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A NEW OVOVIVIPAROUS SPECIES OF *TECTARIUS* (GASTROPODA: LITTORINIDAE) FROM NIUE, SOUTH PACIFIC, WITH A MOLECULAR PHYLOGENY OF THE GENUS

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ABSTRACT

A new ovoviviparous littorinid gastropod, *Tectarius (Echininiopsis) niuensis*, from Niue, west of the Cook Islands, is described. This is distinguished from the only other ovoviviparous member of the genus, *T. (E.) viviparus* (Rosewater, 1982) from the Mariana Islands, here redescribed in detail. The new species is remarkable for its high-level habitat in the littoral fringe on wave-exposed karstic limestone cliffs, for its variation in shell shape according to tidal level, shell colour polymorphism, calcified operculum and penis with a single mamilliform penial gland. In a cladistic analysis of morphological characters, including single representatives of each of the three other subgenera of *Tectarius (Tectarius, Echininus, Tectininus)*, these two ovoviviparous species appear as sister-taxa. This is confirmed by a molecular phylogenetic analysis of the same species, based on the sequence of a portion of the 16S ribosomal RNA mitochondrial gene. Neither analysis unequivocally confirms the monophyly of *Tectarius*. The divergence of DNA sequences within *Tectarius* suggests that the genus arose in the Upper Cretaceous, much earlier than the oldest (Upper Eocene) fossils. Only 4 of the 175 species of Littorinidae are known to be ovoviviparous (with brooding through metamorphosis) and the possible adaptive significance of this type of development is discussed. Hitherto, its rarity had been explained by early extinction of poorly-dispersed brooding taxa. However, ovoviviparity may have persisted in *Echininiopsis* for at least 35 million years, and has not precluded colonization of islands 6300 km apart.

INTRODUCTION

The genus *Tectarius* is one of the most poorly known groups of those littorinid gastropods that are found at high intertidal levels on marine shores (Littorinidae: subfamily Littorininae). This is surprising, since the genus includes the largest members of an otherwise extremely well-studied family. Such relative neglect is explained by their geographical distribution for, with the exception of a single species in the Caribbean, all occur in relatively remote localities on islands in the southern and western Pacific Ocean and on the coast of northwestern Australia. The Pacific species appear to be found exclusively (and the Caribbean species most commonly) upon karstic limestone, at the highest limits of the littoral fringe. In the Pacific the distribution of the genus as a whole is almost coincident with that of elevated limestone ('makatea') islands given by Stoddart (1992). In a revision of the classification of the Littorinidae, the genus *Tectarius* was redefined to include 8 species (and one of uncertain specific status), of which some had previously been placed in *Echininus* (Reid, 1989a; see detailed review of classification below). This revision was based on cladistic analysis of a range of anatomical characters, but nevertheless the genus was poorly characterized, with only a single unreversed synapomorphy.

Here, we report the discovery of a new species of *Tectarius* from Niue, west of the Cook Islands. This is superficially similar in appearance to *T. viviparus* (Rosewater, 1982) from the southern Mariana Islands, and likewise has ovoviviparous development. Anatomical comparisons by one of us (DGR) have revealed a number of differences, and independent DNA studies by the other (JBG) have found a 12.2% difference in the base sequence of the 16S ribosomal RNA mitochondrial gene, strongly suggesting that the two are distinct species.

This finding raises several interesting questions. The reproductive strategies of littorinids have long been known to be exceptionally diverse, and have been used to demonstrate adaptive trends (Reid, 1989a, 1996). Hitherto, only three of the approximately 175 known species of the family have been discovered to be ovoviviparous with brooding through metamorphosis (i.e. lacking a planktotrophic veliger larva), and these species occur in three contrasting habitats. The addition of another prompts a reexamination of the question of the adaptive value of this developmental strategy. Furthermore, it is of interest whether the two cases of ovoviviparity in *Tectarius* arose independently, or are descendants from an ovoviviparous ancestor; this is so because ovoviviparity has been considered a 'short-term' evolutionary strategy likely to lead to early extinction (Reid, 1989a), as a consequence of poor dispersal capability (reviews by Jablonski & Lutz, 1983; Jablonski, 1986). If these two species of *Tectarius* share a common ovoviviparous ancestor, it is therefore remarkable that they now occur on islands 6300 km apart.

The aim of this paper is first to describe the new species of *Tectarius* and to distinguish it from the similar *T. viviparus*. Anatomical material of three additional *Tectarius* species was available, and using morphological characters from these we reexamine the phylogeny of the genus and its possible monophyly. The resulting morphological phylogeny is compared with a mitochondrial gene phylogeny for the same species. Finally, we briefly consider the fossil record and biogeography of *Tectarius,* and the adaptive value of ovoviviparity in the Littorinidae as a whole.

REVIEW OF THE CLASSIFICATION OF THE GENUS *TECTARIUS*

The genus *Tectarius* has had a complex taxonomic history. The early history will here only be briefly summarized (for detailed generic and specific synonymies see Clench & Abbott, 1942; Abbott, 1954; Rosewater, 1972, 1973), before considering recent changes in more detail. As a consequence of their sculptured, trochoidal shells, the species discovered in the eighteenth and early nineteenth centuries were initially described in trochoidean genera. Even the generic name *Tectarius* itself was initially used as an incorrect spelling of the trochid genus *Tectus* (Keen, 1966), although it has since been validated as a new name (Melville & China, 1969). It was not until after the first anatomical description by Quoy & Gaimard (1834) that the littorinid affinities of the group were recognized (Deshayes & Milne-Edwards, 1843; and independently by Gray, 1839, 1840). At least six generic names were based on members of the group during this period (see Rosewater, 1972), but in early iconographies the species were included in the broad genus *Littorina* (Philippi, 1846–1848; Reeve, 1857). H. & A. Adams (1854) separated those littorinids with nodulose and spinose shells as *Tectarius*, and those that in addition were umbilicate and possessed a multispiral operculum, as *Echinella*. This view was reinforced by the radular studies of Troschel (1858), although using the names *Tectus* and *Nina* respectively. However, in 1887 Tryon simply classified all the trochoidal, strongly sculptured littorinids as *Tectarius*. This classification persisted in the influential works of Thiele (1929) and Wenz (1938), although by using a combination of characters of the shell, operculum and radula, the subgenera *Nodilittorina*, *Cenchritis*, *Echinellopsis* and *Nina* were distinguished.

In order to understand the modern classification of this group of littorinids, the taxonomic treatments by successive authors of the type species of six generic and subgeneric names are summarized in Table 1. Clench & Abbott (1942) retained the broad genus *Tectarius*, but removed (and renamed) the genus *Echininus*, because of its multispiral operculum. Anatomical characterization of these strongly-sculptured littorinids was first attempted by Abbott (1954). He distinguished the genus *Nodilittorina* from *Tectarius*, using characters of the penis, radula and egg capsules, and refined the definition of *Echininus* to include penial and radular features. *Tectarius* itself remained largely unknown anatomically, and Abbott therefore included in it the Caribbean species *'T.' (Cenchritis) muricatus*. Fischer (1971) recommended the elevation of *Cenchritis* to generic rank, although purely from comparisons of shells and opercula. In his influential monographs of Indo-Pacific Littorinidae, Rosewater (1970, 1972, 1973) followed the generic and subgeneric arrangement of Abbott (1954). However, he went further, creating new subfamilies for each of the genera *Tectarius* and *Echininus*, although the only consistent character purportedly distinguishing them from each other and from the rest of the

Table 1. Summary of generic and subgeneric classifications of type species of *Nodilittorina*, *Cenchritis* and the four recognized subgenera of *Tectarius* in significant taxonomic works published since 1942. A valid senior synonyms of one type species is given in square brackets. *, Clench & Abbott (1942) did not mention *Littorina pyramidalis* by name, but did include related Caribbean species in *Tectarius*.

Type species	Clench & Abbott (1942)	Abbot (1954) Rosewater (1970, 1972, 1973)	Rosewater (1982)	Bandel & Kadolsky	Reid (1989a)
Littorina pyramidalis Quoy & Gaimard, 1833	*Tectarius**	*Nodilittorina*	–	*Nodilittorina*	*Nodilittorina*
Turbo muricatus Linnaeus, 1758	*Tectarius*	*Tectarius (Cenchritis)*	–	*Cenchritis*	*Cenchritis*
Tectarius coronatus Valenciennes, 1832	*Tectarius*	*Tectarius (Tectarius)*	–	*Tectarius*	*Tectarius (Tectarius)*
Trochus cumingii Philippi, 1846	*Echininus (Echininus)*	*Echininus (Echininus)*	*Echininus*	*Echininus*	*Tectarius (Echininus)*
Litorina nodulosa Pfeiffer, 1839 [= *Litorina antonii* Philippi, 1846]	*Echininus (Tectininus)*	*Echininus (Tectininus)*	*Tectininus*	*Nodilittorina (Tectininus)*	*Tectarius (Tectininus)*
Echininus viviparus Rosewater, 1982	–	–	*Echininus*	–	*Tectarius (Echininiopsis)*

Littorinidae was the operculum, mesospiral in *Tectarius* and multispiral in *Echininus*. In 1982 Rosewater described a new species, *Echininus viviparus*, and reaffirmed the status of the Echininae, while also raising *Tectininus* to generic rank on account of its unique radula. In the same year Bandel & Kadolsky (1982) reviewed the known characters of the penis, spawn, operculum, radula and shell of nine littorinid genera, stressing features of the penis and radula in generic diagnoses. As a result, the genus *Nodilittorina* was more clearly delimited than before, although *Tectininus* was included as a subgenus, but both *Tectarius* and *Echininus* were retained at generic level. The most recent reclassification of this group was the result of a cladistic analysis of a wide range of morphological characters from all known subgeneric taxa of the Littorinidae (Reid, 1989a). The surprising conclusion was that *Tectarius*, *Echininus* and *Tectininus* were sufficiently closely related, as indicated mainly by reproductive anatomy, that they should be recognized merely as subgenera of the single genus *Tectarius*. This inclusive genus was defined by synapomorphies of the mesospiral to multispiral operculum, numerous mamilliform glands of the penis, and narrow to vestigial rachidian tooth of the radula (although none of these is unique in the family as a whole). A new subgenus, *Echininiopsis*, was proposed for the single ovoviviparous species then known. Generic and subgeneric diagnoses, and synonymies, were given by Reid (1989a).

The most recent species-level revisions of the taxa now included in *Tectarius* are those of Rosewater (1972, 1973, 1982). Following these accounts, Reid (1989a) listed all eight species then known, five in the subgenus *Tectarius* and one each in the subgenera *Echininus*, *Tectininus* and *Echininiopsis*. There is some doubt about the composition of *Echininus*; Rosewater (1972) recognized two allopatric subspecies (*E. cumingii cumingii* (Philippi, 1846) and *E. c. spinulosus* (Philippi, 1847)) with divergent shell characters, and further information (anatomical and/or genetic) is required to confirm that they are conspecific (see p. 233).

MATERIALS AND METHODS

The material examined is deposited in the Natural History Museum, London (BMNH), and some paratypes of the new species in the National Museum of Natural History, Washington, D.C. (USNM). The morphological description of the new species was based upon two samples from Anaana Point, Niue (19°02'S, 169°55'W, west of the Cook Islands, collected by G. Paulay on 17 October 1991 (BMNH 1996064 to 1996068). Six males were dissected, and sperm samples extracted from three; ten females were dissected, and four radulae (two from each sex) were examined. The redescription of *Tectarius viviparus* was based upon two collections, from Pago Bay (BMNH 1996070) and from Tagachan (BMNH 1996069), both on the island of Guam in the Mariana Islands, made in August and September, 1985, by J.D. Taylor. Five males and seven females were dissected; two sperm samples and four radulae (two from each sex) were examined. All material had been relaxed in 7.5% (volume of hydrated crystals to volume of fresh water) magnesium chloride solution, fixed in 10% seawater formalin buffered with borax, and stored in 80% ethanol.

