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Abstract

The phylogeny of the genus *Echinolittorina*, and phylogeography of some of its members, have previously been examined using molecular data, so that species can now be defined by a combination of phylogenetic, morphological and geographical criteria. The 26 species recognized in the Indo-West Pacific biogeographical region form a monophyletic group, here defined as the subgenus *Granulilittorina* Habe & Kosuge, 1966. Morphological descriptions are provided for these 26 species, including details of shell, pigmentation of headfoot, reproductive anatomy, spermatozoa, egg capsules and radulae. Diagnoses include reference to mitochondrial gene sequences (COI). A key is based on shells, tentacle pigmentation, penial shape and geographical distribution. Seven new species are described: *E. marisrubri*, *E. omanensis*, *E. austrotrochoides*, *E. marquesensis*, *E. wallaceana*, *E. tricincta*, *E. philippinensis*. Three name changes are proposed: *E. malaccana* (Philippi, 1847) and *E. cecillei* (Philippi, 1851) are valid names for two members of the former '*E. trochoides*' group; *E. biangulata* (von Martens, 1897) replaces '*E. quadricincta*'. Full synonymies are given for all taxa, and the taxonomic, evolutionary and ecological literature reviewed. Distribution maps are based on examination of 1701 samples and reliable literature records. The contrast between continental and oceanic distribution patterns is emphasized; one clade of five species and two additional species are shown to have an association with upwelling areas. All species are known (or predicted from protoconch size and oviduct anatomy) to have planktotrophic development, and rare extralimital records suggest a maximum open-water dispersal distance of 1000–2100 km. The most useful morphological characters for identification are the shell, penial shape and copulatory bursa in the pallial oviduct. Sister species can be morphologically similar, but are almost always entirely allopatric, so that distributional information is important for identification. Substantial intraspecific variation is present in the shell shape and sculpture of most species; where there is a pronounced geographical pattern this may have a genetic basis, but ecophenotypic effects are also implicated, e.g. by predictable associations in some species of strongly nodulose sculpture with limestone substrates and with dry habitats where growth rate may be slow. Morphological characters are superimposed on a molecular phylogeny to demonstrate the synapomorphies of clades. This is essentially a morphostatic radiation of largely allopatric species with little morphological differentiation; ecological divergence is limited to specialization to oceanic, continental or upwelling areas and to small differences in zonation level.

Key words: shell sculpture, penis, radula, oceanic distribution, upwelling, morphostatic radiation, littoral fringe

Introduction

Littorinid gastropods are among the dominant large invertebrates at high tidal levels on hard substrates of seashores throughout the temperate and tropical oceans. As a consequence of this accessibility and ubiquity, they have been the subject of a large volume of research on ecology, genetics and physiology (reviews by McQuaid 1996a, b; Reid 1996). The systematics of the group (particularly of the subfamily Littorininae) have also been intensively studied over the past 40 years, initially using morphological characters (e.g. Rosewater 1970; Bandel & Kadolsky 1982; Reid 1986a, 1989a, 1996, 2002a, b) and more recently by the application of molecular phylogenetic methods (Reid *et al*. 1996; Williams *et al*. 2003; Williams & Reid 2004). The combination of detailed knowledge of their biology and phylogenetic systematics, together with their worldwide distribution and ease of collection, have ensured that the Littorinidae have become model organisms for the study of global patterns of biogeography and speciation (Reid *et al*. 1996; Williams *et al*. 2003; Williams & Reid 2004; Reid *et al*. 2006).

In recent times the taxonomic study of the Littorinidae of the Indo-West Pacific (IWP) was pioneered by Rosewater (1970, 1972, 1982; Ponder & Rosewater 1979; Rosewater & Kadolsky 1981). Since then there have been systematic revisions of the IWP members of the littorinine genera *Littoraria* (Reid 1986a, 2001b; Stuckey & Reid 2002), *Mainwaringia* (Reid 1986b), *Peasiella* (Reid 1989b; Reid & Mak 1998), *Littorina* (Reid 1996); an addition to *Tectarius* (Reid & Geller 1997); and a revision of the southern temperate species of *Nodilittorina*, *Austrolittorina* and *Afrolittorina* (Reid & Williams 2004). However, apart from brief descriptions of the species in Hong Kong and Southeast Asia (Reid 1992, 2001a), there has not yet been a comprehensive taxonomic account of the largest of the littorinine genera in the IWP—the genus *Echinolittorina*.

In Rosewater's (1970) monograph (slightly modified by Ponder & Rosewater 1979), the IWP species now assigned to *Echinolittorina* were classified in 14 species and subspecies, of which those with smooth shells were assigned to *Littorina (Austrolittorina)*, with nodulose shells to *Nodilittorina (Nodilittorina)* and with granulose shells to *Nodilittorina (Granulilittorina)*. A new emphasis on characters of the radula, penis and spawn led Bandel & Kadolsky (1982) to unite these artificial groups as the single genus *Nodilittorina*. Their classification was largely supported by a cladistic analysis of these and other morphological characters (Reid 1989a). Features of the penis and pallial oviduct were found to discriminate among *Nodilittorina* species with similar shells, and this morphological approach resulted in the recognition of 18 species in the IWP (Reid 1989a, 1992, 2001a, 2002a).

A phylogenetic analysis of all worldwide *Nodilittorina* species, based on morphological characters, resulted in poor resolution, but did suggest that the genus was not monophyletic (Reid 2002a). Subsequently, DNA-sequence analysis confirmed that '*Nodilittorina*' was a polyphyletic assemblage of four clades—the monotypic Australian *Nodilittorina*, the two small southern-temperate genera *Austrolittorina* and *Afrolittorina*, and the worldwide tropical genus *Echinolittorina* (Williams *et al*. 2003). There followed a global study of the molecular phylogeny and geographical distribution of all known *Echinolittorina* species (Williams & Reid 2004). This demonstrated the monophyly of the IWP members and the basal placement of the species in the Atlantic and Eastern Pacific Oceans (Fig. 1). Based on almost complete allopatry of sister taxa, it was concluded that speciation has been entirely allopatric in this genus. Within the IWP no prevailing geographical pattern of speciation events was found, and the high regional diversity of species in the East Indies Triangle was shown to be mainly the result of a mosaic of allopatric distributions, rather than of overlap of widespread species. At the species level, a combination of molecular and morphological data defined 59 evolutionarily significant units (ESUs) worldwide. In the Eastern Pacific Ocean these largely corresponded with the 16 morphospecies recognized in an earlier study (Reid 2002b). However, in the IWP the 18 morphospecies (Reid 2002a) were increased to 26 ESUs; the formal nomenclature and species status of these ESUs were not addressed. A subsequent phylogeographic study of larger samples (using mitochondrial COI sequences from 18–92 individuals) from eight of the most widespread of the IWP ESUs confirmed their monophyly and geographical distributions and supported their species status (Reid *et al*. 2006).

The aims of the present work are, therefore: (1) to provide detailed morphological descriptions for the characterization and identification of the 26 IWP species of *Echinolittorina*; (2) to resolve the nomenclature of this group; (3) to record the habitats and distributional records of the species (with special attention to extralimital records that indicate maximum dispersal distances); (4) to assess intraspecific variation; (5) to review the taxonomic and ecological literature; (6) to seek morphological synapomorphies for the clades in the existing molecular phylogeny.

The 26 species treated in this study correspond exactly to the 26 ESUs in the IWP region that were recognized in the molecular study of the entire genus by Williams & Reid (2004). Eight of these were shown to be phylogenetic species by more detailed molecular study (Reid *et al*. 2006). The only taxonomic change introduced here is therefore the formal recognition of all these entities as species. However, there are considerable nomenclatural changes. Seven undescribed species are named, and examination of type specimens and original descriptions have necessitated changes to the valid names of three others.

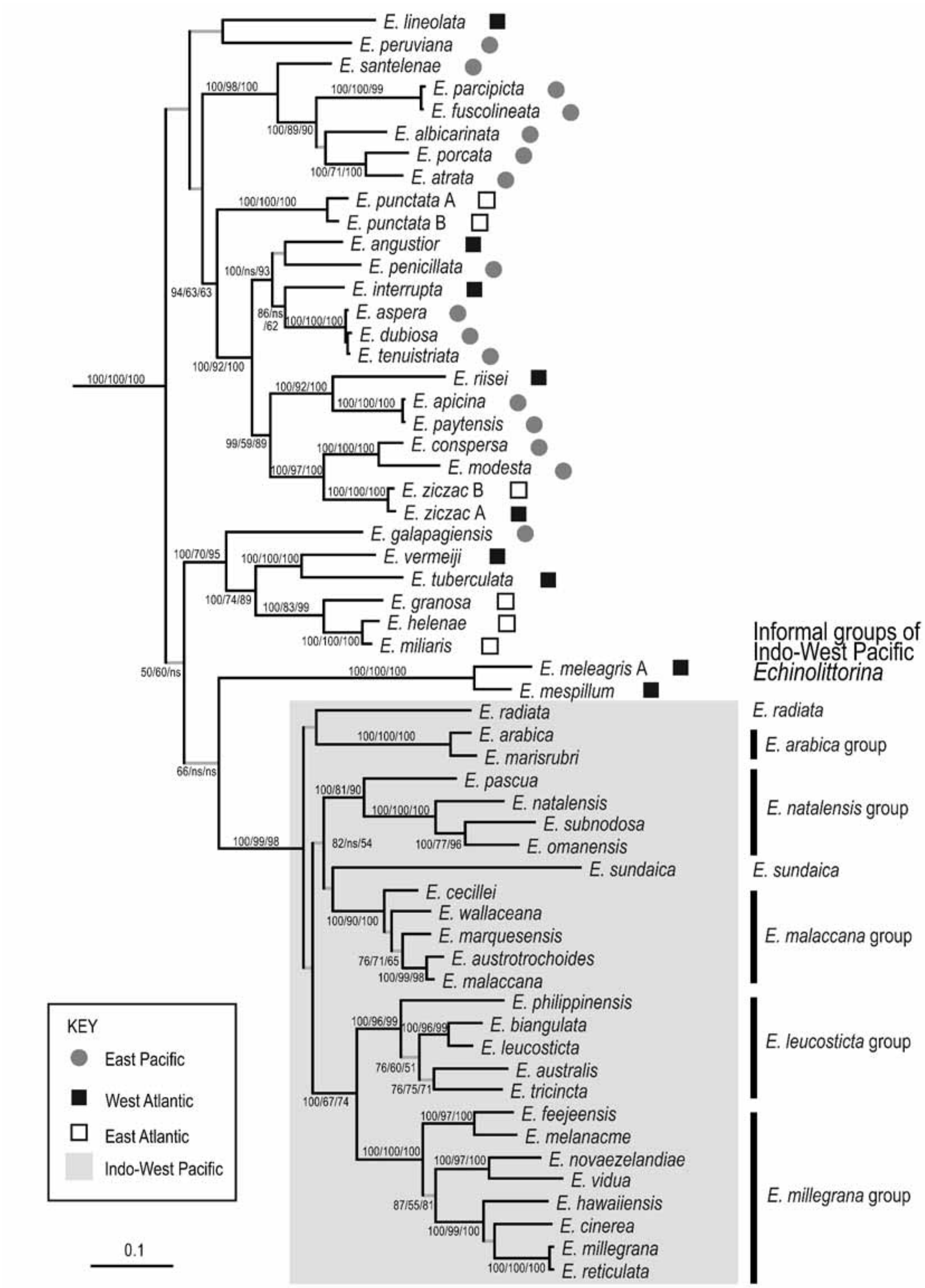

FIGURE 1. Molecular phylogeny of *Echinolittorina* species produced by Bayesian analysis of concatenated gene sequences from 28S rRNA, COI and 12S rRNA genes (outgroups removed). Branches with posterior probability (PP) <90% are grey, branches with PP ⩾ 90% are black. The three measures of nodal support are: posterior probability / bootstrap (neighbour-joining algorithm) / bootstrap (maximum likelihood). Support values are only shown when at least two support values are >50%. Geographical occurrence is shown, with Indo-West Pacific taxa (subgenus *Granulilittorina*) being enclosed in a grey box. Also shown are the informal groups used in the Systematic Descriptions. (Phylogeny after Williams & Reid 2004).

Material and methods

Species concept

The existence of a relatively large amount of molecular data on the IWP *Echinolittorina* species permits a more precise definition of the species concept than is usually possible in purely morphological studies. Molecular data permit both testing of monophyly and estimation of genetic distance, and are crucial for the definition of phylogenetic species (Wheeler & Meier 2000). Morphological differences (particularly those associated with reproductive structures that may be components of specific mate recognition systems) when found in sympatry are taken as evidence for reproductive isolation, indicating distinct biological species. In sympatry, the phylogenetic and biological species concepts are equivalent, because reproductive isolation maintains fixed genetic differences (Knowlton 2000). However, in allopatry these two species concepts can define quite different groupings, because geographical isolation can maintain small genetic differences that are insufficient to prevent potential interbreeding. In practice, it is recommended that biological species should be diagnosed by concordant patterns in several independent genes (i.e. not mitochondrial genetic data alone) (Avise 2004).

For *Echinolittorina* species this problem is significant, because sister species are almost always allopatric and morphological differences may be slight. In many cases the phylogenetic species defined by a combination of mitochondrial and nuclear genetic data correspond to recognized morphospecies, so that no conflict arises. Where available nuclear genetic sequences (from 28S ribosomal RNA gene; Williams & Reid 2004) are insufficiently variable to confirm the separation of allopatric sister-clades defined by mitochondrial genes (12S rRNA and cytochrome oxidase I), consistent morphological characters (of either shell or anatomy) have been taken to indicate nuclear genetic differences, and therefore to support species status. In such cases the Kimura two-parameter (K2P) genetic distance (Kimura 1980) estimated from COI sequences was almost always greater than or equal to 6%. Exceptionally, species status has been accepted for one pair with a genetic distance of just 2.70% and only slight morphological differentiation, because their large geographical separation and habitat characteristics appear to preclude the possibility of gene exchange between them (see Remarks on *E. malaccana*). In this case alone, an argument could perhaps have been made for the use of the category ‘subspecies’. However, this would have been an arbitrary decision, resulting in a cumbersome nomenclature, and so this category has not been used. In one case nuclear data showed reciprocal monophyly between allopatric sister taxa, whereas mitochondrial (COI) data did not; the reasons for this anomaly are not known, but consistent morphological differences were again taken as independent evidence of nuclear differentiation, and therefore as support for species status (see Remarks on *E. reticulata*). In the absence of any known nuclear or morphological differentiation, allopatric (but not clearly disjunct) mitochondrial clades with genetic distance of up to 5.9% were not recognized as species (see Remarks on *E. vidua*). These issues are explored more fully elsewhere (Williams & Reid 2004; Reid *et al*. 2006).

Material

This study is based on examination of all Recent material in 8 institutions (AMS, BMNH, IRSNB, MNHN, NNML, USNM, ZISP, ZMA), and additional material has been seen from many others. Personal collections have been made in South Africa, Mozambique, Madagascar, Sudan, Egypt, India, Sri Lanka, Thailand, Malaysia, Singapore, Cambodia, Vietnam, Hong Kong, Taiwan, Japan, Philippines, Indonesia, Australia, New Caledonia, Fiji, Western Samoa, Cook Islands, French Polynesia, Easter Island and Hawaiian Islands, and are deposited in BMNH. A total of 1701 lots have been examined. Fossil material is rare and often unassignable to genus, so will be considered elsewhere.

Institutional abbreviations

AMNZ	Auckland Museum
AMS	Australian Museum, Sydney
ANSP	Academy of Natural Sciences, Philadelphia
BMNH	Natural History Museum, London
BPBM	Bishop Museum, Honolulu
CUMZ	Cambridge University Museum of Zoology
HUJ	Hebrew University, Jerusalem
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels
MNHN	Muséum National d'Histoire Naturelle, Paris
MZB	Museum Zoologi Bogor
NHMW	Naturhistorisches Museum Wien
NNML	National Museum of Natural History, Naturalis, Leiden
NM	Natal Museum, Pietermaritzburg
NMW	National Museum of Wales, Cardiff
NSMT	National Science Museum, Tokyo
NTM	Museum and Art Gallery of the Northern Territory, Darwin
SMF	Naturmuseum Senckenberg, Frankfurt am Main
SMNH	Swedish Museum of Natural History, Stockholm
SMNS	Staatliches Museum für Naturkunde Stuttgart
SNSD	Staatliche Naturhistorische Sammlung Dresden
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
WAM	Western Australian Museum, Perth
ZISP	Zoological Institute, St Petersburg
ZMA	Zoölogisch Museum, Amsterdam
ZMB	Museum für Naturkunde, Humboldt-Universität zu Berlin

Synonymies and types

Synonymies are not exhaustive, but attempt to list all new names and new combinations, and include references to major taxonomic works and faunistic lists, standard identification guides, and significant morphological descriptions. Almost all primary types have been seen, as noted, and the primary type of each valid name is figured. Lectotypes have been designated only for valid names, and in other cases only where syntypes are not all conspecific. Synonymies are presented in condensed format, following each specific name through its generic combinations. For new names, no dash separates the author's name from the new epithet; a dash between the two indicates subsequent usage in a new combination. Misidentifications are indicated by a note in parentheses: 'not' followed by the name in its original form (omitted in the cases of species included in this account) with author and date; '=' is followed by the recognized valid form of the incorrectly used name. A query in front of the full generic plus specific name indicates uncertain inclusion in the synonymy; queries elsewhere (e.g. in front of specific name) are quoted from the original citation. All figures quoted are of shells, unless otherwise indicated.

Taxonomic abbreviations

E.	*Echinolittorina*
L.	*Littorina* (not *Litorina*, which is spelled out in full)
N.	*Nodilittorina*
T.	*Tectarius*

Descriptions

The species are arranged in approximate phylogenetic sequence, beginning with the basal branch in the molecular phylogeny of Williams & Reid (2004; see Fig. 1). For convenience, they are placed into seven 'groups', each monophyletic, but without formal taxonomic rank; these are the *radiata*, *arabica*, *natalensis*, *sundaica*, *malaccana*, *leucosticta* and *millegrana* groups. Diagnoses contain sufficient information to distinguish the species from others in the same informal 'group' or of similar appearance. DNA sequences of the mitochondrial COI gene (available from GenBank) are also given; these are diagnostic in all cases except the pair *E. millegrana* and *E. reticulata*.

Shell dimensions were measured with vernier callipers to 0.1 mm. Shell height (H) is the maximum dimension parallel to the axis of coiling, shell breadth (B) the maximum dimension perpendicular to H, and the length of the aperture (LA) the greatest length from the junction of the outer lip with the penultimate whorl to the anterior lip. Shell shape was quantified as height to breadth ratio (H/B) and as relative spire height (SH = H/LA), and the range of these ratios is given, with extremes in parentheses. The spire profile is described as concave (apical angle increases between successive whorls), straight, or convex (apical angle decreases, giving domed outline). The periphery of the shell is the junction between the upper part of the final whorl and the base; it is usually marked by a slight angulation, or by an enlarged rib (Fig. 2A–C). The parietal area adjacent to the aperture may show evidence of dissolution by the mantle edge, producing a crescentic eroded area (Fig. 2D). A narrow, imperforate pseudumbilicus may be present adjacent to the columella (Fig. 2D), and in some species the eroded parietal area may be continuous with it (Fig. 2B). Significant features of the columella include the length and curvature of the pillar, the presence of a pinched constriction at the base of the pillar, and the presence of a hollowed or flared anterior area (Fig. 2). The inner lip may be sharply raised (Fig. 2A) or smoothly rounded (Fig. 2B). Teleoconch sculpture is described in detail only for the final (body) whorl; earlier (spire) whorls are often eroded and their sculpture is not usefully diagnostic. Sculpture is described in terms of the number of ribs between suture and periphery, and on the shell base; the suture generally runs one or two ribs above the periphery, or is situated at the peripheral rib. If the periphery is not well marked (Fig. 2D) a total number of ribs is given, from suture to base. Narrow ribs are referred to as threads; the spaces between the ribs are grooves. Nodulose sculpture (Fig. 2A) is described by the number of nodules in a single spiral row on the final whorl of the shell. Nodules or granules in successive spiral rows may be aligned to form axial (or oblique) series, sometimes resembling axial ribs (Fig. 2C). Microstriae are fine incised spiral lines that may cover the entire surface and are visible only under low magnification (Fig. 37G). Protoconchs are rarely preserved, and very seldom show recognizable sculpture (Fig. 37H). Even if sculpture has been eroded (Fig. 37G) it may be possible to count the whorls of the protoconch; this was done as described by Reid (1996). The opercular ratio describes the coiling of the operculum and is the ratio of two parallel measurements, the diameter of the spiral part divided by the maximum length (Reid 1996).

Living animals were relaxed and anaesthetized in 7.5% (volume of hydrated crystals to volume of fresh water) magnesium chloride solution. Animals were fixed in 10% seawater formalin (i.e. full-strength 40% formaldehyde solution diluted 1:9 with seawater) buffered with borax, and stored in 80% ethanol. The most important anatomical characters for taxonomic purposes are the penis and oviduct; drawings of these were made by camera lucida and drawing conventions are indicated in Figure 3. For general accounts of the anatomy of littorinids see Reid (1986a, 1989a, 1996, 2002a). The penis of males is visible without dissection on the right side of the headfoot. The wrinkled basal region bifurcates and the lateral branch bears mucus-producing penial glands. Most *Echinolittorina* species possess glands of two types, a mamilliform penial gland (consisting of subepithelial glands around a mucus reservoir, terminating in a raised papilla) and a penial glandular disc (a pad or lobe of subepithelial glands) (Fig. 3A). The smooth penial filament is usually clearly distinguishable from the wrinkled basal part; if this distinction is unclear, the junction between filament and base is taken as level with the top of the lateral branch of the base that bears the penial glands. The sperm groove runs along the antero-dorsal edge of the penial filament.

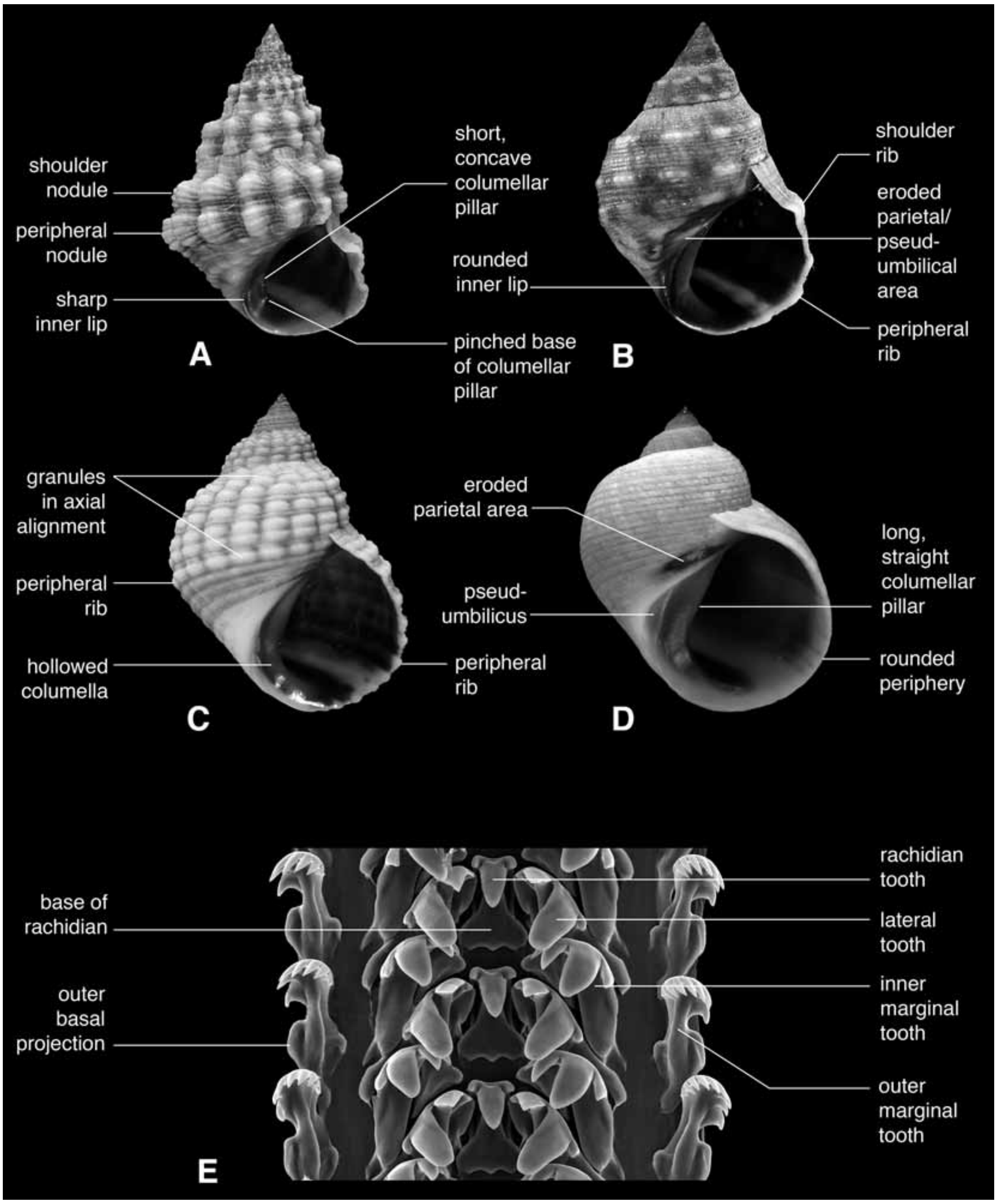

FIGURE 2. Terminology of *Echinolittorina* shells and radulae. **A.** *E. malaccana*. **B.** *E. tricincta*. **C.** *E. reticulata*. **D.** *E. novaezelandiae*. **E.** Radula of *E. pascua* in flat view.

The spermatozoa of *Echinolittorina* are dimorphic, consisting of large, rounded paraspermatozoa that act as carrier cells for the filiform euspermatozoa. Sperm samples were removed from the seminal vesicles of relaxed, living animals, fixed in 0.5% seawater formalin, examined immediately by light microscopy, and drawn by camera lucida. Alternatively, sperm were removed from specimens fixed and stored in formalin, but not from material stored in ethanol (in which shrinkage of paraspermatozoa by about 20% occurs, Reid 1996). Refractile rod-shaped inclusions and granules are visible within the paraspermatozoa. Euspermatozoa are agglutinated in fixed material, and can only be measured when living.

When the shell is gently cracked and removed, the pallial oviduct of females (Fig. 3B) is visible, without dissection, on the right side adjacent to the columellar muscle. The glands of the spiral portion of the pallial oviduct can be distinguished by their colour in fresh and preserved specimens; the albumen gland is translucent white, the distal part of the capsule gland is opaque white or cream, and the small proximal part of the capsule gland translucent reddish or brown. The seminal receptacle is a swollen opalescent bulb, and the egg groove is often characterized by black pigment. To trace the extent of the copulatory bursa, the intact pallial oviduct was removed and gross serial sections of the straight portion were cut with a razor blade. Parasitism by trematodes was not observed in any dissected specimen, and there was no evidence of seasonal regression of the reproductive tract in animals of mature size. For some species, egg capsules were obtained by confining individual females in beakers half-filled with seawater and left overnight. Capsules sink to the bottom, and were drawn using a compound microscope and camera lucida.

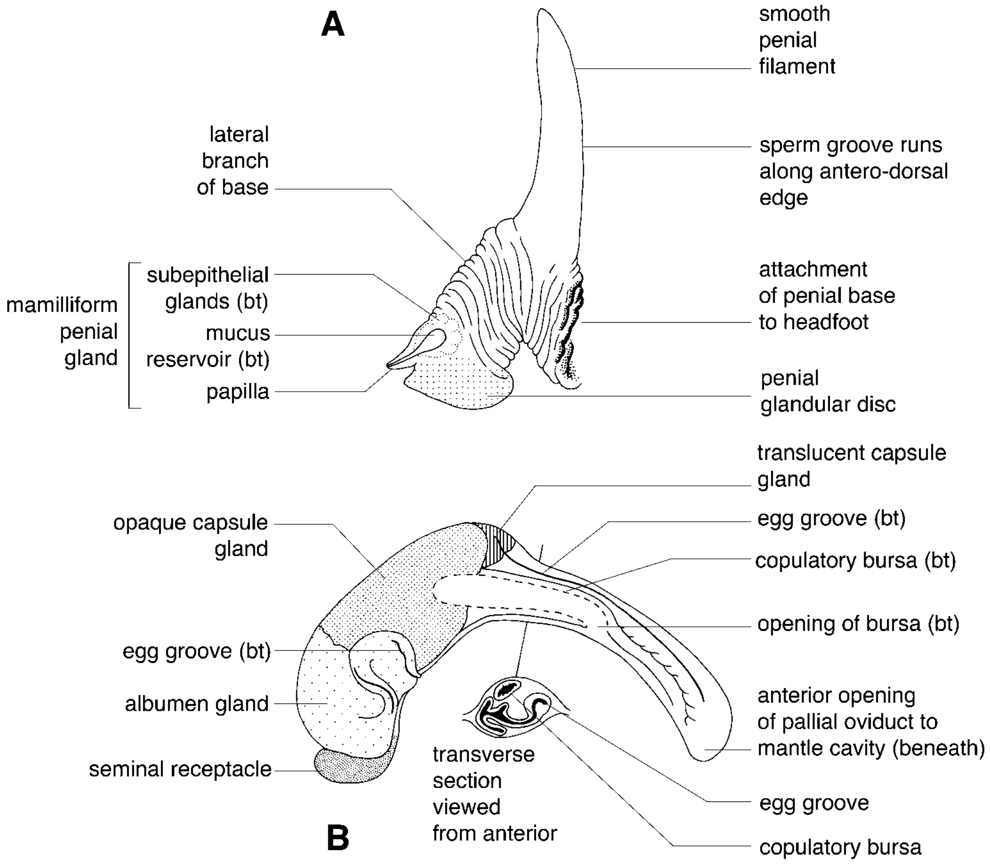

FIGURE 3. Terminology of *Echinolittorina* penes and pallial oviducts. **A.** Penis of *E. wallaceana*. **B.** Pallial oviduct of *E. australis*, with transverse section. The same conventions of shading and line are followed throughout subsequent figures. Abbreviation: bt, structure visible by transparency.

At least three radulae were examined from each species. The relative radular length is the total radular length divided by shell height. Radulae were cleaned by soaking in a hypochlorite bleaching solution at room temperature for about 3 min, rinsed three times in distilled water, mounted on a film of polyvinyl acetate glue on glass, allowed to dry in air, and coated with gold and palladium before examination with a scanning electron microscope. Unworn portions of the radula were viewed in two orientations: in standard flat view from vertically above the radula (to show shapes of tooth bases), and at an angle of 45° from the front end (to show shape of tooth cusps). The shape of the rachidian (central) tooth was quantified as the ratio of the total length (in flat view) to maximum basal width. Numbers and relative sizes of cusps are not given for the five central teeth in each row, because these do not vary: three cusps on rachidian (largest central); four cusps on each of lateral and inner marginal (largest is third from inside in each case) (Fig. 2E). All species show a projection or flange on both the inside and outside of the base of the outer marginal tooth.

Distribution, records, maps and habitat

All distribution records have been personally verified unless otherwise noted. Literature records have only been accepted in cases where a figure or other information leaves no doubt as to the identification. The records listed in the text define the known limits of the range; complete lists of localities are deposited in BMNH and are available upon request. Modern place names are used throughout. All records refer to live-collected specimens. In cases where certain identification requires anatomical or molecular information, records based on shells alone (in which identification is inferred from geographical location) are distinguished on the maps. The distributions indicated on the maps are considered to be fairly complete, as can be judged by the total geographical coverage of all distribution records combined (see Williams & Reid 2004: fig. 1). These littorinids are found in similar habitats on the upper shore and are usually common, so that most species present at a locality are likely to be found together and museum collections are therefore representative. Areas of incomplete coverage include Somalia, western Sumatra, the Java Sea, Makassar Strait, northern New Guinea, eastern Philippines, Solomon Islands, Vanuatu and Micronesia. Absence of records from northwestern India, Bay of Bengal, Malacca Strait, southwestern Borneo, southern New Guinea and the Gulf of Carpentaria is due to the absence of suitable habitats on these sedimentary coastlines with extensive mangrove development.

Zonation on the rocky shore is described according to the system of biologically-defined zones developed by T.A. Stephenson & A. Stephenson (1949) and modified by Lewis (1964). The littoral zone consists of the littoral fringe at the top of the shore (from the upper limit of barnacles to the top of the belt of littorinids and black lichens) and the eulittoral zone (below the upper limit of barnacles). Habitats may be distinguished on a gradient between the extremes of ‘continental’ (typically the shores of continental landmasses, with turbid, nutrient-rich water) or ‘oceanic’ (typically on oceanic islands with clear water of low primary productivity). *Echinolittorina* species may show distinctive tolerances (or requirements) for these contrasting habitats, and the terms ‘continental’, ‘intermediate’ or ‘oceanic’ can also be applied to the animals themselves. Remarks on habitats are the result of personal observation and inference from collection data on museum labels. The term ‘syntopic’ is used to indicate the occurrence of two or more species in the same microhabitat, while ‘sympatric’ indicates geographical overlap of distributions. Notes on ecology (including behaviour, reproduction etc) are quoted from the literature.

Identification

With experience, the majority of *Echinolittorina* species can be identified from their shell characters alone, although many species show considerable intraspecific variation. It is not uncommon for extreme shell variants of a single species to range from spirally striate to strongly granulose or nodulose, and colour pattern may vary too, although ‘average’ shells are generally distinctive. Shell characters in this genus do not, however, lend themselves to unequivocally diagnostic features. Usually, no more than four (rarely up to seven) *Echinolittorina* species can be found sympatrically at any Indo-West Pacific (IWP) locality, so that locality information is a valuable aid to identification. It is therefore recommended that the key should be used in conjunction with the figures of shells and distribution maps as an initial guide to identification.

The seven informal ‘groups’ in which the species are arranged (see Descriptions above) are defined as monophyletic units by molecular phylogenetic analysis (Williams & Reid 2004). There are also three apomorphic anatomical characters (basal transverse band on cephalic tentacles; small or absent penial glandular disc; bifurcate copulatory bursa) that define some of these same groups with relatively high consistency (see Discussion and Table 2) and so can be used to recognize them. Nevertheless, because the IWP *Echinolittorina* species are a ‘morphostatic radiation’ (see Discussion) without pronounced morphological divergence, there are few anatomical characters that are diagnostic of species within these groups. In some cases there are subtle differences in the shape of penis or oviduct, so that reference to the anatomical drawings may aid identification. However, the penis is not such a reliable species-discriminating character as in some other littorinid genera (e.g. *Littoraria*, Reid 1986a, 2001b; *Littorina*, Reid 1996). If penis shape functions as a recognition or isolation mechanism in nature (Reid 1996), then this difference may be a reflection of the predominant allopatry of sister species in *Echinolittorina* (Williams & Reid 2004), whereas sympatry of close relatives (perhaps leading to reinforcement of isolating mechanisms) is more frequent in other littorinid genera. Identification by sequence data from the mitochondrial COI gene is reliable in all but one case (the sister-species pair *E. millegrana* and *E. reticulata*), but at the present time this remains a relatively laborious and costly solution. Importantly, since members of the same group are almost always allopatric, locality information is normally sufficient to distinguish them.

Excluded species

The following are not members of Littorinidae, but the names have been used for IWP *Echinolittorina* species.

Tectaria armata Issel, 1869: 192–193, pl. 2, fig. 7 (Suez [Red Sea])

This name has occasionally been assigned to Littorinidae (Weinkauff 1882; Tryon 1887) and was once used for *Echinolittorina subnodosa* (e.g. Safriel & Lipkin 1964), but is a member of the family Trochidae (= *Perrinia stellata* (A. Adams, 1864)).

Littorina beccarii Tapparone-Canefri, 1875: 1031 (Sorong [Irian Jaya, Indonesia])

This unfigured species was said to be very close to *L. lamellosa* Montrouzier in Souverbie, 1861, and so is presumably likewise a *Fossarus* (Planaxidae), as also noted by Rosewater (1970).

Littorina lamellosa Montrouzier in Souverbie, 1861: 273, pl. 11, fig. 5 (Art, Archipel Calédonien [I. Art, New Caledonia])

As noted by Tryon (1887) and Rosewater (1970) this is a *Fossarus* (Planaxidae). The name was sometimes used in the late nineteenth century for museum collections of strongly sculptured specimens of *Echinolittorina cinerea*.

Among members of other genera of Littorinidae, the name *L. pyramidalis* Quoy & Gaimard, 1833 has frequently been used for nodulose *Echinolittorina* species, but is the sole member of *Nodilittorina sensu stricto* and restricted to eastern Australia (Reid & Williams 2004). There has also been confusion of IWP *Echinolittorina* species with congeners from the Atlantic Ocean. These include *L. granularis* Gray, 1839 (= *E. miliaris*); *L. miliaris* Quoy & Gaimard, 1833; and *Litorina tuberculata* Menke, 1828 (= *E. tuberculata*).

Systematic descriptions

Genus *Echinolittorina* Habe, 1956

Nodilittorina (Echinolittorina) Habe, 1956a: 96–99 (type by original designation *Litorina tuberculata* Menke, 1828; cited as *Echinolittiorina* in error, p. 96).

Taxonomic history: The complex history of the generic classification of those littorinids now referred to the genus *Echinolittorina* has been reviewed in detail elsewhere (Reid 2002b; Reid & Williams 2004). Briefly, most nineteenth century authors employed the single genus *Littorina* (used in the emended form *Litorina* by some, mainly German, workers). H. Adams & A. Adams (1854) grouped species with elongate and patterned shells (together with the species now classified as *Littoraria*) as *Littorina* subgenus *Melarhaphe*, while those with nodulose shells were placed in the genus *Tectarius* (emended by some authors as *Tectaria* or *Tectarium*, and incorrectly as *Tectus*), and a similar scheme was adopted by Weinkauff (1883) and Tryon (1887). In 1897 von Martens introduced *Nodilittorina* as a subgenus of *Littorina*, for nodulose species with a paucispiral operculum and no columellar tooth (thereby contrasting with *Tectarius*). This subgenus was later transferred to *Tectarius* on the basis of radular similarities, while smooth-shelled species remained in *L. (Melarhaphe)* (Thiele 1929; Wenz 1938). *Nodilittorina* was first used as a full genus, for Indo-Pacific species, by Habe (1951). Abbott (1954) was the first to include details of the penis and spawn in his revision of littorinid genera; he classified the nodulose western Atlantic species as *Nodilittorina tuberculata*, but pointed out its anatomical similarity and close relationship to the smooth-shelled *L. (Melarhaphe) ziczac* (Gmelin, 1791) (i.e. *E. ziczac*). Citing Abbott's (1954) description of the radula of *N. tuberculata*, Habe (1956a) established the new subgenus *Echinolittorina* for this species, retaining *Nodilittorina s.s.* for Indo-Pacific species alone. Subsequently, the genus *Granulilittorina* was erected (Habe & Kosuge 1966a, b) on the basis of the unusual egg capsule of its type species, *G. philippiana* Habe & Kosuge, 1966 (= *E. vidua*). In his monograph of Indo-Pacific littorinids, Rosewater (1970) described characters of penis and spawn, but still used shell sculpture as the basis of his generic classification. Smooth-shelled species currently included in *Echinolittorina* were distributed among five subgenera of *Littorina*, while *Nodilittorina* was divided into three subgenera: *Nodilittorina* with nodulose shells, *Granulilittorina* with granulose sculpture, and the monotypic *Echinolittorina* with nodulose shell and narrow rachidian tooth. Small changes were made by Ponder & Rosewater (1979) and later an additional subgenus, *L. (Fossarilittorina)*, was introduced (Rosewater 1981).

A more natural (i.e. phylogenetic) classification of these species was attempted by Bandel & Kadolsky (1982), who pointed out the evolutionary convergence in characters of the littorinid shell, radula and operculum. Emphasizing penial and spawn characters, they grouped all current *Echinolittorina* species in two genera, *Nodilittorina* and *Fossarilittorina*. This scheme was largely supported by the first attempt at a formal cladistic analysis of littorinid genera (Reid 1986a), although a more thorough analysis (Reid 1989a) recognized only *Nodilittorina*, with three subgenera: *Fossarilittorina*, *Echinolittorina* and *Nodilittorina*. The evidence for the monophyly of the genus *Nodilittorina* was, nevertheless, weak and supported by the sole synapomorphy of tentacle coloration, while the subgenera *Echinolittorina* and *Nodilittorina* were separated only by the position of the copulatory bursa within the pallial oviduct. As taxonomic and anatomical data accumulated, it became clear that a small group of *Nodilittorina* species with smooth shells and southern-temperate distribution could be characterized by the structure of the pallial oviduct, and these were provisionally placed in the subgenus *Austrolittorina* (Reid 2002b). A renewed attempt at a morphological phylogenetic analysis supported this southern-temperate clade, but failed to confirm the monophyly of *Nodilittorina* as a whole, because of pervasive homoplasy of morphological characters (Reid 2002a).

More recently, progress has been made by means of molecular phylogenetic analysis. It has been conclusively demonstrated that *Nodilittorina* (*sensu* Reid 1989a, 2002a, b) is polyphyletic (Williams *et al*. 2003). The southern-temperate species have been removed to the two monophyletic genera *Austrolittorina* and *Afrolittorina* (Williams *et al*. 2003; Reid & Williams 2004). The remaining species consist of a large tropical clade and the unrelated *N. pyramidalis* from southeastern Australia. The latter is the type species of *Nodilittorina* designated by Abbott (1954), and that genus is therefore now monotypic. The earliest available name for the remaining tropical species is *Echinolittorina*, with the western Atlantic *E. tuberculata* as its type (Habe 1956a).

Molecular support for the monophyly and divergence of *Echinolittorina* is strong, based on the combined sequence of two nuclear (28S and 18S rRNA) and two mitochondrial (12S rRNA and cytochrome oxidase I) genes, of which 28S provided the strongest signal (Williams *et al*. 2003; Williams & Reid 2004). Nevertheless, mapping of the known morphological characters of the subfamily Littorininae onto the molecular phylogeny failed to discover any unique morphological synapomorphy for the genus *Echinolittorina* (Reid 2002a; Williams *et al*. 2003). The characters enumerated in the following diagnosis are all either plesiomorphic within the subfamily Littorininae, or are homoplasies that are shared with other genera. Taken together, however, they diagnose the monophyletic taxon recognized by molecular analyses.

Diagnosis: Shell aragonitic; nodulose, granulose, spirally striate or entirely smooth; if smooth or striate then usually with dark axial stripes or axially aligned series of dashes; eroded parietal area may be present, sometimes a small pseudumbilicus; aperture dark with pale spiral band at base (i.e. anterior end) and sometimes another posteriorly. Cephalic tentacles with 2–3 longitudinal black lines, all black, or with broad transverse band at base distal to eye. Operculum paucispiral. Penis with blade-shaped filament (rarely swollen); base usually bifurcate (not so if mamilliform gland absent); usually a single mamilliform gland (sometimes absent, rarely 2); glandular disc of subepithelial glandular tissue usually present; penial vas deferens an open groove or rarely a closed tube. Rod-pieces of paraspermatozoa usually long and straight (rarely small and irregular, or curved). In pallial oviduct egg groove makes a simple loop through albumen gland, straight path through capsule gland and jelly gland; copulatory bursa opens in anterior or posterior position within straight section of pallial oviduct. Spawn a biconvex pelagic capsule with cupola-shaped upper side sculptured by concentric rings, containing single egg; development planktotrophic. Outer marginal radular tooth with flange at inside and at outside of base. Distribution worldwide tropical and warm temperate.

Remarks: As here defined, *Echinolittorina* is the largest genus of Littorinidae, with 59 recognized species worldwide (accepting the molecular ESUs of Williams & Reid 2004 as species).

Subgenus *Granulilittorina* Habe & Kosuge, 1966

Granulilittorina Habe & Kosuge, 1966b (17 May, see Petit & Bieler 1996): 313–314, 328 (type by monotypy *Granulilittorina philippiana* Habe & Kosuge, 1966a = *E. vidua*).

Taxonomic history: The name *Granulilittorina* was first used in the combination *Granulilittorina philippiana* Habe & Kosuge, 1966a (15 January). Nevertheless, since there was no indication that the generic name was new, it must be regarded as a *nomen nudum* (as noted by Petit & Bieler 1996). It was validated by the same authors later the same year, when they published a longer description of '*Granulilittorina philippiana* Habe et Kosuge (gen. et sp. nov.)' (ICZN 1999: Art. 13). The evidence given for the new name was the unusual 'cogwheel' egg capsule and the slightly reduced chromosome count. In fact the egg capsule, so far unique, represents only a minor variation on the common type for *Echinolittorina* (Reid 2002a), while information on chromosome numbers is very incomplete (reviews by Reid 1989a; Thiriot-Quiévreux 2003). This generic name has since been used at generic rank only in the Japanese literature (Habe 1973; Higo 1973; Higo & Goto 1993). Rosewater (1970) employed it as a subgenus of *Nodilittorina*, for those species with granulose sculpture, and included six IWP species and two doubtful Atlantic ones. Later, one of the Atlantic members was removed and another added (Rosewater 1981).

A molecular phylogenetic analysis of all known *Echinolittorina* species showed conclusively that all the IWP species belong to a monophyletic group within the genus (Williams & Reid 2004; Fig. 1). It is appropriate that this significant biogeographic and phylogenetic group should be recognized taxonomically, and the only available name is *Granulilittorina*.

Diagnosis: As for the genus, with the following modifications. Shell aperture dark with pale spiral band at base. Penis with bifurcate base bearing a single mamilliform gland; penial vas deferens an open groove. Copulatory bursa always opening in anterior position within pallial oviduct (as in Fig. 3B, or further towards anterior end). Distribution exclusively Indo-West Pacific.

Remarks: The existence of an IWP clade of '*Nodilittorina*' species was hinted at by Reid's (1989a) separation of *N. (Echinolittorina)* with the copulatory bursa in a posterior position within the pallial oviduct from *N. (Nodilittorina)* with an anterior bursa; members of the former were present only in the Eastern Pacific, Atlantic and southern Africa, whereas the latter group were mainly of IWP distribution. The position of the bursa was later redefined (an anterior state being an opening less than two-thirds of the way back from the anterior end of the pallial oviduct to the anterior extremity of the capsule gland; see Fig. 3B), but this character did not contribute to the resolution of a more thorough morphological phylogenetic analysis of '*Nodilittorina*' (Reid 2002a). Now that the phylogeny of *Echinolittorina* is better resolved, it is clear that all members of the IWP clade show the anterior condition, but that both states occur in the basal clades. A morphological synapomorphy for the subgenus *Granulilittorina* therefore remains elusive.

In the absence of a useful fossil record for *Echinolittorina*, the explanation of the monophyly of the IWP species can only be speculative. Williams & Reid (2004) used the earliest probable fossil (*E. lozoueti* (Dolin & Pacaud, 2000) from the middle Eocene of France) to calibrate the rate of molecular evolution, and thus estimated the origin of the IWP clade at 32.7 million years ago (Ma). This considerably predates the final closure of the Tethyan Seaway at about 18 Ma. If extinction has been insignificant, the basal paraphyly of the Eastern Pacific plus Atlantic clades (Fig. 1) is consistent with an origin of the genus in this region, followed by eastward expansion through the Tethyan Seaway and ultimate isolation of a single lineage in the IWP. However, it is more likely that Neogene extinctions in the Atlantic removed the sister taxa of several IWP lineages, resulting in apparent monophyly of a single IWP clade of greater age than the final closure of the seaway (Williams & Reid 2004). The extreme homoplasy of shell features among littorinids means that the very meagre fossil record of *Echinolittorina*-like shells is difficult to interpret.

Key to species of *Echinolittorina (Granulilittorina)* in Indo-West Pacific

Owing to the high intraspecific variability of shells, to the few anatomical synapomorphies that define clades, and to the fact that the shape of the penis does not always discriminate between sister species, it is impossible to construct an entirely reliable key to these species. Any attempt must involve artificial groupings, subjective descriptions, and omission of extreme or rare shell variants. The following key has been based primarily on shell characters which, although so variable, are nevertheless the most accessible (and, with experience, among the most reliable) characters for identification. To these have been added two of the most useful and accessible anatomical characters, the penis and the coloration of the cephalic tentacles, both visible with only the minimum of dissection. The geographical distribution also provides important evidence for identification, since sister species and members of each of the seven phylogenetic groups are almost invariably allopatric. Identifications should be confirmed by reference to the detailed descriptions, figures and maps. Note that striae, ribs, and rows of granules or nodules, all run in a spiral direction around the shell, unless otherwise noted.

1 Smooth or with faint spiral grooves; tall-spired; small (< 8 mm); black; Sunda Is ... *E. sundaica* (Fig. 24)
- Variably striate, ribbed or granulose (e.g. Fig. 67) 2
- Nodulose (e.g. Fig. 32) 10
2 Cephalic tentacles with basal transverse black band (Figs 41G, 63F) 3
- Cephalic tentacles with 1-3 longitudinal black lines (Figs 5K, L, 25A, 28D, E) 8
3 Penial glandular disc small or absent (Figs 63A, 73A) 4
- Penial glandular disc normal (Figs 28A, 51B) 5
4 Smooth to minutely granulose; white; Sri Lanka .... *E. novaezelandiae* (Fig. 63)
- Finely granulose; brown mottled or reticulate pattern; central Indo-West Pacific (IWP) *E. vidua* (Fig. 59)
- 2–5 strongly granulose carinate ribs; white or with zigzag axial black stripes; Pacific islands .... *E. cinerea* (Fig. 64)
- Striate to granulose; white with large irregular black marks; Hawaiian Is .... *E. hawaiiensis* (Fig. 67)
- Axial rows of granules; white, or with axial brown lines; Indian and Pacific Oceans .... *E. reticulata* (Fig. 69)
- Granules not in axial rows; white; Red Sea and Arabia .... *E. millegrana* (Fig. 72)
5 Grey with black and white dashes on 2–7 ribs 6

-	White, or white finely mottled or lined with grey	7
6	Surface shiny; 3–7 main ribs; India and Sri Lanka	*E. leucosticta* (Fig. 40)
-	Surface dull; 2–4 main ribs, sometimes with small nodules; Java and Sumatra	*E. biangulata* (Fig. 44)
-	Surface dull; 2–3 main ribs with granules and small sharp nodules; western Pacific islands	*E. tricincta* (Fig. 49)
7	Minutely to finely granulose; white with grey herringbone pattern, axial lines or mottling; western Pacific	*E. melanacme* (Fig. 53)
-	Strongly granulose; grey mottled; Fiji Is	*E. feejeensis* (Fig. 57)
-	Striate, granulose or rugose; white to grey; Western Australia	*E. australis* (part) (Fig. 50)
-	Finely granulose; last whorl shouldered; white to grey; Philippines	*E. philippinensis* (Fig. 46)
8	Eroded parietal area (Fig. 2D); strongly granulose ribs with single thread between; dirty white or mottled brown; northwestern Pacific	*E. radiata* (Fig. 4)
-	No eroded parietal area	9
9	Finely or strongly granulose; grey, orange, brown or black; Persian Gulf and Oman	*E. arabica* (Fig. 8)
-	3 rows of small nodules; cream, yellow or orange; Red Sea	*E. marisrubri* (Fig. 11)
10	Penial filament short, triangular (= half total penial length; Fig. 28A); 2 rows of nodules	11
-	Penial filament elongate (> half total penial length; Figs 22A, 39A); 1–3 rows of nodules	12
11	Japan	*E. cecillei* (Fig. 32; Table 1)
-	Marquesas Is	*E. marquesensis* (Fig. 35; Table 1)
-	Australia	*E. austrotrochoides* (Fig. 30; Table 1)
-	India to Southeast Asia	*E. malaccana* (Fig. 27; Table 1)
12	1–2 rows of orange nodules; Western Australia	*E. australis* (part) (Fig. 50E–G)
-	2 rows of whitish nodules; Indonesia	*E. wallaceana* (Fig. 38; Table 1)
-	2 rows of whitish or grey nodules; Easter and Pitcairn Is	*E. pascua* (Fig. 21)
-	2–3 rows of whitish nodules; southern Arabia	*E. omanensis* (Fig. 17)
-	3 rows of whitish nodules; East Africa and Madagascar	*E. natalensis* (Fig. 13)
-	3 rows of whitish nodules; Red Sea	*E. subnodosa* (Fig. 19)

The *Echinolittorina radiata* group

This group contains only the single species *E. radiata*, of which the relationships within the subgenus *Granulilittorina* are uncertain.

Echinolittorina radiata (Souleyet in Eydoux & Souleyet, 1852)

(Figures 4, 5, 6A, B, 7)

Littorina radiata Souleyet in Eydoux & Souleyet, 1852: 562, pl. 31, figs 46, 47 (Touranne, Cochinchine [Da Nang, Vietnam]; lectotype (Rosewater 1970) BMNH 1854.7.24.389, seen, Fig. 4N; 2 paralectotypes MNHN, seen). Fischer, 1891: 171. Serène, 1937: 38.

Nodilittorina (Nodilittorina) radiata—Reid, 1989a: 100. Reid, 1992: 200–201, figs 1i (penis), 2h (oviduct), pl. 3d–h.

Nodilittorina (Granulilittorina) radiata—Kurozumi, 1994: 366, pl. 2, fig. 1.

Nodilittorina radiata—Mak, 1995: 53–59, figs 1b, 2b (spawn). Higo *et al*., 1999: 91. Hasegawa, 2000: 141, pl. 70, fig. 21. Reid, 2001a: 440–441, figs 2D, E, 3F (penis). Reid, 2002a: 259–281. Lee & Chao, 2003: 32, pl. 3, fig. 61. Thach, 2005: 54, pl. 8, fig. 28.

Echinolittorina radiata—Williams *et al*., 2003: 63, 83. Williams & Reid, 2004: 2227–2251.

Litorina exigua Dunker, 1860: 226–227 (Japan; lectotype (Rosewater 1970) Dunker, 1861: pl. 2, fig. 3). Dunker, 1861: 13, pl. 2, fig. 3. Dunker, 1882: 111. Weinkauff, 1882: 95–96, pl. 13, figs 13, 16 (in part; includes *E. miliaris*).

Litorina (Tectaria) exigua—Weinkauff, 1883: 226.

Littorina exigua—Pilsbry, 1895: 61.

Nodilittorina (Granulilittorina) exigua—Rosewater, 1970: 500–502, pl. 386, figs 1-6, pl. 387 (map). Fujioka & Kurozumi, 1980: 51–54, fig. 1C.

Granulilittorina exigua—Kuroda *et al*., 1971: 58, pl. 16, figs 32–34. Higo, 1973: 47. Okutani, 1986: 70–71, figs. Choe, 1992: 291–291, fig. 83. Higo & Goto, 1993: 73.

Nodilittorina exigua—Ohgaki, 1985a: 462. Ohtsuka & Yoshioka, 1985: 232, fig. 4C, D (spawn). Ma, 2004: 33, fig. 12 (map, as *N. pyramidalis* in error) (in part, includes *E. vidua*).

Littorina miliaris—Nevill, 1885: 154 (in part, includes *E. natalensis*; not *L. miliaris* Quoy & Gaimard, 1833 = *E. miliaris*).

Litorina (Hamus) granularis—Watson, 1886: 576–577 (not *L. granularis* Gray, 1839 = *E. miliaris*). Pilsbry, 1895: 62 (not Gray, 1839).

Tectarius granularis—Tryon, 1887: 260, pl. 45, fig. 4 (in part, includes *E. millegrana*, *E. miliaris*, *E. vidua*, *E. cinerea*; not Gray, 1839). Kuroda & Habe, 1952: 89 (not Gray, 1839). Hirase & Taki, 1954: pl. 79, fig. 10 (not Gray, 1839).

Littorina (Melarhaphe) granularis—von Martens, 1897: 206–207 (as *Melarrhaphe*; in part, probably includes *E. vidua*, *E. melanacme*; not Gray, 1839).

Littorina granularis—Yen, 1936a: 2–3 (not Gray, 1839). Yen, 1936b: 191, pl. 16, fig. 17 (not Gray, 1839).

Littorivaga (?) *granularis*—Kuroda, 1940: 102–102 (not Gray, 1839).

Littorina (Littorivaga ?) granularis—Kuroda, 1941: 82, pl. 6, fig. 9 (not Gray, 1839).

Nodilittorina granularis—Habe, 1951: 92, pl. 14, figs 7, 8, 16 (not Gray, 1839). Habe, 1955: 206–207, figs 1, 2 (spawn) (not Gray, 1839). Habe, 1956b: 117–121, fig. C (spawn) (not Gray, 1839). Habe, 1958a: 8, pl. 1, fig. 8 (not Gray, 1839). Kojima, 1960: 118, fig. 1 (spawn) (not Gray, 1839). Kira, 1962: 22–23, pl. 12, fig. 24 (not Gray, 1839). Oyama & Takemura, 1963: *Nodilittorina* fig. 1 (not Gray, 1839).

Tectarius millegranus—Dautzenberg & Fischer, 1905: 151–152 (not Philippi, 1848).

Littorina (Littorivaga?) millegrana—Hirase, 1934: 47, pl. 79, fig. 10 (not Philippi, 1848).

Nodilittorina (Granulilittorina) millegrana—Rosewater, 1970: 491–494, pl. 380, figs 2, 3 (in part, includes *E. melanacme*, *E. feejeensis*, *E. vidua*, *E. novaezelandiae*, *E. millegrana*, *E. reticulata*; not Philippi, 1848).

Taxonomic history: The specific name *granularis* was applied by Tryon (1887) to a group of at least five *Echinolittorina* species with granulose shells, but following Watson (1886) and Yen (1936a, b) this name became associated with the present species, and was widely used in the Japanese literature of the mid-twentieth century. However, as first noted by Rosewater (1970), *L. granularis* Gray, 1839 is a synonym of *E. miliaris*, endemic to Ascension Island in the southeastern Atlantic. (The type of *L. granularis* in BMNH is a worn shell without locality, but shows the characteristic sculpture of *E. miliaris* and the two white apertural bands present in most non-Indo-West-Pacific members of the genus.) Accordingly, Rosewater (1970) revived the name *N. exigua* for the present species, distinguishing it from a complex of six species under the name *N. millegrana*. This distinction was based on shell characters alone and was unclear; furthermore the lectotype of *L. radiata* was figured as a member of the latter group. Among the members of the conchologically similar *E. millegrana* group, *E. radiata* is only commonly sympatric with *E. vidua*, and their separation (but under different names) was already well recognized (e.g. Yen 1936a, b; Kuroda 1941; Habe 1951). Their diagnostic shell characters were further discussed by Ohgaki (1985a). The priority of the name *radiata* was pointed out by Reid (1989a) and the name and identity of the species established by subsequent redescriptions (Reid 1992, 2001a).

Diagnosis: Shell turbinate; 5–8 granulose ribs at and above periphery, single thread between each rib, granules not aligned in axial series; white with faint fine brown marbled pattern. Japan, Korea, China, Vietnam. COI: GenBank AJ623039, AJ623040.

Material examined: 87 lots (including 13 penes, 7 sperm samples, 19 pallial oviducts, 9 radulae).

Shell (Fig. 4): Mature shell height 4.4–12.8 mm. Shape high turbinate (H/B = 1.19–1.51, SH = 1.36–1.69); spire whorls rounded, suture distinct; spire profile straight; periphery of last whorl weakly angled at periphery and sometimes also at shoulder. Columella concave, hollowed and slightly pinched at base; eroded parietal area; often an imperforate pseudumbilical area adjacent to columella; often a slightly produced anterior lip to aperture. Sculpture of last whorl: 5–8 strongly or weakly granulose ribs at and above periphery; granular sculpture not usually aligned in axial series; ribs usually subequal, but peripheral rib and shoulder rib may be slightly more prominent (Fig. 4E, J); single thread between each rib (rarely two or none); spiral microstriae cover entire surface; base with 4–8 ribs; surface usually eroded. Protoconch 0.28–0.30 mm diameter, 2.9 whorls. Colour: dirty white, fawn or pale blue-grey, spire whorls blue-grey to purple-brown; pattern usually faint, sometimes absent, brown marks between granules on ribs, brown marbling over whole surface in darkest shells, but with cream spiral line on base and another adjacent to columella; aperture brown with pale band at base; columella brown.

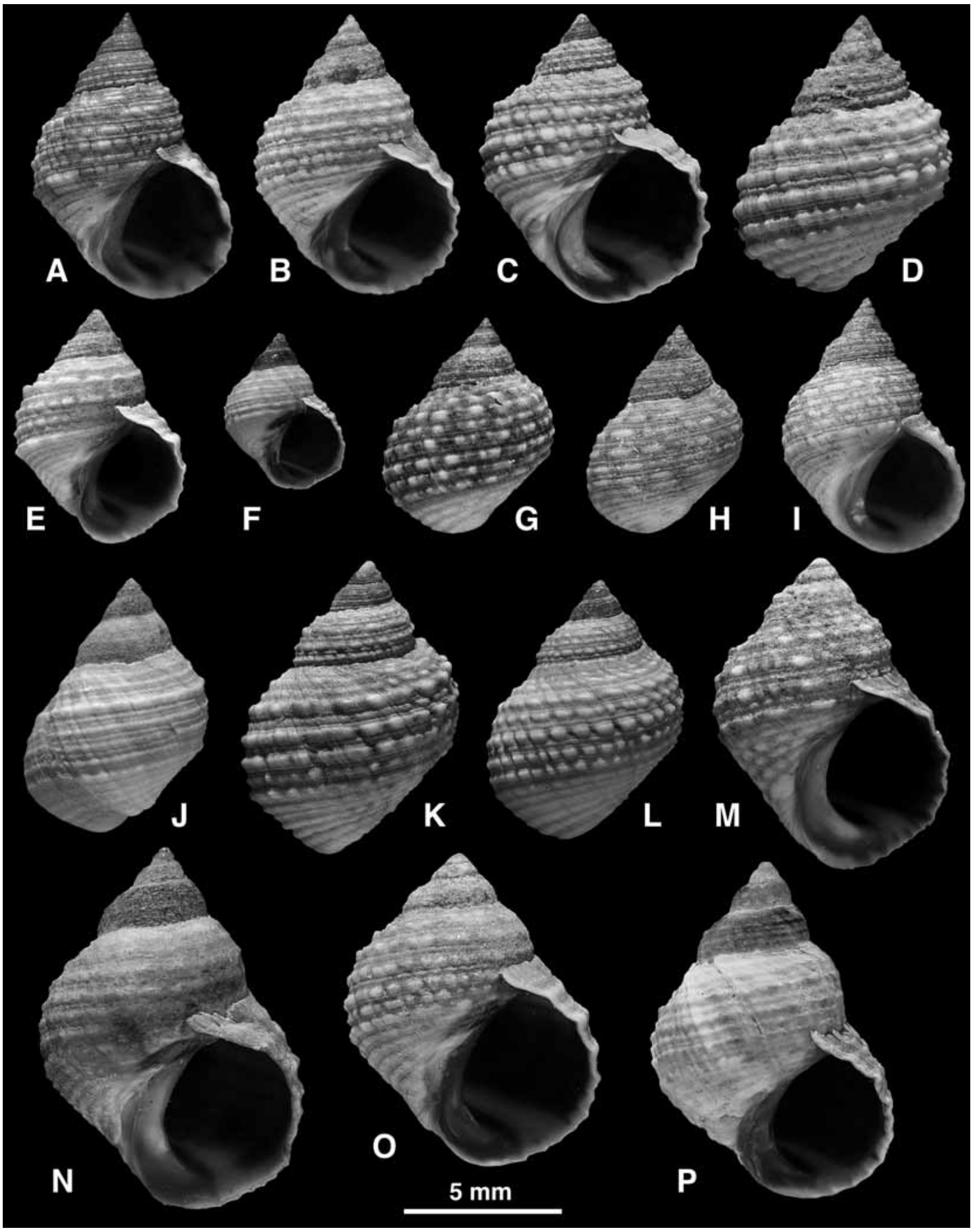

FIGURE 4. *Echinolittorina radiata*. **A,** Hoi Ha, Mirs Bay, Hong Kong (BMNH 20030888). **B, G,** Cat Ba Bay, Ha Long Bay, Vietnam (BMNH 20030889). **C, O,** Otsu, Ibaraki, Japan (BMNH 20030890). **D, P,** Nogita, Kyushu, Japan (BMNH 20030891). **E, J,** Haikou, Hainan I., China (BMNH 20030892). **F,** Yantai, Qingdao, China (BMNH 20030893). **H, I,** Sai Kung, Hong Kong (BMNH 20030894). **K–M,** Tsutsu, Tsushima I., Japan (BMNH 20030895). **N,** *Littorina radiata* Souleyet, in Eydoux & Souleyet, 1852, lectotype, Touranne, Cochinchine [Da Nang, Vietnam] (BMNH 1854.7.24.389).

Animal (Fig. 5): Head (Fig. 5K–M) black, with or without unpigmented stripe across snout, tentacle pale around eye, with two longitudinal black lines (sometimes only lower line present); sides of foot grey to black. Opercular ratio 0.46–0.54. Penis (Fig. 5A–E): filament stout, lower half wrinkled and not clearly differentiated from wrinkled base, smooth tip bluntly triangular, filament 0.5–0.6 total length of penis, sperm groove ends subterminally; mamilliform gland and glandular disc of similar size, borne on short projection of base; penis unpigmented, or slightly pigmented at base. Euspermatozoa 66–84 µm; paraspermatozoa (Fig. 5I, J) spherical to slightly oval, 11–14 µm diameter, containing 1–3(4) rectangular rod-pieces, equal to or shorter than cell diameter, hexagonal in section, and large distinct granules. Pallial oviduct (Fig. 5F, G): distal part swollen and bent back beneath straight section; bursa opening near swollen part and extending back to albumen gland. Spawn (Fig. 5H) an asymmetrically biconvex pelagic capsule 200–244 µm diameter (160 µm, Habe 1955) with broad peripheral rim, cupola-shaped upper side sculptured by 5–7 concentric rings (Kojima 1960, illustrated a probably aberrant capsule with 3 rings), containing single ovum 50–78 µm diameter (Habe 1955, 1956b; Kojima 1960; Ohtsuka & Yoshioka 1985; Mak 1995). Development predicted to be planktotrophic.

Radula (Fig. 6A, B): Relative radula length 2.80–6.49. Rachidian: length/width 1.14–1.42; tip of major cusp rounded. Lateral and inner marginal: major cusp on each of similar size, tips blunt to rounded. Outer marginal: 6–8 cusps.

Range (Fig. 7): Japan, Korea, China, Taiwan, Vietnam. Range limits: Shakotan, Hokkaido, Japan (Ohgaki 1983b); Shimamaki, Hokkaido, Japan (BMNH); Hakodate, Hokkaido, Japan (USNM 276842); Kuroshima, Kagoshima Pref., Japan (Uozumi Colln); Yahazu, Yaku-shima, Kagoshima Pref., Japan (BMNH); Akuseki-jima, Tokara Is, Japan (Kurozumi 1994); Senkaku Is, Japan (Fujioka & Kurozumi 1980); Sokcho, S. Korea (Song *et al*. 2000); Pusan, S. Korea (BMNH); Inchon, S. Korea (Song *et al*. 2000); Yantai, near Qingdao, China (BMNH 20030893, ZISP); Tiaoshi, 20 km NW Keelung, Taiwan (BMNH); Longkang, Oluanpi Peninsula, Taiwan (BMNH); Do Son, Hai Phong, Vietnam (BMNH 20030897; MNHN); Nha Trang, Vietnam (BMNH 20010355).

The species appears to occur all around the Yellow Sea; Ma (2004) records it from the entire Chinese coast and Song *et al*. (2000) from localities in South Korea. The species is rare at Nha Trang, Vietnam, and in the south of Taiwan. On Hokkaido it is common only at the southern tip (Ohgaki 1983b). It is apparently absent from most of the Ryukyu Island chain (absence from Ishigaki noted by Ohgaki 1998), occurring only in the north up to 220 km from the mainland of Kyushu (Kurozumi 1994) and in the south in the Senkaku Islands 150 km northeast of Taiwan (Fujioka & Kurozumi 1980). (A single collection from ‘Okinawa’, NSMT 41643, is probably unreliable.) It is also absent from the Ogasawara Islands. It is therefore a species of continental habitats, absent from oceanic islands.

Habitat and ecology: Juveniles can be found among barnacles in the eulittoral zone, but adults extend upwards into the lower littoral fringe. Substrates include granite, basalt, slate, sandstone, limestone and concrete and the species occurs on both sheltered and exposed coastlines.

Various aspects of the ecology and behaviour of this species have been studied. Its zonation has been described in Hong Kong (Ohgaki 1985a; Williams 1994), China (Fan 1981; Morton 1990; You 1990), Korea (Lee & Hyun 1997) and throughout Japan (Ohgushi 1956; Habe 1958b; Yajima & Kosaka 1979; Tsuchiya 1979; Ohgaki 1985b, c, 1988b; Tanaka *et al*. 1985). In Hong Kong it is zoned at and above mean high water of spring tides; this is below and in the lower part of the range of *E. malaccana* and above the level of *Littorina brevicula* (Ohgaki 1985a; Williams 1994). Field manipulations indicate that competitive interactions between these three littorinids may influence their relative zonation (Dudgeon & Yipp 1986). Compared with the others, *E. radiata* has only a modest desiccation resistance, showing 50% survival after 31 days (Yipp *et al*. 1986). Likewise, in Japan it usually occupies a level above *L. brevicula* (Ohgushi 1956). At Tanabe Bay in southern Honshu it occurs below *E. cecillei* and above *E. vidua*, and occupies both sheltered and exposed sites (Habe 1958b). Vertical zonation is related to the height of waves and shows seasonal variation (Ohgaki 1989).

On each tide the animals migrate vertically to remain in the splash zone (Hukuda 1950; Ohgaki 1985c; Kato 1985, 1986a, b) and the vertical range is restored following dislodgement by rain (Ohgaki 1988b). At high tidal levels there may be long periods of quiescence and activity is stimulated by rain (Britton & McMahon 1992).

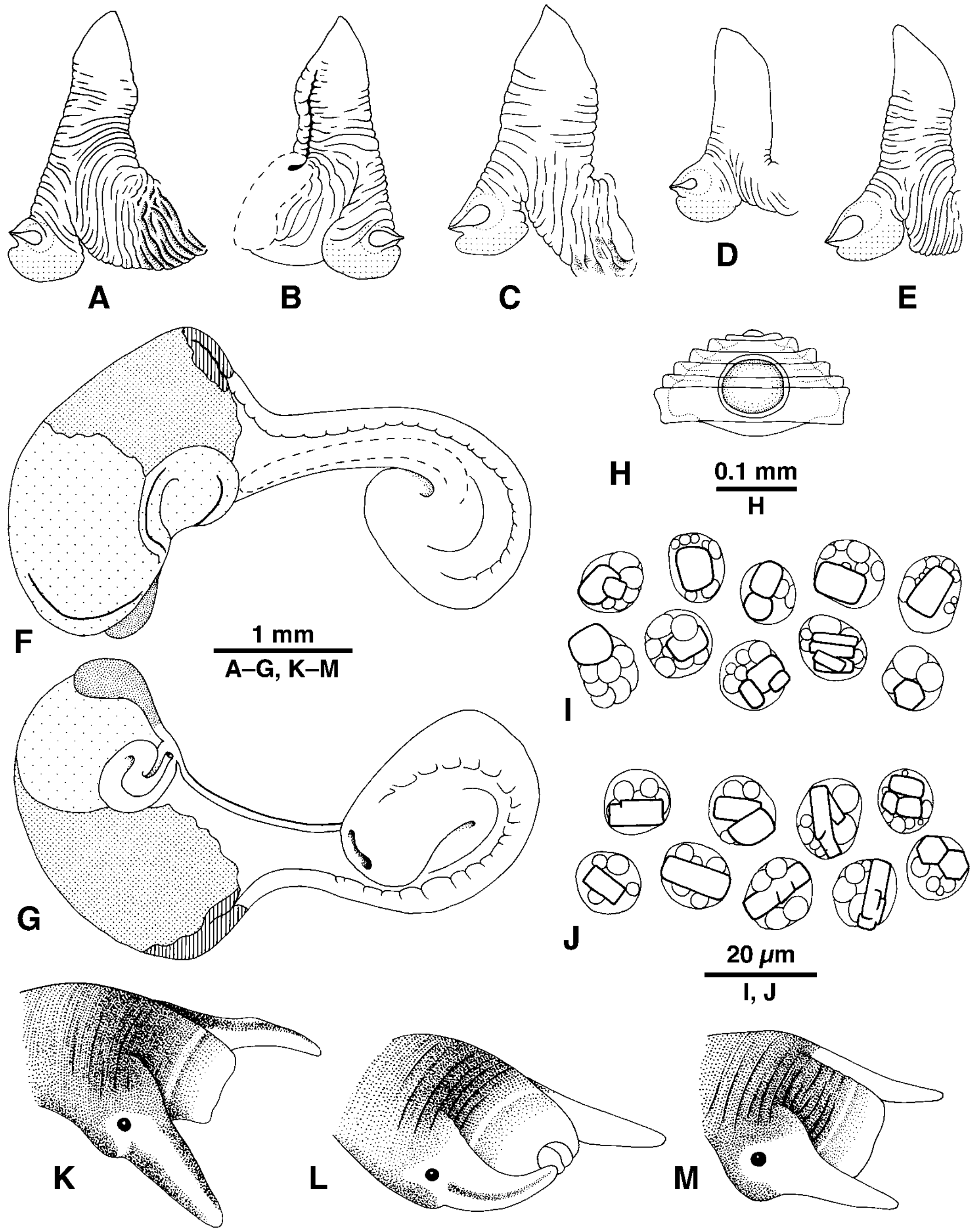

FIGURE 5. *Echinolittorina radiata*. **A–E,** penes. **F, G,** pallial oviduct. **H,** pelagic egg capsule (after Mak, 1995). **I, J,** paraspermatozoa. **K–M,** heads. **A–C, I,** Asamushi, Honshu, Japan (BMNH 20030896; **A, B,** lateral and medial views of same specimen; shell H **A, B** = 7.5 mm, **C** = 7.0 mm). **D,** Do Son, Hai Phong, Vietnam (BMHH 20030897; shell H = 6.5 mm). **E, K–M,** Sai Kung, Hong Kong (BMNH 20030894; shell H **E** = 5.0 mm, **K** = 5.3 mm, **L** = 6.4 mm, **M** = 6.6 mm). **F, G,** Nejiko, Hirado I., Kyushu, Japan (BMNH 20030898; lateral and medial views of same specimen; shell H = 9.1 mm). **H,** Hong Kong. **J,** Aberdeen, Hong Kong (BMNH 20030899). Shading conventions as in Figure 3.

