientific investigations. II. Biology. Pp. 1–8.

Hershler, R. & G. M. Davis. 1980. The morphology of *Hydrobia truncata* (Gastropoda: Hydrobiidae): relevance to systematics of *Hydrobia*. Biological Bulletin 158:195–219.

Houbrick, R. S. 1979. Classification and systematic relationships of the Abyssochrysidae, a relict family of bathyal snails (Prosobranchia: Gastropoda). Smithsonian Contributions to Zoology 290:1–21.

Houbrick, R. S. 1981. Anatomy, biology and systematics of *Campanile symbolicum* with reference to adaptive radiation of the Cerithiacea (Gastropoda: Prosobranchia). Malacologia 21:263–289.

Houbrick, R. S. 1987. Anatomy of *Alaba* and *Litiopa* (Prosobranchia: Litiopidae): systematic implications. The Nautilus 101:9–18.

Houbrick, R. S. 1988. Cerithoidean phylogeny. Malacological Review, Supplement 4:88–128.

Houbrick, R. S. 1989. *Campanile* revisited: implications for cerithioidean phylogeny. American Malacological Bulletin 7:1–6.

Huber, G. 1993. On the cerebral nervous system of marine Heterobranchia (Gastropoda). Journal of Molluscan Studies 59:381–420.

Johansson, J. 1939. Anatomische Studien über die Gastropodenfamilien Rissoidae und Littorinidae. Zoologiska Bidrag från Uppsala 18:287–396.

Kabat, A. R. 1991. The classification of the Naticidae (Mollusca: Gastropoda): review and analysis of the supraspecific taxa. Bulletin of the Museum of Comparative Zoology 152: 417–449.

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Explanation of Figure 35

Radulae, Littorinidae. Figure A. *Haloconcha reflexa,* syntype. Figure B. *Lacuna vincta,* Swedish west coast, Koster Area. Figures C, F. *Lacuna notorcadensis,* paratype, NMWZ 1955.158.157. Figure D. *Laevilitorina* (*Macquariella*) *antarctica,* South Georgia, Cumberland Bay, 1–2 m, on algae, SMNH 2794. Figure E. *Laevilitorina wandelensis* (holotype of *Lacuna notorcadensis*), RSM 1921.143.623. Scale lines in µm.

Kase, T. 1990. Late Cretaceous gastropods from the Izumi Group of Southwest Japan. Journal of Paleontology 64:563–578.

Lamy, E. 1905. Gastropodes prosobranches recueillis par l'expedition française du Dr Charcot. Bulletin du Museum National d'histoire Naturelle de Paris 11:475–483.

Lamy, E. 1906. Mollusques Gastropodes et Pelecypodes. Expédition antarctique française (1903–1905) (L. Joubin Ed.). Pp. 1–19.

Martens, E. **von** & G. **Pfeffer**. 1886. Die Mollusken von Süd-Georgien nach den Ausbeute der deutschen Station. Jahrbuch der hamburgischen wissenschaftlichen Anstalten 3:65–135.

McLean, J. H. 1992. Systematic review of the family Choristellidae (Archaeogastropoda: Lepetellacea) with descriptions of new species. The Veliger 35:273–294.

Melvill, J. C. & R. **Standen**. 1907. The marine Mollusca of the Scottish National Antarctic Expedition. Transactions of the Royal Society of Edinburgh 46:119–157.

Melvill, J. C. & R. **Standen**. 1912. The marine Mollusca of the Scottish National Antarctic Expedition. Transactions of the Royal Society of Edinburgh 48:333–366.

Mestayer, M. K. 1916. Preliminary list of Mollusca from dredgings taken off the northern coasts of New Zealand. Transactions and Proceedings of the New Zealand Institute 48:122–130.

Pelseneer, P. 1903. Mollusques (Amphineures, Gastropodes et Lamellibranches). Résultats du S.Y. Belgica en 1897–1899, Zoologie. 85 pp.

Ponder, W. F. 1988. The truncatelloidean (= rissoacean) radiation—a preliminary phylogeny. Malacological Review, Supplement 4:129–164.

Ponder, W. F.& E. K. **Yoo**. 1980. A review of the genera of the Cingulopsidae with a revision of the Australian and tropical Indo-Pacific species (Mollusca: Gastropoda: Prosobranchia). Records of the Australian Museum 33:1–88.

Powell, A. W. B. 1927. Deep-water Mollusca from Southwest Otago, with descriptions of 2 new genera and 22 new species. Records of the Canterbury Museum 3:113–124.

Powell, A. W. B. 1937. New species of marine Mollusca from New Zealand. Discovery Reports 15:153–222.

Powell, A. W. B. 1940. The marine Mollusca of the Aupourian Province New Zealand. Transactions and Proceedings of the New Zealand Institute 70:205–248.

Powell, A. W. B. 1951. Antarctic and subantarctic Mollusca: Pelecypoda and Gastropoda. Discovery Reports 26:147–196.

Powell, A. W. B. 1958. Mollusca from the Victoria-Ross Quadrants of Antarctica. B.A.N.Z. Antarctic Research Expedition 1920–1931 6(9):167–215.

Powell, A. W. B. 1960. Antarctic and subantarctic mollusca. Records of the Auckland Institute and Museum 5:117–193.

Powell, A. W. B. 1979. New Zealand Mollusca. Collins: Auckland, Sydney, London. xiv + 500 pp.

Reid, D. G. 1989. The comparative morphology, phylogeny and evolution of the gastropod family Littorinidae. Philisophical Transactions of the Royal Society of London Series B. 324:1–110.

Suter, H. 1908. Additions to the marine molluscan fauna of New Zealand, with descriptions of new species. Proceedings of the Malacological Society of London 8:22–42.

Suter, H. 1913. Manual of New Zealand Mollusca. Wellington, New Zealand. 1120 pp.

Taylor, J. D. & J. A. **Miller**. 1989. The morphology of the osphradium in relation to feeding habits in meso- and neogastropods. Journal of Molluscan Studies 55:227–237.

Thiele, J. 1912. Die antarktischen Schnecken und Muscheln. Wissenschaftliche Ergebnisse der deutschen Südpolarexpedition 1901–03 13:183–285.

Thiele, J. 1913. Die Antarktischen Schnecken und Muscheln [review of Thiele 1912]. Zentralblatt für Zoologie, Allgemeine und experimentelle Biologie 2:86.

Tomlin, J. R. **le** B. 1930. Some preoccupied generic names. Proceedings of the Malacological Society of London 19:22–24.

Trew, A. 1987. James Cosmo Melvill's New Molluscan Names. National Museum of Wales: Cardiff. 84 pp.

Warén, A. 1991. New and little known Mollusca from Iceland and Scandinavia. Sarsia 76:53–124.

Warén, A., S. **Gofas** & W. F. **Ponder**. (in preparation). Review and systematic position of "vitrinellid- and skeneidlike" gastropod genera.

Warén, A. & S. **Hain**. 1992. *Laevipilina antarctica* and *Micropilina arntzi,* two new monoplacophorans from the Antarctic. The Veliger 35:165–176.

Warén, A. & W. F. **Ponder**. 1991. New species, anatomy, and systematic position of the hydrothermal vent and hydrocarbon seep gastropod family Provannidae fam.n. (Caenogastropoda). Zoologica Scripta 20:27–56.

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Habitat Affinities and Distributions of Land Gastropods from the Ruby Mountains and East Humboldt Range of Northeastern Nevada

by

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Abstract. The habitat affinities, distributions, and densities of 16 species of land snails and one species of slug were determined for two high elevation, cold desert mountain ranges in northeastern Nevada. Five habitat types were identified, and 28 collection stations representing these habitat types were established. Perennial streams lined with deciduous trees had the highest number of species (12) and the highest density (126.8 specimens/m^2) from the study area. Other habitat types described are the mountain brush community (9 species, 57.1 specimens/m^2); the wet meadow community (10 species, 22.5 specimens/m^2); the xeric pinyon pine and Utah Juniper community (8 species, 22.8 specimens/m^2); and the subalpine conifers (4 species, 4 specimens/m^2). Land gastropods were most diverse and abundant in deep canyons at elevations of approximately 2250 meters, and in aspen litter with a metamorphic bedrock that is conducive to water retention during the dry spring and summer months.

Gastropod communities seen today in these mountains suggest a once widespread Pleistocene fauna that has become fragmented and isolated in the more mesic habitats during the Holocene.

The larger or medium-sized land snails, which include species of the genera *Oreohelix, Microphysula,* and *Discus,* occur most often in canyons on the west slopes of this study area. Some smaller land snails, such as species of *Vertigo, Pupilla, Vallonia,* and one small species of *Oreohelix,* depend heavily on microhabitats in the more xeric, pinyon pine-juniper woodlands located in deep limestone canyons and beneath cliff faces, associated with drought-tolerant shrubs.

INTRODUCTION

Little is known about the habitat affinities and local distributions of land snails from the high elevation, cold desert of the northern Great Basin of the western United States. The gastropod fauna of the Great Basin is typical of the Rocky Mountain Province of North America (Henderson, 1931) and has many similarities to the gastropod fauna of the Wasatch Mountains in Utah at the eastern edge of the Great Basin (Chamberlin & Jones, 1929). Several species in central and northern Nevada appear to be common on the approximately 100 mountain ranges that line up in a parallel north to south orientation. Land gastropods are relatively rare in the intervening valleys. Approximately 30 species of snails and two species of slugs occur primarily in mesic, wooded habitats within deep canyons and on north-facing slopes that retain a snow cover into late spring. Xeric, shrub-dominated valleys, foothills, and alkali flats present a formidable barrier to dispersal by the more mesic adapted gastropods of the Great Basin. The diversity and distribution of snails and slugs in these mountain ranges appear to be in a state of non-equilibrium in which local populations are going extinct without much replacement by immigration of similar taxa from the Rocky Mountains to the north and east (Pratt, 1985).

Various studies in North America have shown a strong correlation between land snail species richness and vegetational cover (Karlin, 1961; Boag & Wishart, 1982; Kralka, 1986). Other studies have pointed out the importance of soil and rock types for building shells (Coney et al., 1982; Cameron, 1986). Elevation, slope aspect, slope angle, and annual precipitation affect species richness and population densities of land snails on some mountain ranges in western North America (Hoff, 1962; Boag & Wishart, 1982; Kralka, 1986). No such study has been conducted on land snails in the Great Basin.

This study was undertaken to determine the habitat affinities and distributions of land gastropods from the Ruby Mountains and East Humboldt Range, both representing high elevation, mesic environments in northeastern Nevada. Five habitat types were characterized according to their dominant vegetation, elevation, geological features, and soil-rock type. Collection stations were established in each of the five habitat types to determine gastropod species richness, density, and distributions. This information adds to the existing knowledge of the ecology and zoogeography of gastropods found in the Rocky Mountains of North America (Chamberlin & Jones, 1929; Karlin, 1961; Beetle, 1989).

SETTING

The climate of the Great Basin desert is greatly influenced by the rain shadow effect caused by the Sierra Nevada and Cascade ranges to the west, which creates a mid-latitude, high elevation, cold desert. Winter storms from the west provide most of the precipitation that is received in northeastern Nevada, and 80% of that is in the form of snow (Lewis, 1972). The East Humboldt Range and the northern half of the Ruby Mountains average approximately 126 cm of precipitation between elevations of 2200 and 3200 meters. Elevations between 1600 and 2200 meters average 55 cm of precipitation. The summers are short, hot, and dry with a mean July maximum of 29.9°C and mean July minimum of 11.1°C. The winters are long and cold with a mean January maximum of 3.78°C and a mean January minimum of −9.22°C. Annually, there is a mean of 210 days in which the temperature is 0°C and below (Lewis, 1972).

The Ruby Mountains and the East Humboldt Range are a metamorphic core complex in the form of an asymmetric fault block, beginning just south of the town of Wells and extending 125 km south to the Elko-White Pine county line (Figure 1). This complex is approximately 28 km wide at its widest point in the central Ruby Mountains and 15 km wide at its narrowest point at Secret Pass, which separates the East Humboldt Range from the Ruby Mountains (Coats, 1987).

The most abundant rock types in the East Humboldt Range and in the northern two-thirds of the Ruby Mountains are quartzite, gneiss, and some granite. Soil development is poor in once glaciated canyons and along the mountain crest. These rock types make up 78% of the total mass of the East Humboldt Range and Ruby Mountains, and facilitate the retention of water at higher elevations because of their non-porous nature. Several subalpine lakes and long-lasting snow banks contribute to a general availability of water. The remaining 22% of this complex, south of Harrison Pass (Figure 1), is composed predominantly of carbonate rock, both dolomite and limestone, with some metamorphic rock as well (Coats, 1987).

Approximately 35% of the central Ruby Mountains and 27% of the East Humboldt Range were perennially covered with ice and snow during glacial stages of the Pleistocene. Glacial advances during the Illinoian and Wisconsin stages carved out deep, bowl-shaped canyons, such as Lamoille Canyon (Figure 1: station 13), which today are wooded and well watered. The majority of these glaciated canyons developed on the western slope, which has a more gentle

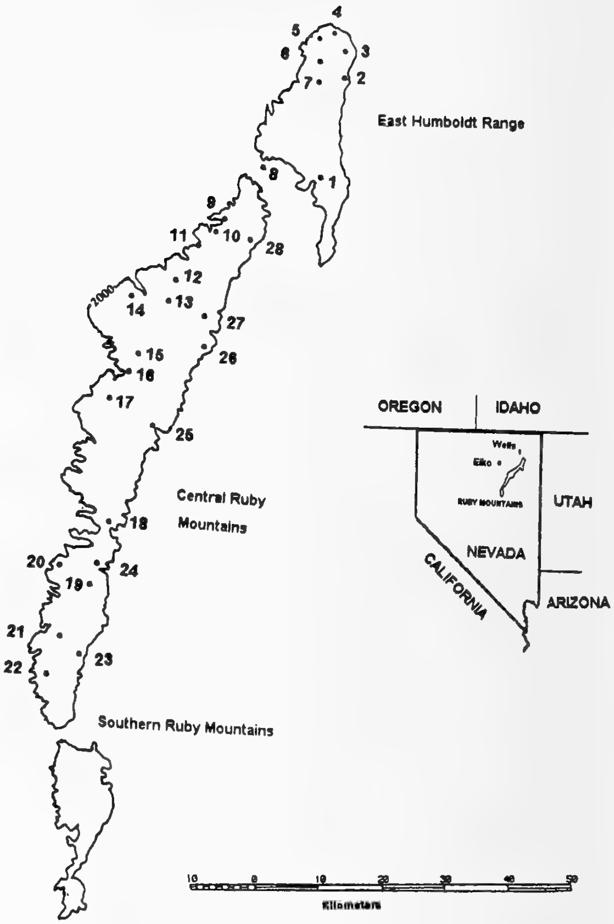

Figure 1

Geographical locations of 28 collection stations established in the East Humboldt Range and Ruby Mountains of northeastern Nevada. Place names are those used on the Elko and Ruby Lake quadrangles, U.S. Geological Survey 30 × 60-Minute Series, Topographic. Roman numerals represent the habitat types sampled at each station. Refer to Table 1 for habitat listings. 1. Horse Creek (I), 2. Winchell Creek (I), 3. Angel Creek (I), 4. Trout Creek (I), 5. Grey's Lake (I), 6. Herder Creek (I), 7. Ackler Creek (I, II, III), 8. Secret Creek (I, II), 9. Soldier Creek (I, IV), 10. John Day Creek (I), 11. Cold Creek (I, III), 12. Talbot Creek (I, III, V), 13. Lamoille Canyon (I, II, V), 14. Sietz Canyon (I), 15. Kleckner Creek (I, III, V), 16. Long Canyon (I), 17. Rattlesnake Canyon (I, III), 18. Harrison Pass (I, III), 19. Pearl Peak (I, IV), 20. Brown Creek (I, II), 21. Mitchell Creek (I, III), 22. Willow Creek (I), 23. Broncho Charlie Canyon (IV), 24. Indian Creek (IV), 25. Overland Creek (I), 26. Thompson Creek (I), 27. Lutts Creek (I, IV), 28. Ruby Guard Station (II).

incline of 75–156 meters per kilometer, more extensive and complex plant communities, and receives the most moisture from east-tracking Pacific storms. The eastern slope has a steeper incline of 15–66 meters per kilometer. Only a few signs of extensive glaciation occur here (Figure 1: station 27). Plant communities are less developed and less watered in east slope canyons (Sharp, 1938).

MATERIALS AND METHODS

Land gastropods were collected, identified, and counted from 28 stations established in the Ruby Mountains and East Humboldt Range in northeastern Nevada (Figure 1). Each station typically had more than one of five habitat types, and three samples were taken from each of the 45 habitat sites, for a total of 135 samples (Table 1). A station generally included a single riparian zone with deciduous trees and small, widely dispersed meadows usually associated with perennial springs. The more xeric mountain brush, pinyon pine/Utah juniper, and white bark pine/rock slide communities were generally found on the slopes above the riparian zones. Collections were made each spring and summer between 1988 and 1993, for a total of 125 trips to the study area. Collecting was concentrated in those habitat types that were known to have snail populations.

Seventy-five samples (Figure 1: stations 1–22 and 25–27) were collected along perennial streams wooded with a narrow strip of quaking aspen (*Populus tremuloides*), long-leafed cottonwood (*Populus angustifolia*), and an understory of shrubs, forbs, and grasses (Table 1).