Anatomical drawings were made by camera lucida. Sperm were removed from the seminal vesicle and examined at a magnification of ×1000 by light microscopy. Radulae were cleaned of tissue by soaking in a hypochlorite bleaching solution at room temperature, rinsed in distilled water, mounted on a film of polyvinyl acetate glue and allowed to dry in air, then coated with gold and palladium before examination in a scanning electron microscope. Radulae were viewed in three orientations: in standard flat view from vertically above the radula (to show shapes of teeth), at an angle of 45° from the front end of the radula (to show shapes of tooth cusps), and at an angle of 45° from the side of the radula (to show relief). The shape of the rachidian tooth was quantified as the ratio of the total length (in flat view) to the maximum basal width. Embryonic shells removed from the mantle cavity were also examined by scanning electron microscopy.

Shell dimensions were measured with vernier calipers to 0.1 mm. For the purpose of diagnosis, shell shape was quantified simply as the ratio of the maximum height (H) parallel to the axis of coiling, to the maximum breadth (B) perpendicular to this. For comparisons of shapes in three samples of shells (*T. viviparus* from Pago Bay; samples of the new species from each of two microhabitats), an analysis of covariance was performed with the program Genstat 5 (1988). Protoconch whorls were counted as recommended by Reid (1996). Opercular coiling was described by the opercular ratio (OR), the ratio of the diameter of the spiral part to the maximum length (Reid, 1996). Relative radular length was defined as the total radular length divided by shell height.

Phylogenetic relationships within the genus *Tectarius* were investigated using both morphological and molecular characters, and the results of the two approaches compared. The same species were used for both morphological and molecular analyses. In addition to the new species and *T. viviparus*, three other *Tectarius* species were available: *T. antonii*, *T.*

grandinatus and *T. cumingii* (thus representing all four subgenera of *Tectarius*). Based on the morphological phylogeny of Reid (1989a), three other littorinids were used as an outgroup: *Peasiella tantilla*, *Nodilittorina trochoides* and *Cenchritis muricatus*. Localities and authorities for these species are listed in Table 2.

For the morphological analysis, 21 characters of the shell and anatomy were scored. Many of these have previously been described by Reid (1989a, b); additional or modified characters are discussed in the Results. A Wagner parsimony analysis was performed using PAUP, version 3.1.1 (Swofford, 1993). Four characters were ordered (Table 3) and all were unweighted.

Specimens for DNA analysis were prepared by cracking the shells before storage in either DNE (20% DMSO, 250 mM EDTA, NaCl to saturation), 90% isopropanol or 100% ethanol. Each tissue sample was homogenized in a microcentrifuge tube in 500 µl 1X CTAB extraction buffer (50 mM Tris-HCl at pH 8.0, 0.7 M NaCl, 10 mM EDTA, 1% CTAB (hexadecyltrimethylammonium bromide), 0.1% 2-mercaptoethanol) and incubated at 55°C for 3–16 hr. Each sample was then twice extracted with chloroform:isoamyl-alcohol (24:1), and nucleic acids were precipitated with one volume of ice cold isopropanol. Nucleic acids were pelleted in a microfuge, dried under vacuum, and resuspended in 500 µl of TE (10 mM Tris and 1 mM EDTA, pH 8.0).

A segment of the 16S rRNA gene was amplified using a modification of widely used universal primers (16SAR and 16SBR) (Palumbi, Martin, Romano, McMillan, Stice & Grabowski, 1991). Primers were made degenerate at several positions to increase their utility for a wider variety of organisms. Primer sequences were D16SAR:5′ CGC CTG TTT AHY AAA AAC AT 3′ and D16SBR: 5′ CCG GTC TGA ACT CAG MTC AYG T 3′. For each reaction, 0.5 µl of the total cellular DNA preparation was used as template in 25 ml PCR mixes. The reaction mix consisted of 10 mM Tris (pH 8.3), 1.5 mM $MgCl_2$, 50 mM KCl, 0.01% Triton-X 100, 0.01% gelatin, 0.01% NP-40, 200 mM of each dNTP, 1 unit AmpliTaq DNA polymerase (Perkin-Elmer), and 25 pmoles of each primer. Reaction mixes were subjected to 30 cycles of 10 s at 98°C, 30 s at 54°C, and 1 min at 72°C on an automated thermocycler (MJR, Norwalk, CT). Five µl of each amplification was checked by electrophoresis and ethidium bromide staining on a 1.2% agarose gel. The remaining 20 µl of each amplification reaction was gel purified by excision from a second 1.2% agarose gel. Gel slices were placed in a spin column, which consisted of 0.7 ml microfuge tubes packed one quarter full with sterile polyester fibre. The spin columns were placed in 1.5 ml microfuge tubes and centrifuged at full speed for 5 min to elute the gel buffer containing DNA. A pinhole in the bottom of the spin column allowed the buffer to collect in the larger outer tube. DNA was then precipitated by addition of 1/10 volume of NaOAc and 2.5 volumes of ice-cold 100% ethanol, followed by incubation at −70°C for at least 30 min. DNA was then pelleted by centrifugation, dried under vacuum and resuspended in 20 µl of TE. Five µl of purified PCR product was then sequenced using forward and reverse PCR primers, α-33P dATP, and a Perkin-Elmer Amplicycle cycle-sequencing kit following the manufacturer's protocol. Sequencing reactions were electrophoresed on 6% TBE-acrylamide gels (19:1 acrylamide: bis-acrylamide) containing 42% urea with a TBE (89 mM Tris base, 89 mM boric acid, 2 mM EDTA, pH 8.0) running buffer. Sodium acetate was added to the bottom buffer tank to a concentration of 3M to

Table 2. Locality information for the five species of *Tectarius* and three outgroup taxa used in the morphological (M) and molecular (D) phylogenetic analyses.

Species	Locality	Analysis
Peasiella tantilla (Gould, 1849)	Kailua Bay, Oahu, Hawaii	D
	Kaneohe Bay, Oahu, Hawaii	M
Cenchritis muricatus (Linnaeus, 1758)	5 km W of Nassau, Bahama Islands	D
	Jupiter Inlet, Florida	M
Nodilittorina trochoides (Gray, 1839)	Cape d'Aguilar, Hong Kong	D
	Shek-O, Hong Kong	M
Tectarius (Tectininus) antonii (Philippi, 1846)	Eight-mile Rock, Grand Bahama Island	D
	Jupiter Inlet, Florida	M
Tectarius (Tectarius) grandinatus (Gmelin, 1791)	Avana Harbour, Rarotonga, Cook Islands	D, M
Tectarius (Echininus) cumingii (Philippi, 1846)	Avana Harbour, Rarotonga, Cook Islands	D, M
	Madang, Papua New Guinea	M
Tectarius (Echininiopsis) viviparus (Rosewater, 1982)	Mangilao, Guam, Mariana Islands	D
	Pago Bay, Guam	M
	Tagachan, Guam	M
Tectarius (Echininiopsis) niuensis new species	Anaana Point, Niue Island	D, M

create a salt gradient that slowed migration near the bottom of the gel, allowing longer reads. Gels were dried under vacuum and exposed overnight to autoradiography film. Sequences were read manually and entered into the computer program DNAid+ 1.8 (F. Dardel, Laboratoire de Biochimie, École Polytechnique, 91128 Palaiseau, France) for alignment of forward and reverse sequences.

For *Nodilittorina trochoides* a published 16S sequence was used (Reid, Rumbak & Thomas, 1996). The new DNA sequences from *Tectarius cumingii*, *T. grandinatus*, *T. niuensis* and *T. viviparus* have GenBank accession numbers U66351–U66354. In addition, unpublished 16S sequences were used for *Peasiella tantilla*, *Cenchritis muricatus* and *Tectarius antonii* (Thomas, Reid & Rumbak, in prep.). The eight sequences were aligned using ClustalW (Thompson, Higgins & Gibson, 1994). Parsimony analysis was performed using PAUP.

SYSTEMATIC DESCRIPTIONS

Genus *Tectarius* Valenciennes, 1832
Subgenus *Echininiopsis* Reid, 1989

Tectarius (Echininiopsis) viviparus
(Rosewater, 1982)
Figures 1G–K; 2B, D, G, I; 3; 5A–D; 6

Echininus cumingi spinulosus—Rosewater, 1972: 527–528 (in part; includes *Tectarius spinulosus* (Philippi, 1847)).

Echininus viviparus Rosewater, 1982: 69–79; figs 1–6 (Machong Point, Rota, Mariana Islands; holotype USNM 792356; 15 paratypes USNM 803296; seen).

Tectarius (Echininiopsis) viviparus—Reid, 1989: 95; figs 1r, 7b, 9r, 14b.

Shell (Fig. 1G–K). Mature shell height 5.0–10.4 mm (to 12.3 mm, Rosewater, 1982); H/B = 1.03–1.20 (mean = 1.14 ± 0.039 95% confidence limits; n = 10); probably sexually dimorphic in size, largest female 9.5 mm, largest male 6.2 mm (mean of 7 females 7.17 mm and of 4 males 5.4 mm; in *t*-test $P < 0.05$). Teleoconch 4–5 whorls. Shape trochoidal; sutures moderately impressed; not umbilicate. Sculpture (Fig. 2D) of 5 spiral ribs at and above periphery of last whorl, bearing conspicuous rounded nodules; two rows of nodules, at periphery and at shoulder, are most prominent; minor cords may develop between ribs in largest specimens. Base with 5–6 spiral ribs, becoming larger and more strongly nodulose towards periphery. Entire surface covered with fine spiral microstriae if well preserved. Aperture almost circular. Columella short, hollowed, pinched at base so that pillar ends in slight nodule. Colour dimorphic; shells either salmon-orange, fading to pinkish with paler nodules, interior of aperture bright salmon-orange; or ochraceous cream, fading to pale cream, interior ochraceous orange; colour frequencies: 100% orange in sample from Pago Bay (n = 72), 50% orange in sample from Tagachan (n = 26); columella coloured as interior. Protoconch (Fig. 2B, D, I) 1.4 whorls, 520–540 μm diameter; virtually smooth, but for fine, irregular wrinkling and growth lines visible at high magnification; terminated by a simple growth line (not a sinusigera rib).

Operculum (Fig. 2G). Ear-shaped, paucispiral (following definition of Reid, 1989a), more than 5 whorls visible; opercular ratio, 0.71–0.74; entirely corneous.

Anatomy (Fig. 3). Head-foot of normal littorinine appearance; head and sides of foot unpigmented, but for pale grey cephalic tentacles in some specimens. Penis (Fig. 3A–E) simple, unbranched, sperm groove opens slightly subterminally at tip of filament; base wrinkled, bearing 6–8 mamilliform penial glands in single row along postero-ventral edge; short, bluntly pointed filament (i.e. distal to apical penial gland) 18–27% total length of penis; unpigmented, but with scattered rust-red granules over wrinkled base. Prostate gland open. Sperm: euspermatozoa not preserved; paraspermatozoa (Fig. 3F, G) 19–27 μm, each containing single large rod-piece, spindle-shaped or cylindrical with rounded ends, granules large and distinct. Pallial oviduct (Fig. 3H, I): simple spiral of opaque albumen gland followed by translucent albumen gland (probably including covering gland, not visibly differentiated); capsule glands absent; long straight section with slender copulatory bursa (extending back two thirds of the distance from the anterior opening into mantle cavity towards posterior spiral section). Development ovoviviparous, with intracapsular metamorphosis; up to 138 embryos, within thin spherical coverings, are brooded to crawling stage in a single layer on roof of mantle cavity.