The breeding season is extended in the southern parts of the range. Spawning occurs in July and August at Asamushi in the north of Honshu (Kojima 1958a, 1960; Hirai 1963). At Shirahama it spawns from mid-June to early September, and egg release is associated with strong waves and high tide, rather than the lunar phase (Ohgaki 1981). In Hong Kong the spawning season lasts from April to October (Mak 1998). Recruits appear

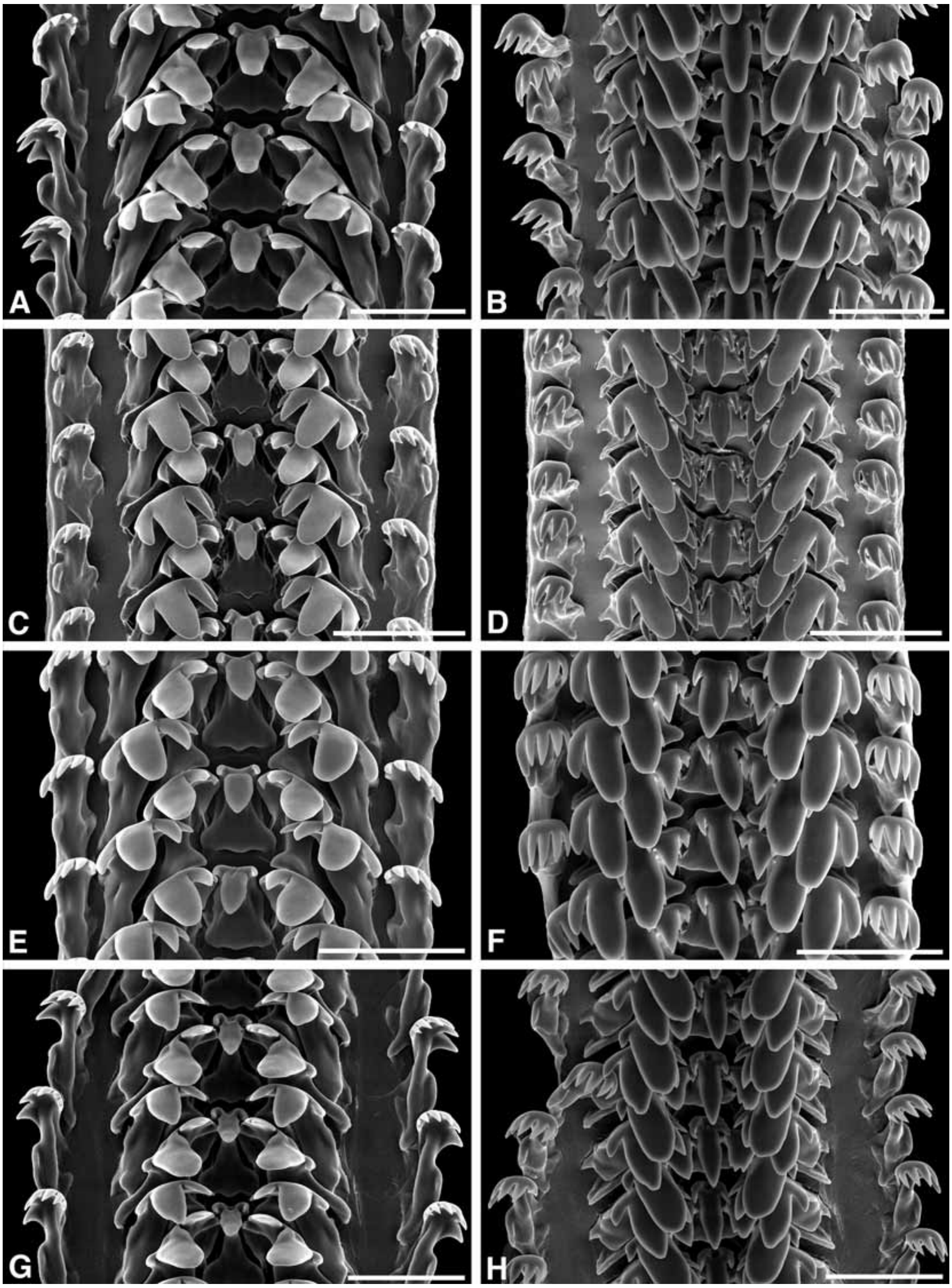

FIGURE 6. Radulae of *Echinolittorina* species (two views of each radula, flat and at 45°). **A, B,** *E. radiata*; Kinkasan I., Miyagi Pref., Japan (BMNH 20050563; shell H = 8.7 mm). **C, D,** *E. arabica*; Hamriya, Sharjah (BMNH 20030871; shell H = 8.4 mm). **E, F,** *E. marisrubri* new species, paratype; Port Safaga, Egypt (BMNH 20030886; shell H = 10.6 mm). **G, H,** *E. omanensis* new species, paratype; Wadi Sayq, Jabal Qamr, Dhofar, Oman (BMNH 20040220; shell H = 14.2 mm). Scale bars = 50 µm.

in the lower part of the vertical range and mean size of snails is larger at higher levels (Ohgaki 1985b; Tanaka *et al*. 1985). Mature animals of both sexes and also immature individuals are found at lower levels during the summer, so this migration may be related to feeding or avoidance of environmental stress, rather than spawning (Ohgaki 1988a; Ito *et al.* 1998). In Hong Kong *E. radiata* grazes the epilithic biofilm of cyanobacteria (Mak & Williams 1999). Radular length decreases in summer at lower tidal levels as a consequence of increased foraging activity (Ito *et al.* 2002). Growth rate has been recorded in Hokkaido (Miyamoto *et al.* 1995), and the relation between total weight, body and shell weight measured (Tokeshi *et al.* 2000). The frequency of mucus attachment to the substrate at the outer lip has been studied by Wada & Ito (2000).

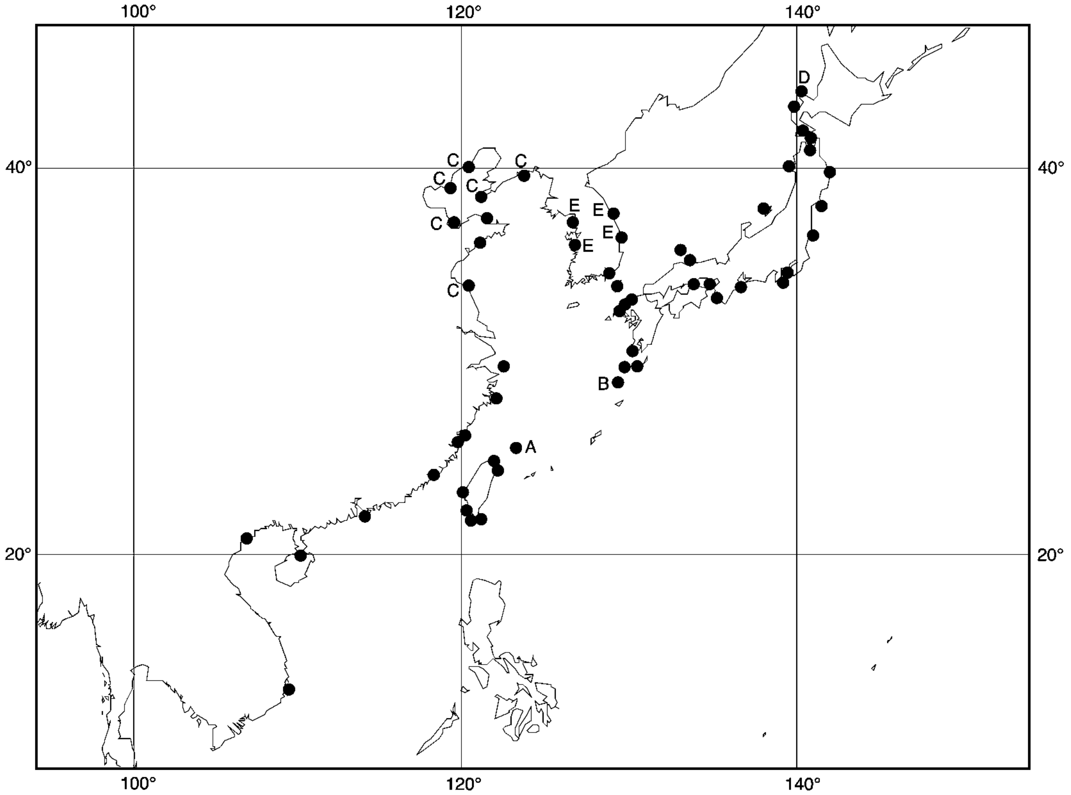

FIGURE 7. Distribution of *Echinolittorina radiata*. Literature records: A, Fujioka & Kurozumi (1981); B, Kurozumi (1994); C, Ma (2004); D, Ohgaki (1983b); E, Song *et al.* (2000).

Remarks: Unusually in the genus *Echinolittorina*, the distribution of *E. radiata* lies almost entirely outside tropical latitudes. Under the influence of the warm Tsushima Current in the Japan Sea and the Kuroshio Current flowing up the east coast of Japan, it extends to 43°N in Hokkaido. This is a continental species, absent from the Ryukyu and Ogasawara Islands where marine productivity is low. Phylogeography has been examined in Korea using cytochrome-*b* sequence data (Song *et al.* 2000).

Superficially the granulose shell resembles those of the members of the *E. millegrana* group, but *E. radiata* does not possess the unique tentacle coloration of that group, nor the curved paraspermatozoan rod-pieces of most of its members. Molecular data do not support a relationship with any other species within the Indo-Pacific radiation (Williams & Reid 2004).

Of the few sympatric species, confusion is only possible with *E. vidua*; the shell of *E. radiata* differs from that of *E. vidua* (Fig. 59) in its slightly taller spire, profile often slightly angled at periphery and shoulder (rounded in *E. vidua*), usually larger and coarsely granulose ribs with single thread between (finer and more numerous ribs and granules in *E. vidua*), dirty white colour sometimes with indistinct brown pattern (often distinct brown stripes and tessellation in *E. vidua*), slightly produced anterior lip of aperture (rounded in *E. vidua*), brown columella and lip (brown columella, but white anterior and inner apertural lip in *E. vidua*); the penis, paraspermatozoa, oviduct, egg capsules and head pigmentation are all clearly different in these two species (Figs 5, 60). There is also an ecological difference; in Hong Kong only *E. radiata* is found on the sheltered shore of Tolo Harbour, whereas both occur on exposed coasts (Ohgaki 1985a). In this respect, and in its geographical distribution (e.g. on the Ryukyu Islands) *E. vidua* is a more oceanic species than *E. radiata*. This species occurs with others (*E. melanacme*, *E. tricincta*, *E. reticulata*) in Taiwan, and with *E. melanacme* in Vietnam, but confusion should not occur.

The *Echinolittorina arabica* group

This group consists of the two sister species, *E. arabica* and *E. marisrubri* n.sp. Until 1990 they were not distinguished from *E. subnodosa*.

Echinolittorina arabica (El Assal, 1990)

(Figures 6C, D, 8, 9, 10)

Nodilittorina (Granulilittorina) subnodosa—Rosewater, 1970: 495–496, pl. 383, figs 4–6, pl. 383a (map) (in part, includes *E. subnodosa*, *E. marisrubri*; not Philippi, 1847).
Nodilittorina subnodosa—Biggs, 1973: 355 (not Philippi, 1847).
Nodilittorina arabica El Assal, 1990: 293–298, figs 2, 3 (operculum), 5 (radula), 6 (penis) (Arabian Gulf, Saudi Arabia [restricted to Ras Met'eb, Dammam, Saudi Arabia, the locality of the syntypes]; lectotype BMNH 1990089/1 (here designated, Fig. 8L) and paralectotype BMNH 1990089/2, seen; 4 lectotypes in alcohol, BMNH 1990089/3–6, seen). Reid, 2002a: 259–281 (in part, includes *E. marisrubri*).
Nodilittorina (Nodilittorina) arabica—Bosch *et al*., 1995: 45, fig. 115.
Echinolittorina arabica—Williams *et al*., 2003: 83 (in part, includes *E. marisrubri*).
Echinolittorina arabica A—Williams & Reid, 2004: 2227–2251.

Taxonomic history: Rosewater (1970) considered specimens from the Persian Gulf to be smooth variants of *E. subnodosa*, and this taxonomy was followed for 20 years. Anatomical study during a larger project (Reid 1989a) indicated that *E. subnodosa* was distinct from the *E. arabica* group, although specimens from the Red Sea and Persian Gulf were not then separated. El Assal (1990) made unacknowledged use of information provided by Reid and proceeded to name the species from the Persian Gulf, without any anatomical comparison and making no mention of the similar specimens from the Red Sea. Thereafter, *E. arabica* was considered to occur in both the Persian Gulf and Red Sea (Bosch *et al*. 1995; Dekker & Orlin 2000; Reid 2002a) and the sister species of the *E. arabica* group were only separated following molecular study (Williams & Reid 2004).

Diagnosis: Shell turbinate; smooth with 16–22 minutely granulose threads at and above periphery and rugose suture, or granulose with 2–5 rows of granules at and above periphery; colour grey, cream, orange, brown or black. Persian Gulf and Gulf of Oman. COI: GenBank AJ622981, AJ622982.

Material examined: 54 lots (including 13 penes, 2 sperm samples, 6 pallial oviducts, 4 radulae).

Shell (Fig. 8): Mature shell height 5.4–13.9 mm. Shape turbinate to conical (H/B = 1.20–1.53; SH = 1.47–2.11); spire whorls lightly rounded to almost flat, suture distinct; spire profile slightly convex, concave at apex; periphery of last whorl weakly angled. Columella short, concave, slightly hollowed at base; no eroded parietal area; sometimes a pseudumbilicus in large shells. Sculpture granulose, nodulose, rugose or smooth; last whorl of strongly sculptured shells (Fig. 8A–F, H): 2–5 rows of granules or nodules, usually most prominent at periphery and shoulder, with granulose threads between; smooth shells (Fig. 8G, I–L) with up to16–22 fine minutely or indistinctly granulose threads above periphery; suture and adjacent posterior part of last whorl often coarsely rugose; spiral microstriae cover entire surface, but surface often eroded; base with 5–12 threads or weakly granulose ribs. Protoconch 0.26–0.29 mm diameter, 2.6–2.8 whorls. Colour: pale grey, cream, orange, brown or black, sometimes with broad dark band in middle of whorl and another on base; pattern usually absent, but sometimes a faint spiral pattern of brown marks between granules; aperture brown with pale band at base; columella white.

Animal (Fig. 9): Head grey to black, with or without unpigmented stripe across snout, tentacle pale around eye, with two longitudinal grey to black lines; sides of foot grey to black. Opercular ratio 0.47–0.59. Penis (Fig. 9A–G): filament strap-shaped to pointed, sometimes slightly narrowed at base, filament 0.6–0.8 total length of penis, sperm groove extends to tip; mamilliform gland and glandular disc of similar size, borne on short projection of base; penis unpigmented or slightly pigmented at base. Euspermatozoa not known; paraspermatozoa (Fig. 9J, K) oval, with 1–2 rod-pieces 14–26 µm, usually one rod-piece strongly projecting and slightly curved, the other shorter and not projecting; cytoplasm filled with large round granules. Pallial oviduct (Fig. 9H, I): bursa opening at midpoint of straight section and extending back to albumen gland. Spawn not known. Development predicted to be planktotrophic.

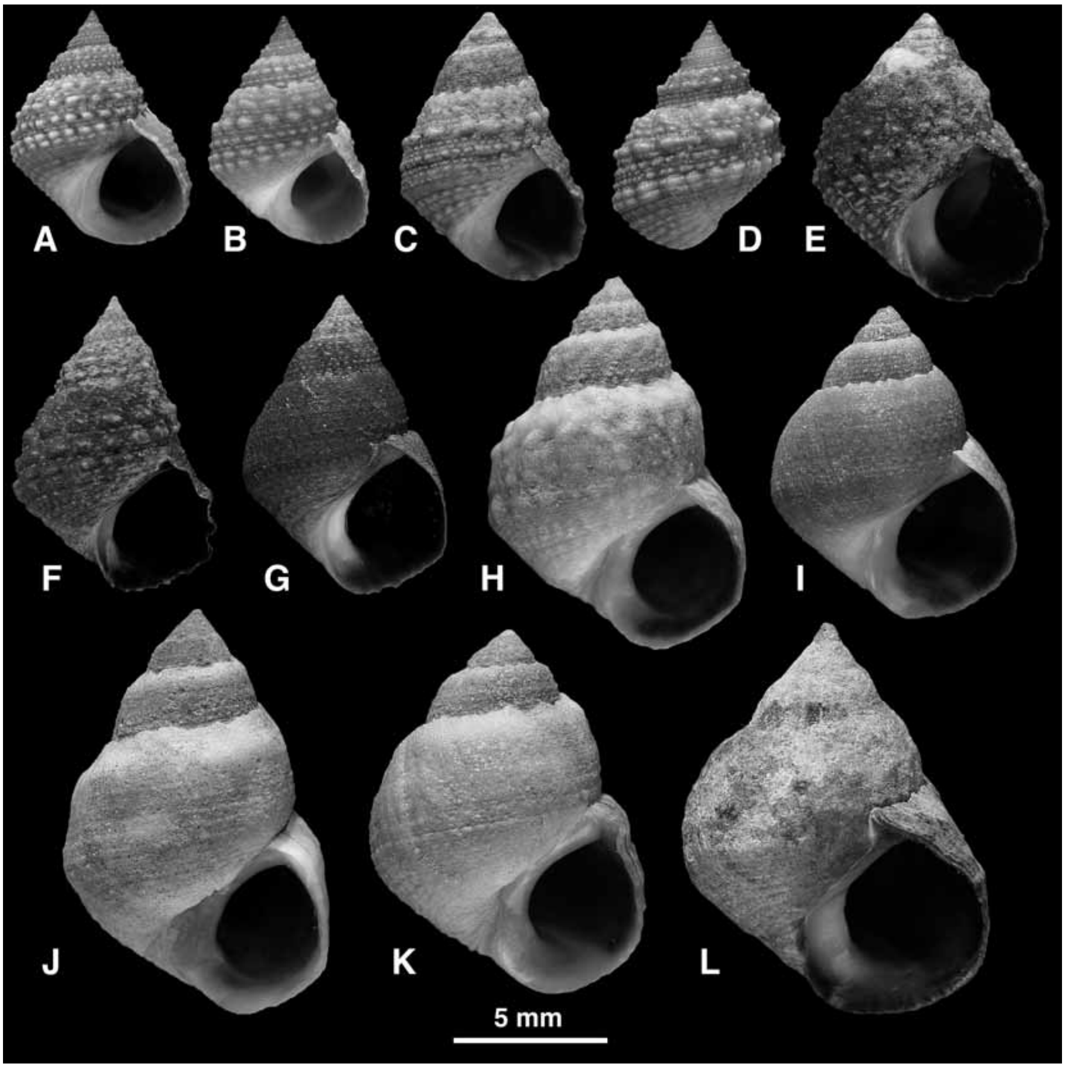

FIGURE 8. *Echinolittorina arabica*. **A, B,** Hamriya, Sharjah (BMNH 20030871). **C,** Ras al-Hadd, Oman (BMNH 20030872). **D,** Hormuz, Iran (BMNH 20030873). **E,** Fujairah, United Arab Emirates (BMNH 20030874). **F, G,** Ras al-Khaimah Khor, United Arab Emirates (BMNH 20030875). **H, I,** United Arab Emirates (BMNH 20030876). **J, K,** Khor al-Bazm, United Arab Emirates (BMNH 20030877). **L,** *Nodilittorina arabica* El Assal, 1990, lectotype, Ras Met'eb, Dammam, Saudi Arabia (BMNH 1990089/1).

Radula (Fig. 6C, D): Relative radula length 2.36–3.92. Rachidian: length/width 1.45–1.70; tip of major cusp pointed. Lateral and inner marginal: major cusp on each of similar size, tips rounded. Outer marginal: 5 cusps.

Range (Fig. 10): Persian Gulf and Gulf of Oman. Range limits: Kuwait (BMNH 20030878); Bushire, Iran (USNM 679285); Ras Mushayrib, United Arab Emirates (BMNH); Hormuz I., Iran (BMNH 20030873); Fujaira, United Arab Emirates (BMNH 20030874); Al Bustan, E of Muscat, Oman (ZMA); Ras al-Hadd, Oman (BMNH 20030872). The southern range limit at Ras al-Hadd and absence from the Arabian Sea coast of the Arabian Peninsula are probably correct, for *E. arabica* has not been found among the 34 samples of other *Echinolittorina* species available from between Masirah and Aden.

Habitat and ecology: *Echinolittorina arabica* occurs on a wide range of hard substrates in the uppermost eulittoral zone and low littoral fringe, but always in sheltered situations. It has been recorded on limestone, beachrock and concrete sea walls. It can be found on the trunks and pneumatophores of the mangrove *Avicennia* and among saltmarsh plants, and may crawl over firm sand and mud surfaces at low tide (G.R. Feulner, pers. comm.). It is abundant on the extensive black cyanobacterial mats ('sabkas') of the Gulf coast of the United Arab Emirates (Biggs 1973). It tolerates salinity of up to 50 ppt and water temperatures of up to 34°C (Biggs 1973).

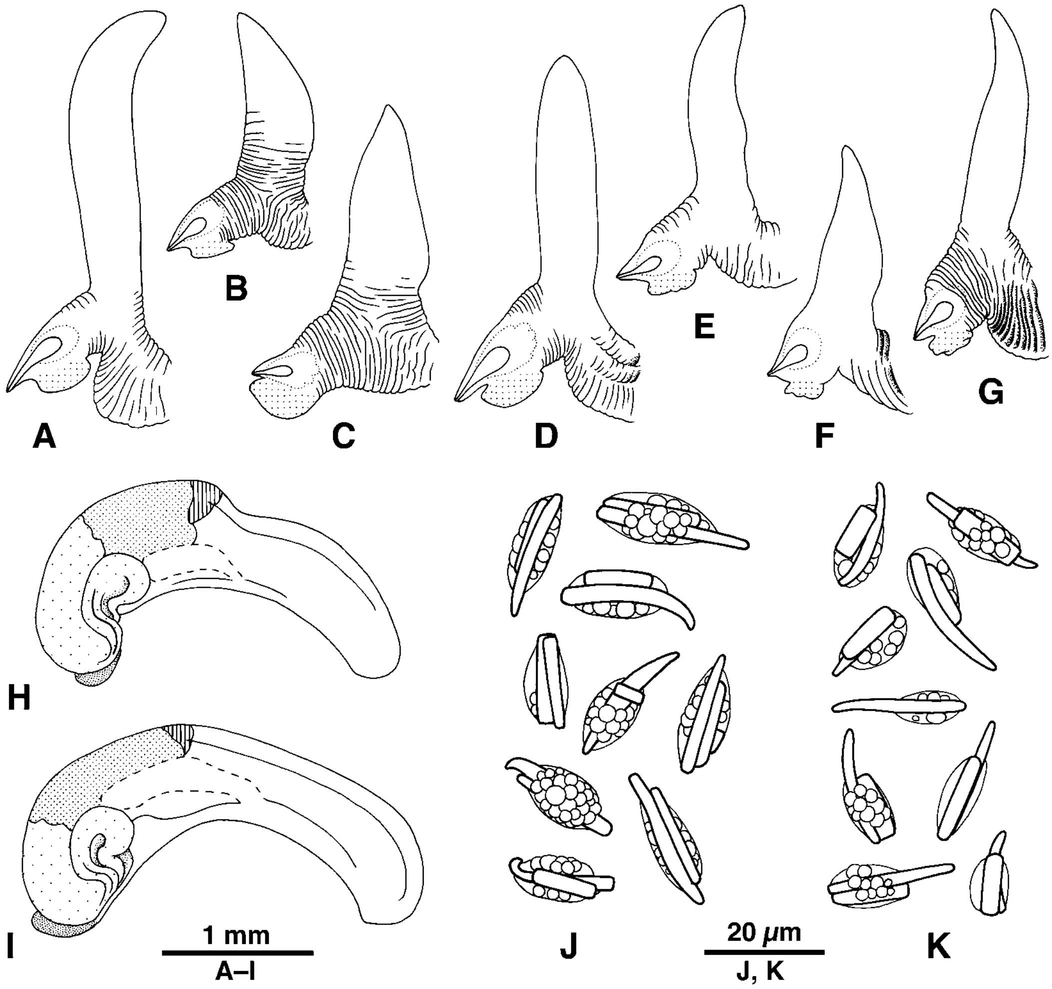

FIGURE 9. *Echinolittorina arabica*. **A–G**, penes. **H, I,** pallial oviducts. **J, K,** paraspermatozoa. **A,** Kuwait (BMNH 20030878; shell H = 7.8 mm). **B–D, J, K,** Dubai, United Arab Emirates (BMNH 20030879; shell H **B** = 6.6 mm, **C** = 7.0 mm, **D** = 7.3 mm). **E,** Ghemeis Peninsula, Abu Dhabi, United Arab Emirates (BMNH 20030880; shell H = 7.6 mm). **F,** Fujaira, United Arab Emirates (BMNH 20030881; shell H = 7.7 mm). **G,** Ras al-Khaimah Khor, United Arab Emirates (BMNH 20030875; shell H = 8.4 mm). **H,** Hamriya, Sharjah, United Arab Emirates (BMNH 20030871; shell H = 7.7 mm). **I,** Al Bustan, Muscat, Oman (ZMA; shell H = 9.2 mm). Shading conventions as in Figure 3.

Remarks: The shell of this species is among the most variable in the genus, ranging from coarsely granulose to smooth. Although available samples differ in their degree of sculpture, it is unclear whether there is any correlation with habitat type. Extremes of sculpture can be found in the same microhabitat (e.g. Fig. 8F and G together in the same mangrove habitat). The great majority of shells are of the smooth type. Despite the sheltered environment, the shells from the cyanobacterial mats on tidal flats of the southern Persian Gulf are of considerable thickness and curiously eroded (Fig. 8H–K). In addition, this species is extremely variable in colour and some samples are polymorphic, varying from black to orange or cream. Most samples from the black cyanobacterial mats have black to brown shells, as do those from mangroves, whereas samples from rock substrates are paler brown to orange (BMNH; G.R. Feulner and R. Hornby pers. comm.); this might imply an ecophenotypic effect through diet, or visual selection, and deserves further study. G.R. Feulner (pers. comm.) has suggested that crab predation plays an important role in determining the abundance of this species in the eastern Persian Gulf and Oman. Evidence of damage by crabs can sometimes be seen on the shells, and the shells can be remarkably solid (Fig. 8J, K).

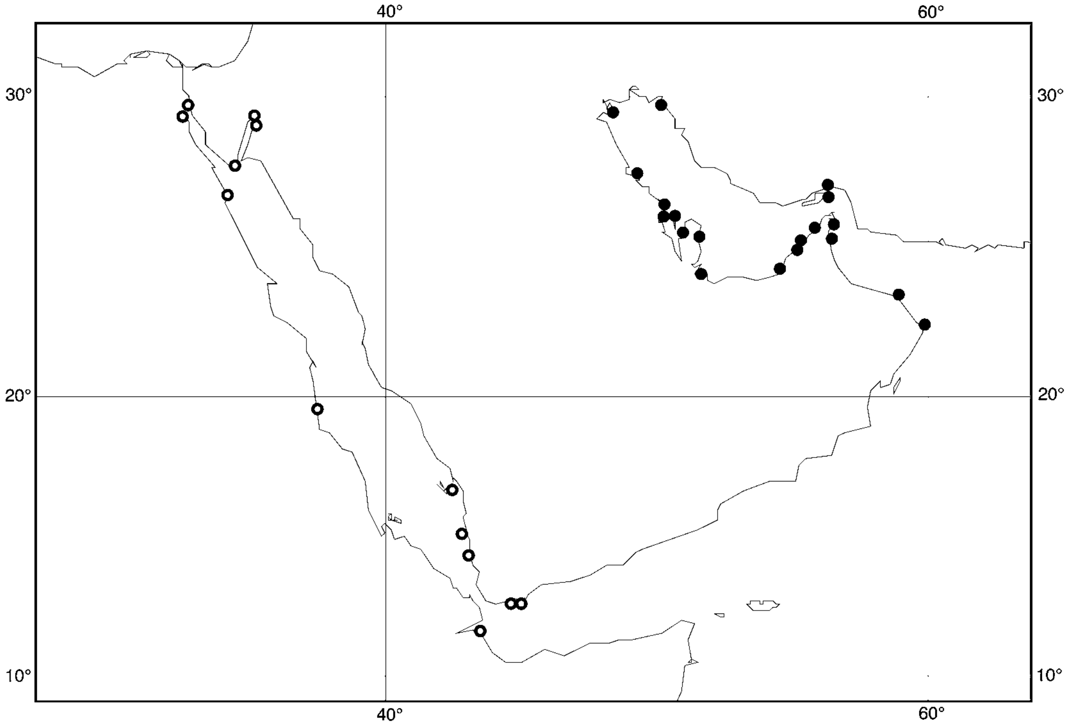

FIGURE 10. Distribution of *Echinolittorina arabica* (solid circles) and *E. marisrubri* (open circles).

Molecular data indicate that *E. arabica* and *E. marisrubri* are sister taxa (Williams & Reid 2004) with a close relationship (K2P genetic distance for COI = 6.24%). The geographical range of *E. arabica* is restricted to the sheltered and relatively eutrophic shores of the Persian and Oman Gulfs. Its absence from the Arabian Sea coast of Oman and Yemen (and perhaps the separation of these sister species) may be attributed to the stronger exposure, or to the summer upwelling that reduces temperatures and imposes a strongly seasonal nutrient regime (Wilson 2000). During low sea-level stands of glacial intervals the Persian Gulf dried out over most of its extent (Sheppard *et al.* 1992), so that recolonization of this part of the range must have taken place during the Holocene. The ability to live on mangroves and algal mats, and to crawl on mud and sand, are highly unusual in the genus *Echinolittorina*, and unknown in other IWP species.

There are no obvious anatomical differences between *E. arabica* and *E. marisrubri*; details of the pallial oviduct, the shape of the penis, the curved rods of the paraspermatozoa, and the 5–6 cusps of the outer marginal teeth, are all similar. However, shells of the two are almost always distinct. Typically, those of *E. arabica* are turbinate with rounded whorls, usually smooth with 16–22 minutely granular threads at and above the periphery (Fig. 8G, I–L), sometimes rugose (Fig. 8E, H) or occasionally with 2–5 rows of small nodules (Fig. 8A–C). In contrast, shells of *E. marisrubri* are more conical with flatter whorls, bearing three rows of nodules and a beaded rib between each row, and brown to black shells are not known (Fig. 11A, G–I). Rare weakly sculptured shells of *E. marisrubri* have only eight beaded ribs at and above the periphery (Fig. 11D). Difficulty may be experienced with some of the most nodulose forms of *E. arabica* (Fig. 8C, D, F) that are similar to moderately nodulose *E. marisrubri* (Fig. 11B, C, E); in the latter there remain fewer ribs (8–13 at and above periphery), and it is the peripheral row of nodules that is largest, whereas in *E. arabica* the shoulder nodules are largest. Although nuclear genetic data are limited, these shell differences support the recognition of two distinct species. Furthermore, there may be an ecological difference, because the range of *E. marisrubri* extends into the oligotrophic northern Red Sea.

In the Persian Gulf and Gulf of Oman *E. arabica* is broadly sympatric with *E. millegrana*. The latter species predominates in more exposed microhabitats and localities, and its shells can resemble those of granulose forms of *E. arabica*. The shell of *E. millegrana* is almost always white, the rounded whorls lack peripheral and shoulder angulation, and the surface is more uniformly granulose (Fig. 72).

Echinolittorina marisrubri **new species**

(Figures 6E, F, 10, 11, 12)

Nodilittorina (Granulilittorina) subnodosa—Rosewater, 1970: 495–496, pl. 383, figs 7–10, pl. 383a (map) (in part, includes *E. subnodosa*, *E. arabica*; not Philippi, 1847).

Nodilittorina (Nodilittorina) subnodosa—Sabelli & Taviani, 1984: 95–100, pl. 1 (radula, penis), figs 3–5 (not Philippi, 1847).

Nodilittorina subnodosa—Sharabati, 1984: pl. 6, figs 4, 4a (not Philippi, 1847). Verbinnen & Dirkx, 2005: 112, fig. 5 (not Philippi, 1847).

Nodilittorina arabica—Dekker & Orlin, 2000: 20 (not El Assal, 1990). Reid, 2002a: 259–281 (in part, includes *E. arabica*; not El Assal, 1990).

Echinolittorina arabica—Williams *et al*., 2003: 83 (in part, includes *E. arabica*; not El Assal, 1990).

Echinolittorina arabica B—Williams & Reid, 2004: 2227–2251.

Types: Holotype BMNH 20030885 (Fig. 11G); 10 dry and 36 alcohol paratypes BMNH 20030886 (Fig. 12A, B, E, F); Port Safaga, Egypt.

Etymology: Latin, from the Red Sea.

Taxonomic history: Together with *E. arabica* this species was included with *E. subnodosa* by Rosewater (1970). Sabelli & Taviani (1984) and Verbinnen & Dirkx (2005) correctly distinguished the two nodulose species in the Red Sea, but misidentified *E. subnodosa* as *N. natalensis* and *E. marisrubri* as *N. subnodosa*. Following the description of *E. arabica* by El Assal (1990), that name was applied to *E. marisrubri* also (Dekker & Orlin 2000; Reid 2002a), and the two were only distinguished with molecular data (Williams & Reid 2004).

Diagnosis: Shell conical; 3 rows of nodules at and above periphery, with 1 beaded rib and smaller threads between; cream, yellow or orange, nodules white; Red Sea. COI: GenBank AJ622979, AJ622980.

Material examined: 22 lots (including 5 penes, 2 sperm samples, 6 pallial oviducts, 3 radulae).

Shell (Fig. 11): Mature shell height 6.7–11.8 mm. Shape high turbinate to conical (H/B = 1.29–1.52; SH = 1.53–1.87); spire whorls flat or slightly rounded, suture distinct; spire profile slightly convex, often concave at apex; periphery of last whorl weakly angled. Columella short, concave, slightly hollowed at base; no eroded parietal area. Sculpture of last whorl: usually 3 rows of pointed nodules at periphery, shoulder and near suture, with single beaded rib (occasionally 2 or more) and 1 or more threads in each interspace, in total 8–13 ribs and threads at and above periphery; posterior row of nodules may be absent; suture and adjacent posterior part of last whorl usually rugose; in smoothest shells (Fig. 11D) 8 subequal granulose ribs at and above periphery and nodules absent; spiral microstriae cover entire surface; base with 3–7 nodulose ribs, 1–2 threads in interspaces. Protoconch 0.29–0.30 mm diameter. Colour: cream, pale yellow, orange or grey; spire whorls brownish; nodules paler or white; sometimes a faint spiral pattern of brown marks between nodules and granules on ribs; aperture brown with pale band at base; columella cream to dark brown.

Animal (Fig. 12): Head pale to dark grey, with or without unpigmented stripe across snout, tentacle pale around eye, with two longitudinal grey to black lines; sides of foot grey to black. Opercular ratio 0.51–0.61. Penis (Fig. 12A–E): filament blade-shaped, tip rounded, base narrowed, filament 0.7–0.8 total length of penis, sperm groove extends to tip; mamilliform gland and glandular disc of similar size, borne on short projection of base; penis unpigmented or slightly pigmented at base. Euspermatozoa 86–100 µm; paraspermatozoa (Fig. 12G, H) oval, with 1–3 rod-pieces 14–27 µm, either slightly projecting and straight with rounded ends, or strongly projecting and slightly curved, cytoplasm filled with large round granules. Pallial oviduct (Fig. 12F): bursa opening at midpoint of straight section and extending back to albumen gland. Spawn a pelagic capsule 250 µm diameter, 150 µm high, cupola-shaped upper side sculptured by 3 concentric rings, containing single ovum 70 µm diameter (Hulings 1986; as *N. subnodosa* but probably this species). Development planktotrophic (Hulings 1986).

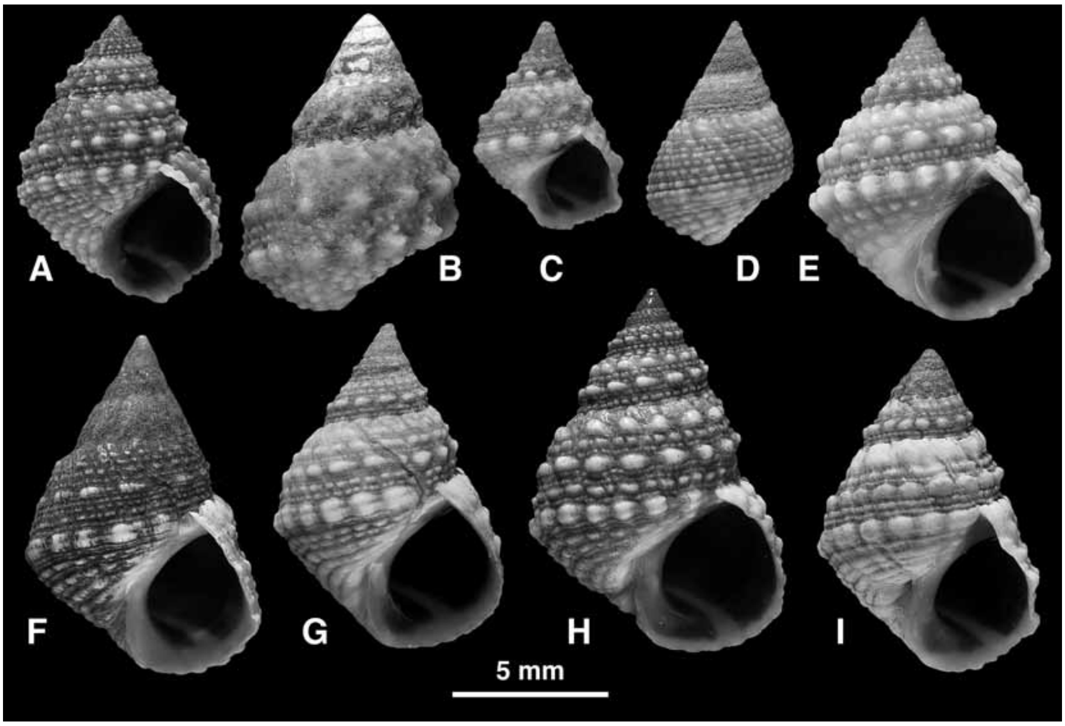

FIGURE 11. *Echinolittorina marisrubri* new species. **A,** Little Aden, Yemen (BMNH 20030882). **B, C,** Safaga, Egypt (NNML). **D,** Eilat, Israel (BMNH 20030883). **E, H,** Red Sea (BMNH 20030884). **F,** paratype (BMNH 20030886). **G,** holotype, Port Safaga, Egypt (BMNH 20030885). **I,** Hind Kadam, Sudan (BMNH 1891.1.31.49).

Radula (Fig. 6E, F): Relative radula length 2.60–3.12. Rachidian: length/width 1.32–1.52; tip of major cusp pointed. Lateral and inner marginal: major cusp on each of similar size, tips rounded. Outer marginal: 5–6 cusps.

Range (Fig. 10): Red Sea and western Gulf of Aden. Range limits: Suez Canal, Egypt (BMNH 1928.3.26.76); Eilat, Israel (BMNH 20030883); Djibouti (MNHN); Conquest Bay, Aden, Yemen (BMNH). The coast of Somalia is poorly sampled, but absence of this species from the Arabian Sea coast east of Aden is believed to be genuine.

Habitat and ecology: Substrate records include rocks on both sandy and muddy beaches, coral limestone cliffs and piers; it is found in the upper eulittoral zone or littoral fringe. In the Gulf of Aqaba this species occupies a zone above that of *E. millegrana*; its rate of water loss has been measured and it survived out of water for 17 days in the field (Hulings 1987, as *N. subnodosa*, but average size = 7.3 mm, so probably this species). Reproduction occurs from June to September in the Gulf of Aqaba (Hulings 1986, as *N. subnodosa*). Most available samples show high frequencies of repaired shell breakage (Fig. 11F, G), probably attributable to attempted predation by crabs.

Remarks: The new species is closely related to its sister taxon *E. arabica* (Williams & Reid 2004; see Remarks on that species for discrimination).

This species is poorly represented in museum collections; it is apparently not rare, but may have been overlooked in favour of the larger and superficially similar *E. subnodosa* with which it is sympatric. Shells of *E. subnodosa* are larger (to 18.7 mm) and broader, also with three rows of nodules, but the rows are widely spaced and the intervening threads are not granulose; there are brown lines connecting the nodules (Fig. 19). Males may be separated by the shape of the penial filament, smooth and strap-shaped in *E. marisrubri* (Fig. 12A–E), but tapering and with annular wrinkles in *E. subnodosa* (Fig. 20A–D). The new species just overlaps with *E. omanensis* at Aden; shells of the latter are grey or blackish with three rows of white nodules, of which those in the anterior row are axially elongate, and the intervening threads are not granulose (Fig. 17). From the western Indian Ocean, *E. natalensis* displays similar features to *E. omanensis*, but is less elongate (Fig. 13).

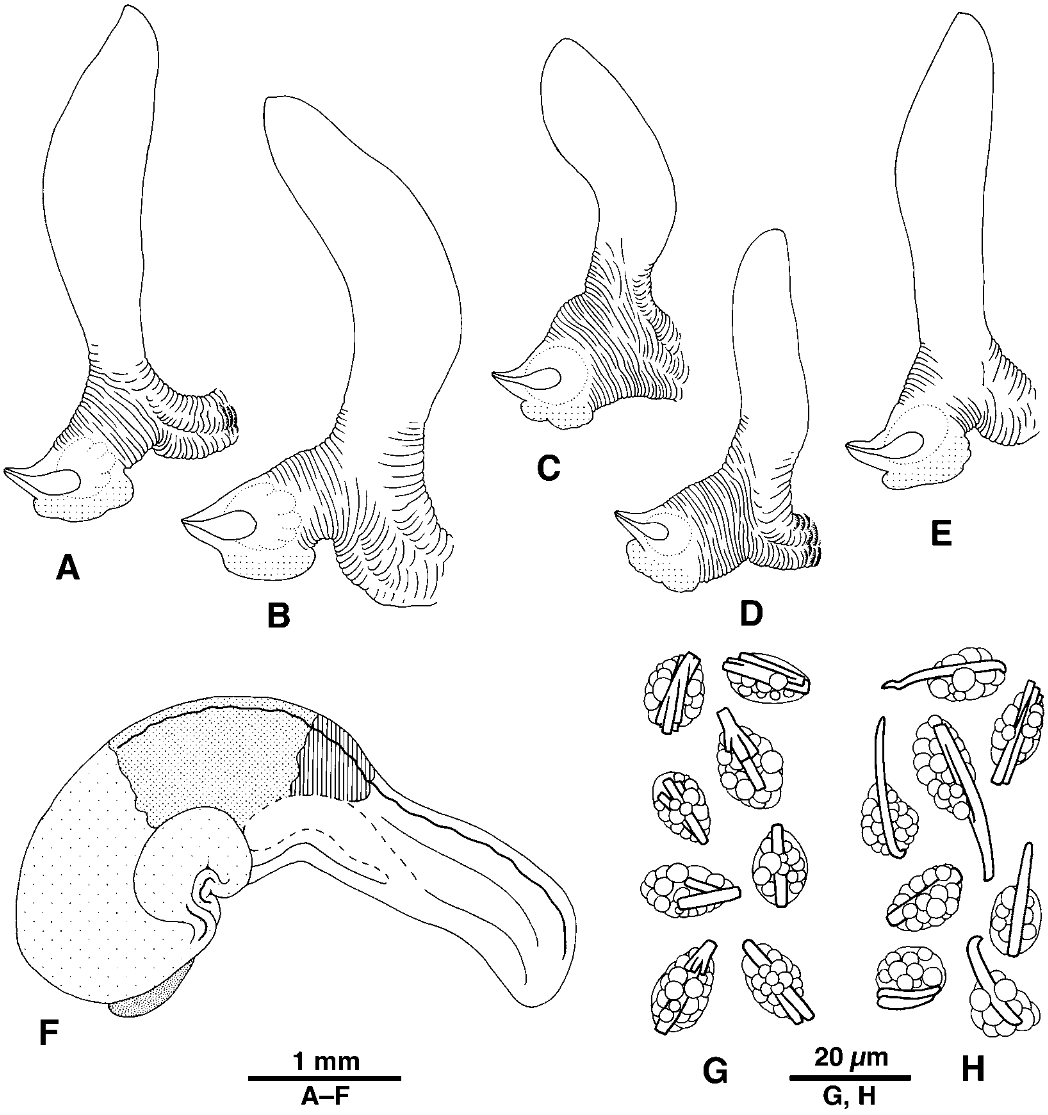

FIGURE 12. *Echinolittorina marisrubri* new species. **A–E,** penes. **F,** pallial oviduct. **G, H,** paraspermatozoa. **A, B, E, F,** paratypes; Port Safaga, Egypt (BMNH 20030886; shell H **A** = 10.7 mm, **B** = 10.4 mm, **E** = 9.3 mm, **F** = 10.3 mm). **C, D, G, H,** Ras Mohammed, Sinai, Egypt (BMNH 20030887; shell H **C** = 9.6 mm, **D** = 10.2 mm). Shading conventions as in Figure 3.

There have been few observations of the habitat of this species. It occurs throughout the Red Sea, and therefore in both the oligotrophic northern part and in the more nutrient-rich south that is under the influence of water from the Gulf of Aden (Sheppard 2000). Absence from the Arabian Sea coast of Arabia might be due to the monsoon-driven summer upwelling of cool water (Wilson 2000).

During glacial low sea-level stands the water depth in the shallow Bab el Mandab seaway at the mouth of the Red Sea was reduced to a mere 15 m. Evaporation then exceeded inflow from the Gulf of Aden so the Red Sea became hypersaline; salinities in the central and northern parts are estimated to have exceeded 50 ‰ (Siddall *et al*. 2003). Most marine organisms would not have been able to survive such extremes and the most recent recolonization took place following the last glaciation, about 15000 years ago (Sheppard *et al*. 1992). It follows that species now endemic to the Red Sea, such as *E. marisrubri*, must either have survived in refugia in the very south of the Red Sea or in the Gulf of Aden, or otherwise must have originated very recently. The age of separation of *E. marisrubri* and *E. arabica* can be estimated as 1.3–2.4 Ma (COI K2P distance = 6.24% and using evolutionary rates from Williams & Reid 2004). The present distribution of *E. marisrubri* (Fig. 10) suggests that only a very small refugium may have existed outside the mouth of the Red Sea. However, during glacial intervals the strength of the upwelling along the southern coast of Arabia was much reduced (Sheppard *et al*. 1992) and the distribution of *E. marisrubri* may then have been more extensive in the Gulf of Aden.

The *Echinolittorina natalensis* group

This group consists of *E. natalensis*, *E. omanensis* n.sp. and *E. subnodosa* from the western Indian Ocean, Arabia and Red Sea respectively, and a fourth species *E. pascua* from the distant locality of the southeastern extremity of Polynesia. All share similar nodulose shells, resembling those of the *E. malaccana* group with which, however, they are never sympatric. The most notable difference in the shells of the two groups is that those of the *E. natalensis* group (except *E. omanensis*) are slightly broader and (except *E. pascua*) usually bear three rows of nodules on the final whorl; shells of the *E. malaccana* group are usually more tall-spired and almost always bear only two rows of nodules. Anatomically, the *E. natalensis* group shares a tapering, wrinkled penial filament, short paraspermatozoan rod-pieces, and a single long bursa opening at about one third to half of the length of the straight section of the pallial oviduct; these characters are distinct from those of the *E. malaccana* group. Sequences of two mitochondrial genes support the monophyly of these four species (Williams & Reid 2004).

Echinolittorina natalensis (Krauss in Philippi, 1847)

(Figures 13, 14, 15A–D, 16)

Litorina natalensis Krauss in Philippi, 1847a: vol. 2: 160, *Litorina* pl. 3, fig. 4 (Ora Natal in Africa australi [coast of Natal, South Africa]; lectotype (Janus 1961: pl. 3, figs 7, 8) SMNS ZI0050942 (Fig. 13M), seen; 13 paralectotypes SMNS ZI0050943, not seen; 17 probable paralectotypes SMNH 4971; 2 additional ex Krauss lots SMF (Herbert & Warén 1999), not seen; additional ex Krauss material possibly in NNML (van Bruggen 1992), not seen). Krauss, 1848: 102. Weinkauff, 1882: 92–93, pl. 13, figs 6, 7.

Tectarius natalensis—H. Adams & A. Adams, 1854: 315. Bartsch, 1915: 120. Dautzenberg, 1932: 61. Barnard, 1963: 191, fig. 37b (radula), 37c. Kensley, 1973: 66, fig. 202.

Littorina natalensis—Reeve, 1858: sp. 102, pl. 18, fig. 102a, b.

Littorina (Nodilittorina) natalensis—von Martens, 1897: 205.

Tectarius (Nodilittorina) natalensis—Janus, 1961: 7, pl. 3, figs 7, 8.

Nodilittorina (Nodilittorina) natalensis—Rosewater, 1970: 489–490, pl. 376, figs 1–6, pl. 377 (map) (in part, includes *E. omanensis*). Kilburn, 1972: 405. Reid, 1989a: 100.

Nodilittorina natalensis—Kilburn & Rippey, 1982: 51, pl. 10, fig. 5. Potter & Schleyer, 1991: 1–15, pl. 2.5 (radula). Reid, 2002a: 259–281 (in part, includes *E. omanensis*).

Echinolittorina natalensis—Williams *et al*., 2003: 83 (in part, includes *E. omanensis*). Williams & Reid, 2004: 2227–2251.

Litorina nodosa—Weinkauff, 1883: 226 (in part, includes *E. australis*, *E. subnodosa*, *E. malaccana* group; not Gray, 1839 = *E. australis*).

Tectarius nodosus—Tryon, 1887: 259, pl. 47, fig. 67 (in part, includes *E. australis*, *E. subnodosa*, *E. miliaris*; not Gray, 1839).

Nodilittorina nodulosa—Fischer, 1969: 119–129 (in part, includes *N. pyramidalis*, *E. omanensis*, *E. malaccana*, *E. austrotrochoides*, *E. cecillei*, *E. marquesensis*, *E. wallaceana*; not Gmelin, 1791 = *E. malaccana* group or *E. pascua*). Fischer, 1971: 31–32 (in part, includes *E. omanensis*, *E. malaccana*; not Gmelin, 1791).

Littorina miliaris—Nevill, 1885: 154 (in part, includes *E. radiata*; not Quoy & Gaimard, 1833 = *E. miliaris*).

Tectarius malaccanus—Dautzenberg, 1923: 49 (not Philippi, 1847). Dautzenberg, 1929: 495–496 (not Philippi, 1847). Dautzenberg, 1932: 61 (not Philippi, 1847).

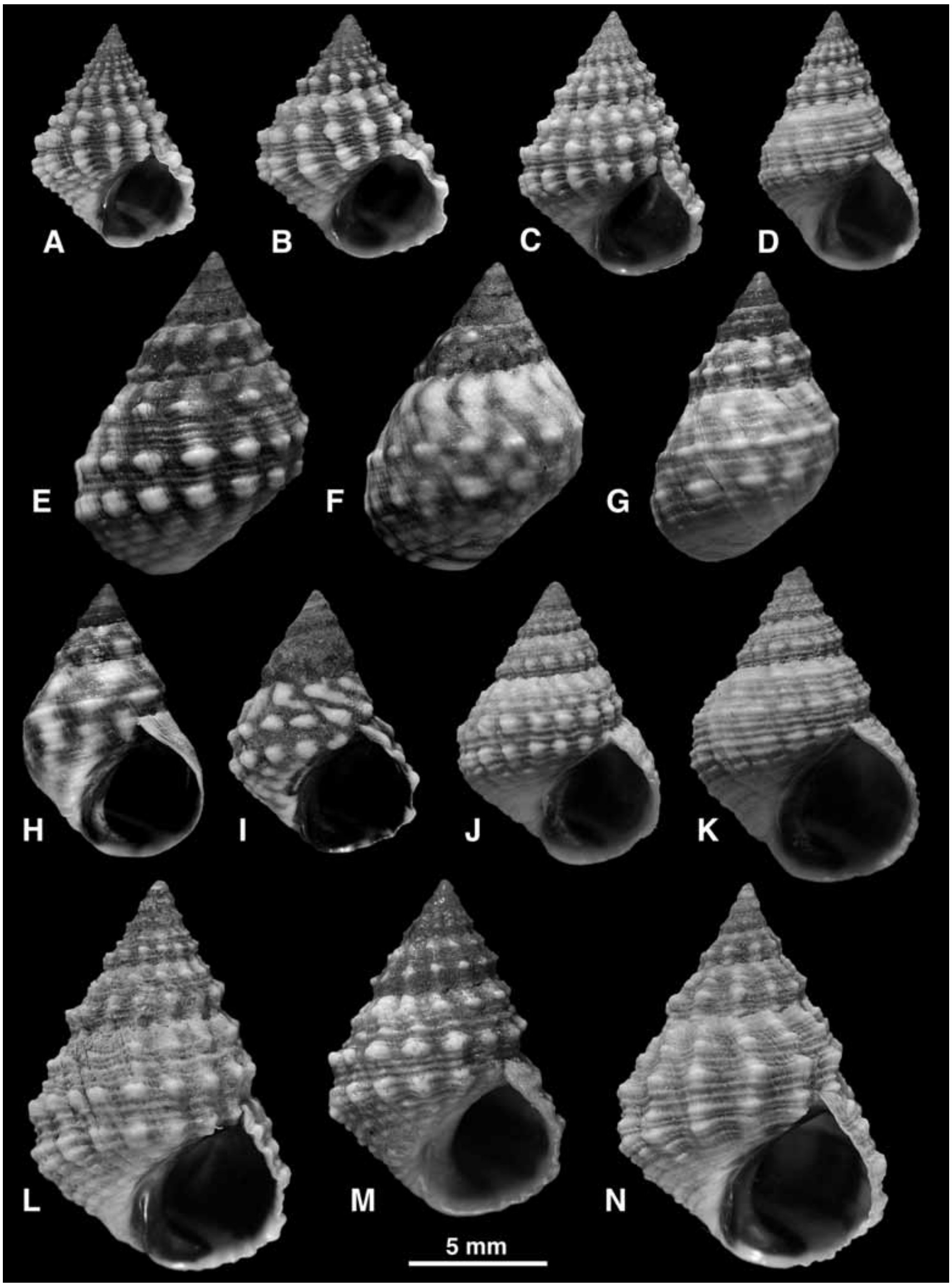

FIGURE 13. *Echinolittorina natalensis*. **A–C,** Tiwi Beach, Kenya (BMNH 20040209). **D, J, K,** North Pier, Durban, South Africa (BMNH 20040210). **E, F,** Ankarena, Île Ste Marie, Madagascar (BMNH 20030679). **G, H,** no locality [probably eastern Madagascar] (MNHN). **I, L, N,** Libanona Beach, Tolagnaro, Madagascar (BMNH 20030691). **M,** *Litorina natalensis* Krauss in Philippi, 1847, lectotype, Natal, South Africa (SMNS ZI.0050942).

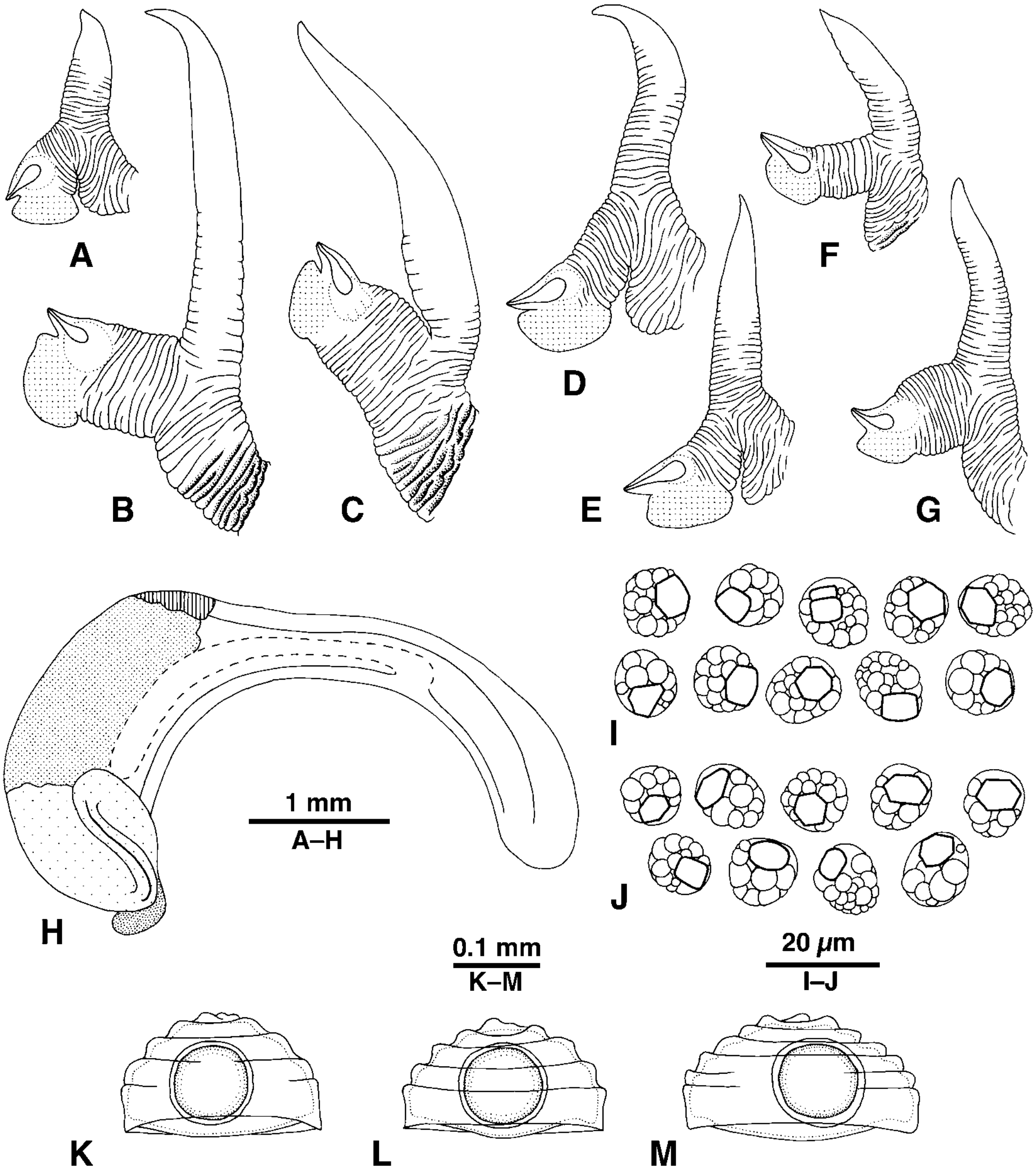

FIGURE 14. *Echinolittorina natalensis*. **A–G,** penes. **H,** pallial oviduct. **I, J,** paraspermatozoa. **K–M,** pelagic egg capsules. **A,** Amanzimtoti, Kwazulu-Natal, South Africa (BMNH 20040211; shell H = 6.3 mm). **B, C,** Ankarena, Île Ste Marie, Madagascar (BMNH 20030679; shell H **B** = 10.8 mm, **C** = 10.5 mm). **D, E, K–M,** North Pier, Durban, South Africa (BMNH 20040210; shell H **D** = 10.0 mm, **E** = 9.4 mm). **F, I, J,** Oysterbay, Dar-es-Salaam, Tanzania (BMNH 20040212; shell H = 6.5 mm). **G, H,** Libanona Beach, Tolagnaro, Madagascar (BMNH 20030691; shell H **G** = 7.8 mm, **H** = 10.0 mm). Shading conventions as in Figure 3.

Taxonomic history: Despite its superficial similarity to nodulose species in other parts of the world, this species has had a relatively uncomplicated taxonomic history and most authors have accepted it as distinct since its description. Weinkauff (1883; followed by Tryon 1887) considered it conspecific with the larger *E. subnodosa* from the Red Sea, and united these two under the name *Litorina nodosa*, together with nodulose forms of *E. australis* from Australia. These three taxa were clearly distinguished by Rosewater (1970). Until now, nodulose shells from southern Arabia have generally been included with *E. natalensis* (Rosewater 1970; Mienis 1973; Bosch *et al.* 1995; Reid 2002a), but these are here described as *E. omanensis*. Surprisingly, no authors appear to have synonymized *E. natalensis* with members of the *E. malaccana* group and confusion between them has been minimal. It is not clear why Dautzenberg (1923, 1929, 1932) separated *T. natalensis* and *T.*

malaccanus from Madagascar; the only nodulose species known to occur there is *E. natalensis*. Nevertheless, Fischer (1969, 1971) continued to maintain that *N. nodulosa* (= *E. malaccana* group) occurred in the western Indian Ocean, based on Dautzenberg (1929) and a misidentification of the Arabian *E. omanensis*.

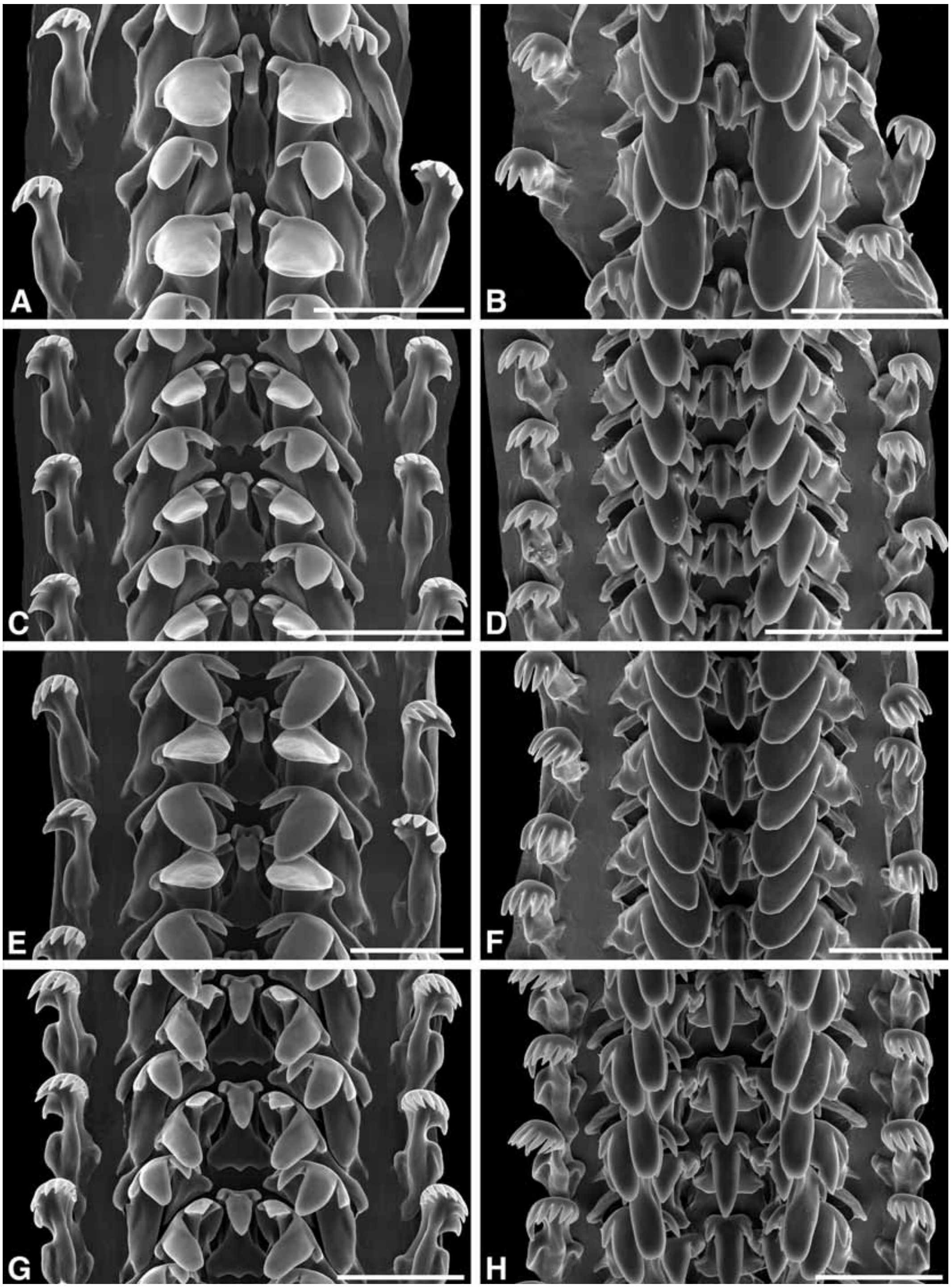

FIGURE 15. Radulae of *Echinolittorina* species (two views of each radula, flat and at 45°). **A–D,** *E. natalensis*. **A, B,** Libanona Beach, Tolagnaro, Madagascar (BMNH 20030691; shell H = 8.9 mm). **C, D,** Tiwi Beach, Kenya (BMNH 20040209; shell H = 9.0 mm). **E, F,** *E. subnodosa*; El-Qalawi, 30.5 km S Port Safaga, Egypt (BMNH 20040229; shell H = 14.2 mm). **G, H,** *E. pascua*; Hanga Tee, Easter I. (BMNH 20040232; shell H = 14.0 mm). Scale bars = 50 µm.

Diagnosis: Shell conical, 3 rows of pointed nodules on last whorl, peripheral nodules crossed by 2 spiral ribs; 15–24 sharp spiral threads on last whorl (including base); grey, brown or black with white nodules. South and East Africa, Madagascar. COI: GenBank AJ623019, AJ623020.

Material examined: 60 lots (including 17 penes, 3 sperm samples; 12 pallial oviducts, 1 sample of egg capsules, 4 radulae).

Shell (Fig. 13): Mature shell height 6.3–15.8 mm. Shape conical (H/B = 1.26–1.66; SH = 1.56–1.98); spire whorls lightly rounded, suture distinct; spire profile almost straight, slightly concave at apex; periphery of last whorl weakly angled. Columella short, concave, hollowed at base; small eroded parietal area. Sculpture of last whorl: 3 rows of pointed nodules at periphery, mid-whorl and shoulder, aligned to form 12–18 axial series; entire surface with sharp spiral threads, 10–15 at and above periphery, and microstriae; peripheral nodules crossed by 2 spiral threads; base with 5–9 nodulose threads; in strongly sculptured shells (Fig. 13A) the axially aligned nodules form varix-like ridges; in smooth shells (Fig. 13F–H) the nodules become obsolete on last whorl, remaining only as 1–3 slightly raised ribs. Protoconch 0.23–0.25 mm diameter, 2.3–2.4 whorls. Colour: purple-brown (fading to grey-pink), orange-brown at apex, nodules white; in darkest shells an irregular axial pattern of black and grey stripes (Fig. 13I); in smooth shells the positions of the 3 rows of nodules may be marked by bands of black and white spots (Fig. 13F); aperture brown to black with pale band at base; columella purple-brown to black.

Animal (Fig. 14): Head black, no unpigmented stripe across snout, tentacle pale around eye and inner side of base, with two longitudinal grey to black lines, usually partly fused and extending to half tentacle length, but sometimes extending full length, or tentacle black with unpigmented tip; sides of foot mottled black or all black. Opercular ratio 0.49–0.58. Penis (Fig. 14A–G): filament gradually tapering to pointed tip, with fine annular wrinkles for most of its length, filament 0.6–0.7 total length of penis, sperm groove extends to tip; mamilliform gland equal to or smaller than glandular disc, borne together on projection of base; penis unpigmented or slightly pigmented at base. Euspermatozoa 114–121 µm; paraspermatozoa (Fig. 14I, J) spherical to oval, 10–14 µm diameter, filled with large round granules, containing single short rectangular rod-piece, hexagonal in section and not projecting from cell. Pallial oviduct (Fig. 14H): bursa opening at one third to one half length of straight section (from anterior) and extending back to albumen gland. Spawn (Fig. 14K–M): an asymmetrically biconvex pelagic capsule 220–285 µm diameter with broad peripheral rim on which faint diagonal striations can sometimes be seen, cupola-shaped upper side sculptured by 5–6 spiral or concentric rings (rings occasionally absent in aberrant capsules), containing single ovum 88–100 µm diameter. Development predicted to be planktotrophic.

Radula (Fig. 15A–D): Relative radula length 2.67–8.0 (mean 4.55, Potter & Schleyer 1991). Rachidian: length/width 1.89–3.85, sometimes narrow (Fig. 15A); tip of major cusp pointed. Lateral and inner marginal: tips of major cusps rounded; major cusp of lateral slightly (Fig. 15C, D) or considerably (Fig. 15A, B) larger than that of inner marginal; outermost cusp of inner marginal may be absent (Fig. 15A). Outer marginal: 5–6 cusps.

Range (Fig. 16): Southwestern Indian Ocean from South Africa to Kenya, Madagascar and Seychelles. Range limits: Cove Rock, East London, South Africa (Kilburn 1972); Umngazana Head, South Africa (BMNH); Bazaruto I., Mozambique (NM J7152); Wimbi, Pemba, Mozambique (BMNH 20060279); Oysterbay, Dar es Salaam, Tanzania (BMNH 20060284); Datamu, 20 miles N Mombasa, Kenya (BMNH); Picard, Aldabra (BMNH); Mahé, Seychelles (IRSNB); Baie de Diego Suarez, Madagascar (IRSNB); Tolagnaro, Madagascar (BMNH 20030691); Toliara, Madagascar (IRSNB); Europa Atoll (IRSNB). The species is apparently rare in the Seychelles; only a single shell has been recorded and its occurrence requires confirmation. It does occur on the atolls of Europa and Aldabra, but was not recorded in a survey of the littorinids of the Comores (Warmoes *et al.* 1990). Occurrence between Bazaruto in southern Mozambique and Dar es Salaam, and in western Madagascar, is apparently sporadic. The southern limit is East London, where a single shell was recorded by Kilburn (1972).

Habitat and ecology: This species occurs on a variety of substrates, including coral limestone, beachrock, sandstone, conglomerate, granite and concrete. It is abundant in the littoral fringe on shores of moderate to high exposure. In Natal *E. natalensis* occupies a zone between *Littoraria glabrata* in the littoral fringe and *Afrolittorina africana* lower on the shore, and prefers eroded sandstone (Eyre & Stephenson 1938; Kilburn 1972); it occurs mainly in crevices, and reaches densities of 2000 per m^2 (Potter 1987). At Inhaca Island it is found at and above MHWS on calcareous sandstone, in a zone between the same two sympatric littorinids, at densities of up to to 1000 per m^2, and only on exposed shores (Kalk 1958). At Toliara, Madagascar, it is found on eroded limestone cliffs, but not on concrete (Plante 1964; as *Tectarius malaccanus*). Translocation, diet and competition for food have been studied by Potter (1987) and Potter & Schleyer (1991).

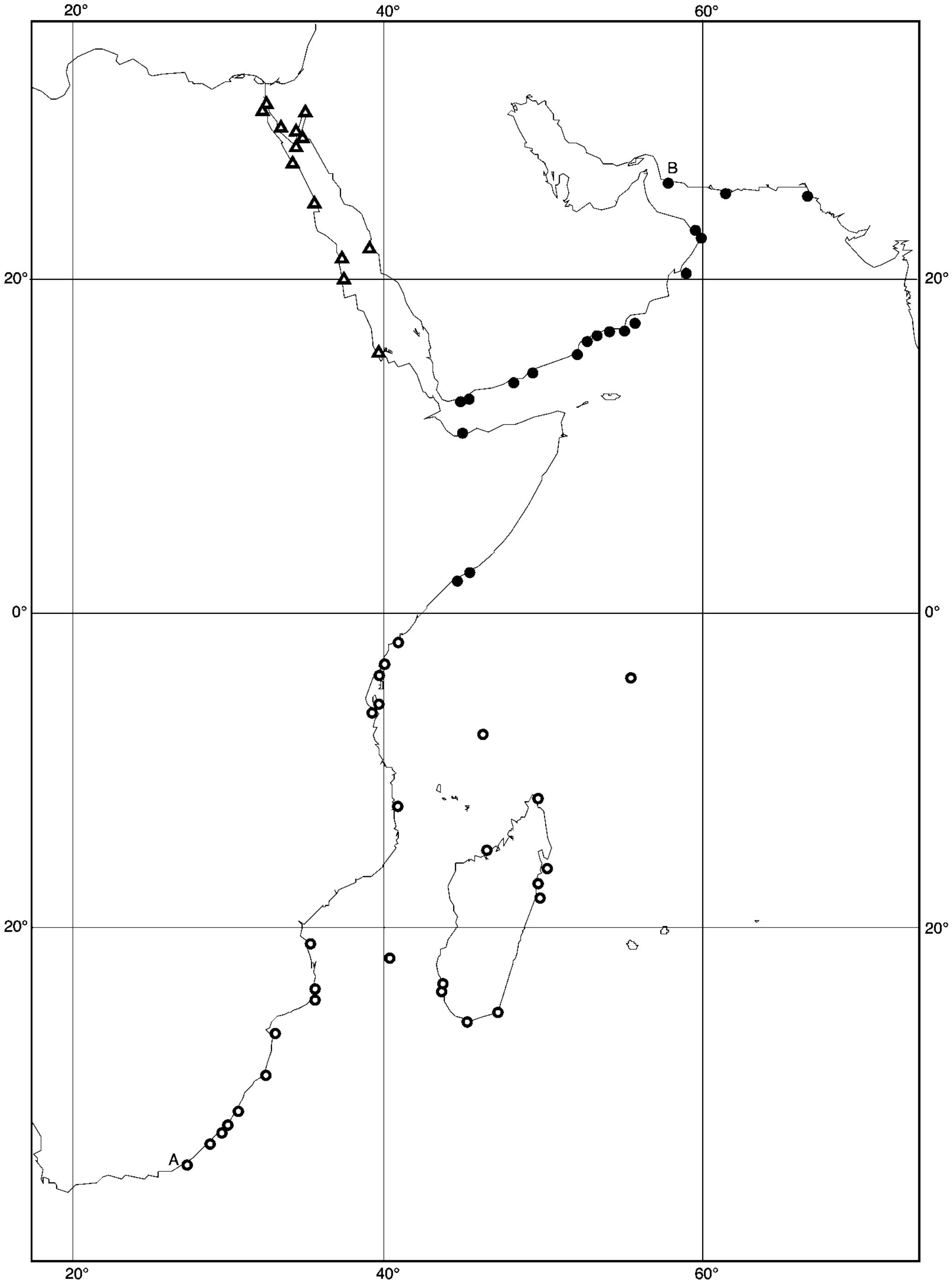

FIGURE 16. Distribution of *Echinolittorina natalensis* (open circles), *E. omanensis* (solid circles) and *E. subnodosa* (open triangles). Literature records: A, Kilburn (1972); B, Melvill & Standen (1901).

Remarks: Although found mainly on the continental shores of East Africa and Madagascar, this species can be classed as oceanic in character, because it occurs in areas of low primary productivity (Rutgers University Primary Productivity Study) and on shores that are often exposed to strong wave action. To the south, its distribution in South Africa is extended by the warm Agulhas Current and is presumably ultimately limited by low temperatures. Elsewhere, the lack of records from central Mozambique, the eastern and western coasts of Madagascar, and to the north of the records in Kenya, can be ascribed to lack of suitable habitat on these predominantly sedimentary coastlines (Myers & Whittington 2000; Cooke et al. 2000; Carbone & Accordi 2000). The westward-flowing South Equatorial Current may prevent the colonization of the Mascarene Islands.

The small shell with three rows of nodules is usually easily recognized and unlikely to be confused with any other within its area of distribution. However, the nodules occasionally become weak on the last whorl. A distinctive regional form occurs in western Madagascar, from Ile Sainte Marie to Tolagnaro, in which the spire is normal and nodulose, but the last whorl may be macroscopically smooth (retaining spiral threads), with a black-and-white striped or marbled pattern (Fig. 13F–I). These smooth shells superficially resemble *E. biangulata* from the eastern Indian Ocean (Fig. 44) and *E. tricincta* from the western Pacific (Fig. 48). However, they occur together with typically nodulose shells and intermediates, and no anatomical differences can be detected. Precise dates of collection are not available for the studied museum specimens of this smooth form, but most were collected in the late nineteenth and early twentieth century. Recent collecting in Ile Sainte Marie, Tamatave and Tolagnaro (pers. obs. 2003) revealed no entirely smooth shells among abundant normal forms, and only a low frequency (less than 5%) of moderately smooth types (Fig. 13F). There may also be an ecophenotypic component to sculptural variation, because shells from limestone substrates are the most strongly sculptured (Fig. 13A–C). On a sea wall in Dar es Salaam strongly sculptured shells (similar to those in Fig. 13A–C) were found on blocks of coral limestone, whereas shells on an immediately adjacent stretch of concrete wall were more smooth (resembling those in Fig. 13D, G; pers. obs. 2006).

This species shows more striking radular variation than any of its IWP congeners. Of the four radulae examined, only one from Tolagnaro, Madagascar, was found with extreme reduction of the rachidian and enlargement of the lateral tooth cusps (Fig. 15A, B) and this occurred on a sandstone substrate together with an individual with a radula of normal type (similar to that illustrated in Fig. 15C, D from limestone in Kenya). Similar variation occurs in *E. australis*, and the possibility of ecophenotypic plasticity deserves investigation (see Discussion).

There are no obvious anatomical differences between the three allopatric species *E. natalensis*, *E. omanensis* and *E. subnodosa*, although shells of each are almost always distinctive. Molecular evidence supports their recognition as separate species, with *E. natalensis* sister to the other two (Williams & Reid 2004). Of the three, those most similar in shell characters are the nodulose forms of *E. natalensis* and *E. omanensis*. *Echinolittorina omanensis* (Fig. 17) is a narrower shell; there are usually two rows of rounded nodules on the last whorl (three rows of more pointed ‘prickly’ nodules in *E. natalensis*); the nodules in the peripheral row are axially elongate and crossed by three or four spiral ribs (two spiral threads on peripheral nodules of *E. natalensis*); the base is rarely nodulose; the spiral sculpture is of 10–16 spiral ribs on the last whorl (15–24 sharp spiral threads in *E. natalensis*). Confusion between *E. natalensis* and *E. subnodosa* is less likely; the latter (Fig. 19) has a larger shell, concave spire profile and three widely-spaced rows of pointed nodules.

***Echinolittorina omanensis* new species**

(Figures 6G, H, 16, 17, 18)

Littorina (Tectus) trochoides—Nevill, 1885: 156–157 (in part, includes *E. marquesensis*, *E. malaccana*; not Gray, 1839 = *E. pascua*).

Nodilittorina (Nodilittorina) trochoides—Reid, 1992: 202 (in part, includes *E. malaccana*, *E. austrotrochoides*, *E. cecil-*

lei; not Gray, 1839).