Twelve samples (Figure 1: stations 7, 13, 20, and 28) were collected in mid-elevation (2250 m) mountain brush communities (Table 1). These plant communities dominate the Ruby Mountains and East Humboldt Range and include several species of sagebrush (*Artemisia* spp.), serviceberry (*Amelanchier alnifolia*), bitterbrush (*Purshia tridentata*), snowberry (*Symphoricarpus oreophilus*), and curlleaf mountain mahogany (*Cercocarpus ledifolius*). An understory of forbs and grasses is usually present.

Twenty-four samples (Figure 1: stations 7, 8, 11, 12, 15, 17, 18, and 21) were collected from wet meadow communities (Table 1). These communities were dominated by willows (*Salix* sp.), sedges (*Juncus* spp.), and several species of grasses and forbs. Fifteen samples (Figure 1:

Table 1

Mean density (shells and live animals/m^2) and range for 17 species of gastropods found in five habitat types in the Ruby Mountains and East Humboldt Range of northeastern Nevada. Values for each habitat type include: the number of samples collected, the total number of species, the mean number of species with a ±SD, and the mean number of specimens (shells and live animals)/m^2 with a ±SD.

Habitat types Samples/habitat	I 75	II 12	III 24	IV 15	V 9
Species			Shells and live animals/m^2 and (range)		
Oreohelix strigosa	9.3 (4–89)	—	—	3.3 (12–63)	—
Oreohelix subrudis	2.0 (1–6)	—	—	—	—
Oreohelix hemphilli	22.0 (11–28)	5.5 (2–11)	—	0.7 (2–5)	—
Microphysula ingersolli	15.2 (5–90)	4.2 (2–8)	—	4.2 (2–9)	1.0 (1–3)
Discus whitneyi	5.0 (2–14)	0.5 (2–4)	3.6 (1–8)	0.4 (2–4)	0.5 (2–4)
Vitrina pellucida	9.1 (2–45)	2.3 (1–7)	5.9 (4–10)	2.0 (3–7)	1.5 (2–5)
Punctum conspectum	4.3 (2–27)	1.3 (2–5)	1.4 (2–8)	—	—
Vallonia cyclophorella	48.8 (2–208)	28.5 (10–68)	—	5.0 (2–21)	1.0 (1–5)
Euconulus fulvus	4.1 (1–25)	0.3 (1–3)	48 (2–9)	—	—
Pupilla hebes	0.9 (1–3)	12.0 (8–40)	—	1.8 (1–3)	—
Pupilla blandi	5.4 (5–32)	2.5 (2–8)	—	5.4 (5–20)	—
Vertigo gouldi	—	—	0.5 (1–4)	—	—
Vertigo concinnula	0.2 (1–3)	—	0.9 (2–6)	—	—
Vertigo ovata	—	—	0.5 (1–3)	—	—
Vertigo modesta	—	—	1.1 (2–5)	—	—
Catinella rehderi	—	—	2.9 (2–9)	—	—
Deroceras laeve	—	—	0.9 (2–3)	—	—
Total species/habitat	12	9	10	8	4
Mean no. species/sample (±SD)	6.38 (±0.18)	5.75 (±01.3)	6.13 (±0.19)	4.60 (±0.36)	3.30 (±0.16)
Mean specimens/m^2/sample (±SD)	126.8 (±12.8)	57.1 (±7.4)	22.5 (±1.9)	22.8 (±2.0)	4.0 (±0.5)

I. Aspen and cottonwood, perennial streams.
II. Mountain brush, forbs, and grasses.
III. Wet meadows.
IV. Xeric pinyon pine and Utah juniper.
V. Subalpine confiers and rockslides.

stations 9, 19, 23, 24, and 27) were collected in habitats that are centered primarily in the southern third of the Ruby Mountains on limestone and dolomite bedrock. Their plant communities were dominated by short-statured, evergreen conifers and an understory of shrubs, forbs, grasses, and much bare ground. The dominant trees are the single-leafed pinyon pine (*Pinus monophylla*) and the Utah juniper (*Juniperus osteosperma*). Only three perennial streams are located in this area (Figure 1: stations 20, 21, and 22).

Nine samples (Figure 1: stations 12, 13, and 15) were collected from the high elevation subalpine zone (Table 1). At elevations of 2700 m and above, there are scattered stands of whitebark pine (*Pinus albicaulis*) and limber pine (*Pinus flexilis*) with an understory of shrubby cinquefoil (*Potentilla fruticosa*), willows, sagebrush, forbs, and grasses. Large areas of boulders, cliffs, and morainal deposits are generally barren of plants and snails at this elevation (Lewis, 1972).

Soil and litter samples were taken using a 20 cm × 20 cm wooden frame that was randomly thrown within each of the five described habitats. Within the grid area, litter, soil, and gravel were collected to a depth of approximately 5 cm, placed in plastic bags, labeled, and taken to the laboratory. Each litter and soil sample was then sieved through sequential sizes of wire mesh—2 mm, 5 mm, 10 mm, and 15 mm.

All live gastropods and empty shells were identified with the aid of Pilsbry's *Land Mollusca of North America* (1939, 1946, and 1948) and with the help of Drs. W. L. Pratt and T. J. Frest, and museum specimens. All shells and slugs are deposited in the collections of the Biology Department at Great Basin College. Elevation, soil, and rock types were recorded for each collection station by reference to topographic and geomorphic maps (Coats, 1987). A coefficient of similarity was calculated for species composition between each possible habitat pair (Table 2). The similarity coefficient SC = (2C)/(A + B), where C is the number of species in common, and A and B are the number of species in habitats A and B. The similarity coefficients were used to construct a dendrogram (Figure 2) by cluster analysis using an unweighted pair-group method (Sneath & Sokal, 1973).

Table 2

Similarity matrix showing coefficients of similarity S (percent similarity in species between two habitats) of land snail communities from five habitat types in the Ruby Mountains and East Humboldt Range of northeastern Nevada.

	Habitat types				
	I	II	III	IV	V
I	—				
II	86	—			
III	45	42	—		
IV	80	82	22	—	
V	50	29	29	67	—

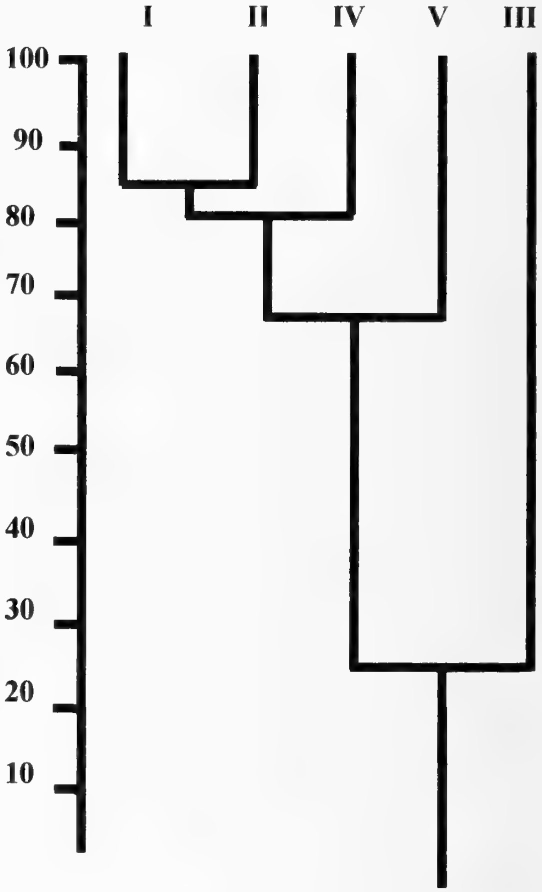

Figure 2

Cluster analysis showing the percent similarities of land snail communities in five habitat types from the Ruby Mountains and East Humboldt Range of northeastern Nevada.

RESULTS

Sixteen land snail species and one species of slug were recorded (Table 1). The highest land mollusk density (126.8 specimens/m^2), counting both live animals and empty shells, and the highest number of species (12) were found in the aspen-cottonwood riparian habitats (Figure 1: stations 1–22, 25, 26, and 27). A mean number of 6.38 species per sample came from the 75 samples collected from this habitat (Table 1).

Snails were relatively common in the dominant, more xeric mountain shrub habitats (Figure 1: stations 7, 13, 20, and 28). The four stations in this habitat type held nine species of land snails with the second highest density (57.1 specimens/m^2). A mean number of 5.75 species per sample came from the 12 samples collected from this habitat. This group of species was also present in the aspen-cottonwood riparian habitat, as well as the xeric pinyon pine and Utah juniper habitats with a few exceptions (Table 1).

Nine species of land snails and one species of slug were recorded from eight wet meadow habitats (Figure 1: stations 7, 8, 11, 12, 15, 17, 18, and 21). Gastropods were most abundant beneath large rocks and rotting, woody vegetation. Of the nine species collected, three species of *Vertigo, Catinella rehderi* (Pilsbry, 1948), and the only species of slug, *Deroceras laeve* (Müller, 1774), were found exclusively in these wet meadow stations. The other five species recorded here were shared with habitats I and II (Table 1). In the wet meadows, a density of 22.5 specimens/m^2 was recorded, and a mean number of 6.13 species per sample came from the 24 samples collected from this habitat (Table 1).

The mid-elevation (2250 m) pinyon pine and Utah juniper woodlands (Figure 1: stations 9, 19, 23, 24, and 27) had eight species of land snails at a density of 22.8 specimens/m^2 (Table 1). A mean number 4.60 species per sample came from the 15 samples collected from this habitat. *Vallonia cyclophorella* (Sterki, 1893), *Pupilla blandi* (E. S. Morse, 1865), *Pupilla hebes* (Ancey, 1881), and a small oreohelicid, *Oreohelix hemphilli* (Newcomb, 1869), were all present in this more xeric habitat. The remaining species were isolated in small perennial springs with deciduous vegetation, and were shared with habitats I, II, III, and V (Table 1).

The three stations (Figure 1: 12, 13, and 15) located in the high elevation subalpine zone had four species, *Microphysula ingersolli* (Bland, 1874), *Discus whitneyi* (Newcomb, 1864), *Vitrina pellucida* (Müller, 1774), and *Vallonia cyclophorella.* They were found at a density of only four specimens/m^2 and a mean number of 3.3 species per sample from the nine samples collected (Table 1).

Sixteen stations surveyed on the west slope of the Ruby Mountains and the East Humboldt Range averaged 7.6 species per sample, while twelve stations on the eastern slopes averaged 5.3 species per sample. Actual shell densities for the west slope versus east slope were not calculated, but samples from the west slope had consistently more shells than the east slope samples. Land snails in the study area occupied an elevational range of 1900 m to 3350 m, with the highest density and species richness at approximately 2250 m. Twelve stations were located in deep, loamy soils on top of metamorphic granite and gneiss. An average of 7.1 species per sample was associated with this soil and rock type. Ten stations were located among rocks and boulders of igneous quartz and gneiss with a poor to moderate soil and litter development. An average of 6.3 species per sample occurred here. Six stations established in the southern Ruby Mountains had an average of 3.5 species per sample that occur in the dolomite and limestone canyons.

Table 2 shows calculated values for the percent similarity of species among the five habitat types. The aspen/cottonwood riparian community (86%), the mountain-brush community (82%), and the pinyon pine and Utah juniper woodlands (80%) all share a similar molluscan fauna. The high elevation subalpine habitat is relatively similar to the previous three habitats (average of 60% similarity), while the wet meadow habitats (habitat III) were the least similar to the pinyon pine-Utah juniper habitat (22%) and the subalpine habitat (29%). The wet meadow habitat shared slightly less than half the species with the aspen/cottonwood riparian habitats (45%) and the mountain brush habitats (42%). This can be expected since wet meadows are restricted to perennial riparian zones with surrounding mountain brush communities. Figure 2 shows these relationships in the form of a dendrogram.

DISCUSSION

The highest species richness and shell density was found in canyons with perennial streams bordered by woodlands of deciduous trees and shrubs. Species composition found in the Ruby Mountains and East Humboldt Range is most similar to gastropod assemblages found in canyons and meadows of the Wasatch Mountains of Utah (Chamberlin & Jones, 1929) and from the Rocky Mountains of Montana and Colorado (Karlin, 1961).

Populations of land snails emigrating from the northern Rocky Mountains became isolated on Great Basin mountain ranges during the later part of the Miocene Epoch and into the Pliocene (Pratt, 1985). The Pleistocene epoch brought wet, cold winters and cool summers. This climatic change was responsible for the formation of several glaciers on the windward slope of the Ruby Mountains and East Humboldt Range. Storms coming from the Pacific Ocean and the Arctic dropped large amounts of snow on the west slope, and cool, short summers facilitated the movement of glaciers, such as Lamoille Canyon (Figure 1: station 13), down to the present valley floor at 1875 m. The mountain crest created a local rain shadow effect on the eastern slope resulting in the formation of only one large glacier, the present day Lutts Creek (Figure 1: station 27) (Sharp, 1938). This combination of glaciated canyons, a rock type that retains water, the presence of perennial streams, and a gentle slope allows for the growth of extensive deciduous forest and shrub lands accounting for the greater species richness and shell densities that occur on the western slopes.

A core of gastropod species occurred in some combination in each of the five habitat types (Table 1); these include *Oreohelix strigosa* (Gould, 1846), *Oreohelix subrudis* (Reeve, 1854), *Microphysula ingersolli, Discus whitneyi, Vitrina pellucida, Punctum conspectum* (Bland, 1865), *Vallonia cyclophorella, Euconulus fulvus* (Müller, 1774), *Pupilla hebes,* and *Pupilla blandi.* In habitats I, II, and IV there were seven to nine shared species of gastropods (Table 1), which have a high affinity for similar habitats (Figure 2), and have a high percent similarity in shared species (Table 2). Gastropods found in habitats I and II possibly represent an original, widespread community that may have been present before or during the Pleistocene in mesic habitats.

Habitat III is host to five obligate meadow species, which accounts for its low percent similarity with the other four habitats (Figure 2). However, five core species from habitat III are shared with the other four habitats, again suggesting a once widespread gastropod fauna (Table 1).

Comparing the shared gastropod species (Table 1) and their percent similarities (Table 2), the aspen-cottonwood riparian (I), mountain brush community (II), and pinyon pine-Utah juniper woodlands (IV), suggests that these three groups are also derived from a similar core of mesic adapted species. Six shared species (Figure 2) of gastropods found in habitat IV are restricted to aspen and willow found around three small perennial springs (Figure 1: stations 20, 21, and 22) located within the pinyon pine and Utah juniper woodlands (Table 1). These species may represent isolated populations of a once widespread mesic fauna which were stranded at these mesic sites during the Holocene.

The pinyon pine and Utah juniper woodlands moved into the southern Ruby Mountains some 6500 years ago in response to the drying climate during the Holocene (Grayson, 1993). Except for those species restricted to perennial springs, only three species, *O. hemphilli, V. cyclophorella,* and *P. hebes,* have adapted to the xeric, pine and juniper woodlands and can be found in microhabitats such as xeric adapted plants beneath north-facing cliff sites, but rarely in the actual pine and juniper litter.

Only four species of gastropods (Table 1) have spread into the higher elevation subalpine conifers and rockslides. These species are derived from the same group of gastropods seen in the other four habitats and appear to represent a similar but depauperate molluscan fauna (Figure 2). This habitat type is also relatively young and was only accessible to snails since the late Holocene as the glaciers melted and conifers and shrubs colonized the higher elevations (Grayson, 1993).

Karlin (1961) has shown that 99% of gastropod species in the west are strongly influenced by the availability of water and decomposing organic matter, usually found beneath aspen and mixed deciduous-coniferous woodlands. Furthermore, in the Rocky Mountains, species-rich faunas are found in such mesic sites regardless of rock types. Apparently these communities of gastropods are obtaining their calcium needs from decomposing, deciduous litter. In the East Humboldt Range and northern half of the Ruby Mountains, gastropod faunas are most diverse in the metamorphic bedrock (average of 7.1 species/sample) associated with mesic plant communities, compared to the limestone and dolomite bedrock of the southern half of the Ruby Mountains (average of 3.5 species/sample) and its more xeric communities. The gastropod fauna of the East Humboldt Range and the Ruby Mountains follow a similar distribution and species richness with gastropod faunas found in the Northern Rockies (Karlin, 1961), along the Wasatch Range of Utah (Chamberlin & Jones, 1929), and New Mexico (Hoff, 1962).

Populations of *Oreohelix strigosa* were found in the deeper glaciated canyons on the west slope of the Ruby Mountains (Figure 1: stations 9, 10, 11, 12, and 13) and one population on the east slope (Figure 1: station 27). This species was absent from 16 other canyons with comparable habitat characteristics, some of which were glaciated (Figure 1: stations 1, 3, 5, 14, 15, 16, and 20). It appears that glaciated canyons may have served as Pleistocene refugia for this species and possibly others. It is unclear why they survived in some canyons but not in others.

In the Ruby Mountains, *Oreohelix strigosa* was most often associated with boulder fields, talus slopes, and stream banks, with a cover of dense shrubs, grasses, and forbs. Most often, there was an canopy of aspen. In Colorado, this was a common habitat used by this species (Henderson, 1931) as well as in Utah (Chamberlin & Jones, 1929) and in Idaho (Solem, 1975).

Oreohelix subrudis was found at only two stations, both of which are on the west slope of the East Humboldt Range, 2200 m (Figure 1: stations 6 and 7). At these two stations, *O. subrudis* was associated with extensive aspen forest with dense litter and nearby perennial streams. Very little brush occurred at these stations. This habitat affinity is somewhat unusual for *O. subrudis.* In Wyoming, this species occurs in a broader range of elevations, from river banks with sparse cottonwood stands and mountain brush to higher elevations in aspen, mixed conifer and deciduous forest. *Oreohelix subrudis* is usually associated with talus slopes, cliff faces, and, in some cases, with other species of *Oreohelix* (Pilsbry, 1939; Chamberlin & Jones, 1929). In Colorado, *O. subrudis* occurs more often in streamside habitat, while *O. strigosa* is found nearby, but prefers the drier stream banks with talus and scree (Ress, 1988; Brandauer, 1988).