Radula (Fig. 5A–D). Total length of radular ribbon 21–33 mm (relative length 3.2–4.8). Radula taenioglossate. Rachidian tooth: length/width ratio 1.67–2.56; central cusp leaf-shaped with pointed or rounded tip; one smaller pointed cusp on either side. Lateral: 4 cusps, third from inside much the largest, with rounded or slightly pointed tip, others smaller and pointed. Inner marginal: 4 cusps, third from inside largest, with rounded or slightly

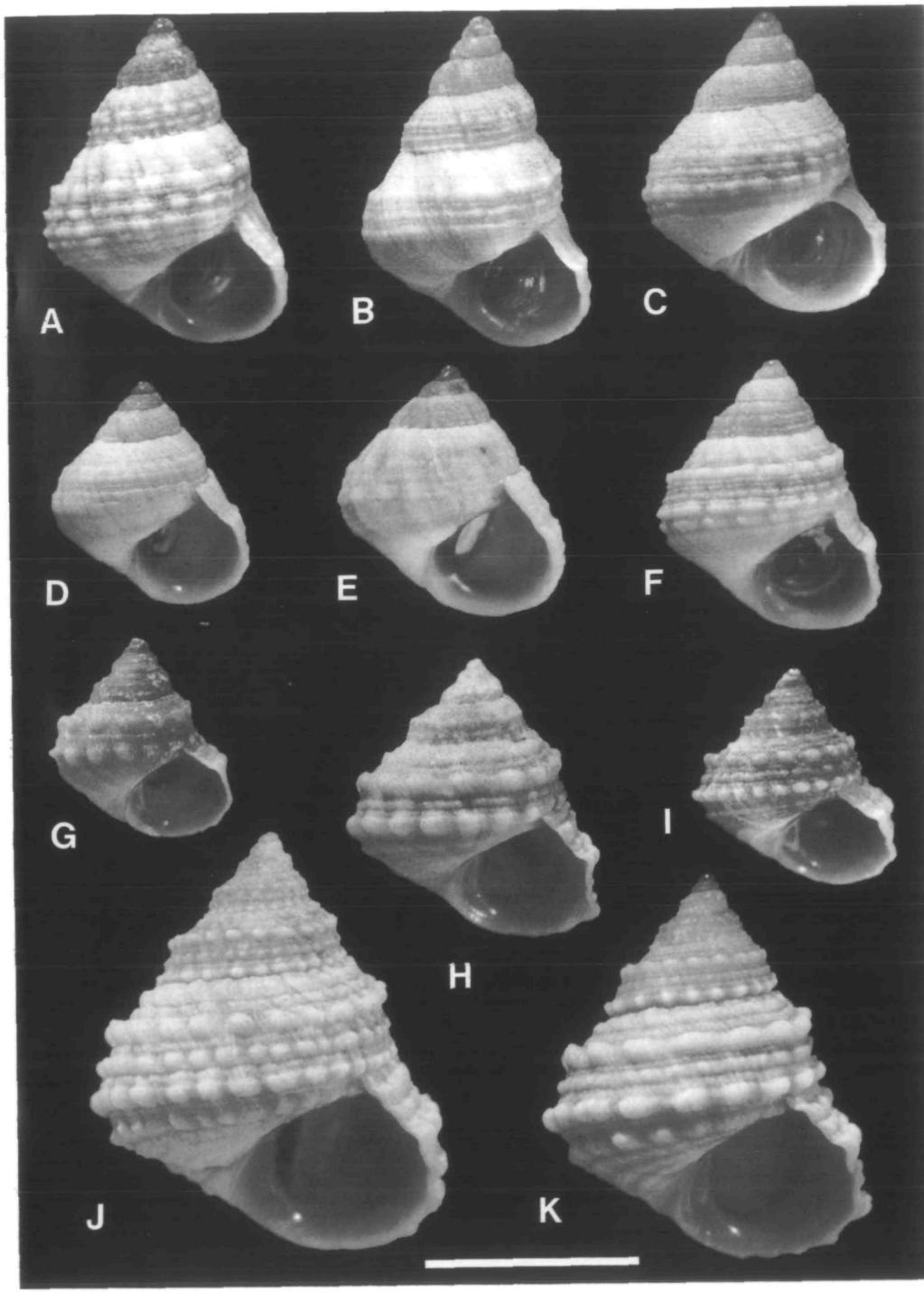

Figure 1. Shells of *Tectarius niuensis* and *T. viviparus*. **A–F.** *T. niuensis* (Anaana Point, Niue Island; **A–C, F,** 10–15 m above sea level; **D, E,** 5–10 m above sea level); **A,** holotype, BMNH 1996064; **B, C, F,** paratypes, BMNH 1996065; **D, E,** paratypes, BMNH 1996066. **G–K.** *T. viviparus* (**G, I–K,** Pago Bay, Guam, BMNH 1996070; **H,** Tagachan, Guam, BMNH 1996069). Scale bar = 5 mm.

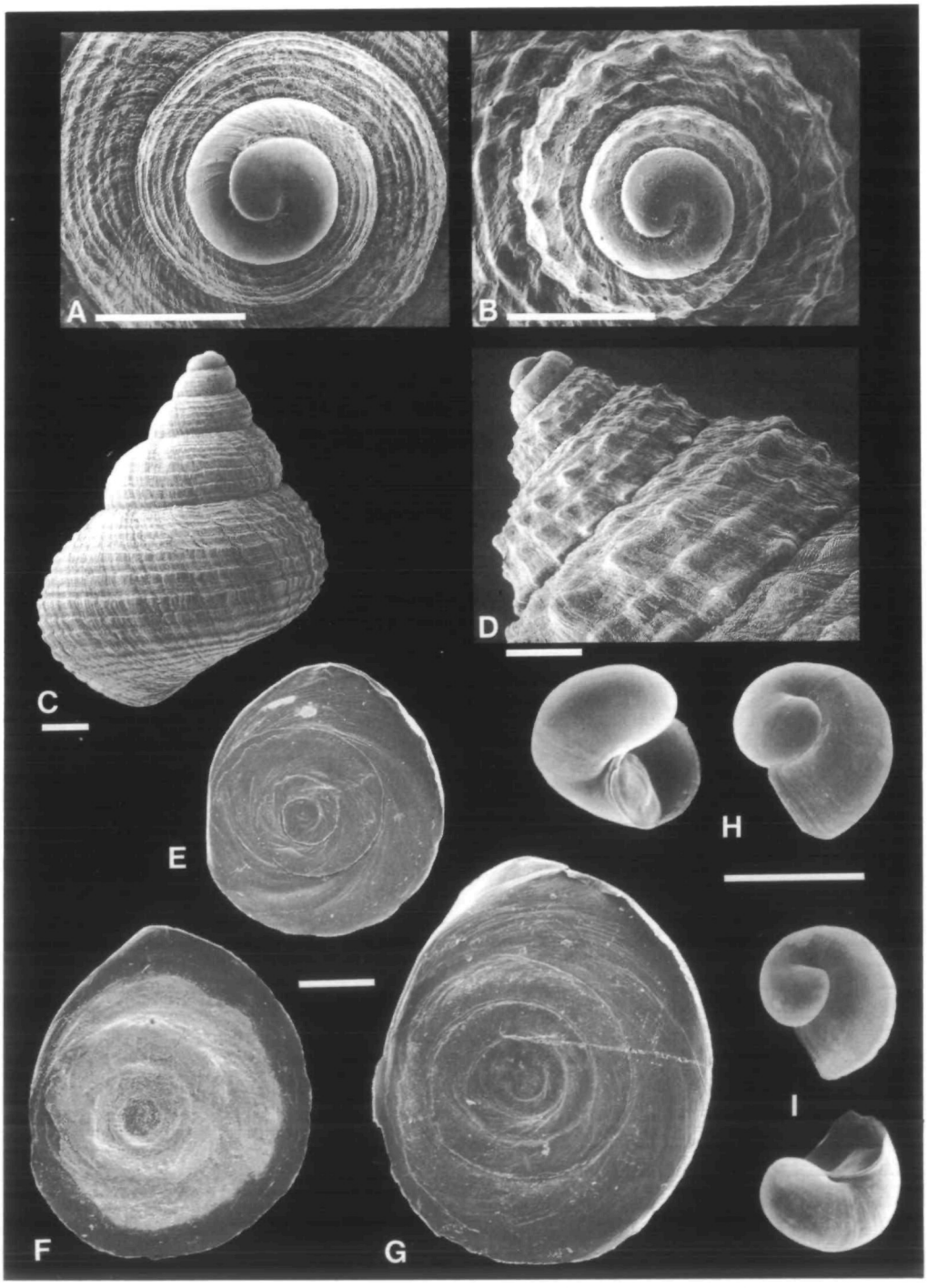

Figure 2. Scanning electron micrographs of shells and opercula of *Tectarius viviparus* (Pago Bay, Guam) and *T. niuensis* (Anaana Point, Niue Island). **A.** Protoconch of *T. niuensis*. **B.** Protoconch of *T. viviparus*. **C.** Juvenile shell of *T. niuensis*. **D.** Detail of apical whorls of teleoconch of *T. viviparus*. **E, F.** Opercula of *T. niuensis*; in **E** the outer calcareous layer has been removed. **G.** Operculum of *T. viviparus*. **H.** Late embryos from mantle cavity of *T. niuensis*. **I.** Late embryos from mantle cavity of *T. viviparus*. Scale bars = 0.5 mm.

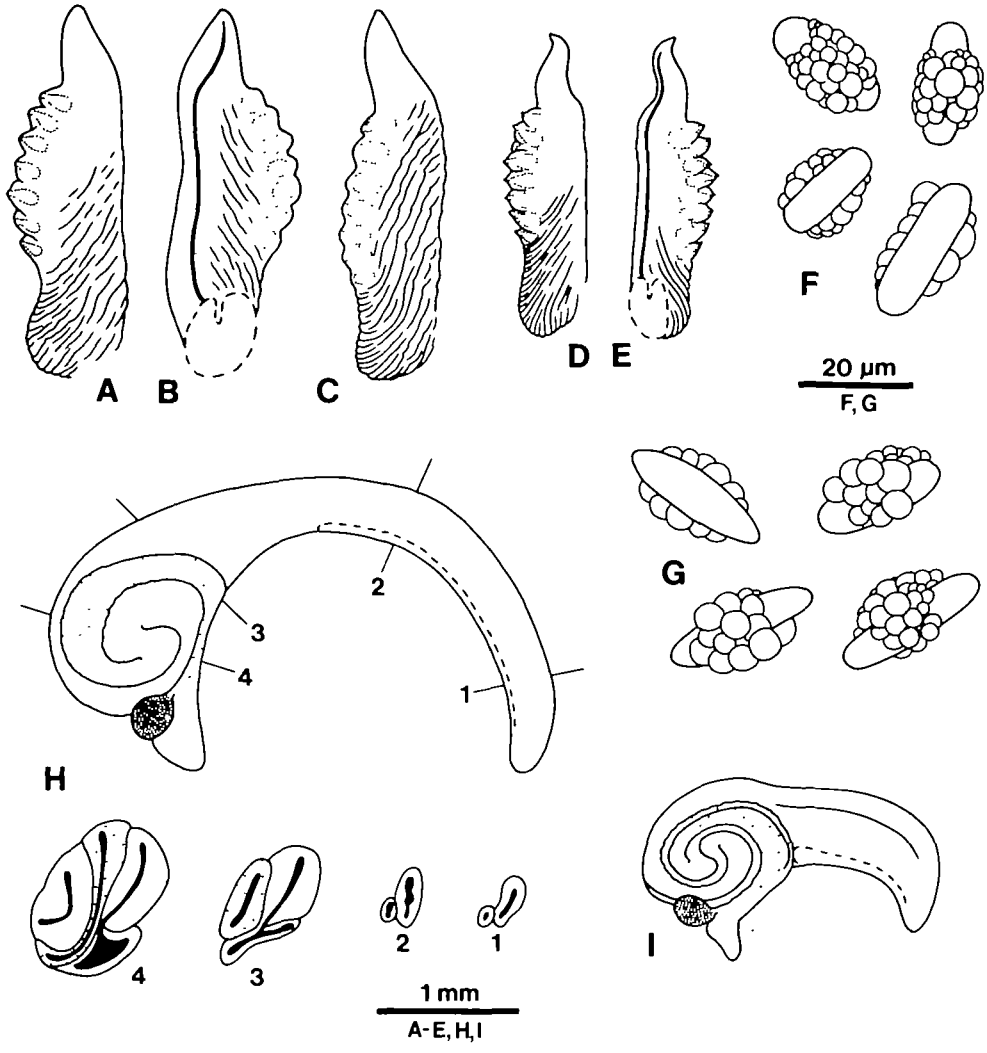

Figure 3. Reproductive anatomy of *Tectarius viviparus*. **A–E.** Penes; **A, B,** and **D, E,** are two views of same penis. **F, G.** Paraspermatozoa from two individuals. **H, I.** Pallial oviducts; 1–4 are sections of **H** viewed from anterior end (i.e. right side of drawing). **A–C, F–H,** Pago Bay, Guam; **D, E, I,** Tagachan, Guam. Shell heights: **A, B,** 6.2 mm; **C,** 6.5 mm; **D, E,** 5.1 mm; **H,** 7.8 mm; **I,** 6.1 mm. Key: dotted outlines, mamilliform penial glands visible by transparency; dashed outlines (**H, I**), copulatory bursa, visible only by dissection; light stipple, opaque albumen gland; dense stipple, seminal receptacle.

pointed tip, others smaller and pointed. Outer marginal: 4 pointed, finger-like cusps; no projection on outer side of base.