Tectarius nodulosus—Melvill & Standen, 1901: 364 (in part, includes *E. malaccana*; not Gmelin, 1791 = *E. malaccana* group or *E. pascua*).

Nodilittorina nodulosa—Fischer, 1969: 119–129 (in part, includes *N. pyramidalis*, *E. natalensis*, *E. malaccana*, *E. austrotrochoides*, *E. cecillei*, *E. marquesensis*, *E. wallaceana*; not Gmelin, 1791). Fischer, 1971: 31–32 (in part, includes *E. natalensis*, *E. malaccana*; not Gmelin, 1791).

Nodilittorina (Nodilittorina) natalensis—Rosewater, 1970: 489–490, pl. 377 (map) (in part, includes *E. natalensis*; not Krauss in Philippi, 1847). Mienis, 1973: 59–61, fig. 3 (not Krauss in Philippi, 1847). Bosch *et al*., 1995: 46, fig. 117 (not Krauss in Philippi, 1847).

Nodilittorina natalensis—Reid, 2002a: 259–281 (in part, includes *E. natalensis*; not Krauss in Philippi, 1847).

Echinolittorina natalensis—Williams *et al*., 2003: 83 (in part, includes *E. natalensis*; not Krauss in Philippi, 1847).

Echinolittorina subnodosa B—Williams & Reid, 2004: 2227–2251.

Types: Holotype BMNH 20040218 (Fig. 17J); 1 dry paratype BMNH 20040219; 6 alcohol paratypes BMNH 20040220; Wadi Sayq, Jabal Qamr, Dhofar, Oman, 16°44’N, 53°20’E.

Etymology: Latin, from Oman.

Taxonomic history: Nodulose shells from southern Arabia and Somalia have sometimes been identified as *E. natalensis* in the past (Rosewater 1970; Mienis 1973; Bosch *et al*. 1995), probably on the basis of geographical proximity. Nevertheless, the narrow shells, often with two rows of nodules, more closely resemble those of the *E. malaccana* group, with which they have also been classified (Nevill 1885; Melvill & Standen 1901; Fischer 1969, 1971; Reid 1992). They were recognized as distinct following molecular study (Williams & Reid 2004).

Diagnosis: Shell high-conical, 2–3 rows of rounded nodules on last whorl, peripheral nodules axially elongated and crossed by 3–4 spiral ribs; 10–16 spiral ribs on last whorl (including base); grey or black with white nodules. Somalia, southern Arabia, Pakistan. COI: GenBank AJ623059, AJ623060.

Material examined: 38 lots (including 15 penes, 1 sperm sample, 5 pallial oviducts, 2 radulae).

Shell (Fig. 17): Mature shell height 4.3–17.2 mm. Shape conical to high-conical (H/B = 1.36–1.75; SH = 1.61–2.27); spire whorls lightly rounded, suture distinct; spire profile almost straight; periphery of last whorl weakly angled. Columella short, concave, hollowed at base; small eroded parietal area. Sculpture of last whorl: 2 rows of rounded nodules at periphery and mid-whorl, nodules rarely pointed (Fig. 17A), often an additional row of smaller nodules at shoulder (Fig. 17A, B, E–H, K, L); nodules aligned to form 9–17 axial series; entire surface with spiral ribs, 7–10 at and above periphery, and microstriae; peripheral nodules axially elongated and crossed by 3–4 ribs; base with 4–6 ribs, occasionally with weak nodules; rarely the nodules on last whorl become weak (Fig. 17I). Protoconch approximately 0.25 mm diameter. Colour: black to purple-brown (fading to blue-grey), nodules white; aperture brown to black with pale band at base; columella purple-brown.

Animal (Fig. 18): Head black, no unpigmented stripe across snout, tentacle pale around eye and sometimes also inner side of base, with two longitudinal grey to black lines, usually partly fused and extending half to full length of tentacle; sides of foot grey to black. Opercular ratio 0.43–0.54. Penis (Fig. 18A–H): filament gradually tapering to pointed tip, with fine annular wrinkles for most of its length, filament 0.5–0.6 total length of penis, sperm groove extends to tip; mamilliform gland about equal to glandular disc, borne together on projection of base; penis unpigmented or slightly pigmented at base. Euspermatozoa not known; paraspermatozoa spherical to oval, 10–14 µm diameter, filled with large round granules, containing single short rectangular rod-piece, hexagonal in section and not projecting from cell. Pallial oviduct (Fig. 18I): bursa opening at half length of straight section and extending back to albumen gland. Development predicted to be planktotrophic.

Radula (Fig. 6G, H): Relative radula length 2.45–9.51. Rachidian: length/width 1.41–1.69; tip of major cusp pointed. Lateral and inner marginal: tips of major cusps rounded; major cusp of lateral slightly larger than that of inner marginal. Outer marginal: 7–8 cusps.

Range (Fig. 16): Somalia, Gulf of Aden, northwestern Arabian Sea to Pakistan. Range limits: Merka, Somalia (HUJ 30002); Mogadishu, Somalia (HUJ 30005, 30967); Berbera, Somalia (BMNH); Little Aden, Yemen (BMNH); Sur, Oman (BMNH); Ras al-Junayz, Ras al-Hadd, Oman (BMNH); Jask, Iran (Melvill & Standen 1901); Ramin, Iran (ZMA); Karachi, Pakistan (BMNH 20040215). The absence of records from most of the coast of Somalia is explained by the inaccessibility of the region. The absence from the southern Gulf of Oman is probably real (there are 10 records of *E. arabica* from Muscat and further north on the coat of Oman, but none of *E. omanensis*), as is that from the Red Sea (there are three records of *E. marisrubri* from the west coast of Yemen).

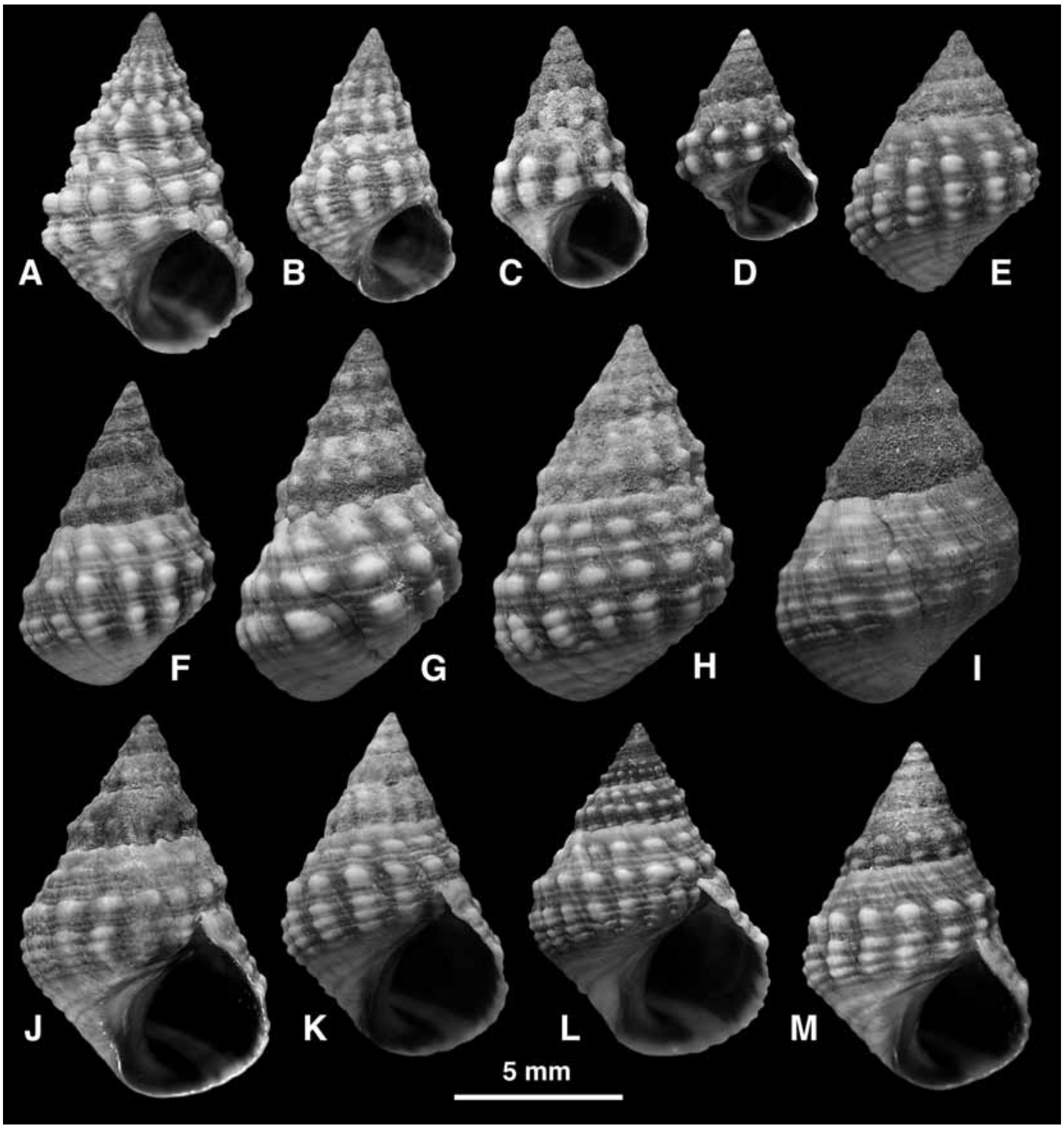

FIGURE 17. *Echinolittorina omanensis* new species. **A, B,** Merca, Somalia (HUJ 30002). **C, F, M,** Mirbat, Dhofar, Oman (BMNH 20040213). **D,** Mughsayl I., Dhofar, Oman (BMNH 20040214). **E,** Karachi, Pakistan (BMNH 20040215). **G, H,** W Mughsayl I., Dhofar, Oman (BMNH 20040217). **I,** Karachi, Pakistan (BMNH 20040216). **J,** holotype, Wadi Sayq, Jabal Qamr, Dhofar, Oman (BMNH 20040218). **K, L,** Mukalla, Aden, Yemen (BMNH 20040221).

Habitat: This species occurs in the littoral fringe on rocks and cliffs, on sheltered and more commonly on wave-exposed coasts (G.R. Feulner pers. comm.). It has been recorded on limestone, basalt and concrete sea walls.

Remarks: The geographical distribution of this species corresponds closely with the area of seasonally high primary productivity associated with the upwelling induced by the southwestern monsoon of the boreal summer (Wilson 2000; Wilson & Klaus 2000; Rutgers University Primary Productivity Study). This coastline is also one of generally high wave exposure. Further south than Mogadishu and Merka (the southernmost records of the species) the coast is protected by coral reefs (Carbone & Accordi 2000). Similarly, the coast of the Gulf of Oman between Ras al-Hadd and Muscat supports reefs and mangroves, while further west a sandy beach stretches to Fujairah (Wilson 2000). The species is present on the exposed, nutrient-rich Makran Coast of Iran and as far east as Karachi, but its eastward distribution is then limited by the sedimentary or estuarine conditions of the Gulfs of Kutch and Khambha, where no *Echinolittorina* species have been reported. *Echinolittorina omanensis* has not been recorded from the Red Sea, despite known inflow from the Gulf of Aden and consequent high summer nutrient levels in the southernmost Red Sea (Sheppard 2000).

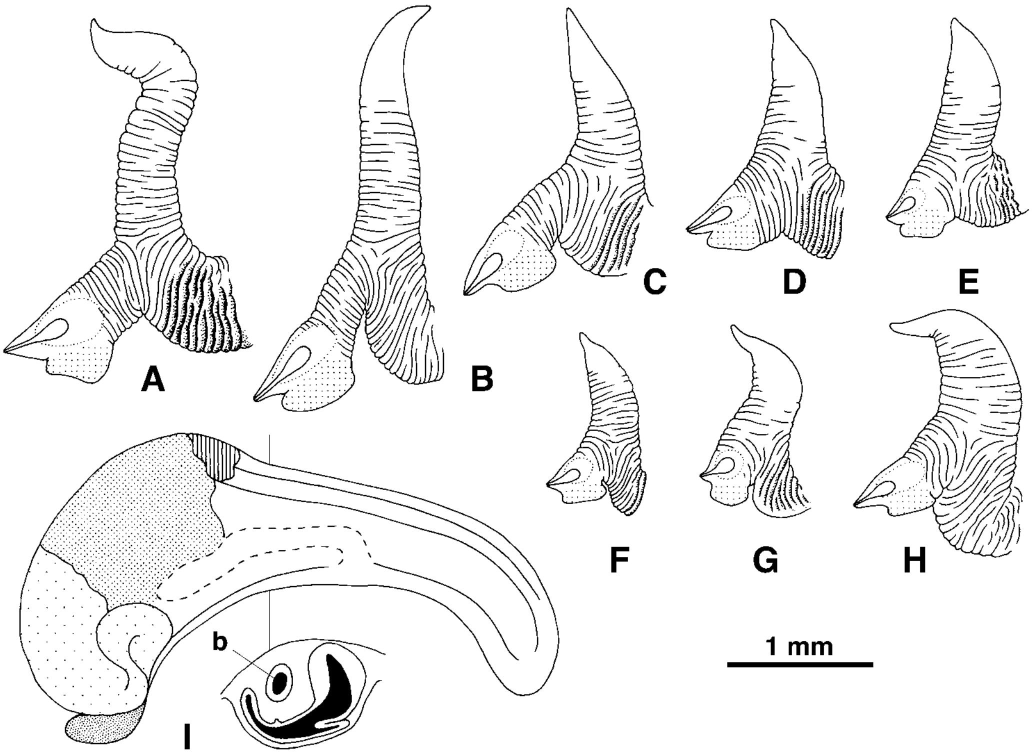

FIGURE 18. *Echinolittorina omanensis* new species. **A–H,** penes. **I,** pallial oviduct, with transverse section. **A, B,** Mukalla, Aden, Yemen (BMNH 20040221; shell H **A** = 10.7 mm, **B** = 10.3 mm). **C, D,** Wadi Kharfot (Wadi Sayq), 10 km W Rahkyut, Dhofar, Oman (ZMA; shell H **C** = 8.7 mm, **D** = 8.6 mm). **E, G,** Wadi Haart, near Salalah, Dhofar, Oman (BMNH 20040222; shell H **E** = 7.0 mm, **G** = 7.6 mm). **F,** Monument Point, N Masirah I., Oman (BMNH 20040223; shell H 5.1 mm). **H, I,** W Mughsayl I., Dhofar, Oman (BMNH 20040217; shell H **H** = 7.5 mm, **I** = 11.4 mm). Abbreviation: b, copulatory bursa. Shading conventions as in Figure 3.

The coastlines of Yemen and Oman have been relatively well collected (material in BMNH, ZMA; G.R. Feulner pers. comm.) and, consequently, it is clear that between Aden and Ras al-Hadd *E. omanensis* is the only abundant species of *Echinolittorina*. Also occurring on this coastline is *E. millegrana* which, while common at Aden and Ras al-Hadd, is scarce at intervening localities; *E. millegrana* occupies a slightly lower tidal level. Predatory intertidal crabs are common on the Arabian coastline and may restrict the microdistribution of *E. omanensis* and its congeners (G.R. Feulner pers. comm.); repaired shell breakages that may have been caused by unsuccessful attacks by crabs are frequent in some samples.

Echinolittorina omanensis overlaps barely or not at all with the remaining *Echinolittorina* species of the western Indian Ocean. In northern Oman, *E. omanensis* has been recorded together with *E. arabica* at only two localities: Ras al-Junayz, Ras al-Hadd (BMNH; both species common) and Sur (BMNH; *E. omanensis* rare, *E. arabica* sparse). At these localities their respective microdistributions are not known, but the habitat characteristics of these species elsewhere suggest that both occupy similar high levels in the littoral fringe, with *E. arabica* restricted to microhabitats that are more sheltered from wave action. In the vicinity of Aden, both *E. omanensis* and *E. marisrubri* have been recorded from Little Aden and Conquest Bay (BMNH), but the latter species is rare. Both species show three rows of nodules on the shell, but the intervening beaded ribs distinguish *E. marisrubri*. At Ras al-Hadd *E. omanensis* is sympatric with rare migrants of *E. leucosticta*.

Sequence data from the mitochondrial COI gene show that the sister species of *E. omanensis* is *E. subnodosa* from the Red Sea (Williams & Reid 2004; see Remarks on *E. subnodosa*).

Separation from members of the conchologically similar *E. malaccana* group is discussed in the Remarks on the *E. natalensis* group and on *E. malaccana* (Fig. 27). Among the other members of the *E. natalensis* group, the shells of *E. omanensis* are most similar to those of *E. natalensis* (Fig. 13; see Remarks on *E. natalensis*) although the two are not known to occur sympatrically. There is some variation in the proportions of the shell of *E. omanensis*, and in the development of a third row of nodules towards the suture, but no entirely smooth forms are known. Three samples have been seen from southern Somalia (see Range above) and in these the shells have more pointed nodules (Fig. 17A, B) and thus the 'prickly' appearance of *E. natalensis*. These samples are geographically closer to *E. natalensis* than to the nearest records of *E. omanensis*, but to the south they are isolated from *E. natalensis* by 800 km of unsuitable sedimentary coastline. They are identified as *E. omanensis* because of their narrow profile, 3–4 ribs crossing the peripheral nodules, and 15–16 spiral ribs on the last whorl. Further collecting is required to establish whether, as expected, this species occurs on the rocky shores of the northern and northwestern coasts of Somalia.

Echinolittorina subnodosa **(Philippi, 1847)**

(Figures 15E, F, 16, 19, 20)

Litorina subnodosa Philippi, 1847a: vol. 2: 161, *Litorina* pl. 3, figs 8, 9 (Mare Rubrum [Red Sea]; lectotype (Rosewater 1970) Philippi, 1847a, *Litorina* pl. 3, fig. 9 (Fig. 19H herein); 3 paralectotypes ZMB 2395, seen). Weinkauff, 1882: 93–94, pl. 13, figs 10, 11.

Tectarius subnodosus—H. Adams & A. Adams, 1854: 315.

Littorina subnodosa—Reeve, 1857: sp. 10, pl. 2, fig. 10. Issel, 1869: 191.

Littorina (Nodilittorina) subnodosa—von Martens, 1897: 205.

Nodilittorina (Granulilittorina) subnodosa—Rosewater, 1970: 495–496, pl. 383, figs 1–3, pl. 383a (map) (in part, includes *E. arabica*, *E. marisrubri*).

Nodilittorina (Nodilittorina) subnodosa—Reid, 1989a: 100.

Nodilittorina subnodosa—Reid, 2002a: 259–281.

Echinolittorina subnodosa—Williams *et al*., 2003: 83.

Echinolittorina subnodosa A—Williams & Reid, 2004: 2227–2251.

Litorina nodosa—Weinkauff, 1883: 226 (in part, includes *E. australis*, *E. natalensis*, *E. malaccana* group; not Gray, 1839 = *E. australis*).

Tectarius nodosus—Tryon, 1887: 259, pl. 47, fig. 65 (in part, includes *E. australis*, *E. natalensis*, *E. miliaris*; not Gray, 1839). Moazzo, 1939: 183 (not Gray, 1839).

Tectarius armatus—Safriel & Lipkin, 1964: 187 (not *Tectaria armata* Issel, 1869 = *Perrinia stellata* A. Adams, 1864, Trochidae).

Nodilittorina (Nodilittorina) natalensis—Sabelli & Taviani, 1984: 95–100, pl. 1 (radula, penis), figs 1, 2 (not Krauss in Philippi, 1847).

Nodilittorina natalensis—Verbinnen & Dirkx, 2005: 111–112, fig. 4 (not Krauss in Philippi, 1847).

Nodilittorina tuberculata—Sharabati, 1984: pl. 6, figs 5, 5a (not *Litorina tuberculata* Menke, 1828 = *E. tuberculata*).

Taxonomic history: The paralectotypes in ZMB were collected by Hemprich & Ehrenberg in the Red Sea (also the source of Philippi's type material of *E. millegrana*) and includes two labels in Philippi's hand. These three shells resemble Philippi's (1847a) fig. 8, but none is the figured shell. Confusion with *E. natalensis* and nodulose forms of the Australian species *E. australis* may be explained by a similar broad shape and three rows of nodules (Weinkauff 1883, as *Litorina nodosa*; followed by Tryon 1887). Following Rosewater (1970) the species was distinguished from these two, but united with *E. arabica* and *E. marisrubri*. Sabelli & Taviani (1984) and Verbinnen & Dirkx (2005) separated the two nodulose species in the Red Sea, *E. subnodosa* and *E. marisrubri*, but under the names *N. natalensis* and *N. subnodosa* respectively, while Sharabati (1984) used *N. tuberculata* (a western Atlantic species) and *N. subnodosa*.

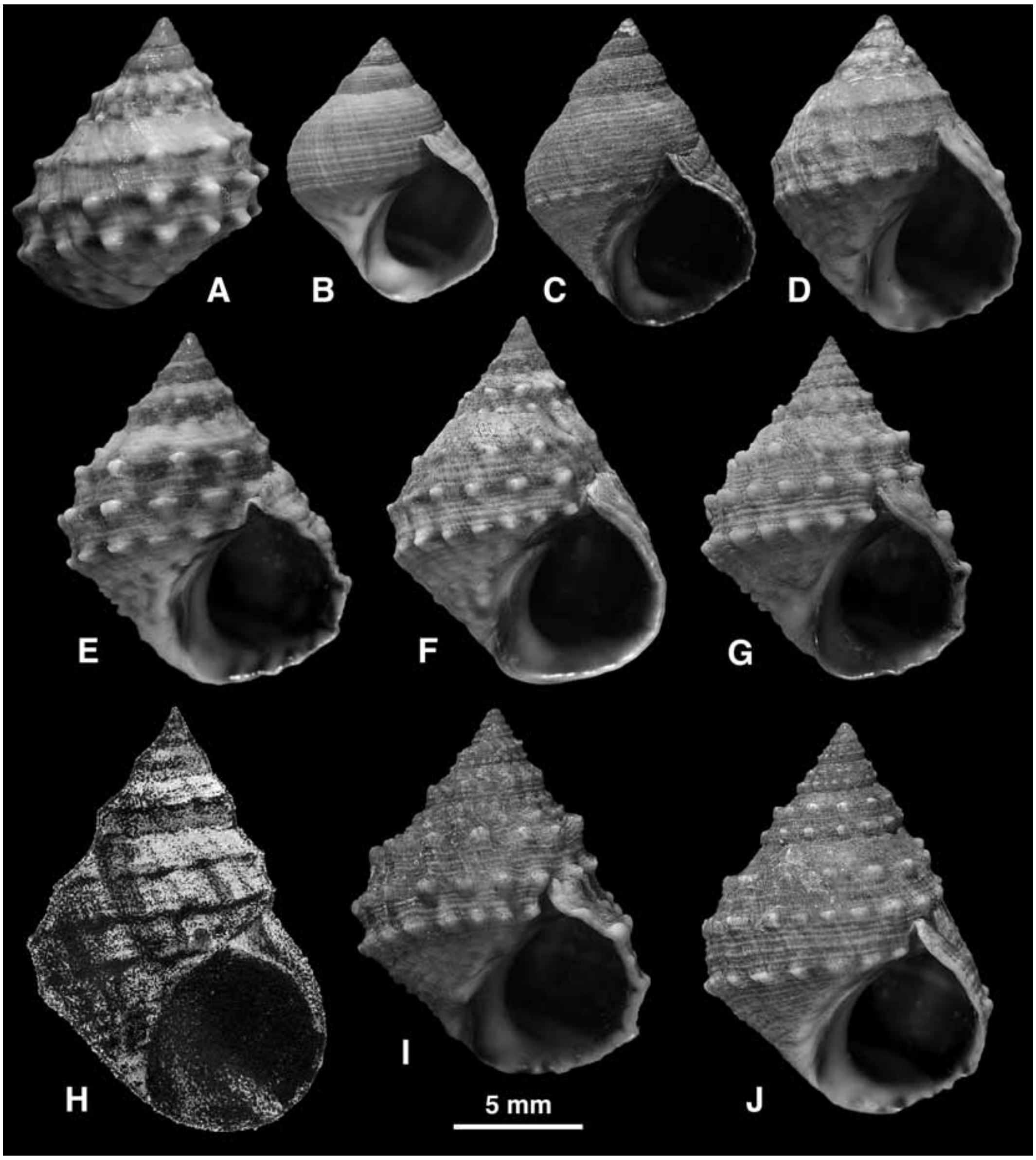

FIGURE 19. *Echinolittorina subnodosa*. **A,** no locality [Red Sea] (BMNH 20040224). **B, C,** Hammam-Fara'un, Gulf of Suez, Egypt (BMNH 20040225). **D–F,** Mukawwar I., Sudan (BMNH 20040226). **G, I,** S of Port Sudan Harbour, Sudan (BMNH 20040227). **H,** *Litorina subnodosa* Philippi, 1847, lectotype figure, Red Sea (Philippi, 1847, *Litorina* pl. 3, fig. 9). **J,** no locality [Red Sea] (BMNH 20040228).

Diagnosis: Shell conical, 3 rows of pointed nodules on last whorl, nodules occupying width of one rib only, so not crossed by spiral ribs; 25–31 spiral ribs on last whorl (including base); grey, a brown spiral line connecting each row of white nodules. Red Sea. COI: GenBank AJ623045, AJ623046.

Material examined: 25 lots (including 7 penes, 2 sperm samples; 6 pallial oviducts, 2 radulae).

Shell (Fig. 19): Mature shell height 8.1–18.7 mm. Shape conical (H/B = 1.16–1.40; SH = 1.35–1.68); spire whorls lightly rounded, suture distinct; spire profile concave at apex; periphery of last whorl weakly angled. Columella short, concave, hollowed at base; eroded parietal area small or absent. Sculpture of last whorl: 3 rows of pointed nodules at periphery, mid-whorl and shoulder, not axially aligned, numbering 13-19 at periphery; rarely an additional row of small nodules near suture; nodules sometimes become obsolete towards end of last whorl, remaining only as enlarged ribs; rarely entire shell lacks nodules (Fig. 19B, C); entire surface with narrow spiral ribs, 16–21 at and above periphery, and microstriae; nodules occupy width of one rib only, so are not crossed by spiral ribs; base with 9–11 ribs, of which up to 4 may be nodulose. Protoconch 0.25–0.27 mm diameter, 2.1–2.2 whorls. Colour: cream to grey, darker grey between shoulder and middle of base; nodules white, each of the 3 major rows connected by a dark brown spiral line; smoother shells sometimes with diffusely marbled or axially zigzag brown pattern; rarely entirely cream or entirely black-brown (Fig. 19B, C); aperture brown, external spiral lines showing through, with pale band at base; columella purple-brown.

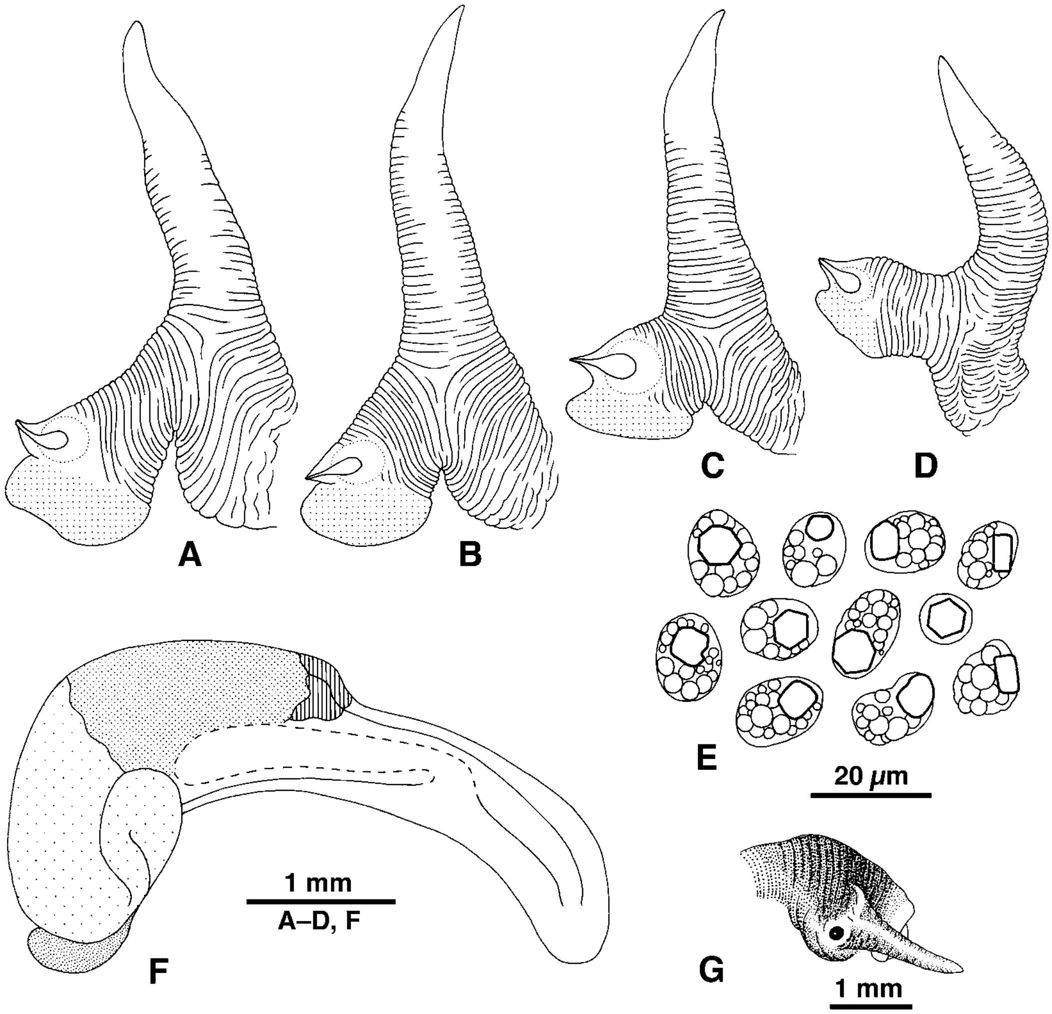

FIGURE 20. *Echinolittorina subnodosa*. **A–D,** penes. **E,** paraspermatozoa. **F,** pallial oviduct. **G,** head. **A,** El-Qalawi, 30.5 km S Port Safaga, Egypt (BMNH 20040229; shell H = 12.5 mm). **B, C, F,** Mukawwar I., Sudan (BMNH 20040226; shell H **B** = 13.0 mm, **C** = 12.3 mm, **F** = 13.1 mm). **D, E, G,** Ras Mohammed, S Sinai, Egypt (BMNH 20040230; shell H = 10.3 mm). Shading conventions as in Figure 3.

Animal (Fig. 20): Head (Fig. 20G) grey to black, no unpigmented stripe across snout, tentacle pale around eye and across base, with two longitudinal grey lines extending almost to tip; sides of foot grey to black. Opercular ratio 0.46–0.56. Penis (Fig. 20A–D): filament gradually tapering to pointed tip, with fine annular wrinkles for most of its length, filament 0.6–0.7 total length of penis, sperm groove extends to tip; mamilliform gland about half size of glandular disc, borne together on projection of base; penis unpigmented or slightly pigmented at base. Euspermatozoa 107–110 µm; paraspermatozoa (Fig. 20E) spherical to oval, 9–

16 µm diameter, filled with large round granules, containing single short rectangular, oval or irregular rod-piece, hexagonal in section and not projecting from cell. Pallial oviduct (Fig. 20F): bursa opening at one third to one half length of straight section (from anterior) and extending back to albumen gland. Development predicted to be planktotrophic.

Radula (Fig. 15E, F): Relative radula length 2.86–4.96. Rachidian: length/width 1.90–2.25; tip of major cusp pointed. Lateral and inner marginal: tips of major cusps rounded; major cusp of lateral slightly larger than that of inner marginal. Outer marginal: 6–8 cusps.

Range (Fig. 16): Red Sea. Range limits: Suez, Egypt (BMNH 1870.12.26.20); Eilat, Israel (USNM 709145); Jeddah, Saudi Arabia (BMNH); Massawa, Eritrea (IRSNB). Restriction to the Red Sea is likely to be correct, because of the numerous records of other *Echinolittorina* species from the Gulf of Aden. The lack of records from the southeastern Red Sea is surprising in view of the five records of *E. marisrubri* and *E. millegrana* from the Red Sea coast of Yemen, and may indicate a real absence.

Habitat: The habitat includes substrates of coral limestone, beachrock and concrete in the littoral fringe.

Remarks: Throughout most of its range this species occurs in the low nutrient regime characteristic of most of the Red Sea and is therefore considerd to be an oceanic species; only the southernmost record, from Massawa (IRSNB), lies in the part of the Red Sea that is influenced by influx of nutrient-rich water from the Gulf of Aden (Sheppard 2000).

Sequence data from the mitochondrial COI gene show that the sister species of *E. subnodosa* is *E. omanensis* (Williams & Reid 2004), with a K2P genetic distance of 10.9%. Depending upon the calibration used, this corresponds to an age of separation of 2.3 or 4.2 Ma. During the glacial intervals of the Plio-Pleistocene the Red Sea became partly isolated, hypersaline and uninhabitable by most marine organisms, and the most recent recolonization began only about 15000 years ago (Sheppard *et al*. 1992; Siddall *et al*. 2003). Although the present distributions of this pair appear to be separated at the mouth of the Red Sea, their speciation therefore cannot be related to recent recolonization and differentiation. The modern distributions of *E. subnodosa* and *E. omanensis* suggest that they are isolated by their ecological requirements (for oceanic and upwelling conditions, respectively), and this may have played a role in their speciation. During glacial intervals the strength of the monsoon-driven upwelling on the southern Arabian coast was reduced (Sheppard *et al*. 1992), and this may have permitted *E. subnodosa* to survive in a refugium in the Gulf of Aden, outside its present range. Meanwhile, the extent of *E. omanensis* may have been correspondingly restricted, maintaining the separation between them. A similar geographical pattern is shown by the likely sister-species pair *Peasiella isseli* (Semper in Issel, 1869) and *Peasiella mauritiana* (Viader, 1951), the former limited to the Red Sea and Aden, while the latter is widespread in the western Indian Ocean (Reid & Mak 1998).

Of the seven species of Littorinidae recorded from the Red Sea (Reid 1986a, 2001b, herein; Reid & Mak 1998), four are endemic to the Red Sea and Arabia (*E. marisrubri*, *E. subnodosa*, *E. millegrana*, *Peasiella isseli*), of which three are restricted to the Red Sea and Aden. Although the details of these patterns differ and their likely causes are varied, this emphasizes the distinct ecology and biogeographic history of the Arabian region and its components (Sheppard *et al*. 1992).

This species is readily distinguished from the others of the *E. natalensis* group in the western Indian Ocean (*E. natalensis*, *E. omanensis*) by its broader shell, with three widely-spaced rows of small nodules (the nodules occupying the width of one rib, and therefore not crossed by spiral sculpture) and a pattern of three spiral brown lines. These three species are not know to occur sympatrically and there are no obvious anatomical differences among them. In the Red Sea *E. marisrubri* is a similar species (Fig. 11) with three rows of nodules, but the shell is smaller, there is a beaded rib between each row of nodules, and the nodules at the periphery are crossed by two spiral threads; penial anatomy and paraspermatozoa differ.

Echinolittorina pascua (Rosewater, 1970)

(Figures 15G, H, 21–23)

? *Trochus nodulosus* Gmelin, 1791: 3582 (Oceano australi [southern Ocean]; lectotype (Clench & Abbott 1942) Chemnitz, 1781: pl. 163, figs 1545, 1546; in part, includes *E. tuberculata* (Menke, 1828); perhaps = *E. malaccana* group; not *Trochus nodulosus* Solander in Brander, 1766).

Tectarius nodulosus—Odhner, 1922: 248.

? *Turbo trochiformis* Dillwyn, 1817: 826 (new name for *Trochus nodulosus* Gmelin, 1791, not *Turbo nodulosus* Gmelin, 1791; not *Turbo trochiformis* Brocchi, 1814; type locality restricted to Southern Ocean [Pacific]).

? *Littorina trochoides* Gray, 1839: 140–141 (no locality; lectotype (Rosewater 1970) BMNH 1887.4.26.1, Fig. 21H; *nomen dubium*). E.A. Smith, 1913: 410.

? *Litorina trochoides*—Philippi, 1847a: vol. 2: 159, *Litorina* pl. 3, fig. 3.

? *Tectarius trochoides*—H. Adams & A. Adams, 1854: 315.

Tectarius pyramidalis—Dall, 1908: 437 (not *L. pyramidalis* Quoy & Gaimard, 1833 = *N. pyramidalis*).

Tectarium pyramidale—Lamy, 1938: 138–139 (not Quoy & Gaimard, 1833).

Nodilittorina (Nodilittorina) pyramidalis pyramidalis—Rosewater, 1970: 481–484, pl. 370, fig. 5 (in part, includes *N. pyramidalis*, *E. malaccana*, *E. austrotrochoides*, *E. cecillei*, *E. marquesensis*, *E. wallaceana*, *E. cinerea*; not Quoy & Gaimard, 1833).

Nodilittorina (Nodilittorina) pyramidalis pascua Rosewater, 1970: 484–485, pl. 370, figs 10–13, pl. 372 (map) (Easter Island; holotype USNM 679290 (Fig. 21I), 24 paratypes USNM 679291, seen; 7 paratypes ANSP 315563, 23 alcohol paratypes ANSP 15238, not seen).

Nodilittorina pyramidalis var. *pascua*—Salvat & Rives, 1975: 263, fig. 40.

Nodilittorina pyramidalis pascua—Rehder, 1980: 25–26, pl. 5, fig. 1. Tsuchida & Shimura, 1986: 83, pl. 1, fig. 2.

Nodilittorina (Nodilittorina) pascua—Reid, 1989a: 100.

Nodilittorina pascua—Reid, 2002a: 259–281.

Echinolittorina pascua—Williams *et al*., 2003: 83. Williams & Reid, 2004: 2227–2251.

Taxonomic history: Confusion surrounding *Trochus nodulosus* Gmelin, 1791 is discussed under the Taxonomic History of the *E. malaccana* group.

The identity of *L. trochoides* Gray, 1839, has been a matter of uncertainty (Philippi 1847a; von Martens 1897), because Gray's original description in *The Zoology of Captain Beechey's Voyage* was brief; he gave no figure or type locality, stating only 'my collection'. The first figure of the species was by Philippi (1847a), of a single specimen received from Cuming (which therefore may have been compared with, or even part of, Gray's original material). Gray's collection was incorporated in the BMNH and in 1887 a lot of eight shells was registered as the type collection of this species. One of these was subsequently designated lectotype (Rosewater 1970). No original label by Gray survives, but the museum register records the locality 'Low Island'. Following its description, the name *trochoides* was used only rarely (Philippi 1847a; Reeve 1858; Nevill 1885; E.A. Smith 1913), and then fell into the synonymy of the nodulose IWP species complex under the name *T.* (or *N.*) *nodulosus* (e.g. Tryon 1887; Fischer 1969) or *N. pyramidalis* (Abbott 1954; Rosewater 1970). It was reestablished as the oldest available name for a tropical IWP species by Reid (1989a) and has become widely used (see Taxonomic History of *E. malaccana* group, and of *E. malaccana*). However, now that this concept of *N. trochoides* is recognized to be a species complex, it is important to discover to which species the name belongs. Only now has thorough comparison been undertaken using much new material, and including nodulose shells from throughout the IWP region. This has revealed extraordinary similarity and convergence among the small, nodulose shells of the *E. malaccana* and *E. natalensis* groups.

Consequently, it is now clear that the lectotype and paralectotypes of *L. trochoides* designated by Rosewater (1970) are small specimens of *E. pascua* (compare Fig. 21F and H). The short, recurved columellar base, partly fused nodules on the last whorl (forming axial flanges), concave profile above the shoulder leading to nodulose suture, dark colour and absence of conspicuously white nodules, strong regular spiral threads, and presence of a single row of small nodules of the base, are all characteristic of *E. pascua*. Some of these features can be found in occasional specimens of the *E. malaccana* group (Figs 27E, H, 32J), but together they unequivocally indicate *E. pascua*. In contrast, shells of the *E. malaccana* group have a sharp inner lip, two rows of white nodules on the last whorl, more rounded whorls, finer and more irregular spiral threads, and 0–4 rows of small nodules on the base. It remains to be determined if the designated specimens are indeed types. Gray (1839) diagnosed the shell as 'black', but added the note 'shell bluish, and the nodules white in some specimens'. The sculpture was described as 'nodulose near the suture, with a series of compressed nodules on the upper and two on the last whorl, with a series of close-set, roundish granules round the edge in front of the last one'. This could describe the sculpture of the last whorl of the nodulose form of *E. pascua*, the 'series of … granules … in front' indicating the single row of small nodules on the base, but is not sufficient to exclude the *E. malaccana* group. The size quoted was 7 by 4 lines (14.8 x 8.4 mm; Gray was usually accurate in his measurements), which is large for the *E. malaccana* group, but common for *E. pascua*; it is also considerably larger than the largest (11.2 mm) of the putative types. In the preface to his work, Gray (1839) admitted that not all the material described came from Beechey's expedition, but stated that specimens from the voyage were deposited in the museums of the Zoological Society and of the Naval Hospital. He did not mention whether any of the material was in his own possession. The route of the voyage is therefore equivocal evidence. Nevertheless, it is interesting that the *Blossom* called at all the recorded localities of *E. pascua* (Easter I. and three islands of the Pitcairn group), as well as at Macao, Ryukyu Islands and Bonin Islands (where members of the *E. malaccana* group could have been obtained) (route described by Beechey 1831). Finally, although 'Low Island' is a common geographical appellation, 'Low Archipelago' was the current name for the Tuamotu Archipelago in the early nineteenth century, in which Easter Island was at that time also included (e.g. Darwin 1842, although Beechey 1831 did not use the name). The shell figured by Philippi (1847a) is large (18 mm, i.e. larger than any specimen of the *E. malaccana* group) and entirely black, but for a pale basal band, and is therefore probably also a specimen of *E. pascua*. (The specimen figured by Reeve 1858, as *L. trochoides* exists in BMNH, and is a member of the *E. malaccana* group that does not correspond with Gray's diagnosis.)

In summary, while the putative types of *L. trochoides* are *E. pascua*, and there is circumstantial evidence that Gray could have obtained specimens of that species, the discrepancy in size and provenance between the type specimens and Gray's inconclusive description, and the lack of clear type locality (or of clear connection with Beechey's voyage), all combine to raise doubts. It would be undesirable to replace the now familiar *E. pascua* with an older name that has not been used in this sense since E.A. Smith (1913), and then only in a list. Furthermore, the name *trochoides* has become familiar (since Reid 1989a) in another sense, for the *E. malaccana* group, to which *E. pascua* does not belong. The epithet *pascua* has not been used sufficiently frequently to justify reversal of precedence (ICZN 1999: Art. 23.9) in order to conserve its current usage. Therefore, stability is best served by considering *L. trochoides* Gray, 1839 a *nomen dubium*. (See also Taxonomic History of *E. malaccana* group for further discussion.)

Rosewater (1970) introduced *pascua* as a subspecies of *N. pyramidalis*, the name then used for most of the nodulose western Pacific littorinids (i.e. *N. pyramidalis s.s.* and *E. malaccana* group). The type collection consisted of the distinctively large, broad, weakly nodulose forms found on Easter Island (Fig. 21I). Neither he nor Reid (1989a, 1992, 2001a) noticed that the smaller, nodulose shells from the limestone rocks of Henderson Island (Fig. 21F, G) were identical with the types of *L. trochoides* (Fig. 21H). Earlier authors had identified *E. pascua* with either *N. pyramidalis* or the *E. malaccana* group, probably on the basis of geographical proximity (*E. marquesensis* of the *E. malaccana* group occurs as far east as the Marquesas Is).

Diagnosis: Shell high conical, 1–2 rows of axially elongate nodules on last whorl; 15–23 spiral threads on last whorl (including base); columella turned out at base to make inner lip rounded and forming a thickened boss; brown to black, nodules same colour or sometimes brown to grey. Easter Island and Pitcairn Group. COI: GenBank AJ623025, AJ623026.

Material examined: 18 lots (including 10 penes, 4 sperm samples; 5 pallial oviducts, 2 radulae).

Shell (Fig. 21): Mature shell height 3.8–15.3 mm (to 17.9 mm, Rehder 1980). Shape conical to high conical (H/B = 1.33–1.68; SH = 1.77–2.33); spire whorls flat or concave between suture and peripheral nodules, suture indistinct; spire profile straight to slightly concave; periphery of last whorl weakly angled. Columella short, concave, turned out at base to make inner lip of aperture rounded (i.e. there is no projecting anterior lip at base of columella, and edge of inner lip is not sharp); inner lip forms a smooth boss continuous with eroded pseudumbilical and parietal area. Sculpture of last whorl: single series of axially elongate nodules from mid-whorl to below periphery, 10–17 at periphery; in strongly sculptured shells nodules are divided to form a paired series and suture is irregularly nodulose (Fig. 21F–H); entire surface with strong, regular, spiral threads, 11–17 at and above periphery, continuous across nodules; microstriae over entire surface; base with 4–7 threads and single row of small nodules (occasionally divided by a spiral groove). Protoconch not well preserved, approx. 0.28 mm diameter, 2.5 whorls. Colour: purple-brown to black, fading to grey, sometimes pale sutural band and basal band, peripheral nodules usually brown to black, sometimes pale grey, basal nodules occupy pale basal band; aperture black-brown, with pale band at base; columella purple-brown.

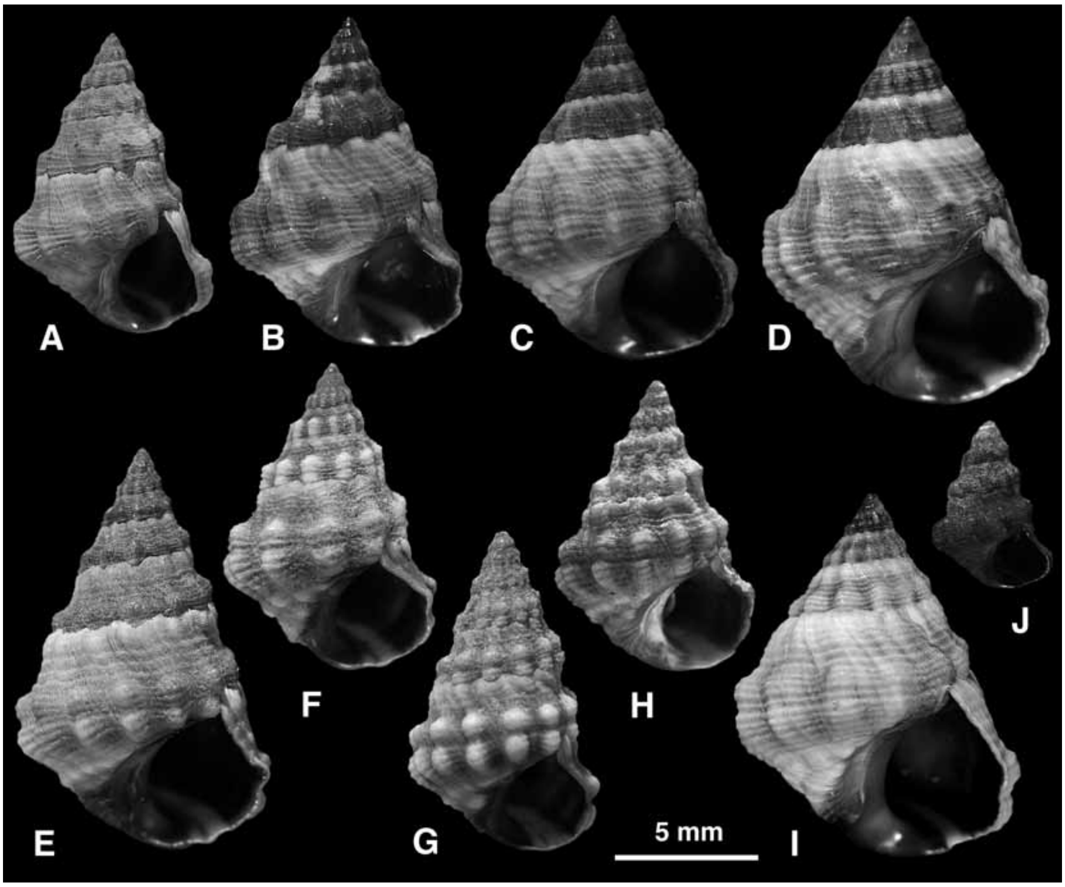

FIGURE 21. *Echinolittorina pascua*. **A, E,** Ovahe, Easter I. (BMNH 20040231). **B–D,** Hanga Tee, Easter I. (BMNH 20040232). **F, G,** North Beach, Henderson I. (BMNH 20040233). **H,** *Littorina trochoides* Gray, 1839, former lectotype, ‘Low Island’ (BMNH 1887.4.26.1). **I,** *Nodilittorina (Nodilittorina) pyramidalis pascua* Rosewater, 1970, holotype, Easter I. (USNM 679290). **J,** Punta Hanga Poukura, Easter I. (BMNH 20040234).

Animal (Fig. 22): Head black, no unpigmented stripe across snout, tentacle dark grey to black (owing to fusion of two longitudinal stripes, as seen in palest animals only), pale around eye and rarely across base, pale at tips; sides of foot black. Opercular ratio 0.48–0.55. Penis (Fig. 22A–E): filament gradually tapering to pointed tip, with fine annular wrinkles for most of its length, filament 0.5–0.6 total length of penis, sperm groove extends to tip; mamilliform gland about half size of glandular disc, borne together on projection of base; penis unpigmented or slightly pigmented at base. Euspermatozoa 114–128 µm; paraspermatozoa (Fig. 22G, H) spherical or slightly oval, 12–17 µm diameter, filled with large round granules, containing 1–2 short irregularly oval to rectangular rod-pieces, hexagonal in section and not projecting from cell. Pallial oviduct

(Fig. 22F): bursa opening at one third to one half length of straight section (from anterior) and extending back almost or fully to albumen gland. Development predicted to be planktotrophic.

Radula (Fig. 15G, H): Relative radula length 4.65–6.64. Rachidian: length/width 1.33–1.50; tip of major cusp pointed. Lateral and inner marginal: major cusp on each of similar size, tips rounded. Outer marginal: 8–10 cusps.

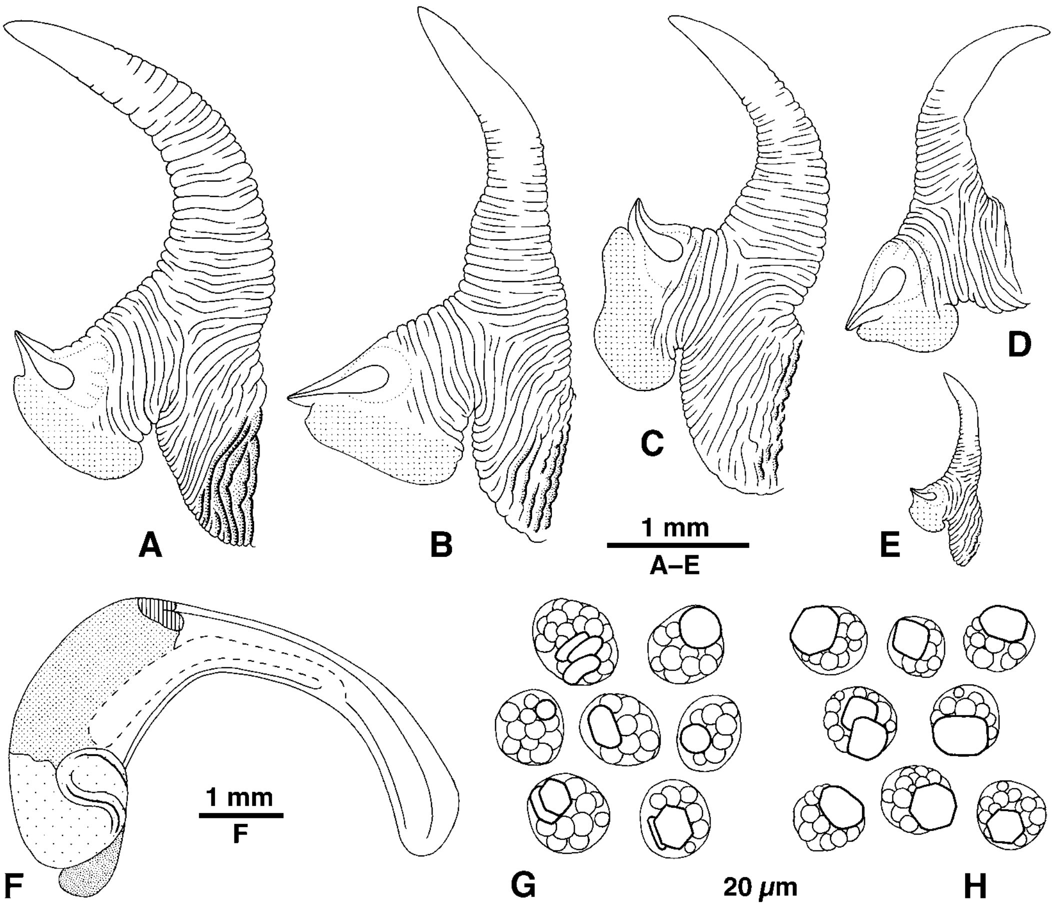

FIGURE 22. *Echinolittorina pascua*. **A–E,** penes. **F,** pallial oviduct. **G, H,** paraspermatozoa. **A–C, F,** Hanga Tee, Easter I. (BMNH 20040232; shell H **A** = 12.2 mm, **B** = 12.9 mm, **C** = 13.5 mm, **F** 13.2 mm). **D,** North Beach, Henderson I. (BMNH 20040233; shell H = 9.9 mm). **E, G,** Punta Hanga Poukura, Easter I. (BMNH 20040234; shell H = 3.8 mm). **H,** Anakena, Easter I. (BMNH 20040235). Shading conventions as in Figure 3.

Range (Fig. 23): Southeastern Polynesia. Range limits: Oeno I. (USNM 789558); Bounty Bay, Pitcairn I. (CUMZ; USNM 793954); North Beach, Henderson I. (CUMZ; BMNH 20040233); Hanga Tee, Easter I. (BMNH 20040232; USNM 756082); Ovahe, Easter I. (BMNH 20040231; USNM 756048).

Habitat: On high volcanic islands this species is abundant on basalt rocks in the littoral fringe, on both strongly exposed shores and in moderately sheltered inlets. On raised coral islands it occurs on limestone.

Remarks: The range of this species is restricted to a few small and isolated islands in the extreme southeast of Polynesia: those of the Pitcairn Group (Pitcairn, Oeno and Henderson Islands, within 200 km of each other) and Easter Island about 1900 km to the east (Rosewater 1970; Rehder 1980; Paulay 1989). On all these islands it is the sole species of *Echinolittorina*. The distance to Easter Island is close to the maximum dispersal distance of 2100 km estimated from extralimital records of *Echinolittorina* species (see Remarks on *E. cinerea* and Discussion), so that conspecificity of the Pitcairn and Easter populations could be questioned. Nevertheless, molecular data from single examples from Henderson and Easter Islands are closely similar, within the expected range for conspecifics (Williams & Reid 2004). If there is gene flow between the populations, it is most likely to occur from east to west in the South Equatorial Current; prevailing surface currents in the Pitcairn Group are from the north east (Paulay & Spencer 1988). There are no records of the species from Ducie Island, an atoll 1570 km west of Easter Island, but during low sea-level stands this may have provided a stepping stone for dispersal. This species is undoubtedly not present on Polynesian islands to the west; the littorinid faunas of the Tuamotu Islands and of Rapa are well known and do not include it. Several authors have noted the existence of a small number of endemic molluscs shared between the Pitcairn and Easter Groups (Rehder 1980; Paulay & Spencer 1988; Preece 1995). The degree of endemism among the impoverished molluscan fauna of Easter Island has been estimated at 36%, attributable to its extreme geographical isolation (Boyko 2003). Only a single, poorly preserved, protoconch was found in available samples, but this did not differ significantly from those of other *Echinolittorina* species, suggesting that there are no peculiarities in the larval development of this species despite the isolation of the islands on which it occurs.

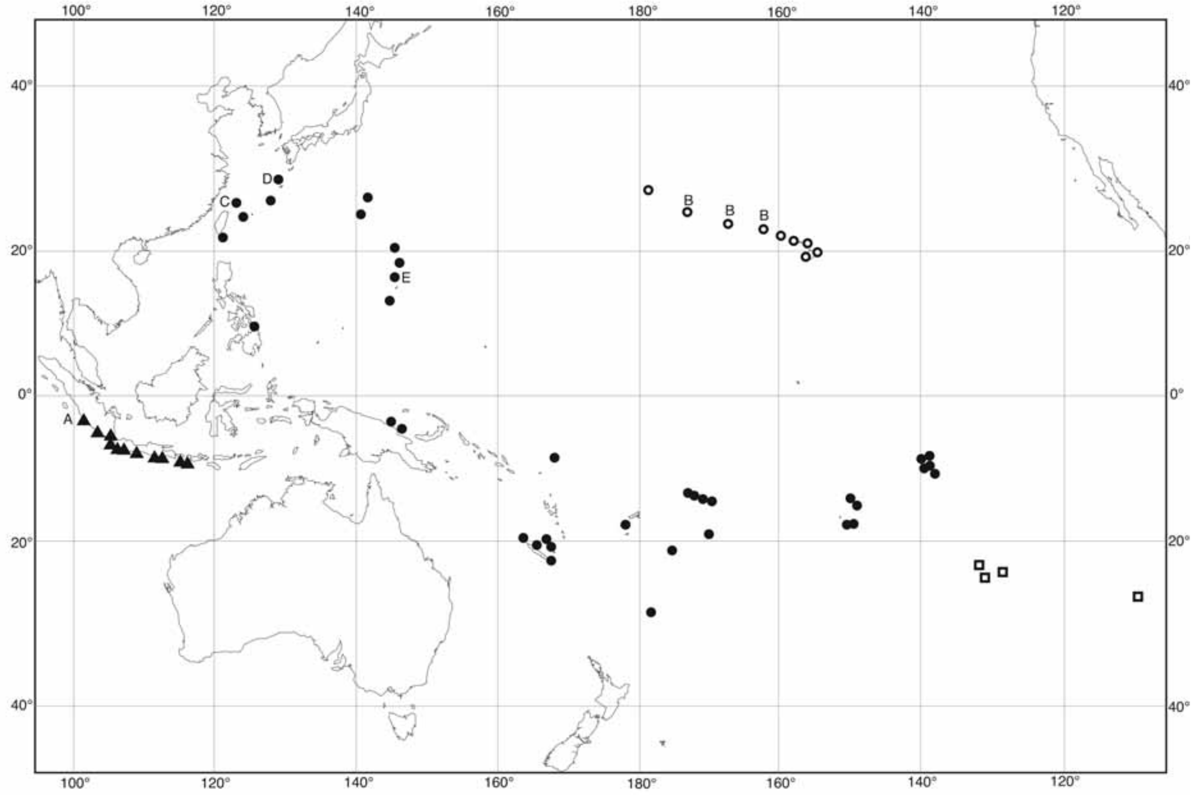

FIGURE 23. Distribution of *Echinolittorina pascua* (open squares), *E. sundaica* (solid triangles), *E. cinerea* (solid circles), and *E. hawaiiensis* (open circles). Literature records: A, Dharma (1997); B, Rosewater (1970); C, Fujioka & Kurozumi (1980); D, Kurozumi (1994); E, Vermeij *et al*. (1984).

The island localities of *E. pascua* fall into two quite different groups. All are situated in oceanic waters of low productivity, but Easter and Pitcairn Islands are volcanic high islands with basalt shores strongly exposed to waves, whereas Henderson is a raised coral island and Oeno an atoll, in both cases sheltered by coral reefs and with only limestone substrates. This supports the apparent indifference of *Echinolittorina* species to the nature of their rock substrate. Specimens from the limestone islands are, however, narrower and more strongly nodulose (Fig. 21F, G) than those from basalt shores, as has been observed in other species (see *E. natalensis*, *E. malaccana*, *E. wallaceana*, *E. hawaiiensis*).

Mitochondrial gene sequences (COI, 12S rRNA, but not nuclear 28S rRNA) suggest that *E. pascua* is sister to the other three species of the *E. natalensis* clade, *E. natalensis*, *E. subnodosa* and *E. omanensis*, all of which are distributed in the western Indian Ocean, about 18000 km (or 180° longitude) distant from *E. pascua*. This is far too great a distance to be explained by dispersal, past or present. Instead, it has been suggested that this clade of *Echinolittorina* was formerly more widespread and has become restricted to the periphery of the IWP region by extinction (Williams & Reid 2004). Interestingly, the five members of the *E. malaccana* clade occupy the intervening area, from western India to the Marquesas Islands, and these two clades are nowhere sympatric. Their habitats and shells are closely similar, and competitive replacement of the *E. natalensis* clade by the *E. malaccana* clade is a possibility. The time of separation of *E. pascua* from the rest of the *E. natalensis* group is estimated at 10–20 Ma (Williams & Reid 2004) and the origins of Oeno and Henderson Islands fall in this range (16 and 13 Ma respectively), whereas Pitcairn and Easter Islands are much younger (less than 1 Ma and 2.5 Ma, respectively) (Preece 1995; Boyko 2003).

No other *Echinolittorina* species are sympatric with *E. pascua*, so no misidentification of correctly localized specimens should occur. Shells of other members of the *E. natalensis* clade (*E. natalensis*, *E. subnodosa* and *E. omanensis*) are similar, but all usually have a third row of nodules at the shoulder, which is absent in *E. pascua*; anatomically, the four species do not differ significantly. Large specimens from Easter and Pitcairn Islands are larger and broader than members of the *E. malaccana* group, have a distinctively rounded inner lip, and usually have a sculpture of axial flanges at the periphery rather than two rows of discrete nodules. However, the narrower and more nodulose shells from limestone islands (Fig. 21F, G) are more similar to those of the *E. malaccana* group (see comparison in Taxonomic History above), although they differ anatomically.

Echinolittorina sundaica group

The relationships of this species are uncertain, so it is placed in a group on its own.

Echinolittorina sundaica (van Regteren Altena, 1945)

(Figures 23–25, 26A, B)

Littorina (Melaraphe) sundaica van Regteren Altena, 1945: 144, 151–152, fig. 2 (Tjilaoet Eureun, south coast of Java [Cilaut Eureun, Java, Indonesia]; holotype NNML 52038, Fig. 24F). Dharma, 1997: 165–166 (map).
Littorina (?Littoraria) sundaica—Rosewater, 1970: 423, 450, pl. 349, figs 1, 2, pl. 350 (map).
Littorina (Austrolittorina) sundaica—Ponder & Rosewater, 1979: 777–779, pl. 2, figs 1-4, pl. 3, figs 1, 2 (radula, penis).
Nodilittorina (Nodilittorina) sundaica—Reid, 1989a: 100.
Nodilittorina sundaica—Reid, 2001a: 442, figs 2F, 3G (penis). Reid, 2002a: 259–281.
Echinolittorina sundaica—Williams *et al*., 2003: 83. Williams & Reid, 2004: 2227–2251.

Taxonomic history: This species is entirely distinctive, but was only named in 1945, probably as a consequence of its small size and restricted distribution.

Diagnosis: Shell small, tall; smooth or with fine incised spiral lines; black to brown, paler or marked with white at suture, pale band on base. Indian Ocean coast of southern Sumatra and Java, Bali. COI: GenBank AJ623047, AJ623048.

Material examined: 21 lots (including 5 penes, 2 sperm samples; 5 pallial oviducts, 4 radulae).

Shell (Fig. 24): Mature shell height 3–8.3 mm. Shape tall (H/B = 1.57–1.89, SH = 1.78–2.52); spire whorls only slightly rounded, suture distinct; spire profile straight; periphery of last whorl slightly angled. Columella short, straight, flattened at base, sometimes slightly pinched; no eroded parietal area. Sculpture of last whorl: smooth but for incised spiral lines, 7–11 above periphery, 7–8 below; periphery marked by wider space between spiral lines, not raised as a rib; sculpture often obsolete towards suture, or entirely absent; surface glossy, no microstriae. Protoconch 0.28 mm diameter, 2.5–2.7 whorls. Colour: dark brown to black, paler at suture, pale band or line on base; sometimes a few irregular white marks at suture, periphery or on base (Fig. 24A), rarely faint grey marbling over surface, but not forming a regular tessellation; aperture dark brown, pale band at base; columella dark brown.

Animal (Fig. 25): Head (Fig. 25A, B) black, usually a narrow unpigmented stripe across snout, tentacle unpigmented with two short longitudinal black lines, lower of which may extend towards tip, unpigmented around eye; sides of foot grey to black. Opercular ratio 0.43–0.47. Penis (Fig. 25A–D): filament tapering to tip, smooth, 0.5 total length of penis, sperm groove extends to tip; mamilliform gland borne on stout projection of base, with glandular disc of similar size; penis unpigmented or slightly pigmented at base. Euspermatozoa not known; paraspermatozoa (Fig. 25F, G) oval to spherical, 11–16 µm diameter, filled with large round granules, 1 (rarely 2) rod-piece with rounded ends, not projecting from cell. Pallial oviduct (Fig. 25E): bursa opening more than halfway along length of straight section (from anterior) and extending back to albumen gland. Development predicted to be planktotrophic.

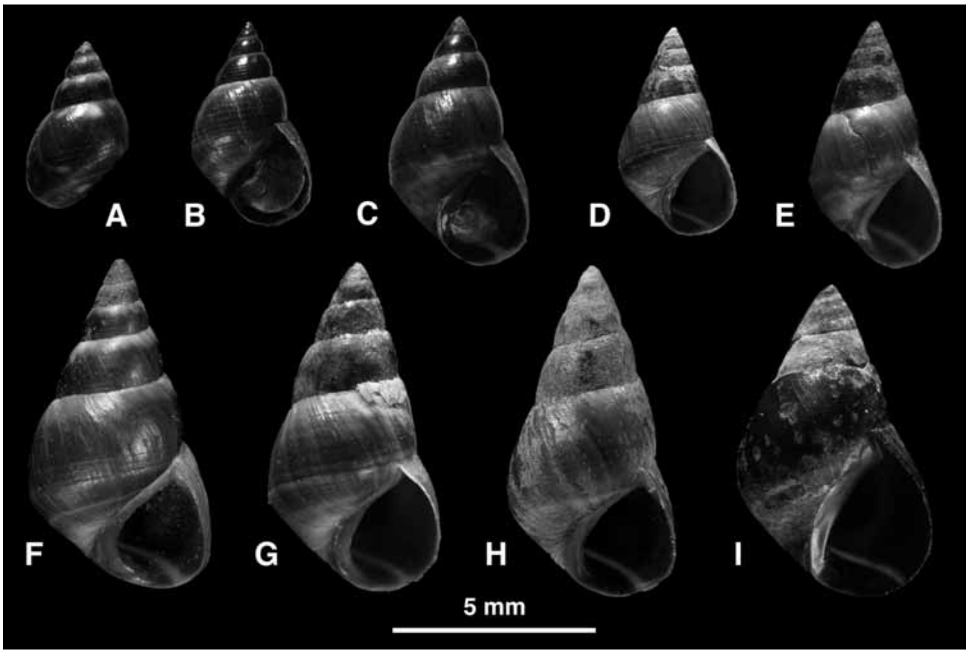

FIGURE 24. *Echinolittorina sundaica*. **A–C,** Tanah Lot, Bali, Indonesia (BMNH 20050020). **D, E, G, H,** Cilaut Eureun, W Java, Indonesia (BMNH 20050021). **F,** *Littorina (Melaraphe) sundaica* van Regteren Altena, 1945, holotype, Tjilaoet Eureun (South coast of Java) [Cilaut Eureun, W Java, Indonesia] (NNML 52038). **I,** Bale Kambang, E Java, Indonesia (BMNH 20050022).

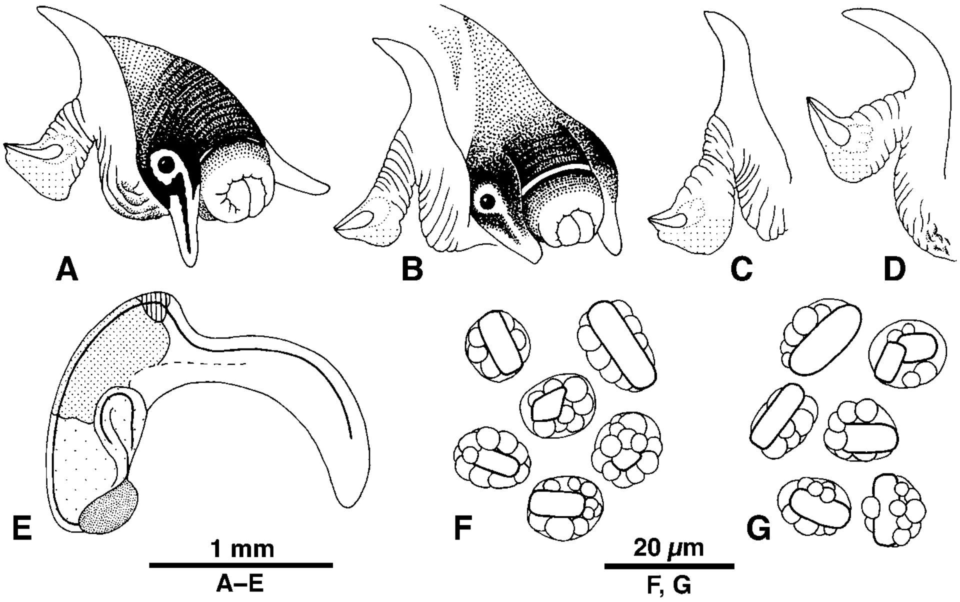

FIGURE 25. *Echinolittorina sundaica*. **A–D,** heads and penes. **E,** pallial oviduct. **F, G,** paraspermatozoa. **A–G,** Tanah Lot, Bali, Indonesia (BMNH 20050020; shell H **A** = 4.9 mm, **B** = 3.9 mm, **C** = 4.1 mm, **D** = 4.6 mm, **E** = 5.2 mm). Shading conventions as in Figure 3.

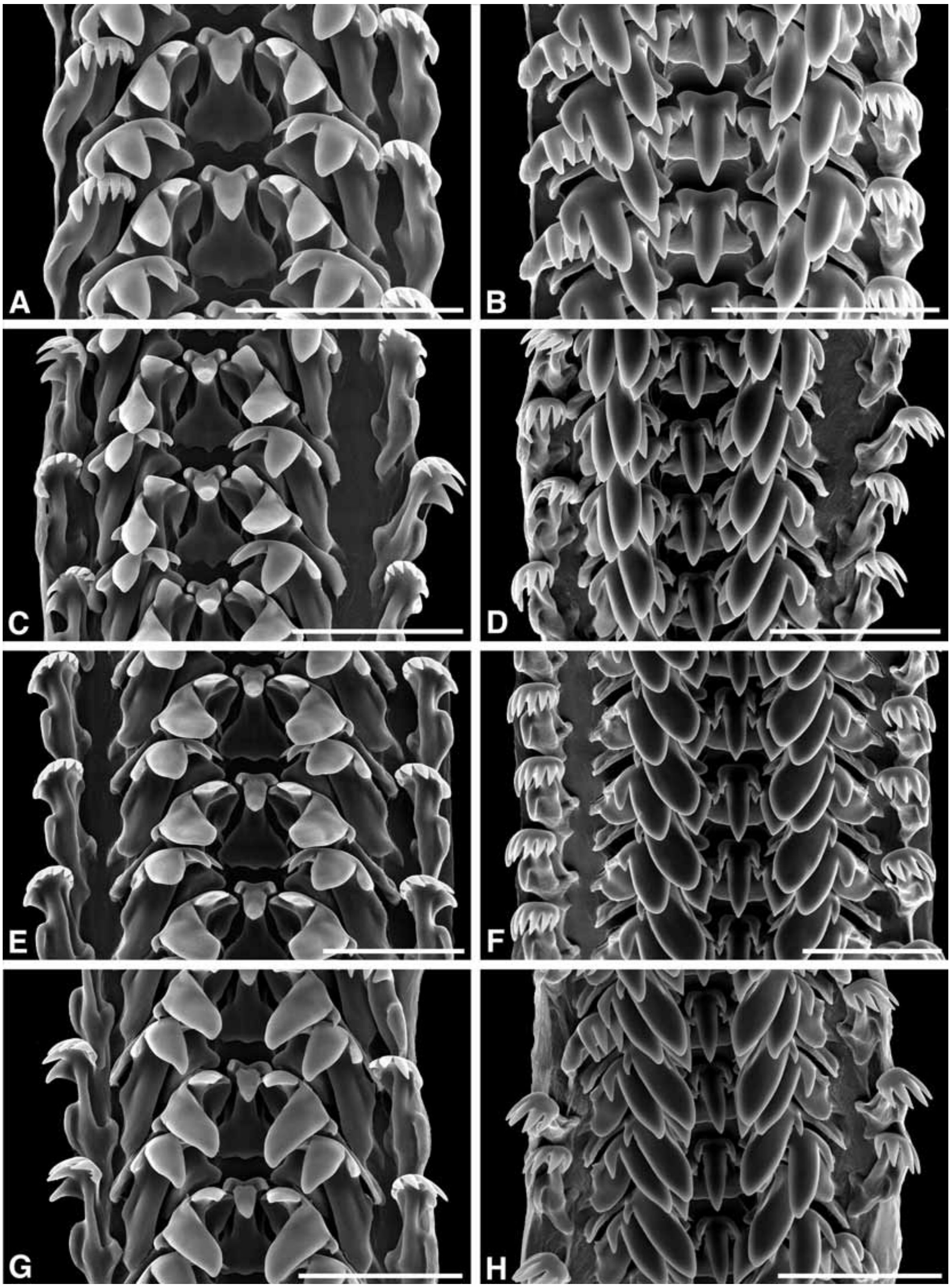

FIGURE 26. Radulae of *Echinolittorina* species (two views of each radula, flat and at 45°). **A, B,** *E. sundaica*; Tanah Lot, Bali, Indonesia (BMNH 20050020; shell H = 5.8 mm). **C, D,** *E. malaccana*, Malapacao I., N Palawan, Philippines (BMNH 20050027; shell H = 7.7 mm). **E, F,** *E. austrotrochoides* new species; Ela Beach, National Capital District, Papua New Guinea (BMNH 20050035; shell H = 10.4 mm). **G, H,** *E. cecillei*; Araki, Kikai-jima, Amami Is, Japan (BMNH 20050047; shell H = 8.0 mm). Scale bars = 50 µm.

Radula (Fig. 26A, B): Relative radula length 1.86–3.70. Rachidian: length/width 1.34–1.46; tip of major cusp pointed. Lateral and inner marginal: major cusp on each of similar size, tips pointed. Outer marginal: 6–7 cusps.

Range (Fig. 23): Indian Ocean coast of southern Sumatra, Java, Bali, Lombok. Range limits: Tapak Pari Beach, Bengkulu City, Sumatra, Indonesia (Dharma 1997); Tembakak, Krui, Lampung, Sumatra (BMNH);

Kalianda, Lampung, Sumatra (BMNH); Labuan, Sunda Strait, West Java, Indonesia (BMNH); Ngliyep, East Java (BMNH); Tanah Lot, Bali, Indonesia (BMNH); Nyang Nyang, Bukit Peninsula, Bali (BMNH); Mawun Beach, 10 km W Kuta, Lombok, Indonesia (BMNH). The species may extend further north in Sumatra; the fauna of the west coast of Sumatra and offshore islands is poorly known (Dharma 1997). Although abundant in Bali, extensive personal collecting in Lombok revealed only a single specimen; the species appears to be limited by 'Wallace's Line' between these two islands.

Habitat: Abundant on moderately exposed shores, in uppermost eulittoral; on basalt, volcanic tuff, concrete (Dharma 1997), often in high-level pools with filamentous green algae.

Remarks: The distribution of *E. sundaica* corresponds closely with a region of coastal upwelling driven by the southeast monsoon; beginning on the southeastern coast of Java in June, the upwelling area intensifies and migrates westward to the southern half of Sumatra, before disappearing in November (Susanto *et al*. 2001). For the rest of the year productivity is generally low, but the upwelling is intensified during El Niño episodes.

Because of its small size and restricted distribution, this species is rare in collections and has been considered enigmatic. With its small, tall, smooth, black shell, it is one of the most distinctive of IWP *Echinolittorina*, but does resemble some temperate littorinids. Members of *Austrolittorina* also have a smooth shell and similar penis; *A. antipodum* (Philippi, 1847) from New Zealand can be small and tall, but the oviduct has an additional loop in the capsule gland (Reid & Williams 2004). *Afrolittorina acutispira* (E.A. Smith, 1892) from southeastern Australia is small and tall, but with a tessellated pattern, blunt penis and two additional loops in the pallial oviduct (Reid & Williams 2004).