The land snails, *Discus whitneyi, Vitrina pellucida,* and *Microphysula ingersolli,* were the most abundant and widespread gastropods in the study area. They all have a strong affinity for deciduous woodlands along perennial streams. Karlin (1961) found *Discus whitneyi* and *Vitrina pellucida* to be most common in quaking aspen woodlands of Colorado, Montana, and New Mexico, but did not find *Microphysula ingersolli.* Chamberlin & Jones (1929) found *M. ingersolli* in canyon woodlands of aspen and maple in the Wasatch Mountains, and Beetle (1989) found this species in similar habitats in the Rocky Mountains in Wyoming. *Microphysula ingersolli* is one of the most widely dispersed and abundant gastropods in the Ruby Mountains and East Humboldt Range, but it is apparently absent from nearby Great Basin mountain ranges such as the Jarbidge to the north and the Cherry Creek Range directly to the south (Ports, unpublished data).

A final assemblage of snails was found in the more xeric pine and juniper woodlands, in limestone canyons of the southern Ruby Mountains (Figure 1). Although this region makes up approximately one-third of the study area, the gastropod community here was relatively small, considering that five of the eight species were found to be closely associated with perennial springs (Table 1). Away from the springs of this region, three species of land snails, *Oreohelix hemphilli, Vallonia cyclophorella,* and *Pupilla hebes,* occur in the litter of shrubs, such as mountain ninebark (*Physocarpus alternans*) and mountain spray (*Holodiscus dumosus*). These drought-resistant shrubs are sheltered by 30 to 50 meter, north-facing, vertical cliffs of limestone. Such a microhabitat serves to moderate the summer heat and provide a more mesic environment compared to the surrounding woodlands. At the higher elevations (above 3100 m) in the southern portion of the Ruby Mountains, these shrubs were few or did not occur at all; however, these three snail species were found beneath dense branches of the woody, mat-forming rock plant, *Petrophytum caespitosa.* This group of snails and its affinity for these xeric conditions is not unique to the southern Ruby Mountains and indeed has been found in six mountain ranges to the south and east of the Ruby Mountains. These mountain ranges are also dominated by limestone canyons, pinyon pine and Utah juniper woodlands, and the same species shrubs and cliff sites found in the southern Ruby Mountains (Ports, unpublished data).

The gastropod fauna of the Ruby Mountains and East Humboldt Range is typical of what would be expected in the central and eastern Great Basin on mountain ranges with peaks of 3000 m or more. Deep glaciated canyons act as refugia, with extensive deciduous forests and streams that enhance species richness. These conditions also exist in the Schell Creek Range, Deep Creek Range, and the Snake Range, all to the southeast of the study area, and these mountains have a similar fauna. The Ruby Mountains and East Humboldt Range fauna illustrate the potential for isolation and endemism, especially in *Oreohelix.* There is also the potential for local extinctions due to long-term climatic changes, such as severe drought and the loss of the limited (such as aspen forests) but critical habitat to livestock grazing, mining, and modification of water resources that would impact on spring and stream vegetation.

ACKNOWLEDGMENTS

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LITERATURE CITED

Beetle, D. E. 1989. Checklist of recent Mollusca of Wyoming, U.S.A. The Great Basin Naturalist 49(4):637–645.

Boag, D. A. & W. D. **Wishart.** 1982. Distribution and abundance of terrestrial gastropods on a winter range of bighorn sheep in southwestern Alberta. Canadian Journal of Zoology 60:2633–2640.

Brandauer, N. E. 1988. Family Oreohelicidae (Gastropoda: Pulmonata) in Colorado. Natural History Inventory of Colorado, No. 9. University of Colorado Museum, Boulder, Colorado. 32 pp.

Cameron, R. D. 1986. Environment and diversities of forest snail faunas from coastal British Columbia. Malacologia 27(2):341–355.

Chamberlin, R. C. & D. T. **Jones.** 1929. A descriptive catalog of the Mollusca of Utah. Bulletin of the University of Utah 19(4):203.

Coats, R. R. 1987. Geology of Elko County, Nevada. Nevada Bureau of Mines and Geology, Bulletin 101. 112 pp.

Coney, C. C., W. A. **Tarpley,** J. C. **Warden** & J. W. **Nagel.** 1982. Ecological studies of land snails in the Hiwassee river basin of Tennessee, U.S.A. Malacological Review 15:69–106.

Grayson, D. K. 1993. The Desert's Past: A Natural Prehistory of the Great Basin. Smithsonian Institution Press: Washington D.C. xix–356 pp.

Henderson, J. 1931. Molluscan provinces in the western United States. University of Colorado Studies 18:177–186.

Hoff, C. C. 1962. Some terrestrial Gastropoda from New Mexico. The Southwestern Naturalist 7(1):51–63.

Karlin, E. J. 1961. Ecological relationships between vegetation and the distribution of land snails in Montana, Colorado, and New Mexico. American Midland Naturalist 65(1):60–66.

Kralka, R. A. 1986. Population characteristics of terrestrial gastropods in boreal forest habitats. American Midland Naturalist 115(1):156–164.

Lewis, M. E. 1972. Flora of the Ruby Mountains and East Humboldt Range with Special Emphasis on the Lamoille Canyon Area. Humboldt National Forest, United States Forest Service, United States Department of Agriculture. 55 pp.

Pilsbry, H. A. 1939. Land Mollusca of North America (north of Mexico). Academy of Natural Sciences of Philadelphia Monograph 3, 1(1):i–vvii, 1–573, i–ix.

Pilsbry, H. A. 1946. Land Mollusca of North America (north of Mexico). Academy of Natural Sciences of Philadelphia Monograph 3, 2(1):i–viii, 1–520.

Pilsbry, H. A. 1948. Land Mollusca of North America (north of Mexico). Academy of Natural Sciences of Philadelphia Monograph 3, 2(2):i–xlviii, 521–1113.

Pratt, W. L. 1985. Insular biogeography of central Great Basin land snails: extinction without replacement. Journal of the Arizona-Nevada Academy of Sciences 20:14.

Rees, B. B. 1988. Electrophoretic and morphological characteristics of two species of *Oreohelix,* the mountain snail. Malacological Review 21:129–132.

Sharp, R. P. 1938. Pleistocene glaciation in the Ruby-East Humboldt Range, northeastern Nevada. Journal of Geomorphologyy 1(4):296–323.

Sneath, P. H. A. & R. R. **Sokal.** 1973. Numerical Taxonomy. 2nd ed. W. H. Freeman: San Francisco. 573 pp.

Solem, A. 1975. Notes on Salmon River Valley oreohelicid land snails, with description of *Oreohelix waltoni.* The Veliger 18(1):16–30.

The Veliger 39(4):342–347 (October 1, 1996)

THE VELIGER

Ventilation Rate of Cuttlefish, *Sepia officinalis*, in Response to Visual Stimuli

by

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Abstract. Ventilation rate can provide information about the detectability and salience of stimuli. Octopus ventilation rate responds to chemical stimuli; here we tested whether cuttlefish ventilation rate is sensitive to visual stimuli. We measured the changes in ventilation rate of juvenile *Sepia officinalis* in response to a general disturbance (being moved to a new tank), to the sight of prey items (live fish and live crabs), and to the sight of conspecifics (familiar and unfamiliar). Ventilation rate increased relative to controls in all cases, but most to general disturbance. Responses to prey items were stronger than reponses to conspecifics, a finding consistent with the semi-solitary lives of free-living juvenile cuttlefish. Although cuttlefish prefer crabs to fish and hunt them differently, no differences in responses were found between types of prey. Responses to familiar and unfamiliar conspecifics also did not differ. We conclude that analysis of ventilation rates is a good method for measuring the perception and relative significance of broad classes of visual stimuli in cuttlefish.

INTRODUCTION

It is not always easy to discern what animals perceive. The appearance of stimuli important to an animal can cause increased alertness, with a possible concomitant increase in ventilation rate (hereafter, referred to as "arousal"). A directly observable behavior, ventilation rate has the potential for providing a convenient measure of the relative salience of different stimuli. To investigate this possibility, we measured changes in ventilation rates of cuttlefish in response to visual stimuli.

Cephalopods change the rate or volume of water respired in response to changes in activity level. The common octopus, *Octopus vulgaris* Cuvier, 1797, increases its ventilation rate with even small increases in activity level (Boyle, 1983). The common cuttlefish, *Sepia officinalis* Linnaeus, 1758, increases ventilation volume, with a reduction in ventilation rate, when it jets (Trueman & Packard, 1968).

Cephalopods also change the rate or volume of water respired in response to chemical stimuli. In *Octopus vulgaris,* ventilation rate increased in response to crab extract and to water from a crab holding tank (Boyle, 1983). Ventilation rate in the octopus *Eledone cirrhosa* Lamarck, 1798, changed in response to several common chemical constituents of arthropod flesh (betaine, glycine, proline, alanine, lactic acid, and serine) (Boyle, 1986). Chase & Wells (1986) observed respiratory changes in *O. vulgaris* in response to weak solutions of glutamic acid, glycine, and adenosine 5′-monophosphate.

The feasibility of using ventilation rate to measure responses to chemical stimuli was demonstrated by Boyle (1983), using two different methods: (1) direct observation by an experimenter, and (2) automated measurement of the electrical impedance of the water surface, which fluctuates with the disturbances caused by ventilation movements. Automated measurements were sometimes disrupted by movements of the subject within the enclosed space or by spontaneous bursts of hyperventilation. In the experiments reported here, we measured ventilation rates by the simpler method of direct observation.

We measured the ventilation rates of *Sepia officinalis* in response to visual stimuli: live fish, crabs, shrimp, and familiar and strange conspecifics. We addressed four questions: is ventilation rate affected by (1) general disturbance (moving the animal into the test tank); (2) the presence of a food item (live shrimp); (3) the sight of a conspecific (familiar or unfamiliar); and (4) the type of live stimuli (fish, crab and other cuttlefish)? We discuss the possible relationship between relative magnitudes of ventilation changes and significance of stimuli to the cuttlefish.

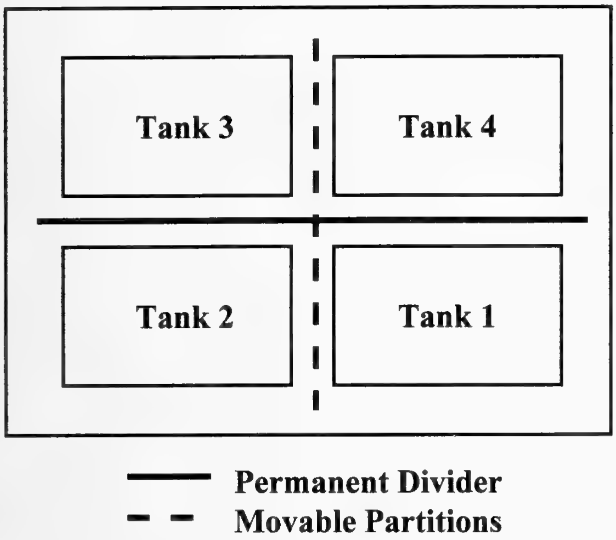

Figure 1

Schematic of test tanks. Tanks had glass bottoms, and cuttlefish were viewed from below in order to observe the ventilation movements of their funnels.

MATERIALS AND METHODS

Subjects (7.5–10.5 cm mantle length) were taken from a cohort of juvenile laboratory-cultured *Sepia officinalis* (Forsythe et al., 1991). This cohort of approximately 120 animals was maintained in groups of about 10 cuttlefish per 1.52 m diameter round tank. All 12 holding tanks, as well as the test tank, were interconnected to the same recirculating water system (see Forsythe et al., 1991). Water was obtained from the Gulf of Mexico, and ranged from 19–21°C with a salinity of 35 ppt. Light was provided with a combination of natural light and artificial light on a 12 hr light/12 hr dark cycle. The animals were fed frozen shrimp twice a day *ad libitum*.

The test tank was a glass-bottomed aquarium (109 × 90 × 90 cm). Stout timbers set on building blocks supported the tank along the outside perimeter and allowed an experimenter to view the tanks from beneath. The outer side walls of the tank were covered with dark green camouflage cloth. Four identical smaller aquariums (51 × 25 × 40 cm) were placed within the test tank in a 2 × 2 array (Figure 1). A lid made from plastic mesh fit over the four smaller tanks. A permanent opaque divider separated the tanks into two pairs; movable opaque partitions could be placed between the two tanks of each pair. A

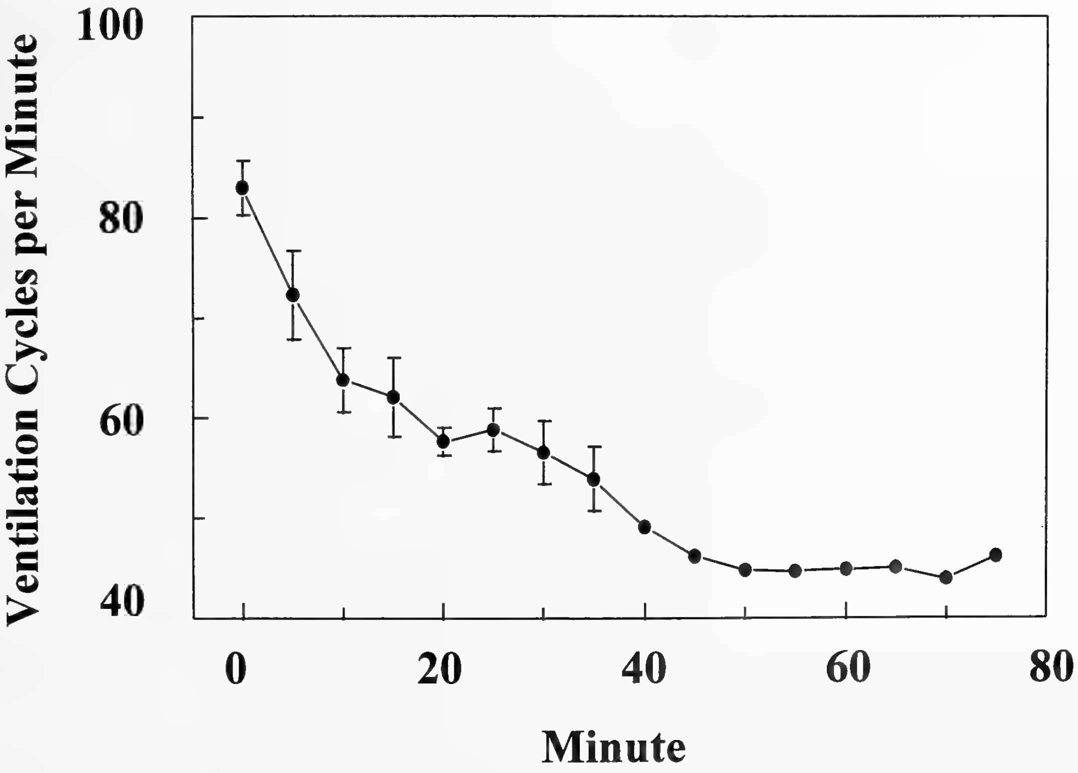

Figure 2

Experiment 1: Ventilation rate of cuttlefish ($n = 20$) after being transferred from holding tanks to test tanks (mean ± SE).

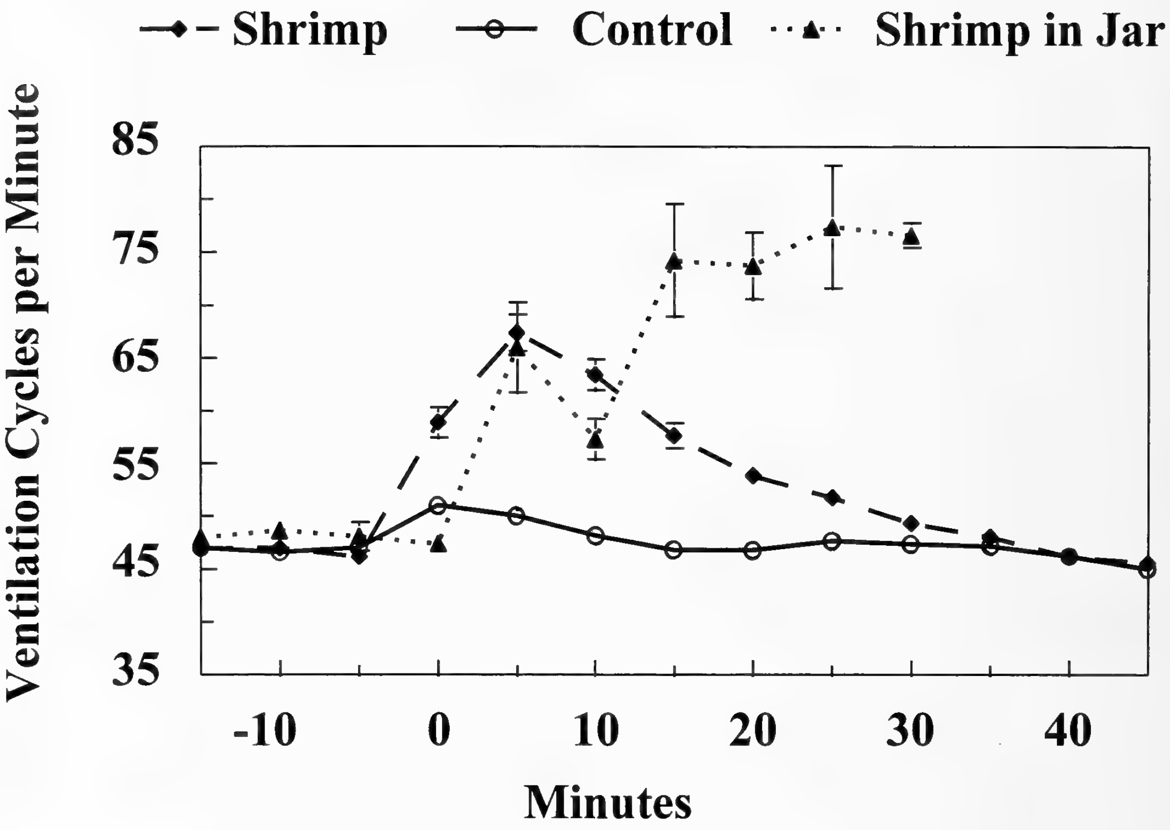

Figure 3

Experiment 2: Ventilation rate in response to the appearance of a prey item at minute 0 (mean ± SE).

small desk lamp (60 watts) was placed below the test tank, shining upward. The experimenter lay quietly beneath the tank, observing the ventral sides of the subjects.