Habitat. In the high intertidal and littoral fringe on strongly wave-exposed shores of karstic limestone; often wetted only by spray from surf or blowholes; 'sometimes found at considerable distances landward from the tops of sea cliffs 20–50 feet [6–15 m] high' (Rosewater, 1982). It may not be entirely restricted to limestone shores, since Vermeij (1971) recorded it (as *Echininus cumingii spinulosus*) also on basalt.

Range (Fig. 6). Southern Mariana Islands: Guam, Rota, Tinian and Saipan (Rosewater, 1982). A record of '*Echininus cumingii*' from Maug in the Northern Mariana Islands (Eldredge, Tsuda, Moore, Chernin & Neudecker,

1977) is a misidentification of a *Nodilittorina* species (observation of original material in University of Guam Marine Laboratory, by G. Paulay, pers. comm.). It is absent from the basaltic shores of the Northern Mariana Islands (Vermeij, Kay & Eldredge, 1983).

Tectarius (Echininiopsis) niuensis new species
Figures 1A–F; 2A, C, E, F, H; 4; 5E–H; 6

Types. Holotype BMNH 1996064; 7 dry paratypes BMNH 1996065; 8 dry paratypes BMNH 1996066; 67 alcohol paratypes BMNH 1996067; 102 alcohol paratypes BMNH 1996068; 10 alcohol paratypes USNM 880184. Type locality Anaana Point, Niue Island, west of Cook Islands.

Etymology. After the type locality.

Shell (Fig. 1A–F). Mature shell height 5.0–8.0 mm; H/B = 1.13–1.51 (H/B differs significantly in two samples from type locality: at 5–10 m above sea level, mean = 1.21 ± 0.045 95% confidence limits, n = 10; at 10–15 m above sea level, mean = 1.33 ± 0.075 95% confidence limits, n = 10); no significant sexual dimorphism in size (mean of 10 females 5.71 mm and of 6 males 5.40 mm; in *t*-test $P > 0.05$). Teleoconch 3.5–4.5 whorls. Shape turbinate to conical, with rounded periphery; sutures moderately impressed; largest specimens sometimes minutely umbilicate. Sculpture (Fig. 2C) of 6–12 spiral ribs and smaller cords at and above periphery of last whorl, of which the larger ribs (especially 2 or 3 ribs between shoulder and periphery which are most prominent) often bear small, rounded nodules; nodulation obsolete in some specimens, and ribs are then made minutely rugose by intersecting axial growth lines (Fig. 1B, D). Base with 6–10 fine spiral ribs, slightly rugose towards periphery, but becoming obsolete towards columella. Entire surface covered with fine spiral microstriae if well preserved. Aperture almost circular. Columella short, not hollowed or pinched. Colour dimorphic; shells either pale salmon-orange, fading to pinkish with paler nodules, interior of aperture bright salmon-orange; or ochraceous cream, fading to whitish, interior pale ochraceous orange; colour frequencies: 58% orange in 5–10 m sample (n = 120), 57% orange in 10–15 m sample (n = 75); all have a purplish brown stain on the columella. Protoconch (Fig. 2A, H) 1.4–1.5 whorls, 550–570 μm diameter; virtually smooth, but for fine, irregular wrinkling and growth lines visible at high magnification; terminated by a simple growth line (not a sinusigera rib).

Operculum (Fig. 2E, F). Ear-shaped, paucispiral (following definition of Reid, 1989a), 4 whorls visible; opercular ratio 0.68–0.74; corneous, but with an amorphous deposit of aragonitic calcium carbonate (confirmed by x-ray diffraction) overlaying most of outer surface, with exception of central nucleus and narrow margin.

Anatomy (Fig. 4). Head-foot of normal littorinine appearance; head and sides of foot entirely unpigmented in most individuals, occasionally slight grey pigment on back of head. Penis (Fig. 4A–C) simple, unbranched, sperm groove open to tip of filament; base wrinkled, bearing single mamilliform penial gland on postero-ventral edge; tapering filament (i.e. distal to penial gland) 30–45% total length of penis; unpigmented. Prostate gland open. Sperm: euspermatozoa not well preserved, but are attached in bunches to paraspermatozoa; paraspermatozoa (Fig. 4D, E) 23–39 μm, each containing single long rod-piece with rounded ends, granules large and distinct. Pallial oviduct (Fig. 4G, H): spiral reduced to simple backward loop, of opaque albumen gland followed by translucent albumen gland (probably including covering gland, not visibly differentiated); capsule glands absent; long straight section with no separate copulatory bursa. Development ovoviviparous, with intracapsular metamorphosis; up to 28 embryos, within thin spherical coverings, are brooded to crawling stage, close-packed within mantle cavity (Fig. 4F).

Radula (Fig. 5E–H). Total length of radular ribbon 11–13 mm (relative length 1.8–2.2). Radula taenioglossate. Rachidian tooth: length/width ratio 1.12–1.33; central cusp leaf-shaped with rounded or slightly pointed tip; one smaller pointed cusp on either side. Lateral: 4 cusps, third from inside much the largest, with rounded tip, others smaller and pointed. Inner marginal: 4 cusps, third from inside largest, with rounded tip, others smaller and pointed. Outer marginal: 5 pointed, finger-like cusps; a knob-like projection on outer side of base.

Habitat. In the littoral fringe on strongly wave-exposed shores (not protected by fringing reef) of karstic limestone; on steep cliffs, 5–15 m above sea level, wetted only by spray from surf (G. Paulay, pers. comm).

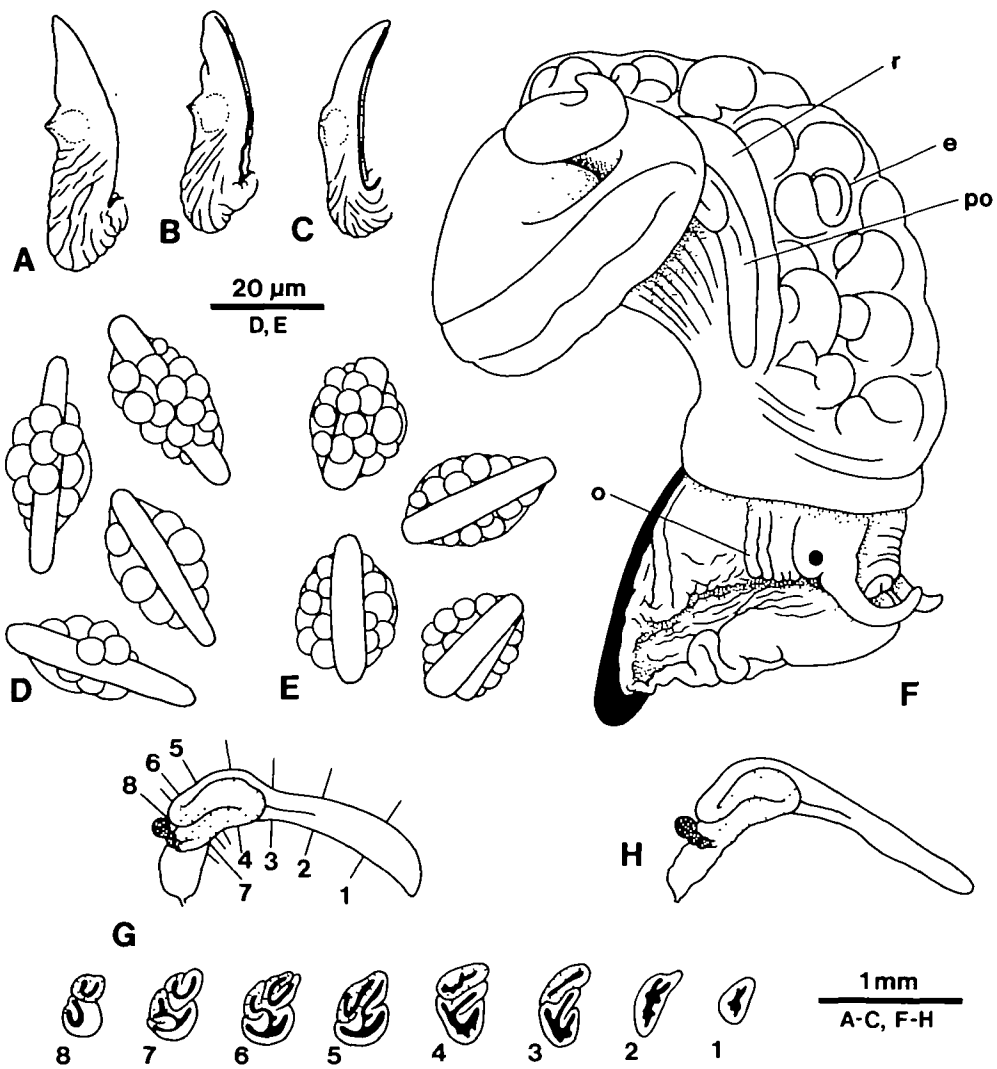

Figure 4. Reproductive anatomy of *Tectarius niuensis* (Anaana Point, Niue Island). **A–C.** Penes. **D, E.** Paraspermatozoa from two individuals. **F.** Female removed from shell, showing embryos in mantle cavity. **G, H.** Pallial oviducts; 1–8 are sections of **G** viewed from anterior end (i.e. right side of drawing). Shell heights: **A,** 5.3 mm; **B,** 6.0 mm; **C,** 5.0 mm; **F,** 6.0 mm; **G,** 5.9 mm; **H,** 6.5 mm. Key: dotted outlines, mamilliform penial glands visible by transparency; light stipple (**G, H**), opaque albumen gland; dense stipple (**G, H**), seminal receptacle. Abbreviations: e, embryos in mantle cavity; o, ovipositor; po, pallial oviduct; r, rectum.

Range (Fig. 6). Recorded only from the type locality on Niue Island, west of Cook Islands.

Similar species. Confusion is most likely with the other member of the subgenus, *T. (Echininiopsis) viviparus*, redescribed above. However, there are numerous diagnostic differences (summarized in Table 3). From the shells alone, the new species is recognized by its smaller size, generally taller spire (especially in the sample from the higher tidal level at the type locality), less prominent (or