The peculiar shell led to doubt about the classification of this species. It was first described in the subgenus *Melarhaphe*, at the time widely used for smooth-shelled tropical '*Littorina*' species. Rosewater (1970) restricted the definition of this subgenus, and doubtfully included it in the subgenus *Littoraria*. With the benefit of penial and radular characters, Ponder & Rosewater (1979) transferred it to the subgenus *Austrolittorina*. Following cladistic treatment of the family, this subgenus was included in the large genus *Nodilittorina* (Reid 1989a). Finally, both anatomical (Reid 2002a) and molecular evidence (Williams *et al*. 2003; Williams & Reid 2004) excluded *E. sundaica* from the temperate genus *Austrolittorina* and demonstrated its membership of the tropical clade *Echinolittorina*. Within the IWP clade of *Echinolittorina* species the relationships of *E. sundaica* are uncertain. There is weak molecular support for a sister-relationship with the five species of the *E. malaccana* group (Williams & Reid 2004), but the only morphological similarities are the generalized form of the penis and the tall shell.

The *Echinolittorina malaccana* group

This is the group formerly known by the name *E. trochoides* (Williams & Reid 2004; Reid *et al*. 2006). It consists of five species (*E. malaccana*, *E. austrotrochoides* n.sp., *E. cecillei*, *E. marquesensis* n.sp., *E. wallaceana* n.sp.) with nodulose shells and a combined distribution stretching from India to northern Australia, southern Japan and the Marquesas Islands. Besides a relatively tall shell with two rows of nodules on the last whorl, these species share a penis with narrowly triangular filament lacking annular wrinkles, and all but one (*E. wallaceana*) have a unique synapomorphy in the bifurcate copulatory bursa. Molecular data strongly support their monophyly (Williams & Reid 2004). The shells are similar to those of the *E. natalensis* group, but members of these two groups are never sympatric. Confusion is also likely with the larger *Nodilittorina pyramidalis*, endemic to southeastern Australia.

The nomenclature of this group is complex, owing to lack of clear conchological differences among the species and also to similarity with other nodulose *Echinolittorina* (especially the *E. natalensis* group and *E. tuberculata* in the western Atlantic) and to *N. pyramidalis*. Gmelin's (1791) introduction of the earliest name associated with the group, *Trochus nodulosus*, was accompanied by a reference to two figures by Chemnitz (1781) and the observation: '*Habitat in* Oceano australi, *et* (*minor*) mari, Americam meridionalem *alluente*, …' (italics original). The two figures of Chemnitz (1781), and his detailed description, were of a 'larger form' based on shells obtained from Cook's expeditions to 'southern lands' (i.e. Pacific Ocean), but he also briefly mentioned a 'smaller form' from the West Indies. Gmelin (1791) appears to have based his description of this species entirely on that of Chemnitz (1781) and the mention of two localities has resulted in persistent confusion about its identity (Dillwyn 1817; Philippi 1846; Weinkauff 1882; Watson 1886; Iredale 1924; Clench & Abbott 1942; Abbott 1954; Fischer 1967; Bandel & Kadolsky 1982; Reid & Williams 2004). Because Chemnitz's figures (formally designated as lectotype by Clench & Abbott 1942) were from the Pacific and this form was regarded as the typical one by Gmelin, the name *Trochus nodulosus* must be applied to a Pacific taxon. Although it has been interpreted as a synonym of *N. pyramidalis* (Philippi 1846; Weinkauff 1882; Iredale 1924), the tall spire with white nodules, nodulose base and relatively narrow columella of Chemnitz's figures instead suggest a member of the *E. malaccana* group (Reid & Williams 2004); only the size of the figures (18 mm) argues against this, being 1–2 mm larger than any shells of this group. The large size, single row of nodules on the base, and rounded aperture without anterior lip are perhaps an even better match for some forms of *E. pascua* (e.g. Fig. 21G). Cook did indeed visit Easter Island in the South Seas, but his Pacific voyages also took him to localities where any of the members of the *E. malaccana* group could have been collected. In the absence of a precise type locality, *Trochus nodulosus* cannot be confidently placed in the synonymy of any particular member of the *E. malaccana* group or of *E. pascua*. For convenience it is listed under *E. malaccana s.s.* (together with other names of uncertain identity in this group). Despite these uncertainties, the name *nodulosus* has been widely used (see Synonymy below); it is, however, unavailable, being a junior primary homonym, as pointed out by Clench & Abbott (1942). Dillwyn (1817) replaced the name by *Turbo trochiformis*, probably not for this reason, but because he placed the species in the genus *Turbo* where it was preoccupied by *Turbo nodulosus* Gmelin, 1791 (Weinkauff 1882; Fischer 1967). Dillwyn's new name was likewise a junior primary homonym.

While the *E. malaccana* group was believed to be a single species (e.g. Reid 1989a, 1992; Reid & Williams 2004) its synonymy was considered straightforward. Now that it is divided into five allopatric species without diagnostic conchological differences, the lack of precise type localities has caused difficulties. The types of *Litorina rubra* Anton, 1838 are lost (Schneibs 1995) and there was no type locality, but the description of two rows of white nodules on the last whorl could apply to a member of the *E. malaccana* group (Rosewater & Kadolsky 1981) or to other nodulose species; it is here considered a dubious and forgotten name. The oldest available name in this group was claimed to be *Littorina trochoides* Gray, 1839, by Reid (1989). Unfortunately, it now appears that this name, with no original type locality, may have been based on specimens of *E. pascua* and it is here considered a *nomen dubium* (see Taxonomic History of *E. pascua* above). An alternative course of action would have been to apply to the ICZN to set aside the types of *L. trochoides* and designate a neotype to preserve prevailing usage (ICZN 1999: Art. 75.6). Nevertheless, in this case prevailing usage is incorrect; *E.* '*trochoides*' is a complex of five species, none of which has an outstanding claim to bear the name. *Litorina vilis* Menke in Philippi, 1846, is another taxon without type locality that must be considered a *nomen dubium*. The first name in this group with both type specimens and type locality is *Litorina malaccana* Philippi, 1847; this is the most widespread member and its name can be applied to the group as a whole.

The synonymies below indicate the long and confused taxonomic history of this species group. Although Gmelin (1791, following Chemnitz 1781) introduced the name *Trochus nodulosus* for shells from both the Southern Ocean and West Indies, the locality was restricted to the former (i.e. Pacific) by Dillwyn (1817), and Menke (1828) renamed the West Indian species *Litorina tuberculata*. Nevertheless, Deshayes (1843) still united Pacific and West Indian species as *Littorina nodulosa*, while recognizing the Australian *L. pyramidalis* as distinct. Philippi (1846–7) divided the nodulose littorinids into many more species on the basis of subtle differences in shell shape and sculpture; besides *Litorina pyramidalis* from Australia, he separated the West Indian species as *Litorina trochiformis* (an incorrect usage of Dillwyn's name) and in the IWP he recognized *Litorina natalensis*, *Litorina trochoides*, *Litorina vilis*, *Litorina malaccana* and later (Philippi 1851) also named *Litorina cecillei*. This arrangement was largely followed by Reeve (1857–8) and Weinkauff (1882), although Weinkauff subsequently (1883) considered *Litorina vilis* a variety of *Litorina nodosa*. In a work on shells of the South Seas, von Martens & Langkavel (1871) returned to the concept of a single nodulose species, synonymizing *trochoides*, *vilis* and the endemic Marquesan species under *Litorina pyramidalis*. Nevertheless, later von Martens (1897) distinguished the East Indian *L. vilis* (doubtfully including *L. malaccana*) from the Australian *L. pyramidalis*. Nevill (1885) had also separated these two, but used the name *L. trochoides* for the former, and also remarked that this might be the same as *L. natalensis*. It was, therefore, a retrograde step when Tryon (1887) reverted to an extraordinarily broad species concept, using the name *Tectarius nodulosus* for many of the small, prickly littorinids from the wordwide tropics (including *E. tuberculata* and *T. antonii* from the western Atlantic, *N. pyramidalis* and the *E. malaccana* group). Curiously, he included the superficially similar *E. natalensis* with *T. nodosus*.

During most of the twentieth century a broad species concept prevailed. Abbott (1954) united the *E. malaccana* group with *N. pyramidalis* under the latter name. This classification was followed in the influential monograph of IWP littorinids by Rosewater (1970), who also described *E. pascua* as a subspecies of *N. pyramidalis*. A similarly broad species concept was held by Fischer (1967, 1969, 1971) in a series of publications on nodulose littorinids, although he reinstated the oldest name, *N. nodulosa*. Meanwhile, in Australia the obvious difference between the large *N. pyramidalis* in New South Wales and small *E. austrotrochoides* in Queensland and the north of the country led Hedley (1910) to list both *T. nodulosus* and *T. malaccanus*, while Allan (1950) used the names *N. tuberculata* and *N. malaccana* respectively. Both Iredale & Allan (1940) and Endean *et al*. (1956a) commented on the likely presence of two species in eastern Australia. Based on information from reproductive anatomy, Reid (1989a) listed *N. pyramidalis*, *N. pascua* and *N. trochoides* as distinct, the last including all the members of the *E. malaccana* group. Detailed descriptions of *N. trochoides* were given by Reid (1992, 2001a), and of *N. pyramidalis* by Reid & Williams (2004). The first suggestion that *N. trochoides* was a complex of species was made by Reid (2002a), who pointed out the distinct penis of specimens from the Marquesas Islands. Molecular data showed conclusively that the tropical '*Nodilittorina*' species were genetically distant from the type species *N. pyramidalis*, and led to their placement in a separate genus, *Echinolittorina* (Williams *et al*. 2003). Finally, molecular phylogenetic analysis of the worldwide radiation of *Echinolittorina* suggested that *E. trochoides* should be divided into five allopatric taxa (Williams & Reid 2004), and these were supported as distinct species by more extensive sampling of mitochondrial COI sequences by Reid *et al*. (2006). These species are here discriminated morphologically for the first time (see Remarks on *E. malaccana* below) and three new names are introduced.

***Echinolittorina malaccana* (Philippi, 1847)**

(Figures 26C, D, 27–29)

? *Trochus nodulosus* Gmelin, 1791: 3582 (Oceano australi [southern Ocean]; lectotype (Clench & Abbott 1942) Chemnitz, 1781: pl. 163, figs 1545, 1546; in part, includes *E. tuberculata* (Menke, 1828); perhaps = *E. pascua*; not *Trochus nodulosus* Solander in Brander, 1766).

? *Littorina nodulosa*—Deshayes, 1843: 205–206 (in part, includes *E. tuberculata*).

Tectarius nodulosus—Tryon, 1887: 258, pl. 47, figs 61–64 (in part, includes *N. pyramidalis, E. tuberculata, E. marquesensis*, *T. antonii*). Melvill & Standen, 1901: 364 (in part, includes *E. omanensis*). Dautzenberg & Fischer, 1905: 149–150. Yen, 1935: 14-15.

Nodilittorina nodulosa—Fischer, 1967: 47–80 (in part, includes *N. pyramidalis*, *E. austrotrochoides*, *E. cecillei*, *E. marquesensis*). Fischer, 1969: 119–129 (in part, includes *N. pyramidalis, E. natalensis, E. omanensis, E. austrotrochoides*, *E. cecillei*, *E. marquesensis*, *E. wallaceana*). Fischer, 1971: 31–32 (in part, includes *E. natalensis*, *E. omanensis*). Starmühlner, 1974: 55, pl. 1G, 4G.

? *Turbo trochiformis* Dillwyn, 1817: 826 (new name for *Trochus nodulosus* Gmelin, 1791, not *Turbo nodulosus* Gmelin, 1791; not *Turbo trochiformis* Brocchi, 1814; type locality restricted to Southern Ocean [Pacific]).

? *Tectarius trochiformis*—H. Adams & A. Adams, 1854: 315.

? *Litorina rubra* Anton, 1838: 53 (no locality; types lost, Schneibs 1995; *nomen dubium*).

? *Tectarius rubra*—Tryon, 1887: 260.

? *Littorina trochoides* Gray, 1839: 140–141 (no locality; lectotype (Rosewater 1970) BMNH 1887.4.26.1, Fig. 21H, is conspecific with *E. pascua*; *nomen dubium*, see Taxonomic History of *E. pascua*). ? Reeve, 1858: sp. 105, pl. 18, fig. 105.

Litorina trochoides—Weinkauff, 1882: 98–99, pl. 14, figs 6, 7 (in part, includes *E. marquesensis*).

Litorina (Tectaria) trochoides—Weinkauff, 1883: 225 (in part, includes *E. marquesensis*).

Littorina (Tectus) trochoides—Nevill, 1885: 156–157 (in part, includes *E. marquesensis*, *E. omanensis*).

Nodilittorina (Nodilittorina) trochoides—Reid, 1989a: 100 (in part, includes *E. austrotrochoides*, *E. wallaceana*, *E. cecillei*). Reid, 1992: 202, figs 1j (penis), 2i (oviduct), pl. 3a–c (in part, includes *E. austrotrochoides*, *E. cecillei*, *E. omanensis*). Subba Rao, 2003: 120, pl. 19, figs 5, 6.

Nodilittorina trochoides—Mak, 1995: 53–59, figs 1a, 2a (spawn). Tan & Chou, 2000: 61, fig. Reid, 2001a: 442–444, figs 2G, H, 3C (penis) (in part, includes *E. austrotrochoides*, *E. cecillei*, *E. wallaceana*). Swennen *et al*., 2001: 113, fig. 310. Reid, 2002a: 259–281, fig. 2E (penis) (in part, includes *E. austrotrochoides*, *E. cecillei*, *E. wallaceana*). Lee & Chao, 2003: 32, pl. 3, fig. 62. Thach, 2005: 54, pl. 8, fig. 26.

Echinolittorina trochoides—Williams *et al*., 2003: 83 (in part, includes *E. austrotrochoides*, *E. cecillei*, *E. wallaceana*). Sanpanich *et al*., 2004: figs 2b, 3 (map).

Echinolittorina trochoides A—Williams & Reid, 2004: 2227–2251.

? *Litorina vilis* Menke in Philippi, 1846a: 145–146, *Litorina* pl. 2, fig. 21 (no locality; types not in SMF, presumed lost; *nomen dubium*). Weinkauff, 1882: 93, pl. 13, figs 9, 12.

Tectarius vilis—H. Adams & A. Adams, 1854: 315. Hidalgo, 1905: 209.

? *Littorina vilis*—Reeve, 1857: sp. 12, pl. 2, fig. 12.

Littorina (Nodilittorina) vilis—von Martens, 1897: 204–205 (in part; includes *E. austrotrochoides*, *E. marquesensis*, *E. wallaceana*).

Tectarius (Nodilittorina) vilis—Oostingh, 1927: 3. Kuroda, 1941: 83.

Nodilittorina vilis—Habe, 1951: 90 (in part, includes *E. cecillei*).

Litorina malaccana Philippi, 1847b: 15, *Litorina* pl. 6, fig. 17 (Pulo Pinang [Penang, Malaysia]; lectotype BMNH 20050028/1 (here designated, Fig. 27A) + 6 paralectotypes BMNH 20050028/2, seen). Dunker, 1882: 111 (in part, includes *E. cecillei*). Weinkauff, 1882: 90–91, pl. 13, figs 1, 4.

Littorina malaccana—Reeve, 1857: sp. 7, pl. 2, fig. 7.

Litorina (Tectaria) malaccana—Weinkauff, 1883: 225.

Tectarius malaccanus—Adam & Leloup, 1938: 81 (in part, includes *E. wallaceana*). Suvatti, 1950: 47.

Littorina monilifera Souleyet in Eydoux & Souleyet, 1852: 559, pl. 31, figs 37–39 (Touranne, Cochinchine [Da Nang, Vietnam]; 3 syntypes BMNH 1854.7.24.390, seen; 8 syntypes MNHN, seen). Fischer, 1891: 171.

? *Litorina nodosa*—Weinkauff, 1883: 226 (in part, includes *E. australis*, *E. subnodosa*, *E. natalensis*, *E. malaccana* group; not Gray, 1839 = *E. australis*).

Littorina pyramidalis—von Martens, 1887: 192 (not Quoy & Gaimard, 1833 = *N. pyramidalis*).

Nodilittorina pyramidalis—Abbott, 1954: 456 (in part, includes *N. pyramidalis*, *E. austrotrochoides*, *E. cecillei*, *E. wallaceana*; not Quoy & Gaimard, 1833). Berry, 1986: fig. 1 (spawn) (not Quoy & Gaimard, 1833). Atapattu, 1972: 161 (not Quoy & Gaimard, 1833). Ma, 2004: 33, fig. 12 (map, as '*N. exigua*' in error), pl. 14, fig. G (not Quoy & Gaimard, 1833).

Nodilittorina (Nodilittorina) pyramidalis pyramidalis—Rosewater, 1970: 481–484, pl. 370, figs 3–5, 8, 9, pl. 371, fig. A (radula), B (penis), pl. 372 (map) (in part, includes *N. pyramidalis*, *E. pascua*, *E. austrotrochoides*, *E. cecillei*, *E. marquesensis*, *E. wallaceana*, *E. cinerea*; not Quoy & Gaimard, 1833).

Nodilittorina (Nodilittorina) pyramidalis—Ma, 1985: 191–192, pl. 1, fig. 4 (not Quoy & Gaimard, 1833).

Littorina pyramidalis pyramidalis—Veerappan, 1988: 77–82, figs 2 (headfoot), 3 (penis), 6 (radula).

Taxonomic history: In the Synonymy above, those entries with a query apply to unspecified members of the *E. malaccana* group (see remarks on *E. malaccana* group above). As established earlier (see Taxonomic History of *E. pascua*), the putative lectotype and paralectotypes of *L. trochoides* Gray, 1839, are conspecific with *E. pascua* and the name is considered a *nomen dubium*. This necessitates a change of name for this species and its species group.

The oldest name for the present species with both type specimens and type locality (and therefore unequivocal identity) is *Litorina malaccana* Philippi, 1847. The type material from the Cuming Collection has been newly identified in BMNH, based on an original label bearing identification and locality in Philippi's hand. Philippi's material was collected by his brother, but it is known that he exchanged material with Cuming. Since its introduction, the specific name *malaccana* has seldom been used, having been applied to members of this species group (most recently by Allan 1950, for *E. austrotrochoides*) and to *E. natalensis* (Dautzenberg 1932, 1929, 1932).

Diagnosis: Shell high-conical, spire profile straight to slightly convex, base slightly convex; 2 rows of 9–18 rounded nodules on last whorl, peripheral nodules crossed by 2–3 threads, threads on base often nodulose; aperture rounded anteriorly, anterior lip not projecting; grey or black with white to cream nodules. Penial filament triangular, pointed, 0.4–0.5 total length of penis; copulatory bursa divided, ventral branch equal to or longer than dorsal branch. India, Southeast Asia, South China Sea, Philippines, Sulawesi; restricted to continental settings. COI: GenBank AJ623055, AJ623056.

Material examined: 165 lots (including 57 penes, 30 pallial oviducts, 6 sperm samples, 5 radulae).

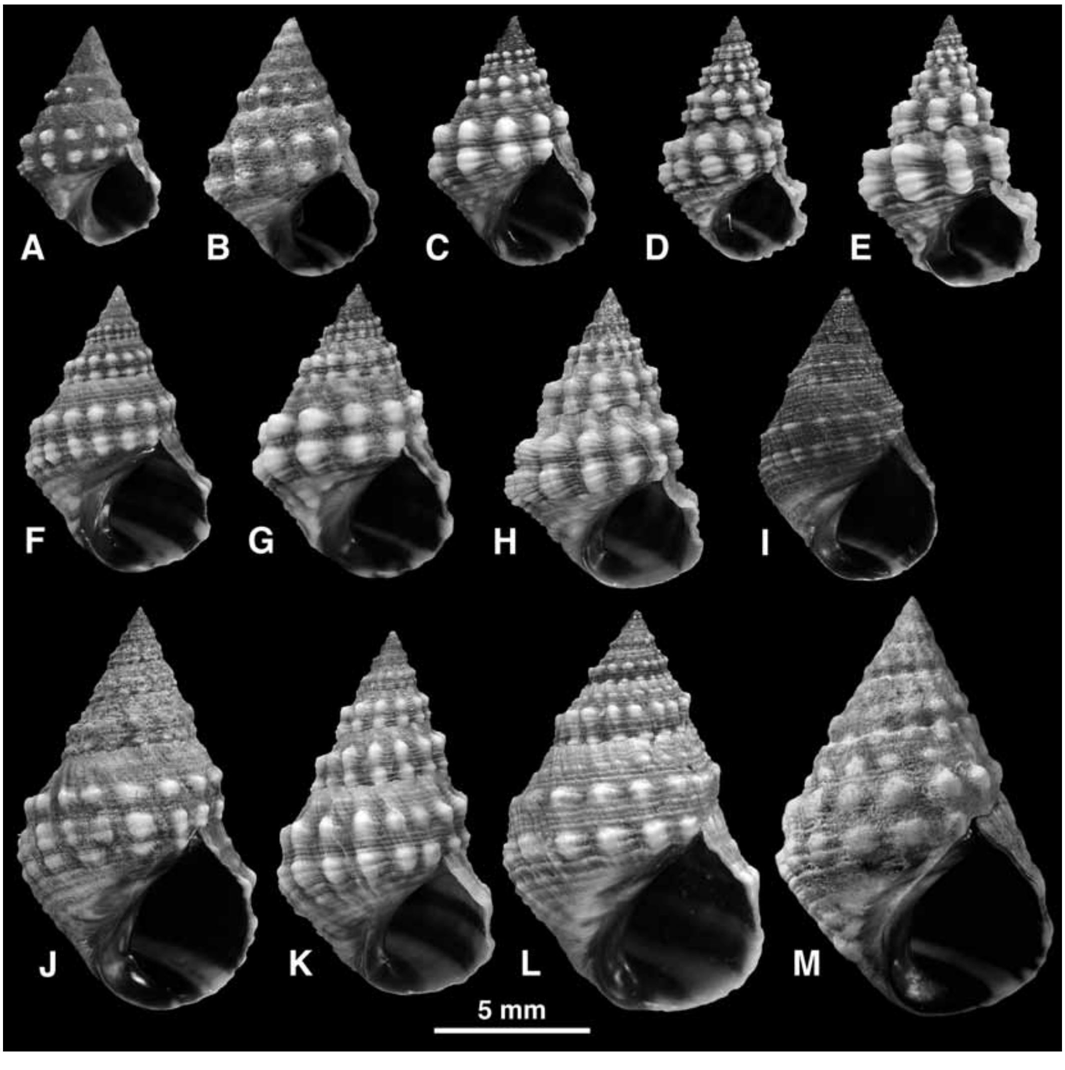

FIGURE 27. *Echinolittorina malaccana*. **A,** *Litorina malaccana* Philippi, 1847, lectotype, Penang, Malaysia (BMNH 20050028/1). **B,** Cape D'Aguilar, Hong Kong (BMNH 20050026). **C, G,** Kudat, Sabah, Malaysia (BMNH 20050024). **D, E,** Bunaken I., Manado, Sulawesi, Indonesia (BMNH 20020615). **F,** Kamenti, Kapataran, Sulawesi, Indonesia (BMNH 20020605). **H, K,** Malapacao I., N Palawan, Philippines (BMNH 20050027). **I, J,** Kovalam, Kerala, India (BMNH 20000714). **L,** Sanya, Skali Molin, Hainan, China (BMNH 20050025. **M,** Polhena, Matara, Sri Lanka (BMNH 20050029).

Shell (Fig. 27): Mature shell height 5.0–16.6 mm. Shape conical to high-conical (H/B = 1.34–1.88; SH = 1.63–2.59); spire whorls almost flat to lightly rounded, suture not distinct; spire profile straight to slightly convex; periphery of last whorl rounded; base profile slightly convex. Columella short, concave, hollowed but not flared at base, anterior lip rounded (slightly projecting in juveniles); usually a small eroded parietal and pseudumbilical area. Sculpture of last whorl: 2 (rarely 3, Fig. 27J, M) rows of rounded nodules, at periphery and shoulder, axially aligned in 9–18 pairs, occasionally fused to form axial ribs in strongly sculptured shells (Fig. 27E); entire surface (including base) with 12–26 narrow spiral threads and microstriae, peripheral nodules crossed by 2–3 major threads; basal threads (below peripheral nodules) 3–8, often bearing small nodules (Fig. 27A–H, K, M). Protoconch 0.28–0.30 mm diameter, 2.6–2.7 whorls. Colour: black to dark brown (fading to blue-grey), paler at suture and on base, nodules white to cream; sometimes black with three cream spiral bands corresponding to two rows of nodules and band on base; aperture dark brown with pale band at base, sometimes two additional pale bands above; columella dark brown.

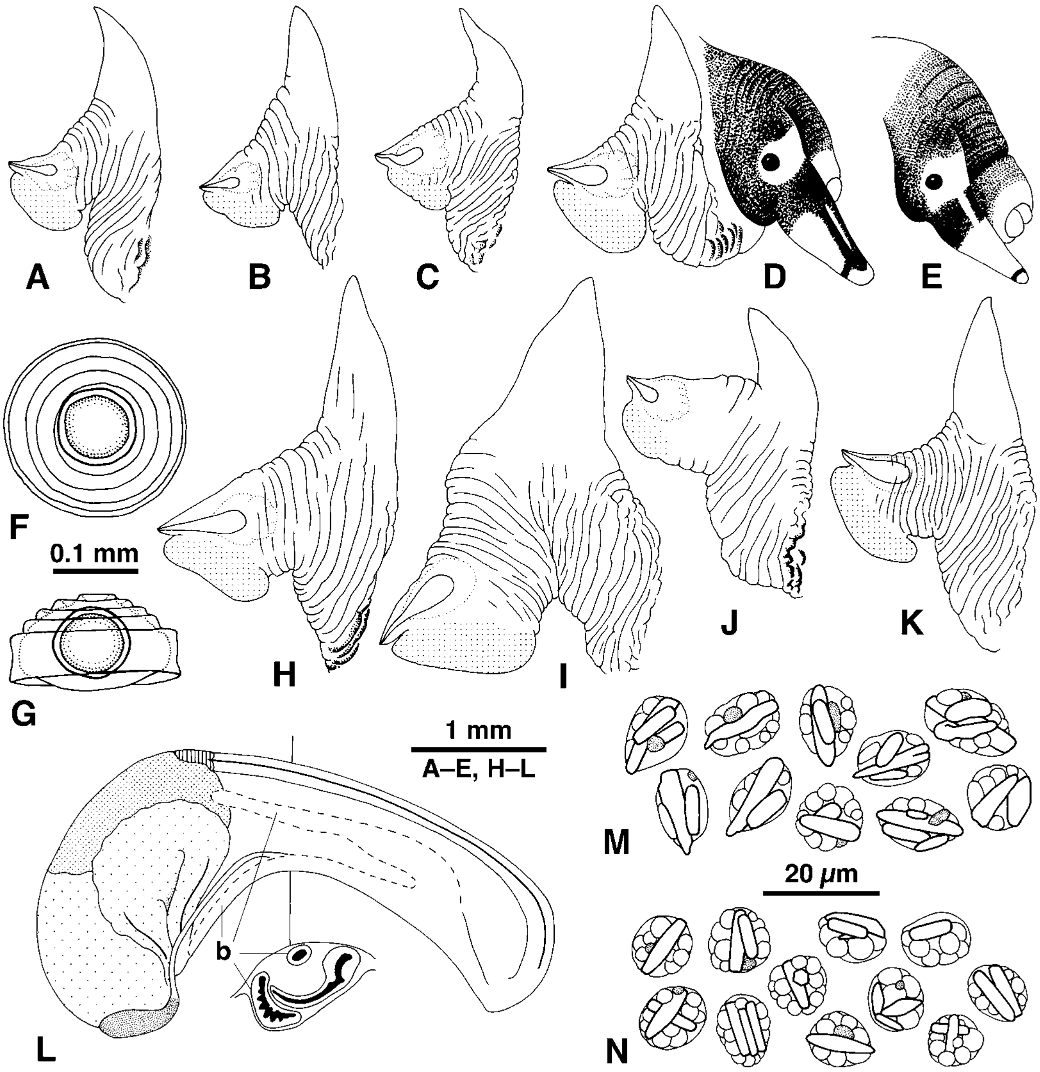

FIGURE 28. *Echinolittorina malaccana*. **A–D, H–K,** penes. **D, E,** heads. **F, G,** pelagic egg capsule (after Mak 1995). **L,** pallial oviduct, with transverse section. **M, N,** paraspermatozoa. **A, B,** Kudat, Sabah, Malaysia (BMNH 20050024; shell H **A** = 7.9 mm, **B** = 7.6 mm). **C, L,** Santubong, Sarawak, Malaysia (BMNH 20020624; shell H **C** = 6.9 mm, **L** = 8.9 mm). **D, E,** Nha Trang, Vietnam (BMNH 20010354; shell H **D** = 7.4 mm, **E** = 6.4 mm). **F, G,** Hong Kong. **H, M,** Polhena, Matara, Sri Lanka (BMNH 20050029; shell H = 11.0 mm). **I,** Kamenti, Kapataran, Sulawesi, Indonesia (BMNH 20020605; shell H = 10.5 mm). **J,** Galle Fort, Sri Lanka (BMNH 20050030; shell H = 7.6 mm). **K,** Xi Zi, Kaohsiung, Taiwan (BMNH 20050031; shell H = 8.8.mm). **N,** Shek O, Hong Kong (BMNH 20050032). Abbreviation: b, copulatory bursa. Shading conventions as in Figure 3; stippled granules in paraspermatozoa are probable nuclei.

Animal (Fig. 28): Head (Fig. 28D, E) black; tentacle unpigmented with two black longitudinal stripes at base usually fused to form a transverse band and two spots or black band behind tip, tentacle often darker with black stripes extending almost to tip, always unpigmented around eye and across base; sides of foot black. Opercular ratio 0.46–0.62. Penis (Fig. 28A–D, H–K): filament triangular, tapering to pointed tip, smooth, 0.4–0.5 total length of penis; mamilliform gland equal to or smaller than glandular disc, borne together on stout projection of base; penis unpigmented or slightly pigmented at base; sperm groove extends to tip. Euspermatozoa 71–76 µm; paraspermatozoa (Fig. 28M, N) oval to spherical, 10–19 µm diameter, filled with large round granules, usually one granule more refringent than others (probable nucleus), rod-pieces straight-sided to fusiform, ends rounded, not (or only slightly) projecting. Pallial oviduct (Fig. 28L): bursa opening at one quarter to one third length of straight section (from anterior), divided into two, ventral branch (extending beneath albumen gland) 1.0–1.3 length of dorsal branch that extends back to albumen gland. Spawn (Fig. 28F, G) an asymmetrically biconvex pelagic capsule 154–207 µm, cupola-shaped upper side sculptured by 4–5 concentric rings, containing single ovum 57-66 µm diameter (Berry 1986; Mak 1995). Development predicted to be planktotrophic.

Radula (Fig. 26C, D): Relative radula length 1.86–5.28. Rachidian: length/width 1.29–1.38; tip of major cusp pointed. Lateral and inner marginal: major cusp on each of similar size, tips rounded to slightly pointed. Outer marginal: 6–8 cusps.

Range (Fig. 29): India, mainland coast of Southeast Asia, Southern China, Taiwan, Philippines, Borneo, Sulawesi. Range limits: Colaba, Bombay, India (BMNH); Madras, India (BMNH, ?); Polhena, Matara, Sri Lanka (BMNH 20050029); Cape Negrais, Arakan, Burma (BMNH 1882.8.7.55, ?); Andaman Islands (IRSNB); Pulau Pandan, Sumatra (ZMA, ?); Spider I., Fukien, China (USNM 340905, ?); Zhejiang Prov., China (Ma 2004, ?); Tiaoshi, 20 km NW Keelung, Taiwan (BMNH); Chialoshui, Taiwan (BMNH); Duncalan Beach, Catarman, Samar I., Philippines (BMNH); Panglao, Bohol I., Philippines (BMNH); Kamenti, Kapataran, Sulawesi (BMNH); Bola, Buton I., Sulawesi (BMNH); Latuhalat, Ambon, Indonesia (NNML); Hatuhuran, Piru Bay, Seram (NNML); Sungailiat, Bangka I., Indonesia (ZMA); Tandjung Klajang, Belitung I., Indonesia (F. de Graaf Colln, ?); Bantam, Java (USNM 260880, ?); Jakarta Bay, Java (ZMA, ?).

Unequivocal identification requires anatomical or molecular information; the records listed with a query are based on shells alone and confirmation is required. In China the species extends as far north as Zhejiang Province (Ma 2004). The distribution in northern Java, Kalimantan, western Sulawesi and southern Philippines is poorly known owing to lack of collecting in these areas. However, the absence from southern Java, the Moluccas and the southern Banda Sea is apparently real (see records of *E. wallaceana* in this region, Fig. 34). One uncertainty is whether *E. malaccana* occurs on the southern shores of the Java Sea; shell material from northwestern Java is here mapped as this species, but could belong to *E. wallaceana* (Fig. 34). Syntopy with the conchologically almost identical *E. wallaceana* has been recorded at six localities in western Sulawesi, Ambon and the central Philippines (see Range of *E. wallaceana*). Another uncertainty is the identification of three samples from Ambon and another from Seram; characters of the penis and oviduct are those of *E. malaccana* and *E. austrotrochoides*, but no molecular data are available to distinguish between these possibilities. Ambon and Seram are closer to the known range of *E. malaccana* (600 km to northeastern Sulawesi) than to that of *E. austrotrochoides* (900 km to Arnhemland in northern Australia), so the records are tentatively included here for the former. However, these islands lie on the eastern (Australian) side of the ‘oceanic eastern Indonesian corridor’ that has been proposed as the barrier that separates these two species (Reid *et al*. 2006).

Habitat and ecology: This species is common in the upper littoral fringe, reaching higher levels than any sympatric congener. It has been found on basalt, volcanic tuff, granite, shale, coral limestone, sandstone, concrete and rarely on mangrove trunks, in sheltered to moderately exposed sites. It is most abundant in continental settings, and is more tolerant of turbidity and slightly estuarine conditions than any other *Echinolittorina* in the IWP. It is generally uncommon on karstic limestone in clear-water habitats with fringing reefs, as in the Philippines and Sulawesi.

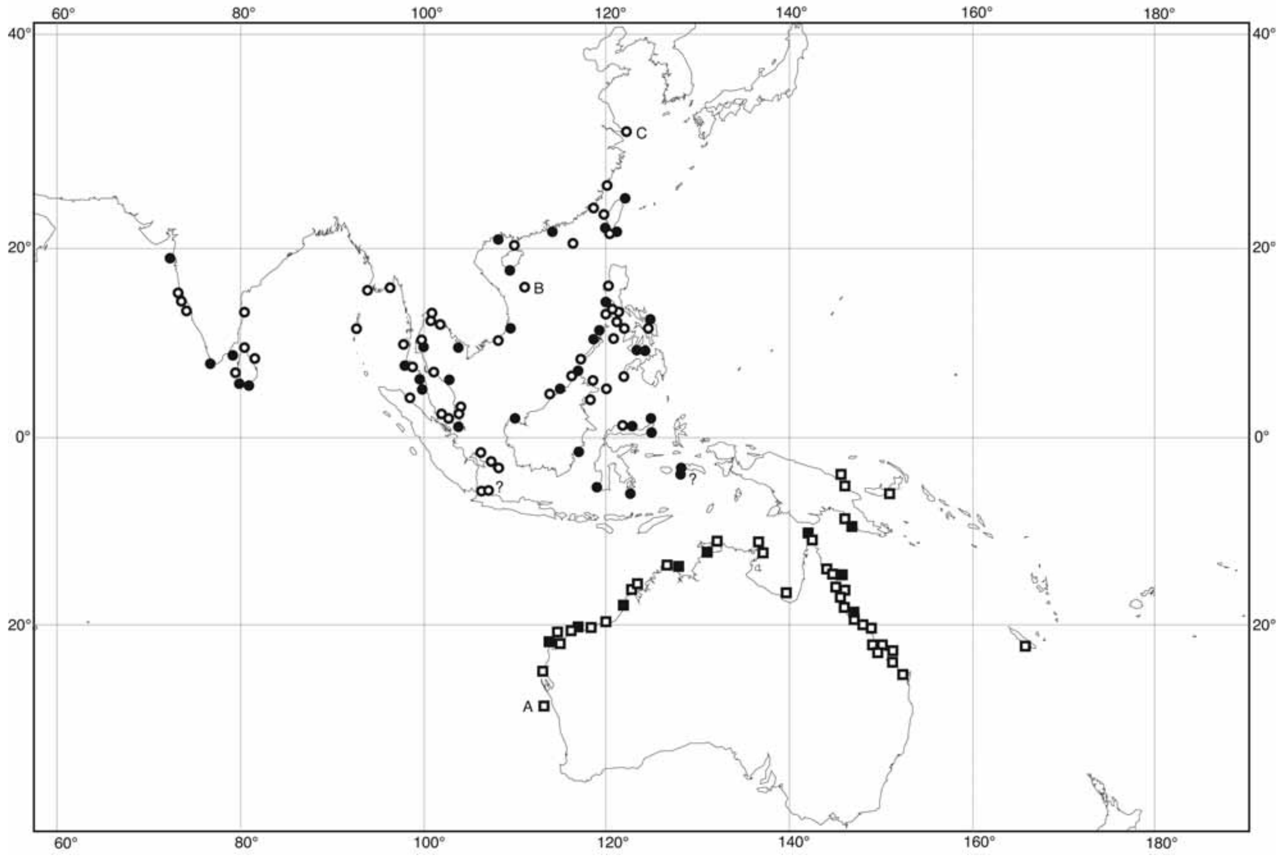

FIGURE 29. Distribution of *Echinolittorina malaccana* (circles) and *E. austrotrochoides* (squares). Solid symbols are records confirmed by COI mtDNA sequences (35 localities listed in Reid *et al*. 2006) or anatomy (distinguishing these two species from others in the *E. malaccana* group, but not from each other); open symbols are based on shells alone. Literature records: A, Johnson & Black (1997); B, Ma (1985); C, Ma (2004). The queries indicate uncertainty of identification in two significant areas (see Range of *E. malaccana*).

In Sri Lanka it is more numerous on western and southern coasts than elsewhere (Atapattu 1972); it is larger at higher levels and reaches densities of 150 per 1/16 m^2 at Mt Lavinia (Starmühlner 1974). In the nearby Gulf of Mannar it occupies the entire littoral fringe, above the level of *E. leucosticta*, and larger animals are again found at higher levels (Rao & Sundaram 1974; Pillai & Appukuttan 1980). Zonation has been recorded in Thailand (Tsuchiya & Lirdwitayapasit 1986) and here it has occasionally been found on trees at the seaward fringes of mangrove forests (*Rhizophora* and *Avicennia*, Sanpanich *et al*. 2004). Its ecology has been extensively studied in Hong Kong and southern China, where it reaches densities of 162 m^{-2} (Dudgeon & Yipp 1986; Yipp *et al*. 1986; Yi & Li 1990; You 1990; Williams 1994). The species is common in the sheltered muddy conditions of Tolo Harbour as well as on the open coast of Hong Kong, and can occur up to 6.5 m above mean high-water of spring tides under strongly exposed conditions (Ohgaki 1985a). In zonation studies involving field manipulations it is a dominant competitor over *E. radiata* (Dudgeon & Yipp 1986). At high levels it may endure long periods of quiescence, becoming active after rain (Britton & McMahon 1992), and shows high resistance to desiccation (50% survived 64 days; Yipp *et al*. 1986). At lower levels it moves upshore to feed when wetted by waves and returns to crevices as the tide recedes (Williams 1994). The snails graze the epilithic biofilm of cyanobacteria and control its development (Mak & Williams 1999). In Hong Kong spawning was recorded between April and October (Mak 1998), while in Penang breeding was observed during March–June and spawning took place mainly during spring tides (Berry 1986).

Remarks: This was considered to be one of the best known of the IWP *Echinolittorina* species, following recent redescription (Reid 1992, 2001a) and numerous ecological studies (see above). Nevertheless, sequence analysis of mitochondrial DNA revealed five divergent and reciprocally monophyletic clades with almost entirely allopatric distributions (Williams & Reid 2004; Reid *et al*. 2006). Closer examination found corresponding small but consistent anatomical differences (shapes of penial filament and copulatory bursa) among four clades, implying nuclear genetic differentiation among them. Furthermore, two of the clades (*E. malaccana* and *E. wallaceana*, see Range of the latter) are occasionally syntopic, and anatomical characters remain distinct at the localities of sympatry. This is evidence for the species status of these four clades under both phylogenetic and biological species concepts (Reid *et al*. 2006; Material and Methods). However, the two most closely related of the five clades distinguished by the mitochondrial COI gene (i.e. *E. malaccana* and *E. austrotrochoides*) are entirely allopatric, and there is no diagnostic morphological difference between them (slight differences in shell and penis are pointed out below). The genetic (K2P) distance between them based on COI is 2.70% (cf. 6.24-8.99% for comparisons among the four morphological groups of the *E. malaccana* group; Reid *et al*. 2006). The closest approach between their confirmed ranges is 1000 km (a straight line from Sulawesi to NW Australia, or perhaps about 1300 km by transport in the Indonesian Throughflow current, but see discussion below about uncertainty of distribution in the Banda Sea), which is less than the known maximum dispersal distances of *Echinolittorina* species (Reid *et al*. 2006; Discussion), so that migration and gene flow from north to south might theoretically occur if interbreeding were possible. However, the intervening area (southern Banda, Flores and Timor Seas) is, so far as is known, occupied by *E. wallaceana* alone, and this stretch of oceanic habitat is apparently unsuitable for either *E. malaccana* or *E. austrotrochoides*. These two are here considered distinct species, but it would be desirable to test this decision with a suitable nuclear genetic marker.

Comparisons among the five species of the *E. malaccana* group are summarized in Table 1. Aside from the genetic data, the most obvious differences are in distributional range, for only at six localities in western Sulawesi, Ambon and the central Philippines are two (*E. malaccana* and *E. wallaceana*) known to be sympatric. There is a striking contrast in habitat type; both *E. malaccana* and its sister *E. austrotrochoides* are found on productive, nutrient-rich continental coastlines and are tolerant of some freshwater influence and turbidity, whereas the remaining three are found on oceanic coasts with regimes of low productivity (Rutgers University Primary Productivity Study). Differences in the shell are too slight to be diagnostic, although some trends can be seen. In comparison with *E. austrotrochoides* (Fig. 30) the shell of *E. malaccana* often shows a more convex spire and base, and the columella is not flared or projecting (except in immature shells, Fig. 27A). Where they are sympatric, *E. malaccana* shows small nodules on the basal ribs, whereas *E. wallaceana* (Fig. 38) does not, but this distinction is not consistent across their ranges. The shape of the penial filament is strikingly large and elongate in *E. wallaceana*, narrow in *E. marquesensis* and small in *E. cecillei*, although in the last of these there is variation that overlaps with all of the other taxa. The filament of *E. austrotrochoides* is often slightly more sharply tapered at the tip than the triangular filament of *E. malaccana*. In females, the copulatory bursa is undivided in *E. wallaceana*, but bifurcates into ventral and dorsal branches in the others. The ventral branch is as large or larger than the dorsal in *E. malaccana* and *E. austrotrochoides*, but much smaller in *E. marquesensis* and of intermediate size in *E. cecillei*.

Members of the *E. natalensis* group can be extremely similar in shell characters to the *E. malaccana* group. In *E. natalensis* (Fig. 13) the shell is slightly broader than in the *E. malaccana* group and there are usually three rows of sharp nodules on the last whorl (not two as in the *E. malaccana* group). *Echinolittorina omanensis* (Fig. 17) is even more similar in outline, but again often bears three, not two, rows of nodules. Nodulose forms of *E. pascua* (Fig. 21F–H) are distinguished by the short, recurved columellar base, partial fusion of the nodules to form axial flanges, concave profile above the shoulder, absence of such conspicuously white nodules, stronger and more regular spiral threads over the surface, and presence of a single row of small nodules of the base.

TABLE 1. Summary of characters for identification of the five species of the *Echinolittorina malaccana* group.

Character	*E. malaccana*	*E. austrotrochoides*	*E. cecillei*	*E. marquesensis*	*E. wallaceana*
1. Geographical range	Fig. 29 India , SE Asia, China, Philippines, Borneo, Sulawesi	Fig. 29 Australia (Queensland, Northern Territory, Western Australia), New Guinea	Fig. 34 Ryukyu Is, S Japan, Ogasawara Is, Mariana Is	Fig. 34 Marquesas Is	Fig. 34 S Java, Banda Sea, Moluccas, Philippines
2. Habitat type	continental	continental	oceanic	oceanic	oceanic
3. Shell —spire profile	Fig. 27 straight to convex	Fig. 30 straight to concave	Fig. 32 straight to convex	Fig. 35 convex	Fig. 38 straight
—base profile	convex	concave	convex	convex	concave to convex
—columella; anterior lip	not flared; rounded	flared; projecting	flared; rounded	flared; rounded	flared; rounded
—basal threads	usually nodulose	often nodulose	rarely nodulose	often nodulose	rarely nodulose
4. Penis —filament shape	Fig. 28A–D, H–K triangular	Fig. 31A–I tapering	Fig. 33A–M small, tapering	Fig. 36A–E narrow	Fig. 39A–H elongate
—filament to total length	0.4–0.5	0.5	0.4-0.5	0.4–0.5	0.5–0.6
5. Copulatory bursa	Fig. 28L divided; ventral branch equal to or longer than dorsal branch	Fig. 31J divided; ventral branch equal to or longer than dorsal branch	Fig. 33N, O divided; ventral branch less than half length of dorsal branch	Fig. 36F, G divided; ventral branch less than half length of dorsal branch	Fig. 39I undivided; dorsal bursa only

Like other nodulose members of the *E. malaccana* and *E. natalensis* groups, the sculpture is strongest and the spire tallest in shells from limestone (Fig. 27D, E, H, K). In shells from the Indian Ocean (Fig. 27I, J, M) the spire whorls are flatter than elsewhere, and nodules sometimes unusually weak (Fig. 27I).

DNA sequence analysis of the COI gene clearly indicates that *E. malaccana* and *E. austrotrochoides* are sister species, but do not resolve the relationships among the remaining members of this group (Williams & Reid 2004; Reid *et al*. 2006). The presence of the unique synapomorphy of the bifurcate bursa in four members and normal bursa in *E. wallaceana*, might suggest that the latter is the basal member.

The distribution of *E. malaccana* appears to be limited by its requirement for continental oceanographic conditions with high primary productivity (Rutgers University Primary Productivity Study). It has been suggested that this explains its absences from the oceanic eastern Indonesian corridor through the Banda Sea and from western Sumatra and southern Java, areas that are occupied instead by *E. wallaceana* (Reid *et al*. 2006; compare Figs 29 and 34). However, recently new material has been seen from Ambon, geographically within the Banda Sea, but on the eastern side of the oceanic corridor. Identification of this material would require genetic data. If it could be confirmed as *E. malaccana* (as suggested by proximity) then this species evidently crosses the supposed oceanic barrier. If, on the other hand, it is *E. austrotrochoides*, then the distribution of that species is more extensive than previously known; furthermore, the gap between the ranges of these two sister species would then be reduced to just 600 km. Records of *Echinolittorina* species in the Banda Sea are not numerous (see Fig. 34) and their distribution requires further study.

In India *E. malaccana* does not extend north of Mumbai on the west coast nor of Chennai on the east coast, owing to lack of suitable rocky substrate. Molecular phylogeographic analysis has shown that *E. malaccana* has a deep genetic divergence between one clade in the Indian and another in the Pacific Ocean, reflecting episodes of isolation during the low sea levels of glacial intervals (Reid *et al*. 2006) and perhaps continuing limitation of gene flow through the Strait of Malacca. This disjunction may explain the distinctive shell morphology of specimens from the Indian Ocean.

Echinolittorina austrotrochoides **new species**

(Figures 26E, F, 29–31)

Littorina (Nodilittorina) vilis—von Martens, 1897: 204–205 (in part; includes *E. malaccana*, *E. marquesensis*, *E. wallaceana*; *Litorina vilis* Menke in Philippi, 1846, is a *nomen dubium*).

Tectarius malaccanus—Hedley, 1910: 355 (not Philippi, 1847). T.A. Stephenson *et al*., 1931: 61.

Nodilittorina malaccana—Allan, 1950: 80 (not Philippi, 1847).

Nodilittorina pyramidalis—Endean *et al*., 1956a: 127 (in part, includes *N. pyramidalis*; not Quoy & Gaimard, 1833). Wilson & Gillett, 1971: 30, pl. 11, figs 11, 11a (in part, includes *N. pyramidalis*; not Quoy & Gaimard, 1833).

Nodilittorina (Nodilittorina) pyramidalis pyramidalis—Rosewater, 1970: 481–484, pl. 326, figs 9, 11, pl. 372 (map) (in part, includes *N. pyramidalis*, *E. pascua*, *E. malaccana*, *E. cecillei*, *E. marquesensis*, *E. wallaceana*, *E. cinerea*; not Quoy & Gaimard, 1833).

Nodilittorina (Nodilittorina) pyramidalis—Wilson, 1993: 147, pl. 18, fig. 5a, b (in part, includes *N. pyramidalis*; not Quoy & Gaimard, 1833).

Nodilittorina nodulosa—Fischer, 1967: 47–80 (in part, includes *N. pyramidalis*, *E. malaccana*, *E. cecillei*, *E. marquesensis*; *Trochus nodulosus* Gmelin, 1791 = *E. malaccana* group or *E. pascua*). Fischer, 1969: 119–129 (in part, includes *N. pyramidalis*, *E. natalensis*, *E. omanensis*, *E. malaccana*, *E. cecillei*, *E. marquesensis*, *E. wallaceana*).

Nodilittorina (Nodilittorina) trochoides—Reid, 1992: 202 (in part, includes *E. malaccana*, *E. cecillei*, *E. omanensis*; *L. trochoides* Gray, 1839 is a *nomen dubium*).

Nodilittorina trochoides—Reid, 2001a: 442–444 (in part, includes *E. malaccana*, *E. cecillei*, *E. wallaceana*).

Echinolittorina trochoides—Williams *et al*., 2003: 83 (in part, includes *E. malaccana*, *E. cecillei*, *E. wallaceana*). Reid & Williams, 2004: 85 (in part, includes *E. malaccana*, *E. cecillei*, *E. wallaceana*).

Echinolittorina trochoides B—Williams & Reid, 2004: 2227–2251.

Types: Holotype AMS C205631 (Fig. 30A); 6 dry paratypes AMS C205632; 37 dry paratypes BMNH 20050036; 67 alcohol paratypes BMNH 20050041 (Fig. 31A, B, F, J–L); Picnic Bay, Magnetic Island, Queensland, Australia.

Etymology: Latin, southern *trochoides*, as a reminder of the former application of that name to this group of species.

Taxonomic history: See also remarks on *E. malaccana* group and Synonymy of *E. malaccana*. Until molecular data were available, this species was not distinguished from other members of the *E. malaccana* group. It was referred to as *E. trochoides* B by Williams & Reid (2004) and Reid *et al*. (2006).

Diagnosis: Shell conical, spire profile straight to slightly concave, base slightly concave; 2 rows of 8–17 nodules on last whorl, peripheral nodules crossed by 2–3 threads, threads on base sometimes nodulose; projecting anterior lip, aperture trapezoid; grey or black with white to cream nodules. Penial filament tapering, half total length of penis; copulatory bursa divided, ventral branch equal to or longer than dorsal branch. Australia, New Guinea. COI: GenBank AJ623053, AJ623054.

Material examined: 95 lots (including 15 penes, 9 pallial oviducts, 3 sperm samples, 3 radulae).

Shell (Fig. 30): Mature shell height 5.0–15.4 mm. Shape conical to high-conical (H/B = 1.31–1.69; SH = 1.62–2.17); spire whorls lightly rounded, suture not distinct; spire profile straight to slightly concave; periphery of last whorl angled or rounded; profile of base slightly concave. Columella concave, hollowed at base, flared to form projecting anterior lip; apertural outline trapezoid; usually a small eroded parietal and pseudumbilical area. Sculpture of last whorl: 2 rows of rounded to pointed nodules, at periphery and shoulder, axially aligned in 8–17 pairs; entire surface (including base) with 14–24 strong narrow spiral threads and microstriae, peripheral nodules crossed by 2–3 major threads; basal threads (below peripheral nodules) 5–8, sometimes bearing small nodules (Fig. 30G–I). Protoconch 0.26 mm diameter, 2.6 whorls. Colour: black to dark brown (fading to blue-grey), paler at suture and on base, nodules white to cream; aperture dark brown with pale band at base; columella dark brown.

Animal (Fig. 31): Head black; tentacle unpigmented with two black longitudinal stripes at base usually fused to form a transverse band and two spots or black band behind tip, tentacle may be darker with black stripes extending almost to tip, always unpigmented around eye and across base; sides of foot black. Opercular ratio 0.49–0.60. Penis (Fig. 31A–I): filament narrowly triangular, tapering to pointed tip, smooth, half total length of penis; mamilliform gland equal to or smaller than glandular disc, borne together on stout projection of base; penis unpigmented or slightly pigmented at base; sperm groove extends to tip. Euspermatozoa 72–76 µm; paraspermatozoa (Fig. 31K, L) oval to spherical, 9–22 µm diameter, filled with round granules, rod-pieces straight-sided to fusiform, ends rounded, not (or only slightly) projecting. Pallial oviduct (Fig. 31J): bursa opening at one quarter to one third length of straight section (from anterior), divided into two, ventral branch (extending beneath albumen gland) 1.0–1.3 length of dorsal branch that extends back to albumen gland. Development predicted to be planktotrophic.

Radula (Fig. 26E, F): Relative radula length 2.39–5.58. Rachidian: length/width 1.14–1.41; tip of major cusp pointed. Lateral and inner marginal: major cusp on each of similar size, tips rounded to pointed. Outer marginal: 6–8 cusps.

Range (Fig. 29): Tropical Australia, eastern New Guinea, New Caledonia. Range limits: Manam I., Papua New Guinea (IRSNB, ?); Cape Dampier, New Britain, Papua New Guinea (AMS, ?); Ela Beach, National Capital District, Papua New Guinea (BMNH 20050035); Point Vernon, Hervey Bay, Queensland, Australia (AMS C386753); Point Quobba, Western Australia (AMS); Wallabi Group, Abrolhos Is, Western Australia (Johnson & Black 1997); N'Go Bay, New Caledonia (USNM 725032, ?).

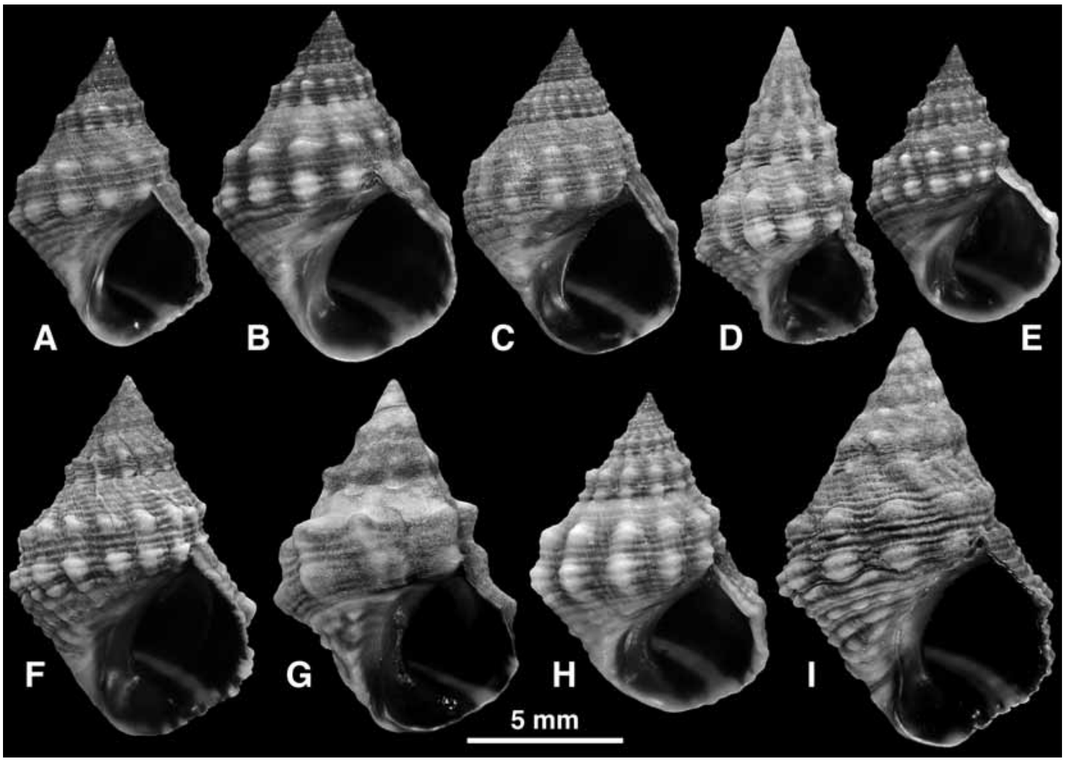

FIGURE 30. *Echinolittorina austrotrochoides* new species. **A,** holotype, Picnic Bay, Magnetic I., Queensland, Australia (AMS C205631). **B, C,** St Paul's Mission, Moa I., Torres Strait, Queensland, Australia (BMNH 20050033). **D,** Karratha, Western Australia (BMNH 20050034). **E,** Ela Beach, National Capital District, Papua New Guinea (BMNH 20050035). **F, G,** Gantheaume Point, Broome, Western Australia (BMNH 20050037). **H,** Point Murat, Cape Vlamingh, Western Australia (BMNH 20050038). **I,** Fall Point, Roebuck Bay, Western Australia (BMNH 20050039).

Unequivocal identification requires anatomical or molecular information; those records listed with a query are based on shells alone and confirmation is required. The southern limit in eastern Australia is Point Vernon in Hervey Bay (Endean *et al.* 1956a; Reid & Williams 2004). Only a single shell has been seen from New Caledonia (USNM 725032) despite intensive collecting effort there. The distribution in New Guinea and nearby islands is poorly documented. However, the absence from southern Java, the Moluccas and the southern Banda Sea is apparently real (see records of *E. wallaceana* in this region, Fig. 34). Specimens with the anatomical features of *E. malaccana* and *E. austrotrochoides* have been seen from Ceram and Ambon in the northern Banda Sea and in the absence of genetic data it is not known to which of these species they belong (see Range of *E. malaccana*). In Western Australia the species is rare south of Northwest Cape (single shell from Point Quobba, AMS; two specimens recorded from Abrolhos Is by Johnson & Black 1997); extension of the range south to Fremantle (Wells 1980) requires confirmation.

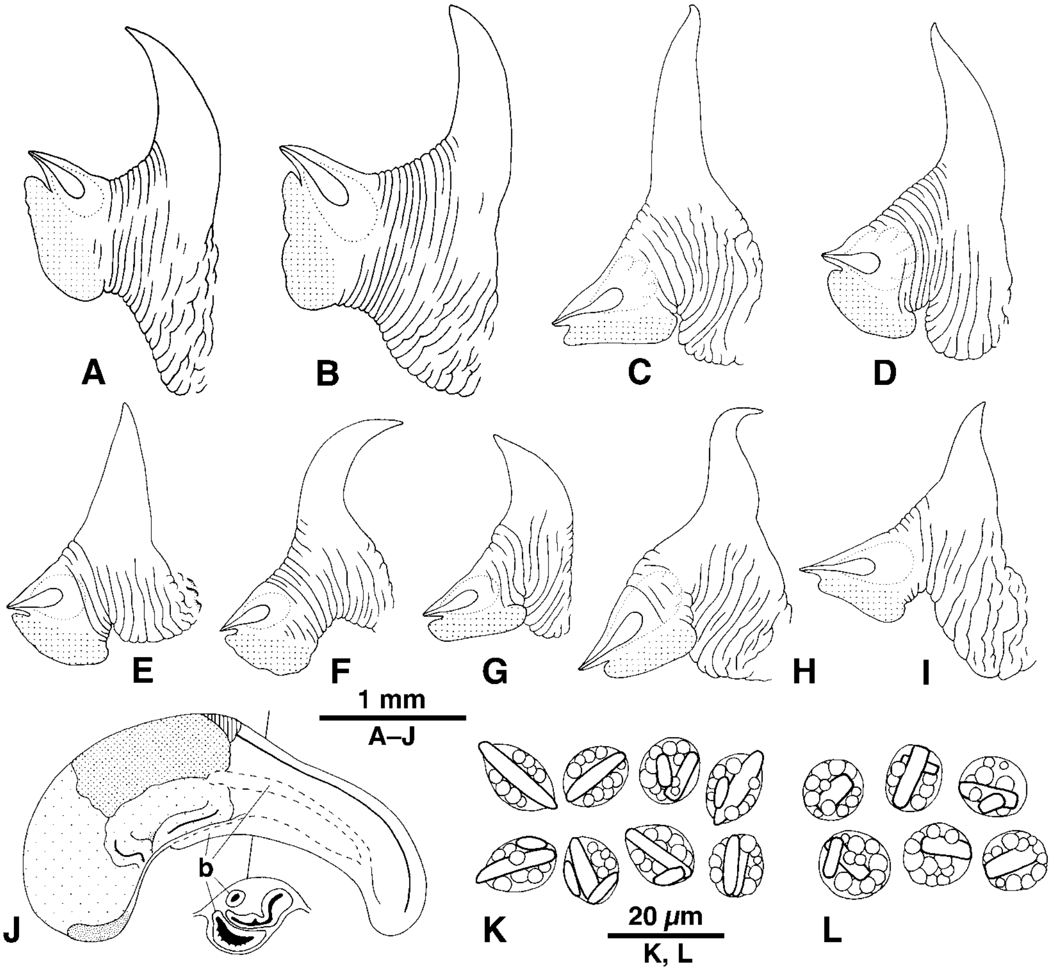

FIGURE 31. *Echinolittorina austrotrochoides* new species. **A–I,** penes. **J,** pallial oviduct, with transverse section. **K, L,** paraspermatozoa. **A, B, F, J–L,** paratypes, Picnic Bay, Magnetic I., Queensland, Australia (BMNH 20050041; shell H **A** = 7.0 mm, **B** = 9.2 mm, **F** = 8.2 mm, **J** = 9.0 mm). **C–E,** Ela Beach, National Capital District, Papua New Guinea (BMNH 20050035; shell H **C** = 9.2 mm, **D** = 8.2 mm, **E** = 9.3 mm). **G,** Port of Broome, Western Australia (BMNH 20050040; shell H = 6.3 mm). **H, I,** Karratha, Western Australia (BMNH 20050034; shell H **H** = 8.3 mm, **I** = 7.5 mm). Abbreviation: b, copulatory bursa. Shading conventions as in Figure 3.

Habitat and ecology: This species is common in the upper littoral fringe. It occurs on basalt, granite, limestone, sandstone and concrete, in sheltered to moderately exposed sites in continental settings. On the Queensland mainland it occupies the highest levels of the littoral fringe, above the zone of *E. melanacme* and *E. vidua* (Endean *et al.* 1956a), but on the offshore islands it extends to a lower level, around mean high water or high water of neap tides (Endean *et al.* 1956b; W. Stephenson *et al.* 1958). It was described as a typical mainland species, of sparse occurrence on islands such as Heron Island (Endean *et al.* 1956b). Black & Johnson (2001) described zonation and demography at Ningaloo, Western Australia; this species occurred at the highest level on the shore and showed high survival and slow growth, taking nearly 3 years to reach half maximum size.

Remarks: See Remarks on *E. malaccana* and Table 1 for differentiation from other members of the *E. malaccana* group. The decision to treat the pair of sister taxa, *E. malaccana* and *E. austrotrochoides*, as distinct species is discussed in the Remarks on the former, together with the uncertainty about the identification of samples from the Banda Sea. Anatomically, *E. austrotrochoides* cannot be distinguished from *E. malaccana*, although the penial filament is usually slightly longer and more slender in the former. However, the shells of *E. austrotrochoides* are characterized by a slightly concave spire outline, slightly concave base, and relatively large aperture of trapezoid shape, with a projecting anterior lip; these features separate most shells from others in the *E. malaccana* group. COI sequence data provide unequivocal identification of each species in the group.

Like that of *E. malaccana* the distribution of this species is apparently limited by its requirement for a tropical environment with continental oceanographic conditions. Assuming that the single record from New Caledonia is reliable and correctly identified, it suggests that a rare dispersal event (presumably as a pelagic larva) occurred from the closest established populations, some 1500 km away on the coast of Queensland. COI sequence data show no evidence of phylogeographic structure within Australia (Reid *et al*. 2006), but allozymes do reveal some differentiation between populations from the east and west coasts (Stuckey 2003), reflecting historical episodes of isolation during low sea-level stands.

In eastern Australia the distribution of *E. austrotrochoides* and the conchologically similar *N. pyramidalis* hardly overlap, the latter being found only at and south of the Keppel Islands, and there are only two records of sympatric occurrence (Reid & Williams 2004). The distinction between the *E. malaccana* group (as *E. trochoides*) and *N. pyramidalis* was described by Reid & Williams (2004). Comparing only the two species in Australia: the shell of *N. pyramidalis* reaches 27 mm (cf. 15.4 mm in *E. austrotrochoides*), is broader (H/B = 1.23–1.46, cf. 1.31–1.69), has a single row of nodules on the penultimate whorl (usually 2 visible in *E. austrotrochoides*), basal ribs are never nodulose (sometimes nodulose in *E. austrotrochoides*), and there are two pale bands within the dark aperture (cf. a single band). The papillate penial filament of male *N. pyramidalis* and additional loop of the capsule gland in females are diagnostic anatomical differences.

There is some variation in the shells of *E. austrotrochoides*; as in other members of the *E. malaccana* group shells from limestone are tall and show strong sculpture (Fig. 30D).

Echinolittorina cecillei (Philippi, 1851)

(Figures 26G, H, 32–34)

Litorina cecillei Philippi, 1851: 78 (Insulae Liew-kiew [Ryukyu Is, Japan]; lectotype MNHN (here designated, Fig. 32F) and paralectotype MNHN, seen). Weinkauff, 1882: 105.

Litorina (Tectaria) cecillei—Weinkauff, 1883: 226.

Tectarius cecillei—Tryon, 1887: 260.

Litorina malaccana—Dunker, 1882: 111 (in part, includes *E. malaccana*; not Philippi, 1847).

Littorina malaccana—Pilsbry, 1895: 61 (not Philippi, 1847).

Tectarius (Nodilittorina) trochoides—Hirase, 1934: 47, pl. 79, fig. 14 (*L. trochoides* Gray, 1839 is a *nomen dubium*).

Nodilittorina (Nodilittorina) trochoides—Reid, 1992: 202 (in part, includes *E. malaccana*, *E. austrotrochoides*, *E. omanensis*). Kurozumi, 1994: 366.

Nodilittorina trochoides—Fukuda, 1995: 39, 67. Higo *et al*., 1999: 91. Hasegawa, 2000: 141, pl. 70, fig. 26. Reid, 2001a: 442–444 (in part, includes *E. malaccana*, *E. austrotrochoides*, *E. wallaceana*).

Echinolittorina trochoides—Williams *et al*., 2003: 83 (in part, includes *E. malaccana*, *E. austrotrochoides*, *E. wallaceana*).

Echinolittorina trochoides E—Williams & Reid, 2004: 2227–2251.

? *Littorina-capsula multistriata* Tokioka, 1950: 152, fig. 6.2 (spawn) (Ago and Tanabe Bays, Japan; name unavailable, see Reid & Mak 1998: 16–17).

Nodilittorina vilis—Habe, 1951: 90, pl. 14, figs 11, 12 (in part, includes *E. malaccana*; *Litorina vilis* Menke in Philippi, 1846 is a *nomen dubium*). Oyama & Takemura, 1963: *Nodilittorina* fig. 10.

Tectarius vilis—Kuroda & Habe, 1952: 89. Hirase & Taki, 1954: pl. 79, fig. 14.

Nodilittorina pyramidalis—Habe, 1956a: 96–99, fig. 4 (radula) (not Quoy & Gaimard, 1833). Habe, 1956b: 117–121, fig. D (spawn) (not Quoy & Gaimard, 1833). Kojima, 1958b: 233–237, fig. 2 (not Quoy & Gaimard, 1833). Kira, 1962: 23, pl. 12, fig. 25 (not Quoy & Gaimard, 1833). Higo, 1973: 47 (not Quoy & Gaimard, 1833). Okutani, 1986: 70–71, figs (not Quoy & Gaimard, 1833). Asakura *et al*., 1993: 11 (not Quoy & Gaimard, 1833). Fukuda, 1993: 38–39 (not Quoy & Gaimard, 1833). Higo & Goto, 1993: 74 (not Quoy & Gaimard, 1833).

Nodilittorina (Nodilittorina) pyramidalis pyramidalis—Rosewater, 1970: 481–484, pl. 372 (map) (in part, includes *N. pyramidalis*, *E. pascua*, *E. malaccana*, *E. austrotrochoides*, *E. marquesensis*, *E. wallaceana*, *E. cinerea*; not Quoy & Gaimard, 1833).

Nodilittorina nodulosa—Fischer, 1967: 47–80 (in part, includes *N. pyramidalis*, *E. malaccana*, *E. austrotrochoides*, *E. marquesensis*; *Trochus nodulosus* Gmelin, 1791 = *E. malaccana* group or *E. pascua*). Fischer, 1969: 119–129 (in part, includes *N. pyramidalis*, *E. natalensis*, *E. omanensis*, *E. malaccana*, *E. austrotrochoides*, *E. marquesensis*, *E. wallaceana*).

Taxonomic history: See also remarks on *E. malaccana* group and Synonymy of *E. malaccana*.

Philippi (1851) described this species from material collected by Cécille and sent to him by Largilliert. A lectotype is here designated from two syntypes in MNHN, from the collection of Largilliert, formerly in the Rouen Museum. A modern label gives the locality of the syntypes as ‘Chine’, but Philippi was more precise. Following its introduction, the name was listed by Tryon (1887), but has not since appeared in the literature.

Habe (1956b) indicated that *Littorina-capsula multistriata* Tokioka, 1950, an egg capsule with six spiral ridges, belongs to this species, but Kojima (1958b) pointed out 10 spiral ridges in capsules liberated by *E. cecillei*. It is not clear if this represents intraspecific variation; Tokioka’s (1950) capsule also falls within the range of variation of *E. radiata*. The names given to littorinid egg capsules by Tokioka (1950) have been judged to be unavailable, because they were introduced provisionally, when the species that produced them were not known (Reid & Mak 1998; ICZN 1999: Art. 1.3.5).

Diagnosis: Shell high-conical, base slightly convex; 2 rows of 10–16 pointed nodules on last whorl, peripheral nodules crossed by 2–3 threads, threads on base usually not nodulose; columella slightly flared at base, anterior lip rounded; grey or black with white to cream nodules. Penial filament small, half total length of penis or less; copulatory bursa divided, ventral branch 0.3–0.7 length of dorsal branch. Ryukyu Is, south coast of Japan, Ogasawara Is, Mariana Is. COI: GenBank AJ623057, AJ623058.

Material examined: 47 lots (including 46 penes, 21 pallial oviducts, 3 radulae).

Shell (Fig. 32): Mature shell height 3.9–16.3 mm. Shape conical to high-conical (H/B = 1.39–1.73; SH = 1.74–2.37); spire whorls lightly rounded, suture not distinct; spire profile straight to slightly convex; periphery of last whorl weakly angled; profile of base slightly convex. Columella short, concave, hollowed and only slightly flared at base; anterior lip usually rounded, occasionally projecting (Fig. 32J–L); usually a small eroded parietal and pseudumbilical area. Sculpture of last whorl: 2 rows of rounded to pointed nodules, at periphery and shoulder, axially aligned in 10–16 pairs; entire surface (including base) with 13–23 narrow spiral threads and microstriae, peripheral nodules crossed by 2–3 major threads; basal threads (below peripheral nodules) 4–8, only rarely becoming nodulose (Fig. 32G, J). Protoconch 0.26–0.33 mm diameter, 2.8 whorls. Colour: black to dark brown (fading to blue-grey), paler at suture and on base, nodules white to cream; aperture dark brown with pale band at base; columella dark brown.

Animal (Fig. 33): Head black, occasionally a narrow unpigmented stripe across snout, tentacle unpigmented with two short black longitudinal stripes at base (sometimes fused to form a transverse band; sometimes extending to just behind tentacle tip) and two spots or black band behind tip, unpigmented around eye and across base; sides of foot black. Opercular ratio 0.46–0.69. Penis (Fig. 33A–M): filament small, tapering to pointed tip, smooth, about 0.4–0.5 total length of penis; mamilliform gland equal to or smaller than glandular disc, borne together on stout projection of base; penis unpigmented or slightly pigmented at base; sperm groove extends to tip. Spermatozoa not known. Pallial oviduct (Fig. 33N, O): bursa opening at one quarter to one third length of straight section (from anterior), divided into two, ventral branch 0.3–0.7 length of dorsal branch (measured from their point of separation) that extends back to albumen gland. Spawn (Fig. 33Q, R) an asymmetrically biconvex pelagic capsule 160–220 µm, cupola-shaped upper side sculptured by 6–10 concentric rings, containing single ovum 75 µm diameter (Habe 1956b; Kojima 1958b). Development predicted to be planktotrophic.

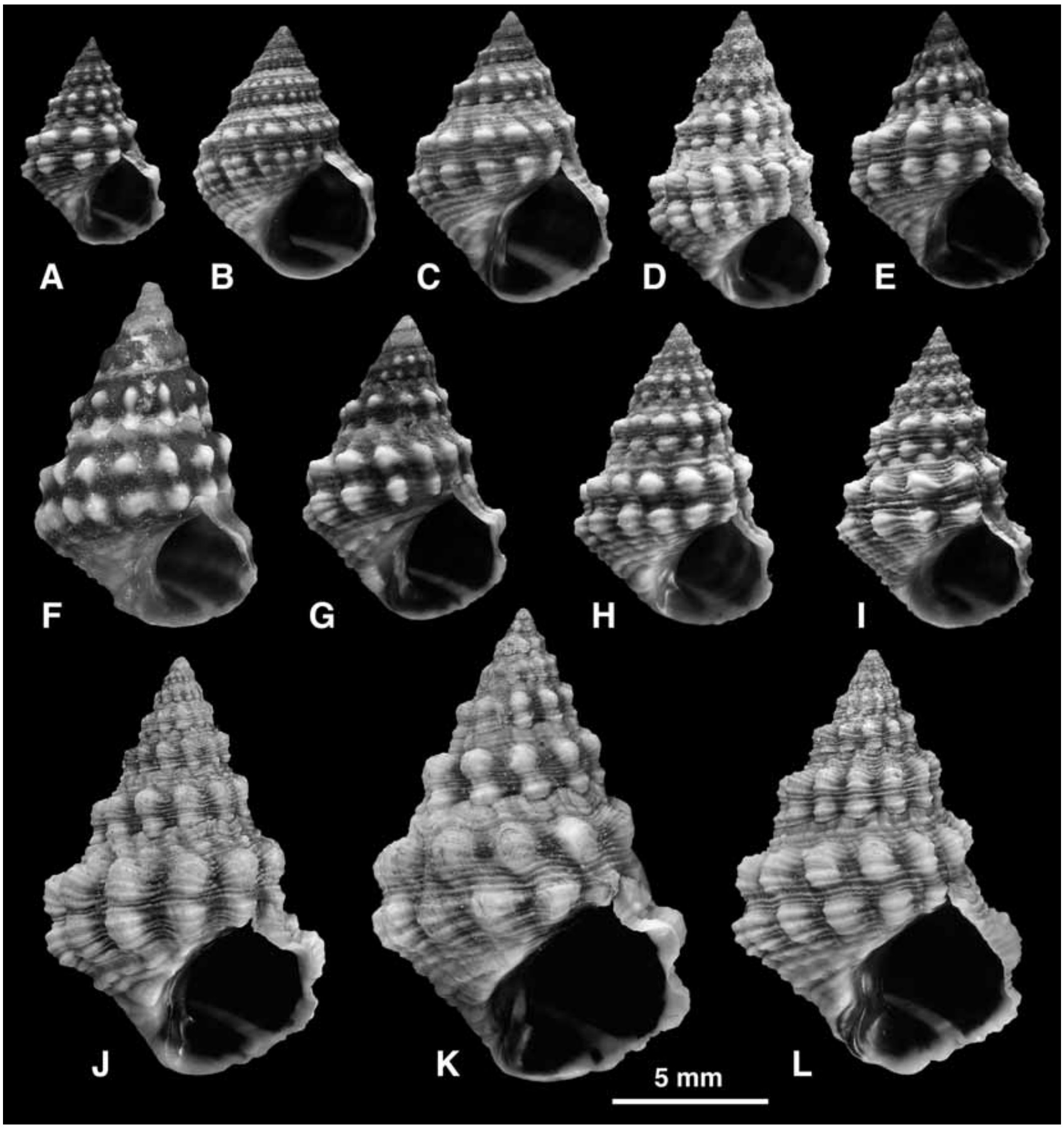

FIGURE 32. *Echinolittorina cecillei*. **A,** Miyanohama, Chichi-shima, Ogasawara Is, Japan (BMNH 20050042). **B, C,** Buma, Awa, Nago-shi, Okinawa, Japan (BMNH 20050043). **D,** Nakazato, Kikai-jima, Amami Is, Japan (BMNH 20050044). **E,** Taredo, Mitsune, Hachijo-jima, Japan (BMNH 20050045). **F,** *Litorina cecillei* Philippi, 1851, lectotype (MNHN). **G, H,** Tsubaki, Wakayama, Japan (BMNH 20050046). **I,** Araki, Kikai-jima, Amami Is, Japan (BMNH 20050047). **J–K,** Zanpa, Okinawa, Japan (BMNH 20050048).