Subjects were selected at random from the 12 holding tanks and placed in the test tank 1 hour before trials. When trials began, the experimenter recorded at 5 minute intervals the total time for 30 inhale/exhale cycles for each subject. Cycles could be observed directly from the ventilation movement of the funnel with the pressure changes of inhalation and exhalation. We compared ventilation rates before and after each event for each subject. Pre-event rates were determined by averaging the three measurements immediately prior to the event. Post-event rates were determined by averaging highest recorded rate after the event with the two recorded rates that immediately followed the peak rate.

1. General Disturbance

We recorded the responses of cuttlefish to the general disturbance of being moved to the test tank. One cuttlefish was placed into each of the four small tanks. Subjects were in visual isolation with all barriers in place. Ventilation rate was measured starting immediately after the subjects were placed into the test tanks. Sixteen subjects were observed for 1 hour; an additional four subjects were observed for 1 hour and 20 minutes.

2. Presence of Food

We recorded the response of cuttlefish to the presence of familiar food items. An inverted PVC cap, about 5 cm in diameter, was placed over a live shrimp in two of the small aquariums; in the other two aquariums the cap was empty (control). Subjects were again placed into each of the tanks, in visual isolation. After 1 hour had elapsed, caps were inverted by means of an attached string. Ventilation rate was measured at 5 minute intervals starting 15 minutes before the cap was inverted, for a total of 1 hour and 15 minutes. Twelve subjects were used, six with the shrimp and six with the control condition. For an additional two subjects, the cap and shrimp were confined within a glass jar in order to determine the effect of solely visual stimulation.

3. Sight of Conspecifics

In this experiment, we recorded the response of cuttlefish to the sight of familiar and unfamiliar conspecifics. One

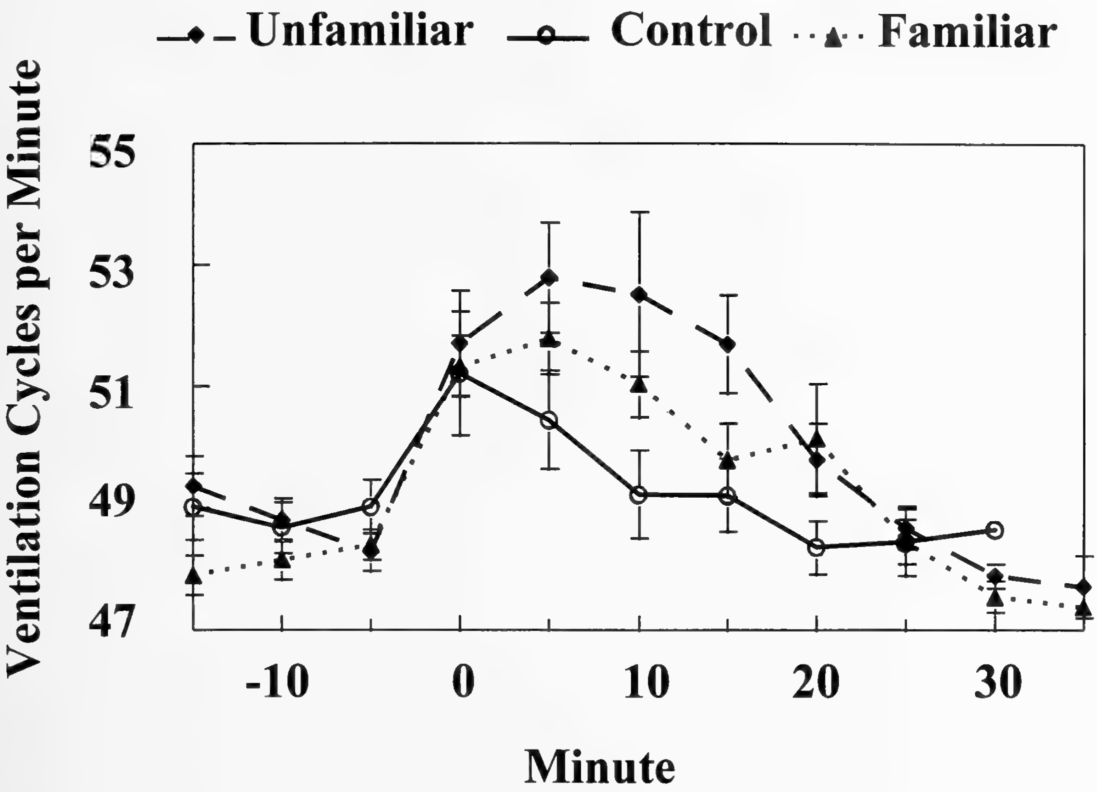

Figure 4

Experiment 3: Ventilation rate in response to the appearance of a conspecific (familiar or unfamiliar) or an empty tank (control) at minute 0 (mean ± SE).

cuttlefish was placed into each of the four small tanks. Subjects were in visual isolation. After 1 hour, the movable partitions were raised by means of an attached string. Each animal could thus see one other subject. For five pairs of subjects, both animals came from the same holding tank (familiar conspecific); for five other pairs, each individual came from a different holding tank (unfamiliar conspecific). For a further eight subjects, the adjacent tank was empty (control). Ventilation rate was measured starting 15 minutes before the barriers were raised, for a total of 1 hour and 15 minutes.

4. Differences between Stimuli

We tested whether cuttlefish arousal, as measured by ventilation rate, differed between similar-sized stimuli. We compared responses to a crab and a fish, each roughly the same size as the subject when viewed from the cuttlefish's perspective (fish total length, crab carapace width, and cuttlefish mantle length), with the responses we found in Experiment 3 to familiar and unfamiliar conspecifics.

For each pair of tanks, one cuttlefish was placed in one of the small tanks; in the other, a large glass jar was placed containing either a blue crab (*Callinectes sapidus* Rathbun, 1896) or a gulf killifish (*Fundulus grandis* Baird & Girard, 1853). The movable partition separated the tanks. After 1 hour, the movable partition was raised. Ventilation rate was measured statrting 15 minutes before the barriers were raised, for a total of 1 hour and 15 minutes. The fish was used for four subjects; the crab was used for four other subjects. Results were compared with those of Experiment 3 with familiar and unfamiliar conspecifics.

RESULTS

1. General Disturbance

Immediately after the subject was moved to the test tank (the disturbance, time 0), ventilation rates averaged 83 ventilation cycles per minute. After 50 minutes, average rates had slowed to 45 cycles per minute, a decrease of about 45%. Rates then stabilized (Figure 2).

2. Presence of Food

Treatment (control, live shrimp, live shrimp in glass jar) had a significant effect ($F = 157.51$; $df = 2,13$; $P < 0.001$) (Figure 3); ventilation rates increased about 40% in re-

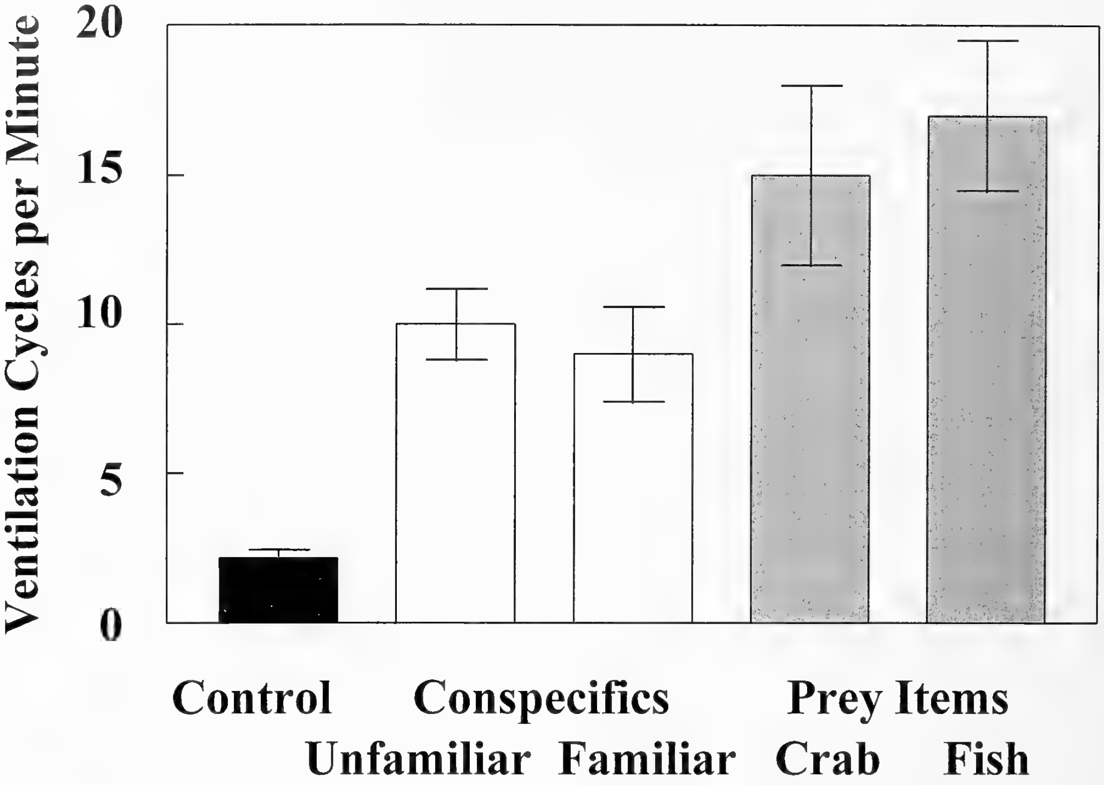

Figure 5

Experiment 4: Ventilation rate increase in response to stimuli, each of the same overall size as the subjects (mean ± SE).

sponse to the presence of the shrimp, as compared to controls. *A priori* tests between means showed that responses with the glass jar were significantly different from those without the glass jar (F = 21.36; df = 1,13; $P < 0.001$).

3. Sight of Conspecifics

In the test for response to conspecifics, treatment (control, familiar conspecific, unfamiliar conspecific) had a very small, yet statistically significant effect (F = 3.53; df = 2,25; $P < 0.05$) (Figure 4). *A priori* tests between the means showed that there was no difference in response to a familiar and an unfamiliar conspecific (F = 0.80; df = 1,25; $P \sim 0.45$).

4. Differences between Stimuli

In the experiment on the reaction of cuttlefish to other living animals of the same size as themselves, we found a small but significant difference in ventilation rate between presentation of other cuttlefish (familiar or unfamiliar) and other animals (crab or killifish) (F = 14.39; df = 2.25; $P < 0.001$) (Figure 5). There was no difference between their response to a crab and a killifish (t = 2.10, df = 3, $P > 0.05$).

DISCUSSION

Disturbance had an effect on ventilation rates of cuttlefish, as did the sight of conspecifics and other animals. These results are consistent with and extend those of Boyle (1983) and Chase & Wells (1986) on the effect of chemical stimuli on octopus ventilation rate. Ventilation rate thus appears to be a good overall indication of cephalopod arousal.

The largest influence on ventilation rate was that of the general disturbance. After the transfer to the test tank (Experiment 1), ventilation rate gradually decreased to the resting rate, a pattern consistent with an interpretation of habituating to their new surroundings.

When presented with prey items (Experiment 2), cuttlefish became quite active and focused intently on the shrimp at the same time that ventilation rates increased. Response to the shrimp in the glass jar differed significantly from that without the jar. This difference was probably a result of sustained responses by the subjects unable to reach the shrimp rather than any effect of the absence of chemosensory information. Initial response to the sight of the shrimp did not differ between the two groups (Figure 3).

Response to the sight of another cuttlefish (Experiment

3) was quite different from that to prey items. Subjects were less active and their activity was less focused in any particular direction. Ventilation rate rose only slightly more than that of controls. We found no significant difference between the response to familiar and to unfamiliar conspecifics. Although results appear suggestive that a difference might be found had we used a larger sample size or more sensitive method (Figure 4), Boal (in press) has found similar lack of evidence for social recognition in adults of the same species.

Response did not differ between the crab and fish presentations (Experiment 4). Both are prey items when they are smaller than the cuttlefish. Cuttlefish will attempt to capture same- or even larger-sized crabs and fish if they are hungry enough. In the laboratory, the cuttlefish appear to prefer crabs over fish. They also approach them differently when preying upon them (Nixon, 1987). It may be that our results did not reflect these differences because our sample size was quite small ($n = 8$). Another possible explanation is that the two live prey items were equally arousing when presented alone to hungry cuttlefish accustomed to receiving only dead food. Satiated animals might respond differently.

The cuttlefish did not respond equally to all live stimuli of approximately the same size; they were clearly more interested in food than in each other (Experiment 4). Our subjects were juveniles; results with sexually mature adults might be different.

We find it noteworthy that with this simple experimental design we were able to support results obtained with more sophisticated equipment (Boyle, 1983, 1986). Cephalopod ventilation rate is indeed responsive to visual stimuli, as well as to chemical stimuli. The magnitudes of changes in ventilation rates were consistent with interpretations of differing salience. Ventilation rate provides a robust, objective, and quantifiable behavioral measure for testing animal perception, and is sensitive enough to demonstrate discrimination between classes of stimuli.

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LITERATURE CITED

BOAL, J. G. In press. Absence of social recognition in laboratory-reared cuttlefish, *Sepia officinalis* L. (Mollusca: Cephalopoda). Animal Behavior.

BOYLE, P. R. 1983. Ventilation rate and arousal in the octopus. The Journal of Experimental Marine Biology and Ecology 69:129–136.

BOYLE, P. R. 1986. Response to water-borne chemicals by the octopus *Eledone cirrhosa* (Lamarck, 1798). The Journal of Experimental Marine Biology and Ecology 104:23–30.

CHASE, R. & M. J. WELLS. 1986. Chemotactic behaviour in Octopus. The Journal of Comparative Physiology A 158: 375–381.

FORSYTHE, J. W., R. T. HANLON & R. DERUSHA. 1991. Pilot large-scale culture of *Sepia* in biomedical research. Pp. 313–323 in E. Boucaud-Camou (ed.), The Cuttlefish: First International Symposium on the Cuttlefish *Sepia*. Centre de Publications de l'Université de Caen: France.

NIXON, M. 1987. Cephalopod diets. Pp. 201–219 in P. R. Boyle (ed.), Cephalopod Life Cycles, Vol. II. Comparative Reviews. Academic Press: New York.

TRUEMAN, E. R. & A. PACKARD. 1968. Motor performances of some Cephalopods. The Journal of Experimental Biology 49:495–507.

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THE VELIGER

Two New Species of Nudibranch Mollusks from the Gulf of the Farallones and Cordell Bank National Marine Sanctuaries, Central California

by

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Abstract. Two new species of nudibranchs are described from the central coast of California. *Armina* ***cordellensis*** is unique among described taxa in having low tubercles not arranged in distinct longitudinal rows. The radular teeth are elongate and minutely denticulate.

Aeolidia ***farallonensis*** is unique among described species in possessing a lateral anus and irregularly rugose rhinophores. The jaws are proportionately larger than in other described species. The anal position is situated ventral to the notum, a feature that is unique among described members of the Aeolidiidae.

INTRODUCTION

The opisthobranch fauna of the Pacific coast of North America has been recently reviewed (Behrens, 1991). More than 200 species have been reported from the region, including 26 undescribed species. Since then, several additional species have been recorded from deep waters off the coast of southern California (Gosliner, 1996).

Specimens of two apparently new species were examined from material held in the collections of the California Academy of Sciences. Neither species was observed alive. Both species differ markedly from sympatric congeners present in the eastern Pacific. Both species are known from relatively little material, but are sufficiently different from closely related taxa that there is little question of their distinctness.

This paper describes the anatomy of these species and compares them to morphologically similar species.

DESCRIPTIONS

ARMINIDAE

Armina Rafinesque, 1814

Armina **cordellensis** Gosliner & Behrens, sp. nov.

(Figures 1, 2)

Type material: Holotype, California Academy of Sciences, CASIZ 105717, Craine's Point, Cordell Bank, 20 km w of Point Reyes, 37°59′30″N, 123°24′30″W, 46–52 m depth, 20 October 1978, R. Schmeider et al.

Etymology: This species is named for the type locality, Cordell Bank.