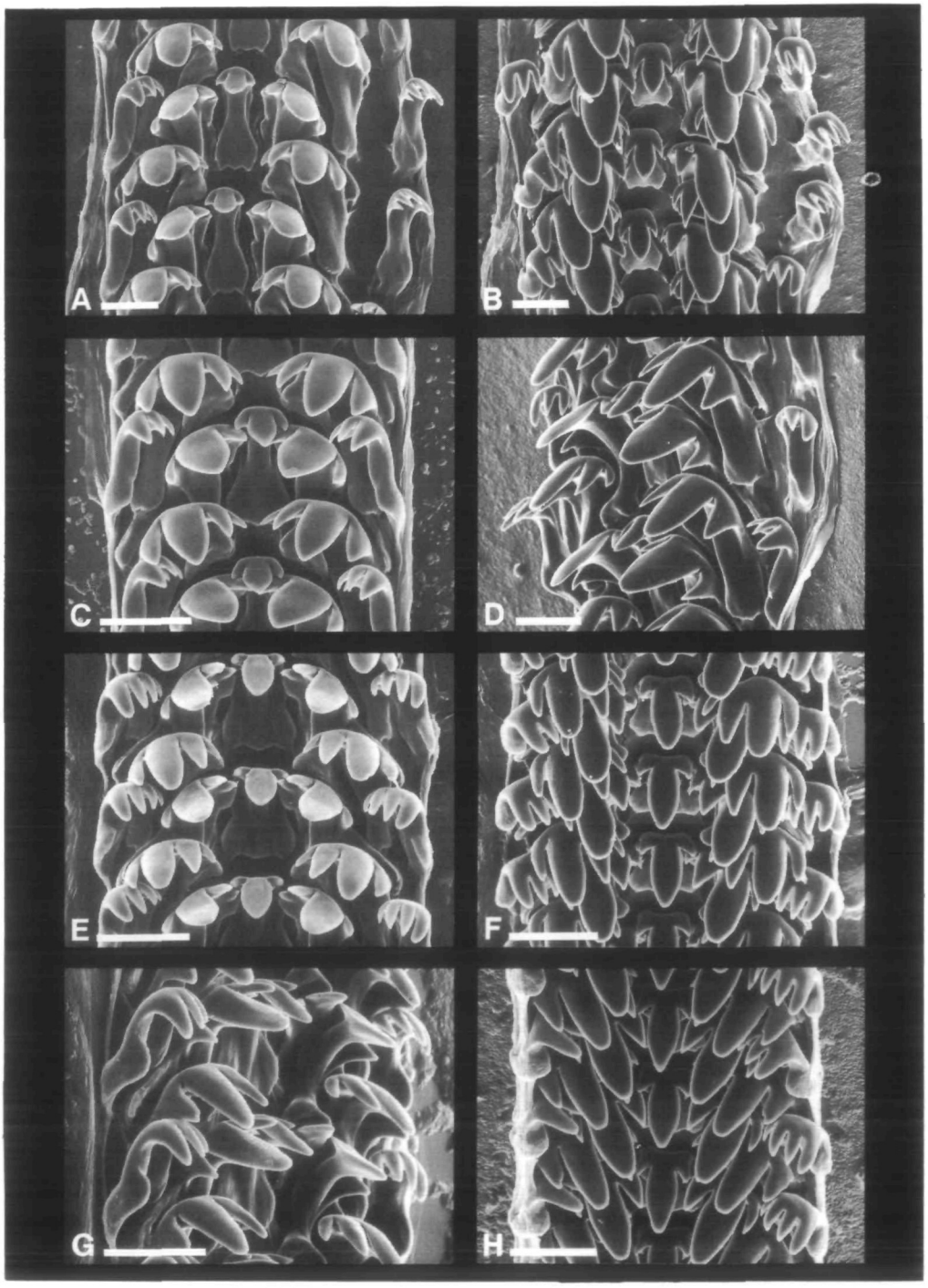

Figure 5. Scanning electron micrographs of radulae of *Tectarius viviparus* (Pago Bay, Guam) and *T. niuensis* (Anaana Point, Niue Island). **A, B, D.** Three views of radula (flat, at 45°, at 45° from side) of *T. viviparus* (shell H = 6.9 mm). **C.** Radula of *T. viviparus* (flat; shell H = 5.3 mm). **E–G.** Three views of radula (flat, at 45°, at 45° from side) of *T. niuensis* (shell H = 6.0 mm). **H.** Radula of *T. niuensis* (at 45°; shell H = 6.2 mm). Scale bars = 20 μm.

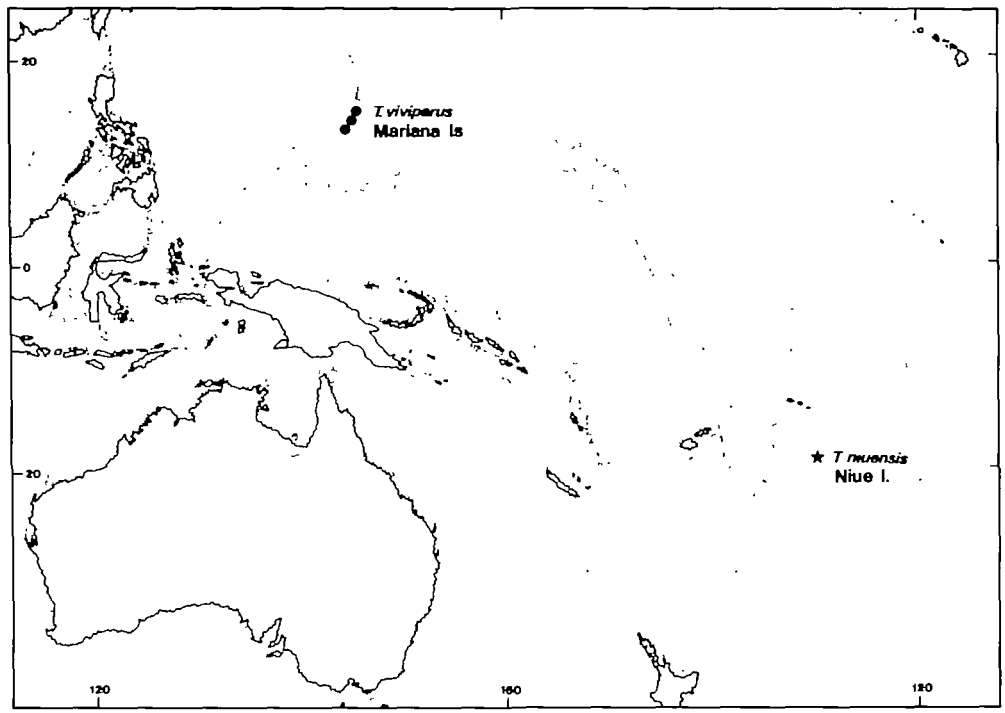

Figure 6. Distribution of *Tectarius viviparus* (dots; after Rosewater, 1982) and *T. niuensis* (asterisk).

even absent) nodular sculpture, more rounded margin and dark columella. The externally calcified operculum is only known in the new species, although the layer is brittle and sometimes becomes partly detached. Anatomically, the penis, oviduct and radula are each diagnostic. Furthermore, their geographical ranges are widely distant.

The only other *Tectarius* in the southern and western Pacific with which confusion could possibly arise is *T. (Echininus) cumingii* (Philippi, 1846). This was divided by Rosewater (1972) into two subspecies, the typical one from New Guinea to the Society Islands, and *T. cumingii spinulosus* (Philippi, 1847) from the Philippines to southern Japan. Whether these two are indeed conspecific has yet to be confirmed by anatomical examination, and shell features suggest that they might be distinct (see p. 233). The former is a low-trochoidal shell with two rows of strong spines at the periphery and at the shoulder, while the latter is quite similar to *T. viviparus* in sculpture; however, both have a strong row of nodules or small spines just below the suture, and are almost always distinctly umbilicate, distinguishing them from both species of *Echininiopsis*. The operculum of both subspecies of *T. cumingii* is circular, entirely corneous, multispiral (OR = 0.77–0.89) and strongly thickened, in contrast to the paucispiral opercula of the two *Echininiopsis*. Only *T. cumingii cumingii* has been examined anatomically in detail (Reid, 1989a); the base of the penis is bulbous, packed with tubules of large glands, and there are 3–5 large mamilliform penial glands in a cluster at the base of the filament, which is itself covered with numerous minute papillae of smaller mamilliform glands; the pallial oviduct includes a large capsule gland, indicating production of pelagic egg capsules; the protoconch confirms planktotrophic development, being of 1.7 whorls, 360 μm diameter, and terminated by a sinusigera rib. The remaining *Tectarius* species in the Pacific have much larger, generally spinose shells, with which no confusion can arise (Rosewater, 1972, 1973).

There is one other group of trochoidal littorinids in the southern and western Pacific, the genus *Peasiella* (see Reid, 1989b, for detailed account). These have small (up to 6 mm diameter), sharply keeled, umbilicate

Table 3. Comparison of *Tectarius (Echininiopsis) viviparus* and *T. (E.) niuensis*.

Character	*T. viviparus*	*T. niuensis*
Shell	Fig. 1G–K	Fig. 1A–F
Maximum height	12.3 mm	8.0 mm
H/B ratio	1.03–1.20	1.13–1.51
Sculpture	strongly nodulose	small nodules, or absent
Columella	orange	purplish stain
Operculum	Fig. 2G. Corneous, 5 whorls	Fig. 2E, F. Corneous, with outer calcified layer, 4 whorls
Penis	Fig. 3A–E	Fig. 4A–C
Mamilliform glands	6–8	1
Filament	18–27% total length	30–45% total length
Pallial oviduct	Fig. 3H, I	Fig. 4G, H
Spiral pattern	simple spiral	backward loop only
Bursa	present	absent
Radula	Fig. 5A–D	Fig. 5E–H
Rachidian tooth	length-width = 1.67–2.56	length/width = 1.12–1.33
Outer marginal tooth	4 cusps	5 cusps
Range	Fig. 6. Southern Mariana Islands	Fig. 6. Niue Island

shells, with multispiral, corneous opercula. The penis is long and vermiform, with a closed sperm duct and usually a single mamilliform penial gland (sometimes absent). The pallial oviduct has a spiral pattern that differs from that of *Tectarius*, and contains a capsule gland; development is planktotrophic. These are strictly intertidal animals, which are unlikely to be confused with the larger *Tectarius* species of the littoral fringe.

Morphometric analysis. In an analysis of variance of log (H/B) in 30 shells of *T. viviparus* and 30 each of *T. niuensis* from 5–10 m and from 10–15 m above sea level, the differences were statistically significant ($F = 51.78$; d.f. = 2, 87; $P < 0.01$); furthermore, each of the three pairwise comparisons was significantly different. Adding log (H) as a covariate was not statistically significant ($F = 2.12$; d.f. = 1, 86; $P > 0.05$). The two samples of *T. niuensis* therefore differed in shape, irrespective of small differences in size, and both differed in shape, as well as size, from *T. viviparus*.

PHYLOGENETIC ANALYSIS

Morphological analysis

The characters used for the morphological phylogenetic analysis are listed in Table 4, and the character state matrix given in Table 5. Since shell features have traditionally been employed in the classification of these littorinids, 7 characters of the shell have been included; these are self-explanatory. A multispiral operculum is here defined as one with an opercular ratio greater than 0.75 (this same category was used by Reid, 1989a, but inappropriately named 'mesospiral'); additional material has shown that *T. grandinatus* and *T. viviparus* fall into the paucispiral category. Although the opening of the penial vas deferens is slightly subterminal in *T. viviparus* (as noted by Reid, 1989a), its form is more similar to the terminal opening of other taxa than to the markedly subterminal, folded opening of *T. cumingii* and *T. antonii*. The arrangement of the mamilliform penial glands has been described by three characters. Previously, the glandular material in the base of the penis of *T. cumingii* had been identified as of the simple subepithelial type (Reid, 1989a). New material has shown that the base is packed with glandular tubules, which appear to discharge at a weak point of the surface epithelium (not raised in a distinct papilla as in typical mamilliform glands).. It is suggested that these large basal tubular glands are homologous with the pair of large glands in the penial base of *T. antonii*. The penial papillae are minute and very numerous mamilliform glands. The paraspermatozoa of *Tectarius*

Table 4. Characters used in the morphological phylogenetic analysis of *Tectarius* species. Abbreviations: L/W, ratio of length to basal width; OR, opercular ratio; ord, character states ordered in analysis; *, autapomorphic character state.

Character number	Character	Description of character states		
		state 0	state 1	state 2
1	Hollow spines	Absent	Present	
2	Umbilicus	Generally absent	Regularly present	
3	Columellar nodule	Absent	Present	
4	Lirate aperture	Absent	Present*	
5	Apertural colour	Pale callus	Dark brown with white basal stripe	
6	External shell colour	Axial or longitudinal dark pattern	Dark pattern absent	
7	Shell colour polymorphism	Absent	Shell orange or yellow	
8	Opercular shape	Paucispiral (OR < 0.75)	Multispiral (OR ⩾ 0.75)	
9	Opercular calcification	Absent	Outer calcified deposit*	
10	Distal opening of penial vas deferens	At tip of penial filament	Subterminal	
11	Closure of penial vas deferens	Closed tube	Open groove	
12 (ord)	No. of mamilliform penial glands	Absent	1 gland	More than 1 gland
13	Large tubular glands in penial base	Absent	Present	
14	Penial papillae	Absent	Numerous papillae on filament	
15	Paraspermatozoa	Rod-pieces absent	Small, rounded rod-pieces	Long, projecting rod-pieces
16	Copulatory bursa	Vestigial or absent	Anterior position	Posterior position*
17	Capsule glands	Present	Absent	
18 (ord)	Coiling of egg groove	Simple backward loop	Simple spiral	Complex spiral
19	Development	Planktotrophic	Nonplanktotrophic, ovoviviparous	
20 (ord)	Rachidian tooth	L/W < 1.5	L/W = 1.6–3.3	Vestigial*
21 (ord)	Lateral and inner marginal teeth	4 subequal cusps	1 large plus 2–3 smaller cusps	1 large cusp only*

Table 5. Character state matrix for the morphological phylogenetic analysis of *Tectarius* species. For description of characters and character states see Table 4. The outgroup comprises the first three taxa.