Radula (Fig. 26G, H): Relative radula length 1.91–7.41. Rachidian: length/width 1.54–1.85; tip of major cusp pointed. Lateral and inner marginal: major cusp on each of similar size, tips pointed to rounded. Outer marginal: 6-8 cusps.

Range (Fig. 34): Ryukyu Is, south coast of Japan, Ogasawara Is, Mariana Is. Range limits: Higawa-hama, Yonagunijima, Ryukyu Is, Japan (BMNH); Tanegashima, Kagoshima Pref., Japan (Uozumi Colln, ?); Minamidaitojima, Japan (Uozumi Colln, ?); Tsushima, Nagasaki Pref., Japan (Hasegawa 2000); Kamae-cho, Oita Pref., Kyushu, Japan (Dept. Geology, Kyushu Univ., ?); Tsubaki, Wakayama Pref., Japan (BMNH); Wagu, Shima Peninsula, Mie Pref., Japan (USNM 707386, ?); Mitsuishi, Manazuru, Kanagawa Pref., Japan (BMNH); Boso Pen., Chiba Pref., Japan (Hasegawa 2000); Taredo, Mitsune, Hachijo-jima, Japan (BMNH 20050045); Mukoshima, Ogasawara Is, Japan (USNM 637372, ?); Iwojima, Ogasawara Is, Japan (USNM

712055, ?); Uracus I., Mariana Is (USNM 819202, ?); Bandera Peninsula, Pagan I., Mariana Is (BMNH, ?); Apra Bay, Guam, Mariana Is (USNM 256747, ?).

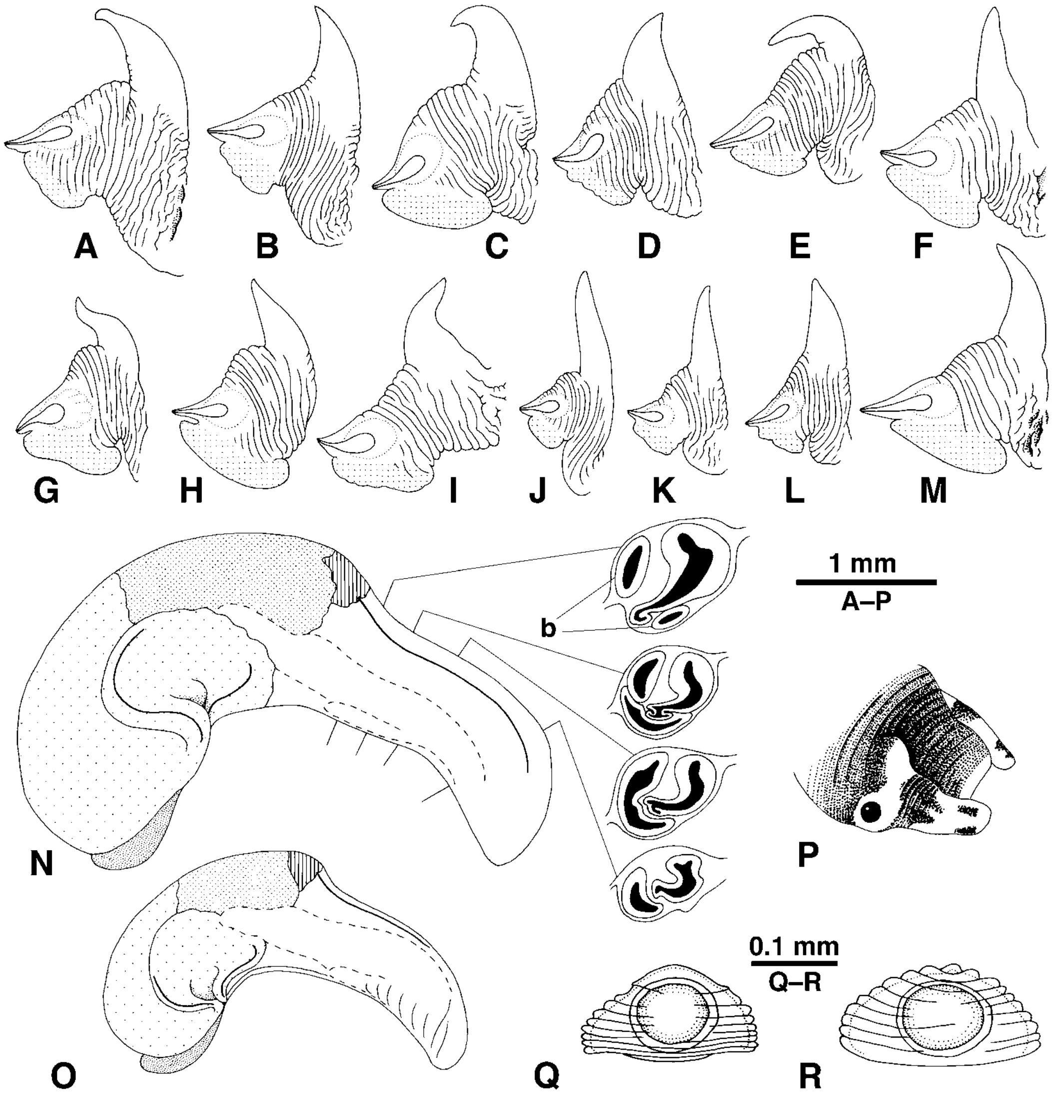

FIGURE 33. *Echinolittorina cecillei*. **A–M,** penes. **N, O,** pallial oviducts, with transverse sections. **P,** head. **Q, R,** pelagic egg capsule (after Kojima 1958). **A,** Harbour, Ishigaki, Japan (BMNH 20050564; shell H = 7.9 mm). **B,** Kannon Saki, Ishigaki, Japan (BMNH 20050049; shell H = 7.1 mm). **C,** Zanpa, Okinawa, Japan (BMNH 20050048; shell H = 9.6 mm). **D, E,** Name Noue, Okinawa, Japan (BMNH 20050050; shell H **D** = 6.2 mm, **E** = 5.4 mm). **F,** Buma, Awa, Nago-shi, Okinawa, Japan (BMNH 20050043; shell H = 7.0 mm). **G,** Miyanohama, Chichi-shima, Ogasawara Is, Japan (BMNH 20050042; shell H = 5.5 mm). **H,** Tsuchi-hama, Amami-oshima, Japan (BMNH 20050051; shell H = 6.4 mm). **I, N, P,** Nakazato, Kikai-jima, Amami Is, Japan (BMNH 20050044; shell H **I** = 7.0 mm, **N, P** = 9.5 mm). **J–L,** Araki, Kikai-jima, Amami Is, Japan (BMNH 20050047; shell H **J** = 5.7 mm, **K** = 5.3 mm, **L** = 5.5 mm). **M,** Taredo, Mitsune, Hachijo-jima, Japan (BMNH 20050045; shell H = 6.8 mm). **O,** Yahazu, Yaku-shima, Japan (BMNH 20050052; shell H = 8.6 mm). Abbreviation: b, copulatory bursa. Shading conventions as in Figure 3.

Unequivocal identification requires anatomical or molecular information; those records listed with a query are based on shells alone and confirmation is required. The species is uncommon on the main islands of Japan, where it is restricted to promontories, peninsulas and islands; the northern limit in the Japan Sea is Tsushima Island and on the Pacific coast the Boso Peninsula (Hasegawa 2000). It is abundant in the Ryukyu and Ogasawara Islands. The species is present in the northern Mariana Islands (Vermeij *et al.* 1984), but there are only two records from the southern Marianas: Guam (1 spec., USNM 256747) and Saipan (2 specs, ANSP

189608). There are no specimens from Guam in the University of Guam (B.D. Smith 2003), so occurrence there may be occasional. Neither anatomical nor molecular information is available from the Mariana Islands.

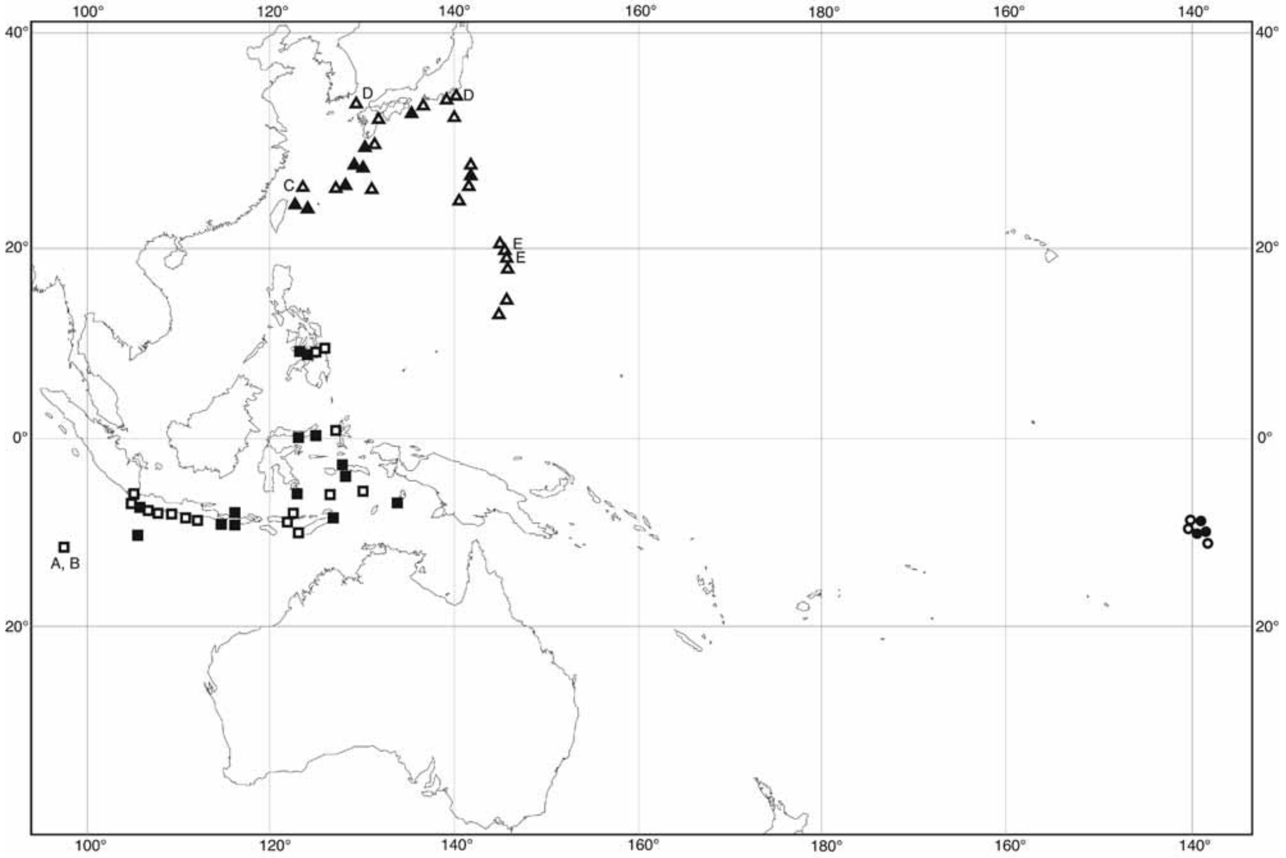

FIGURE 34. Distribution of *Echinolittorina cecillei* (triangles), *E. marquesensis* (circles) and *E. wallaceana* (squares). Solid symbols are records confirmed by COI mtDNA sequences (localities listed in Reid *et al*. 2006) or anatomy; open symbols are based on shells alone. Literature records: A, Maes (1967); B, Wells *et al*. (1990); C, Fujioka & Kurozumi (1980); D, Higo *et al*. (1999) and Hasegawa (2000); E, Vermeij *et al*. (1984).

Habitat and ecology: On rocks including volcanic tuff, concrete and coral limestone, on oceanic coasts. This species is reported to be abundant in the littoral fringe on sheltered and exposed volcanic rocks in the Tokara Islands (Kurozumi 1994) and Ogasawara Islands (Asakura *et al*. 1990; Asakura *et al*. 1991). On the latter it occupies the highest zone of all the littorinids, and attains higher levels and larger size in exposed conditions (Ohgaki 1983a); nevertheless, larger size and lower density were recorded inside than outside a cove on Ishigaki (Ohgaki 1998). It is found at higher levels during spring tides, and shows vertical migration with each tide to avoid wave wash; activity occurs at high tide and also after rain (Ohgaki 1993). At Tanabe Bay it is zoned above *E. radiata*, and is absent from enclosed bays (Habe 1958b).

Remarks: The shell of this species cannot be reliably distinguished from that of *E. malaccana*, although the base of the columella is often slightly more flared (see Remarks on *E. malaccana* and Table 1). The penial filament is usually smaller than that of both *E. malaccana* and *E. austrotrochoides*, but at some localities the shape is variable (Fig. 33J–L) and the filament may be as long as that of *E. wallaceana*. The small size of the ventral bursa distinguishes *E. cecillei* from these other three members of the *E. malaccana* group, but not from *E. marquesensis*. It has not been recorded sympatrically with any of them. At the eastern limit of its range, the distance between the records of *E. cecillei* at Yonagunijima and of *E. malaccana* in Taiwan is only 110 km, but the Kuroshio Current flows northward through this strait (Ichikawa & Beardsley 2002) and may be sufficiently strong to isolate these two species.

As in other members of the group, shells are taller with more prominent nodules on limestone substrates (Fig. 32D, J–L).

The geographical distribution of this species appears to be limited by its preference for oceanic settings. It is almost entirely restricted to islands, and to a few promontories along the southern coast of Japan. Its distribution in the Ryukyu and Ogasawara Islands is connected by the path of the Kuroshio Current, but the latter islands also receive a branch of the North Equatorial Current from the Mariana Islands (Fukuda 1994).

Echinolittorina marquesensis new species

(Figures 34–36, 37A, B)

Litorina pyramidalis—von Martens & Langkavel, 1871: 40 (in part, includes *N. pyramidalis*; not Quoy & Gaimard, 1833).

Tectarium pyramidale—Dautzenberg & Bouge, 1933: 359 (not Quoy & Gaimard, 1833).

Nodilittorina pyramidalis—Rehder, 1969: 30. Salvat & Rives, 1975: 263, fig. 39 (in part, includes *E. pascua*; not Quoy & Gaimard, 1833). Tröndlé & von Cosel, 2005: 279.

Nodilittorina (Nodilittorina) pyramidalis pyramidalis—Rosewater, 1970: 481–484, pl. 372 (map) (in part, includes *N. pyramidalis*, *E. pascua*, *E. malaccana*, *E. austrotrochoides*, *E. cecillei*, *E. wallaceana*, *E. cinerea*; not Quoy & Gaimard, 1833).

Litorina trochoides—Weinkauff, 1882: 98–99, pl. 14, figs 6, 7 (in part, includes *E. malaccana*; *L. trochoides* Gray, 1839 is a *nomen dubium*).

Littorina (Tectus) trochoides—Nevill, 1885: 156–157 (in part, includes *E. malaccana*, *E. omanensis*).

Echinolittorina trochoides C—Williams & Reid, 2004: 2227–2251.

Littorina (Tectus) pyramidalis var. *vilis*—Nevill, 1885: 156 (*Litorina vilis* Menke in Philippi, 1846 is a *nomen dubium*).

Littorina (Nodilittorina) vilis—von Martens, 1897: 204–205 (in part; includes *E. trochoides*, *E. austrotrochoides*, *E. wallaceana*).

Tectarius nodulosus—Tryon, 1887: 258 (in part, includes *N. pyramidalis*, *E. tuberculata*, *E. malaccana*, *Tectarius antonii*; *Trochus nodulosus* Gmelin, 1791 = *E. malaccana* group or *E. pascua*).

Tectarium nodulosum—Dautzenberg & Bouge, 1933: 358–359.

Nodilittorina nodulosa—Fischer, 1967: 47–80 (in part, includes *N. pyramidalis*, *E. malaccana*, *E. austrotrochoides*, *E. cecillei*). Fischer, 1969: 119–129 (in part, includes *N. pyramidalis*, *E. natalensis*, *E. omanensis*, *E. malaccana*, *E. austrotrochoides*, *E. cecillei*, *E. wallaceana*).

Nodilittorina aff. *pascua*—Reid, 2002a: 259–281 (not Rosewater, 1970).

Echinolittorina aff. *pascua*—Williams *et al*., 2003: 83 (not Rosewater, 1970).

Types: Holotype BMNH 20050053 (Fig. 35A); 6 dry paratypes BMNH 20050054 (Fig. 35B–E); 100 alcohol paratypes BMNH 20050055 (Figs 36A–C, F, G, 37A, B); 4 dry paratypes MNHN; Baie de Hané, Ua Huka, Marquesas Islands, French Polynesia.

Etymology: Latin, from the type locality.

Taxonomic history: It has long been known that nodulose littorinids occur in the Marquesas Islands (von Martens & Langkavel 1871), but since their shells show no marked differences from those from the western Pacific, the same names (*pyramidalis, trochoides, vilis, nodulosus*; see remarks on *E. malaccana* group and Synonymy of *E. malaccana*) have generally been used for both. However, a large gap of 7–8000 km separates the Marquesas Islands from the closest records of other members of the *E. malaccana* group or *N. pyramidalis* to the west, which strongly suggests specific differentiation. This gap was less obvious to Rosewater (1970), because he misidentified some nodulose specimens of *E. cinerea* from Samoa and Tonga as members of his *N. pyramidalis pyramidalis* (see Taxonomic History of *E. cinerea*). In fact he drew the taxonomic and biogeographic distinction to the southeast, where he distinguished *N. pyramidalis pascua* on Easter and Pitcairn Islands. The distinctness of the present species was first suggested by its penial shape, but it was initially listed as *N.* aff. *pascua* by reason of geographical proximity and because the character of its bifurcate bursa was not then known (Reid 2002a).

Diagnosis: Shell high-conical, base convex; 2 rows of 12–20 rounded nodules on last whorl, peripheral nodules crossed by 2–4 threads; columella flared at base, anterior lip rounded; grey or black with white nodules. Penial filament small, narrow, less than half total length of penis; copulatory bursa divided, ventral branch 0.3–0.5 length of dorsal branch. Marquesas Is. COI: GenBank AJ623021, AJ623022.

Material examined: 19 lots (including 7 penes, 6 pallial oviducts, 2 radulae).

Shell (Fig. 35): Mature shell height 5.4–12.6 mm. Shape conical (H/B = 1.36–1.60; SH = 1.68–2.05); spire whorls slightly rounded, suture distinct; spire profile slightly convex; periphery of last whorl weakly angled; profile of base convex. Columella short, concave, flared and hollowed at base; anterior lip rounded; parietal area not usually eroded; sometimes a slight pseudumbilical chink adjacent to columellar pillar. Sculpture of last whorl: 2 rows of rounded nodules, at periphery and shoulder, axially aligned in 12–20 pairs; suture rugose, sometimes developing into a third row of nodules; entire surface (including base) with 14–19 narrow spiral threads and microstriae, peripheral nodules crossed by 2–4 major threads; basal threads (below peripheral nodules) 4–7, sometimes becoming nodulose. Colour: black to dark brown (fading to blue-grey), paler at suture and on base, nodules white; aperture dark brown with pale band at base; columella dark brown.

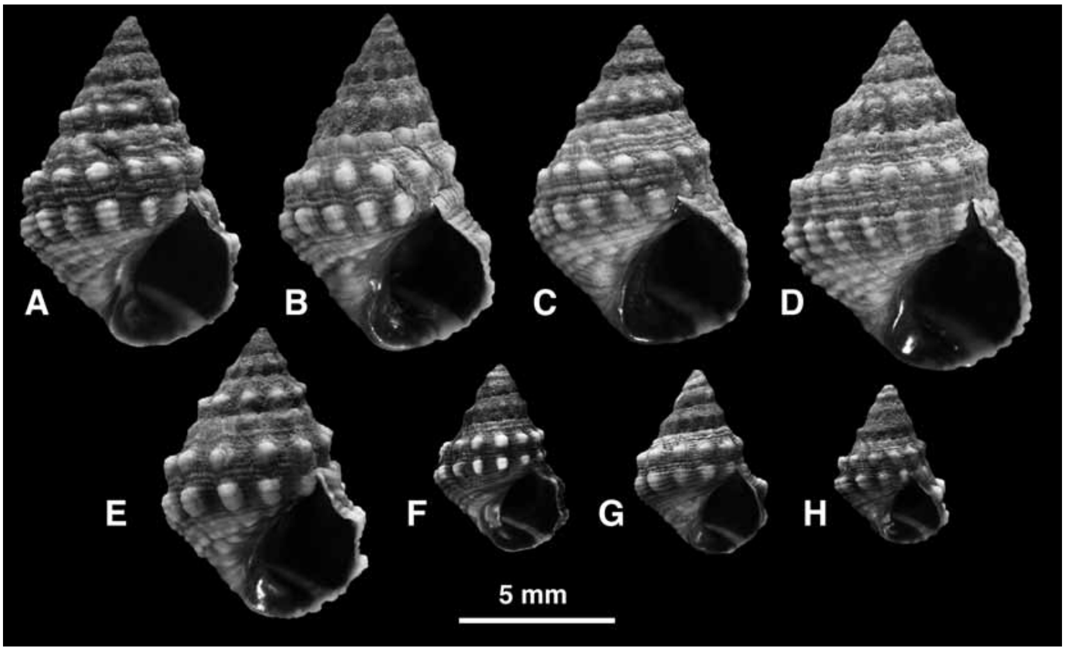

FIGURE 35. *Echinolittorina marquesensis* new species **A,** holotype, Baie de Hané, Ua Huka, Marquesas Is, French Polynesia (BMNH 20050053). **B–E,** paratypes (BMNH 20050054). **F–H,** Taihoae Bay, Nuku Hiva, Marquesas Is, French Polynesia (BMNH 20050056).

Animal (Fig. 36): Head black; tentacle black, unpigmented at tip, around eye and across base; sides of foot black. Opercular ratio 0.44–0.47. Penis (Fig. 36A–E): filament small, narrow, tapering to tip, smooth, 0.4–0.5 total length of penis; mamilliform gland equal to or smaller than glandular disc, borne together on stout projection of base; penis unpigmented; sperm groove extends to tip. Spermatozoa not known. Pallial oviduct (Fig. 36F, G): bursa opening at one third length of straight section (from anterior), divided into two, ventral branch 0.3–0.5 length of dorsal branch (measured from their point of separation) that extends back to albumen gland. Development predicted to be planktotrophic.

Radula (Fig. 37A, B): Relative radula length 3.22–4.84. Rachidian: length/width 1.29–1.55; tip of major cusp pointed. Lateral and inner marginal: major cusp on each of similar size, tips rounded to slightly pointed. Outer marginal: 7–10 cusps.

Range (Fig. 34): Marquesas Is and possibly Tuamotu Is. Marquesas: Nuku Hiva (BMNH 20050056; USNM 794587); Ua Huka (BMNH 20050055); Ua Pou (USNM 798164); Hiva Oe (BMNH); Tahuata (BMNH; USNM 794435); Fatu Hiva (BMNH; USNM 798707). Tuamotus: Ngarumaoa I., Raroia (USNM

711853). The single record from the Tuamotus consists of two specimens; this is either a chance occurrence beyond the normal range, or unreliable. The records of '*N. pyramidalis*' from Samoa and Tonga by Rosewater (1970) are based on *E. cinerea* (R.K. Kawamoto pers. comm.).

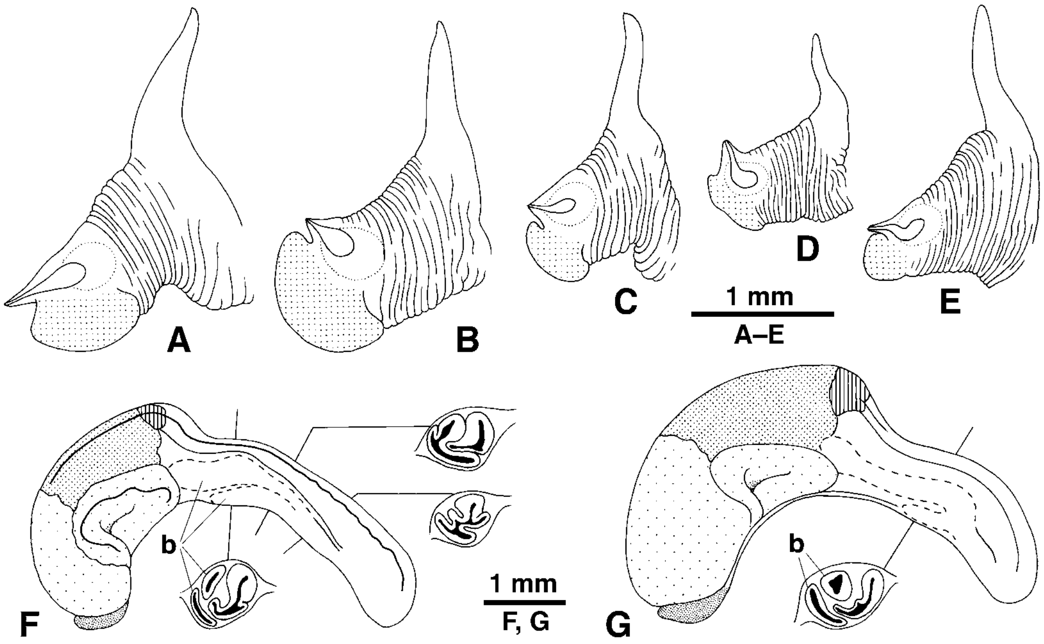

FIGURE 36. *Echinolittorina marquesensis* new species. **A–E,** penes. **F, G,** pallial oviducts, with transverse sections. **A–C, F, G,** paratypes, Baie de Hané, Ua Huka, Marquesas Is, French Polynesia (BMNH 20050055; shell H **A** = 10.4 mm, **B** = 10.9 mm, **C** = 10.0 mm, **F** = 11.4 mm, **G** = 12.4 mm). **D,** Tahuata, Marquesas Is, French Polynesia (BMNH; shell H = 5.4 mm). **E,** Hiva Oe, Marquesas Is, French Polynesia (BMNH; shell H = 7.7 mm). Abbreviation: b, copulatory bursa. Shading conventions as in Figure 3.

Habitat: On basaltic rocks in the littoral fringe, on shores of oceanic high islands.

Remarks: The distance of 7–8000 km between the distributions of *E. marquesensis* and those of other members of the *E. malaccana* group to the west is too great to be traversed by dispersal of pelagic larvae under present-day conditions of current flows. However, during low sea-level intervals in the past it is possible that distributions of oceanic species such as *E. cecillei* or *E. wallaceana* extended further across the Pacific Ocean, if they inhabited the shores of islands that are now partly or entirely submerged. The volcanic islands of the Marquesas group began to form 5.8 Ma (Brousse *et al*. 1990), and the estimated age of *E. marquesensis* is in the range 4–8 Ma (Williams & Reid 2004). The present isolation of the Marquesas Islands is a consequence of oceanic currents in the region, and is reflected in both high endemicity of marine fauna (estimated at 10–20%) and intraspecific phylogeographic structure (Randall 1998; Planes & Fauvelot 2002). The sister-species relationships of this species are not resolved by COI sequence data (Williams & Reid 2004; Reid *et al*. 2006).

Echinolittorina wallaceana new species
(Figures 34, 37C–G, 38, 39)

Littorina moluccana—E.A. Smith, 1887: 518 (error for *malaccana*; not *Litorina malaccana* Philippi, 1847).

Tectarius malaccanus—Adam & Leloup, 1938: 81, fig. 28 (radula) (in part, includes *E. malaccana*; not Philippi, 1847).

Tectarius (Nodilittorina) vilis—Oostingh, 1923: 50–51, fig. 3a–c (*Litorina vilis* Menke in Philippi, 1846 is a *nomen dubium*).

Tectarius vilis—Altena, 1945: 144.

Nodilittorina pyramidalis—Maes, 1967: 109, pl. 4, fig. I (not Quoy & Gaimard, 1833). Wells *et al*., 1990: 26, pl. 8, fig. 34 (not Quoy & Gaimard, 1833).

Nodilittorina (Nodilittorina) pyramidalis pyramidalis—Rosewater, 1970: 481–484, pl. 372 (map) (in part, includes *N. pyramidalis*, *E. pascua*, *E. malaccana*, *E. austrotrochoides*, *E. marquesensis*, *E. cecillei*, *E. cinerea*; not Quoy & Gaimard, 1833).

Nodilittorina nodulosa—Fischer, 1969: 119–129 (in part, includes *N. pyramidalis*, *E. natalensis*, *E. omanensis*, *E. malaccana*, *E. austrotrochoides*, *E. cecillei*, *E. marquesensis*; *Trochus nodulosus* Gmelin, 1791 = *E. malaccana* group or *E. pascua*).

Nodilittorina trochoides—Reid, 2001a: 442–444 (in part, includes *E. malaccana*, *E. austrotrochoides*, *E. cecillei*; *L. trochoides* Gray, 1839 is a *nomen dubium*).

Echinolittorina trochoides—Williams *et al*., 2003: 83 (in part, includes *E. malaccana*, *E. austrotrochoides*, *E. cecillei*).

Echinolittorina trochoides D—Williams & Reid, 2004: 2227–2251.

Types: Holotype BMNH 20050057 (Fig. 38L); 4 dry paratypes BMNH 20050058 (Fig. 38D); 14 alcohol paratypes BMNH 20050058; 3 dry paratypes MZB Gst. 13.233; Awung, south Lombok, Indonesia.

Etymology: Latin, from Wallacea, the region of Southeast Asia between Borneo and New Guinea, where Alfred Russell Wallace undertook pioneering biogeographic studies.

Taxonomic history: See also remarks on *E. malaccana* group and Synonymy of *E. malaccana*. The Moluccas and Java, where this species is chiefly found, have been poorly explored malacologically, so there have been few references to this species in the literature. It was initially distinguished from others in the *E. malaccana* group by DNA sequence data (Williams & Reid 2004), and its morphology is described here for the first time.

Diagnosis: Shell high-conical, base often slightly concave; 2 rows of 9–13 pointed nodules on last whorl, peripheral nodules crossed by 2–3 threads, threads on base not usually nodulose; columella flared at base, but anterior lip usually rounded; grey or black with white to orange nodules. Penial filament more than half total length of penis; single, undivided, copulatory bursa. Oceanic coasts of Java, Banda Sea, Moluccas and southern Philippines. COI: GenBank AJ623051, AJ623052.

Material examined: 54 lots (including 38 penes, 3 sperm samples, 13 pallial oviducts, 2 radulae).

Shell (Fig. 38): Mature shell height 5.9–17.1 mm. Shape conical to high-conical (H/B = 1.28–1.80; SH = 1.64–2.44); spire whorls lightly rounded, suture not distinct; spire profile almost straight; periphery of last whorl weakly angled; profile of base often slightly concave. Columella short, concave, flared and hollowed at base, anterior lip slightly projecting in juveniles (Fig. 38A, F), otherwise rounded; small eroded parietal and pseudumbilical area. Sculpture of last whorl: 2 rows of pointed nodules, at periphery and shoulder, axially aligned in 9–13 (rarely to 15) pairs; entire surface (including base) with 14–21 narrow spiral threads and microstriae, each nodule crossed by 2–3 major threads; basal threads (below peripheral nodules) 4–8, only rarely becoming nodulose (Fig. 38G–I). Protoconch (Fig. 37G, a worn example) 0.28–0.33 mm diameter, 2.7–2.8 whorls. Colour: black to dark brown (fading to blue-grey), paler at suture and on base, nodules white to orange; aperture dark brown with pale band at base; columella dark brown.

Animal (Fig. 39): Head black, occasionally a narrow unpigmented stripe across snout; tentacle unpigmented with two short black longitudinal stripes at base (sometimes fused to form a transverse band; rarely extending towards tentacle tip) and black band behind tip, unpigmented around eye and across base; sides of foot black. Opercular ratio 0.45–0.57. Penis (Fig. 39A–H): filament narrow, with tapering or rounded tip, smooth, about 0.5–0.6 total length of penis; mamilliform gland equal to or smaller than glandular disc, borne together on stout projection of base; penis slightly pigmented at base; sperm groove extends to tip. Euspermatozoa not known; paraspermatozoa oval to spherical, 9–14 µm diameter, filled with large granules, blunt rod-pieces, not projecting from cell (details unclear; ethanol-preserved material). Pallial oviduct (Fig. 39I): bursa single, opening at one third length of straight section (from anterior) and extending back almost to albumen gland. Development predicted to be planktotrophic.

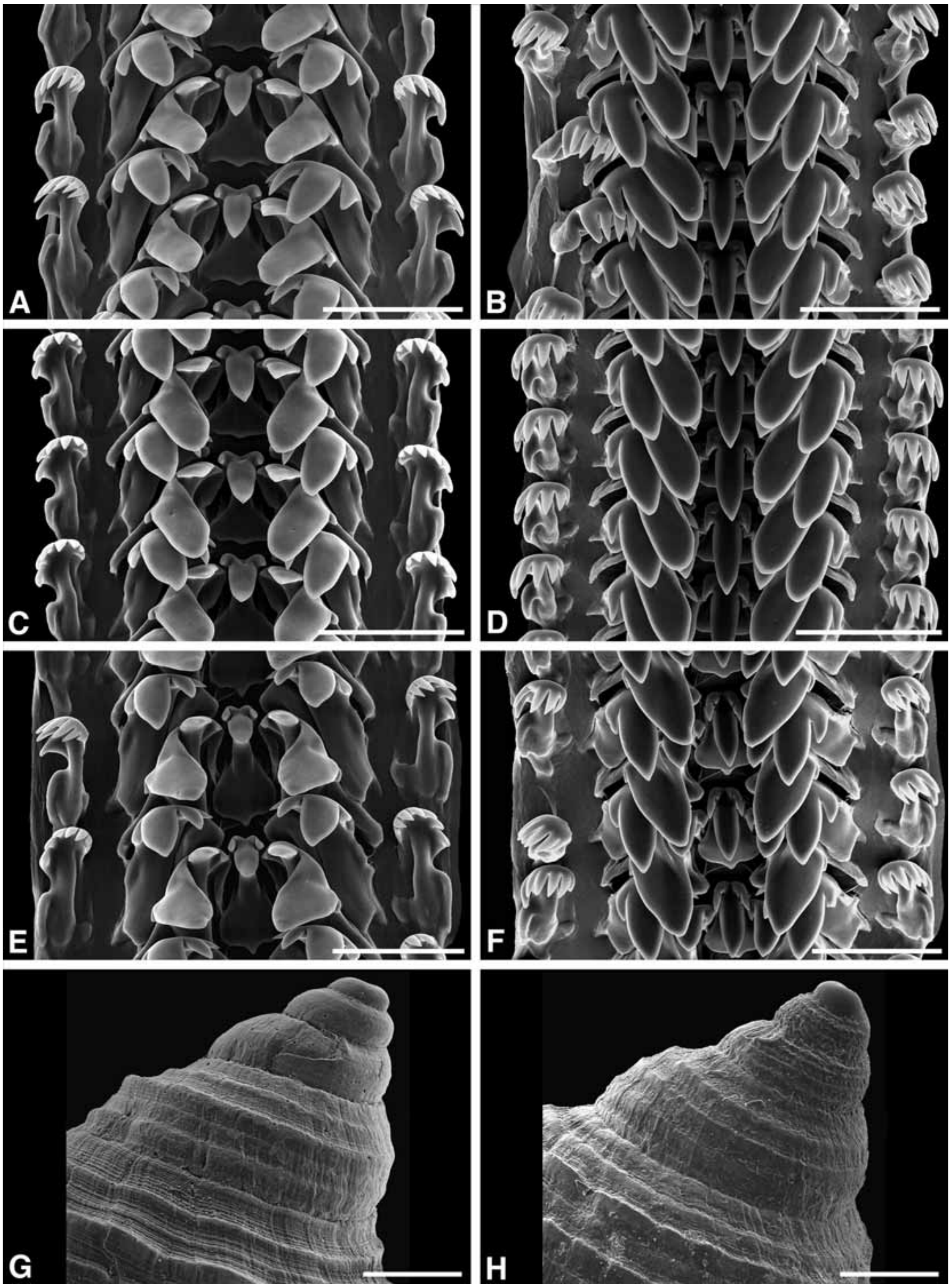

FIGURE 37. Radulae and protoconchs of *Echinolittorina* species (two views of each radula, flat and at 45°). **A, B,** *E. marquesensis* new species; Baie de Hané, Ua Huka, Marquesas Is, French Polynesia (BMNH 20050055; shell H = 12.4 mm). **C–G,** *E. wallaceana* new species. **C, D,** Kamenti, Kapataran, Sulawesi, Indonesia (BMNH 20050062; shell H = 9.2 mm). **E, F,** Mainit, Santander, Cebu I., Philippines (BMNH 20050064; shell H = 8.7 mm). **G,** Protoconch (terminating at sinusigera notch) and early whorls of teleoconch showing microstriae between ribs and threads; protoconch sculpture worn smooth; Latuhalat, Ambon, Indonesia (NNML). **H,** *E. reticulata*; protoconch, showing sculpture, and early whorls of teleoconch; Lamu, Kenya (BMNH). Scale bars **A–F** = 50 µm; scale bars **G, H** = 200 µm.

Radula (Fig. 37C–F): Relative radula length 2.83–5.28. Rachidian: length/width 1.33–1.83; tip of major cusp pointed. Lateral and inner marginal: major cusp on each of similar size (Fig. 37D) or major cusp of lateral larger than that of inner marginal (Fig. 37F), tips rounded to pointed. Outer marginal: 6–7 cusps.

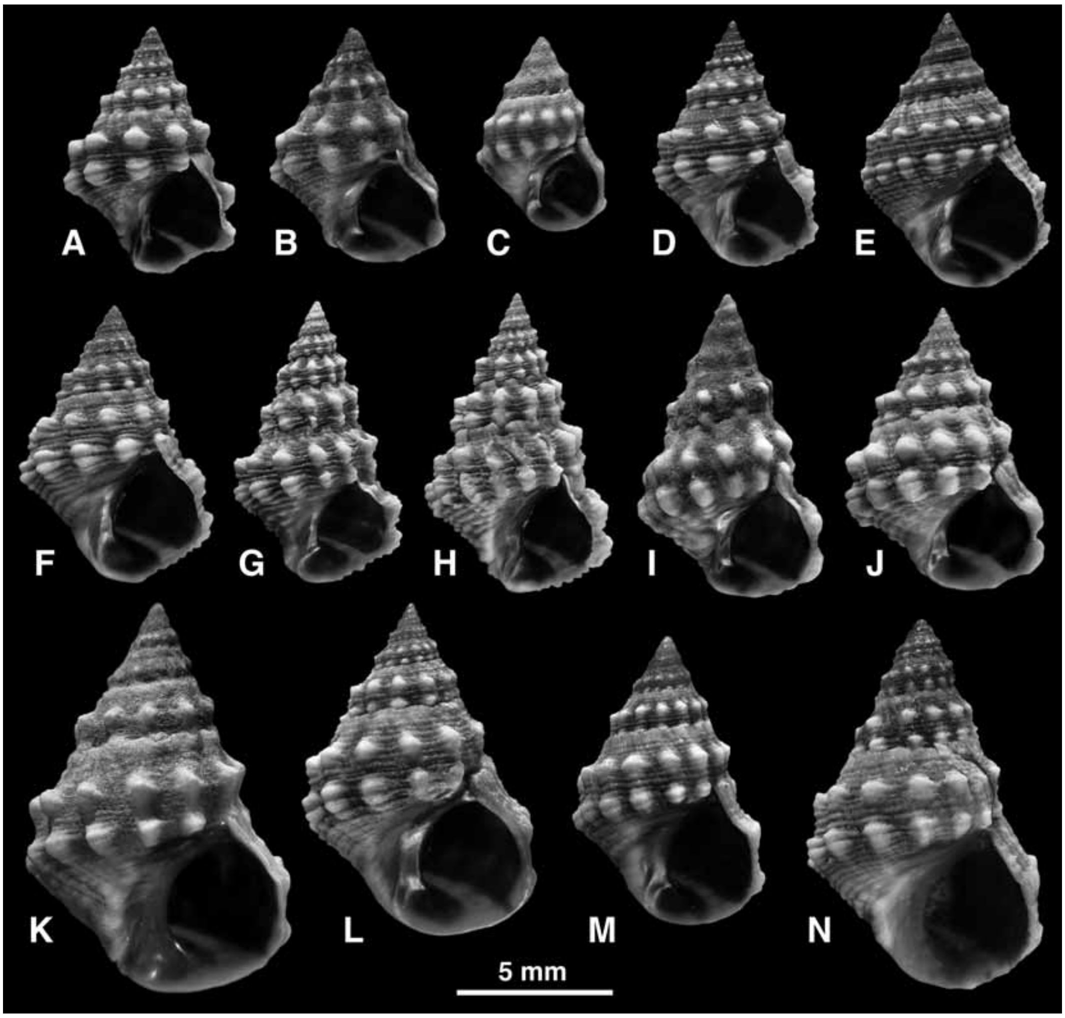

FIGURE 38. *Echinolittorina wallaceana* new species. **A, B,** Bola, Buton I., Sulawesi, Indonesia (BMNH 20050060). **C,** Mawun, Lombok, Indonesia (BMNH 20050061). **D,** paratype, Awung, Lombok, Indonesia (BMNH 20050058). **E, F, M,** Kamenti, Kapataran, Sulawesi, Indonesia (BMNH 20050062). **G, H,** Nyang Nyang, Bali, Indonesia (BMNH 20050063). **I, J,** Mainit, Santander, Cebu I., Philippines (BMNH 20050064). **K,** Cilaut Eureun, W Java, Indonesia (BMNH 20050065). **L,** holotype, Awung, Lombok, Indonesia (BMNH 20050057). **N,** Seroea, Banda Sea, Indonesia (NNML).

Range (Fig. 34): Sunda Strait, south coast of Java, Nusa Tenggara, Banda Sea, Moluccas, central Philippines. Range limits: Cocos-Keeling Is (Maes 1967; Wells *et al*. 1990); Flying Fish Cove, Christmas I. (BMNH); Pulau Sebesi, Sunda Strait, Indonesia (NNML, ?); Samaoe, Timor (NNML, ?); Tg Ngabordamlu, S Trangan, Aru, Indonesia (WAM S10899; USNM 747522); Bola, S. Buton I., Sulawesi, Indonesia (BMNH); Latuhalat, Ambon, Indonesia (NNML); Nusaniwe, Rotsen, Ambon, Indonesia (NNML); Tidore I., Moluccas, Indonesia (BMNH, ?); Kamenti, Kapataran, Sulawesi, Indonesia (BMNH 20050062); Mainit, Santander, Cebu I., Philippines (BMNH); Panglao, Bohol I., Philippines (BMNH).

Unequivocal identification requires anatomical or molecular information; those records listed with a query are based on shells alone and confirmation is required. The distribution in the Philippines is poorly known; there is no available material from southern Mindanao; shells from northeastern Mindanao (USNM) may represent this species, but verification is required. The six known localities of sympatry with *E. malaccana* are those in the Philippines, Sulawesi and Ambon, listed above (three verified by anatomy and DNA, see Reid *et al*. 2006; the others, Buton and Ambon, by anatomy only; see Range of *E. malaccana* for further discussion).

Habitat: This species occurs from the uppermost eulittoral to the highest levels of the littoral fringe, on sheltered and exposed coasts with clear oceanic water; it has been recorded on limestone, basalt and concrete and is usually abundant.

Remarks: This species was first discovered during molecular studies of the *E. malaccana* group (Williams & Reid 2004). Subsequently it was found that males could be distinguished from almost all others in the group by their elongate penial filament (rarely seen also in Japanese specimens that, from their distribution, are presumably *E. cecillei*, Fig. 33J), and females by their single, undivided copulatory bursa (Table 1). Shells are not diagnostic, although in comparison with *E. malaccana* and *E. austrotrochoides* the basal threads are usually slightly finer and not nodulose (compare shells from Kamenti, Sulawesi, Fig. 38E, F, M, with one of *E. malaccana* from the same locality, Fig. 27F; but in the Philippines both species have small nodules on the base, Figs 38I, J and 27H, K). The shell of *E. wallaceana* often has a more ‘prickly’ appearance than others in the *E. malaccana* group, owing to its sharp (rather than rounded) nodules. However, this may simply be the result of the tendency (seen also in *E. malaccana*, *E. austrotrochoides* and *E. cecillei*) of shells from limestone substrates to be more strongly sculptured (Fig. 38A, B, G–K are from limestone, whereas C, D–F, M are not).

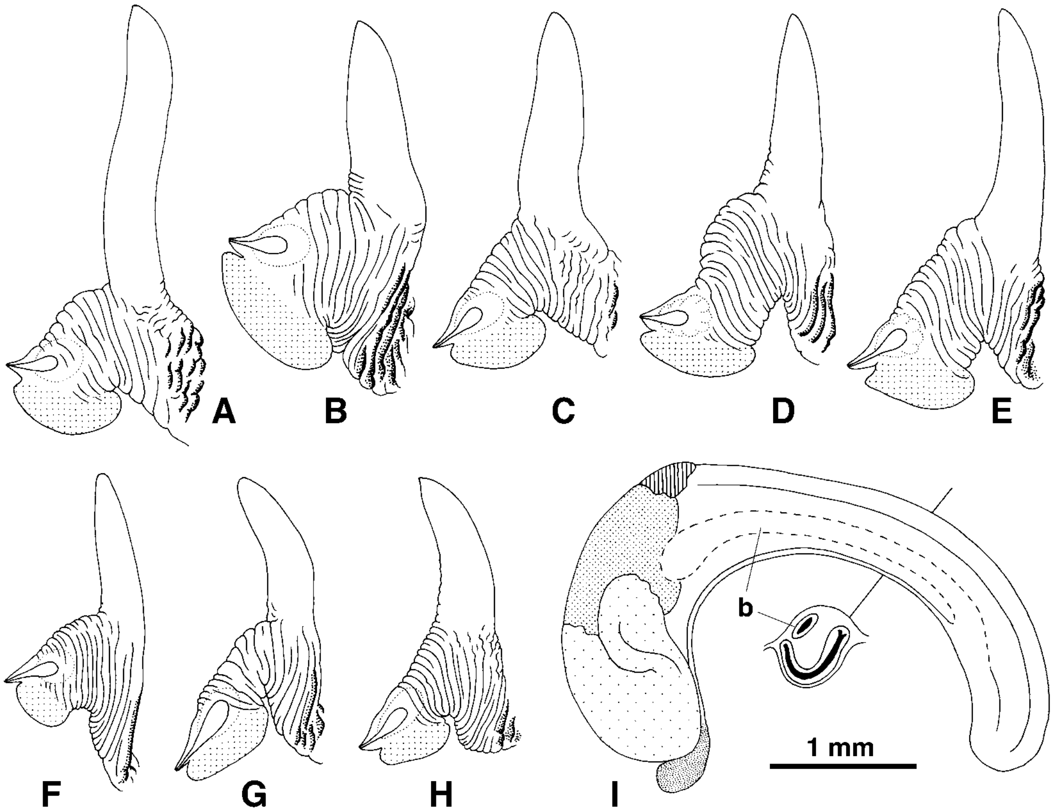

FIGURE 39. *Echinolittorina wallaceana* new species. **A–H,** penes. **I,** pallial oviduct, with transverse section. **A–C, I,** Kamenti, Kapataran, Sulawesi, Indonesia (BMNH 20050062; shell H **A** = 7.3 mm, **B** = 7.8 mm, **C** = 7.4 mm, **I** = 7.5 mm). **D, E,** Mainit, Santander, Cebu I., Philippines (BMNH 20050064; shell H **D** = 7.4 mm, **E** = 7.5 mm). **F, G,** Mawun, Lombok, Indonesia (BMNH 20050061; shell H **F** = 6.1 mm, **G** = 6.9 mm). **H,** Bola, Buton I., Sulawesi, Indonesia (BMNH 20050060; shell H = 6.9 mm). Abbreviation: b, copulatory bursa. Shading conventions as in Figure 3.

The five members of the *E. malaccana* group are almost entirely allopatric; only *E. wallaceana* and *E. malaccana* show limited sympatry, with six recorded localities where both occur. Three of these have been confirmed by COI sequence data (Reid *et al*. 2006; see Range above; but see Remarks on *E. malaccana* for uncertainty about possible sympatry of *E. wallaceana* with *E. austrotrochoides*). The fact that morphological characters remain diagnostic at these localities of sympatry is evidence that these are biological species that are reproductively isolated. Samples at these localities were collected from uniform substrates in the littoral fringe, so it is likely that the two species are syntopic, without marked ecological differences.

The distribution of *E. wallaceana* in Southeast Asia and Australasia appears to be circumscribed by its tolerance or requirement for oceanic habitats of low primary productivity. Its known distribution corresponds remarkably closely with the oceanic 'eastern Indonesian corridor' through the Molucca, Banda and Timor Seas (Reid *et al*. 2006). It is also found on the southern coast of Java, which is an area of generally low oceanic productivity, although with upwelling during July and August (Susanto *et al*. 2001). This distribution does not appear to be connected with the route of the Indonesian Throughflow current that passes mainly from the Celebes Sea southwards through the Makassar Strait; the limited records of this group from these areas are all of *E. malaccana* (cf. Figs 29, 34).

Molecular data have not resolved the closest phylogenetic relationships of *E. wallaceana* (Williams & Reid 2004; Reid *et al*. 2006). Among the *E. malaccana* group, *E. wallaceana* is the only species with a normal, undivided, copulatory bursa; outgroup comparison would therefore suggest that it is the basal member. However, the size of the ventral branch of the bursa among the remaining species is variable, so this evidence is weak.

The *Echinolittorina leucosticta* group

This species group consists of five species (*E. leucosticta*, *E. biangulata*, *E. philippinensis* n.sp., *E. tricincta* n.sp., *E. australis*) with allopatric distributions in India and the central IWP. The first four share similar shells, usually with 2–4 prominent spiral ribs bearing brown and white spots, and have been considered to belong to a single polytypic species (together with *E. feejeensis* and sculptured forms of *E. cinerea*), for which the names *N. leucosticta* or *N. quadricincta* have been employed (Rosewater 1970; Rosewater & Kadolsky 1981). *Echinolittorina leucosticta* was separated as a full species by Reid (2001a, as *N. quadricincta*), but in the absence of diagnostic anatomical characters all five species (together with *E. feejeensis* and *E. melanacme*) were considered as a single informal group in a cladistic analysis of '*Nodilittorina*' (Reid 2002a). Only recently have the four most similar species been distinguished with the aid of molecular data (Williams & Reid 2004). The remaining species, *E. australis*, is now well known, but the extreme plasticity of its shell has been a source of confusion in the past (the name *nodosa* was used for the more strongly sculptured forms). Anatomically there are still no known species-specific characters for any of the five members, nor synapomorphies for the entire group, although their monophyly is strongly supported by sequence analysis of both nuclear 28S rRNA and mitochondrial COI genes (Williams & Reid 2004).

The distribution of this clade is highly unusual; one species occurs on the eastern margin of the Arabian Sea, two on the eastern edge of the Indian Ocean, a fourth in the eastern South China Sea, and the last at the extreme western margin of the Pacific Ocean (Fig. 43). These areas all experience seasonal upwelling of cool, nutrient-rich water, suggesting that the members of this clade share a requirement for (or tolerance of) these oceanographic conditions.

Echinolittorina leucosticta (Philippi, 1847)

(Figures 40, 41, 42A, B, 43)

Litorina leucosticta Philippi, 1847a: vol. 2: 162, *Litorina* pl. 3, fig. 11 (no locality; type locality Bombay [Mumbai], India (Rosewater 1970); lectotype (Rosewater 1970) Philippi, 1847, *Litorina* pl. 3, fig. 11; paralectotype SNSD MTD 1591 (Fig. 40B), seen). Weinkauff, 1882: 60, pl. 8, fig. 1.

Tectarius leucostictus—H. Adams & A. Adams, 1854: 315.

Nodilittorina (Granulilittorina) leucosticta leucosticta—Rosewater, 1970: 497–499, pl. 384, figs 1–5, pl. 385 (map).

Echinolittorina leucosticta—Williams & Reid, 2004: 2227–2251.

Melaraphe subgranosa Dunker in Dunker & Zelebor, 1866: 913 (Madras [Chennai, India]; 100+ syntypes NHMW, 51 seen).

Littorina (Melaraphe) subgranosa—Frauenfeld, 1867: 9, pl. 1, fig. 10a–c.
Litorina subgranosa—Weinkauff, 1882: 103.
Littorina miliaris var. *subgranosa*—Nevill, 1885: 154.
Tectarius granularis var. *subgranosus*—Tryon, 1887: 260, pl. 48, figs 79, 80.
Littorina (Melarrhaphe) subgranosa—von Martens, 1897: 208–209.
Nodilittorina granularis—Atapattu, 1972: 161 (not Gray, 1839 = *E. miliaris*). Starmühlner, 1974: 55, pl. 1H, 2A, 4G (not Gray, 1839).
Nodilittorina (Granulilittorina) quadricincta quadricincta—Rosewater & Kadolsky, 1981: 1233–1234 (not Mühlfeld, 1824 = *E. biangulata*).
Nodilittorina quadricincta quadricincta—Veerappan, 1988: 77–82, figs 1 (headfoot), 4 (penis), 5 (radula) (not Mühlfeld, 1824).
Nodilittorina (Nodilittorina) quadricincta—Reid, 1989a: 100 (not Mühlfeld, 1824). Subba Rao, 2003: 120–121, pl. 19, figs 9, 10 (not Mühlfeld, 1824).
Nodilittorina quadricincta—Reid, 2001a: 440, figs 1D, 3A (penis) (not Mühlfeld, 1824). Reid, 2002a: 259–281 (not Mühlfeld, 1824).
Echinolittorina quadricincta—Williams *et al*., 2003: 83 (not Mühlfeld, 1824).

Taxonomic history: The specimen upon which Philippi (1847a) based his *Litorina leucosticta* was received from Anton, and the figure was designated as a representation of this lost lectotype by Rosewater (1970). In Anton's collection in SNSD there remains a specimen that is apparently from the same sample, because in his catalogue the record of this single shell includes the reference to Philippi's figure followed by the note 'mit disem exemplar' (with this example) (K. Schniebs pers. comm.). This specimen is therefore a paralectotype. Following Philippi's description, the name was almost entirely neglected, presumably because the origin of the species was unknown. The name was used only once in a monograph (Weinkauff 1882, copying Philippi 1847a) until resurrected by Rosewater (1970).

This species was for a time better known as *L. subgranosa*. This name was introduced by Dunker (in Dunker & Zelebor 1866) based on material from Madras collected by the *Novara* expedition. Specimens from the type collection were subsequently illustrated by Frauenfeld (1867); his figures show one tall, shouldered shell (fig. 10a, b) and one with globular shape and more granular sculpture (fig. 10c). This led some authors (Nevill 1885; Rosewater 1970) to suggest that two species were involved, the more globular one corresponding to *E. vidua* which also occurs in India. In fact the type collection of *Melaraphe subgranosa* contains only a single species, showing considerable variation in shape and sculpture (compare Fig. 40F, L). There followed some confusion with *L. granularis* Gray, 1839, a name appied in various senses (to *E. radiata*, *E. melanacme*, *E. vidua*, *E. millegrana*, *E. reticulata*), but actually based on *E. miliaris* from the Atlantic Ocean.

The concept of the present species was established by Rosewater (1970), but he considered it a complex of three subspecies, of which the nominal one was restricted to India and Sri Lanka, while *N. leucosticta biangulata* occurred in Southeast Asia and New Caledonia (i.e. *E. biangulata*, *E. philippinensis* and *E. tricincta*) and *N. leucosticta feejeensis* on the islands of the western Pacific (i.e. *E. feejeensis* and sculptured forms of *E. cinerea*). Later, the name of this species complex was changed to *N. quadricincta*, based on a misidentification (Rosewater & Kadolsky 1981; see Taxonomic History of *E. biangulata*). The subspecies were raised to full species status by Reid (2001a, 2002a) on the basis of consistent differences in shells and small penial differences. The name *E. leucosticta* was reinstated by Williams & Reid (2004).

Diagnosis: Shell with rounded or weakly shouldered whorls, sutures weak, last whorl with numerous ribs and threads of unequal size, of which 3–7 are slightly enlarged but not carinate or nodulose; surface of ribs shiny and lacking spiral microstriae; black to brown with white dashes, spots or flames. India and Sri Lanka. COI: GenBank AJ623037, AJ623038.

Material examined: 44 lots (including 11 penes, 4 sperm samples, 3 pallial oviducts, 2 radulae).

Shell (Fig. 40): Mature shell height 3.9–16.9 mm. Shape turbinate to high turbinate (H/B = 1.25–1.64, SH = 1.34–1.72); spire whorls rounded or slightly angled at shoulder, suture distinct but weakly impressed; spire profile slightly convex; last whorl angled at shoulder and slightly at periphery, often swollen or slightly square in profile. Columella long, straight, slightly hollowed at base; inner lip of aperture slightly rounded and continuous with eroded pseudumbilical and parietal area. Sculpture of last whorl: surface covered by low spiral ribs and threads of unequal size, 11–19 at and above periphery and 4–6 below, with narrow grooves between; usually 3–7 ribs at and above periphery are slightly enlarged; ribs sometimes made finely granulose by intersection with growth lines (Fig. 40F, J), especially on spire, but granules often faint or absent; fine spiral microstriae in grooves only, surface of ribs shiny if well preserved. Protoconch 0.28 mm diameter, 2.5 whorls. Colour: blackish brown, paler at suture and on base; ribs and suture marked by prominent white dashes or spots, rarely fusing to form axial flames of brown and white (Fig. 40I) or a finely marbled pattern (Fig. 40M); aperture dark brown, pale band at base; columella dark purple-brown, inner lip purplish.

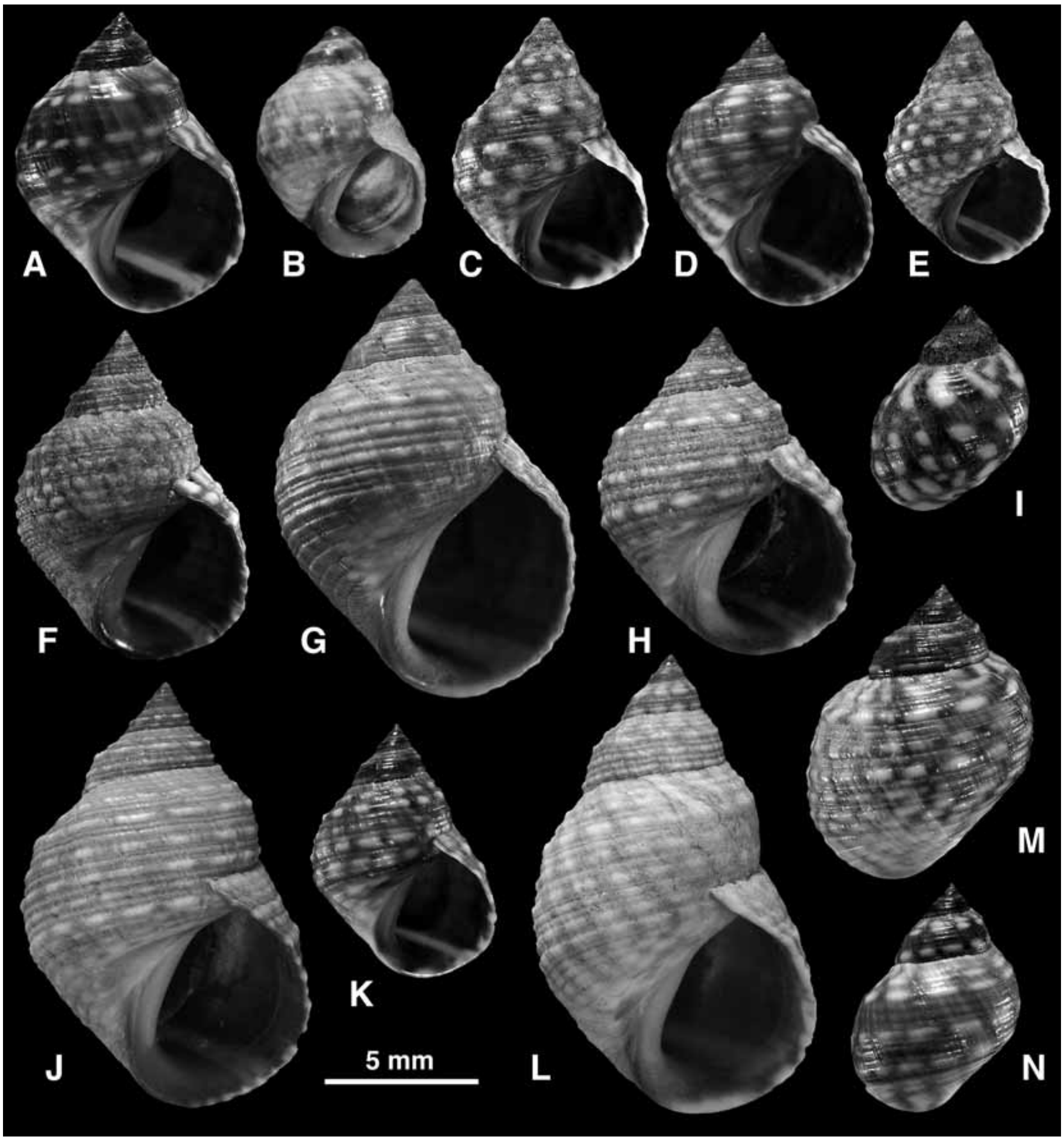

FIGURE 40. *Echinolittorina leucosticta*. **A, D, K, M, N,** Kovalam, Kerala, India (BMNH 20000716). **B,** *Litorina leucosticta* Philippi, 1847, paralectotype SNSD MTD 1591, no locality. **C, E,** Tangalle, Sri Lanka (BMNH 20050077). **F,** Polhena, Sri Lanka (BMNH 20050078). **G,** Cochin, Kerala, India (BMNH 20050079). **H, J, K,** Chennai, India (MNHN). **I,** Hendala, Sri Lanka (BMNH 20050080).

Animal (Fig. 41): Head (Fig. 41G) black, usually a narrow unpigmented stripe across snout; tentacle black at base, unpigmented around eye and across base, black spot at tip; sides of foot black. Opercular ratio 0.28–0.40. Penis (Fig. 41A–E): filament bluntly pointed at tip, with annular wrinkles for half its length, filament 0.5–0.6 total length of penis; mamilliform gland equal in size or larger than glandular disc, borne together on projection of base; penis sometimes pigmented at base; sperm groove extends to tip. Euspermatozoa not known; paraspermatozoa (Fig. 41H, I) spherical, 13–17 µm diameter, filled with large round granules and single irregular, U-shaped or serpentine rod-piece with rounded ends. Pallial oviduct (Fig. 41F): bursa opening at half length of straight section, not reaching albumen gland. Development predicted to be planktotrophic. Barkati & Ahmed (1984) figured cupola-shaped capsules sculptured by 3 concentric rings, with crenulated margin, 118 µm diameter, spawned by '*Nodilittorina picta*' from Karachi, which may be a misidentification of this species.

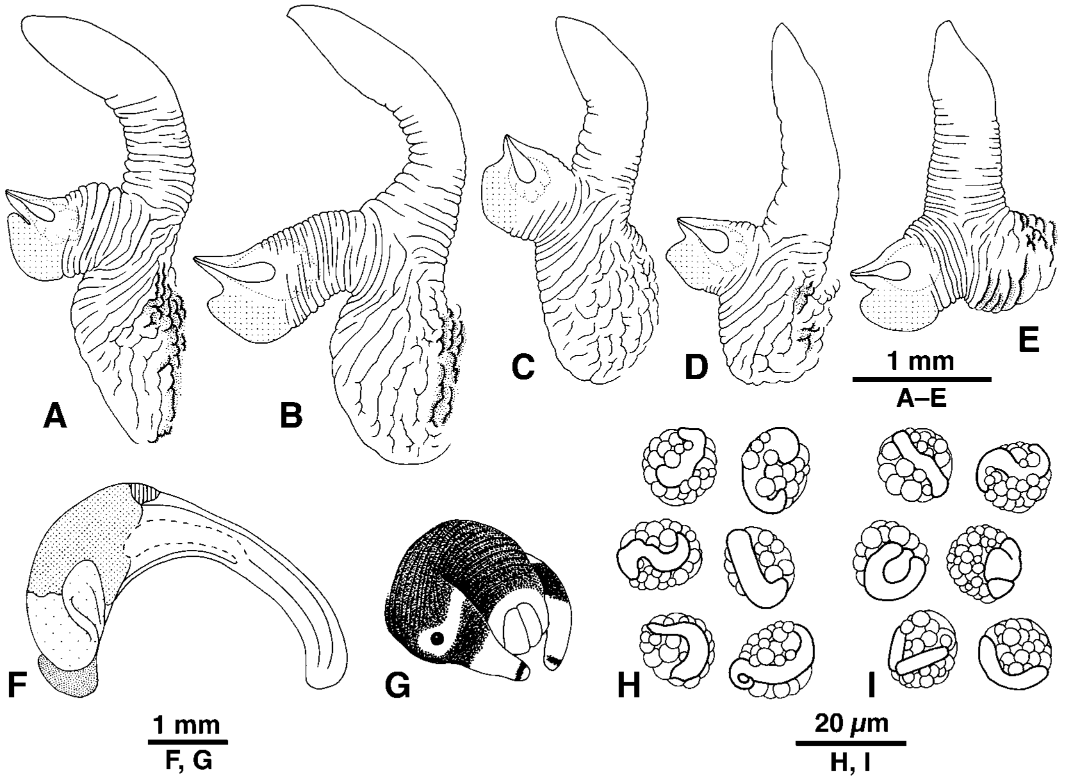

FIGURE 41. *Echinolittorina leucosticta*. **A–E,** penes. **F,** pallial oviduct. **G,** head. **H, I,** paraspermatozoa. **A, B, F–I,** Polhena, near Matara, Sri Lanka (BMNH 20050078; shell H **A** = 9.7 mm, **B** = 10.3 mm, **F** =10.7 mm, **G** = 10.8 mm). **C, D,** Galle Fort, Sri Lanka (BMNH 20050081; shell H **C** = 7.7 mm, **D** = 8.3 mm). **E,** Kovalam, Kerala, India (BMNH 20000716; shell H = 7.9 mm). Shading conventions as in Figure 3.

Radula (Fig. 42A, B): Relative radula length 2.71–5.10. Rachidian: length/width 1.10–1.33; tip of major cusp rounded to slightly pointed. Lateral and inner marginal: major cusp on each of similar size, tips truncated. Outer marginal: 8–9 cusps.

Range (Fig. 43): Oman, Pakistan, India, Sri Lanka, Burma. Range limits: Ras al-Junayz, Ras al-Hadd, Oman (BMNH); East Pier, Karachi, Pakistan (BMNH); Bandra, Mumbai, India (USNM 443611); Cape Comorin, India (BMNH); Rameswaram, India (BMNH); Chennai, India (BMNH; MNHN); Hendala, N Columbo, Sri Lanka (BMNH); Tangalle, Sri Lanka (BMNH 20050077); Cape Negrais, Burma (BMNH 1882.8.7.296).

On the Indian coast this species is abundant between Mumbai and Chennai. In Sri Lanka it is restricted to the south and west coasts (Atapattu 1972). Occurrence in Burma is based on a single specimen from Cape Negrais, a distance of 1500 km across the Bay of Bengal from the closest known population in Chennai. Another extra-limital record is of two specimens from the eastern extremity of Oman; the Oman coast has been well studied and the species is undoubtedly very rare here. The single collection from Karachi is of six specimens; the coast further west is poorly known.

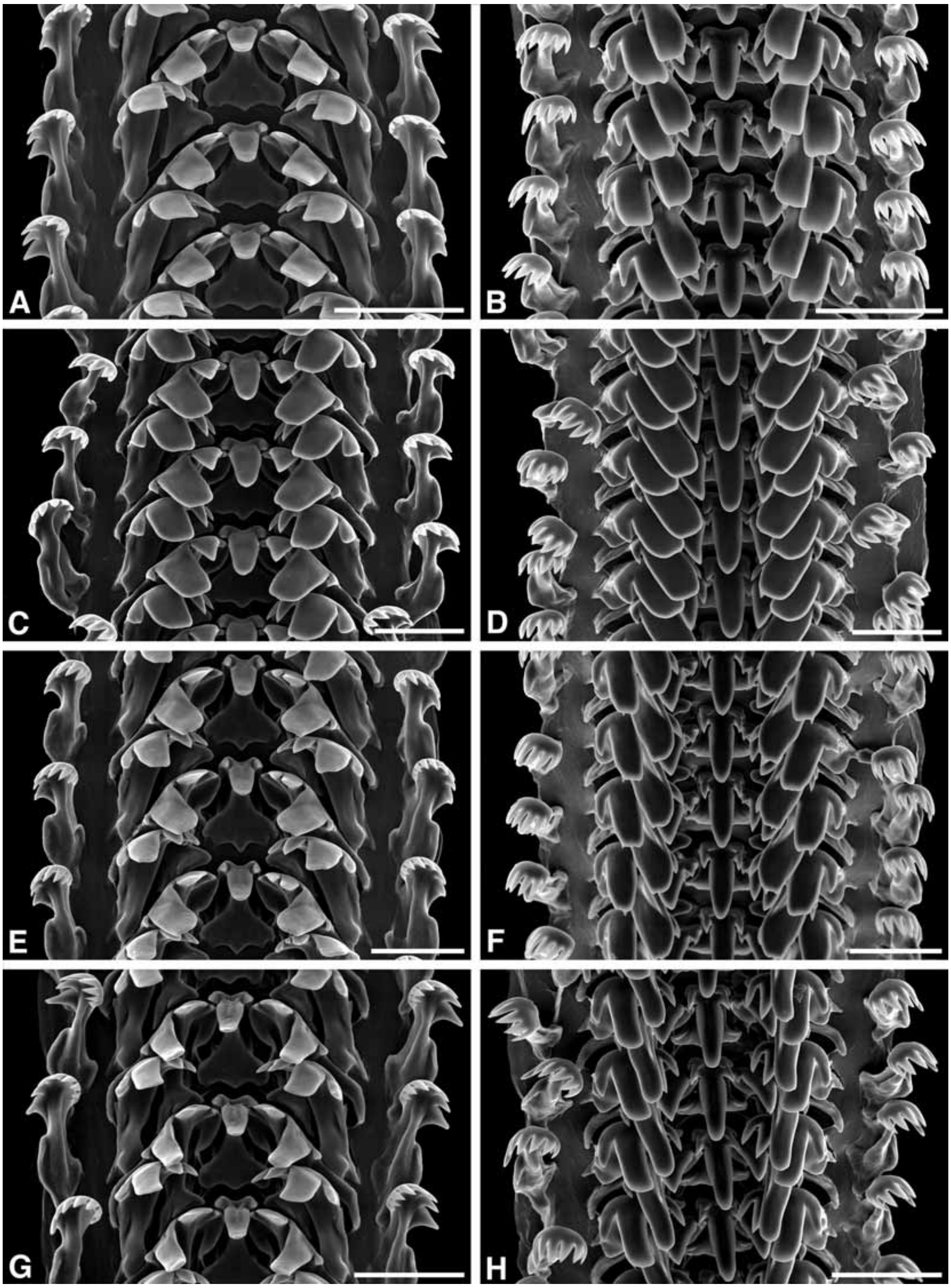

FIGURE 42. Radulae of *Echinolittorina* species (two views of each radula, flat and at 45°). **A, B,** *E. leucosticta*; Polhena, near Matara, Sri Lanka (BMNH 20050078; shell H = 10.7 mm). **C, D,** *E. biangulata*; Pelabuan Ratu, SW Java, Indonesia (BMNH 20050512; shell H = 13.6 mm). **E, F,** *E. philippinensis* new species, paratype; Guintungauan I., Bacuit Archipelago, Palawan, Philippines (BMNH 20050068; shell H = 11.9 mm). **G, H,** *E. tricincta* new species; Anse Ponandou, Secteur de Touho, New Caledonia (MNHN stn 1244; shell H = 10.4 mm). Scale bars = 50 µm.

Habitat: On exposed or moderately exposed rocky shores, in the littoral fringe and mid to upper eulittoral; recorded from granite, beach rock and limestone. There are various, sometimes conflicting, records of the zonation of this species: in the upper eulittoral, down to high water of neap tides (Starmühlner 1974); in the littoral fringe on a sandstone reef, with black lichens (Arudpragasam & Ranatunga 1966); at and below mean high water of spring tides (Rao & Sundaram 1974); in large numbers among weed in the lower eulittoral (Atapattu 1972). It always occupies a zone below the sympatric *E. malaccana* (Rao & Sundaram 1974; Pillai & Appukuttan 1980). According to Atapattu (1969) settlement occurs in the mid-eulittoral zone among oysters, while adults occupy the littoral fringe in the monsoon season and the mid-eulittoral at other times.

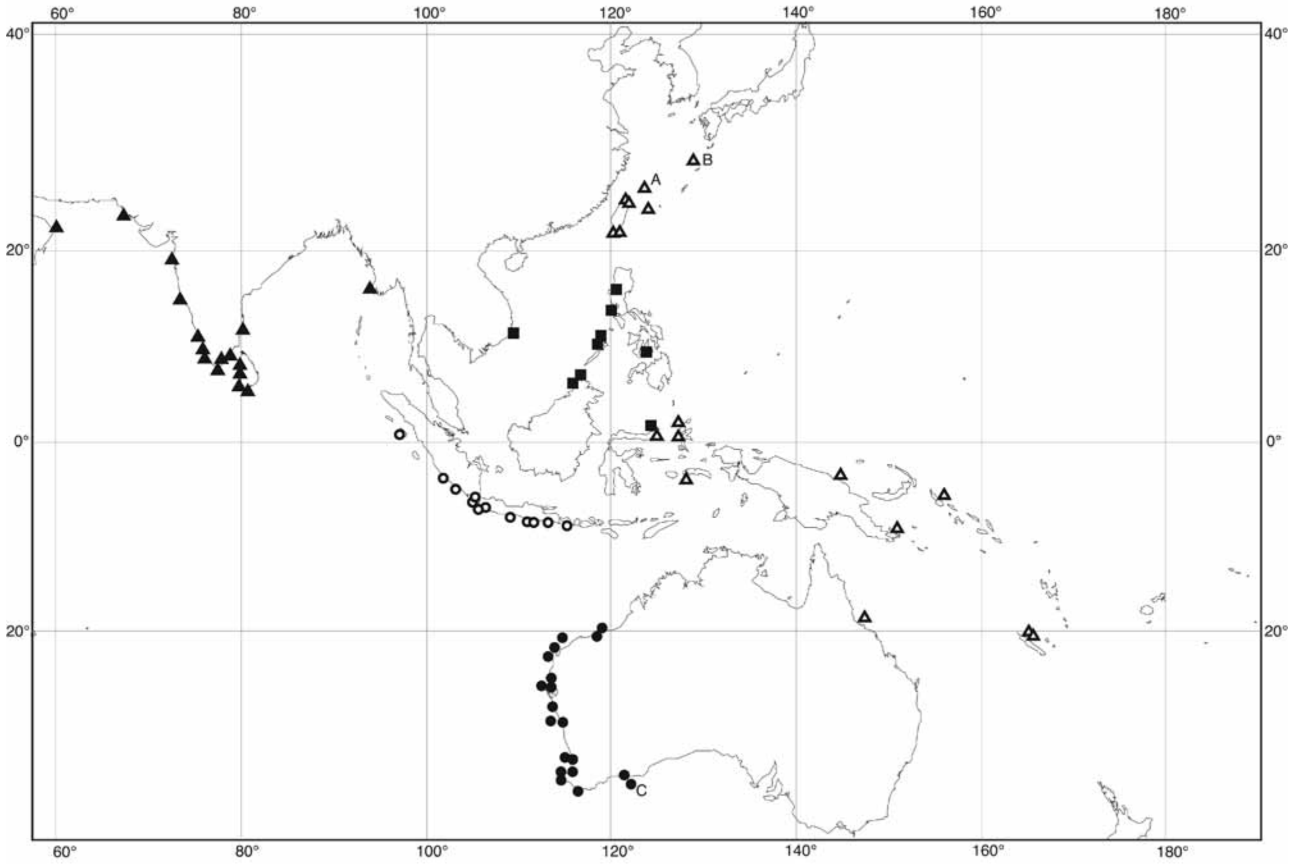

FIGURE 43. Distribution of *Echinolittorina leucosticta* (solid triangles), *E. biangulata* (open circles), *E. australis* (solid circles), *E. philippinensis* (solid squares) and *E. tricincta* (open triangles). Literature records: A, Fujioka & Kurozumi (1981); B, Kurozumi (1994); C, Macpherson (1954).