External morphology: The 60 mm long preserved animal is gray dorsally and on the ventral surface of the foot. Despite the fact that the animal had been preserved in

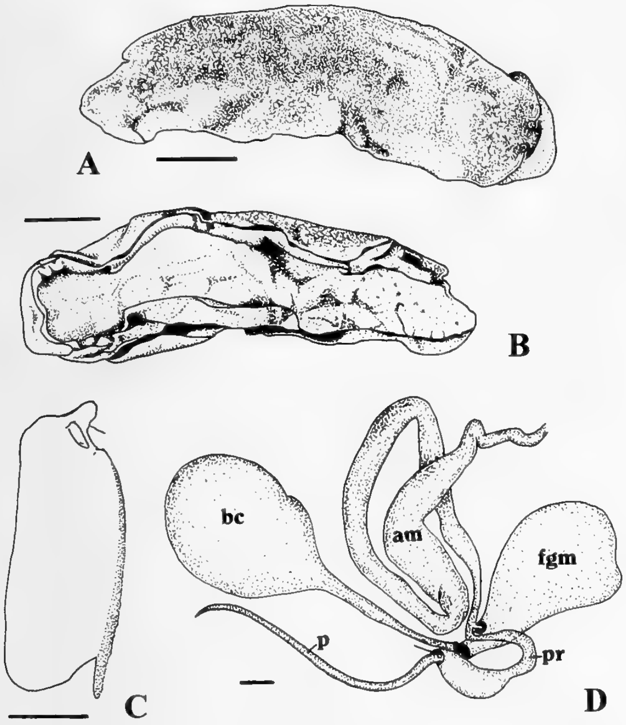

Figure 1

Armina ***cordellensis*** Gosliner & Behrens, sp. nov., holotype, CASIZ 105717. A. Dorsal view of preserved animal, scale = 10 mm. B. Ventral view of preserved animal, scale = 10 mm. C. Jaw, scale = 1.0 mm. D. Reproductive system, scale = 2.0 mm, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate.

alcohol, it appears that its color in life was also grayish, owing to the intensity of the pigment. The notum is granular with irregularly spaced, low rounded tubercles (Figure 1A). There do not appear to be any glandular sacs (cnidosacs) on the notum. The rhinophores are well separated from each other, about 2.5 mm apart, and have a series of longitudinal lamellae on the rounded, but not bulbous clavus. Between the ventral edge of the notum and the foot are a series of lamellar gills. Anteriorly, on each side of the body is a series of longitudinal lamellae. Immediately posterior to the right longitudinal lamellae are the genital apertures. Behind the apertures and extending to the posterior end of the body are 75–80 laterally arranged gill folds. The anus is situated on the right side of the body about three-fourths of the way to the posterior end of the body. The nephroproct is slightly more than halfway between the genital apertures and the anus. The foot (Figure 1B) is elongate and wide, and has a very thin epithelium.

Buccal mass: The buccal mass is elongate, 15 mm in length, and highly muscular. The salivary glands are elongate and straplike and enter the posterior end of the buccal mass. The large chitinous jaws (Figure 1C) are elongate with a long masticatory margin. The masticatory border contains 6–10 rows of triangular denticles (Figure 2A). The radula of the holotype is asymmetrical and has a formula of 48 × 42.1.69. The rachidian teeth (Figure 2B) are broad with a large, triangular central cusp. The cusp is flanked by 8–13 elongate denticles per side. The inner lateral teeth (Figure 2B) are triangular with a relatively short cusp. Approximately seven to nine short, triangular denticles are present on the outer side of each inner lateral tooth. The next several teeth outward increase markedly in the length of the cusp and in the number of denticles. The majority of teeth are elongate and needlelike (Figure 2C). The outer edge of these teeth contains about 25 minute denticles, which are not visible under low magnification, but are evident at higher magnification (Figure 2D).

Reproductive system: The arrangement of the reproductive organs (Figure 1D) is androdiaulic. The ampulla is thick and contains several convolutions. It bifurcates and enters the base of the female gland mass. The other branch is the short, slightly curved prostate. It enters the slightly expanded penial sac. The penis, which is largely protruded, is elongate and flagellar. The large, saccate bursa copulatrix has an elongate duct, which exits adjacent to the female gonopore.

Discussion: Three species of arminids are currently recognized from the Pacific coast of North America. *Armina californica* (Cooper, 1863) can be readily separated from *A.* ***cordellensis*** by aspects of its external anatomy. The rhinophores of *A. californica* are adjacent to each other and have a common stalk, whereas those of *A.* ***cordellensis*** are well separated from each other. *Armina californica* has a series of longitudinal ridges on the notum, whereas *A.* ***cordellensis*** has irregularly arranged tubercles. Internally, the rachidian teeth of *A. californica* have fewer denticles (4–7) than those of *A.* ***cordellensis*** (8–13). The outer laterals of *A. californica* are not as elongate as those of *A.* ***cordellensis*** and have large denticles only near the outer apices rather than minute ones along most of the length of the teeth. The reproductive systems of the two species differ markedly as well. In *A. californica,* the prostate is elongate with several convolutions, whereas in *A.* ***cordellensis*** the prostate consists of a single short loop.

The other two arminids are found farther to the south in subtropical and tropical waters of Baja California and Panama. *Histiomena marginata* Mörch, 1859, is known only from the type material. Mörch described the external anatomy, and Bergh (1876) did not add any significant anatomical details. This species remains poorly known, and the description is so incomplete that it cannot be adequately compared to the present species. No type material or subsequent specimens have been found. *Histiomena convolvula* (Lance, 1962) has a series of convoluted, longitudinal ridges on the notum and a greatly expanded oral veil

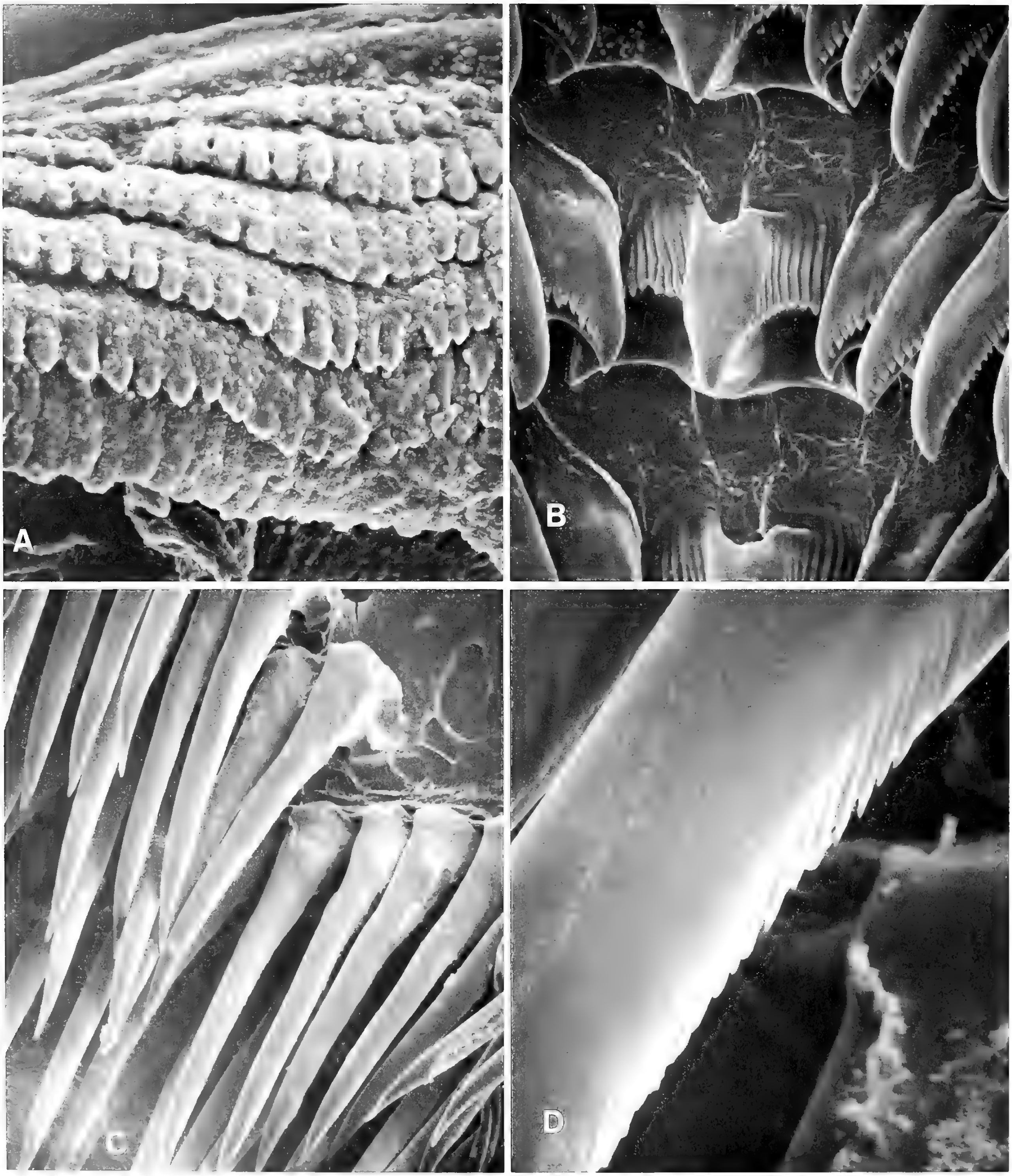

Figure 2

Armina ***cordellensis*** Gosliner & Behrens, sp. nov., holotype, CASIZ 105717, Scanning electron micrographs. A. Jaw denticles, ×500. B. Rachidian and inner lateral teeth, ×400. C. Outer lateral teeth, ×200. D. Outer lateral tooth, ×1500.

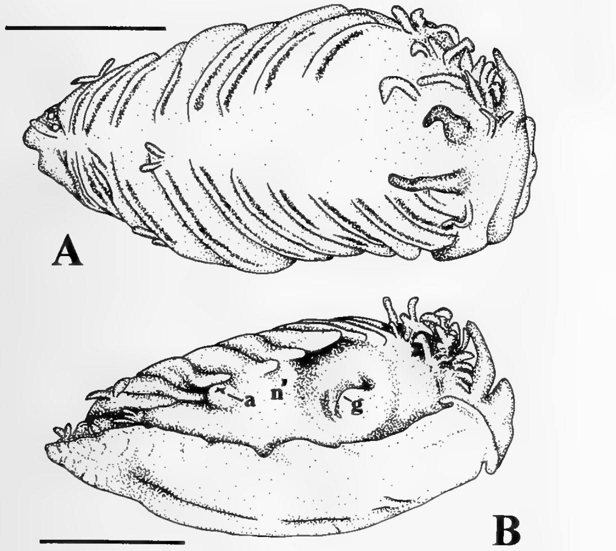

Figure 3

Aeolidia ***farallonensis*** Gosliner & Behrens, sp. nov. A. Dorsal view of preserved holotype, CASIZ 105718, scale = 10 mm. B. Lateral view of holotype, scale = 10 mm.

with an expanded margin. The posterior gills of *H. convolvula* are small fan-shaped structures arranged in four to five irregular rows (Lance, 1962), rather than the uninterrupted rows of simple lateral lamellae found in *A.* ***cordellensis.*** The rachidian radular teeth of *H. convolvula* are rectangular and lack the large triangular cusp found in *A.* ***cordellensis.*** There are more lateral teeth per half-row (88) in *H. convolvula* than in *A.* ***cordellensis*** (a maximum of 69 teeth per half-row).

Armina ***cordellensis*** is most similar to several species placed in *Linguella* Blainville, 1823, considered as a subgenus or synonym of *Armina* by modern workers. Species in this taxon have widely separated rhinophores without distinct tubercles between the anterior end of the notum and the rhinophores. The six described species, *A. fallax* (Bergh, 1880), *A. iaira* (Bergh, 1865), *A. punctilucens* (Bergh, 1874), *A. quadrilateralis* (Bergh, 1860), *A. sarasinica* (Bergh, 1890), and *A. variolosa* (Bergh, 1904), are all known from the Indo-Pacific tropics. Most of these species are known only from their original description and are incompletely described. *Armina sarasinica* differs from *A.* ***cordellensis*** in having fewer, more elongate denticles on the rachidian teeth (Bergh, 1890). *Armina variolosa* is uniformly reddish and has tubercles arranged in distinct longitudinal rows (Baba, 1955), whereas *A.* ***cordellensis*** is probably gray in life and has scattered tubercles. Also, in *A. variolosa* the genital apertures are anterior to the longitudinal gill lamellae whereas in *A.* ***cordellensis*** they are posteriorly situated. *A. variolosa* also has fewer lateral teeth (22–26) than *A.* ***cordellensis*** (42–69).

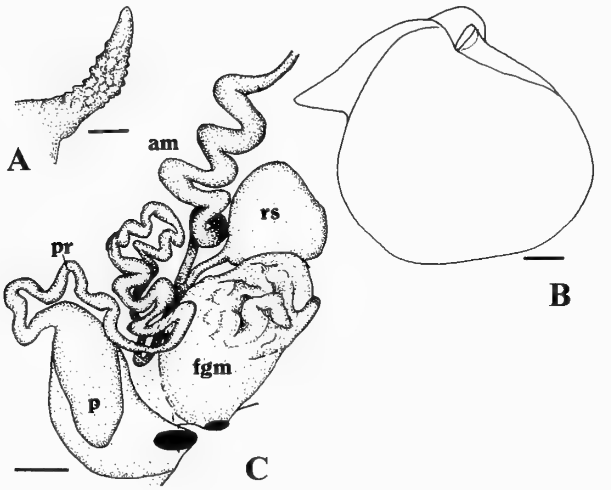

Figure 4

Aeolidia ***farallonensis*** Gosliner & Behrens, sp. nov. A. Rhinophore, scale = 1.0 mm. B. Jaw, scale = 1.0 mm. C. Reproductive system of paratype, CASIZ 105719, scale = 2.0 mm, am = ampulla, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis.

AEOLIDIIDAE

Aeolidia Cuvier, 1798

Aeolidia ***farallonensis*** Gosliner & Behrens, sp. nov.

(Figures 3–5)

Type material: Holotype, California Academy of Sciences, CASIZ 105718, off Farallones Islands, Gulf of Farallones, 37°27.9′N, 123°02′W, trawled from 510 m depth, 13 December 1985, Robert Van Syoc. Paratype, dissected, California Academy of Sciences, CASIZ 105719, off Farallones Islands, 37°35.3′N, 123°14.5′W, trawled between 1405–1491 m depth, 13 December 1985, Robert Van Syoc.

Etymology: This species is named for the Farallones Islands, from which the type material was collected.

External morphology: Both the holotype (Figure 3A, B) and paratype are largely devoid of cerata. Only a few scattered cerata remain attached to the notum. The preserved specimens are approximately 25 mm in length. The rhinophores (Figure 4A) are rugose with fine papillations scattered along their length. The oral tentacles are elongate and evenly tapered. The cerata are arranged on diagonal ridges. There are 13 ridges per side in both specimens examined. The anteriormost row contains 12 cerata while the seventh row has 38 cerata, based on the number of attachment bases that are still visible. The cerata appear to be dorsoventrally flattened in the few remaining cerata, but only small cerata are present. The anus, nephroproct, and genital aperture are visible on the right side of the body (Figure 3B). The genital aperture is situated ventral to the fourth to sixth ceratal rows in the paratype and

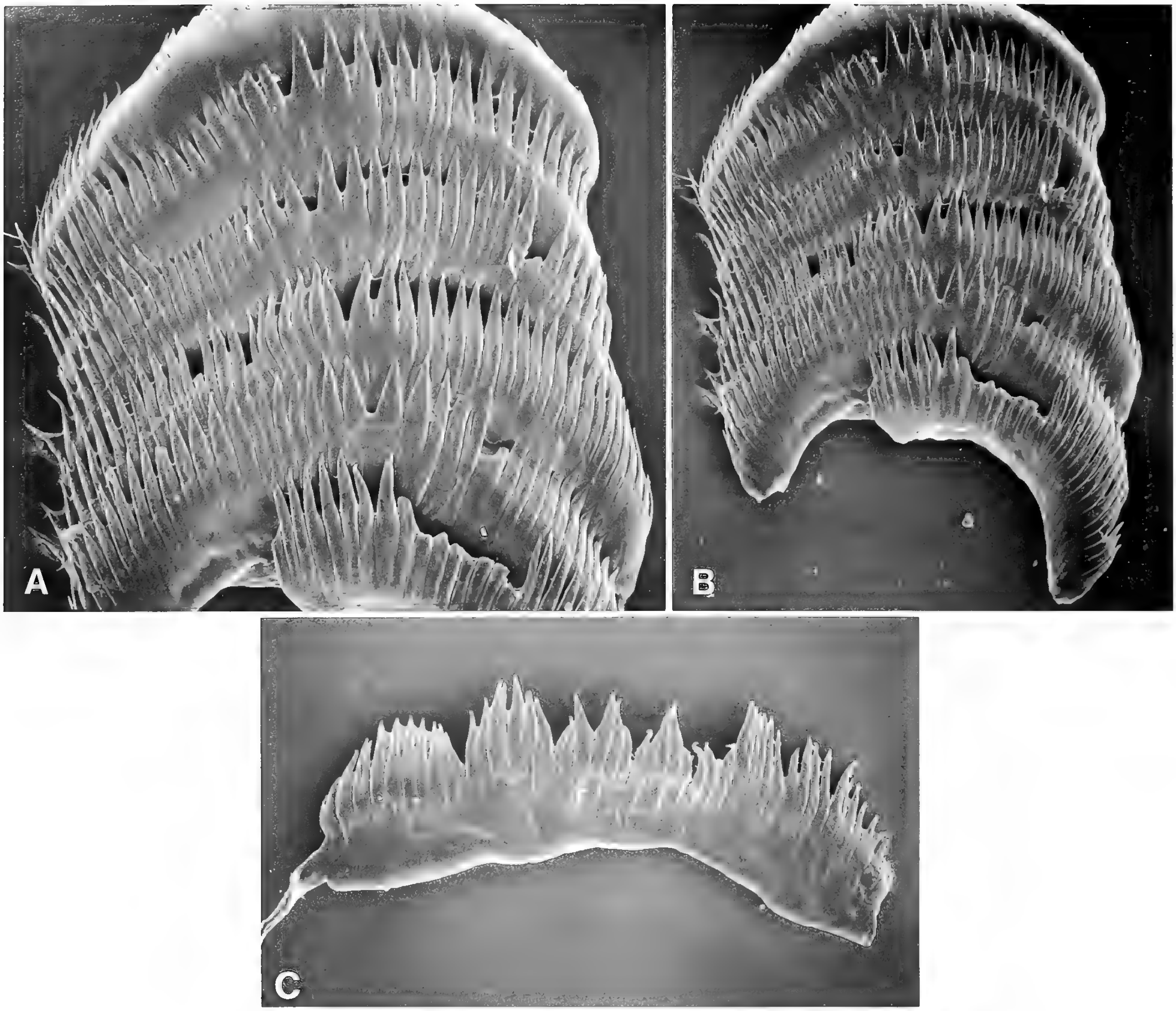

Figure 5

Aeolidia ***farallonensis*** Gosliner & Behrens, sp. nov. Scanning electron micrographs of radular teeth of paratype, CASIZ 105719. A. ×110 B. ×80. C. ×120.

between the fifth to seventh rows in the holotype. The nephroproct is found at the base of the seventh or eighth ceratal row. The anus is pleuroproctic, situated ventral to the ceratal rows. In the holotype it is found below the ninth and tenth ceratal rows, while it is found ventral to the eighth and ninth ceratal rows in the paratype. The anterior end of the foot is thickened, and short angular foot corners are present (Figure 3B).