Species	Character number																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Peasiella tantilla	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Nodilittorina trochoides	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0
Cenchritis muricatus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	1
Tectarius (Tectininus) antonii	1	0	0	0	1	0	0	1	0	1	1	2	1	1	1	2	0	0	0	2	2
Tectarius (Tectarius) grandinatus	1	0	1	1	0	0	0	0	0	0	1	2	0	1	2	1	0	2	0	1	1
Tectarius (Echininus) cumingii	1	1	0	0	0	0	0	1	0	1	1	2	1	1	0	1	0	1	0	1	1
Tectarius (Echininiopsis) viviparus	0	0	1	0	0	1	1	0	0	0	1	2	0	0	2	1	1	1	1	1	0
Tectarius (Echininiopsis) niuensis	0	0	0	0	0	1	1	0	1	0	1	1	0	0	2	0	1	0	1	0	0

species have previously been described only in *T. antonii* (Reid, 1989a). Those of *T. grandinatus* are almost identical to those of *T. niuensis* (Fig. 4D, E). In *T. antonii* the paraspermatozoa are 16–23 μm in diameter, round or slightly oval, containing large round granules and one or two irregularly rounded rod-pieces. Those of *T. cumingii* are similar in shape, 20–24 μm in diameter, also with large round granules, but lacking obvious rod-pieces; however, only a single sample of sperm was available in this species, and it has not been possible to confirm that it was typical. The coiling of the egg groove in the pallial oviduct has been included as a character; in state 0 there is a simple backward loop only (as in *T. niuensis*; see also Reid, 1989a: fig. 9n, q); in state 1 the loop is twisted through one turn to form a simple spiral (as in *T. viviparus*; see also Reid, 1989a: fig. 9p, r); in state 2 there are more turns to the spiral (Reid, 1989a: fig. 9m, o).

In the parsimony analysis of the morphological data set, 6 minimum length trees were found (length 41 steps; consistency index = 0.611, excluding autapomorphic states). In five of these, the tree could not be rooted such that the ingroup was monophyletic. The topology of the strict (and 50% majority-rule) consensus tree is shown in Figure 7. Evidence for the monophyly of the genus *Tectarius* is therefore equivocal. The sister-group relationship of *T. (Echininus) cumingii* and *T. (Tectininus) antonii* is supported by three character-state changes, the multispiral operculum (character number 8), the subterminal opening of the penial vas deferens (10) and the large tubular glands in the penial base (13), of which the latter is unique in the Littorinidae and therefore probably a reliable synapomorphy. Further optimization of characters on the consensus tree is not possible, because of the unresolved polychotomy. However, character states can be reconstructed on the one of the most parsimonious trees in which the genus *Tectarius* is monophyletic. In this case, two characters (hollow spines, and penial papillae; numbers 1 and 14) support the clustering of the subgenus *Tectarius* with the subgenera *Echininus* and *Tectininus*, but since neither of these characters is unique in the family, the evidence is weak. The sister-group relationship of the two species *T. viviparus* and *T. niuensis* is supported by four characters: absence of colour pattern, colour polymorphism, absence of capsule glands, and ovoviviparous development (numbers 6, 7, 17, 19). The occurrence of colour polymorphism is unique among the genera included in the analysis, and is therefore regarded as a strong synapomorphy. There are no unequivocal synapomorphies of the genus *Tectarius*, but possible synapomorphies include multiplication of the mamilliform penial glands (number 12; assuming reversion to a single gland in *T. niuensis*) and narrowing of the rachidian tooth (number 20; assuming reversion to a broader tooth in *T. niuensis*).

If the analysis is run with all characters specified as unordered, the topology of the ingroup remains unaltered, and its monophyly is still unresolved. If the two characters connected with development (17, 19) are excluded from the analysis, the sister-group relationship of *T. viviparus* and *T. niuensis* is no longer supported, so that the morphological data set does not provide independent support for the single origin of ovoviviparity within *Tectarius*. If all shell characters (1–7) are excluded, 7 minimum length trees are

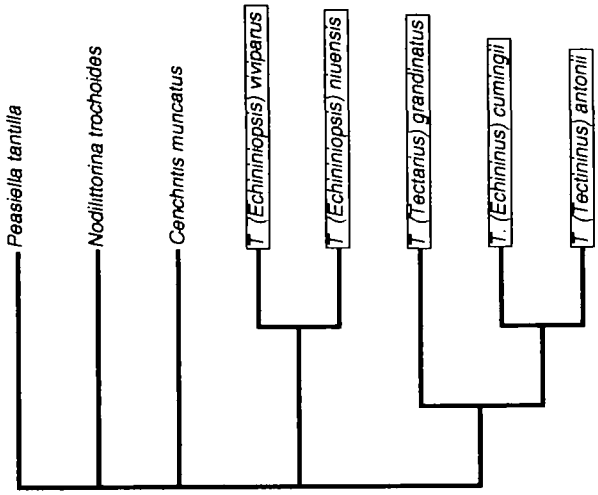

Figure 7. Strict consensus of 6 most-parsimonious trees produced by analysis of morphological characters of 5 species of *Tectarius* (Table 4) with PAUP. No unambiguous characters support the monophyly of the genus *Tectarius* (taxa in boxes). See text for details of character optimization on the tree.

produced, of which a strict consensus supports *T. cumingii* and *T. antonii* as sister-species, whereas the remaining taxa form a polychotomy.

Molecular analysis

The sequences of the 16S rRNA gene fragment that were used in the molecular phylogenetic analysis are shown aligned in Figure 8. Aligment was facilitated by several highly conserved regions, although alignment in two regions was uncertain due to both sequence variability and insertion/deletion events. There are 170 variable positions (including insertions and deletions) among the 436 sites aligned. A search for the most parsimonious trees was bootstrapped using the general heuristic option of PAUP with 2000 replications. The resulting tree (Fig. 9) shows support (87% of bootstrap replications) for the sister-species pair *T. viviparus* and *T. niuensis*, and these form a weakly supported clade (64%) with *T. grandinatus*. *Tectarius cumingii* and *T. antonii* are moderately well supported sister-species (73%), and join *Peasiella tantilla* and *Cenchritis muricatus* in a weakly supported clade (59%). The monophyly of the genus *Tectarius* is therefore not supported, but the evidence against it is weak.

DISCUSSION

Morphology of Tectarius niuensis

The genus *Tectarius* includes the largest member of the family Littorinidae, *T. (Tectarius) pagodus* (Linnaeus, 1758), which attains a shell height of 61 mm (Rosewater, 1972). *Tectarius viviparus* was hitherto the smallest member of this genus, but the new species is smaller still. Both these members of the subgenus *Echininiopsis* are remarkable for their habitat at the upper extreme of the littoral fringe on wave-exposed coasts, up to 15 m above the water level, where they appear to be wetted only by spray and rain. Little is known about the habitats of other *Tectarius* species, but at Avana Harbour on Rarotonga, in the Cook Islands, the large *T. (T.) grandinatus* (Gmelin, 1791) (H up to 33 mm) was found on karstic limestone at the top of the eulittoral zone, just washed by waves, whereas the smaller *T. (Echininus) cumingii* (H up to 18 mm) was found up to 1–2 m further from the water level, in pits on the eroded, sun-baked limestone platform, even among the bases of halophytic land plants (DGR, pers. obs.). Although the two *Echininiopsis* have not been found sympatrically with other *Tectarius* species, they appear to continue the trend towards smaller size at

```
N. trochoides   ACGGCCGCGGTACTCTGACCGTGCAAAGGTAGCATAATCATTTGCCCTAT  50
T. antonii      ..................................................
T. cumingii     ..................................................
T. grandinatus  ..................................................
T. niuensis     ..........................................C.....T...
T. viviparus    ..................................................
C. muricatus    ..................................................
P. tantilla     ..................................................

N. trochoides   AATTGAGGGCTAGTATGAAGGGTTTGACAAGGGCTTTTCTGTCTCTGTGA 100
T. antonii      ..................................GCCC........ACAG
T. cumingii     ..................................ACCC..........AG
T. grandinatus  ..C.......................G......G.C..C.........
T. niuensis     ......A......C.....A........G...AT.A.A........A.A.
T. viviparus    ..C.......C............C....G....T.G.A..........A.
C. muricatus    ..................................-....C..........
P. tantilla     ..........................T.A..AAAG.......A..AG

N. trochoides   AAA--TTGTTGGAATTTATTTTTTAGATGAAGAAATCTAAATGGAATTAA 150
T. antonii      .G.AT..TC.....C.....C.....G.......CC....G.AA......
T. cumingii     ...--.AA.C.........C..A...G......T.C...G..AC......
T. grandinatus  ..G--.AAA.A...G.....C.....G.......CC......AA......
T. niuensis     G..--..AC.AA..A...........G........C......AA......
T. viviparus    G..--.CCC.AA..A.....C.....G.A......C......AA......
C. muricatus    ...--.CAA.....C..............................A......
P. tantilla     ...--.AC..............A..G.......GC..T...AAG.....

N. trochoides   AAGACAAGAAGACCCTATCGAGCTTAAAAATTATTTTTGATATAAAAAAA 200
T. antonii      ..............................C.AC.A...AG....G...
T. cumingii     ..............................C.A..G....C....G...
T. grandinatus  ............................G.C-...G...A.C.....GT
T. niuensis     ..............................C.....A....GCC......
T. viviparus    ............................TC.....A.........C...
C. muricatus    T..............................A..TC..CT.GGG.
P. tantilla     ..........................GTCA...AGAAT.C.TTTTG..

N. trochoides   GCATT---TTGTATTTTTATTCACAAAAGAATTTTGGTTGGGGCGACTAA 250
T. antonii      .TGACAAA.CAC....C.T....T...-A.T..................
T. cumingii     AT.C.ATCA.A.T.C.C.TCA..A.T.-ATT....A...........C..
T. grandinatus  A.TCC---CA....C..CC....T...GA.T..................
T. niuensis     C.CAC----.......-.T....T...-A.....................C..
T. viviparus    ..CA.CTA...C..C.CCC....T...-A.....................C..
C. muricatus    CT..AACTA.AG..CCC.T.C..T...-A.....................G.
P. tantilla     CT.G.---.A....C..T..TT.T..-AC.....A..............

N. trochoides   GGAACAAAAAAAGCTTCTTTTATTTTTAAAGATATATTTATTTTGATCCA 300
T. antonii      ......GTC..........-----..A.CCTT.A.A.CAAT..-A......
T. cumingii     .........T...A....C.---C..ACCT.A.AC..C.ATC.-A......
T. grandinatus  ..................----.C...T..A.C...CCATAA....C...
T. niuensis     ................C.---C.A.....CTATAT.A..CC-........
T. viviparus    ..................----..ACA...AT..C...ATAA........
C. muricatus    ........C..........----..AA.TT.A.CCAC.A.TC.GA.....G
P. tantilla     ........C.G......C.---.G.AA...A...G..A.T.G.AT..TG.
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Figure 8. Aligned DNA sequences of a segment of the mitochondrial 16S rRNA gene from 5 species of *Tectarius*, *Peasiella tantilla*, *Cenchritis muricatus* and *Nodilittorina trochoides*.

```
N. trochoides    TAT-CTGGTTGTGATTAAAAGAATTAGTTACCGTAGGGATAACAGCATAA 350
T. antonii       ..C--.TT..A...C.....................................
T. cumingii      ..C--CAA..A....C......C.....................C......
T. grandinatus   C..-..CA.............A.C.....................................
T. niuensis      C.C--.CA.............A.....................................
T. viviparus     C.C--CTA.............A.....................................
C. muricatus     CGCCT.TA.C.C.....................................
P. tantilla      .CCA.GCT.C........T....A.....................

N. trochoides    TCTTTTTTGAGAGTTCTTATCGAAAGAA-AGGTTTGTGACCTCGATGTTG 400
T. antonii       ................CC.......A..-.....................-..
T. cumingii      ..............C..........A..-.....................
T. grandinatus   ................C........AG.-.....................
T. niuensis      ............C..C........A..?.....................
T. viviparus     ............C..CC.......A..-G.....................
C. muricatus     ............CC..........A..-.....................
P. tantilla      ...C.C.......C.............G-.....................