Remarks: Analysis of both 28S rRNA and COI sequence data confirm that the sister species of *E. leucosticta* is *E. biangulata* (Williams & Reid 2004). The latter, in Sumatra and Java, is geographically the closest of this group to *E. leucosticta*, although the shells of *E. biangulata* are more similar to those of *E. tricincta*. The shortest distance between the known ranges of *E. leucosticta* and *E. biangulata* is almost 2000 km (Sri Lanka to Nias I.), while the extralimital records of the former in Burma suggest that transport of pelagic larvae can occur over distances of at least 1500 km across the Bay of Bengal. The consistent morphological differences in the shells of these two, and their genetic distance (COI K2P distance = 7.8%), support their recognition as distinct species.

The members of the *E. leucosticta* group cannot be distinguished from each other by unique anatomical features, but their distributions are allopatric and their shells are mostly distinctive. The pair *E. biangulata* (Fig. 44) and *E. tricincta* (Fig. 48) are most similar to *E. leucosticta*, but in the latter the profile is only slightly shouldered, the ribs are never carinate or nodulose, and the ribs lack microstriae and are therefore shiny.

Much of the distribution of this species is on coastlines with moderate oceanic primary production (Rutgers University Primary Productivity Study), but it also includes sites in Oman, Karachi and the Gulf of Mannar where productivity is high. Absence from the east coast of Sri Lanka (Attapatu 1972) may be related to the low productivity of this oceanic stretch of coastline. Another feature of the distribution is that the species is common only on exposed or semi-exposed coasts; the species is scarce in the northern Gulf of Mannar, for example. The closest correlation, however, is with areas of coastal upwelling; this is driven by the summer monsoon on the west coast of India, and by the winter monsoon on the west coast of Sri Lanka (Luis & Kawamura 2004). Occurrence north of Mumbai in the Arabian Sea and north of Chennai in the Bay of Bengal is limited by sedimentary shorelines.

Barkati & Ahmed (1984) compared the spawning habits of two littorinids from Karachi, identified as '*Nodilittorina picta*' and '*N. leucosticta leucosticta*'. The pelagic capsules of the former resemble those of *E. vidua*, whereas the latter was described as ovoviviparous, releasing veligers. The protoconch of *E. leucosticta* is of the planktotrophic type and its large capsule gland indicate spawning of egg capsules; this record of ovoviviparity must therefore be based on misidentification, perhaps of *Littoraria intermedia* (Philippi, 1846).

Echinolittorina biangulata **(von Martens, 1897)**

(Figures 42C, D, 43–45)

? *Trochus quadricinctus* Mühlfeld, 1824: 210, pl. 7, fig. 6a, b (Ostindische Meer [East Indies Sea]; lectotype (Rosewater & Kadolsky 1981; type locality incorrectly restricted to Bombay) Mühlfeld, 1824: pl. 7, fig. 6a, b; *nomen dubium*).

Nodilittorina (Nodilittorina) quadricincta—Reid, 1989a: 100 (in part, includes *E. leucosticta*).

Echinolittorina quadricincta A—Williams & Reid, 2004: 2227–2251.

Litorina subgranosa—Böttger, 1890: 169 (not Dunker in Dunker & Zelebor, 1866 = *E. leucosticta*).

Littorina (Melarrhaphe) biangulata von Martens, 1897: 209–210, pl. 9, fig. 26 (Benkulen, west coast of Sumatra [Bengkulu, Sumatra, Indonesia]; lectotype (here designated, Fig. 44K) ZMA Moll. 2.97.001, seen; 10 paralectotypes ZMB 109.925).

Nodilittorina (Granulilittorina) leucosticta biangulata—Rosewater, 1970: 499–500, pl. 384, figs 6–9, pl. 385 (map) (in part, includes *E. tricincta*, *E. philippinensis*).

Nodilittorina (Granulilittorina) quadricincta biangulata—Rosewater & Kadolsky, 1981: 1234 (in part, includes *E. tricincta*, *E. philippinensis*).

Nodilittorina biangulata—Reid, 2001a: 436 (in part, includes *E. tricincta*, *E. philippinensis*). Reid, 2002a: 259–281 (in part, includes *E. tricincta*, *E. philippinensis*).

Echinolittorina biangulata—Williams *et al*., 2003: 83 (in part, includes *E. tricincta*, *E. philippinensis*).

Nodilittorina leucosticta feejeensis—Cernohorsky, 1972: 56 (in part, includes *E. cinerea*, *E. feejeensis*; not Reeve, 1857).

Taxonomic history: The name *Trochus quadricinctus* was introduced by Mühlfeld (1824), with a detailed description, accurate figure and type locality 'East Indies Sea'. No type specimens have been traced; they are not present in NHMW (A. Eschner pers. comm.). The name was apparently not used again until resurrected by Rosewater & Kadolsky (1981). They identified it as the Indian species until then known as *N. leucosticta* (Philippi, 1847), and adopted *N. quadricincta* as its valid name, designating the figure as lectotype and restricting the type locality to Bombay. However, Mühlfeld's figure shows a shell with four strongly raised ribs, whereas in *E. leucosticta* the ribs are usually more numerous and never so pronounced; the shouldered, carinate and somewhat elongate shape is also unlike that of most specimens of *E. leucosticta* (Fig. 40). The original type locality further militates against identification as *E. leucosticta*, a species endemic to India and Sri Lanka and not found in the 'East Indies' (i.e. Indonesia and central IWP). Nevertheless, *Trochus quadricinctus* cannot be confidently identified as the present species, because both *E. tricincta* (Fig. 48A, D, M, N) and *E. philippinensis* (Fig. 46J) can sometimes resemble Mühlfeld's figure, and occur in the 'East Indies'. The name is therefore considered a *nomen dubium*. The next available name, *Littorina biangulata* von Martens, 1897, is supported by type specimens and a clear type locality, and has been used more frequently in the recent literature.

Shells from Java were first identified as *Litorina subgranosa*, a synonym of the Indian *E. leucosticta*, by Böttger (1890), emphasizing the similarity between the two species (see Taxonomic History of *E. leucosticta*). Following its description by von Martens (1897), *E. biangulata* was not mentioned again in the primary literature until used by Rosewater (1970) in the form *N. leucosticta biangulata*, to designate the three species here named *E. biangulata*, *E. tricincta* and *E. philippinensis*. This name was changed to *N. quadricincta biangulata*, following the misidentification discussed above (Rosewater & Kadolsky 1981), and *N. biangulata* was later considered a full species (Reid 2001a, 2002a). Most recently, the three species included under this name were distinguished using DNA sequence analysis by Williams & Reid (2004), who provisionally used the names *E. quadricincta* A, B and C for *E. biangulata*, *E. tricincta* and *E. philippinensis* respectively.

Diagnosis: Shell angled at shoulder and periphery, with spiral threads and 2–4 raised or carinate, sometimes nodulose, ribs on last whorl; spire whorls with marked shoulder angle; surface dull because of fine spiral microstriae; brown with white dashes or nodules on prominent ribs. Western Sumatra and southern Java. COI: GenBank AJ623035, AJ623036.

Material examined: 20 lots (including 3 penes, 6 pallial oviducts, 2 radulae).

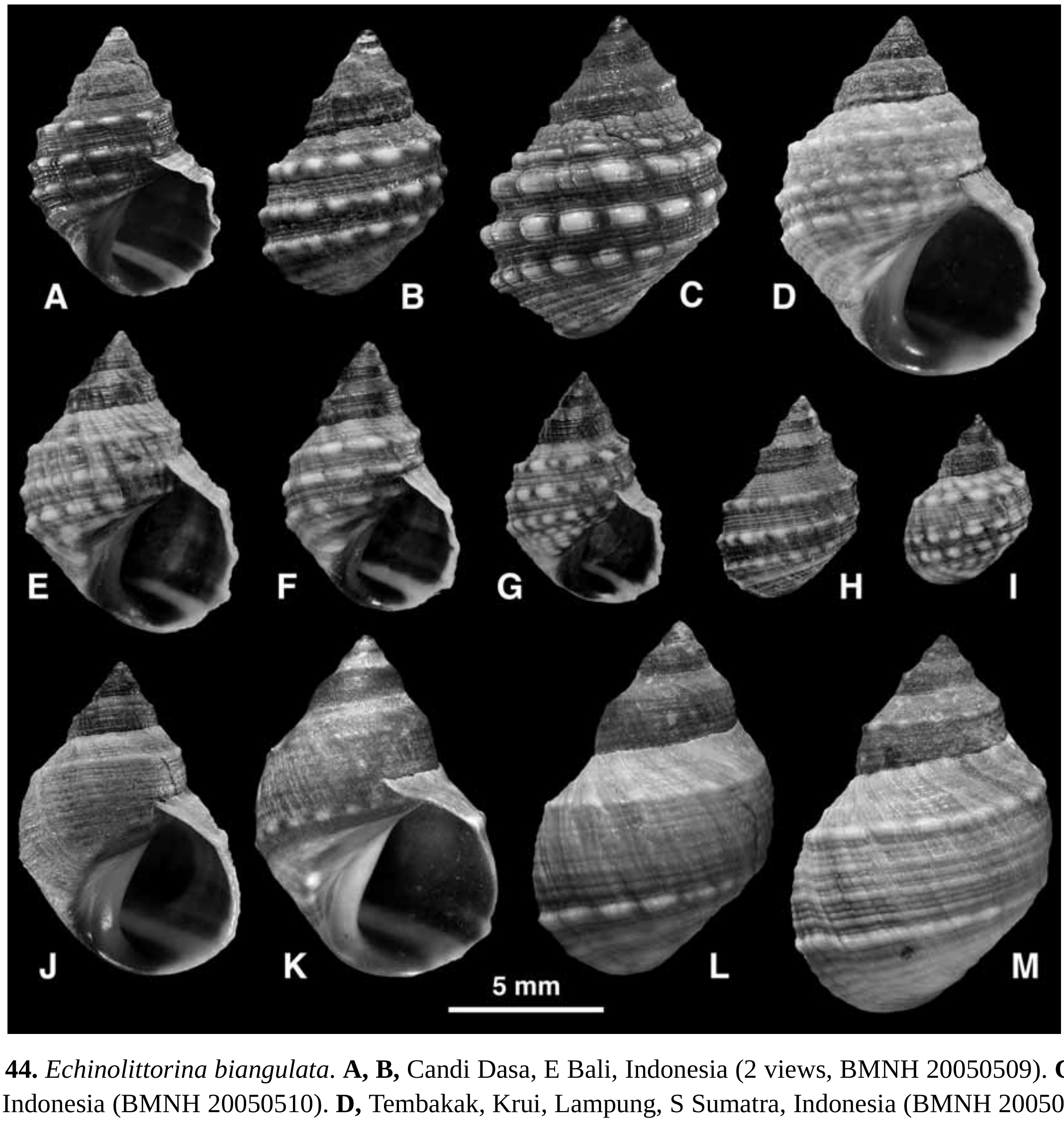

FIGURE 44. *Echinolittorina biangulata*. **A, B,** Candi Dasa, E Bali, Indonesia (2 views, BMNH 20050509). **C,** Sundak, SW Java, Indonesia (BMNH 20050510). **D,** Tembakak, Krui, Lampung, S Sumatra, Indonesia (BMNH 20050511). **E–I,** Pelabuan Ratu, SW Java, Indonesia (BMNH 20050512). **J,** Bale Kambang, Malang, SE Java, Indonesia (BMNH 20050513). **K,** *Littorina biangulata* von Martens, 1897, lectotype ZMA Moll. 2.97.001, Bengkulu, Sumatra, Indonesia. **L,** Bengkulu Harbour, Sumatra, Indonesia (H. Kool Colln). **M,** Bengkulu Harbour, Sumatra, Indonesia (BMNH 20050514).

Shell (Fig. 44): Mature shell height 4.9–13.6 mm. Shape high turbinate (H/B = 1.33–1.56, SH = 1.49–1.79); spire whorls angled at shoulder, suture distinct; spire profile almost straight; last whorl angled at shoulder and slightly at periphery. Columella long, straight, wide, only slightly hollowed at base; inner lip of aperture smoothly rounded and continuous with eroded pseudumbilical and parietal area. Sculpture of last whorl: surface covered by sharp spiral threads of unequal size, 6–9 below periphery, 16–23 above; usually 2–4 prominent or carinate ribs (at shoulder and periphery only, Fig. 44K–M, or shoulder, mid-whorl, periphery and on base, Fig. 44A, B, F, H) that may bear 14-20 elongate nodules or irregular granules; occasionally only shoulder rib is prominent (Fig. 44J), or ribs absent; surface made dull by fine spiral microstriae. Protoconch not seen. Colour: dark brown, fading to fawn or blue-grey in larger specimens; cream band on base, and area extending to columella usually also pale; the prominent ribs with cream nodules and brown spots between; aperture dark brown with cream band at base; columella pale to dark purple-brown, inner lip purplish.

Animal (Fig. 45): Head dark grey to black; tentacle black at base, unpigmented around eye and sometimes in a narrow stripe across base, black at tip; sides of foot grey to black. Opercular ratio 0.34–0.40. Penis (Fig. 45A–C): filament rounded at tip, filament 0.6 total length of penis; mamilliform gland equal in size to glandular disc, borne together on short projection of base; penis slightly pigmented at base; sperm groove extends to tip. Spermatozoa not known. Pallial oviduct (Fig. 45D): bursa opening at half length of straight section, extending back almost to albumen gland. Development predicted to be planktotrophic.

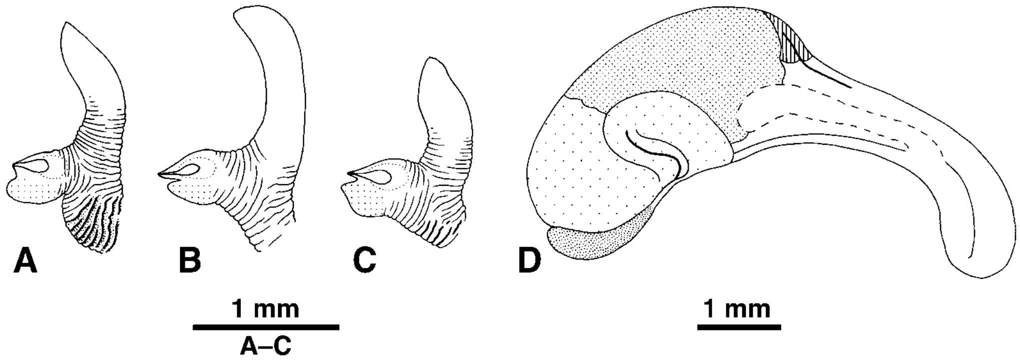

FIGURE 45. *Echinolittorina biangulata*. **A–C,** penes. **D,** pallial oviduct. **A,** Sukahujan, Malimping, SW Java, Indonesia (BMNH 20050515; shell H = 6.0 mm). **B–D,** Pelabuan Ratu, SW Java, Indonesia (BMNH 20050512; shell H **B** = 5.4 mm, **C** = 4.9 mm, **D** = 13.6 mm). Shading conventions as in Figure 3.

Radula (Fig. 42C, D): Relative radula length 3.21–4.34. Rachidian: length/width 1.04–1.08; tip of major cusp rounded. Lateral and inner marginal: major cusp on each of similar size, tips rounded to truncated. Outer marginal: 7–9 cusps.

Range (Fig. 43): West coast of Sumatra, south coast of Java, Bali. Range limits: Pulau Nias, Sumatra, Indonesia (USNM 654444); Bengkulu, Sumatra (BMNH 20050514); Kalianda, Lampung, Sumatra (BMNH); Sukahujan, Malimping, Java, Indonesia (BMNH 20050515); Bale Kambang, Malang, Java (BMNH 20050513); Candi Dasa, Bali, Indonesia (BMNH 20050509). It was not found during extensive collecting in Lombok, but the distribution in Sumatra is poorly known.

Habitat: On wave-exposed basaltic rocks and sea walls in splash zone.

Remarks: This is one of the rarest littorinids in collections and has seldom been mentioned in the literature, but this reflects its restricted and relatively inaccessible distribution. It is apparently common in its range. This species is found on the exposed oceanic coastlines of Indonesian islands facing the Indian Ocean, where primary productivity is low for most of the year. Beginning in June, monsoon-driven upwelling occurs on the coast of Java, moving westwards to central Sumatra before disappearing in November (Susanto *et al.* 2001). An almost identical distribution is shown by *E. sundaica*, although this has not been recorded as far north as Pulau Nias (Fig. 23).

This is the sister species of *E. leucosticta* (see Remarks on that species). Shells are, however, more similar to those of *E. tricincta* (Fig. 48). Compared with that species, the shells of *E. biangulata* are frequently carinate, rarely granulose, and (if present) the nodules are rounded and laterally elongate; shells of *E. tricincta* are seldom carinate, often finely granulose, and nodules (if present) are pointed. Nevertheless, these species are sometimes indistinguishable morphologically from each other, and from rare examples of *E. philippinensis* (Fig. 46J).

***Echinolittorina philippinensis* new species**

(Figures 42E, F, 43, 46, 47)

Nodilittorina (Granulilittorina) leucosticta biangulata—Rosewater, 1970: 499–500, pl. 384, figs 12, 13, pl. 385 (map) (in part, includes *E. biangulata*, *E. tricincta*; not von Martens, 1897).

Nodilittorina (Granulilittorina) quadricincta biangulata—Rosewater & Kadolsky, 1981: 1234 (in part, includes *E. biangulata*, *E. tricincta*; not von Martens, 1897).

Nodilittorina biangulata—Reid, 2001a: 436, figs 1B, 3B (penis) (in part, includes *E. biangulata*, *E. tricincta*; not von Martens, 1897). Reid, 2002a: 259–281, fig. 3C (paraspermatozoa) (in part, includes *E. biangulata*, *E. tricincta*; not von Martens, 1897).

Echinolittorina biangulata—Williams *et al.*, 2003: 83 (in part, includes *E. biangulata*, *E. tricincta*; not von Martens, 1897).

Echinolittorina quadricincta C—Williams & Reid, 2004: 2227–2251.

Types: Holotype BMNH 20050066 (Fig. 46A); 16 dry paratypes BMNH 20050067 (Fig. 46B–D, H, K, L); 100 alcohol paratypes BMNH 20050068 (Figs 42E, F, 47); Guintungauan Island, Bacuit Archipelago, Palawan, Philippines.

Etymology: Latin, from the Philippines.

Taxonomic history: This species has been mentioned infrequently in the literature. It was grouped with *E. biangulata* and *E. tricincta* as *N. leucosticta biangulata* by Rosewater (1970); this name was subsequently changed to *N. quadricincta biangulata* (Rosewater & Kadolsky 1981; see Taxonomic History of *E. leucosticta* and *E. biangulata*). This grouping of three species persisted when *N. biangulata* was raised to specific rank (Reid 2001a, 2002a), and the three were only recognized as distinct as a result of molecular analysis (Williams & Reid 2004).

Diagnosis: Shell angled at shoulder and sometimes at periphery, with numerous spiral ribs and threads of unequal size, of which shoulder rib and 1–3 ribs at periphery are enlarged, carinate or granulose; surface dull because of fine spiral microstriae; spire brown with white or spotted ribs, last 2 whorls white or blue-grey. Mainly Philippines. COI: GenBank AJ622989, AJ622990.

Material examined: 14 lots (including 9 penes, 3 sperm samples, 5 pallial oviducts, 2 radulae).

Shell (Fig. 46): Mature shell height 6.0–16.1 mm. Shape high turbinate (H/B = 1.24–1.59, SH = 1.40–1.85); spire whorls rounded or angled at shoulder, suture distinct; spire profile almost straight; last whorl angled at shoulder, rounded at periphery. Columella long, straight, hollowed at base; inner lip of aperture slightly rounded and continuous with eroded pseudumbilical and parietal area. Sculpture of last whorl: surface covered by spiral ribs and threads of unequal size, 26–35 in total; usually rib at shoulder and 1–3 ribs at periphery are enlarged (occasionally carinate, Fig. 46G, I), sometimes up to 5 ribs may be enlarged; larger ribs are made minutely (or rarely coarsely, Fig. 46G) granulose by intersection with growth lines, but granules are not conspicuously axially aligned; granules sometimes obsolete or eroded away on last whorl; surface made dull by fine spiral microstriae. Protoconch 0.26–0.28 mm diameter, 2.5–2.6 whorls. Colour: apical 3 whorls brown with white or white-dashed ribs, fading to orange; most shells fade to white to blue-grey on last 2 whorls, ribs paler; occasionally last whorl grey-brown, base pale, ribs with white granules separated by brown spots (Fig. 46J); aperture pale to dark brown, with pale band at base and sometimes also at periphery and shoulder; columella pale to dark purple-brown, inner lip purplish.

Animal (Fig. 47): Head (Fig. 47G, H) grey to black with narrow unpigmented stripe across snout; tentacle black at base, unpigmented around eye and across base, usually a black spot at tip; sides of foot grey to black. Opercular ratio 0.34–0.41. Penis (Fig. 47A–E): filament rounded at tip, with annular wrinkles for half its length, filament 0.5–0.6 total length of penis; mamilliform gland equal in size to or larger than glandular disc, borne together on long projection of base; penis usually pigmented at base; sperm groove extends to tip. Euspermatozoa 100–121 µm; paraspermatozoa (Fig. 47I, J) spherical, 11–16 µm diameter, filled with large round granules and single U-shaped to serpentine rod-piece with rounded ends. Pallial oviduct (Fig. 47F): bursa opening at half length of straight section, extending back to albumen gland, usually dilated posteriorly. Development predicted to be planktotrophic.

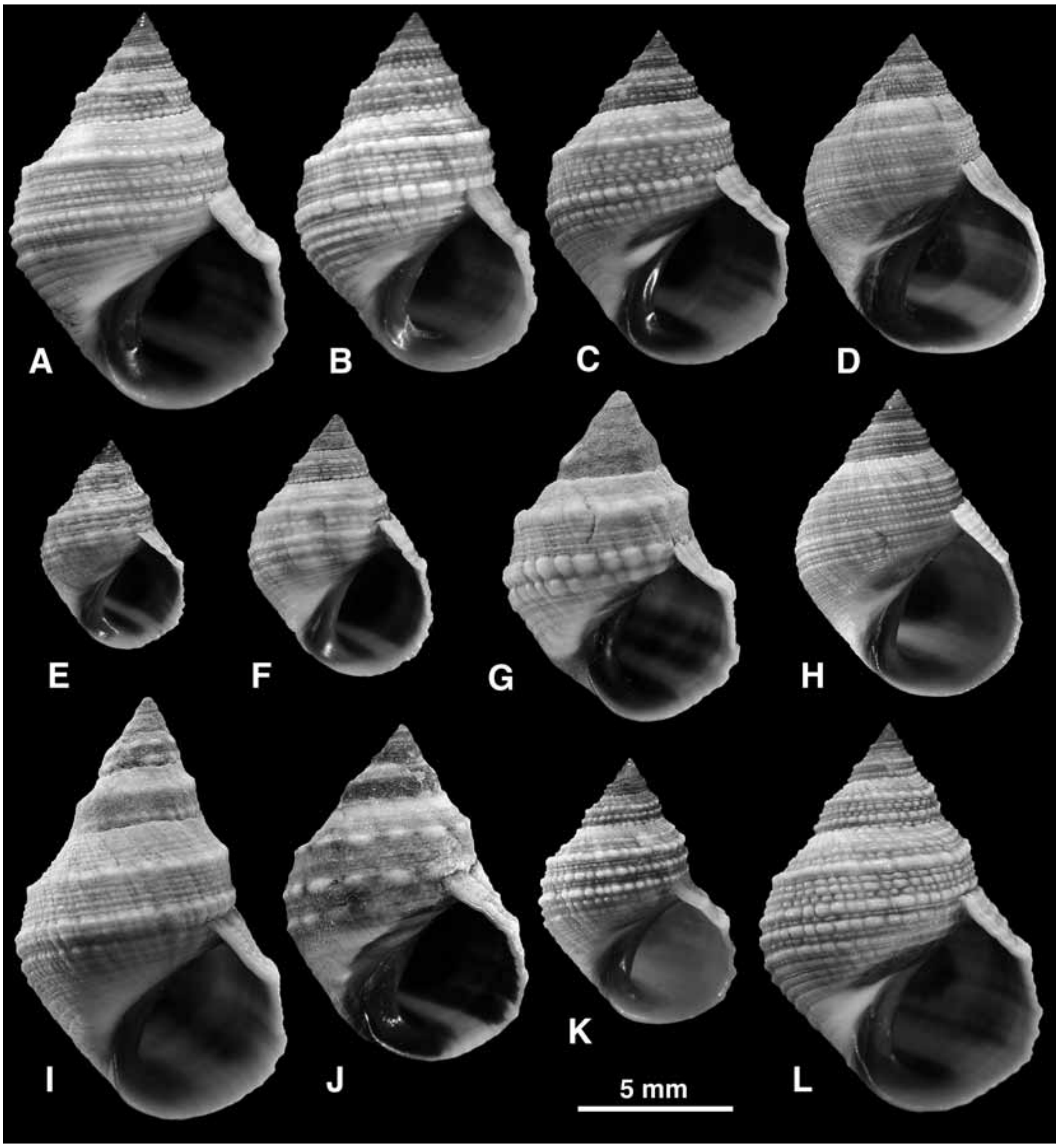

FIGURE 46. *Echinolittorina philippinensis* new species. **A,** holotype, Guintungauan I., Bacuit Archipelago, Palawan, Philippines (BMNH 20050066). **B–D, H, K, L,** paratypes, Guintungauan I., Bacuit Archipelago, Palawan, Philippines (BMNH 20050067). **E, F,** Sabang, Palawan, Philippines (BMNH 20050069). **G, I,** Mainit, Santander, Cebu I., Philippines (BMNH 20050070). **J,** Kudat, Sabah, Malaysia (BMNH 20050071).

Radula (Fig. 42E, F): Relative radula length 3.37–4.49. Rachidian: length/width 1.07–1.31; tip of major cusp rounded. Lateral and inner marginal: major cusp on each of similar size, tips rounded to truncated. Outer marginal: 7–8 cusps.

Range (Fig. 43): Philippines, north Sulawesi, north Borneo, south Vietnam. Range limits: Camp Wallace, La Union, Luzon, Philippines (USNM 233396); Panglao, Bohol, Philippines (BMNH); Santander, Cebu, Philippines (BMNH 20050070); Mokupa, Manado Bay, Sulawesi, Indonesia (BMNH); Gaya I., Sabah, Malaysia (USNM 658324; ZMA); Yen I., Nha Trang Bay, Vietnam (Institute of Oceanography, Nha Trang). This species has a localized distribution and is only known to be abundant in northwestern Palawan, although abundance was not recorded at the three localities in Luzon (USNM). It is uncommon in Cebu and Sabah. In southern Vietnam and northern Sulawesi it is very rare, so these areas are probably outside the normal range.

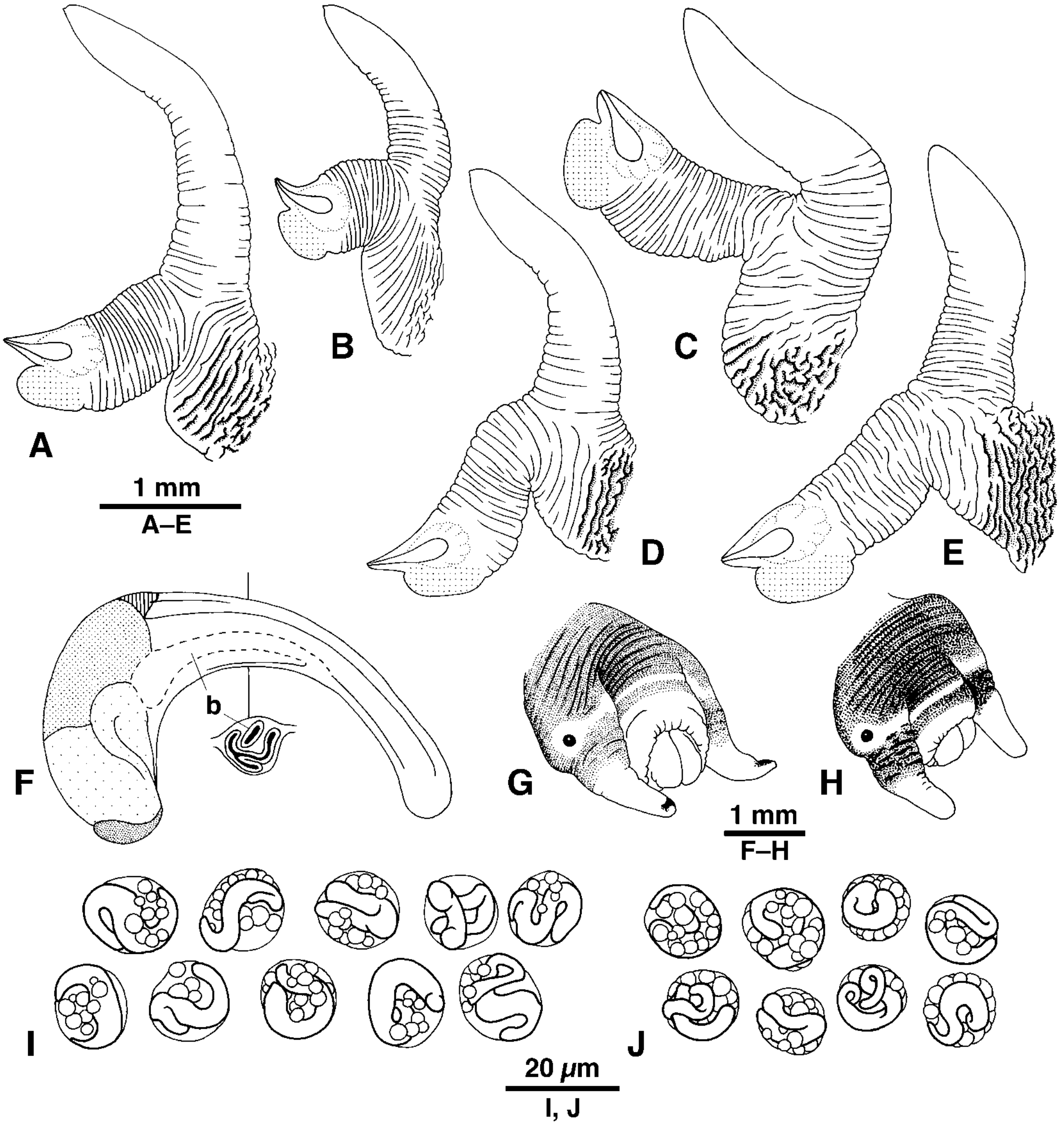

FIGURE 47. *Echinolittorina philippinensis* new species. **A–E,** penes. **F,** pallial oviduct with transverse section. **G, H,** heads. **I, J,** paraspermatozoa. **A–J,** paratypes, Guintungauan I., Bacuit Archipelago, Palawan, Philippines (BMNH 20050068; shell H **A** = 10.4 mm, **B** = 8.6 mm, **C** = 9.0 mm, **D** = 9.0 mm, **E** = 9.3 mm, **F** = 10.8 mm, **G** = 11.9 mm, **H** = 10.4 mm). Abbreviation: b, copulatory bursa. Shading conventions as in Figure 3.

Habitat: In the Philippines this species is abundant on karstic limestone cliffs that are sheltered by fringing reefs, where water is clear. The microhabitats are usually shaded crevices, overhangs and in the shade of trees, in the littoral fringe and uppermost eulittoral zone. It is also recorded from sandstone, shale and basalt.

Remarks: Records of littorinids from the Philippines are quite numerous (see maps of *E. malaccana* Fig. 29 and *E. melanacme* Fig. 56), yet this species is recorded from only eight localities in the islands, all from the western and central regions, indicating a restricted range. All records are from areas of low to moderate oceanic primary production (Rutgers University Primary Productivity Study) and at a local scale in Cebu it occurs only where the water is clear (pers. obs.). Excluding the extralimital records from Vietnam and Sulawesi, all but two are from the eastern margin of the South China Sea, where there is evidence of upwelling phenomena. Off western Borneo the northeast monsoon drives upwelling during the boreal winter (Xie & Hsieh 1995); in northwestern Palawan divers have reported cold water and plankton blooms from January to April (Goreau *et al*. 1997); and off the west coast of Luzon a major upwelling zone observed from October to January is driven by basin circulation rather than wind patterns (Shaw *et al*. 1996). There is no evidence of upwelling in the central Philippines, although human activities do result in eutrophication. The single record from southern Vietnam implies occasional dispersal of larvae across the 1100 km of the South China Sea. In northern Sulawesi rare specimens were found at a locality just 150 km by sea from the closest record of *E. tricincta*; no sympatric occurrences have yet been recorded, perhaps because the present species favours more sheltered locations.

The relationships of this species are not clearly resolved; analysis of DNA sequence from the 12S rRNA gene suggests that it may be the sister taxon of the remaining four members of the *E. leucosticta* group (Williams & Reid 2004). Most shells are readily distinguished from others in this group by their finely granular sculpture and whitish coloration. However, specimens from Sabah (Fig. 46J) lack granules and are indistinguishable from smooth examples of *E. tricincta* (Fig. 48M, N); the identification of this material is based on its geographical location. Nevertheless, intermediate specimens (Fig. 46E, F) suggest that these relatively smooth shells may be within the range of variation of this species. They may perhaps represent a sculptural type found on non-limestone substrates. There are no distinguishing anatomical features, so confirmation of this identification would require molecular evidence. In the Philippines *E. philippinensis* is often syntopic with *E. reticulata*, another granulose white shell. The latter (Fig. 69) is easily recognized by its rounded (not shouldered) whorls, larger granules in distinct axial alignment, and lack of an eroded parietal and pseudumbilical area.

Echinolittorina tricincta **new species**

(Figures 42G, H, 43, 48, 49)

Littorivaga (?) *subnodosa*—Kuroda, 1940: 102 (not Philippi, 1847).

Littorina (Littorivaga ?*) subnodosa*—Kuroda, 1941: 82, pl. 6, figs 5, 6 (not Philippi, 1847).

Nodilittorina subnodosa—Habe, 1951: 92, pl. 14, fig. 1 (not Philippi, 1847). Oyama & Takemura, 1963: *Nodilittorina* fig. 4 (as *subnodosus*; not Philippi, 1847). Higo, 1973: 47 (not Philippi, 1847).

Tectarius subnodosus—Kuroda & Habe, 1952: 89 (not Philippi, 1847).

Nodilittorina (Granulilittorina) subnodosa—Fujioka & Kurozumi, 1980: 53–54, fig. 1A (not Philippi, 1847).

Nodilittorina (Granulilittorina) leucosticta biangulata—Rosewater, 1970: 499–500, pl. 384, figs 10, 11, pl. 385 (map) (in part, includes *E. biangulata*, *E. philippinensis*; not von Martens, 1897). Kurozumi, 1994: 366–367, pl. 2, fig. 5 (not von Martens, 1897).

Nodilittorina (Granulilittorina) quadricincta biangulata—Rosewater & Kadolsky, 1981: 1234 (in part, includes *E. biangulata*, *E. philippinensis*; not von Martens, 1897).

Nodilittorina leucosticta biangulata—Higo & Goto, 1993: 74 (not von Martens, 1897). Higo *et al*., 1999: 91 (not von Martens, 1897). Hasegawa, 2000: 141, pl. 70, fig. 23 (not von Martens, 1897).

Nodilittorina biangulata—Reid, 2001a: 436, fig. 1A (in part, includes *E. biangulata*, *E. philippinensis*; not von Martens, 1897). Reid, 2002a: 259–281 (in part, includes *E. biangulata*, *E. philippinensis*; not von Martens, 1897).

Echinolittorina biangulata—Williams *et al*., 2003: 83 (in part, includes *E. biangulata*, *E. philippinensis*; not von Martens, 1897).

Echinolittorina quadricincta B—Williams & Reid, 2004: 2227–2251.

Types: Holotype BMNH 20050072 (Fig. 48A); 7 dry paratypes BMNH 20050073 (Fig. 48B–F); 9 alcohol paratypes BMNH 20020609 (Fig. 49A, B, E, I, J); 3 dry paratypes MZB Gst. 13.234; Kamenti, Kapataran, Sulawesi, Indonesia.

Etymology: Latin, three-girdled.

Taxonomic history: Until 1970, all literature references to this species were to its occurrence in Taiwan and the Ryukyu Islands. Following Kuroda (1940, 1941) it was identified as *L. subnodosa*. Although the latter (Fig. 19) is a larger species endemic to the Red Sea, its shell with three spiral bands bearing sharp white nodules does bear superficial resemblance to that of *E. tricincta*. Rosewater (1970) had material of this species only from New Caledonia, and identified it (together with *E. biangulata* and *E. philippinensis*) as *N. leucosticta biangulata*, later changed to *N. quadricincta biangulata* (Rosewater & Kadolsky 1981) (see Taxonomic History of *E. leucosticta*, *E. biangulata*, *E. philippinensis*). The members of the *E. leucosticta* group have only recently been distinguished, using molecular data (Williams & Reid 2004).

Diagnosis: Shell angled at shoulder, with spiral threads and 1–3 raised or carinate ribs on last whorl, sometimes bearing granules or sharp nodules; surface dull because of fine spiral microstriae; brown with white dashes on prominent ribs, fading to blue-grey. Western Pacific islands from Taiwan to New Caledonia. COI: GenBank AJ622987, AJ622988.

Material examined: 36 lots (including 10 penes, 1 sperm sample, 4 pallial oviducts, 5 radulae).

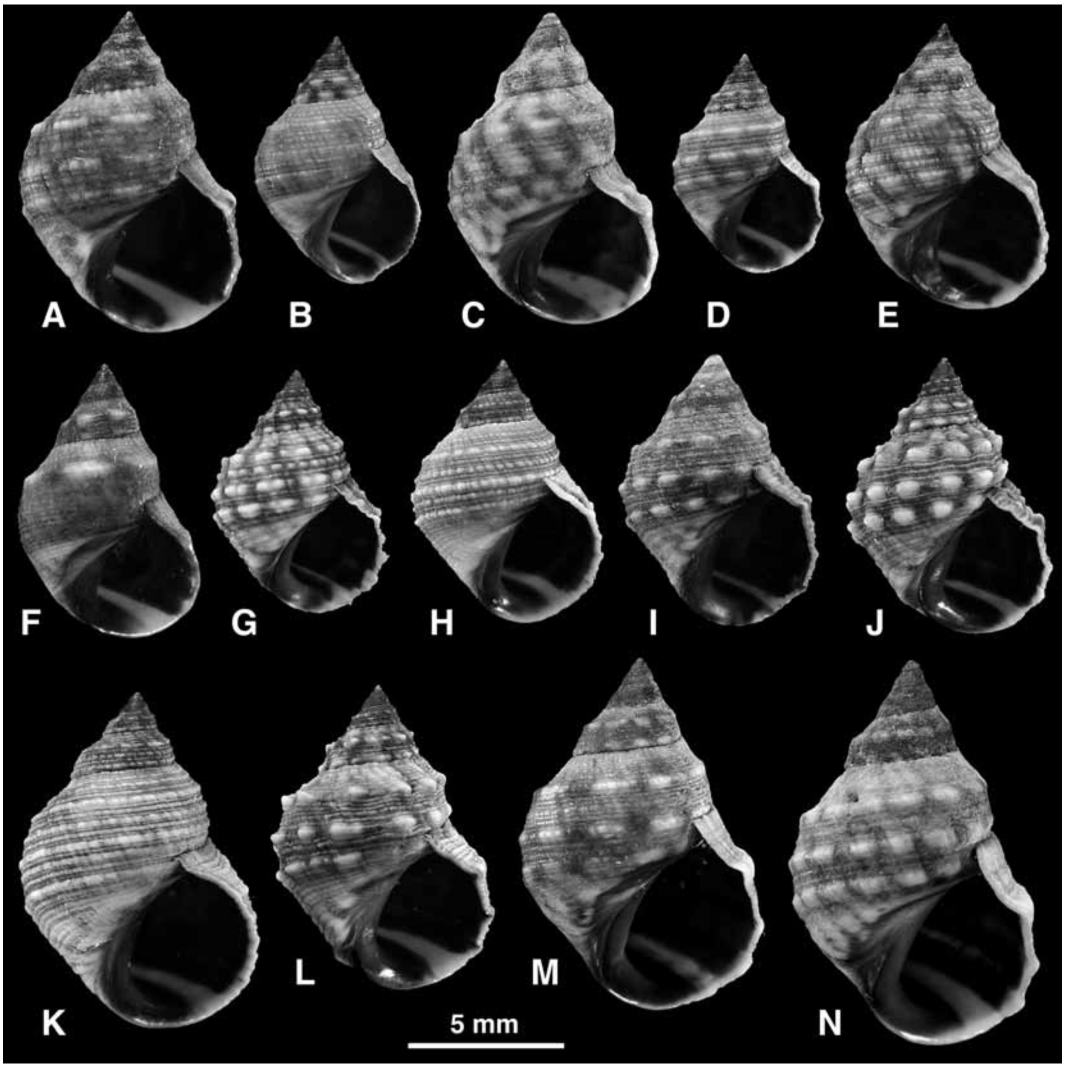

FIGURE 48. *Echinolittorina tricincta* new species. **A,** holotype, Kamenti, Kapataran, Sulawesi, Indonesia (BMNH 20050072). **B–F,** paratypes, Kamenti, Kapataran, Sulawesi, Indonesia (BMNH 20050073). **G, H, J–L,** Chialoshui, SE Taiwan (BMNH 20050074). **I,** Tali, 20 km SE Keelung, Taiwan (BMNH 20040075). **M, N,** Anse Ponandou, New Caledonia (BMNH 20050076).

Shell (Fig. 48): Mature shell height 5.5–14.7 mm. Shape high turbinate (H/B = 1.39–1.54, SH = 1.45–1.69); spire whorls slightly angled at shoulder and with 2 enlarged ribs visible at suture and periphery, suture distinct; spire profile straight to slightly concave towards apex; last whorl angled at shoulder and slightly at periphery. Columella long, straight, slightly hollowed at base; inner lip of aperture slightly rounded and continuous with eroded pseudumbilical and parietal area. Sculpture of last whorl: surface covered by spiral ribs and threads of unequal size, 15–20 at and above periphery and 7–11 below; usually 3 ribs are enlarged or sometimes carinate (at shoulder, mid-point and periphery; rarely only shoulder rib, Fig. 48F; or up to 6 subequal ribs above periphery, Fig. 48H, K); larger ribs are made coarsely or minutely granulose by intersection with growth lines, but granules are not conspicuously axially aligned; granules sometimes obsolete or eroded away on last whorl; rarely the three large ribs are represented by rows of as few as 13 sharp nodules (Fig. 48J, L); surface made dull by fine spiral microstriae. Protoconch 0.28 mm diameter, 2.5–2.6 whorls. Colour: apical 3 whorls brown to black, with white dashes on ribs; most shells fade to blue-grey on last 2 whorls, with whitish base, ribs with white dashes separated by brown spots (Fig. 48A, I, M); occasionally last whorl with brown axial flames (Fig. 48C); aperture dark brown, pale band at base and sometimes faint bands at periphery and shoulder; columella dark purple-brown, inner lip purplish.

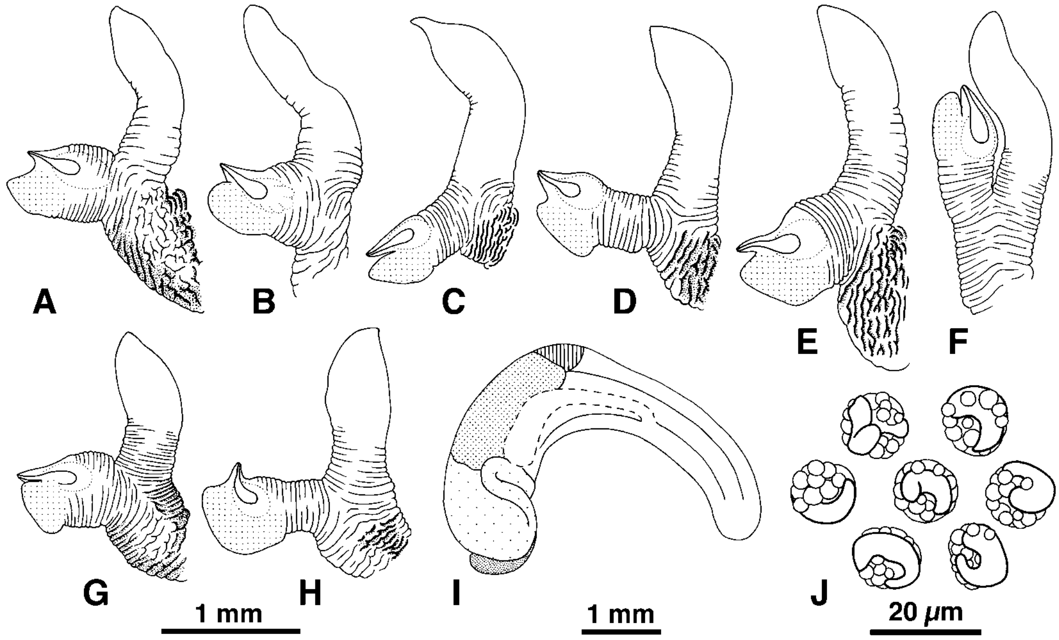

FIGURE 49. *Echinolittorina tricincta* new species. **A–H,** penes. **I,** pallial oviduct. **J,** paraspermatozoa. **A, B, E, I, J,** paratypes, Kamenti, Kapataran, Sulawesi, Indonesia (BMNH 20020609; shell H **A** = 7.2 mm, **B** = 7.7 mm, **E** = 8.5 mm, **I** = 9.7 mm). **C,** Anse Ponandou, Secteur de Touho, New Caledonia (MNHN stn 1244; shell H = 9.7 mm). **D,** Tali, 20 km SE Keelung, Taiwan (BMNH 20040075; shell H = 7.1 mm). **F, G,** Xi Zi, Kaohsiung, Taiwan (BMNH; shell H **F** = 8.2 mm, **G** = 7.8 mm). **H,** National Sun Yat-Sen University, Kaohsiung, Taiwan (BMNH; shell H = 8.8 mm). Shading conventions as in Figure 3.

Animal (Fig. 49): Head black, sometimes a narrow unpigmented stripe across snout; tentacle black at base or occasionally almost to tip, unpigmented around eye and across base, usually a black spot at tip; sides of foot black. Opercular ratio 0.33–0.40. Penis (Fig. 49A–H): filament bluntly pointed or occasionally slightly mucronate at tip, with annular wrinkles for half its length, terminal half slightly swollen, filament 0.5–0.7 total length of penis; mamilliform gland about equal in size to glandular disc, borne together on projection of base; penis usually pigmented at base; sperm groove extends to tip. Euspermatozoa 86–100 µm; paraspermatozoa (Fig. 49J) spherical, 11–13 µm diameter, filled with large round granules and single U-shaped rod-piece with rounded ends. Pallial oviduct (Fig. 49I): bursa opening at half length of straight section, extending back to albumen gland, slightly dilated posteriorly. Development predicted to be planktotrophic.

Radula (Fig. 42G, H): Relative radula length 2.34–4.58. Rachidian: length/width 1.31–1.58; tip of major cusp rounded. Lateral and inner marginal: major cusp on each of similar size, tips rounded to truncated. Outer marginal: 7–9 cusps.

Range (Fig. 43): Ryukyu Is, Taiwan, Moluccas, Papua New Guinea, northeastern Australia, New Caledonia. Range limits: Yokoate-jima, Tokara Is, Japan (Kurozumi 1994); Senkaku Is, Japan (Fujioka & Kurozumi 1980); Inoda Harbour, Ishigaki, Japan (BMNH); Yehliu, 10 km NE Keelung, Taiwan (BMNH); Tali, 20 km SE Keelung, Taiwan (BMNH 20040075); Chialoshui, 10 km E Hengchun, Taiwan (BMNH 20050074); Kahatola I., S Loloda Is, Moluccas, Indonesia (USNM 671207); Kamenti, Kapataran, Sulawesi, Indonesia (BMNH 20020609); Latuhalat, Ambon, Indonesia (NNM); Manam I., Papua New Guinea (IRSNB); Aropa Point, Kieta, Bougainville I., Papua New Guinea (AMS C067255); Urasi I., Milne Bay Prov., Papua New Guinea (IRSNB); Picnic Bay, Magnetic I., Queensland, Australia (BMNH); Hienghene, E New Caledonia (AMS; USNM 637368); Poindimié, E New Caledonia (AMS; USNM 795331).

Despite its 6000-km range from the Ryukyu Islands to New Caledonia, few records are available for this species. It is abundant on the exposed eastern coast of Taiwan and on a short stretch of the northeastern coast of New Caledonia, but at the other recorded localities it appears to be scarce. It has not been found at Okinawa, and only a single shell is reported from the Tokara Islands (Kurozumi 1994). Only a single specimen has been found in Queensland, despite intensive collecting, so this is evidently an extra-limital record. Relatively little collecting of littorinids has been done on the exposed east coast of the Philippines.

Habitat: On exposed and moderately exposed rocky shores with clear, oceanic water; recorded from basalt, granite, sandstone, limestone and concrete, often on open or vertical surfaces. This species extends lower on the shore than all sympatric littorinids, being found in the low littoral fringe and upper part of the barnacle zone.

Remarks: *Echinolittorina tricincta* is found in areas with low to moderate levels of oceanic primary productivity (Rutgers University Primary Productivity Study). It is only known to be abundant in two areas, one on the exposed eastern coast of Taiwan (at two localities, Tali and Chialoshui, listed above) and the other on a short stretch of the northeastern coast of New Caledonia where there are gaps in the barrier reef. This apparent preference for wave-exposed sites may explain the paucity of records of this widely distributed species; on the western fringes of the Pacific Ocean exposed rocky shores that are not sheltered by reefs are scarce and often inaccessible. This habitat contrasts with that of the more sheltered sites where *E. philippinensis* occurs, and may explain why in Sulawesi *E. philippinensis* was found on the sheltered north coast while *E. tricincta* occurred on the more exposed coast facing the Molucca Sea.

There is also a possible correlation between the occurrence of *E. tricincta* and areas of upwelling, although the distribution of such areas in the western Pacific is not well documented. There is a major upwelling area off northeastern Taiwan (Chen 1995), but there is no record of upwelling off the southeast of the island. Monsoon-driven upwelling occurs during the boreal winter to the north of Halmahera (Xie & Hsieh 1995) and on the northern coast of New Guinea (Kuroda 2000), and during the boreal summer in the eastern Banda Sea (Moore *et al*. 2003). (Records of littorinids in the eastern Banda Sea are scarce and distributions therefore poorly known; for *E. tricincta* there is a single record from Ambon.) Summer upwelling also occurs off northeastern New Guinea (Xie & Hsieh, 1995). There is a strong summer phytoplankton bloom off the north and northeastern coasts of New Caledonia during the summer, and chlorophyll enrichment around the Solomon Islands, but the origins of these blooms are unknown (Dupouy *et al*. 2004).

There is a large gap in the known distribution, between Taiwan and the Molucca Sea, but preliminary molecular data indicate that these populations are conspecific (12S sequence from Taiwan, S.T. Williams & D.G. Reid unpublished, almost identical to those reported from Sulawesi, Williams & Reid 2004).

DNA-sequence data suggest that the sister species of *E. tricincta* is *E. australis*, but support for this relationship is not strong (Williams & Reid 2004). The shell of the latter is unlikely to be confused with that of *E.*

tricincta, being larger, thicker and often bearing strong nodules (Fig. 50). Much more similar, and sometimes indistinguishable, are the shells of *E. biangulata* (Fig. 44; see Remarks on that species, and on *E. philippinensis*). Anatomically, all members of the *E. leucosticta* group are closely similar, but the distal part of the penial filament of *E. tricincta* is often more swollent than in the others. In Taiwan *E. tricincta* occurs on the same shores as *E. malaccana* (Fig. 27), but at lower tidal levels; the two can be similar (Fig. 48J, L), but nodulose specimens of *E. tricincta* are distinguished by their three, not two, rows of nodules and their rounded, not sharp, inner lip. Some shells from Taiwan (Figs 48H, K) also approach the sympatric *E. radiata* (Fig. 4) and *E. melanacme* (Fig. 53), but *E. tricincta* differs in the two prominent ribs visible on the spire whorls and in the rounded inner columellar lip. Also found in Taiwan is *E. cinerea* (Fig. 64), but shells of that species have four prominent ribs on the last whorl and a sharp inner apertural lip. Anatomical features distinguish *E. tricincta* from *E. malaccana*, *E. radiata*, *E. melanacme* and *E. cinerea*.

Echinolittorina australis **(Gray, 1826)**

(Figures 43, 50–52)

Littorina australis Gray, 1826: 483 (no locality, but described in *Narrative of a survey of the intertropical and western coasts of Australia*; neotype (Rosewater 1970) WAM S15402 (formerly 292-70), South Mole [Arthur's Head], at the mouth of the Swan River, Western Australia (Fig. 50A), seen; not *L. australis* Gray, 1839 = *Bembicium nanum* (Lamarck, 1822)).

Litorina australis—Menke, 1844: 57.

Nodilittorina (Nodilittorina) australis—Rosewater, 1970: 485–487, pl. 325, figs 19, 20, pl. 373, figs 1–4, pl. 374 (map). Reid, 1989a: 99. Wilson, 1993: 147, pl. 18, fig. 10a, b.

Nodilittorina australis—Wells & Bryce, 1986: 50, pl. 10, fig. 113. Johnson & Black, 1999: 111–119, fig. 2. Yeap *et al*., 2001: 63–76. Reid, 2002a: 259–281.

Echinolittorina australis—Williams *et al*., 2003: 83. Williams & Reid, 2004: 2227–2251.

Littorina nodosa Gray, 1839: 139 (no locality; lectotype (Rosewater 1970) BMNH 1887.4.26.10 (Fig. 50F), seen; 2 paralectotypes BMNH 1887.4.26.11–12; seen; type locality (Rosewater 1970) north coast of Western Australia). Reeve, 1857: sp. 13, pl. 2, fig. 13.

Litorina nodosa—Philippi, 1847a: vol. 2: 160–161, *Litorina* pl. 3, figs 6, 7. Weinkauff, 1882: 94–95, pl. 13, figs 14, 15.

Tectarius nodosus—H. Adams & A. Adams, 1854: 315. Tryon, 1887: 259, pl. 47, fig. 66, pl. 48, fig. 83 (in part, includes *E. natalensis*, *E. subnodosa*, *E. miliaris*).

Litorina (Tectaria) nodosa—Weinkauff, 1883: 226 (in part, includes *E. subnodosa*, *E. natalensis*, *E. malaccana* group).

Nodilittorina (Nodilittorina) nodosa—Rosewater, 1970: 487–488, pl. 325, figs 21, 22, pl. 373, figs 5-10, pl. 374 (map). Wilson, 1993: 147, pl. 18, fig. 11a, b.

Nodilittorina nodosa—Wells & Bryce, 1986: 50, pl. 10, fig. 116.

Litorina rugosa Menke, 1843: 9 (ad scopulos calcareos collis Arthurshead, od ostium fluvii cygnorum [from calcareous cliffs of hill Arthurshead, at mouth of Swan River, Western Australia]; types lost). Philippi, 1846a: vol. 2: 101, *Litorina* pl. 1, fig. 5. Weinkauff, 1882: 66–67, pl. 8, figs 14, 15. Weinkauff, 1883: 214.

Littorina rugosa—Reeve, 1857: sp. 32, pl. 7, fig. 32a, b.

Tectarius rugosus—Tryon, 1887: 259–260, pl. 48, fig. 70.

Nodilittorina rugosa—Macpherson, 1954: 59. Hodgkin *et al*., 1966: 33, pl. 11, fig. 5. Wilson & Gillett, 1971: 30, pl. 11, figs 10, 10a.

Nodilittorina (Nodilittorina) australis x *nodosa* hybrids—Rosewater, 1970: 488–489, pl. 373, figs 11–16.

Nodolittorina praetermissa—Schneider, 2003: 4–6, fig. 1 (not *Litorina praetermissa* May, 1909 = *Afrolittorina praetermissa*).

Taxonomic history: The extraordinary intraspecific variation in the shell of this species has led to persistent taxonomic confusion. Gray described the species twice, the large spirally striated form as *L. australis* Gray, 1826 and the small nodulose form as *L. nodosa* Gray, 1839 (Fig. 50A, F). The former was named again as *Litorina rugosa* Menke, 1843, although Menke (1844) himself pointed out that his species was a synonym of *L. australis*. Nevertheless, it was the names *L. rugosa* and *L. nodosa* that became accepted in the literature for the striate and the nodulose forms respectively (Philippi 1846, 1847a; Reeve 1857; Weinkauff 1882), while the name *L. australis* was overlooked. Later, Weinkauff (1883) listed *Litorina subnodosa*, *Litorina natalensis* and *Litorina vilis* as varieties of *Litorina nodosa*, and this was followed by Tryon (1887), who cited the three rows of nodules shared by some of these species. Despite the broad species concept implied by this surprising synonymy, both these authors continued to maintain *L. rugosa* as a separate species, and this name continued in use, as *N. rugosa*, for nearly a century (Wilson & Gillett 1971).

Rosewater (1970) resurrected the name *N. australis* for the large, striate form, but continued to maintain it as a species distinct from *N. nodosa*; shells of intermediate appearance (and even with sculpture changing from nodulose to striate during growth) were identified as interspecific hybrids. These names gained acceptance in the Australian literature (Wells & Bryce 1986; Wilson 1993), but they were synonymized by Reid (1989a) on the basis of their similar reproductive anatomy. This was confirmed by allozyme frequencies (Johnson & Black 1999) and the phenotypic plasticity of this species was finally spectacularly established by reciprocal transfer experiments (Johnson & Black 1999; Yeap *et al*. 2001).

Diagnosis: Shell reaching large size, usually heavy and swollen; sculpture extremely variable, from 1–2 rows of large nodules to spirally striate with granulose or rugose surface; white, or black with cream to orange nodules. Western Australia. COI: GenBank AJ622985, AJ622986.

Material examined: 81 lots (including 9 penes, 1 sperm sample, 9 pallial oviducts, 3 radulae).

Shell (Fig. 50): Mature shell height 8.0–23.1 mm. Shape turbinate to high turbinate (H/B = 1.11–1.61, SH = 1.32–1.78); spire whorls rounded or flattened, suture usually distinct; spire profile straight to slightly concave towards apex; last whorl may be rounded, angled at periphery, or angled at shoulder and periphery. Columella concave, slightly hollowed at base; inner lip of aperture slightly rounded, continuous with eroded parietal area and sometimes a small pseudumbilical area. Extraordinarily variable in sculpture; surface of last whorl covered by 13–19 rounded ribs (8–12 at and above periphery, 5–7 below) with narrow grooves between; in weakly sculptured shells the spire whorls are crossed by axial ribs, but these become weak or absent on last whorl, where spiral ribs are weakly granulose or smooth (Fig. 50B, I); commonly, last whorl bears 9–15 axial, usually curved, rugose ribs between suture and periphery, weakening towards end of whorl (Fig. 50A, C, D, L, N–P); in nodulose shells the axial rugae develop as rounded nodules (usually a row at suture and at periphery, Fig. 50F, G; sometimes up to 4 rows, Fig. 50H, J; rarely single row at periphery, Fig. 50E); transitional shells with nodulose spire and striated final whorl can be found (Fig. 50K); nodulose shells usually of small size (less than 12 mm, but rarely up to 21 mm); ribs glossy if well preserved, with spiral microstriae in grooves only. Protoconch 0.28–0.30 mm diameter, 2.5–2.7 whorls. Colour: white to cream, usually grey to blackish between axial rugae and in spiral grooves, sometimes persisting as a marbled pattern on final whorl of weakly sculptured shells; nodulose shells grey to black with red, orange or cream nodules, pale zone on base; aperture cream to brown, pale basal band visible in darker shells, and occasionally a peripheral band also; columella cream, fawn or purple-brown.

Animal (Fig. 51) Head grey with a narrow unpigmented stripe across snout; tentacle base pale to dark grey, unpigmented around eye and across base, rarely a black spot at tip; sides of foot grey. Opercular ratio 0.38–0.40. Penis (Fig. 51B–F): filament bluntly rounded to slightly pointed at tip, with annular wrinkles for half its length, terminal third may be blade-shaped, filament 0.6–0.8 total length of penis; mamilliform gland equal in size or smaller than glandular disc, borne together on projection of base; penis not pigmented at base; sperm groove extends to tip. Euspermatozoa not known; paraspermatozoa: spherical, with single U-shaped or annular rod-piece with rounded ends (preservation poor in available material). Pallial oviduct (Fig. 51A): bursa opening at half length of straight section, not reaching or just touching albumen gland. Development predicted to be planktotrophic.

Radula (Fig. 52): Relative radula length 3.37–7.84. Rachidian: length/width 1.40–2.00; tip of major cusp rounded or pointed. Lateral and inner marginal: major cusp on each of similar size (Fig. 52B) or major cusp of lateral larger than that of inner marginal (Fig. 52D), tips rounded. Outer marginal: 6–7 cusps.

Range (Fig. 43): Temperate and subtropical Western Australia. Range limits: Eleven-Mile Beach, Esperance, Western Australia (BMNH 20050086); Boxer I., Recherche Archipelago, Western Australia (Macpherson 1954); W Denmark, Western Australia (AMS C107499); Barrow I., Western Australia (USNM 691675); Port Hedland, Western Australia (USNM 835618); Cape Keraudren, Western Australia (AMS).

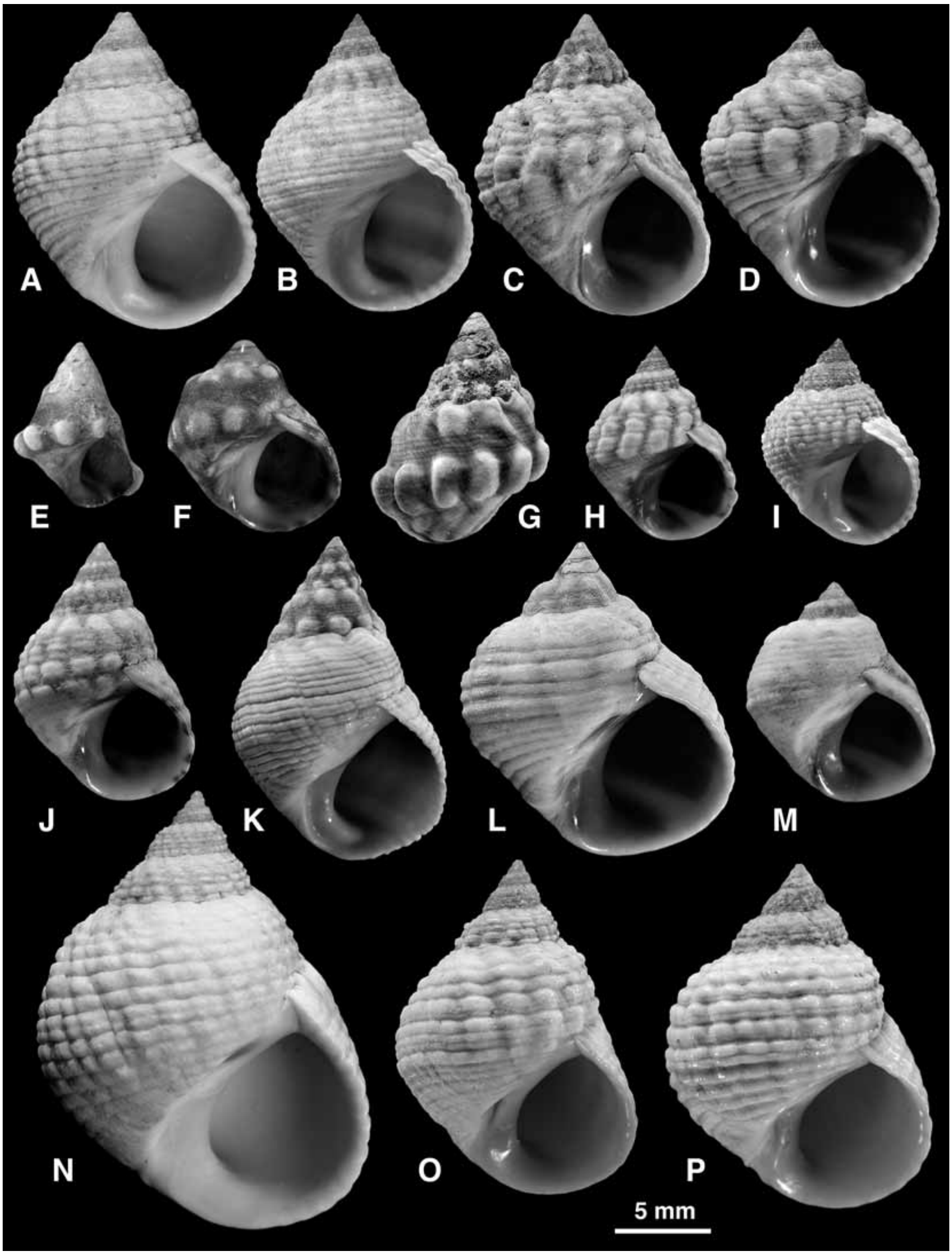

FIGURE 50. *Echinolittorina australis*. **A,** *Littorina australis* Gray, 1826, neotype, South Mole, mouth of Swan River, Fremantle, Western Australia (WAM S15402). **B, I,** Trigg I., Western Australia (BMNH 20050082). **C, J, H, M,** Point Murat, Cape Vlamingh, Cape Range, Western Australia (BMNH 20050083). **D, L,** Ricey Bay, Rottnest I., Western Australia (BMNH 20050084). **E,** no locality (BMNH 20050085). **F,** *Littorina nodosa* Gray, 1839, lectotype, no locality (BMNH 1887.4.26.10). **G,** Eleven-Mile Beach, Esperance, Western Australia (BMNH 20050086). **K,** Kalbarri, Western Australia (BMNH 20050087). **N,** no locality (BMNH 20050088). **O, P,** East Wallabi I., Abrolhos Is, Western Australia (BMNH 20050089).

Esperance has long been quoted as the southeastern limit of the distribution (Hodgkin *et al*. 1966; Rosewater 1970). There is a single record from Cape Northumberland, Port MacDonnel, South Australia (AMS, 10 specimens), 1600 km to the east, but this is presumed to be unreliable since the littorinids of southeastern Australia are well recorded (e.g. Reid & Williams 2004), and such a large collection of a rare immigrant is unlikely. The northern limit is problematic. There are three records from Vansittart Bay in the tropical zone of Western Australia (AMS C45180; USNM 684714, 862118; also quoted by Rosewater 1970); the one in AMS was collected by W. Burrows, whose record of *Austrolittorina unifasciata* (Gray, 1826) from the same locality was dismissed as unreliable by Reid & Williams (2004). The northernmost reliable record is here taken as Cape Keraudren, approximately 1000 km to the southwest.

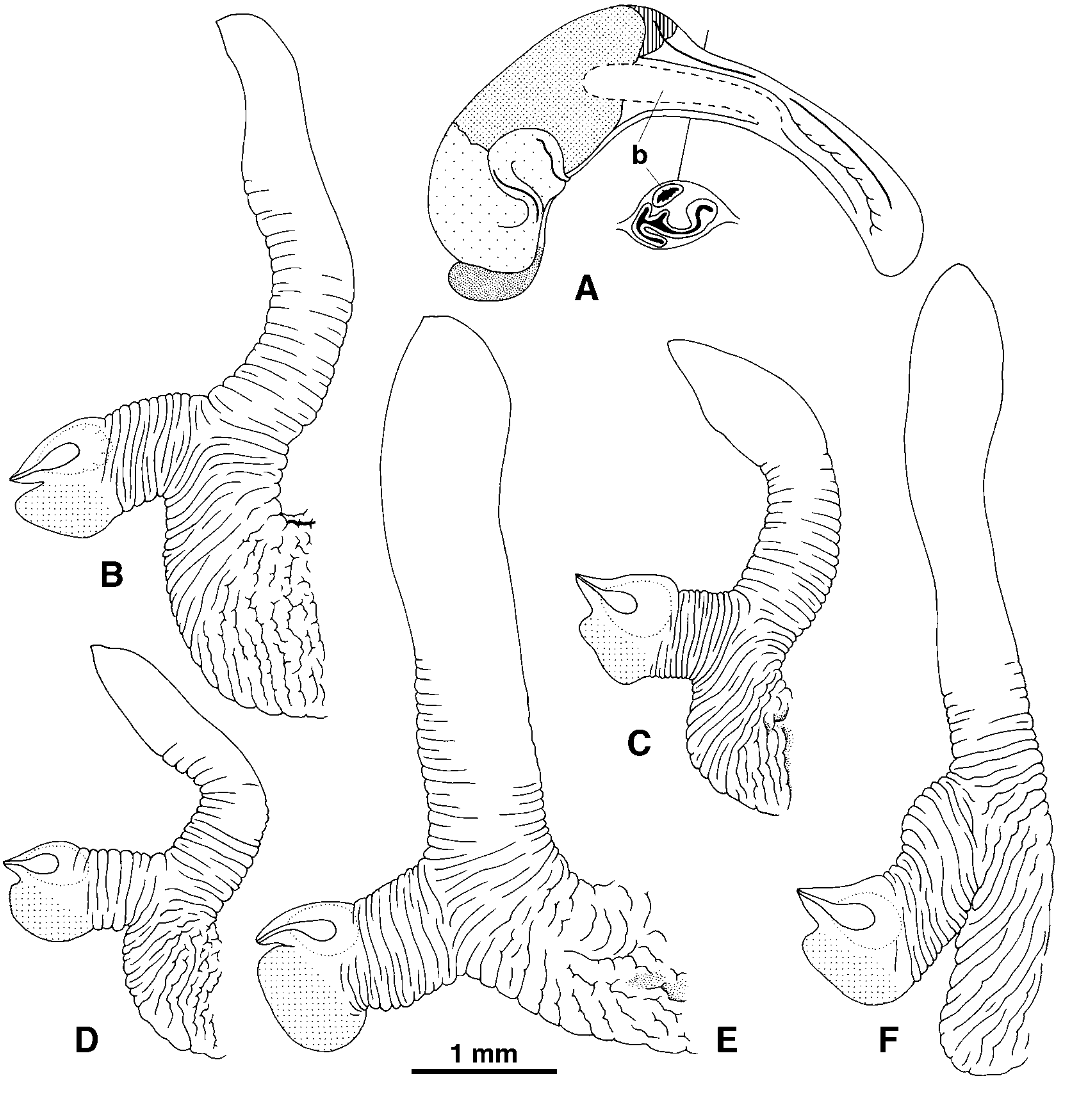

FIGURE 51. *Echinolittorina australis.* **A,** pallial oviduct. **B–F,** penes. **A–D,** Point Murat, Cape Vlamingh, Cape Range, Western Australia (BMNH 20050083; shell H **A** = 9.7 mm, **B** = 12.3 mm, **C** = 11.0 mm, **D** = 9.4 mm). **E,** Ricey Bay, Rottnest I., Western Australia (BMNH 20050084; shell H = 18.7 mm). **F,** Kalbarri, Western Australia (BMNH 20050087; shell H = 12.8 mm). Abbreviation: b, copulatory bursa. Shading conventions as in Figure 3.

Habitat and ecology: On exposed rock platforms and cliffs, also on sheltered coasts; frequently on limestone, but also recorded from sandstone; in littoral fringe and uppermost eulittoral. At Ningaloo, Black & Johnson (2001) observed zonation between the lower *E. vidua* and the higher *E. austrotrochoides*; this species showed an intermediate growth rate, reaching half its maximum size in 1.2 years. In the Abrolhos Islands it occurs on large rocks in the splash zone, on exposed and sheltered shores (Johnson & Black 1997). Zonation at Rottnest Island was described by Black *et al.* (1979) and at Ningaloo by Johnson & Black (1999).

Remarks: This is the largest member of the genus *Echinolittorina,* shells reaching 23.4 mm in height

(Rosewater 1970). It is most remarkable for its extreme variation in shell form, which is as pronounced as in any other species of this notoriously variable family (e.g. Reid 1996, 2002b). The basis of shell variability in *E. australis* has been investigated in detail (Johnson & Black 1999; Yeap *et al*. 2001), and there is a close parallel with descriptions of the variation of the Atlantic *Tectarius striatus* (King & Broderip, 1832) (Britton 1995; Reid 1996; De Wolf *et al*. 1997; all as *L. striata*). The two extreme shell forms, striate and nodulose, were considered distinct species by Rosewater (1970, as *N. australis* and *N. nodosa* respectively), with occasional hybridization. Consistent with this interpretation, they occupy broadly the same geographical range and at many localities both types can be found in discrete groups on different parts of the shore. Nevertheless, at other localities the two forms are intermixed and intermediates occur; these may show sharp transitions from nodulose to striate morphology (Fig. 50K), but only very rarely (less than 1% of natural intermediates) are transitions found in the opposite direction (Johnson & Black 1999). Furthermore, there is a connection with size, for the nodulose form does not usually exceed 15 mm (exceptionally to 21 mm, BMNH), and many shells display a tendency to become gradually less nodulose on later whorls (Fig. 50B). Allozyme analysis revealed no differences between the two forms, and preliminary transfer experiments suggested that the switch from nodulose to striate was a response to habitat (Johnson & Black 1999). Observations at Rottnest Island showed that striate forms were found only on vertical, relatively shaded, limestone faces exposed to wave action, whereas nodulose forms occurred only on rugged, sloping shores in full sun. A large series of transplant experiments demonstrated asymmetry in the developmental response, most of the nodulose forms becoming more striate in character when transplanted to vertical shores, whereas only about half of the striate shells showed a response when transplanted to the open habitat (Yeap *et al*. 2001). Investigating the adaptive significance of the plasticity, it was found that the nodulose shell form (with higher surface area) cools more quickly, whereas striate animals emerge more rapidly when submerged; these characteristics are clearly adaptive in sunny and wave-exposed habitats respectively. These authors argued that the asymmetry of the plasticity may also be functional, because smaller snails are more affected by heat stress, whereas large ones are more susceptible to dislodgement by waves. Nevertheless, there was also evidence of some developmental constraint, because the nodulose shell type was more likely to develop under conditions of slower growth, probably reflecting the rate-limiting process of shell deposition. These studies also demonstrated the high degree of canalization of the development of the two shell morphs, in which sculpture (striate and nodulose) and colour (white, or brown with orange nodules, respectively) are strongly but not completely correlated. Although the experimental evidence is convincing, one inconsistency in the adaptive explanation is that (contrary to the suggestion by Yeap *et al*. 2001, based on maps in Rosewater 1970) the nodulose form is not absent in the cooler southern parts of the distribution. Only nodulose forms have been seen from Esperance at the extreme southeast of the range, both forms occur at the southern extreme in the vicinity of Denmark, and the four northernmost records (Barrow I.; Port Hedland; Cape Keraudren) are all of striate shells.

This species also shows variation in radular tooth form (Fig. 52), similar to that of *E. natalensis* (Fig. 15A–D), but less pronounced. It is not known whether this might have an ecophenotypic basis, as in the case of shell form.

Echinolittorina australis extends to higher latitudes than any other IWP member of the genus, with the exception of *E. radiata* in Japan. Its distribution corresponds closely with the route of the southward Leeuwin Current along the western Australian coastline and extends well into the southern Australian temperate region or 'Flindersian Province' (Wilson & Allen 1987). The easternmost records of the species in the vicinity of Esperance are close to the limit of the influence of this warm current, and suggest temperature limitation on its range. This current had been thought to inhibit the upwelling that is found on most eastern ocean margins, but it has recently been shown that wind-driven upwelling does occur in the extreme southwest of Western Australia during the austral summer, providing a source for the cooler Capes Current that flows northwards along the inner continental shelf (Gersbach *et al*. 1999). Upwelling also occurs on the northwestern coast of Australia around Port Hedland between March and September (Wyrtki 1961). As with other members of the *E. leu-*

costicta group, therefore, there is evidence for an association with upwelling areas.