Buccal mass: The buccal mass is thick and muscular. The jaws are thick and massive. The jaws of the paratype (Figure 4B) are 9 mm long and 9 mm wide. The masticatory border is elongate and completely devoid of any denticles. The radula of the paratype is uniseriate and contains 30 teeth. The teeth (Figure 5) are pectinate with 38–53 shallow, triangular denticles. There is no median denticle. The two innermost denticles are widest and divergent, forming a "v" between them. The denticles vary in height and curvature.

Reproductive system: The reproductive system (Figure 4C) is androdiaulic. The ampulla is thin and highly convoluted. It bifurcates to the female gland mass and the elongate and extremely convoluted vas deferens. The large, saccate receptaculum seminis has a moderately long duct which joins the ampulla immediately prior to the bifur-

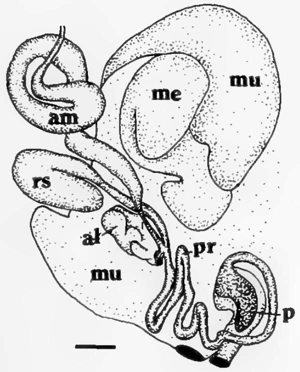

Figure 6

Aeolidia papillosa (Linnaeus, 1761). Reproductive system of specimen from Channel Islands, California, CASIZ 064212, scale = 1.0 mm, al = albumen gland, am = ampulla, me = membrane gland, mu = mucous gland, p = penis, pr = prostate, rs = receptaculum seminis.

cation of the female gland mass and vas deferens. The penial bulb is large and is occupied largely by the large, muscular, bulbous penial papillae, which are devoid of any armature.

Discussion: The systematics of the genus *Aeolidia* remains the subject of some confusion. Presently, only a single species, *A. papillosa* (Linnaeus, 1761), is recognized (Marcus, 1959, 1961), though populations are widely separated in the North Atlantic, North Pacific, and the subspecies, *A. papillosa serotina* Bergh, 1873, in the southern Atlantic and Pacific of South America. The present material of *A.* ***farallonensis*** differs from all described material of *A. papillosa* and from North Atlantic (New Hampshire and Maine) and North Pacific material (central and southern California) of *A. papillosa* examined in this study. The present material of *A.* ***farallonensis*** has rugose to papillate rhinophores, whereas the rhinophores of all specimens of *A. papillosa* are entirely smooth. The foot corners of *A.* ***farallonensis*** appear to be more highly developed than in *A. papillosa*. Specimens of *A. papillosa* have more ceratal rows (17) than specimens of *A.* ***farallonensis*** of a comparable size (13). The most obvious difference between the two species is the position of the anus. In all specimens of *A. papillosa,* the anus is cleioproctic (high up on the body), situated well within the space between the ceratal rows, whereas in *A.* ***farallonensis*** the anus is situated below the most ventral cerata in the pleuroproctic position. A pleuroproctic anus is considered plesiomorphic for aeolidaceans (Gosliner & Kuzirian, 1990). There appear to be more cerata per row in specimens of *A.* ***farallonensis.*** In *A.* ***farallonensis***, there were up to 38 cerata per row, whereas in specimens of *A. papillosa* there were a maximum of 19–25 cerata per row.

Internally, the jaws of *Aeolidia* ***farallonensis*** are almost twice as long and more than twice the width of those of a specimen of *A. papillosa* of the same size. The radular teeth are similar in the two species in number of teeth and denticles. The shape of the teeth seems more highly arched with more evenly graded, parallel denticles in specimens of *A. papillosa.* In *A. papillosa,* there is usually a small median denticle, whereas in *A.* ***farallonensis*** the two adjacent denticles at the median are strongly divergent rather than parallel.

The reproductive system of the two species is similar. It has not been depicted in most previous descriptions of *A. papillosa,* except by Odhner (1939) and is shown here in Figure 6. The vas deferens of *A.* ***farallonensis*** is much longer and more highly convoluted than that of *A. papillosa,* and the penial papilla is proportionately larger in *A.* ***farallonensis.***

Although some questions remain as to the systematic status of specimens presently united as *A. papillosa,* all material is clearly distinct from *A.* ***farallonensis.***

ACKNOWLEDGMENTS

We thank the staff of the Gulf of the Farallones and Cordell Bank National Marine Sanctuaries for financial support of publication costs of this work. Robert Van Syoc collected the specimens of *Aeolidia* ***farallonensis.*** Robert Schmeider and many other divers collected valuable material from Cordell Banks, in which the present specimen of *Armina* ***cordellensis*** was included. Staff of the Photography Department of the California Academy of Sciences prepared the prints of the scanning electron micrographs.

LITERATURE CITED

BABA, K. 1955. Opisthobranchia of Sagami Bay. Supplement. Iwanami shoten: Tokyo. 59 pp.

BEHRENS, D. W. 1991. Pacific Coast Nudibranchs. 2nd ed. Sea Challengers: Monterey. 107 pp.

BERGH, R. 1876. Neue Beitröge zur Kenntniss der Pleurophyllidien. Malakozoologische Blatter 23:1–14.

BERGH, R. 1890. Weitere Beitröge zur Kenntniss der Pleurophyllidien. Verhandlungen der k. k. zoologisch-botanischen Gesellschaft in Wien 40:1–14.

GOSLINER, T. 1996. Opisthobranchia. Pp. 1–52. in F. G. Hochberg and P. Scott (eds), Taxonomic Atlas of the Santa Maria Basin. Vol. 8. Mollusca. Santa Barbara Museum of Natural History: Santa Barbara California.

GOSLINER, T. & A. KUZIRIAN. 1990. Two new species of Flabellinidae (Opisthobranchia: Aeolidacea) from Baja California. Proceedings of the California Academy of Sciences 47(1):1–15.

LANCE, J. 1962. A new species of *Armina* (Gastropoda: Nudibranchia) from the Gulf of California. The Veliger 5(1): 51–54.

MARCUS, E. 1959. Reports of the Lund University Chile Expedition 1948–49, 36. Lamellariacea und Opisthobranchia. Lunds Universitets Arsskrift N.F. 2 55 (9):1–133.

MARCUS, E. 1961. Opisthobranch mollusks from California. The Veliger 3(supplement):1–85.

ODHNER, N. 1939. Opisthobranchiate Mollusca from the western and northern coasts of Norway. Det Kongelige Norske Videnskabersselskabs Skrifter 1:1–93.

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NOTES, INFORMATION & NEWS

Analysis of Sugars in the Hemolymph and Digestive Gland-Gonad Complex (DGG) of *Biomphalaria glabrata* and *Helisoma trivolvis* (Colorado and Pennsylvania Strains) Maintained on Restricted Diets

by

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Glucose is the most common monosaccharide reported to be present in numerous species of gastropods (Livingstone & de Zwann, 1983). According to this review, other sugars have also been reported in the hemolymph and tissues of gastropods, including fructose, xylose, ribose, and galactose in the freshwater snail *Lymnaea luteola*; galactose, fucose, and mannose in the land snail *Helix pomatia*; maltose, maltotriose, and maltotetrose in the slug *Ariolimax columbianus*; and trehalose in several species of freshwater and marine snails. More recently, Anderton et al. (1993) reported the presence of trehalose and glucose in the medically important planorbid snail *Biomphalaria glabrata* (Say, 1818), and Conaway et al. (1995) noted similar findings for two strains of the North American planorbid snail *Helisoma trivolvis* (Say, 1816).

In the above-mentioned reports, snail diets were not controlled, i.e., snails were fed leaf lettuce *ad libitum*. Recent work has been done in which planorbid snails were maintained either without food (starved) or on restricted diets. Studies on the effects of restricted diets on the levels of hemolymph glucose in *B. glabrata* have given contradictory results. Using spectrophotometry, Christie et al. (1974) and Stanislawski & Becker (1979) found that hemolymph glucose levels decreased in starved *B. glabrata*, but Thompson & Mejia-Scales (1993) reported an elevation in glucose concentration levels in those snails deprived of food. A purpose of this research was to resolve these disparities by use of high performance thin layer chromatography (HPTLC) to determine hemolymph glucose levels in *B. glabrata* and *H. trivolvis* snails (Colorado and Pennsylvania strains) maintained on restricted diets. Additionally, glucose levels in the digestive gland-gonad complex (DGG) of these snails were examined. HPTLC analyses of the sugars in the hemolymph and DGG of these snails were also carried out, and results compared with previous studies on sugars in gastropods.

Materials and Methods

Stock cultures of an albino strain (M-line) of *B. glabrata* (10–12 mm shell diameter) and two strains of *H. trivolvis* (Colorado and Pennsylvania) snails (9–15 mm shell diameter) were maintained in artificial spring water under diffuse overhead fluorescent light for 12 hr/day at 22–24°C, and were fed boiled leaf lettuce supplemented with Tetramin fish food (Duncan et al., 1987). A group of seven snails of each strain was removed from a stock culture and placed in a plastic beaker containing 300 mL of artificial spring water. A wire screen (2 mm mesh) was placed 2.5 cm from the bottom of the plastic container so that fecal matter would fall through the mesh and prevent snail coprophagy. Each group of snails was maintained on one of three feeding regimens for 1 week. The unrestricted group was fed boiled leaf lettuce (*Lactuca sativa*) *ad libitum* with one weekly supplement of Tetramin (fish food). The restricted group was given 15 mg of boiled lettuce every other day, and the starved group was maintained without food. All snails were maintained at 22–24°C with a 12 hour light:12 hr dark photoperiod. Food for the unrestricted group and water for each group were changed daily.

After 1 week, the hemolymph and DGG samples from four to seven snails per group were prepared as described previously (Anderton et al., 1993). Each experiment was repeated three to five times for each strain of snail. All hemolymph and DGG samples were initially reconstituted in 200 μL of 70% ethanol.

HPTLC was performed on Merck high performance preadsorbent silica gel plates (No. 13 153) following the procedures described in detail earlier (Conaway et al., 1995). The layer was impregnated with sodium bisulfite and citrate buffer and developed for a distance of 7 cm by ascending chromatography three times in the same direction with ethanol-glacial acetic acid-methanol-water (60:15:15:10) or acetonitrile-water (85:15), and sugar zones were detected with 1-naphthol-sulfuric acid reagent.

Quantification of glucose was carried out by scanning sample and standard zones at 515 nm using a Shimadzu CS-930 densitometer, as was also described earlier (Conaway et al., 1995). If the scan area of at least one of the 2.00–8.00 μL aliquots of reconstituted hemolymph samples or the 1.00–7.50 μL aliquots of reconstituted DGG sample was not bracketed by the areas of the spotted standards (Conaway et al., 1995), samples were quantitatively concentrated by nitrogen blow-down and reconstituted in a smaller volume (typically 30.0 μL), or diluted, as necessary. The concentration of glucose was calculated using the equations described previously (Anderton et al., 1993), with incorporation of dilution or concentration factors as needed. The Student's t-test was employed to determine the significance of differences between the mean concentrations of glucose in the hemolymph and DGG of the three strains of snails. A value of $P < 0.05$ was considered to be significant.

To identify other sugars in the hemolymph and DGG of the three snail types, 1.20 μL of 1.00 μg/μL standard solutions of glucose, trehalose, maltose, fructose, sucrose, xylose, mannose, lactose, raffinose, galactose, fucose, melezitose, and ribose were spotted on the same plate with the sample solutions, and R_f values of standard and sample zones were compared in both mobile phases. In order to confirm the identify of sugars made on the basis of a match in sample and standard R_f values, a spiked sample was prepared by mixing equal volumes of a 1.00 μg/μL standard of the presumed sugar and reconstituted hemolymph or DGG sample. The spiked sample was spotted on a plate along with the sugar standard and unspiked sample.

Results

Hemolymph and DGG glucose concentrations resulting from the feeding experiments for the three snail strains are given in Table 1. The data in this table indicate that glucose concentrations were highly variable. The Student's t-test, which was used to test the significance of the differences in the glucose levels in the hemolymph and DGG of the snails depending on their diets, was carried out as follows: unrestricted vs. restricted, unrestricted vs. starved, and restricted vs. starved for all snail strains. The results of these tests gave values of $P > 0.05$ for all comparisons, indicating that restricted diets do not have a significant difference on hemolymph or DGG concentrations. Calibration curves of the glucose standards produced during these quantitative analyses had linearity correlation coefficients (R values) of 0.94–0.99.

Contrary to the findings of Anderton et al. (1993) and Conaway et al. (1995), maltose rather than trehalose was identified as a major sugar in addition to glucose in the hemolymph and DGG samples of the snail samples. This identification was indicated by an exact match in R_f values between sample and maltose standard zones in both the acetonitrile-water and ethyl acetate-acetic acid-methanol-water solvent systems, and was confirmed by the spiking experiments. Samples spiked with trehalose gave an extra zone that lined up with the trehalose standard, whereas the samples spiked with maltose gave only a single, symmetrical zone that was more intense but had an identical R_f value compared to the maltose standard and unspiked sample zones. Table 2 lists R_f values in both solvent systems for standards of all sugars studied.

Table 1

Effect of restricted diets on hemolymph glucose concentration and % glucose levels in the DGG of *Biomphalaria glabrata* and *Helisoma trivolvis* (Colorado and Pennsylvania strains).

Snail strain	Type of diet	Mean ± SE glucose in hemolymph (mg/dL)	Mean ± SE % glucose in DGG
B. glabrata	Unrestricted	101 ± 17	0.15 ± 0.03*
	Restricted	64 ± 22	0.42 ± 0.01
	Starved	59 ± 10	0.20 ± 0.04
H. trivolvis (CO)	Unrestricted	32 ± 11	0.027 ± 0.002
	Restricted	22 ± 8	0.023 ± 0.004
	Starved	14 ± 2	0.021 ± 0.003
H. trivolvis (PA)	Unrestricted	10 ± 2	0.021 ± 0.004
	Restricted	5.3 ± 0.6	0.018 ± 0.001
	Starved	8 ± 1	0.018 ± 0.003

* $n = 2$; $n = 3$–5 samples in all other trials.

Table 2

R_f values of standards on a high performance silica gel plate impregnated wth sodium bisulfite and citrate buffer and developed with (1) acetonitrile-water (85:15) or (2) ethyl acetate-acetic acid-methanol-water (60:15:15:10).

Sugar	R_f value	
	Solvent (1)	Solvent (2)
Glucose	0.41	0.70
Trehalose	0.19	0.48
Maltose	0.22	0.54
Fructose	0.45	0.70
Sucrose	0.28	0.60
Xylose	0.56	0.80
Mannose	0.43	0.72
Lactose	0.19	0.45
Raffinose	0.082	0.33
Galactose	0.34	0.66
Fucose	0.58	0.78
Melezitose	0.13	0.39
Ribose	0.58	0.78

Discussion

The two mobile phases employed in our analyses were originally recommended by Fell (1990), who performed three unidimensional developments for the acetonitrile-water solvent but only one for the acidic solvent. We used three developments with each mobile phase because of the improved resolution achieved, resulting in more certain identification of the sugar zones.

Thompson & Mejia-Scales (1993) showed a significant decline in hemolymph glucose levels of *B. glabrata* snails maintained on restricted diets. In this study, there was no significant decline in hemolymph glucose levels in either *B. glabrata* or *H. trivolvis* snails maintained on restricted diets. Thompson & Mejia-Scales (1993) did not examine sugar levels of the DGG of *B. glabrata* snails maintained on restricted diets.

Some differences are apparent between the Thompson & Mejia-Scales (1993) study and our present study that may account, at least in part, for the disparate findings. They maintained their snails for 4 weeks at 26°C with a photoperiod of 16 hr light:8 hr dark, whereas our snails were kept for 1 week at 22–24°C with a 12 hr:12 hr light: dark photoperiod. Moreover, analysis in the Thompson & Mejia-Scales (1993) study was by spectrophotometry, whereas HPTLC was used in our study.