N. trochoides    GACTAGAATATCCTGAGAGGTGCAGAAGCCTTCAAG 436
T. antonii       .........G......T....??...C.........
T. cumingii      ................T.............-......
T. grandinatus   ................T....-.............
T. niuensis      ................T..................A
T. viviparus     ............C..C..................A
C. muricatus     ................A....??..CC.........
P. tantilla      .....A.G........T.....T..CC.........
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Figure 8. *Continued.*

levels further from the sea. All members of this exclusively tropical genus of the high shore have shells that are nodulose or spinose, and are pale in colour, fading to whitish. As in other high-shore littorinids (Vermeij, 1973), these traits may be adaptive in relation to convective heat loss and reflection of sunlight. Small size may also be adaptive at the highest levels of the shore, increasing the relative surface area for convection and reradiation of heat, although an interspecific trend of decreasing size at higher levels is not evident in other littorinid assemblages (Vermeij, 1973). Other considerations, such as fecundity, may be more important determinants of body size.

The difference in shell shape of the samples of *T. niuensis* from the two levels on the shore is interesting. In addition to being more tall-spired, the sample from the upper level (10–15 m above sea level) is also more strongly nodulose (compare Fig. 1D, E from 5–10 m with Fig. 1A–C, F from 10–15 m). Interspecific trends of increasing spire height and sculpture with zonation level have been noted in other tropical littorinids, and explained respectively as adaptive in relation to reduction of the relative size of the aperture (and hence of the area of the foot in contact with the hot substratum while crawling) and to convective heat dissipation (Vermeij, 1973). Intraspecific trends in shell form with tidal level on a similarly small scale have been described in some temperate littorinids with non-planktotrophic development, such as *Littorina saxatilis* (Olivi, 1792), and since the variation has a partly genetic basis, adaptive explanations can be suggested (review by Reid, 1996), although not in relation to heat stress. The taller-spired, more nodulose shells of *T. niuensis* at higher levels may well be functional in relation to heat stress, but since the genetic basis of the intraspecific difference is unknown, it cannot be said that these traits are necessarily adaptive. Genetic differentiation over a distance of only 10 m is a possibility, for (as in the case of *Littorina saxatilis*) ovoviviparous development will restrict gene flow. An ecophenotypic explanation (which does not require genotypic adaptation) is also possible; for example, if food supply or feeding time are more limited at higher levels, growth may be slower, with a direct influence on shell shape and sculpture (see review of ecophenotypic effects on shell shape in *Littorina* by Reid, 1996). Intraspecific trends of increasing spire height with shore level have also been

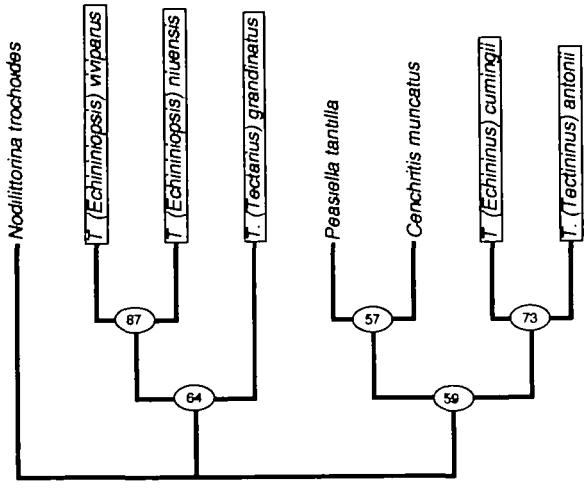

Figure 9. Bootstrapped maximum-parsimony tree based on analysis of 16S rRNA gene sequences from 5 *Tectarius* species with three outgroup taxa (*Peasiella tantilla*, *Cenchritis muricatus* and *Nodilittorina trochoides*), produced with PAUP. Numbers on nodes are the percentage of replicates in which the taxa of each clade occur together.

found in some planktotrophic littorinids, for example *Nodilittorina punctata* (Gmelin, 1791) (Vermeij, 1793) and *N. unifasciata* (Gray, 1826) (Chapman, 1995), and in *Littorina striata* King & Broderip, 1832, nodulosity increases in the same way (Reid, 1996). In these planktotrophic species, high gene flow has been presumed to preclude genotypic differentiation, and ecophenotypic mechanisms have been invoked. Nevertheless, in the planktotrophic *Nodilittorina hawaiiensis* Rosewater & Kadolsky, 1981, small-scale intraspecific variation in shell nodulosity has been claimed to have a genetic basis (Struhsaker, 1968, as *Littorina picta*).

Many littorinid species show intraspecific variation in shell coloration, but discrete variation, or polymorphism, has hitherto been described in a few members of only two genera, *Littoraria* (Reid, 1986) and *Littorina* (review by Reid, 1996). The discovery of polymorphism in both *Tectarius viviparus* and *T. niuensis* is therefore noteworthy. In other littorinids there is a correlation between the most striking shell colour polymorphism and a visually varied background, as in the cases of *Littoraria* species which inhabit mangrove vegetation (Reid, 1987) and two species of the *Littorina obtusata* group which live in association with intertidal fucoid algae (Reid, 1996). Polymorphism may be maintained in various ways, but this association has led to the suggestion that such cases may be maintained by frequency-dependent selection by visual predators (Reid, 1987; Cook & Garbett, 1992). Little is known of the visual properties of the habitats of the two *Tectarius* species, but the pitted, eroded limestone on which they are found may perhaps present a varied pattern. This, however, should also be the case in other *Tectarius* species which all occur on similar substrates. The two polymorphic species differ from the rest in apparently occupying habitats even further from the sea; conceivably, they may there be exposed to a range of visually-hunting terrestrial predators, such as birds, which might promote visual polymorphism. It should be noted that the colour polymorphism of these two species is most noticeable in juvenile shells and when the shells are wet; when dry and faded the difference between the two morphs is less distinct.

Among *Tectarius* species, the operculum is most nearly circular, and most tightly wound ('mesospiral' of Reid, 1989a; 'multispiral' of Rosewater, 1972, and Bandel & Kadolsky, 1982), in *T. cumingii* and *T. antonii*. Although other *Tectarius* species have opercula that are often more tightly coiled (OR 0.62–0.74) than those of temperate littorinids (e.g. 0.38–0.72 in

Littorina species, Reid, 1996), no sharp distinction can be made. Functionally, tight coiling serves to thicken the operculum, and to fit a more circular aperture (Bandel & Kadolsky, 1982); both may reduce evaporative water loss in these littorinids of the tropical littoral fringe. The partly calcified operculum of *T. niuensis* appears to be unique among marine members of the family. Curiously, Bandel & Kadolsky (1982) listed a calcified operculum as one of the characters of their genus *Echininus*, although all examples of *T. (Echininus) cumingii cumingii* and *T. (E.) cumingii spinulosus* that have been examined during this study have had entirely corneous opercula. Perhaps this character may be variable within the subgenus *Echininus*, or alternatively these authors may have included examples of the new species in their concept of *Echininus*. Elsewhere in the Littorinidae, only the freshwater genus *Cremnoconchus* has a calcified operculum, although in that case there are proteinaceous layers over both internal and external surfaces. The terrestrial family Pomatiasidae (a possible sister-group of the Littorinidae, Reid, 1989a) also has an externally calcified operculum. The association with a semi-terrestrial or entirely non-marine habitat in these three cases is notable, but it is not clear whether there might be a common functional interpretation. A role in calcium metabolism seems unlikely; for *Cremnoconchus*, calcium may be limiting (as suggested by the frequent erosion of the shell), whereas this cannot be the case for calciphilic pomatiasids, nor for *T. niuensis* inhabiting coralline limestone. A protective thickening of the operculum is a possibility.

The penes of both *Tectarius viviparus* and *T. niuensis* are of more simple structure than those of other members of the genus, since the mamilliform glands are fewer in number and are all of the same size (penes of other *Tectarius* species are described by Reid, 1989a). One of the principal synapomorphies of the subfamily Littorininae is the presence in the pallial oviduct of capsule glands, which secrete the pelagic egg capsule. In the two species of *Tectarius* described here, as in all other ovoviviparous members of the subfamily, these glands have been lost; the absence of capsule glands can therefore be used to predict this aspect of development. Ovoviviparity, and the method of brooding, in littorinids are discussed below. The absence of the copulatory bursa, observed in *T. niuensis*, is unusual in the Littorinidae, having been observed only in two species of *Pellilitorina* (Reid, 1989a), three of *Peasiella* (Reid, 1989b) and in some small examples of *Littorina saxatilis* (Reid, 1996). Typically, the rachidian tooth of *Tectarius* species is narrowed (as in *T. viviparus*, or more so); the rectangular shape of that of *T. niuensis* is unique in the genus, and resembles the plesiomorphic condition in the family (Reid, 1989a).

Phylogenetic relationships and classification of Tectarius

Neither the morphological nor the molecular phylogenetic analyses provide unequivocal support for the monophyly of the genus *Tectarius* as currently constituted (Reid, 1989a). In the morphological analysis, monophyly was supported by only one of the six most parsimonious trees. There were no unequivocal morphological synapomorphies of the genus, but possible synapomorphies (equivocal, since they are open to alternative optimizations) include multiplication of the mamilliform penial glands (this requires reversion to a single gland in *T. niuensis*) and narrowing of the rachidian tooth (this requires reversion to a broader tooth in *T. niuensis*). However, neither of these character states is unique in the Littorinidae (Reid, 1989a), so the evidence for monophyly is weak. In a previous morphological phylogenetic analysis of all littorinid subgenera (Reid, 1989a) there were three possible synapomorphies for *Tectarius*. There, it was concluded that the reduced rachidian tooth was a good synapomorphy for the genus, but *T. niuensis* (which is an exception) was not then known. Furthermore, marked narrowing of the rachidian tooth has also been described in some members of the genus *Nodilittorina* (Bandel & Kadolsky, 1982), indicating convergence in this character. A second possible synapomorphy was the multispiral operculum, but additional material and the discovery of the new species have shown that this is restricted to *T. antonii* and *T. cumingii*. The third possible synapomorphy in the previous analysis was the presence of many mamilliform penial glands of several types; this character has been recoded here, but multiplication of the glands remains as a possible synapomorphy, although a parallel development has occurred in *Littorina* (Reid, 1996).

A further four or five species of *Tectarius* are known. Shell, penial and opercular characters of the type species, *T. coronatus*

Valenciennes, 1832, were described by Rosewater (1972, 1973). Preliminary anatomical studies of three others (*T. pagodus* (Linnaeus, 1758), *T. rusticus* (Philippi, 1846) and *T. tectumpersicum* (Linnaeus, 1758)) indicate that they are closely related to *T. grandinatus* and likewise belong to the nominate subgenus. As noted earlier, the taxon *T. (Echininus) cumingii spinulosus* is of uncertain status; in addition to the conchological differences described by Rosewater (1972), the limited anatomical material available suggests that it differs from the nominate subspecies only in having 2–3, rather than 7–12, typical mamilliform glands on the penis. Further investigation may prove it to be specifically distinct, but it is undoubtedly closely related to *T. (E.) c. cumingii* (see p. 233). Inclusion of these additional species in the morphological analysis would not therefore alter the tree topology, unless further characters were to be discovered.

In the molecular analysis there was weak evidence against the monophyly of *Tectarius*, since *T. cumingii* and *T. antonii* were separated from the remaining three *Tectarius* species. However, the bootstrap values were low. A more rigorous test of the monophyly of the genus will be possible when molecular data from a wider range of littorinid taxa are analysed (Thomas *et al.*, in prep.). The inclusion of other species of *Tectarius* in the molecular analysis, and the sequencing of additional genes, might improve resolution of these phylogenetic relationships.

At present, it would be premature to alter the generic and subgeneric classification of *Tectarius*. Nevertheless, some systematic conclusions can be drawn. Both molecular and morphological analyses support the sister-species relationship of the two ovoviviparous taxa, which are placed together in the subgenus *Echininiopsis*. As reviewed earlier (Table 1), there has been controversy about the classification of *T. antonii*, which was placed in the genus *Nodilittorina* by Bandel & Kadolsky (1982), because of characters of its shell, radula and spawn. Both the analyses presented here support the conclusion of Reid (1989a) that this species is not related to *Nodilittorina*; in fact it shows the closest relationship with *Tectarius (Echininus) cumingii*, as has in the past sometimes been indicated by their inclusion together in the genus *Echininus* (Clench & Abbott, 1942; Abbott, 1954; Rosewater, 1970, 1972). If future work refutes the monophyly of *Tectarius*, it may be appropriate once again to recognize *Echininus* at generic rank.