The relationships of this species are not clearly resolved by available molecular data, but there is weak support for a sister relationship with *E. tricincta* (Williams & Reid 2004; COI K2P distance = 10.3%). It is not sympatric with any other member of the *E. leucosticta* group, and its shell does not resemble those of the others; anatomically, however, all members are closely similar. In the north of its range, *E. australis* is sympatric with *E. austrotrochoides* (e.g. Black & Johnson 2001; Fig. 30); nodulose shells of the former are distinguished by their fewer, larger and more rounded nodules. White, granulose forms of *E. australis* bear some resemblance to *E. reticulata* (Fig. 69); the latter is smaller and the granules on the shell are clearly aligned in axial rows, but the two are not sympatric.

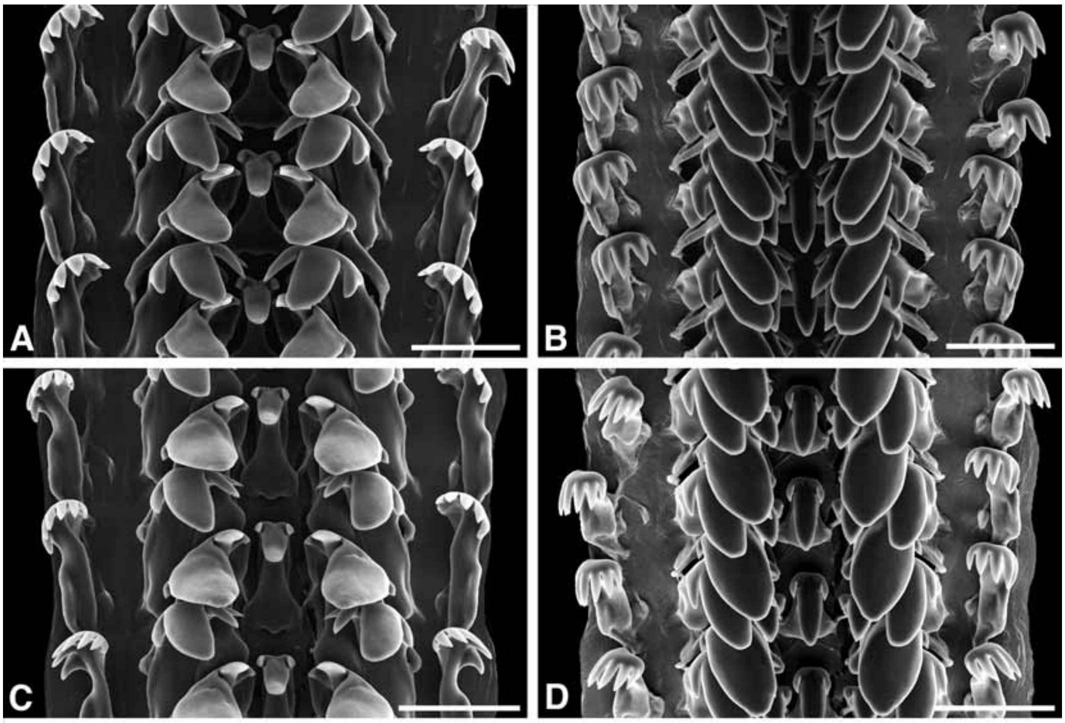

FIGURE 52. Radulae of *Echinolittorina australis* (two views of each radula, flat and at 45°). **A, B,** nodulose shell, Kalbarri, Western Australia (BMNH 20050087; shell H = 10.4 mm). **C, D,** striate shell, Point Murat, Cape Vlamingh, Cape Range, Western Australia (BMNH 20050083; shell H = 11.0 mm). Scale bars = 50 µm.

The *Echinolittorina millegrana* group

Included in this group are eight species: *E. melanacme*, *E. feejeensis*, *E. vidua*, *E. novaezelandiae*, *E. cinerea*, *E. hawaiiensis*, *E. millegrana* and *E. reticulata*. They share superficially similar granulose shells, reflected in the fact that most have at some time been misidentified as *L. granularis* (not Gray, 1839 = *E. miliaris*). For example, Tryon's (1887) concept of *T. granularis* included *E. millegrana*, *E. cinerea* and *E. vidua* of this group, besides *E. radiata* and *E. miliaris*. Rosewater's (1970) classification included five of the eight members of this group (*E. melanacme*, *E. vidua*, *E. novaezelandiae*, *E. millegrana*, *E. reticulata*, besides several misidentified examples of *E. feejeensis* and *E. radiata*) under the name *N. millegrana*. This name was widely used in this broad sense until penial and shell differences led to the recognition of most of the constituent species (Reid 1989a, 1992, 2001a). The sister-species pair *E. melanacme* and *E. feejeensis* are the most similar and were only recently separated by DNA-sequence data (Williams & Reid 2004). Morphologically, all but *E. melanacme* and *E. feejeensis* share the synapomorphy of a reduced penial glandular disc (Reid 2002a), but the monophyly of all eight members is strongly supported by DNA-sequence data (Williams & Reid 2004).

Echinolittorina melanacme (E.A. Smith, 1876)

(Figures 53, 54, 55A, B, 56)

? *Littorina picta* Philippi, 1846b: 139 (ad insulas Sandwich [Hawaiian Islands]; not *Litorina obtusata picta* Menke, 1845).

Litorina picta—Weinkauff, 1882: 70, pl. 9, fig. 6 (in part; includes *E. hawaiiensis*, *Littoraria intermedia*).

Litorina picta var. *marmorata* Philippi, 1847a: vol. 2: 167, *Litorina* pl. 3, fig. 26 (provincia Ilocos borealis insulae Luçon [Ilocos Norte, Luzon, Philippines] (restricted by Rosewater 1970); lectotype (Rosewater 1970) Philippi, 1847a, *Litorina* pl. 3, fig. 26; not *Litorina marmorata* Pfeiffer, 1839).

Littorina novaezelandiae—Fischer, 1860: 202 (not Reeve, 1857).

Littorina (Melaraphe) novaezelandiae—Tryon, 1887: 249, pl. 44, fig. 77 (in part, includes *E. novaezelandiae*; not Reeve, 1857).

Nodilittorina (Nodilittorina) novaezelandiae—Reid, 1989a: 100 (in part, includes *E. novaezelandiae*, *E. feejeensis*; not Reeve, 1857).

Nodilittorina novaezelandiae—Ohgaki, 1998: 157–161 (not Reeve, 1857). Tan & Chou, 2000: 62, fig. (not Reeve, 1857).

Littorina melanacme E.A. Smith, 1876: 552, pl. 30, fig. 21 (San Christoval [San Cristobal], Solomon Islands; lectotype (here designated) BMNH 1876.1.10.67/1 (Fig. 53O), seen; 1 paralectotype BMNH 1876.1.10.67/2, seen; 2 probable paralectotypes BMNH 1968371, seen).

? *Litorina melanacme*—Hedley, 1910: 355 (probably includes *E. vidua*).

Melaraphe melanacme—Endean *et al*., 1956a: 88–146 (in part; includes *E. vidua*).

Echinolittorina melanacme—Williams & Reid, 2004: 2227–2251.

Litorina pusilla—Böttger, 1890: 168 (not Philippi, 1847 = *E. lineolata* (d'Orbigny, 1840)).

Littorina (Melarrhaphe) ventricosa var. *strubelli* von Martens, 1897: 208 (Krakatau, Niederländisch Ost-Indien [Indonesia]; 3 syntypes SMF, not seen).

Littorina eudeli G.B. Sowerby III, 1915: 167, pl. 10, fig. 5 (Pondicherry [India], in error; 1 syntype BMNH 1919.12.31.33, seen; 3 syntypes AMS, seen; 4 syntypes USNM 341790, seen).

Tectarius granularis—Adam & Leloup, 1938: 80, fig. 27 (radula) (in part, includes *E. reticulata*, *E. vidua*; not *L. granularis* Gray, 1839 = *E. miliaris*).

Littorina punctata—Risbec, 1942: 61–64, pl. 2, figs 13–22 (radula, penis, anatomy) (not *Turbo punctatus* Gmelin, 1791 = *E. punctata*).

Nodilittorina (Granulilittorina) millegrana—Rosewater, 1970: 491–494, pl. 378, figs 1–4, pl. 380, figs 6, 7, 13, 14, pl. 382 (map) (in part, includes *E. radiata*, *E. feejeensis*, *E. vidua*, *E. novaezelandiae*, *E. millegrana*, *E. reticulata*; not Philippi, 1848). Ma, 1985: 192, pl. 1, fig. 5 (not Philippi, 1848).

Nodilittorina millegrana—Cernohorsky, 1972: 56, pl. 12, fig. 10 (not Philippi, 1848). Ma, 2004: 33, pl. 14, fig. E (right) (in part, includes *E. reticulata*; not Philippi, 1848).

Nodilittorina (Granulilittorina) vidua—Kurozumi, 1994: 366, pl. 2, fig. 2 (not Gould, 1859).

Nodilittorina vidua—Hasegawa, 2000: 141, pl. 70, fig. (in part, includes *E. vidua*; not Gould, 1859).

Nodilittorina feejeensis—Reid, 2001a: 437–439, figs 1F, G, 3H (penis) (in part, includes *E. feejeensis*; not Reeve, 1857). Reid, 2002a: 259–281 (in part, includes *E. feejeensis*; not Reeve, 1857). Thach, 2005: 54, pl. 8, figs 18, 23 (not Reeve, 1857).

Echinolittorina feejeensis—Williams *et al*., 2003: 83 (in part, includes *E. feejeensis*; not Reeve, 1857). Sanpanich *et al*., 2004: fig. 2a, 3 (map) (not Reeve, 1857).

Taxonomic history: The identity of *Littorina picta* Philippi, 1846 is problematic, because the original description is not diagnostic. Philippi (1846b) described a band on the upper part of the whorls and another on the base, longitudinal brown lines and transverse striae, gave dimensions of 4 by 3 lines (taking 1 German line = 2.18 mm, this is 8.7 x 6.5 mm), and mentioned that it has 'nearly the shape and size of *L. basteroti*' (i.e. the European *Melarhaphe neritoides* (L.)) and 'the colouring of the interrupted variety of *L. ziczac*' (*L. ziczac* var. *interrupta* C.B. Adams in Philippi, 1847 = western Atlantic *E. interrupta*). These dimensions and species comparisons suggest a small, striate, high-turbinate shell with fine axial lines and two spiral bands. This is a better description of the 'herringbone' colour form of *E. melanacme* from Southeast Asia and the Philippines (Fig. 53D, F) than of the coarsely patterned, striate forms of *E. hawaiiensis* (Fig. 67A–H). Furthermore, he mentioned a 'var. β' with the mid-part of the last whorl marbled with white, as can also be found in the present species (Fig. 53H). However, for the typical form he gave the locality Sandwich Islands (i.e. Hawaiian Islands) where the only *Echinolittorina* species is the endemic *E. hawaiiensis*. Philippi (1847a) later added the locality Ilocos Norte on the Philippine island of Luzon for *L. picta*, and his only illustration is a shell that is clearly the present species, although this was indicated as ‘var. b. *marmorata*’ and no locality was given. Philippi was very discerning in his descriptions of littorinids and is unlikely to have confused two such different species as *E. melanacme* and *E. hawaiiensis*. It is therefore possible that *L. picta* was based on a sample of *E. melanacme* with incorrect locality data. However, subsequent authors appear to have been influenced more by the Hawaiian locality, and have usually identified *L. picta* as the Hawaiian species. The first to do so was Reeve (1857: figs 80a, b, 81) who illustrated two shells of the smooth, patterned form of *E. hawaiiensis* and noted that ‘the specimen of *L. picta* here represented is Dr Philippi’s var. *marmorata*’. It was this that may have persuaded Rosewater to designate a lectotype for *L. picta* from a sample of three shells in BMNH that are closely similar to (but not identical with) those figured by Reeve. These are from the Cuming Collection, from which Philippi (1846b) described *L. picta*, but there is no documentary evidence to link them with Philippi, and they are obviously not var. *marmorata* (as illustrated by Philippi 1847a). This lectotype does not match Philippi’s description because it is a larger and taller shell (9.7 x 6.5 mm), worn smooth, with a coarse pattern of six oblique brown stripes and only a single brown band on the last whorl (Fig. 67A). The two paralectotypes are even larger (12.3 and 12.6 mm), also smooth, but do have two brown bands. While the lectotype designation is apparently incorrect, the evidence for the identity of *L. picta* is not conclusive, and it is fortunate that this name must be rejected as a junior homonym. For the sake of stability of the replacement name *E. hawaiiensis*, however, it is important that *L. picta* should continue to be regarded as a synonym of that species (see Taxonomic History of *E. hawaiiensis*).

Littorina melanacme was described by E.A. Smith (1876) from the Solomon Islands; since then the name appears to have been used only for Australian material, and then only for *E. vidua* or for a probable mixture of the two species (Hedley 1910; Fischer 1940; Endean *et al*. 1956a, b; W. Stephenson *et al*. 1958). The name *E. melanacme* was resurrected by Williams & Reid (2004). *Littorina (Melarrhaphe) ventricosa* var. *strubelli* von Martens, 1897 is a distinctive colour form found in the vicinity of the Sunda Strait (Fig. 53A, B), initially misidentified as *Litorina pusilla* (Böttger 1890). *Littorina eudeli* Sowerby, 1915 was based on material with the locality ‘Pondicherry’, but this species has not been recorded from India.

Owing to its variable shell, this species has frequently been misidentified or united with others. Rosewater’s (1970) broad concept of *N. millegrana* included the present species and up to six others, and was widely followed. E.A. Smith (1876) himself mentioned the similarity of his *L. melanacme* to *L. novaezelandiae*. The latter is endemic to Sri Lanka, but its rather smooth, pale, often patulous shell could easily be interpreted as a geographical form of *E. melanacme*, explaining the misidentification by several authors (Fischer 1860; Tryon 1887; Reid 1989a). Anatomical comparison revealed this error and the identification was changed to *N. feejeensis* (Reid 2001a, 2002a). The name had to be changed yet again when molecular evidence indicated that specimens from Fiji belonged to a distinct species (Williams & Reid 2004).

Diagnosis: Shell high-turbinate to patulous, often slightly shouldered; fine spiral ribs are smooth or finely granulose, separated by narrow grooves; colour variable, finely tessellated with dark grey-brown, or grey-white with dark herringbone pattern or oblique axial lines; columella and inner lip purple-brown. Penial glandular disc is a lobe, together with penial gland on long branch of base; filament long, tapering. SE Andaman Sea, Southeast Asia, Indonesia, W Pacific from Okinawa to Queensland and New Caledonia. COI: GenBank AJ622999, AJ623000.

Material examined: 222 lots (including 26 penes, 10 sperm samples, 9 pallial oviducts, 8 radulae).

Shell (Fig. 53): Mature shell height 5.3–14.0 mm. Shape variable, high-turbinate to patulous (H/B = 1.22–1.60, SH = 1.40–1.82); spire whorls rounded, suture distinct; spire profile concave at apex; last whorl rounded or slightly angled at periphery, often slightly shouldered. Sexually dimorphic: females taller, narrower, larger (Fig. 53A, F–L, P, R); males patulous, smaller (Fig. 53B–E, N, Q). Columella usually long, straight, wide, flattened but only slightly pinched at base; eroded parietal area present or absent; sometimes an imperforate pseudumbilical chink adjacent to columella. Sculpture of last whorl: 16–19 ribs, of which 5–6 are on base, separated by incised lines or narrow grooves, rarely with single interpolated threads (Fig. 53M, R); ribs above periphery sometimes finely granulose, granules not axially aligned, rarely with larger pointed granules (Fig. 53M); spiral microstriae only in grooves. Protoconch 0.26–0.31 mm diameter, 2.7–3.0 whorls. Colour: grey-white to fawn; pattern of fine dark grey to grey-brown axial lines that may be continuous and oblique (Fig. 53A, B, common in Sumatra and Java), zigzag (Fig. 53G, J, M), interrupted in herringbone fashion by 1–2 spiral lines above periphery and one below (Fig. 53D, F, I, K, L), or may break into finely tesselated or marbled pattern over mid-part of whorl (Fig. 53H) or entire whorl (Fig. 53N–Q, predominant pattern in Queensland and New Caledonia), rarely entirely dark brown except for white flames on base (in Palau); apical 2–3 teleoconch whorls brown to black, no spiral lines; aperture brown to dark brown, external pattern showing through, pale band at base; columella and inner lip purple-brown.

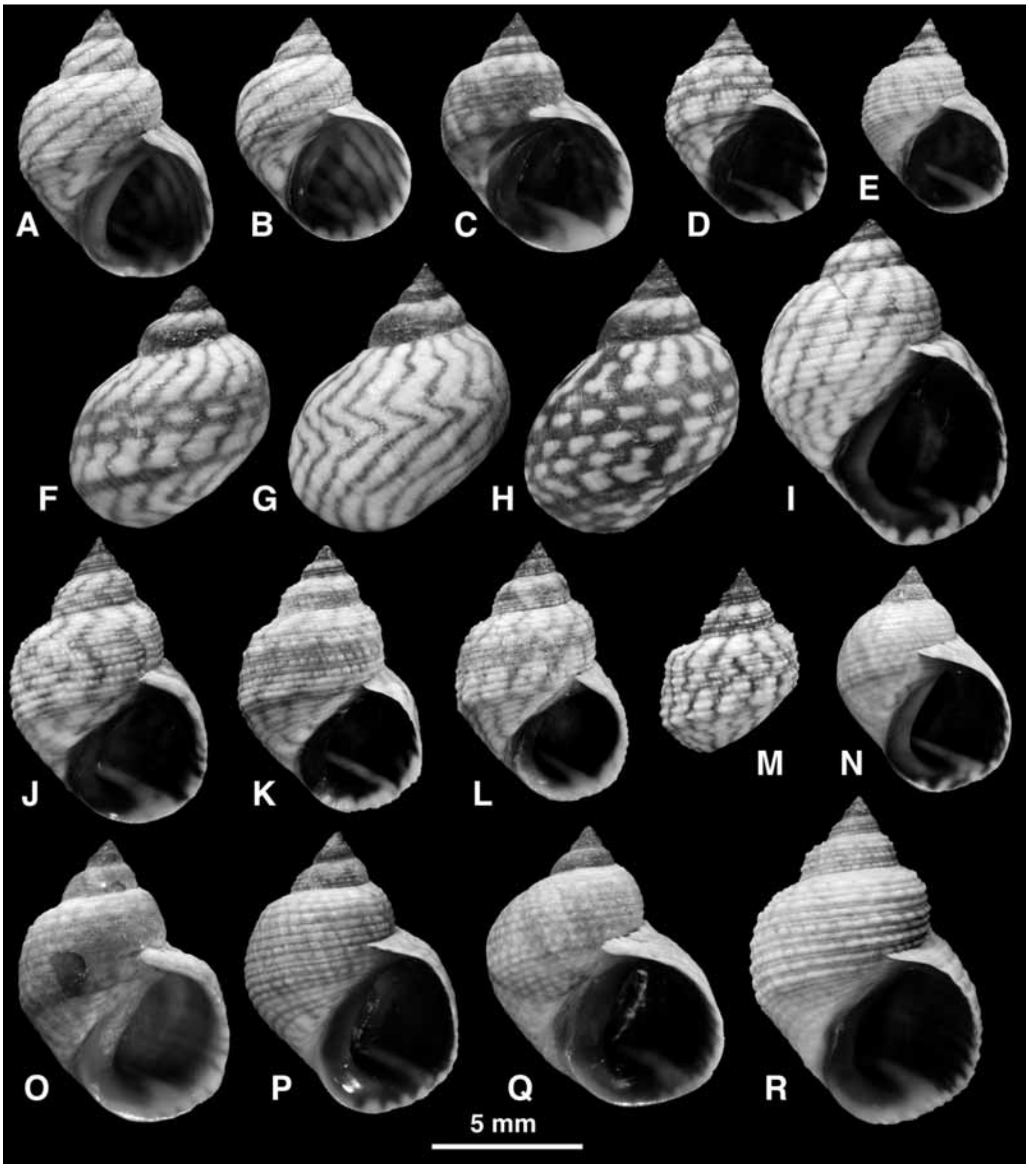

FIGURE 53. *Echinolittorina melanacme*. **A, B,** Pulau Sebesi, Lampung, Sumatra, Indonesia (BMNH 20050516; female, male). **C,** Kamenti, Kapataran, Sulawesi, Indonesia (BMNH 20020606; male). **D, E, J,** Guintungauan I., Bacuit Archipelago, Palawan, Philippines (BMNH 20050517; male, male, female). **F–I,** Nha Trang, Vietnam (BMNH 20010353; females). **K,** Chialoshui, SE Taiwan (BMNH 20050518; female). **L,** Ogan Saki, Ishigaki, Japan (BMNH 20050519; female). **M,** Bunaken I., Manado, Sulawesi, Indonesia (BMNH 20020616). **N,** 10 km N Cape Tribulation, Queensland, Australia (BMNH 20050520; male). **O,** *Littorina melanacme* E.A. Smith, 1876, lectotype, San Cristobal, Solomon Is (BMNH 1876.1.10.67/1). **P, Q,** Mont Dore, New Caledonia (BMNH 20050521; female, male). **R,** Baie de Kanidera, Île des Pins, New Caledonia (BMNH 20050522; female).

Animal (Fig. 54): Head (Fig. 54I) grey to black, unpigmented stripe across snout present or absent, tentacle unpigmented with broad grey to black band across base, black line or speck at tip, unpigmented around eye; sides of foot grey to black. Opercular ratio 0.38–0.45. Penis (Fig. 54A–G): filament long, gradually tapering to minutely rounded tip, smooth and without annular wrinkles, filament 0.6–0.8 total length of penis, sperm groove extends to tip, core of filament red in living animals; mamilliform gland borne on relatively long, stout projection of base, together with glandular disc of approximately equal size that projects as small, often pointed, lobe; penis unpigmented or slightly pigmented at base. Euspermatozoa 92–107 µm; paraspermatozoa (Fig. 54J–L) oval to spherical, 11–18 µm diameter, filled with large round granules, rod-pieces usually curved or semi-circular, sometimes fibrous and indistinct, not projecting. Pallial oviduct (Fig. 54H): straight section slightly recurved at anterior end; bursa opening at anterior end of straight section and extending back almost to albumen gland. Development predicted to be planktotrophic.

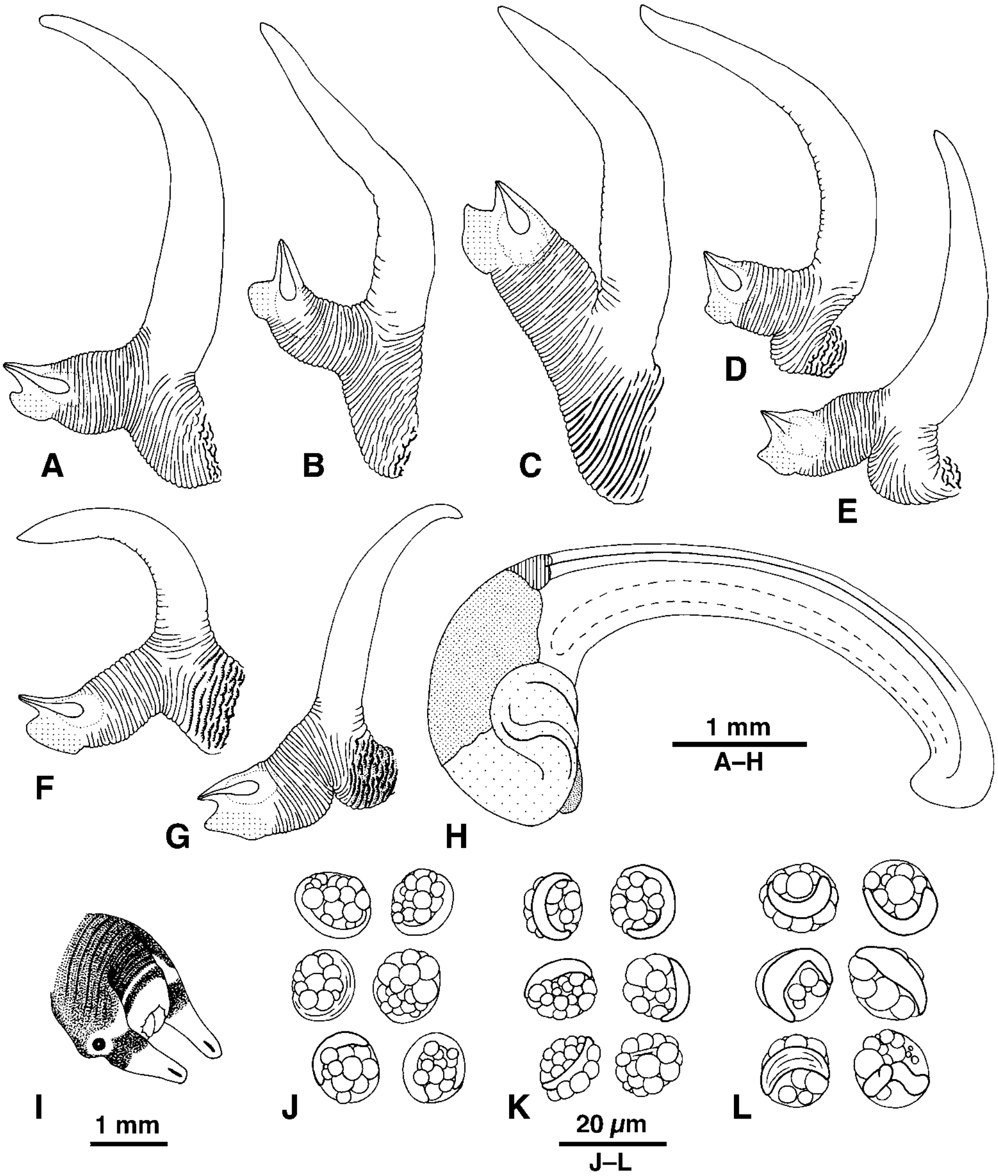

FIGURE 54. *Echinolittorina melanacme*. **A–G,** penes. **H,** pallial oviduct. **I,** head. **J–L,** paraspermatozoa. **A, B, H,** Kudat, Sabah, Malaysia (BMNH 20050523; shell H **A** = 9.5 mm, **B** = 8.5 mm, **H** = 10.3 mm). **C, I, K,** Nha Trang, Vietnam (BMNH 20010353; shell H **C** = 8.6 mm, **I** = 8.4 mm). **D,** Ogan Saki, Ishigaki, Japan (BMNH 20050519; shell H = 7.0 mm). **E,** Kamenti, Kapataran, Sulawesi, Indonesia (BMNH 20020606; shell H = 10.0 mm). **F, J,** Guintungauan I., Bacuit Archipelago, Palawan, Philippines (BMNH 20050517; shell H **F** = 6.7 mm). **G,** Anse Vata, Nouméa, New Caledonia (BMNH 20050524; shell H = 6.9 mm). **L,** Pulau Manukan, Sabah, Malaysia (BMNH 20050525). Shading conventions as in Figure 3.

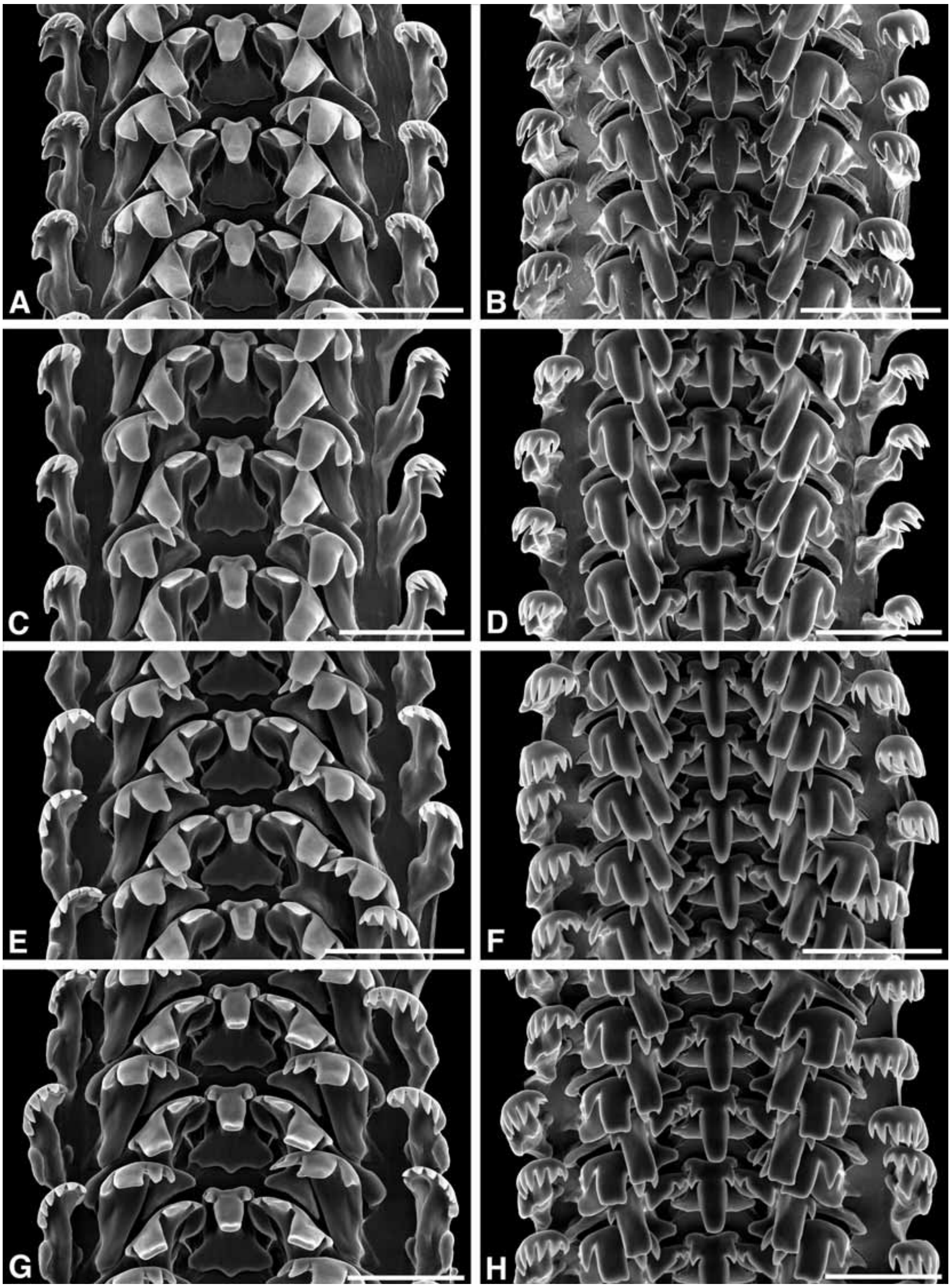

FIGURE 55. Radulae of *Echinolittorina* species (two views of each radula, flat and at 45°). **A, B,** *E. melanacme*; Guintungauan I., Bacuit Archipelago, Palawan, Philippines (BMNH 20050517; shell H = 9.0 mm). **C, D,** *E. feejeensis*; New Town Beach, Nadi, Viti Levu, Fiji (BMNH 20050528; shell H = 10.0 mm). **E, F,** *E. vidua*; Awung, Lombok, Indonesia (BMNH 20040643; shell H = 9.0 mm). **G, H,** *E. novaezelandiae*; Mirissa, near Weligama, Sri Lanka (BMNH 20040631; shell H = 11.2 mm). Scale bars = 50 µm.

Radula (Fig. 55A, B): Relative radula length 2.00–3.36. Rachidian: length/width 1.21–1.38; tip of major cusp rounded or occasionally pointed. Lateral and inner marginal: major cusp on each of similar size, tips truncated to rounded. Outer marginal: 6–8 cusps.

Range (Fig. 56): Southeastern Andaman Sea, mainland of Southeast Asia to Ryukyu Is, Philippines, eastern Indonesia, southern Sumatra and western Java, Palau, Papua New Guinea, Queensland, Solomon Is and New Caledonia. Range limits: Phuket I., W Thailand (Sanpanich *et al*. 2004); Ko Phi Phi, W Thailand (USNM 661503); Pulau Anyut, Malacca Strait, Malaysia (USNM 660921); Batam, Sekupang, Indonesia (BMNH); Ko Pha Ngan, E Thailand (BMNH); Bight of Bangkok, Thailand (Sanpanich *et al*. 2004); Nha Trang, Vietnam (BMNH 20010353); Xisha (Paracel) Is, China (Ma 1985); Sanya, Hainan I., China (BMNH); Cape d'Aguilar, Hong Kong (BMNH); Tali, 20 km SE Keelung, Taiwan (BMNH); Buma, Nago-shi, Okinawa, Japan (BMNH); Nakano-shima, Tokara Is, Japan (Kurozumi 1994); Ilocos Norte, Luzon, Philippines (Philippi 1847a); Davao City, Mindanao, Philippines (WAM S.10897; USNM 747824); Koror, Palau (BMNH; USNM 701900); Pulau Manukan, off Kota Kinabalu, Sabah, Malaysia (BMNH 20050525); SE Belitung I., Indonesia (F. de Graaf Colln); Bengkulu, Sumatra, Indonesia (BMNH); Pelabuan Ratu, Java, Indonesia (ZMA); Senggigi, Lombok, Indonesia (BMNH); Matasiri, Laut I., Indonesia (BMNH); Dili Bay, East Timor (BMNH); Morotai, Halmahera, Indonesia (USNM 542543); Abroeki I., Geelvink Bay, Irian Jaya, Indonesia (ANSP 208495); Matupi I., Rabaul, Papua New Guinea (AMS C39799); Ela Beach, National Capital District, Papua New Guinea (BMNH); Lizard I., Queensland, Australia (BMNH; AMS); Cape Cleveland, Queensland, Australia (USNM 623201); Heron I., Queensland, Australia (AMS); Fulakora Point, Sta Isabel, Solomon Is (BMNH); Koumac, New Caledonia (MNHN), Île des Pins, New Caledonia (BMNH 20050522; AMS C.71798); Baie du Santal, Lifou, Loyalty Is (MNHN).

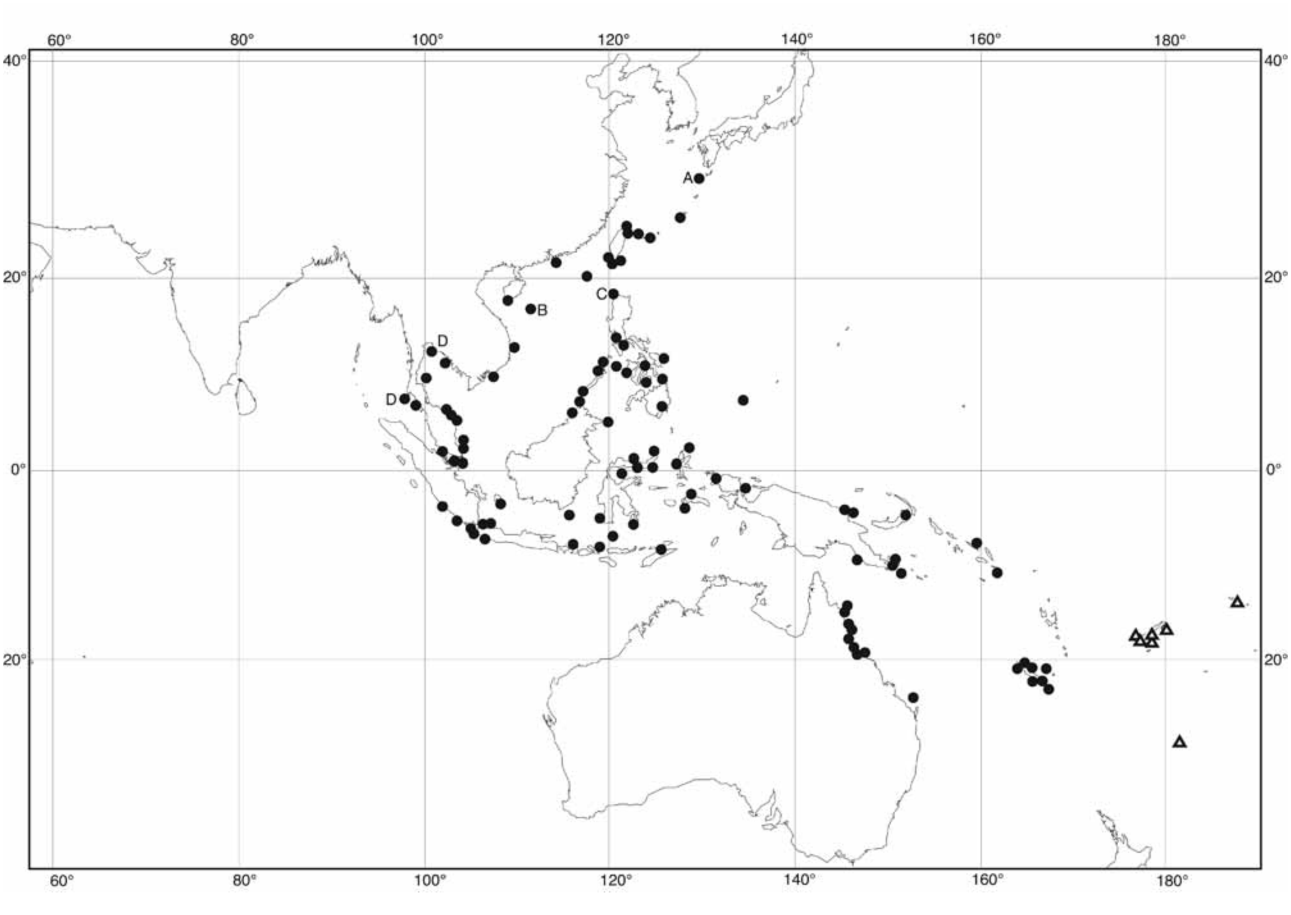

FIGURE 56. Distribution of *Echinolittorina melanacme* (solid circles) and *E. feejeensis* (open triangles). Literature records: A, Kurozumi (1994); B, Ma (1985); C, Philippi (1847a); D, Sanpanich *et al.* (2004).

This species just extends into the Indian Ocean in the extreme southwest of Thailand, Strait of Malacca, southwestern Sumatra and western Java; there are numerous records of other littorinids from Thailand and southern Java, so the limits in these areas are probably approximately correct. Records extend around the

Southeast Asian mainland as far as Hong Kong, but the species is rare in Singapore, in the Gulf of Thailand, absent from Ha Long Bay, Vietnam, and only two specimens are known from Hong Kong; in this region it is mainly recorded from offshore islands and is only common in areas of clear oceanic water, as on the east coast of Peninsular Malaysia and at Nha Trang, Vietnam. Similarly, it is rare or absent from the west coast of Taiwan, but common on the oceanic east coast, and is common in Ishigaki and moderately so in Okinawa, reaching as far north as the Tokara Islands (Kurozumi 1994). It is abundant throughout the Philippines and eastern Indonesia, in the west of New Guinea, the Solomon Islands and New Caledonia, and extends to Palau in Micronesia. It is also abundant in Queensland, but only between Lizard Island and Townsville, with an outlying record from Heron Island. It is undoubtedly absent from the Arafura Sea and Western Australia, and also apparently from the muddy coasts of Sarawak and most of the Java Sea.

Habitat: This species can be found on substrates including basalt, sandstone, beachrock, granite, limestone and concrete, at levels from the lower littoral fringe to the uppermost eulittoral. It is only common in areas with clear oceanic water; on continental shores where water is turbid it is rare or absent. It tolerates sheltered and moderately exposed situations, often on shores behind fringing reefs, and is rare or absent in strongly wave-exposed conditions.

On Ishigaki this species was common only on the open coast, and scarce within a sheltered cove (Ohgaki 1998). In Thailand it was found only in clear-water situations on offshore islands (Sanpanich *et al*. 2004). Ecological observations on '*Melaraphe melanacme*' in northern Queensland probably included both the present species and sympatric *E. vidua* (Endean *et al*. 1956a, b).

Remarks: The occurrence of this species is closely correlated with areas of clear oceanic water of low to moderate productivity. On a geographical scale (Rutgers University Primary Productivity Study) this accounts for its rarity on the mainland coast of East Asia, and absence from continental areas in Sarawak and much of the Java Sea. In Australia its distribution corresponds closely with the area of lowest productivity on the tropical coast, while it is absent from the more productive areas of far northern and southern Queensland, and the Arafura Sea. Few collections are available from Kalimantan, but it is likely to be rare or absent there. The absence from much of the oceanic coast of southern Java may be explained by intolerance of strongly exposed situations or upwelling conditions. At a local level, on continents and large islands it is only common on promontories, offshore islets and open coastlines (e.g. Ohgaki 1998; Sanpanich *et al*. 2004). On the oceanic-continental gradient it is intermediate between the extremely oceanic species *E. reticulata* and the more continental *E. vidua*, and its range overlaps that of both these species. In comparison with *E. vidua* it extends further on to the Pacific Plate, reaching Palau, the Solomon Is and New Caledonia, which may also reflect its more oceanic character.

Three regional forms can be recognized on the basis of sculpture and colour variation. Throughout most of the range, from Thailand to Irian Jaya to Okinawa, shells are strikingly patterned with dark grey or grey-brown axial lines, often interrupted by 1–2 spiral bands to give a characteristic herringbone pattern (extremely dark in Guam), and are usually granulose (Fig. 53C–M). In a small area of southern Sumatra and western Java around the Sunda Strait all shells are white with narrow oblique brown lines, smooth and with fine incised lines (Fig. 53A, B). In the Coral Sea (Papua New Guinea, Solomon Is, New Caledonia and Queensland) the shells are fawn with a finely tessellated grey-brown pattern, striate, and not at all or only finely granulose (Fig. 53N–R). There is some intergradation between these forms (e.g. the range of colour pattern in a single sample from Vietnam, Fig. 53F–I). These three forms apparently correspond to three partially isolated areas of the distribution. Much of the coastline of the Java Sea is of unsuitable muddy or mangrove environment, so that gene flow between the Sunda Strait and the main distributional area in the South China Sea and eastern Indonesia may be reduced. The absence of the species from the Arafura Sea suggests that genetic contact between the main area and the Coral Sea is only maintained via the north coast of New Guinea. In contrast, limited COI sequence data show a shallow phylogenetic division (K2P genetic distance = 1.01%) between four haplotypes from Sulawesi and six from throughout the rest of the range (Thailand, Okinawa, Philippines, Lombok, Queensland, New Caledonia), and very little differentiation among the latter group (S.T. Williams & D.G. Reid unpublished).

Sexual dimorphism in the shell of this species is of the same type seen in other littorinids (Reid 1986a, 1996), in which females are larger and males more patulous (i.e. relatively lower spire and larger aperture). Most *Echinolittorina* species show slightly larger females, but here the size and shape dimorphism is more marked than in any congener.

Specimens from limestone substrates show slightly taller and more strongly sculptured shells (Fig. 53D, E, J, M, R) than those from other rock types, suggesting a possible ecophenotypic effect.

Available molecular data show that the sister species of *E. melanacme* is *E. feejeensis*, and there is some support for these two being the sister lineage of the remaining members of the *E. millegrana* group (Williams & Reid 2004). The latter relationship is consistent with the synapomorphy of the reduced or absent penial glandular disc shared among *E. vidua*, *E. novaezelandiae*, *E. cinerea*, *E. hawaiiensis*, *E. millegrana* and *E. reticulata* (Reid 2002a).

Confusion is most likely to arise with *E. vidua*, with which *E. melanacme* is often sympatric. Shells of the latter show a predominantly dull grey-brown colour and frequent 'herringbone' pattern; the inner apertural edge is not distinctively paler than the adjacent columella; the outline is often slightly shouldered and males are patulous. In *E. vidua* (Fig. 59) the pattern is brown (not greyish) and 'herringbone' effects are rare; the inner apertural lip is white, outlining the purplish columella; the outline is rounded and rarely shouldered or patulous; sculpture is often more noticeably and regularly granular. The long, tapering penial filament and large glandular disc, anterior extent of bursa, and black tentacle tips are anatomical characters of *E. melanacme* that are absent in *E. vidua*. On the western margin of the Pacific Ocean this species is sympatric with *E. tricincta* (Fig. 48); most shells of the latter are readily distinguished by their 1–3 enlarged ribs, but a few (Fig. 48K) are similar in shape and sculpture to *E. melanacme* (cf. Fig. 53K, R) and anatomical confirmation may be necessary. Comparison should also be made with *E. novaezelandiae* (Fig. 62) and with *E. feejeensis* (Fig. 57), but since these are limited to Sri Lanka and to Fiji, respectively, there is no geographical overlap with *E. melanacme*.

***Echinolittorina feejeensis* (Reeve, 1857)**

(Figures 55C, D, 56–58)

Littorina feejeensis Reeve, 1857: sp. 82, pl. 15, fig. 82a, b (Feejee [Fiji] Islands; lectotype (Rosewater 1970) + 5 paralectotypes BMNH 1968319, Fig. 57A, seen).

Nodilittorina (Granulilittorina) leucosticta feejeensis—Rosewater 1970: 500, pl. 384, figs 14-17, pl. 385 (map) (in part, includes *E. cinerea*).

Nodilittorina leucosticta feejeensis—Cernohorsky, 1972: 56, pl. 12, fig. 11 (in part, includes *E. cinerea*, *E. biangulata*).

Nodilittorina (Granulilittorina) quadricincta feejeensis—Rosewater & Kadolsky, 1981: 1234 (in part, includes *E. cinerea*).

Nodilittorina feejeensis—Reid, 2001a: 437–439, figs 1H (in part; includes *E. melanacme*). Reid, 2002a: 259–281 (in part; includes *E. melanacme*).

Echinolittorina feejeensis—Williams *et al.*, 2003: 83 (in part, includes *E. melanacme*). Williams & Reid, 2004: 2227–2251.

Litorina vitiensis 'Reeve' von Martens & Langkavel, 1871: 40 (emendation of *L. feejeensis* Reeve, 1857).

Littorina miliaris var. *fijiensis* 'Reeve' Nevill, 1885: 154 (emendation of *L. feejeensis* Reeve, 1857; in part, includes *E. cinerea*).

Litorina (Melaraphe) vitensis Dunker, 1871: 150–151 (ad insulas Vitenses [Fiji Is]; types unknown).

Littorina vitiensis 'Dunker' Godeffroy, 1874: 105 (emendation of *Litorina vitensis* Dunker, 1871). Weinkauff, 1882: 84–85, pl. 11, figs 10, 11. Weinkauff, 1883: 221.

Littorina plena var. *vitiensis*—Nevill, 1885: 139.

Tectarius miliaris—Tryon, 1887: 259, pl. 48, fig. 76 (in part, includes *E. miliaris*, *E. reticulata*; not Quoy & Gaimard, 1833 = *E. miliaris*).

Nodilittorina (Granulilittorina) millegrana—Rosewater, 1970: 491–494, pl. 382 (map) (in part, includes *E. radiata*, *E. melanacme*, *E. vidua*, *E. novaezelandiae*, *E. millegrana*, *E. reticulata*; not Philippi, 1848).

Nodilittorina millegrana—Brook & Marshall, 1998: 215 (not Philippi, 1848).

Nodilittorina (Nodilittorina) novaezelandiae—Reid, 1989a: 100, fig. 5I (head) (in part, includes *E. novaezelandiae*, *E. melanacme*; not Reeve, 1857).

Taxonomic history: These distinctively granulose shells from Fiji (formerly Feejee or Viti Islands) were first named *L. feejeensis* by Reeve (1857) and later *Litorina vitensis* by Dunker (1871); Weinkauff (1882) pointed out their synonymy, but used the junior name. Both names were emended without justification by several authors. Tryon's (1887) concept of *Tectarius miliaris* was a heterogeneous assemblage of *E. miliaris* from Ascension Island, *E. reticulata* and *E. feejeensis*. The present species did not appear in the primary literature for almost a century until Rosewater (1970) used *N. leucosticta feejeensis* (subsequently changed to *N. quadricincta feejeensis*; Rosewater & Kadolsky 1981) for strongly sculptured shells of both *E. feejeensis* and *E. cinerea*. Cernohorsky (1972) declared that this group defined by Rosewater was indistinguishable from shells here named *E. biangulata*, and synonymized them. From his distribution maps, it appears that Rosewater (1970) included smooth forms of *E. feejeensis* under the name *N. millegrana*, accounting for his records of the latter from Fiji, where only *E. feejeensis* and *E. cinerea* occur. Reid (1989a) misidentified *E. feejeensis* and *E. melanacme* as *N. novaezelandiae*, and later used *N. feejeensis* to include *E. feejeensis* and *E. melanacme* (Reid 2001a, 2002a; see Taxonomic History of *E. melanacme*). These sister species were recently separated by molecular data (Williams & Reid 2004).

Diagnosis: Shell turbinate to patulous, often slightly shouldered; finely granulose spiral ribs of which 6 may bear small pointed nodules, separated by narrow grooves; colour grey, nodules cream with brown interspaces; columella and inner lip purple-brown. Penial glandular disc is a lobe, together with penial gland on long branch of base; filament long, tapering. Fiji, Kermadec Is. COI: GenBank AJ623001, AJ623002.

Material examined: 20 lots (including 14 penes, 4 sperm samples, 9 pallial oviducts, 2 radulae).

Shell (Fig. 57): Mature shell height 5.0–11.7 mm. Shape turbinate to patulous (H/B = 1.25–1.42, SH = 1.38–1.68); spire whorls rounded, suture distinct; spire profile concave at apex; last whorl rounded or slightly angled at periphery, often slightly shouldered. Sexually dimorphic: females taller, narrower, larger (Fig. 57C, E, G, I–L, N–P); males patulous, smaller (Fig. 57H, M). Columella usually long, straight, wide, flattened but only slightly pinched at base; eroded parietal area small or absent. Sculpture of last whorl: 15–19 ribs, of which 5–6 are on base, separated by narrow grooves, sometimes with single interpolated threads; in smoother shells only ribs on spire or only those above periphery are weakly granulose (Fig. 57I, J); in sculptured shells all ribs granulose, but 3 ribs at periphery, 2 at and above shoulder, and 1 at mid-point between, bear small pointed nodules (Fig. 57C, D, F, K, L, N–P); granules not usually axially aligned; spiral microstriae only in grooves. Protoconch 0.26 mm diameter, 2.7 whorls. Colour: grey to fawn, paler near suture and on base, nodules cream and separated by brown marks on ribs, sometimes short brown oblique axial stripes at suture and on base; apical 2–3 teleoconch whorls brown, no spiral lines; aperture brown to dark brown, pale band at base; columella and inner lip purple-brown.

Animal (Fig. 58): Head grey to black, unpigmented stripe across snout narrow or absent, tentacle unpigmented with broad grey to black band across up to half of base, black line at tip, sometimes extending back to basal band, unpigmented around eye; sides of foot grey to black. Opercular ratio 0.43–0.50. Penis (Fig. 58A–E): filament long, gradually tapering to minutely rounded tip, smooth and without annular wrinkles, filament 0.6–0.8 total length of penis, sperm groove extends to tip; mamilliform gland borne on relatively long, stout projection of base, together with glandular disc of approximately equal size that projects as small, often pointed, lobe; penis slightly pigmented at base. Euspermatozoa 89–96 µm; paraspermatozoa (Fig. 58F, G) oval to spherical, 11–16 µm diameter, filled with large round granules, rod-pieces fusiform with one or both ends pointed, sometimes curved, occasionally recurved at tip, often projecting from cell, occasionally fibrous and indistinct. Pallial oviduct (Fig. 58H): straight section slightly recurved at anterior end; bursa opening at anterior end of straight section and extending back almost to albumen gland. Development predicted to be planktotrophic.

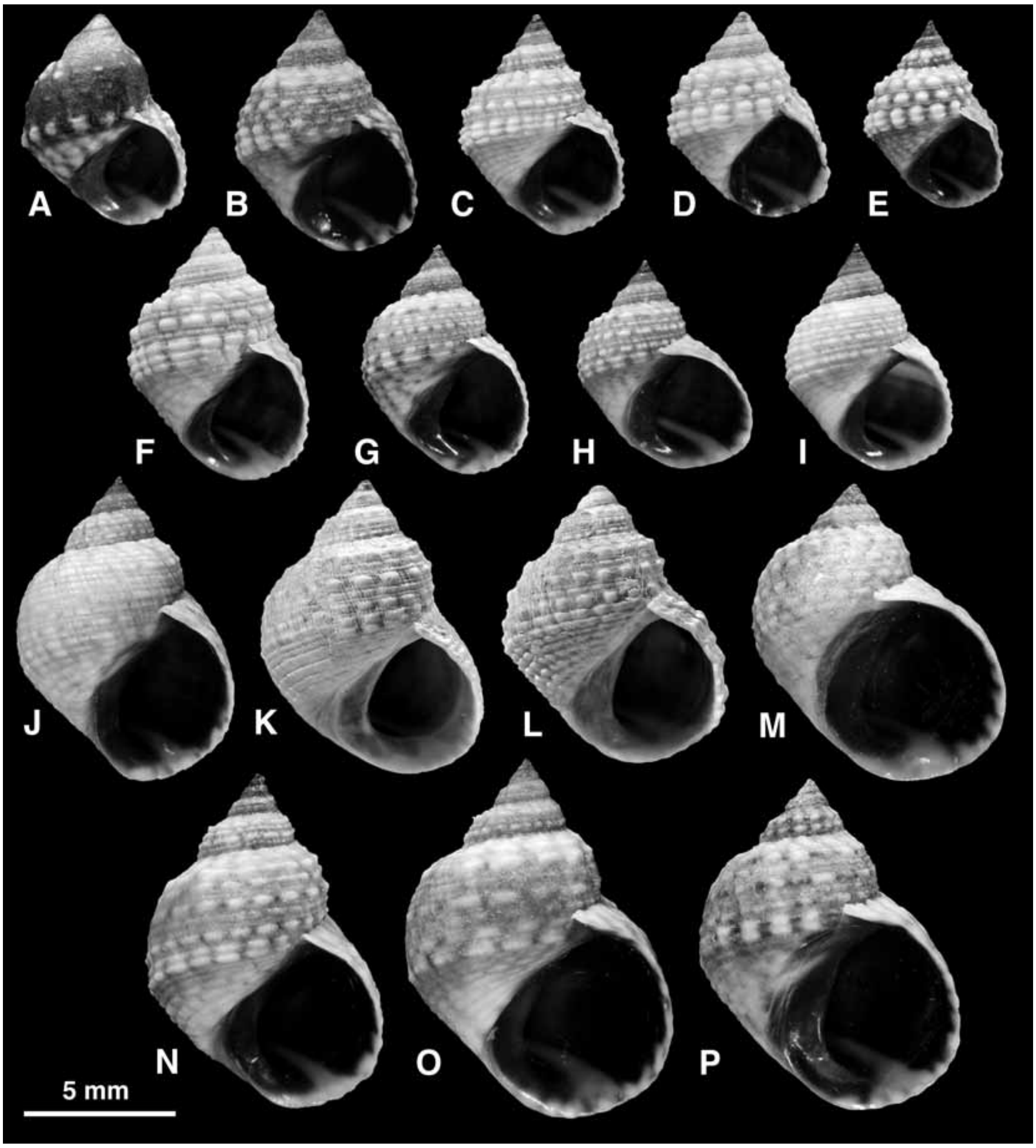

FIGURE 57. *Echinolittorina feejeensis*. **A,** *Littorina feejeensis* Reeve, 1857, lectotype, Fiji Is (BMNH 1968319). **B, D, F,** Matei, Taveuni, Fiji (BMNH 20050527). **C, E, J, N,** New Town Beach, Nadi, Viti Levu, Fiji (BMNH 20050528; females). **G, H, I,** 10 km E Sigatoka, Viti Levu, Fiji (BMNH 20050529; female, male, female). **K, L,** Meyer I., Kermadec Is (AMNZ AK98043; females). **M, O, P,** Matei, Taveuni, Fiji (BMNH 20050526; male, female, female).

Radula (Fig. 55C, D): Relative radula length 2.20–3.29. Rachidian: length/width 1.32–1.38; tip of major cusp rounded. Lateral and inner marginal: major cusp on each of similar size, tips rounded. Outer marginal: 6–8 cusps.

Range (Fig. 56): Fiji Is, Kermadec Is and doubtfully Samoa. Range limits: New Town Beach, Nadi, Viti Levu, Fiji (BMNH 20050528); Laucala Bay, Suva, Viti Levu, Fiji (USNM 794904); Levuka, Ovalau, Fiji (BMNH); Matei, Taveuni, Fiji (BMNH 20050526); W Koro Levu, Taveuni, Fiji (USNM 695622); Meyer I., Kermadec Is (Brook 1998; AMNZ AK98043); Upolu, Samoa (BMNH 1870.12.31.117). Two specimens were collected on Meyer Island in 1995 (Brook & Marshall 1998, as *N. millegrana*), but none was found on a previous expedition (Iredale 1910). The pre-1870 record from Upolu in Samoa requires verification; personal collecting failed to find it there.

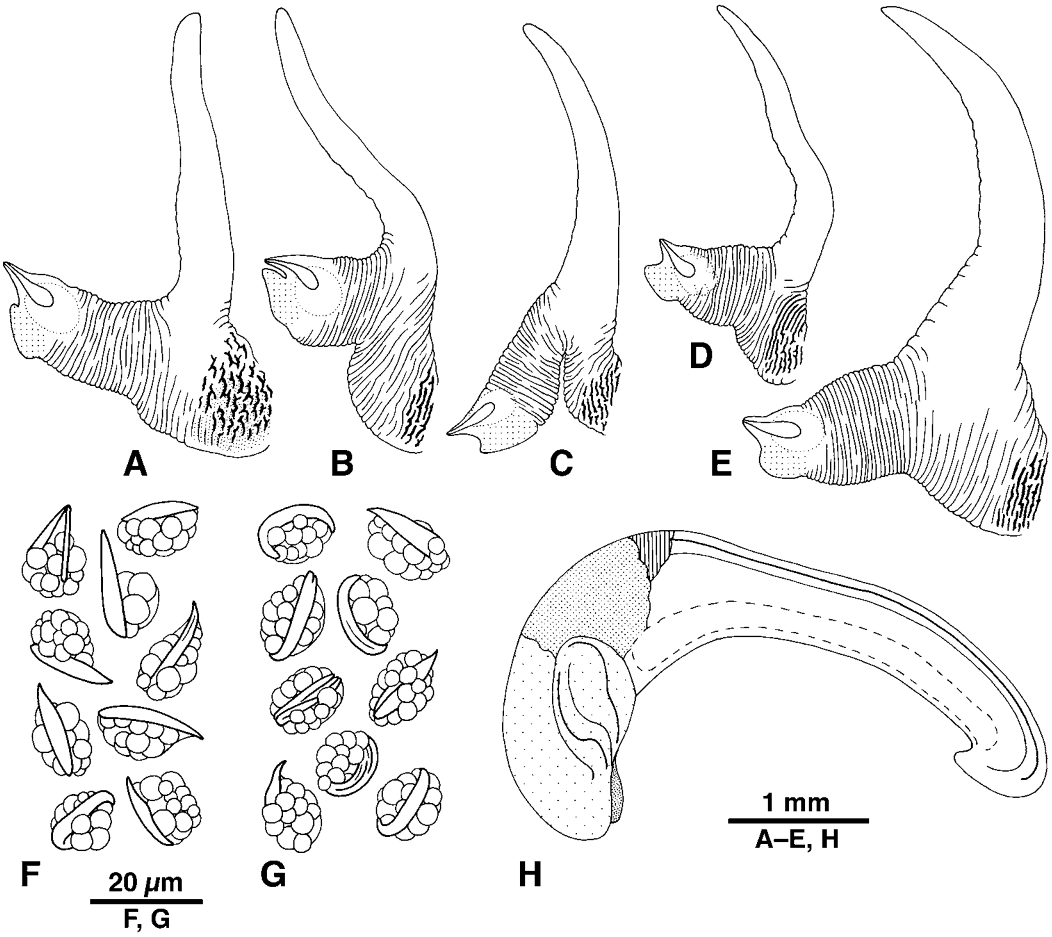

FIGURE 58. *Echinolittorina feejeensis*. **A–E,** penes. **F–G,** paraspermatozoa. **H,** pallial oviduct. **A, B,** New Town Beach, Nadi, Viti Levu, Fiji (BMNH 20050528; shell H **A** = 8.0 mm, **B** = 6.0 mm). **C, F, G,** Matei, Taveuni, Fiji (BMNH 20050527; shell H **C** = 7.0 mm). **E,** Matei, Taveuni, Fiji (BMNH 20050526; shell H = 9.5 mm). **D,** 20 km E Sigatoka, Viti Levu, Fiji (BMNH 20050529; shell H = 6.5 mm). Shading conventions as in Figure 3.

Habitat: Records of habitat are scarce, but this species has been recorded from basalt and concrete, from the lower littoral fringe to the uppermost eulittoral. It has been found only in moderately sheltered situations, often behind fringing reefs, in both clear-water and slightly silty conditions.

Remarks: This is the sister of the widespread central-IWP species *E. melanacme*, and their respective distributions suggest a classic case of founder speciation on a peripheral island group (Williams & Reid 2004). Their K2P genetic distance estimated from mitochondrial COI is 8.24%. Anatomically, the two are almost indistinguishable, although rod-pieces in the paraspermatozoa of *E. feejeensis* are a little longer. The majority of the shells of *E. feejeensis* can be recognized by their stronger sculpture, but the smoother forms (Fig. 57I, J) are not distinct from some shells of *E. melanacme* (Fig. 53R).

This is the only *Echinolittorina* species that is common in Fiji, where it occupies a range of habitats. Smaller shells (often from habitats with clearer water) are more strongly granulose, recalling the ecophenotypic variation of *E. australis* that is connected with habitat and growth rate (Yeap *et al*. 2001).

The single record from the Kermadec Islands shows that occasional dispersal can occur from Fiji, 1000 km to the north. Current patterns in the Kermadec region are poorly known, but in the summer currents do flow southward from tropical regions; this record provides the first clear example of dispersal to the islands by this route (cf. Brook 1998).

Echinolittorina vidua (Gould, 1859)

(Figures 55E, F, 59–61)

Litorina ventricosa Philippi, 1847b (September): vol. 3: 15–16, *Litorina* pl. 6, fig. 19 (Pulo Pinang [Penang, Malaysia]; lectotype (Rosewater 1970) Philippi, 1847b, *Litorina* pl. 6, fig. 19; 2 paralectotypes SMNS ZI0050272, seen; not *Litorina scabra* var. *ventricosa* Philippi, 1847 (April)). E.A. Smith, 1879: 817. Weinkauff, 1882: 79–80, pl. 10, figs 14, 15.

Littorina ventricosa—Reeve, 1858: sp. 93, pl. 17, fig. 93. Nevill, 1885: 152. Melvill & Standen, 1901: 363.

Littorina (Melarhaphe) ventricosa—von Martens, 1897: 207–208 (as *Melarrhaphe*). Oostingh, 1927: 3.

Littorina vidua Gould, 1859: 138 (Ousima [O-shima, Amami Islands, Japan]; types lost (Johnson 1964); neotype (here designated) BMNH 20040645 (Fig. 59O), Tsutsu, Tsushima, Kyushu, Japan). Pilsbry, 1895: 62.

Litorina vidua—Weinkauff, 1882: 103.

Nodilittorina (Nodilittorina) vidua—Reid, 1989a: 100. Reid, 1992: 203, figs 1k (penis), 2j (oviduct), pl. 3i–l. Subba Rao, 2003: 121, pl. 19, figs 3, 4.

Nodilittorina vidua—Mak, 1995: 53–59, figs 1c, 2c (spawn). Higo *et al*., 1999: 91 (in part, includes *E. melanacme*). Hasegawa, 2000: 141, pl. 70, fig. 22 (in part, includes *E. melanacme*). Tan & Chou, 2000: 62, fig. Reid, 2001a: 444–446, figs 2B, C, 3J (penis). Swennen *et al*., 2001: 114, fig. 311. Reid, 2002a: 259–281. Lee & Chao, 2003: 32, pl. 3, fig. 63. Thach, 2005: 54, pl. 8, fig. 20.

Echinolittorina vidua—Williams *et al*., 2003: 63, 83. Williams & Reid, 2004: 2227–2251. Sanpanich *et al*., 2004: figs 2c, 3 (map).

Littorina ventricosa var. *subgranosa*—Nevill, 1885: 152 (not Dunker in Dunker & Zelebor, 1866 = *E. leucosticta*).

Littorina granularis—von Martens, 1887: 192 (not *L. granularis* Gray, 1839 = *E. miliaris*).

Tectarius granularis—Tryon, 1887: 260 (in part, includes *E. radiata*, *E. millegrana*, *E. miliaris*, *E. cinerea*; not Gray, 1839). Adam & Leloup, 1938: 80 (in part, includes *E. reticulata*, *E. melanacme*; not Gray, 1839).

? *Litorina melanacme*—Hedley, 1910: 355 (probably includes *E. melanacme*; not E.A. Smith, 1876).

Melaraphe melanacme—Fischer, 1940: 304 (not E.A. Smith, 1876). Endean *et al*., 1956a: 88–146 (in part; includes *E. melanacme*; not E.A. Smith, 1876).

Littorina chaoi Yen, 1936a: 3–4; figured Yen (1937) unnumbered plate, fig. 2, 2a, b (Pok-hoy, China [Pei-Hai, Gulf of Tonkin]; types unknown).

Littorivaga (?) *picta*—Kuroda, 1940: 102 (not Philippi, 1846 = *E. hawaiiensis*).

Littorina (Littorivaga ?) picta—Kuroda, 1941: 82, pl. 6, figs 7, 8 (not Philippi, 1846).

Nodilittorina picta—Habe, 1951: 93, pl. 14, figs 3, 4 (not Philippi, 1846). Habe, 1956b: 117–121, fig. B (spawn) (not Philippi, 1846). Habe, 1961: 20, pl. 9, fig. 26 (not Philippi, 1846). Oyama & Takemura, 1963: *Nodilittorina* fig. 3 (as *pictus*; in part, includes *E. hawaiiensis*; not Philippi, 1846). ? Barkati & Ahmed, 1984: 91–95, fig. 1 (egg capsules, larval shell) (not Philippi, 1846).

Tectarius pictus—Kuroda & Habe, 1952: 89 (not Philippi, 1846).

Tectarius millegranus—Suvatti, 1950: 47 (not Philippi, 1848).

Nodilittorina (Granulilittorina) millegrana—Rosewater, 1970: 491–494, pl. 326, figs 8, 13, pl. 378, figs 5–7, 10–12, pl. 379, fig. B (penis), pl. 382 (map) (in part, includes *E. radiata*, *E. melanacme*, *E. feejeensis*, *E. novaezelandiae*, *E. millegrana*, *E. reticulata*; not Philippi, 1848). Wilson, 1993: 147, pl. 18, fig. 9a, b (as *Granulittorina*; not Philippi, 1848).

Nodilittorina millegrana—Ohgaki, 1985a: 462. Berry, 1986: fig. 1 (spawn) (not Philippi, 1848).

Granulilittorina millegrana—Habe, 1973: 20, pl. 9, fig. 26. Higo & Goto, 1993: 73 (not Philippi, 1848).

Littorina-capsula hagruma Tokioka & Habe, 1953: 55–56, fig. 11 (spawn) (Tanabe Bay, Japan; name unavailable, see Habe 1977, and Reid & Mak 1998: 16–17).

Granulilittorina philippiana Habe & Kosuge, 1966a (15 January; see Petit & Bieler 1996): 20, pl. 6, fig. 13 (Goza, Shima Peninsula, Honshu, Japan (type locality designated by Habe & Kosuge 1966b); lectotype (Habe & Kosuge 1966b; Habe 1977) NSMT 54881 + 2 paralectotypes NSMT 54882, 54883, not seen; possible additional paralectotypes NSMT 39531 from type locality, and 2 specs NSMT 41625 including probable original figured specimen from Zamboanga, Philippines, not seen; H. Saito pers. comm.). Habe & Kosuge, 1966b (17 May): 313–314, 328. Habe, 1966 (1 July; see Callomon & Petit 2004): 20, pl. 9, fig. 26. Habe, 1968: 28, pl. 9, fig. 26 (see Callomon & Petit 2004). Higo, 1973: 47.

Nodilittorina (Granulilittorina) philippiana—Fujioka & Kurozumi, 1980: 52, 54, fig. 1B.

Nodilittorina exigua—Ma, 2004: 33, pl. 14, fig. H (in part, includes *E. radiata*; not Dunker, 1860).

Taxonomic history: The lectotype figure and extant paralectotypes of *Litorina ventricosa* confirm the identity of Philippi's (1847) species, but the name is a junior homonym of *Litorina scabra* var. *ventricosa* described earlier the same year (var. *ventricosa* is considered of subspecific rank; ICZN 1999: Art. 45.6.4).

No type material is known for *Littorina vidua* (see Johnson 1964) and the original description by Gould (1859) is brief. The species was described from O-shima in the Amami Islands in southern Japan; it was not figured and the few useful features of the Latin description are: ovate-conical shell; intense olive colour with fine yellow tessellation over all; transverse striae; five ventricose whorls; lip with internal lines; dimensions 7 by 4 mm. Gould added, in English: 'Very regular in form, and the reticulations are only seen on close inspection.' Thereafter, the description was simply reproduced (Weinkauff 1882) or the name listed without comment (Pilsbry 1895), and not mentioned again until listed with a query in the synonymy of '*N. millegrana*' (a complex of seven species including the present one) by Rosewater (1970). It was resurrected for the present species by Reid (1992) and has since become widely used (see Synonymy above). The identification depends upon the fine olive and yellow tessellation and the lined aperture noted by Gould (1859), recalling the characteristic brown pattern of this species. The only other Japanese littorinids to which this description might possibly apply are *E. radiata* and *Littoraria sinensis* (Philippi, 1847), but neither is known to occur in the Ryukyu Island chain (Fig. 7; Reid 2001b) and 'olive/yellow tessellation' does not well describe their coloration. However, there are inconsistencies. The dimensions suggest a taller shell (H/B = 1.75, but accuracy of small measurements cannot be assumed). It is curious that no mention was made of the minutely granulose sculpture (but this may sometimes be weak or eroded away). Shells from Okinawa in the central Ryukyu Islands are usually white with one or two spiral brown lines and sometimes axial stripes (Fig. 59G), whereas those from the Japanese mainland are tessellated with brown as suggested by the description; no collections have been seen from the Amami Islands to confirm the appearance of this species at its type locality. Despite these doubts it seems preferable to retain this familiar name and to fix its identity by designating a neotype. This is from the Tsushima Islands in the Korea Strait and is of the brown, tessellated colour form typical of mainland Japan (Fig. 59O). (No COI sequence is available, but the locality is within the expected distribution of haplotype clade 2, see Remarks.)

The species was named *L. chaoi* by Yen (1936), who distinguished it from the sympatric *E. radiata* (as *L. granularis*) by its granulose sculpture, calloused columella, brown pattern and more anterior nucleus of the operculum. The status of the types of *Granulilittorina philippiana* is confused; in January 1966 Habe & Kosuge named the species and figured a shell from Zamboanga; in May 1966 they gave a longer description of the 'new species' and designated a 'holotype' and two 'paratypes' from Goza (here interpreted as selection of lectotype; ICZN 1999, Art. 74.5; see Petit & Bieler 1996, for dates of these publications); registration numbers for these three specimens were subsequently provided by Habe (1977), but these specimens cannot now be found in NSMT (H. Saito pers. comm.).

For much of its history this species has been recognized as distinct. During the later nineteenth and early twentieth centuries it became widely known by the name *L. ventricosa* (Reeve, 1858; E.A. Smith 1879; Weinkauff 1882; Nevill 1885; von Martens 1897; Melvill & Standen 1901; Oostingh 1927). However, this dropped from use as broader species concepts began to prevail; Tryon (1887; followed by Adam & Leloup 1938) included it with four others as *T. granularis*. In the Australian literature it was referred to as *M. melanacme*, including both *E. vidua* and *E. melanacme* (Fischer 1940; Endean *et al.* 1956a). In 1910 Hedley listed both *Litorina melanacme* and *Litorina picta* in his *Marine fauna of Queensland*; it is not known to what he referred by the latter name, but it is unlikely that he was distinguishing *E. melanacme* and *E. vidua*.

In Japan the specific name *picta* was used for this species, in various generic combinations (Kuroda 1940, 1941; Habe 1951, 1956b, 1961; Kuroda & Habe 1952; Oyama & Takemura 1963). However, in 1965 it was suggested by Whipple that *Litorina picta* Philippi, 1846 applied to an endemic Hawaiian species (*E. hawaiiensis*). The present species was then redescribed as *Granulilittorina philippiana* Habe & Kosuge, 1966, under which name it continued to be recognized (Habe & Kosuge 1966a, b; Habe 1966, 1968; Higo 1973; Fujioka & Kurozumi 1980).

Rosewater (1970) reinforced a broad species concept, including the present species together with six others under *N. millegrana*. Although he recognized *N. exigua* (= *E. radiata*) as distinct, these two entities were not clearly separated (he figured the type of *L. radiata* as *N. millegrana*), and only later did Ohgaki (1985a) clarify the separation of *E. radiata* and *E. vidua* (as *N. exigua* and *N. millegrana* respectively) in Hong Kong. Largely on the basis of penial anatomy, Reid (1989a, 1992, 2001a) distinguished the various members of the *E. millegrana* group, including *E. vidua*. The specific name *vidua* is now widely familiar in the taxonomic and ecological literature (Mak 1995; Higo *et al*. 1999; Hasegawa 2000; Tan & Chou 2000; Swennen *et al*. 2001; Reid 2002a; Lee & Chao 2003; Subba Rao 2003; Thach 2005), although some confusion with the similar *E. melanacme* persists.

Diagnosis: Shell turbinate to slightly patulous; fine spiral ribs of unequal size, larger ribs finely granulose due to intersection with strong axial growth lines; colour variable, usually tessellated with brown, or white with spiral brown lines and axial flames, or white; columella broad, pillar purple-brown, edge of inner lip white. Penial glandular disc small; filament tip broad, rounded. Pakistan to Southeast Asia, Indonesia, China, Japan, New Guinea, Australia. COI: GenBank AJ488615, AJ623063, AJ623064, AJ623065.

Material examined: 270 lots (including 92 penes, 5 sperm samples, 8 pallial oviducts, 7 radulae).

Shell (Fig. 59): Mature shell height 4.5–13.6 mm. Shape turbinate to slightly patulous (H/B = 1.13–1.55, SH = 1.27–1.59); spire whorls rounded, suture distinct; spire profile usually concave at apex; periphery of last whorl rounded, sometimes slightly shouldered. Columella long, straight, wide, hollowed and slightly pinched at base; eroded parietal area; occasionally an imperforate pseudumbilical chink adjacent to columella. Sculpture of last whorl: about 13–16 major spiral ribs, but these become divided once or twice at about anterior one third of their width, resulting in an array of ribs of varying width, separated by narrow grooves; larger ribs usually finely granulose where they are crossed by strong axial growth lines, but granules occasionally obsolete (Fig. 59C, R); shoulder rib may be more prominent than others; surface glossy if well preserved, spiral microstriae only in grooves. Protoconch 0.25–0.26 mm diameter, 2.5–2.7 whorls. Colour: highly variable; usually white, cream or pale grey ground colour with pattern of fine brown tessellation on ribs, sometimes forming axial flames, grooves brown; colour of pattern varies from orange to black-brown and may be entirely absent in white or cream shells (Fig. 59J, K); commonly 1–2 brown lines in grooves on shoulder, or a broad shoulder band, with another brown line below periphery (Fig. 59G, H), resulting in herringbone pattern if axial pattern is also developed (Fig. 59I, N); rarely entire shell brown, with pale spots near suture and on base (Fig. 59C, E); apex often black, with black sutural band, or one or more brown lines, extending for 3 whorls of teleoconch, or brown lines may extend to last whorl; apex otherwise yellow; aperture dark brown or (in white shells) orange-brown, or with brown lines, pale band at base; columella purple-brown, but anterior edge and inner lip white, continuing as a white stripe across eroded parietal area.