Regardless of the feeding regimens used in both studies, the range of hemolymph glucose values in *B. glabrata* in mg% was 3.2 to 8.1 in Thompson & Mejia-Scales (1993) and 59.3 to 101.3 in the present study. As mentioned in the previous paragraph, differences between the two studies probably accounted in part for such disparate results.

Our previous reports on sugars in planorbid snails (Anderton et al., 1993; Perez et al., 1994; Conaway et al., 1995) have identified trehalose, in addition to glucose, as major hemolymph carbohydrates. The identification of trehalose in these studies was based on comigration of sample zones at R_f 0.19 with a trehalose standard zone using the acetonitrile-water (85:15) solvent system of Fell (1993). During the present study, comigration of the trehalose standard band and the corresponding snail sample bands did not occur, but a major sugar zone at R_f 0.22 comigrated with maltose and was clearly separated from the trehalose standard band in the acetonitrile-water solvent. Identification of this second major sugar in hemolymph as maltose was confirmed using triple development with the acidic solvent system of Fell (1993) and spiking experiments in both solvents, as described above. The presence of maltose in gastropods has been reported previously (see review in Livingstone & de Zwann, 1983). Other zones were detected in the chromatograms of hemolymph and DGG samples, but they did not line up with any of the standard zones and could not be identified.

We are not sure of the occurrence of trehalose in planorbid snails. Fairbairn (1958) first reported on the presence of trehalose in *B. glabrata* based on spectrophotometric analysis. Our earlier HPTLC studies (not confirmed in the present study) based on comigration of a significant sugar zone with an authentic trehalose standard also suggested significant amounts of trehalose in *B. glabrata,* the concentrations of which were reported (Anderton et al., 1993; Perez et al., 1994; Conaway et al., 1995). Unpublished observations by S. N. Thompson (personal communication, 1995) based on HPTLC analysis of *B. glabrata* hemolymph extract suggested the presence of trace amounts of trehalose; moreover, unpublished observations by N. Wisnewski (personal communication, 1992) based on gas chromatography/mass spectrometry (GC/MS) analyses indicated the presence of trehalose in both the hemolymph and DGG of *B. glabrata.* The qualitative and quantitative analysis of trehalose in planorbid snails needs further examination.

Acknowledgments

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Literature Cited

ANDERTON, C. A., B. FRIED & J. SHERMA. 1993. HPTLC determination of sugars in the hemolymph and digestive gland-gonad complex of *Biomphalaria glabrata* snails. Journal of Planar Chromatography-Modern TLC 6:51–54.

CHRISTIE, J. D., W. B. FOSTER & L. A. STAUBER. 1974. The effect of parasitism and starvation on carbohydrate reserves of *Biomphalaria glabrata.* Journal of Invertebrate Pathology 23:55–62.

CONAWAY, C. A., B. FRIED & J. SHERMA. 1995. High performance thin layer chromatographic analysis of sugars in *Helisoma trivolvis* (Pennsylvania strain) infected with larval *Echinostoma trivolvis* and in uninfected *H. trivolvis* (Pennsylvania and Colorado strains). Journal of Planar Chromatography-Modern TLC 8:184–187.

DUNCAN, M., B. FRIED & J. SHERMA. 1987. Lipids in fed and starved *Biomphalaria glabrata* (Gastropoda). Comparative Biochemistry and Physiology 86A:663–665.

FAIRBAIRN, D. 1958. Trehalose and glucose in helminths and other invertebrates. Canadian Journal of Zoology 36:787–795.

FELL, R. D. 1990. The qualitative and quantitative analysis of insect hemolymph sugars by high performance thin-layer chromatography. Comparative Biochemistry and Physiology 95A:539–544.

LIVINGSTONE, D. R. & A. DE ZWANN. 1983. Carbohydrate metabolism of gastropods. Pp. 177–242 in P. W. Hochachka (ed.), Mollusca, Vol. 1, Metabolic Biochemistry and Molecular Biomechanics. Academic Press: Orlando, Florida.

PEREZ, M. K., B. FRIED & J. SHERMA. 1994. High Performance thin-layer chromatographic analysis of sugars in *Biomphalaria glabrata* (Gastropoda) infected with *Echinostoma caproni* (Trematoda). Journal of Parasitology 80:336–338.

STANISLAWSKI, E. & W. BECKER. 1979. Influences of semisynthetic diets, starvation and infection with *Schistosoma mansoni* (Trematoda) on the metabolism of *Biomphalaria glabrata* (Gastropoda). Comparative Biochemistry and Physiology 63A:527–533.

THOMPSON, S. N. & V. MEJIA-SCALES. 1993. Effects of restricted food intake on hemolymph glucose concentration and digestive gland-gonad lipid level in the schistosome vector *Biomphalaria glabrata* (Say) (Gastropoda: Planorbidae). The Veliger 36:425–432.

New Records of Phylliroidae (Opisthobranchia: Nudibranchia) from the Gulf of California, Mexico

by

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Nudibranchs of the family Phylliroidae lead a pelagic existence, spending their entire life cycles in the open ocean. They have been considered parasites of medusae and siphonophores by Ankel (1952), Martin & Brinckmann (1963), Martin (1966), and Sentz-Braconnot & Carré (1966). Recently, Lalli & Gilmer (1989) re-examined the particular nutritional types of members of this family and their species relationships with other planktonic animals. They suggested that the association with coelenterates is clearly one of predator and prey. This paper reports the occurrence of two species of Phylliroidae in the Gulf of California. Both are well known from the Mediterranean Sea (Ankel, 1952; Rose, 1957; Martin & Brinckmann, 1963). They also occur in the Atlantic Ocean (Van der Spoel, 1970; Abbott, 1974), but their records in the Pacific Ocean are scarce.

Taxonomy and Geographic Distribution

Suborder Dendronotina Odhner, 1934

Superfamily DENDRONOTOIDEA Odhner, 1934

Family PHYLLIROIDAE Férussac, 1821

Genus *Phylliroe* Péron & Lesueur, 1810

Phylliroe bucephala Péron & Lesueur, 1810

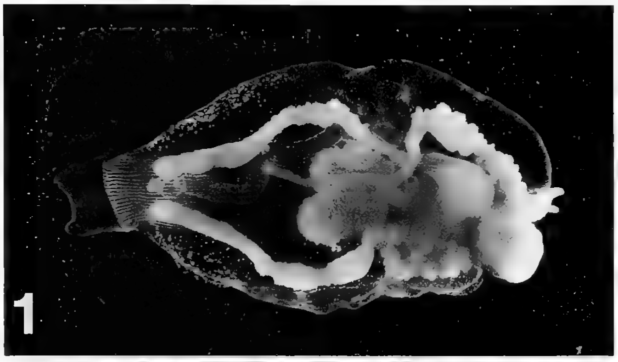
(Figure 1)

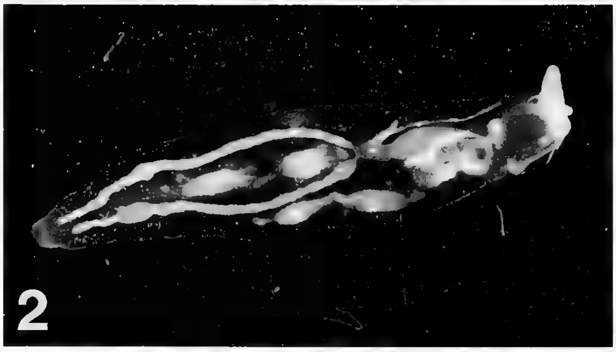
Previous records in the Pacific Ocean: New Zealand, Hauraki Gulf between Mokohinau Islands and Kawan Island, and off Cape Bret (Powell, 1937, 1979). Coastal waters off New South Wales, Australia (Dakin & Colefax, 1940). North-east Pacific off North American coast at 33°19′N, 128°27′W (Dales, 1953). West coast of Mexico, between latitudes 14° and 24°N (Keen, 1971).

Material examined: It was collected by Centro Interdisciplinario de Ciencias Marinas (CICIMAR), Instituto Politécnico Nacional in La Paz, Baja California, México, during the GOLCA 8404 cruise in March and April 1984, with oblique net-tows from a depth of 200–0 m. Station data are: sta. 92 (26°16′N, 110°29′W) 31 March, 1 specimen; sta. 95 (25°50′N, 110°12′W) 1 April, 3 specimens; sta. 98 (26°22′N, 109°43′W) 1 April, 1 specimen; sta. 105 (25°14′N, 110°16′W) 2 April, 1 specimen; sta. 110 (25°09′N, 109°20′W) 3 April, 1 specimen; sta. 123 (24°27′N, 108°30′W) 4 April, 1 specimen; sta. 125-A (24°02′N, 108°18′W) 6 April, 1 specimen.

Additional material: Specimens were sorted from zooplankton samples collected with open-closed net (Leavitt 1 m), during the El Golfo 6311-12 cruise (November–December, 1963) of the Scripps Institution of Oceanography, University of California, San Diego (SIO) in the following localities: sta. III (26°32′N, 111°03′W) 19 November, 50 m depth, 1 specimen; sta. III-A (26°36′N, 110°03′W) 20 November, 40 m depth, 1 specimen; sta. III-A (26°36′N, 110°03′W) 20 November, 50 m depth, 2 specimens; sta. III-B (26°32′N, 111°03′W) 20 November, 60 m depth, 5 specimens.

Measurements in millimeters: Largest: 19.0 length, 8.0 width; smallest: 4.0 length, 1.7 width.





Explanation of Figures 1 and 2

Figure 1. *Phylliroe bucephala* from the GOLCA 8404 cruise, sta. 123. L.I.UNAM3767. A preserved specimen in formalin. Size: 17 × 8 mm.

Figure 2. *Cephalopyge trematoides* from the GOLCA 8404 cruise, sta. 117-A. L.I.UNAM3776. A preserved specimen in formalin. Size: 5.9 × 0.7 mm.

Genus *Cephalopyge* Hanel, 1905

Cephalopyge trematoides (Chun, 1889)

(Figure 2)

Previous records in the Pacific Ocean: Shimizu Bay, Japan (Baba, 1933); off coast of New South Wales, Australia (Dakin & Colefax, 1936, 1937); North-eastern Pacific, 28°30′N, 117°58′W (Dales, 1953); Camp Cove, Port Jackson, New South Wales, Australia, North-eastern Pacific, 28°38.1′N, 115°15.9′W; 33°24′N, 117°55′W (Steinberg, 1956).

Material examined: It was collected by CICIMAR, Instituto Politécnico Nacional, La Paz, Baja California Sur, during the GOLCA 8404 cruise in March and April 1984, with oblique net-tows from a depth of 200–0 m. Station data are: sta. 61 (27°33′N, 112°23′W) 26 March, 1 specimen; sta. 93 (25°39′N, 110°40′W) 31 March, 2 specimens; sta. 100 (26°15′N, 109°25′W) 1 April, 1 specimen; sta. 106 (24°41′N, 110°19′W) 2 April, 2 specimens; sta. 108 (24°53′N, 109°55′W) 3 April, 1 specimen; sta. 110 (25°08′N, 109°20′W) 3 April, 1 specimen; sta. 116 (24°45′N, 109°04′W)

4 April, 1 specimen; sta. 117 A (24°24′N, 110°04′W) 4 April, 4 specimens; sta. 120 (24°03′N, 109°20′W) 5 April, 1 specimen; sta. 122 (24°14′N, 108°46′W) 5 April, 1 specimen; sta. 123 (24°47′N, 108°29′W) 5 April, 1 specimen; sta. 129 (23°47′N, 108°03′W) 7 April, 1 specimen; sta. 134 (23°07′N, 109°20′W) 7 April, 1 specimen.

Additional material: A zooplankton sample from the El Golfo 6311-12 cruise (November–December, 1963) of the Scripps Institution of Oceanography, University of California, San Diego. It was taken with open-closed net (Leavitt 1 m) in the Station II-A (25°36′N, 110°15′W) 17 November, 40 m depth, 1 specimen.

Measurements in millimeters: Largest: 7.5 length, 0.7 width; smallest: 2.7 length, 0.5 width.

Comments: Detailed descriptions and illustrations of this species are given by Stubbings (1937, as *Cephalopyge arabica*), and Steinberg (1956). In the studied specimens it was not possible to find the radula, possibly because of preservation in formalin. However, in a specimen which was dissected, the jaws had a very small papilla, possibly the odontophore.

The sizes of the specimens are smaller than those recorded by Steinberg (1956) for specimens of *C. trematoides* from the southwestern Pacific, and are similar or somewhat smaller than those of specimens of *Cephalopyge* described by other authors such as Chun (1889, in Stubbings, 1937), André (1906), and Stubbings (1937).

All specimens of *P. bucephala* and *C. trematoides* collected by CICIMAR from the GOLCA 8404 cruise were deposited in the Laboratorio de Invertebrados, Facultad de Ciencias, Universidad Nacional Autónoma de México, and all specimens from the El Golfo 6311-12 cruise were deposited in the Scripps Institution of Oceanography, planktonic invertebrates collection.

Discussion

The species of the family Phylliroidae are best known from the Mediterranean Sea and Atlantic Ocean. Few records of these nudibranchs exist in the Pacific Ocean. Most have been made from the southwestern Pacific, in the waters of New Zealand and Australia (Dakin & Colefax, 1940; Powell 1937, 1979; Steinberg, 1956). Baba (1933) recorded a new species, *Cephalopyge orientalis*, from Japanese waters, but Steinberg (1956) placed it in synonymy with *C. trematoides*.

There are fewer records from the eastern Pacific. Dales (1953) recorded one specimen of *Phylliroe bucephala* and one *Cephalopyge trematoides*, collected at 33°19′N, 128°27′W, and 28°30′N, 117°58′W, respectively, off the coast of Baja California. Steinberg (1956) recorded *Cephalopyge trematoides* from two localities (28°38.1′N, 115°15.9′W; 33°24′N, 117°55′W). Lance (1961) mentioned *Cephalopyge trematoides* in his distributional list of Southern California opisthobranchs as "usually collected accidentally in plankton tows." These are the first records of *Phylliroe bucephala* from the Gulf of California. Keen (1971) mentioned that "numerous free-swimming adults have been collected during plankton tows by the Scripps Institution of Oceanography off the west coast of México between latitudes 14° and 24°N." However, there are no records of this species in the invertebrate collections of SIO (M. Ohman and A. Towndsend, personal communication), so Keen's records are apparently from the Pacific.

Stubbings (1937) mentioned that the distribution of some species of *Cephalopyge* is almost worldwide in tropical and subtropical waters. However, the specimens of the Phylliroidae are difficult to see in zooplankton samples because of their very small size, and they can escape through the meshes of the net, and if caught, they are readily overlooked in sorting large masses of zooplankton.

From this study, it is possible to conclude that these animals are in fact hidden in the zooplankton masses; however, they do not escape due to their small size, and it is necessary to carefully check the whole sample with the stereoscope microscope in order to find them. It is possible that the largest specimens have evasion capacity and could not be captured by the net. Under these circumstances and by the exhaustive revision of 77 and 70 zooplankton samples from two cruises in the Gulf of California and the western coast of Baja California, including the Guadalupe, Cedros, and Socorro Islands, it is possible to conclude that *Phylliroe bucephala* and *Cephalopyge trematoides* were widespread in the southern region of the Gulf of California during March–April of 1984; and they were in only two and one localities, respectively, during November–December of 1963 at depths of 40–60 m.

Acknowledgments

I would like to thank Marco Sánchez Hidalgo and Mark Ohman for permitting me to examine the collections of zooplankton samples under their care in CICIMAR, IPN, México and SIO, UCSD, respectively, and for the use of facilities to sort the specimens from these samples. I am particularly grateful to Annie Towndsend who assisted me in the revision of zooplankton samples during my visit at SIO. I would also like to thank Jim Lance for his valuable criticism, and Margaret Knight for her substantial help in the preparation of the manuscript. My appreciation also is due to Hans Bertsch for his critical review and recommendations on the manuscript. I am grateful to Maricela Vicencio Aguilar for her cooperation. José Antonio Hernández made the photographs in the Laboratorio de Microcine, Facultad de Ciencias, UNAM. This research was supported by grants from CONACYT, México, and DGAPA, UNAM.

Literature Cited

ABBOTT R. T. 1974. American Seashells. The Marine Mollusca of the Atlantic and Pacific Coasts of North America. 2nd ed. Van Nostrand Reinhold: New York. 663 pp.

ANDRÉ E. 1906. Supplement aux Mollusques d'Amboine et description d'un nouveau genre de la familie des Phyllirhoides. Revue swisse Zoologie 14:71–80.

ANKEL, E. 1952. *Phyllirrhoe bucephala* Per. & Les. und die meduse *Mnestra parasites* Krohn. Pubblicazioni della Stazione Zoologica di Napoli 23:91–140.

BABA, K. 1933. A pelagic nudibranch *Cephalopyge orientalis* nov. sp. from Japan. Annotations zoologicae Japonenses 14: 157–160.

CHUN, C. 1889. Bericht uber eine nach den Canarischen Inseln im Winter 1887–88 ausgefuhrte Reise. S. B. preuss. Akademic Wissenshaftlich 1889, 2:519–553.

DAKIN, W. J. & A. N. COLEFAX. 1936. *Ctilopsis,* a rare pelagic nudibranch of the family Phyllorhoidae (Bergh). Proceedings of the Zoological Society of London 2:455–460.

DAKIN, W. J. & A. N. COLEFAX. 1937. A pelagic nudibranch of the family Phyllirhoidae from the waters of New South Wales: a note on the subgenera *Ctilopsis* and *Cephalopyge.* Annals and Magazines of Natural History Series 10(19): 266–271.