Biogeography and fossil record of Tectarius

The genus *Tectarius* has a long, but sparse, fossil record. The earliest undoubted member is *T. elegans* (Faujas), correctly assigned to *Tectarius* by Glibert (1962), from the Stampian stage of the Upper Oligocene in southwestern France (Lozouet, 1986). Specimens have been examined, and closely resemble modern species of the subgenus *Tectarius*. As suggested by Lozouet (1986), '*Trochus*' *deshayesi* Hébert & Renevier, 1854 (illustrated by Boussac, 1911), from the Upper Eocene of the Alps, is perhaps an even older species of the genus. *Tectarius rehderi*, described from the Lower Miocene of the Marshall Islands (Ladd, 1966) is another possible species, but others illustrated by Rosewater (1972) are not considered to be assignable to this genus. These fossil occurrences are too few to provide precise evidence for phylogenetic or biogeographic hypotheses, although it can at least be said that the genus was a component of the Tethyan fauna that occurred in the area of present-day Europe, and that it now survives only in the Caribbean and the southern and western Pacific Ocean.

In the absence of extensive fossil evidence, it is possible to derive approximate ages of clades from the molecular divergence among taxa. Such estimations depend upon the assumption of uniformity of rates of divergence among lineages (i.e. a 'molecular clock') and are difficult and controversial (e.g. Nei, 1987; Gillespie, 1991), but in the present case they are the only source available. The rates of accumulation of transition and transversion substitutions in the 16S mitochondrial gene have been calibrated against the fossil record in the genus *Littorina* (for transitions 0.204% per million years; for transversions 0.0837% per million years; Reid, Rumbak & Thomas, 1996). Such rates may not be uniform even among closely related lineages, and indeed some evidence for rate heterogeneity has been found among littorinine genera (Reid *et al.*, 1996). With this reservation in mind, the percentages of sequence divergence among *Tectarius* species have been examined, and ages estimated using the *Littorina* calibrations (sites with deletions were omitted). Assuming the molecular topology (Fig. 9), but monophyly of *Tectarius*, the six pairwise comparisons of the most distantly related *Tectarius*

species yield an average age for the genus of 90 million years (Ma) (range 77–110 Ma; using transversion differences only, since transition/transversion ratios suggest likely saturation of transition substitutions over this timescale). This would place the origin of the genus in the Upper Cretaceous, far older than available fossils. For the pair *T. antonii* and *T. cumingii* (from the Caribbean and south-western Pacific respectively) there are only two estimates of their age of divergence, based on single comparisons of transitions or transversions, yielding ages of 43 and 79 Ma respectively. These estimates span a wide range, but do suggest that the divergence is an ancient one, predating such events as the Miocene closure of the Tethys Sea (Adams, 1981) and the Pliocene formation of the Panamanian isthmus (Vermeij, 1993), which might have been considered as possible causes of vicariance between Atlantic and Pacific clades.

Performing the same operation for the pair of ovoviviparous sister-species yields ages of 35 Ma and 45 Ma for transitions and transversions respectively. Again this is a wide range, indicative of the considerable errors in this method of coarse approximation. Even allowing that the substitution rate in *Tectarius* might be faster than that in *Littorina* (for example, because of the possible effects of shorter generation time or higher temperature), these figures suggest that the divergence of *T. viviparus* and *T. niuensis* is of considerable antiquity. The known present-day ranges of these species, in the Mariana Islands and on Niue respectively, are separated by about 6300 km. Raised limestone reefs may have been present on the island of Guam as early as the late Miocene, although the cliffs of the Mariana Limestone (on which *T. viviparus* is now found) were only uplifted during the Pleistocene (Tracey, Schlanger, Stark, Doan & May, 1964). The uplift of Niue also occurred relatively recently, during the Pleistocene (Aharon, Goldstein, Wheeler & Jacobson, 1993). There is yet no fossil evidence as to how the modern distribution of the two species has been achieved. The apparently restricted geographical distribution of each is consistent with the fact that tropical gastropods without pelagic larval dispersal, and in which opportunities for rafting are rare, are often narrowly distributed (review by Ó Foighil, 1989; see below). However, although nonplanktotrophic development may restrict dispersal over medium distances, it has been suggested that it may actually enhance very long-distance dispersal, because the progeny of a single fertilized immigrant remain close together and are more likely to establish a viable population (Johannesson, 1988). Conceivably, therefore, the present-day distribution could have been achieved by chance dispersal (or island-hopping) of the ancestral species from the older Mariana Islands southeast through the Pacific. Such dispersal may have taken place via the corridor of limestone islands along the western margin of the Pacific Plate (see map in Stoddart, 1992). Alternatively, and more probably, it may be that the ancestral species had, in the past, a wider distribution, that has since become fragmented. Although elevated limestone islands are now relatively scarce across much of the Pacific (Stoddart, 1992), at times of low sea level in the past the limestone cliff habitat may have been more common. It is well known that during the later Cenozoic, and especially the Pleistocene, successive ice ages have caused large (up to 150 m) and frequent fluctuations of sea level (e.g. Chappell & Shackleton, 1986; Haq, Hardenbol & Vail, 1987). The most severe fall in sea level, about 30 Ma, was sufficient to have exposed most of the existing reef platforms in the western Pacific (Fulthorpe & Schlanger, 1989). The restricted present-day distribution of *T. viviparus* and *T. niuensis* may therefore be relictual, and their divergence the product of vicariance caused by an episode of raised sea level.

It remains possible that further populations of these, or related, species may yet be discovered on other limestone islands in the western Pacific, for example in Tonga, Fiji, Vanuatu, Solomon Islands, Papua New Guinea and Palau. The wave-exposed cliffs on which they occur are difficult of access, and marine species might previously have been overlooked at such high levels of the littoral fringe.

Ovoviviparity in the Littorinidae

The brooding of eggs within the female is rare in littorinids, and in the entire family has been reported in only three (or possibly four) clades, all in the subfamily Littorininae: *Tectarius (Echiniopsis)*, one clade of *Littoraria* (subgenera *Littorinopsis* plus *Bulimilittorina*), *Littorina (Neritrema) saxatilis* and possibly *Cenchritis muricatus* (Reid, 1989a). Of these cases, most involve only a short period of brooding and the release of planktotrophic veliger larvae, as in all 12 species of *Littoraria*

(Littorinopsis) and possibly in *Cenchritis muricatus* (a report of ovoviviparity by Bandel, 1974, is contradicted by other accounts, and it may be facultative, Reid, 1989a). This brief brooding represents only a small modification of the ancestral type of littorinine development, in which pelagic eggs hatch into planktotrophic veligers, and presumably has little influence on fecundity or dispersal. A more profound and significant modification is the retention of larvae beyond metamorphosis, eliminating the planktotrophic larval stage. This has previously been found in only three of the 175 known species of littorinids: *Littorina (Neritrema) saxatilis*, *Littoraria (Bulimilittorina) aberrans* (Philippi, 1846) and *Tectarius (Echininiopsis) viviparus*. This small number is not due to lack of information for, using a combination of oviduct structure and protoconch type, the type of development can be confidently predicted (Reid, 1989a). The new species described here represents a fourth case of brooding through metamorphosis. Among these four species the anatomical modifications giving rise to the brood pouch are of two distinct types. In *Littorina saxatilis* the eggs are retained within the pallial oviduct, in a septate brood pouch which is a modification of the ancestral jelly gland (Reid, 1996). In the remaining three species the eggs are retained in the mantle cavity, as illustrated in Figure 4F.

At first, the rarity of ovoviviparity through metamorphosis in the Littorininae may seem surprising. Members of this subfamily occur almost exclusively in the littoral zone, and usually towards its upper limit and in the littoral fringe. At such high tidal levels, spawning of pelagic eggs (or release of planktotrophic larvae) might seem an inappropriate developmental strategy. It has, however, been argued that because the high intertidal habitat is patchy, but widespread, the survival of offspring can be maximized by wide dispersal of numerous larvae (i.e. '*r*-strategy', see e.g. Jablonski & Lutz, 1983; Grahame & Branch, 1985; Roff, 1992, for reviews). Nevertheless, other theoretical considerations discount the short-term importance of dispersal for enhancing larval survival (Strathmann, 1985). It is well known that at high latitudes planktotrophic development is sometimes suppressed, whether for reasons of food supply and slow growth rate (Thorson, 1950) or pelagic predation (Highsmith, 1985). This accounts for the nonplanktotrophic development (in benthic egg masses) of some species of *Littorina*, the only cold-water clade of Littorininae. The ovoviviparity of *L. saxatilis* is simply an extension of this development pattern, providing superior protection of the embryos, that has occurred relatively recently, about 1.7 million years ago (Reid, 1996). Considerations of dispersal are probably not significant in cold-water littorinids, since rafting of egg masses and of post-larval stages on macroalgae may be common.

The remaining three ovoviviparous littorinines are all tropical; *Littoraria aberrans* occurs in the branches of trees at the landward fringes of mangrove forests in the Panamic province, whereas the two *Tectarius* species are found at the limit of the littoral fringe on limestone shores of Pacific islands. In such habitats, at the limit of the reach of the tides, brooding might increase the short-term survival of larvae. Furthermore, in the two island species, reduced dispersal may itself be advantageous, since pelagic larvae swept away from an isolated oceanic island are unlikely to reach another. On tropical shores benthic egg masses would suffer desiccation at high tidal levels and predation lower down the shore, so that brooding is the only means of achieving nonplanktotrophic development. Despite these considerations, brooding remains rare in tropical high-shore littorinids, even among those typically found on oceanic islands; for example, many of the approximately 45 *Nodilittorina* species occur in just this habitat, yet none brood their larvae. One possible explanation (Reid, 1989a) appeals not to the short-term advantages of brooding for larval survival, but to its long-term evolutionary consequences. It has been found that nonplanktotrophic species of gastropods often show shorter durations in the fossil record, and hence greater likelihood of extinction (Hansen, 1980; Jablonski, 1986; Gili & Martinell, 1994). This may be due to the generally narrower geographical ranges of nonplanktotrophic species (Hansen, 1980; Scheltema, 1989; Kohn & Perron, 1994; although not in *Littorina*, a temperate group that may also disperse by algal rafting, Reid, 1996), which are therefore more susceptible to localized events causing extinction. An additional consideration is that loss of pelagic stages in nonplanktotrophic development results in reduced gene flow and small population size, leading to increased likelihood of speciation (review by Jablonski & Lutz, 1983; Jablonski, 1986). Ovoviviparity through metamorphosis in tropical littorinids was interpreted as an evolutionarily short-term strategy, leading to

early extinction. In support of this view, it was pointed out that both known species in this category were isolated examples within planktotrophic genera (i.e. there were no species-rich ovoviviparous clades), and both showed unusually narrow geographical distributions (Reid, 1989a). The discovery of an additional ovoviviparous *Tectarius* species challenges this view. The two ovoviviparous *Tectarius* are sister-species, and it is most parsimonious to assume that this type of development was inherited from their common ancestor. If so, and since their age of divergence is estimated at 35–45 Ma, their ovoviviparity has persisted for at least this length of time. Furthermore, it has not precluded colonization of islands 6300 km apart.

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Note added in proof

Since going to press, additional material of *Tectarius (Echininus) spinulosus* (Philippi, 1847) has been obtained from Kikaijima, Kagoshima Prefecture, Japan (for which we are grateful to Akihiko Matsukuma). Anatomical examination of 3 males has shown the presence of only 2 typical mamilliform glands on the penis (Rosewater, 1972, gave 2–3); this compares with 7–12 such glands in *T. (E.) cumingii* (Philippi, 1846) (Rosewater, 1972; pers. obs.). The sequence of a 437 base-pair fragment of the 16S rRNA gene differed from the corresponding sequence of *T. (E.) cumingii* at 6.9% of sites (25 transitions, 4 transversions, 1 deletion). This compares with a value of 12.2% (30 transitions, 16 transversions, 6 deletions, in 427 bp) for the sister-species pair of *T. viviparus* and *T. niuensis*. This degree of sequence difference, combined with the apparently consistent difference in penial anatomy, strongly suggests that *T. spinulosus* and *T. cumingii* should be regarded as distinct species. In molecular phylogenetic analyses they appear as sister-taxa.