DAKIN, W. J. & A. N. COLEFAX. 1940. The plankton of the Australian coastal waters off New South Wales. University of Sydney Publications of Zoological Monographies 1:1–215.

DALES, R. P. 1953. North-East Pacific Phyllirhoidae. Annals and Magazines of Natural History Series 12(6):193–194.

KEEN, M. 1971. Sea Shells of Tropical West America. Marine Mollusks from Baja California to Perú. 2nd ed. Stanford University Press: Stanford, California. 1064 pp.

LALLI, C. M. & R. W. GILMER. 1989. Pelagic Snails. The Biology of Holoplanktonic Gastropod Mollusks. Stanford University Press: Stanford, California. 258 pp.

LANCE, J. 1961. A distributional list of Southern California opisthobranchs. The Veliger 4(2):64–69.

MARTIN, R. 1966. An attempt to infect in vitro medusae of *Zanclea costata* (Anthomedusae) with the veliger of *Phyllirrhoe bucephala* (Opisthobranchia). Pubblicazioni della Stazione Zoologica di Napoli 35:130–131.

MARTIN, R. & A. BRINCKMANN. 1963. Zum Brutparasitismus von *Phyllirrhoe bucephala* Per. & Les. (Gastropoda, Nudibranchia) auf der Meduse *Zanclea costata* Gegenb. (Hydrozoa, Anthomedusae). Pubblicazioni della Stazione Zoologica di Napoli 33:206–223.

POWELL, A. W. B. 1937. New species of nudibranchiate Mollusca from Auckland waters. Records of the Auckland Institute and Museum 2(2):119–124.

POWELL, A. W. B. 1979. New Zealand Mollusca. Collins: Sydney. 500 pp.

ROSE, M. 1957. Les mollusques pélagiques. Pp. 474–475, pl. 145 in G. Trégouroff & M. Rose (eds.), Manuel de Planctonologie Méditerranéenne. Centre National de la Recherche Scientifique, Paris.

SENTZ-BRACONNOT, E. & C. CARRÉ. 1966. Sur la biologie du nudibranche pélagique *Cephalopyge trematoides.* Parasitisme sur le siphonophore *Nanomia bijuga,* nutrition, développment. Cahiers Biologie Marine 7:31–38.

STEINBERG, J. E. 1956. The pelagic nudibranch *Cephalopyge trematoides* (Chun, 1889), in New South Wales with a note on other species in this genus. The Proceedings of the Linnean Society of New South Wales 81:184–192.

STUBBINGS, H. 1937. Phyllirhoidae. Scientific Reports John Murray Expeditions 5:1–14.

VAN DER SPOEL, S. 1970. The pelagic Mollusca from the "Atlantide" and "Galathea" expeditions collected in the East Atlantic. Atlantide Reports II:99–139.

The Occurrence of *Mytilopsis leucophaeata* (Conrad, 1831) (Veneroida: Dreissenidae) in Southern New England

by

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The Dreissenidae has had a dynamic biogeographic history, especially in recent times (Nuttall, 1990; Carlton, 1992; Morton, 1993). Much of the group's rapid global spread has been the direct result of human activity. Almost certainly, the enormous potential for dispersal is due to biological factors (Boss, 1982; Morton, 1993), especially the production of a free-swimming larva, a relatively labile ecology enabling them to tolerate, to varying degrees, both fresh and brackish water, and, in extant genera, the sessile nature of the adult mussel. *Mytilopsis leucophaeata* (Conrad, 1831) is the only Recent species of the dreissenid genus *Mytilopsis* Conrad, 1858, known in eastern North America. Until the mid-twentieth century, it was not known from farther north than Chesapeake Bay on the North American Atlantic coast.

Materials and Methods

Housatonic River specimens of *M. leucophaeata* collected in 1992 and 1995 have been placed in the Museum of Zoology, University of Massachusetts (UMA MO.1794, 1831, respectively). Charles River material of the same species has been deposited in the Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ 316062), and the Museum of Zoology, University of Massachusetts, Amherst, Massachusetts (UMA MO.1795). Salinity was determined by a LaMotte Salinity Titration kit (Model POL-H).

Results and Discussion

Mytilopsis leucophaeata was first observed in the lower Hudson River in the late 1930s (Rehder, 1937), and by the 1950s was firmly established throughout the lower Hudson River basin (Jacobson, 1953; Jacobson & Emerson, 1961). The mussel's entry into the Hudson River estuary was believed to be the result of artificial introduction (Jacobson, 1953). In September 1992, one of us (D.G.S.) found a single valve and other fragments of *M. leucophaeata* in the Housatonic River in Shelton, Fairfield County, Connecticut, just south of Twomile Island. The shell material was found in tidally influenced water and was associated with both freshwater and upper estuarine prosobranch and basommatophoran gastropods. Smith (1994) discussed the prosobranch fauna of this part of the Housatonic River. The only other molluscan associates were the freshwater sphaeriid bivalve species *Pisidium compressum* Prime, 1852, and *Pisidium nitidum* Jenyns, 1832. At the time of collection of the *M. leucophaeata* shells, the tide was low and the salinity was < 0.5 ppt (‰). In November 1995, personnel of the Connecticut Department of Environmental Protection collected several live specimens in Shelton, Fairfield County, just north of Twomile Island. A portion of the collection was sent to one of us (D.G.S.) for identification. The species was reported to be common at the site, and salinity was determined to be 1 to 2 ppt (‰).

Farther east and north, several dead specimens were brought to K.J.B. in 1981, having been found attached to buoy lines near a boathouse on the Charles River, Boston, Suffolk County, Massachusetts. These specimens, currently in the MCZ, were presumably the basis for Marelli & Gray's (1985) inclusion of Massachusetts within the North American range of the species. In 1994, several shells were found along shore in Cambridge by D.G.S., and in July 1995, several live specimens were collected along the Boston shore near the locks. The specimens were attached singly to the undersides of rocks in 0.5 m of water. The Charles River is artificially controlled by locks, and at present, the only source of saltwater is the occasional opening of the locks for the passage of boats. The salinity at time of collection was 1.0 ppt (‰); specimens of *M. leucophaeata* were associated with the hydrozoan *Cordylophora lacustris* Allman, 1871, (= *caspia*) the freshwater sponge *Ephydatia fluviatilis* (Linnaeus, 1758), the freshwater mollusks *Physa* sp., *Amnicola limosa* (Say, 1817), and *Anodonta implicata* Say, 1829, and a few dead individuals of the barnacle *Balanus* sp.

Additional searches of the lower Saugatuck River in Westport, Fairfield County, Connecticut, and tidally affected portions of the lower Connecticut River in Connecticut have produced no specimens. Thus, the disjunct occurrence in southern New England of *M. leucophaeata* is most likely the result of introduction, presumably by boat traffic, rather than natural northern dispersal of the species. *Mytilopsis leucophaeata* can be confused with two European dreissenids, the zebra mussel, *Dreissena polymorpha* (Pallas, 1771), and the quagga mussel, *Dreissena bugensis* Andrusov, 1897, introduced into North America in the 1980s and rapidly expanding their range. Young specimens (< 10 mm shell length) of *M. leucophaeata* from the Charles River and the Housatonic River have distinct zigzag markings, a feature not attributed to this species in a recent key distinguishing dreissenids established in North America (McMahon, 1991) and often used to characterize *Dreissena* spp. It is important to evaluate other morphological features characteristic of these species as discussed by McMahon (1991) and Rosenberg & Ludyanskiy (1994) before making a determination of *Dreissena* spp. in southern New England waters.

Acknowledgments

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Literature Cited

Boss, K. J. 1982. Mollusca. Pp. 945–1166 in S. P. Parker (ed.), Synopsis and Classification of Living Organisms. Vol. 1. McGraw-Hill: New York.

Carlton, J. T. 1992. Introduced marine and estuarine mollusks of North America: an end-of-the-20th century perspective. Journal of Shellfish Research 11:489–505.

Jacobson, M. K. 1953. *Congeria leucophaeata* (Conrad) in the Hudson River. The Nautilus 66:125–127.

Jacobson, M. K. & W. K. Emerson. 1961. Shells of the New York City Area. Argonaut Books: Larchmont, New York. 142 pp.

Marelli, D. C. & S. Gray. 1985. Comments on the status of Recent members of the genus *Mytilopsis* (Bivalvia: Dreissenidae). Malacological Review 18:117–122.

McMahon, R. F. 1991. Mollusca: Bivalvia. Pp. 315–399 in J. H. Thorp & A. P. Covich (eds.), Ecology and Classification of North American Freshwater Invertebrates. Academic Press: San Diego, California.

Morton, B. 1993. The anatomy of *Dreissena polymorpha* and the evolution and success of the heteromyarian form in the Dreissenoidea. Pp. 185–215 in T. F. Nalepa & D. W. Schloesser (eds.), Zebra Mussels Biology, Impacts, and Control. Lewis Publishers: Boca Raton, Florida.

Nuttall, C. P. 1990. Review of the Cenozoic heterodont bivalve superfamily Dreissenacea. Palaeontology 33:707–737.

Rehder, H. A.1937. *Congeria leucophaeata* (Con.) in the Hudson River. The Nautilus 50:143.

Rosenberg, G. & M. L. Ludyanskiy. 1994. A nomenclatural review of *Dreissena* (Bivalvia: Dreissenidae), with identification of the quagga mussel as *Dreissena bugensis*. Canadian Journal of Fisheries and Aquatic Sciences 51:1474–1484.

Smith, D. G. 1994. On some Connecticut, USA, snails reported by J.H. Linsley. Malacological Review 27:1–4.

International Commission on Zoological Nomenclature

The following Application was published on 29 March 1996 in Volume 53, Part I of the *Bulletin of Zoological Nomenclature*. Comment or advice on this application is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., c/o The Natural

History Museum, Cromwell Road, London SW7 5BD, U.K.

Case 2962—D. L. G. Karsten (1789) *Museum Leskeanum,* vol. 1 (Regnum Animale): proposed suppression for nomenclatural purposes.

The following Opinions concerning mollusks were published on 29 March 1996 in Volume 53, Part 1 of the *Bulletin of Zoological Nomenclature.* Copies of these Opinions can be obtained free of charge from the Executive Secretary at the address given above.

Opinion 1822. *Helix nitidula* Draparnaud, 1805 and *H. nitens* Michaud, 1831 (currently *Aegopinella nitidula* and *A. nitens;* Mollusca, Gastropoda): specific names conserved and a neotype designated for *H. nitidula.*

Opinion 1823. *Nesopupa* Pilsbry, 1900 (Mollusca, Gastropoda): conserved.

Opinion 182. Megalodontidae Konow, 1897 (Insecta, Hymenoptera): spelling emended to Megalodontesidae, so removing the homonymy with Megalodontidae Morris & Lycett, 1853 (Mollusca, Bivalvia).

Manuscript Reviewers for Volume 39 of *The Veliger*

The following reviewers contributed their time, effort, and expertise to evaluate manuscripts submitted during the course of assembly of Volume 39. The quality of *The Veliger* depends strongly on the voluntary assistance of independent reviewers such as these, and we are grateful to them.

R. F. Ambrose, H. Bertsch, J. S. Bleakney, E. G. Boulding, S. M. Bower, J. C. Britton, S. von Boletsky, B. U. Budelmann, K. A. Campbell, J. T. Carlton, K. B. Clark, E. V. Coan, F. H. A. Costa, M. G. Cuezzo, J. T. Davey, W. P. Elder, W. K. Emerson, N. R. Foster, C. J. Franz, J. H. R. Goddard, T. M. Gosliner, J. Grahame, R. T. Hanlon, M. G. Harasewych, M. Hare, L. G. Harris, M. E. Harte, R. Hershler, F. G. Hochberg, A. J. Kohn, C. M. Lalli, H. Lescinsky, D. R. Lindberg, M. deMaintenon, H. B. Michel, H. K. Mienis, S. V. Millen, F. P. Monroy, D. R. Moore, M. Norman, D. Ó Foighil, D. K. Padilla, J. A. Pechenik, D. G. Reid, P. D. Reynolds, R. Robertson, P. U. Rodda, G. Rosenberg, R. Seapy, S. van der Spoel, R. L. Squires, R. Toll, S. Turner, G. J. Vermeij, J. Voltzow, R. L. Walker, S. E. Walker, T. R. Waller, K. Warheit, A. Warén.

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BOOKS, PERIODICALS & PAMPHLETS

Mediterranean Sepiolidae [Les Sépioles de Méditerranée]

edited by SIGURD V. BOLETZKY. 1995. Bulletin de I'Institut océanographique, Monaco, Numéro spécial 16; Service des Publications, Musee océanographique, Avenue Saint-Martin, MC 98000, Monaco. 104 pp. Price 100 FF (+22 FF for shipping and handling) (US $21).

Despite the fact that the sepiolids represent an abundant and diverse assemblage of Mediterranean cephalopods, they have not been studied as extensively as those groups that have more substantial fisheries in this geographic area, such as the octopods. However, a database is accumulating on this group, as they provide good model systems for a variety of basic biological questions, because of their small size, relatively fast growth rates, and the ability to raise them under laboratory conditions.

This monograph, edited by S. v. Boletzky, offers not only a good introduction to the Mediterranean sepiolids, but also to this family of cephalopods in general. The contribution contains a series of well-reviewed papers that resulted from a meeting held in the early 1990s of the working group on cephalopods of the International Commission for Scientific Exploration of the Mediterranean. The volume consists of an introduction by C. Volpi, M. Borri & S. v. Boletzky and 11 contributed papers on various aspects of the biology of the Mediterranean Sepiolidae. Most of the articles include a sizeable bibliography, which when considered together probably cover most of the available literature on this family of cephalopods.

Following the well-written introduction, which provides a good "roadmap" for the subsequent articles, the contributions focus primarily on the systematics and biogeography of the Mediterranean sepiolid species. The chapter by G. Bello provides a both usable and elaborate key for the three subfamilies, seven genera, and 23 species that comprise this family. Three of the manuscripts (by Sartor & Belcari; Volpi, Borri & Zucchi; and, Wurtz, Matricardi & Repetto) cover the distribution and abundance of species off of the Italian coast; another contribution covers these issues for species of the northwestern Mediterranean (by Villanueva); and one article (by Orsi Relini) focuses on the distribution and abundance of a midwater species of sepiolid, *Heteroteuthis dispar,* from the Ligurian Sea. Articles by Boucher-Rondoni, Martin, & Peduzzi and Ragonese & Jereb explore the use of two different types of characters, antigenicity of eye lens proteins and biometry, respectively, in the systematics of sepiolids. In their contribution, Bello & Biagi challenge the notion that members of the sepiolid subfamilies Sepiolinae and Rossiinae are exclusively benthic or benthopelagic; they present data from capture records indicating that many of these species spend considerable periods of time great distances from the substrate. The closing contribution of the monograph, by S. v. Boletzky, provides a cladistic analysis of the sepiolids in relation to other major cephalopod taxa. The volume includes one article that is not concerned with systematics and biogeography, by Gabel-Deickert, on reproductive patterns in the sepiolids, with a concentration on one particular species, *Sepiola affinis.* This contribution will be valuable to those experimental scientists who are considering the raising of Mediterranean sepiolids under laboratory conditions.

In summary, this monograph is short and of somewhat limited scope, but full of useful information concerning this subset of the Mediterranean fauna. This volume would be a valuable and essential component of the libraries of researchers studying the biology of sepiolid squids.

Margaret McFall-Ngai

Revision der Gattung *Vallonia* Risso 1826 (Mollusca: Gastropoda: Valloniidae)

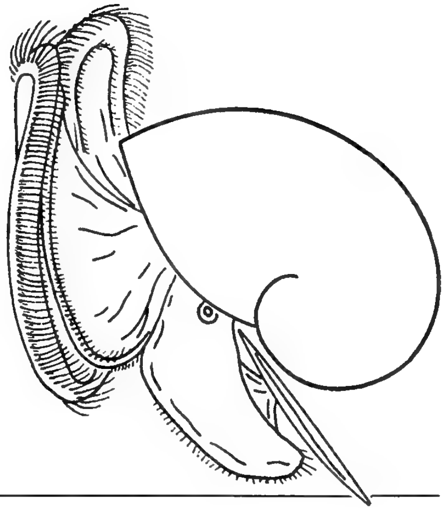
by JOCHEN GERBER. 1996. Schriften zur Malakozoologie aus dem Haus der Natur—Cismar, 8. 227 pp., 85 figs. Ostholstein, Germany. ISBN 3-925 919-22-8 (paperbound), 3-925 919-23-6 (hard cover).

This paper presents a careful and thorough revision of the known fossil and Recent nominal taxa of the Holarctic pulmonate land snail genus *Vallonia.* Forty species and subspecies regarded as valid are treated comprehensively; a key aids in their identification. Eight new species and subspecies are described. Neotypes are designated for five nominal taxa and lectotypes for many others. Special terminology used in the description of the minute valloniid shell is defined by reference to clear illustrations. The species concepts are employed in light of *Vallonia*'s predominantly self-fertilizing mode of reproduction.

A chart of hypothetical phylogenetic relationships (fig. 12) is plotted on a Cenozoic time scale. Some attempt is made (p. 32) to designate plesiomorphic and apomorphic states of a few shell characters, partly by outgroup comparison but also by stratigraphic precedence and the assumption that "common equals primitive." The branching diagram leans heavily on stratigraphy; it is not evaluated against criteria of parsimony, and discussions of character-states are pulled in, apparently on an *ad hoc* basis, to support various nodes and line segments.

B. Roth

THE VELIGER



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