Animal (Fig. 60): Head (Fig. 60L, M) grey to black, unpigmented stripe across snout, tentacle unpigmented with broad black band (rarely faint) across base, unpigmented around eye; sides of foot grey to black, rarely unpigmented. Opercular ratio 0.35–0.43. Penis (Fig. 60A–K): filament strap-shaped, usually broadening towards rounded tip, tip sometimes minutely mucronate, smooth and without annular wrinkles, filament 0.7–0.9 total length of penis, sperm groove extends to tip; mamilliform gland borne on short projection of base, together with extremely small glandular disc (represented only by patch of tissue adjacent to mamilliform gland, not projecting as a lobe); penis unpigmented or slightly pigmented at base. Euspermatozoa 121–139 µm; paraspermatozoa (Fig. 60P) oval to spherical, 12–17 µm diameter, filled with large round granules, rod-pieces indistinct, probably represented by 1–2 refringent granules, additional straight or arcuate fibrous inclusions sometimes present. Pallial oviduct (Fig. 60N): bursa opening at one third length of straight section (from anterior) and extending back to albumen gland. Spawn (Fig. 60O) a drum-shaped pelagic capsule 160–260 µm diameter (160 µm, Tokioka & Habe 1953; 170-190 µm, Habe 1956b; 240–260 µm, Berry 1986; 200–220 µm, Mak 1995), its sides sculptured by 15–26 vertical ridges thus resembling a cogwheel when viewed from above, cupola-shaped upper side sculptured by 2–5 concentric rings (Berry 1986, illustrated a flattened capsule with cogwheel margin and no cupola or rings), containing single ovum 64–80 µm diameter (Tokioka & Habe 1953; Habe 1956b; Berry 1986; Mak 1995). Development predicted to be planktotrophic.

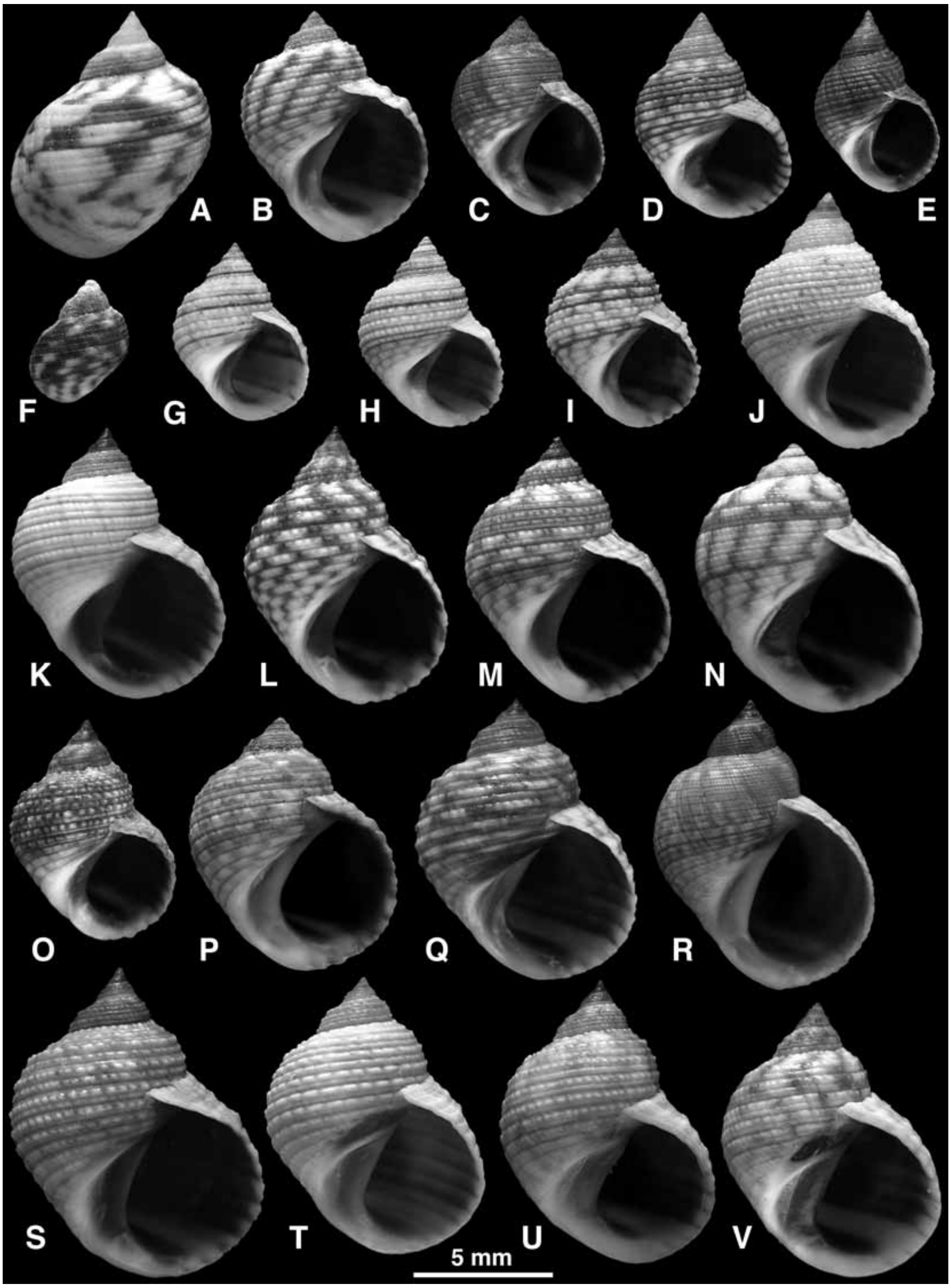

FIGURE 59. *Echinolittorina vidua*. **A,** Gantheaume Point, Broome, Western Australia (BMNH 20040634). **B,** Ela Beach, National Capital District, Papua New Guinea (BMNH 20040635). **C,** Cape Pallarenda, Townsville, Queensland (BMNH 20040636). **D,** Cape Keraudren, Western Australia (BMNH 20040637). **E,** Watering Cove, Dampier, Western Australia (BMNH 20040638). **F,** East Coast Park, Singapore (BMNH 20040640). **G,** Buma, Awa, Nago-shi, Okinawa, Japan (BMNH 20040641). **H, I,** Duncalan Beach, Catarman, Samar I., Philippines (BMNH 20040642). **J, K,** Awung, Lombok, Indonesia (BMNH 20040643). **L,** Maya, Cebu I., Philippines (BMNH 20040644). **M, N,** Kamenti, Kapataran, Sulawesi, Indonesia (BMNH 20020608). **O,** *Littorina vidua* Gould, 1859, neotype, Tsutsu, Tsushima, Japan (BMNH 20040645). **P,** Peng Chau, Mirs Bay, Hong Kong (BMNH 20040646). **Q,** Kovalam, Kerala, India (BMNH 20000715). **R,** Bombay, India (BMNH 20040647). **S,** Cat Loi, Nha Trang, Vietnam (BMNH 20040648). **T,** Sanya, Skali Molin, Hainan, China (BMNH 20040649). **U, V,** Hat Rin Beach, Ko Pha Ngan, Thailand (BMNH 20040650; female, male).

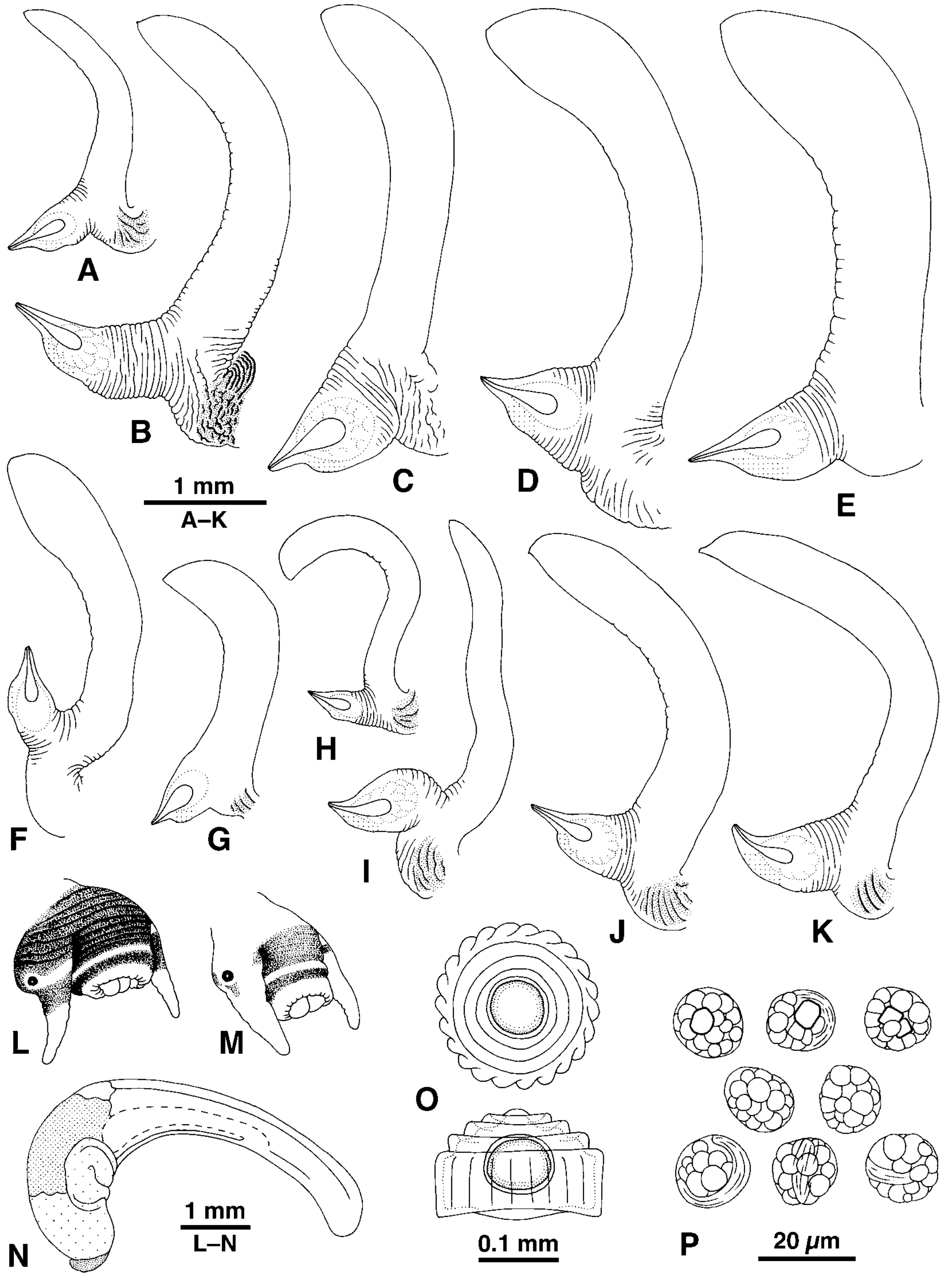

FIGURE 60. *Echinolittorina vidua*. **A–K,** penes. **L, M,** heads. **N,** pallial oviduct. **O,** pelagic egg capsule (after Mak 1995). **P,** paraspermatozoa. **A, P,** Borongan, Samar I., Philippines (BMNH 20040651; shell H **A** = 5.4 mm). **B,** Mirissa, near Weligama, Sri Lanka (BMNH 20040652; shell H = 8.1 mm). **C, M,** Point Murat, Cape Vlamingh, Western Australia (BMNH 20040639; shell H = 6.2 mm). **D,** Hat Rin Beach, Ko Pha Ngan, Thailand (BMNH 20040650; shell H = 10.0 mm). **E,** Ela Beach, National Capital District, Papua New Guinea (BMNH 20040635; shell H = 7.8 mm). **F,** St John's I., Singapore (BMNH 20040653; shell H = 6.0 mm). **G,** from same lot as neotype of *Littorina vidua* Gould, 1859, Tsutsu, Tsushima, Japan (BMNH 20040645; shell H = 5.4 mm). **H,** Tanah Lot, Bali, Indonesia (BMNH 20040654; shell H = 4.9 mm). **I,** Duncalan Beach, Catarman, Samar I., Philippines (BMNH 20040642; shell H = 6.0 mm). **J,** Awung, Lombok, Indonesia (BMNH 20040643; shell H = 7.2 mm). **K,** Sabang, Palawan I., Philippines (BMNH 20040655; shell H = 7.4 mm). **L,** Maya, Cebu I., Philippines (BMNH 20040644; shell H = 10.6 mm). **N,** Laelae I., Makassar, Sulawesi, Indonesia (BMNH 20020561; shell H = 9.2 mm). **O,** Hong Kong. Shading conventions as in Figure 3.

Radula (Fig. 55E, F): Relative radula length 1.56–3.52. Rachidian: length/width 1.07–1.55; tip of major cusp rounded to truncated. Lateral and inner marginal: major cusp on each of similar size, tips rounded to truncated. Outer marginal: 6–7 cusps.

Range (Fig. 61): Central IWP, including Pakistan, India, Southeast Asia, Indonesia, tropical Australia, New Guinea and southern Japan. Range limits: Karachi, Pakistan (BMNH); Madras, India (BMNH 1867.8.12.78); Galle, Sri Lanka (USNM 672392); Mirissa, Weligama, Sri Lanka (BMNH); Cape Negrais, Arakan, Burma (BMNH 1882.8.7.47–50); Penang, Malaysia (BMNH); Tanjong Tiram, Sumatra, Indonesia (ZMA); Pulu Weh, Sumatra, Indonesia (NNML, ZMA); Nanga Bay, Flores, Indonesia (ZMA); Point Murat, Cape Vlamingh, Western Australia (BMNH); Peel I., Moreton Bay, Queensland, Australia (AMS); Scarborough, Moreton Bay, Queensland, Australia (Endean *et al*. 1956a); Chinaman's Beach, near Balmoral, Sydney, NSW, Australia (AMS); Madang, Papua New Guinea (AMS C71611); Sorong, Irian Jaya, Indonesia (BMNH); Borongan, Samar, Philippines (BMNH); Pao Tai, Xiamen, China (BMNH); Chialoshui, Taiwan (BMNH); Tiaoshi, 20 km NW Keelung, Taiwan (BMNH); Senkaku Is, Japan (Fujioka & Kurozumi 1980); Buma, Nago-shi, Okinawa, Japan (BMNH 20040641); Yakushima, Osumi Is, Japan (Uozumi Colln); Tsutsu, Tsushima, Kyushu, Japan (BMNH 20040645); Mishima, Yamaguchi Pref., Japan (Hasegawa 2000); Shirahama, Wakayama Pref., Japan (BMNH); Miura Peninsula, Honshu, Japan (Habe & Kosuge 1966b; Hasegawa 2000); Araike, Mitsune, Hachijojima, Japan (BMNH).

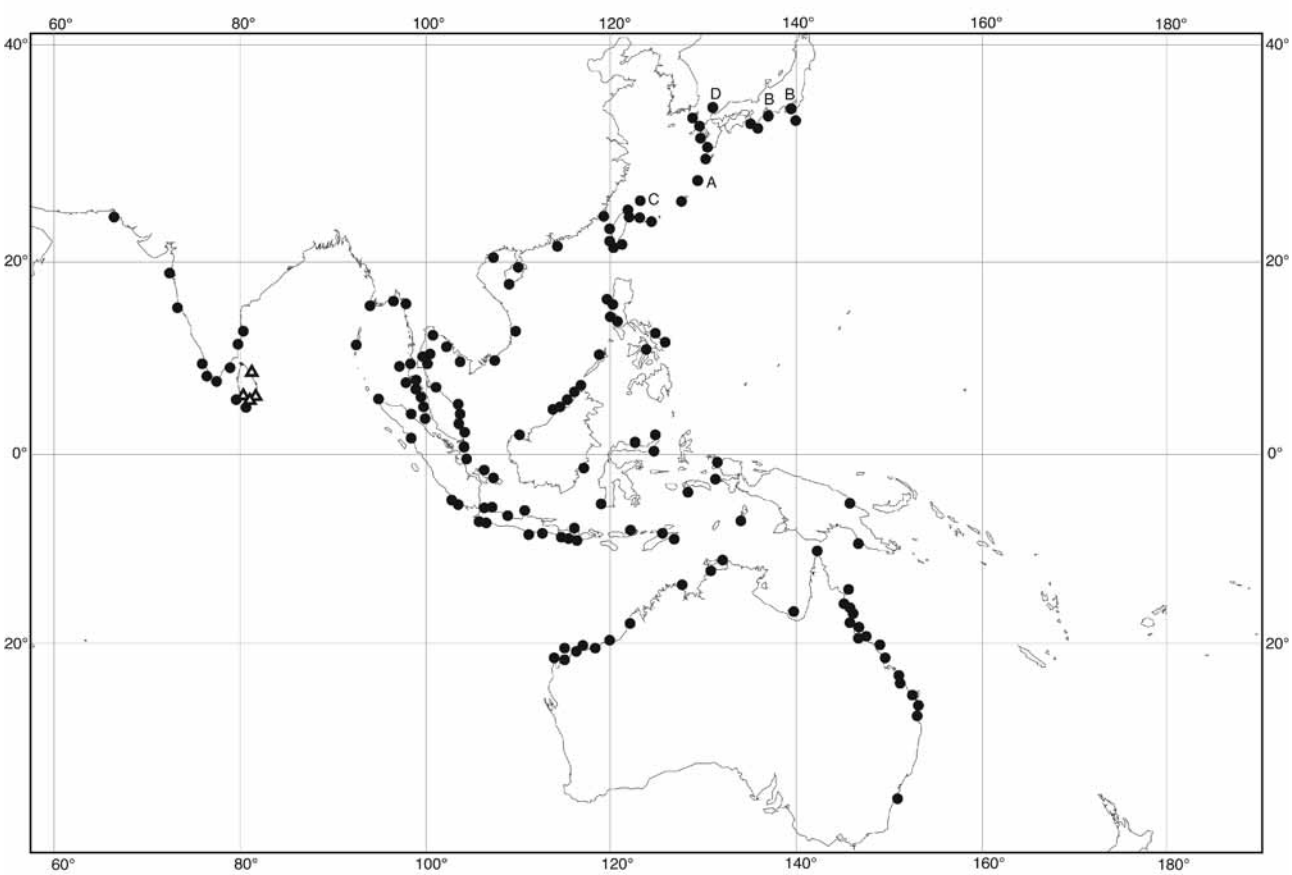

FIGURE 61. Distribution of *Echinolittorina vidua* (solid circles) and *E. novaezelandiae* (open triangles). Literature records: A, Gould (1859; type locality of *E. vidua*). B, Habe & Kosuge (1965a); C, Fujioka & Kurozumi (1980); D, Hasegawa (2000).

Despite its wide distribution and habitat range, *E. vidua* is uncommon in parts of its range. Although common on the west coast of India, only three specimens have been recorded from Sri Lanka. In the central part of its range it is only sporadically distributed in the central Philippines and Sulawesi, and rare in Sabah (pers.

obs.). Sparse museum records suggest that it is also uncommon in the Moluccas and eastern New Guinea (compare with the more numerous records of *E. melanacme* in these areas, Fig. 56). There are also relatively few records from Cape York and Arnhem Land in northern Australia (compare with records of *E. austrotrochoides* in the region, Fig. 29). The southern limit on the east coast of Australia is Moreton Bay (Endean *et al*. 1956a, as *Melaraphe melanacme*). A single specimen has been recorded from the vicinity of Sydney (AMS, collector G.P. Whitley) and may well be a rare occurrence outside the normal range, having been carried south by the East Australian Current. The distribution in the Makassar Strait, Mindanao and the Moluccas is inadequately known. In the Ryukyu Islands there are numerous museum records from Ishigaki and Okinawa, but none to the north until Yakushima (although the type locality, O-shima, lies in this area, see Taxonomic History, above). The species is abundant in eastern and western Australia, Java and Sumatra, and the entire mainland coast of Southeast Asia from Burma to Xiamen, China. It does not extend far out into the western Pacific, but reaches Okinawa and Hachijojima.

Habitat and ecology: This species occurs on sheltered and moderately exposed shores of continents and high islands. It is tolerant of moderately turbid water and is scarce or absent in areas with clear oceanic water. Substrates include granite, slate, basalt, sandstone, concrete, coral limestone and rarely the trunks of trees on the edges of mangrove forests (*Avicennia*, Sanpanich *et al*. 2004; *Sonneratia*). It occupies a lower tidal level than most of its sympatric congeners, extending from the lowermost littoral fringe to the upper eulittoral zone (i.e. largely overlapping with *E. melanacme* but extending slightly lower; only *E. tricincta* extends further down the shore).

In Western Australia Black & Johnson (2001; as *N. millegrana*) found this species zoned lower than *E. austrotrochoides* and *E. australis*, and from its rapid growth rate suggested a possible annual life cycle. On the southern Queensland mainland it occupies a zone from high water of spring tides to below mean high water, below the zone of *E. austrotrochoides*, and is absent where wave action is strong (Endean *et al*. 1956a, as *M. melanacme*; observations in northern Queensland probably included both the present species and sympatric *E. melanacme*, Endean *et al*. 1956a, b). In Hong Kong this species is again the lowest-zoned of the littorinids, found at and just below mean high water of spring tides, where it migrates vertically with the rise and fall of the tide (Williams 1994); it is present only on open coasts and is virtually absent from the sheltered, muddy conditions of Tolo Harbour (Ohgaki 1985a). In Thailand it has been recorded from offshore islands, but not mainland sites (map in Sanpanich *et al*. 2004). Unlike the littorinids of the littoral fringe, this species continues to produce ammonia during periods of emersion, perhaps limiting its zonation (Uglow & Williams 2001). In Hong Kong *E. vidua* grazes the epilithic biofilm of cyanobacteria (Mak & Williams 1999). In Tanabe Bay, Japan, it occurs below *E. radiata* and overlaps with barnacles; here it is absent from enclosed bays (Habe 1958b). Similar zonation, from below *E. malaccana* to the barnacle zone, has been observed in the Gulf of Thailand (Tsuchiya & Lirdwitayapasit 1986), and in Penang between mean high water of spring and neap tides (Berry 1986). Spawning occurs between June and September at Shirahama, Japan (Ohgaki 1981), March and October in Hong Kong (Mak 1998) and, in Penang, between March and June with little evidence of a lunar rhythm (Berry 1986).

Remarks: *Echinolittorina vidua* has a wide distribution in the central IWP, where it is broadly sympatric with *E. malaccana*, *E. austrotrochoides* (Fig. 29) and *E. melanacme* (Fig. 56); it reaches higher latitudes than all of these in both Japan and Australia. On a geographical scale it occurs on the productive, nutrient-rich shores of continental margins and high islands (Rutgers University Primary Productivity Study), and on a local scale it is usually found in sites with moderately turbid water, and is uncommon or absent on shores with clear oceanic water. It therefore shows the characteristics of a continental species. However, its distribution and habitat range appear to be shifted more towards the oceanic end of the spectrum than those of the continental *E. malaccana* and *E. austrotrochoides*. For example, *E. vidua* is present in southern Indonesia and the eastern Banda Sea (where *E. malaccana* and *E. austrotrochoides* do not occur) and it is scarce in northern Australia (where *E. austrotrochoides* is common). On a local scale, in Southeast Asia *E. malaccana* is often seen to extend into more turbid and even slightly estuarine areas than *E. vidua*; in Hong Kong only *E. malaccana* is common in the eutrophic Tolo Channel (Ohgaki 1985a) and in Thailand occurs at mainland sites where *E. vidua* is absent (map in Sanpanich *et al*. 2004). However, comparison of distributions suggests that *E. vidua* is a less oceanic species than *E. melanacme*; the former is common in the inner Gulf of Thailand (where *E. melanacme* is scarce), scarce or absent in the low-productivity areas of Sulawesi and the Moluccas (where *E. melanacme* is common) and extends to more productive areas of the Australian coastline. This is supported by observations at local scales (pers. obs. in Philippines, Taiwan, Sabah, Sarawak, Sulawesi), where the relative abundance of *E. vidua* and *E. melanacme* appears to be correlated with water clarity. However, in disagreement with these generalizations *E. vidua* has been recorded more widely than *E. melanacme* on the exposed, oceanic coastline of western Sumatra and southern Java; possibly this reflects greater tolerance of wave exposure or oceanic upwelling by *E. vidua*, and/or geographical variation in its habitat preferences.

This species has been the subject of a detailed study of the phylogeography of mitochondrial haplotypes (Reid *et al*. 2006). Sequence variation in the COI gene defines six well supported clades restricted to the following areas: (1) Indian Ocean; (2) mainland Southeast Asia, Sarawak, Hong Kong, Taiwan and Japan; (3) Western Australia; (4) Philippines and Taiwan; (5) Okinawa, Taiwan and Sulawesi; (6) eastern Australia (plus one individual from Western Australia) and Lombok. Clades 1–2 and 3–6 are monophyletic groups with lower support. The genetic differentiation among these six clades (K2P distance = 2.15–5.86%) is greater than that known within any other *Echinolittorina* species, and comparable with or greater than that between some species of this genus, so the possible status of the clades as distinct species must be considered.

Although even a single marker can be used to define phylogenetic species, biological species are more likely to be recognized by concordant variation in multiple independent markers (see Material and Methods). Anatomically, the form of the penis does not define any discrete entities within *E. vidua*. Some specimens from the Philippines and Taiwan appear to show a more tapered tip to the penial filament (Fig. 60A, I, K), in contrast to the normal broad and rounded end, but (despite examination of 92 penes) this difference has not been found to be consistent, nor linked with differences in shell morphology. The coloration and sculpture of the shell are variable throughout the geographical range. No geographical trend is evident in the prominence of granular sculpture; relatively smooth and granulose forms are mixed in many populations. Variously tessellated colour forms are present throughout most of the range, but two colour forms are geographically restricted. In both eastern and western Australia the colour pattern is unusually dark; many shells are still tessellated, but some are dark brown from shoulder to below the periphery (Fig. 59C, E). In eastern Sumatra, Java, Bali and Lombok the shells are all white to cream; if pattern is present at all it is merely a brown spiral line at the shoulder, at shoulder and periphery, or in all grooves (Fig. 59J, K). Very similar white shells are found in Okinawa, Taiwan, the Philippines and Sulawesi, although in these areas spiral lines are often present as a band or line at the shoulder and a line on the base, together with axial flames making a 'herringbone' pattern (Fig. 59G–I), and tessellated forms also occur. It is not known that these colour forms have a genetic basis, although this is likely. Neither the 'brown' nor 'white' patterns are found in India, on the mainland of Southeast Asia, Sarawak, or north of the Ryukyu Islands in Japan; in these areas all shells are tessellated to some degree. There is some correspondence with the genetic results, which unite clades 4–6, to the exclusion of the two clades from mainland Asia. Crucially, however, in Taiwan where haplotypes of clades 2, 4 and 5 occur syntopically, shell colour is variable but there is no evidence of a correlation between colour and haplotype. Furthermore, the white shells from Lombok resemble those from Sulawesi, the Philippines and Taiwan (clades 4 and 5) although genetically they belong to clade 6. The eastern and western Australian clades (3 and 6) share the brown colour pattern, yet their haplotypes do not form a single clade. In general, therefore, shell colour pattern appears to correspond more with geographical proximity than haplotype phylogeny.

The geographical distribution and abundance of *E. vidua* are suggestive of the origin and maintenance of some of these molecular clades (Reid *et al*. 2006). Differentiation between Indian and Pacific clades on the Asian mainland may have originated during episodes of low sea levels during Pleistocene glaciations, which largely isolated the two ocean basins. Differentiation on either side of Australia might have had a similar origin, but the presence of the eastern Australian clade in Lombok is difficult to explain. The rarity of this species in northern Australia suggests that gene flow between eastern and western Australia may be limited, but the single eastern haplotype in the west shows that some transport must occur. The distributions of clades do not reveal obvious correspondences with present current flows, such as the Indonesian Throughflow. However, habitat effects may be significant. The absence of the species from most of the oceanic Banda and Molucca Seas may contribute to the genetic break between Sulawesi and Australia. The distribution of clade 5 in Okinawa, Taiwan and Sulawesi is reminiscent of the distribution of *E. tricincta* (Fig. 43), and might suggest that members of this clade have a more oceanic habitat preference than others. At a local scale in Taiwan, however, individuals of this clade can be found in both oceanic and muddy habitats.

Further genetic study of this interesting case is necessary, preferably using nuclear markers. For the present, the available evidence is more consistent with a single species showing pronounced phylogeographic structure (with limited sympatry and likely introgression between the clades defined by COI haplotypes), rather than with six cryptic, reproductively isolated and largely allopatric species.

The egg capsule of this species shows considerable variation in size and shape; the largest capsules are recorded from Penang (240–260 µm, Berry 1986), the smallest from Japan (160–190 µm; Tokioka & Habe 1953; Habe 1956b) and intermediate sizes in Hong Kong (200–220 µm, Mak 1995). The latter two samples are from the distributional area of the same molecular clade. All the recorded egg capsules share the distinctive ‘cogwheel’ appearance, but that figured by Berry (1986) lacks the sculptured cupola. The strong vertical ridges of the peripheral skirt are unusual among littorinine egg capsules, but similar structures have been described in two *Peasiella* species (Reid & Mak 1998). In addition, oblique striations have been illustrated on the skirt of *Tectarius antonii* (Philippi, 1846) and *Echinolittorina riisei* (Mörch, 1876) (Borkowski 1971, as *Echininus nodulosus* and *L. lineolata*, respectively) and are faintly visible in *E. natalensis*.

There is slight sexual dimorphism (Fig. U, V), males being smaller and with a relatively larger aperture; this is similar to that in *E. melanacme*, but less pronounced.

The sister species of *E. vidua* is *E. novaezelandiae* (Williams & Reid 2004), endemic to Sri Lanka; the two are occasionally sympatric and differentiation is described in the Remarks on the latter. Far more similar in shell characters to *E. vidua*, and frequently sympatric or even syntopic with it, is *E. melanacme* (Fig. 53), as discussed in the Remarks on that species. In southern Japan, China and Taiwan there is overlap with *E. radiata* (Fig. 4); the finer and more numerous ribs, brown tessellated pattern and white anterior and inner lips of the shell serve to recognize *E. vidua* in these areas (see Remarks on *E. radiata* for detailed comparison). This species is seldom syntopic with the typically oceanic *E. reticulata*; white shells of *E. vidua* (especially those from eastern Sumatra, Java, Bali and Lombok, Fig. 59J, K) can be similar to the smoother forms of *E. reticulata* (Fig. 69F–H, N), but in the former there is no strong axial alignment of granules, and the columella is wider; penial differences are diagnostic.

Echinolittorina novaezelandiae **(Reeve, 1857)**

(Figures 55G, H, 61–63)

Littorina novaezelandiae Reeve, 1857: sp. 74, pl. 14, fig. 74 (New Zealand [in error, corrected to Trincomali, Sri Lanka, by Rosewater 1970]; lectotype (Biggs, 1966) BMNH 1966124 (Fig. 62H) and 3 paralectotypes BMNH 1966125, seen). Biggs, 1966: 137–139, pl. 7, figs 3–5. Atapattu, 1972: 161.

Littorina (Melaraphe) novaezelandiae—Tryon, 1887: 249, pl. 44, fig. 76 (in part, includes *E. melanacme*).

Nodilittorina (Nodilittorina) novaezelandiae—Reid, 1989a: 100 (in part, includes *E. melanacme*, *E. feejeensis*).

Nodilittorina novaezelandiae—Reid, 2001a: 439–440, figs 2A, 3I (penis). Reid, 2002a: 259–281.

Echinolittorina novaezelandiae—Williams *et al.*, 2003: 83. Williams & Reid, 2004: 2227–2251.

Littorina novaezealandiae ‘Reeve’ Pritchard & Gatliff, 1902: 91 (unjustified emendation of *Littorina novaezelandiae* Reeve, 1857; in part; includes *Afrolittorina praetermissa* (May, 1909)).

Littorina erronea Nevill, 1885: 152–153 (Balapiti, Ceylon [Balapitiya, Sri Lanka]; types probably in Zoological Survey of India, not seen; not *L. pallescens* ? var. *erronea* Nevill, 1885: 148).

Nodilittorina (Granulilittorina) millegrana—Rosewater, 1970: 491–494, pl. 378, figs 8, 9, pl. 380, figs 4, 5, pl. 382 (map) (in part, includes *E. radiata*, *E. melanacme*, *E. feejeensis*, *E. vidua*, *E. millegrana*, *E. reticulata*; not *L. millegrana* Philippi, 1848).

Taxonomic history: Reeve (1857) was mistaken in giving the locality 'New Zealand' for this species, resulting in the unfortunate name. This error was first noted by Nevill (1885; also Biggs 1966 and Rosewater 1970), who apparently judged the name inappropriate and replaced it, although he introduced the new name as a new species.

Despite its narrow occurrence in Sri Lanka and the initial confusion about its origin, this species name has had a long history of use. In part, this is the result of confusion between the present species and the pair here distinguished as *E. melanacme* and *E. feejeensis* (see Synonymies of those species). The name *L. novaezelandiae* was first used for *E. melanacme* in New Caledonia by Fischer (1860), and similarity between these two species was pointed out by E.A. Smith (1876), Nevill (1885) and Tryon (1887). Reid (1989a) mistakenly combined all three species as *N. novaezelandiae*, before limiting the name to the endemic Sri Lankan species on the basis of anatomical evidence (Reid 2001a). Both Biggs (1966) and Atapattu (1972) also used the name *L. novaezelandiae* for the present species, although Rosewater (1970) included it within his broad concept of *N. millegrana*. As noted by Reeve (1857) there is a remarkable resemblance to shells of the temperate species *Afrolittorina africana* (Krauss in Philippi, 1847), and the name *L. novaezelandiae* has also been incorrectly applied to the temperate Australian *Afrolittorina praetermissa* (Pritchard & Gatliff 1902).

Diagnosis: Shell patulous; numerous fine spiral ribs or impressed lines, spire finely granulose due to intersection with axial growth lines; white with faint yellow-brown tessellation; columella broad, pillar purple-brown, inner lip white. Penial glandular disc hardly visible; filament tip pointed. Sri Lanka only. COI: GenBank AJ623023, AJ623024.

Material examined: 12 lots (including 5 penes, 2 sperm samples; 4 pallial oviducts, 2 radulae).

Shell (Fig. 62): Mature shell height 5–12.9 mm. Shape patulous (H/B = 1.09–1.33, SH = 1.22–1.51); spire whorls rounded, suture distinct; spire profile slightly concave at apex; periphery of last whorl rounded. Columella long, straight, wide, hollowed and slightly pinched at base; small eroded parietal area; imperforate pseudumbilical chink adjacent to columella. Sculpture of penultimate whorl: 9–13 low ribs above suture, of which alternate ones are finely granulose where crossed by growth lines; sculpture of last whorl: about 22–35 low ribs of varying width, separated by incised lines, granulose sculpture obsolete or absent, sometimes smooth but for weakly incised lines (Fig. 62J); surface glossy if well preserved, spiral microstriae usually absent, or visible in wider grooves. Protoconch 0.27 mm diameter, 2.5 whorls. Colour: white, usually with faint pattern of fine, yellow-brown tessellation, sometimes with faint brown lines in grooves; apex black or yellow, sometimes with one brown line extending for 3 whorls of teleoconch; aperture orange brown with brown lines at margin corresponding with external grooves, pale band at base; columella purple-brown, but anterior edge and inner lip white, continuing as a white stripe across eroded parietal area.

Animal (Fig. 63): Head (Fig. 63F, G) dark grey, unpigmented stripe across snout; tentacle mainly grey, with unpigmented band across base and around eye, distal half paler or with longitudinal dark streak; sides of foot grey. Opercular ratio 0.30–0.38. Penis (Fig. 63A–D): filament gradually tapering to pointed or slightly mucronate tip, smooth and without annular wrinkles, filament 0.7 total length of penis, sperm groove extends to tip; mamilliform gland borne on short projection of base, together with extremely small glandular disc (hardly visible, represented only by patch of tissue adjacent to mamilliform gland, not projecting as a lobe); penis unpigmented or pigmented at base. Euspermatozoa not known; paraspermatozoa (Fig. 63H, I) spherical, 12–14 µm diameter, filled with large round granules, rod-pieces short rectangular rods up to 9 µm or small irregular polygons. Pallial oviduct (Fig. 63E): bursa opening at about half length of straight section and extending back to albumen gland. Development predicted to be planktotrophic.

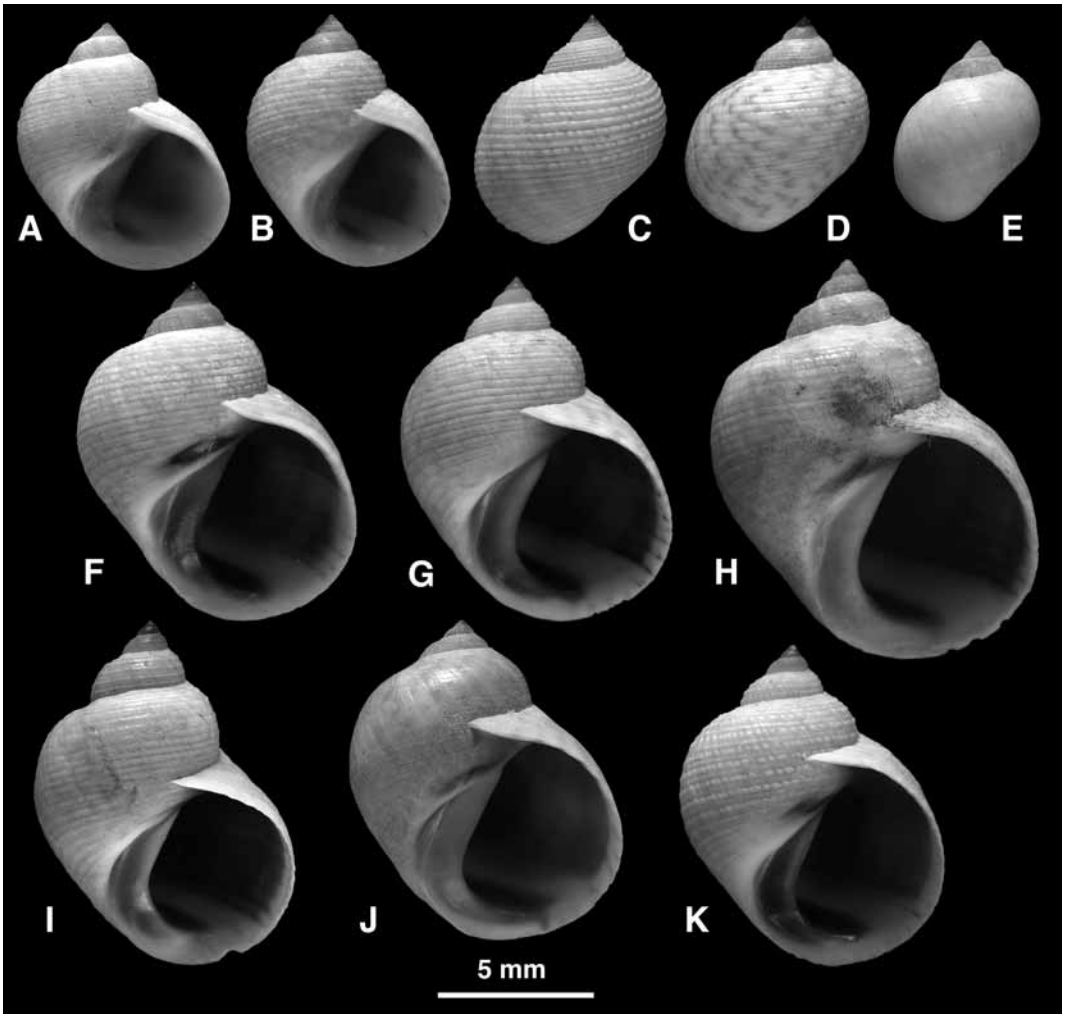

FIGURE 62. *Echinolittorina novaezelandiae*. **A, B, F, G, I, K,** Mirissa, Weligama, Sri Lanka (BMNH 20040631). **C, D,** Tangalle, Sri Lanka (BMNH 20040632). **E,** Trincomalee, Sri Lanka (BMNH 1966122). **H,** *Littorina novaezelandiae* Reeve, 1857, lectotype, 'New Zealand' (in error) (BMNH 1966124). **J,** Sri Lanka (BMNH 20040633).

Radula (Fig. 55G, H): Relative radula length 1.60–1.96. Rachidian: length/width 1.07–1.13; tip of major cusp rounded. Lateral and inner marginal: major cusp on each of similar size, tips truncated. Outer marginal: 6–7 cusps.

Range (Fig. 61): Eastern and southern Sri Lanka. Range limits: Balapitiya (Nevill 1885); Galle (BMNH; USNM 716429); Mirissa, near Weligama (BMNH 20040631); Tangalle (BMNH 20040632); Yala (BMNH); Trincomalee (BMNH 1966123; USNM 637362). There are no records from the west coast north of Balapitiya, despite six records of abundant *E. leucosticta* from this area. At Galle, Mirissa and Tangalle, in the southwest, it is not common (pers. obs.). There are few museum records from eastern Sri Lanka, but Atapattu (1972) records it as the commonest littorinid on the east coast and absent elsewhere except for a few localities on the south coast.

Habitat: Uppermost eulittoral zone on sheltered rocks in areas of clear and only slightly turbid water, and therefore a relatively oceanic species. Atapattu (1972) recorded it in the dry littoral fringe together with *Littoraria undulata*.

Remarks: Molecular data support a sister-species relationship between *E. novaezelandiae* and *E. vidua* (Williams & Reid 2004), but with a relatively large genetic distance (K2P distance based on COI = 11.3%). The narrow range of *E. novaezelandiae* near the periphery of the wide distribution of *E. vidua* could suggest a case of founder speciation, for example by dispersal from the range of *E. vidua* in Southeast Asia or the

Pacific, followed by a more recent dispersal of *E. vidua* to account for its current presence in India (migration around the Bay of Bengal is precluded by estuarine conditions and lack of rock substrate). Nevertheless, the fact that all members of the *E. millegrana* group occupy oceanic habitats, whereas *E. vidua* is a continental species, suggests another possibility. If the ancestor of *E. novaezelandiae* and *E. vidua* was also an oceanic species (as argued by parsimony), it may have occupied the narrow range of *E. novaezelandiae*, and dispersal and habitat shift could have given rise to *E. vidua*.

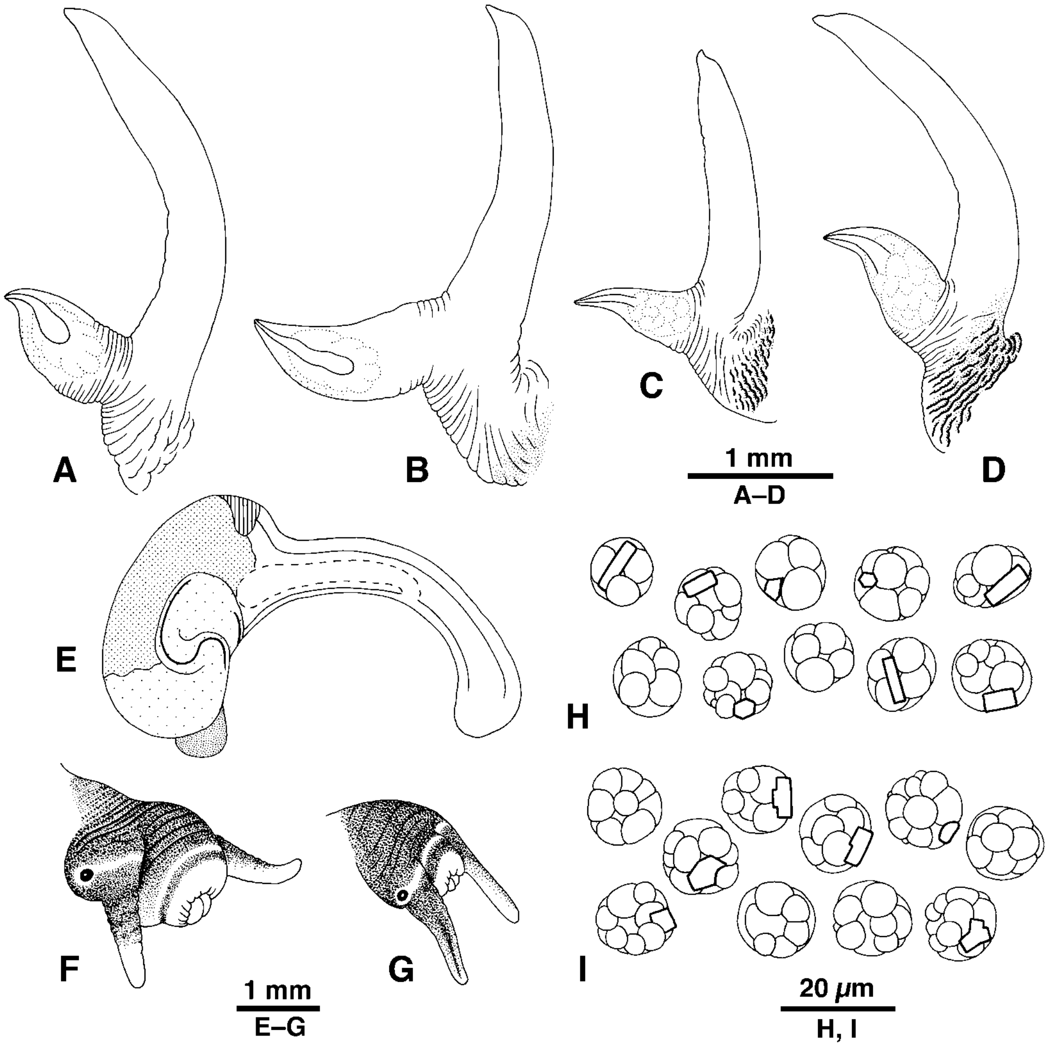

FIGURE 63. *Echinolittorina novaezelandiae*. **A–D,** penes. **E,** pallial oviduct. **F, G,** heads. **H, I,** paraspermatozoa. **A, B, H, I,** Mirissa, near Weligama, Sri Lanka (BMNH 20040631; shell H **A** = 7.0 mm, **B** = 6.7 mm). **C–G,** Tangalle, Sri Lanka (BMNH 20040632; shell H **C**, **G** = 5.9 mm, **D**, **F** = 6.9 mm). Shading conventions as in Figure 3.

Morphologically these two are distinguished by the finer or obsolete sculpture on the last whorl and rounded profile of *E. novaezelandiae* (contrasting with raised and often granulose ribs, and slightly shouldered profile in *E. vidua*). Shells of *E. vidua* (Fig. 59) may be pale in coloration in parts of its range, like *E. novaezelandiae*, but those from Sri Lanka and India (Fig. 59Q, R) are invariably heavily and coarsely tessellated with brown. The penial morphology is similar in both, but the penial tip is more pointed in *E. novaezelandiae* and the penial glandular disc even less noticeable. The tentacle coloration also differs, pigmentation extending further towards the tip in *E. novaezelandiae*. *Echinolittorina vidua* is extremely rare in Sri Lanka, but one specimen has been found syntopically with *E. novaezelandiae* at Mirissa (BMNH), and both are present in a mixed sample from Galle (USNM 672392).

There is a resemblance to the form of *E. melanacme* from the Coral Sea (Fig. 53N–R), but the shell of that species is darker in colour, more coarsely ribbed, and the columella is narrower; male and female reproductive anatomy is distinct in these two. There is also a close resemblance to shells of the temperate southern African *Afrolittorina africana*, but that species has a broad penial filament and a more complex looped structure of the pallial oviduct (Reid & Williams 2004).

This species is virtually restricted to the east coast of Sri Lanka (Atapattu 1972) and therefore has one of the narrowest geographical distributions of any *Echinolittorina*. Absence from the west coast may be explained by an apparent preference for sheltered conditions and clear, oceanic water.

Echinolittorina cinerea **(Pease, 1869)**

(Figures 23, 64, 65, 66A, B)

Littorina cinerea Pease, 1869: 78, pl. 8, fig. 14 (Marquesas Islands; lectotype (Rosewater 1970) ANSP 18811 (Fig. 64D), seen).

Littorina millegrana var. *cinerea*—Nevill, 1885: 153–154 (in part, includes *E. reticulata*).

Tectarium cinereum—Dautzenberg & Bouge, 1933: 358.

Nodilittorina cinerea—Rehder, 1969: 32. Salvat & Rives, 1975: 264, fig. 42. Cernohorsky, 1978: 43, pl. 11, fig. 3. Tröndlé & von Cosel, 2005: 279.

Nodilittorina (Granulilittorina) cinerea—Rosewater, 1970: 505, pl. 382 (map), 386, figs 13–18.

Nodilittorina (Nodilittorina) cinerea—Reid, 1989a: 99.

Nodilittorina cinerea—Reid, 2001a: 436–437, figs 1C, 3D (penis). Reid, 2002a: 259–281.

Echinolittorina cinerea—Williams *et al*., 2003: 83. Williams & Reid, 2004: 2227–2251.

Littorina plena var. *vitiensis*—Nevill, 1885: 139 (not *Litorina vitensis* Dunker, 1871 = *E. feejeensis*).

Littorina miliaris var. *fijiensis*—Nevill, 1885: 154 (not *L. feejeensis* Reeve, 1857).

Tectarius feejeensis—Iredale, 1910: 70, 71 (not Reeve, 1857). Oliver, 1915: 518 (not Reeve, 1857).

Tectarium feejeense—Dautzenberg & Bouge, 1933: 358 (not Reeve, 1857).

Nodilittorina (Granulilittorina) leucosticta feejeensis—Rosewater, 1970: 500, pl. 384, figs 18, 19, pl. 385 (map) (in part, includes *E. feejeensis*; not Reeve, 1857).

Nodilittorina leucosticta feejeensis—Cernohorsky, 1972: 56 (in part, includes *E. feejeensis*, *E. biangulata*; not Reeve, 1857). Higo & Goto, 1993: 74 (not Reeve, 1857).

Nodilittorina (Granulilittorina) quadricincta feejeensis—Rosewater & Kadolsky, 1981: 1234 (in part, includes *E. feejeensis*; not Reeve, 1857). Vermeij *et al*., 1984: 40 (not Reeve, 1857).

Tectarius granularis—Tryon, 1887: 260, pl. 48, fig. 81 (in part, includes *E. radiata*, *E. miliaris*, *E. millegrana*, *E. vidua*; not *L. granularis* Gray, 1839 = *E. miliaris*).

Littorina miliaris—Oyama, 1940: 52 (not Quoy & Gaimard, 1833 = *E. miliaris*).

Nodilittorina miliaris—Habe, 1951: 92, pl. 14, fig. 5 (not Quoy & Gaimard, 1833). Oyama & Takemura, 1963: *Nodilittorina* fig. 5 (not Quoy & Gaimard, 1833). Higo, 1973: 47 (not Quoy & Gaimard, 1833).

Tectarius miliaris—Kuroda & Habe, 1952: 89 (not Quoy & Gaimard, 1833).

Nodilittorina aff. *miliaris*—Fukuda, 1993: 38, pl. 12, fig. 176 (not Quoy & Gaimard, 1833). Fukuda, 1995: 39 (not Quoy & Gaimard, 1833).

Nodilittorina (Nodilittorina) pyramidalis pyramidalis—Rosewater, 1970: 481–484, pl. 372 (map) (in part, includes *N. pyramidalis*, *E. pascua*, *E. malaccana*, *E. austrotrochoides*, *E. marquesensis*, *E. cecillei*, *E. wallaceana*; not *L. pyramidalis* Quoy & Gaimard, 1833 = *N. pyramidalis*).

Nodilittorina leucosticta—Salvat & Rives, 1975: 263, fig. 41 (not Philippi, 1847)

Granulilittorina millegrana—Okutani, 1986: 70–71, fig. (not Philippi, 1848).

Nodilittorina sp.—Asakura & Kurozumi, 1991: 16–18, figs 4, 5. Asakura *et al*., 1993: 11, fig. 3G. Hasegawa, 2000: 141, pl. 70, fig. 25.

Nodilittorina (Granulilittorina) sp. A—Kurozumi & Asakura, 1994: 135.

Nodilittorina (Granulilittorina) sp. B—Kurozumi, 1994: 366, pl. 2, fig. 4.

Nodilittorina novaezelandiae—Brook & Marshall, 1998: 215 (not Reeve, 1857).

Taxonomic history: This variable species ranges in sculpture from smooth to carinate and nodulose, and has consequently been the subject of considerable taxonomic confusion. Pease (1869) described *L. cinerea* from the Marquesas Islands where, as he noted, the sculpture varies from granosely ridged to smooth. Thereafter, this name was applied exclusively to moderately sculptured and smooth shells from the Marquesas Islands (Nevill 1885; Dautzenberg & Bouge 1933; Rosewater 1970; Salvat & Rives 1975; Cernohorsky 1978; Reid 1989a). Meanwhile, strongly sculptured shells, generally with axial stripes and a wider distribution in the South Pacific, were misidentified as *L. feejeensis* (Nevill 1885; Iredale 1910; Oliver 1915; Dautzenberg & Bouge 1933; Rosewater 1970; Cernohorsky 1972; Rosewater & Kadolsky 1981; Vermeij *et al*. 1984; Higo & Goto 1993), here shown to be a species virtually endemic to the Fijian Islands. Meanwhile, in the Japanese literature the same form from the Ryukyu and Ogasawara Islands was identified as *L. miliaris* (Oyama 1940; Habe 1951; Kuroda & Habe 1952; Oyama & Takemura 1963; Higo 1973). However, as discussed by Rosewater (1970), *E. miliaris* is an Atlantic species described from Ascension Island, so the sculptured form was subsequently considered by Japanese workers to be an undescribed species (Asakura & Kurozumi 1991; Asakura *et al*. 1993; Fukuda 1993, 1995; Kurozumi 1994; Kurozumi & Asakura 1994; Hasegawa 2000). Availability of material from throughout the range, and comparison of penes, led Reid (2001a) to conclude that these two contrasting forms represented a single species, and this is supported by limited molecular data (Williams & Reid 2004).

Other names have also been incorrectly applied to this species. It was included by Tryon (1887) in his very broad concept of *T. granularis*. Rosewater's (1970) records of '*N. pyramidalis pyramidalis*' from Samoa and Tonga were based on the most strongly sculptured examples of *E. cinerea* (specimens in BPBM, R. Kawamoto pers. comm.). Salvat & Rives (1975) misidentified black and white shells from Tahiti as *N. leucosticta*. Use of the name *N. novaezelandiae* (e.g. Brook & Marshall 1998) arose as a result of Reid's (1989a) incorrect synonymy of *L. feejeensis* with that species. A name sometimes found on museum material of strongly sculptured shells is *L. lamellosa* Montrouzier in Souverbie, 1861; this is a species of *Fossarus* described from New Caledonia (as also concluded by Rosewater 1970; see Excluded Species).

Diagnosis: Shell turbinate to high turbinate; sculpture variable, from smooth with 14-21 fine incised lines to 2–5 carinate ribs with strong granules; colour variable, unpatterned grey-white, or dark with white granules, or white with axial black lines or zigzag flames. Penial glandular disc minute; filament vermiform, pointed. Islands of South and West Pacific, Polynesia. COI: GenBank AJ622991, AJ622992.

Material examined: 78 lots (including 15 penes, 5 sperm samples, 6 pallial oviducts, 2 radulae).

Shell (Fig. 64): Mature shell height 3.2–13.3 mm. Shape turbinate to high turbinate (H/B = 1.19–1.57, SH = 1.41–2.16); spire whorls rounded or slightly turreted, suture distinct; spire profile straight; periphery of last whorl rounded, sometimes slightly shouldered and angled at periphery. Columella concave, wide, hollowed at base; eroded parietal area small or absent. Sculpture of last whorl highly variable: smooth shells with 14–21 weak, irregularly spaced, incised lines (Fig. 64A); usually one rib at periphery and at shoulder, or up to 5 ribs at and above periphery, and 3–4 on base, are enlarged, separated by 1–2 small riblets (Fig. 64B, C, G, N, O); enlarged ribs at and above periphery usually granulose or minutely lamellose (Fig. 64D, E); strongly sculptured shells with 4 carinate ribs bearing small elongate nodules (Fig. 64I–M); granules or nodules not clearly axially aligned; spiral microstriae only in grooves. Protoconch 0.26 mm diameter. Colour highly variable: smooth shells grey-white; sometimes with irregular dark marks or occasional dark growth lines; grey-brown to black ground with white nodules (Fig. 64F–H); white with black oblique lines or zigzag axial flames (Fig. 64K, M–O); first 1–3 teleoconch whorls brown to black, and in sculptured shells with white granules or white spiral ribs; aperture dark brown with pale band at base; columella purple-brown.

Animal (Fig. 65): Head (Fig. 65B) black, unpigmented stripe across snout, tentacle unpigmented with black base, unpigmented around eye and across base; sides of foot black. Opercular ratio 0.41–0.50. Penis (Fig. 65A–H): filament elongate or vermiform, smooth, pointed at tip, about 0.7–0.9 total length of penis, sperm groove extends to tip; mamilliform gland borne on short projection of base, together with extremely small glandular disc (represented only by patch of tissue adjacent to mamilliform gland, not projecting as a lobe); penis unpigmented or slightly pigmented at base. Euspermatozoa 70–107 µm; paraspermatozoa (Fig. 65J–L) oval to almost spherical, 12–20 µm diameter, filled with large round granules, rod-pieces single (rarely

2), narrowly fusiform, often with one or both ends recurved, sometimes projecting from cell, to 30 µm long. Pallial oviduct (Fig. 65I): bursa opening at one third length of straight section (from anterior) and extending back to albumen gland. Development predicted to be planktotrophic.

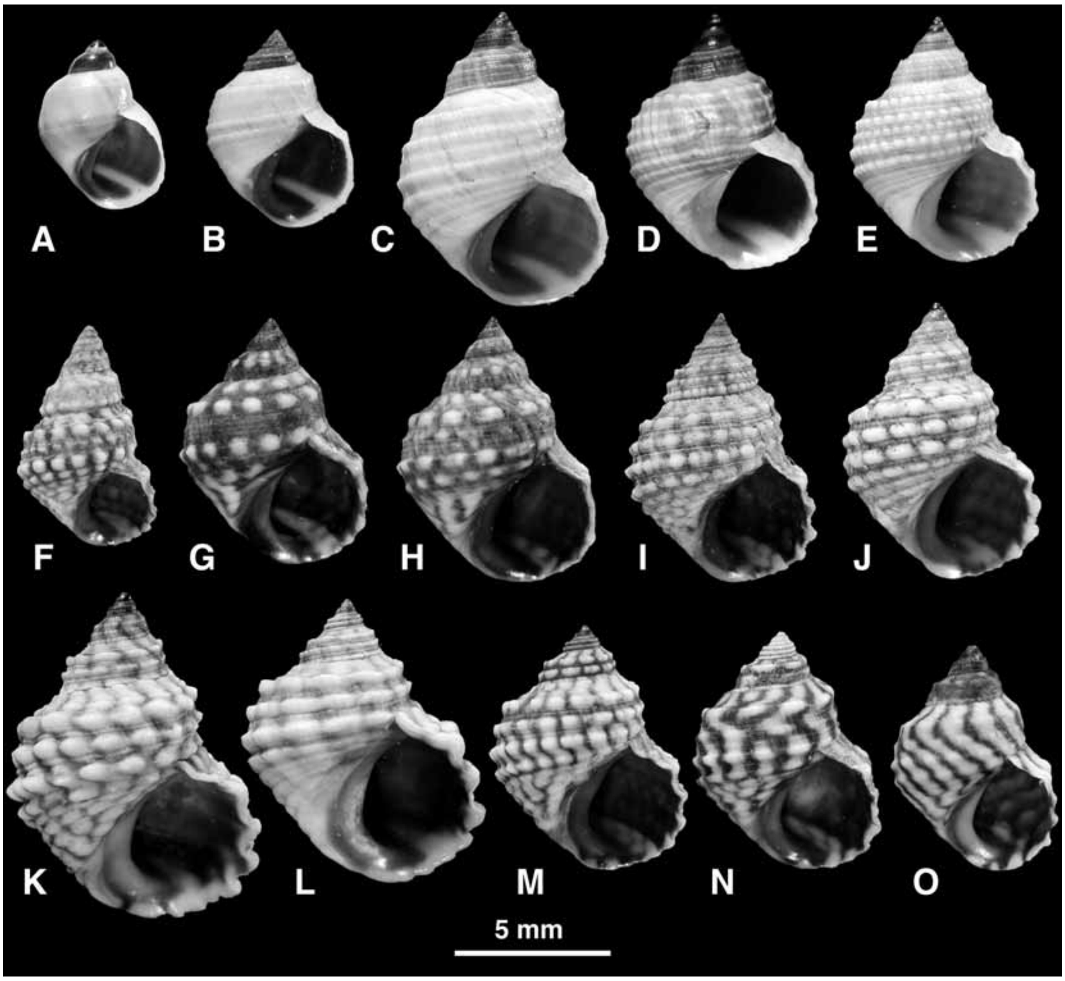

FIGURE 64. *Echinolittorina cinerea*. **A,** Hiva Oa, Marquesas Is (BMNH 20050530). **B,** Taihoae Bay, Nuku Hiva, Marquesas Is (BMNH 20050531). **C, E,** Atuona Bay, Hiva Oa, Marquesas Is (USNM 637351). **D,** *Littorina cinerea* Pease, 1869, lectotype, Marquesas Is (ANSP 18811). **F,** Arahoho Blowhole, Tahiti, French Polynesia (BMNH 20050532). **G,** Puputeai, Arue, Tahiti, French Polynesia (USNM 668461). **H,** Pointe de Tapahi, Tahiti, French Polynesia (BMNH 20050533). **I, M, N,** O Le Pupu, 'Upolu, Western Samoa (BMNH 20050534). **J,** Ogné, Île Ouvéa, Loyalty Is, New Caledonia (BMNH 20050535). **K,** no locality (BMNH 20050536). **L,** no locality (BMNH 1851.11.3.469). **O,** Tutuila, American Samoa (USNM 488720).

Radula (Fig. 66A, B): Relative radula length 1.56–2.60. Rachidian: length/width 1.11–1.16; tip of major cusp pointed. Lateral and inner marginal: major cusp on each of similar size, tips rounded to pointed. Outer marginal: 6–8 cusps.

Range (Fig. 23): South and West Pacific. Range limits: Yokoate-jima, Tokara Is, Japan (Kurozumi 1994); Buma, Nago-shi, Okinawa, Japan (BMNH); Kannon-saki, Ishigaki, Japan (BMNH); Chialoshui, 10 km E Hengchun, Taiwan (BMNH); Sagisi I., Surigao, Mindanao, Philippines (USNM 707181); Chichijima, Ogasawara Is, Japan (BMNH 20050539); Uracus I., Mariana Is (USNM 819203); Bandera, Pagan, Mariana Is (BMNH; USNM 819204); Anatahan, Mariana Is (Vermeij *et al.* 1984); Guam, Mariana Is (MNHN); Manam I., Papua New Guinea (IRSNB); Vanikoro I. (AMS C52049); Île des Pins, New Caledonia (IRSNB); Lifou, Loyalty Is (USNM 422638; IRSNB; MNHN); Raoul (Sunday) I., Kermadec Is (AMS C380518; USNM 214758; MNHN); Taga Blowholes, Savai'i, W Samoa (BMNH 20050537); Pointe de Tapahi, Tahiti (BMNH

20050533); Makatea, Tuamotu Is (USNM 637346); Baie de Hané, Ua Huka, Marquesas Is (BMNH 20050538); Hiva Oa, Marquesas Is (BMNH 20050530; USNM 637351).

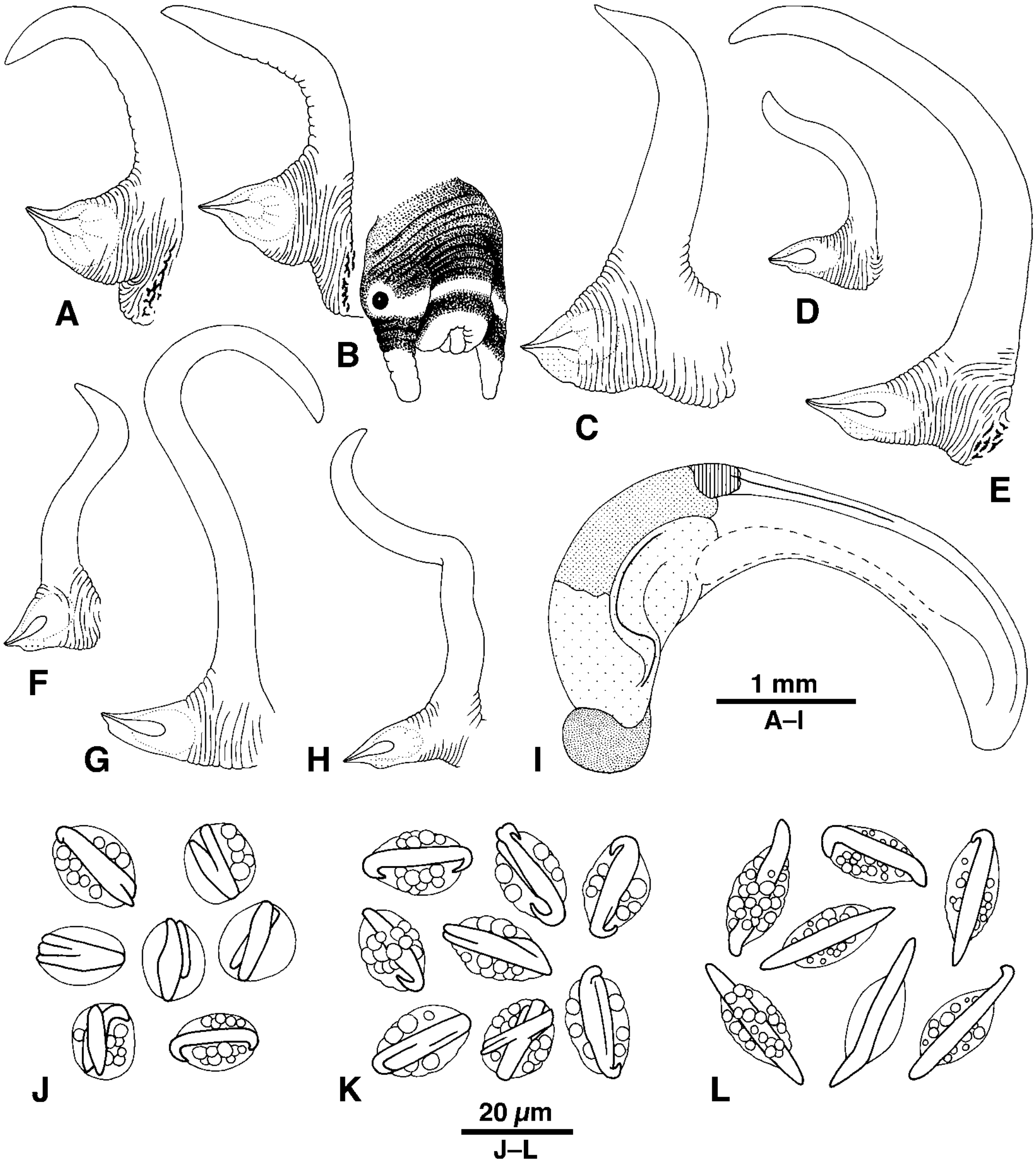

FIGURE 65. *Echinolittorina cinerea*. **A–H,** penes. **B,** head. **I,** pallial oviduct. **J–L,** paraspermatozoa. **A, B, J,** Taga Blowholes, Savai'i, Western Samoa (BMNH 20050537; shell H **A** = 5.1 mm, **B** = 5.4 mm). **C, I, K, L,** Pointe de Tapahi, Tahiti, French Polynesia (BMNH 20050533; shell H **C** = 8.1 mm; **I** = 9.9 mm). **D,** Baie de Hané, Ua Huka, Marquesas Is (BMNH 20050538; shell H = 3.6 mm). **E, H,** Manam I., Papua New Guinea (IRSNB; shell H **E** = 7.1 mm, **H** = 4.9 mm). **F,** Miyanohama, Chichijima, Ogasawara Is, Japan (BMNH 20050539; shell H = 4.9 mm). **G,** Ogné, Île Ouvéa, Loyalty Is., New Caledonia (BMNH 20050535; shell H = 7.0 mm). Shading conventions as in Figure 3.

This species is common in the Ogasawara Islands (Fukuda 1993). Occurrence in the northern Mariana Islands is well documented, but recent collecting has not revealed it in Guam (Vermeij *et al.* 1984, as *N. quadricincta feejeensis*; B.D. Smith 2003), so the MNHN record may be unreliable. Records further west are extremely rare; only a single specimen is known from each of Taiwan, Ishigaki, Okinawa and the Philippines (listed above), and two from the Tokara Islands (Kurozumi 1994). There are numerous collections available from the Loyalty Islands, Samoa, Tahiti and the Marquesas Islands and the species is evidently common there. Records from New Guinea, New Caledonia and Fiji are sparse. Occurrence on the Kermadec Islands is apparently sporadic; most of the collections available in museums (AMS, MNHN, USNM, Wellington Museum) were made by Iredale in 1908, who reported a few localized colonies (Iredale 1910). The absence from the central Pacific (Marshall, Gilbert and Line Is) is real (cf. distribution map of *Littoraria coccinea* in Rosewater 1970, indicating collecting effort in the same habitat in this area). However, the littorinid fauna of the Solomon Islands, Vanuata, Tuvalu and outer islands of Fiji (where this species can be expected to occur) is poorly known.

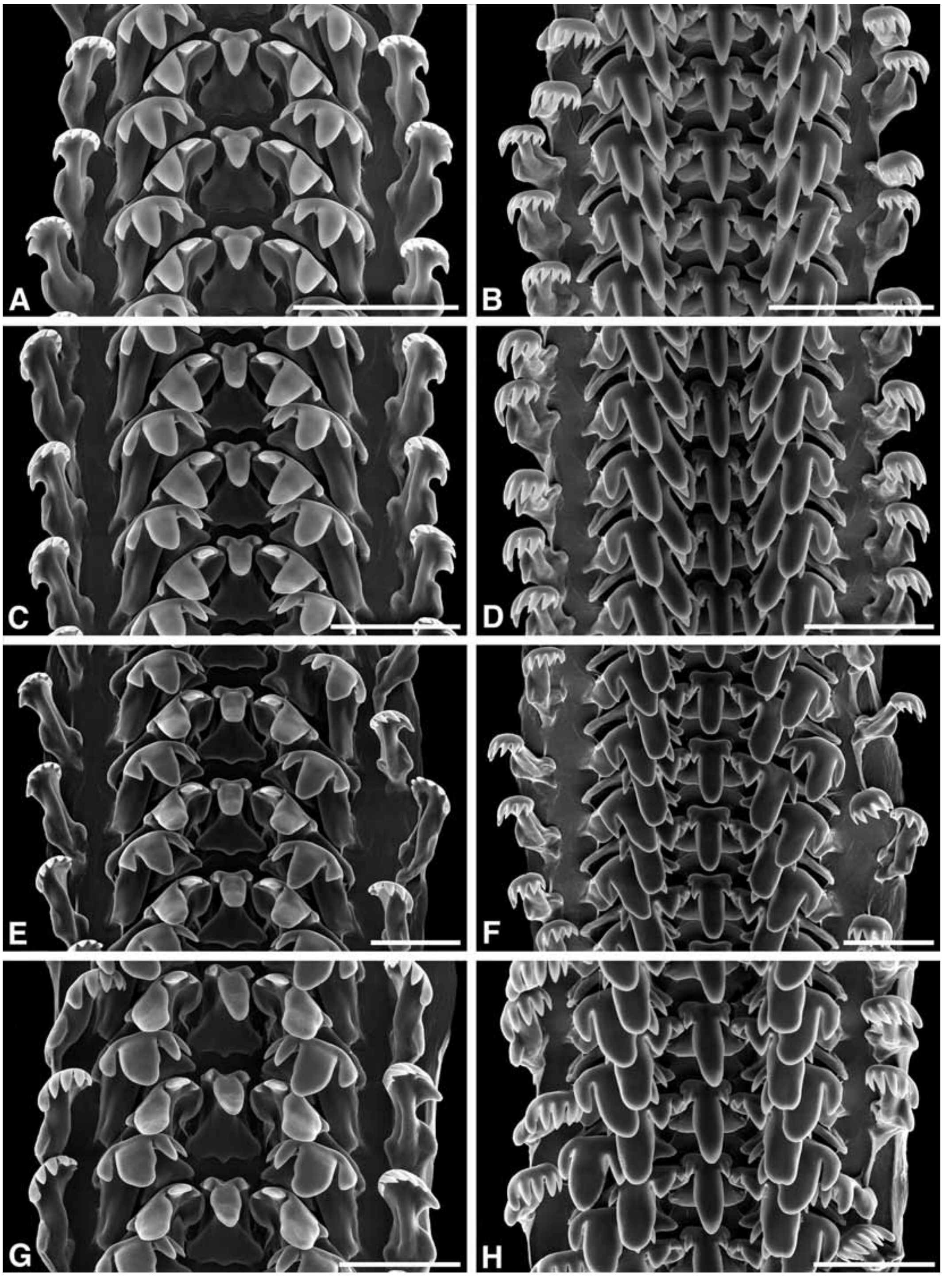

FIGURE 66. Radulae of *Echinolittorina* species (two views of each radula, flat and at 45°). **A, B,** *E. cinerea*; Baie de Hané, Ua Huka, Marquesas Is (BMNH 20050538; shell H = 5.0 mm). **C, D,** *E. hawaiiensis*; Keaau, Hawaii, Hawaiian Is (BMNH 20050540; shell H = 8.2 mm). **E, F,** *E. reticulata*; Anakena, Île Ste Marie, Madagascar (BMNH 20030678; shell H = 10.6 mm). **G, H,** *E. millegrana*; Hamriya, Sharjah, United Arab Emirates (BMNH 20050550; shell H = 8.7 mm). Scale bars = 50 µm.

Habitat: Uppermost eulittoral and littoral fringe, below the level of *E. marquesensis* where the species are sympatric in the Marquesas Islands, sometimes at edges of small pools with algae. Most records are from basalt, but the species is also found on coral limestone and sandstone; usually on wave-exposed coasts not sheltered by reefs, always in oceanic situations with clear water. Occurrence in the upper eulittoral has been recorded in the Tokara Islands (Kurozumi 1994). In the Ogasawara Islands it is common at and just above the mean high water mark of spring tides, at the lower limit of the range of the more abundant *E. cecillei* (Ohgaki 1983a; Asakura *et al*. 1990, 1991).

Remarks: This is a highly variable *Echinolittorina* species, with shells ranging from almost smooth to strongly carinate and granulose, and from white to patterned. There is a pronounced geographical pattern in this shell variation and three regional forms can be distinguished. Specimens from the Marquesas Islands are grey-white and without conspicuous dark pattern; they are frequently smooth, but the two ribs at periphery and shoulder (rarely more) may be enlarged and granules are weak or absent (Fig. 64A–E). The form in Tahiti is distinctive, with dark coloration (brown to black ground, with white granules) and often only the peripheral and shoulder ribs are enlarged (Fig. 64F–H). Elsewhere (Tuamotu Is, Samoa, Kermadec Is, Western Pacific) the shells are strongly sculptured with 4–5 strong ribs at and above the periphery, which bear granules or small nodules, and the coloration is often a striking pattern of black lines on a white ground (Fig. 64I–O). Extremes of the range of each of these forms overlap. COI sequences are available for single individuals from the Ogasawara Islands, Samoa, Tahiti and the Marquesas Islands, and show negligible variation (Williams & Reid 2004; S.T. Williams & D.G. Reid unpublished).

It is not clear if there is also an environmental component to the shell variation; all shell types can be found on basalt, but shells of the few samples from limestone (including Tuamotu Is, Niue, Lifu) are always strongly sculptured.

Together with *E. pascua*, *E. hawaiiensis* and *E. marquesensis*, this is one of the IWP *Echinolittorina* species with the most oceanic of distribution patterns and habitat requirements. It is restricted to regions with low primary productivity (Rutgers University Primary Productivity Study), where it occupies strongly exposed shores with clear water. Its distribution is also virtually limited to the Pacific and Philippine Plates, but this is likely to be a consequence of its habitat, rather than its historical biogeography. The rare records from the Ryukyu Islands, Taiwan and Philippines probably represent chance migrations of larvae across the 1300–2100 km from the Mariana and Ogasawara Islands under the influence of the North Equatorial Current.

Molecular data show that this species forms a monophyletic group together with *E. hawaiiensis* and the pair *E. millegrana* and *E. reticulata*, but the relationships are not further resolved (Williams & Reid 2004). Both smooth and sculptured forms of *E. cinerea* could be confused with *E. hawaiiensis* (Fig. 67); the latter bears more numerous incised lines on the last whorl of smooth shells (26–47, cf. 14-21 in *E. cinerea*), while in carinate forms the ribs bear rounded granules rather than elongate nodules; the colour pattern is of large, irregular patches in *E. hawaiiensis*; the two species are entirely allopatric. One similar species with which *E. cinerea* is occasionally sympatric is *E. reticulata*, which reaches Taiwan, the Ryukyu, Ogasawara and Mariana Islands at the eastern extremity of its range. That species is recognized by its white shell with axially aligned granules, between which there may be brown axial lines (Fig. 69); in similar shells of *E. cinerea* (Fig. 64E, M) the granules are not conspicuously aligned and the pattern is of oblique and zigzag lines. The form of *E. cinerea* from Tahiti (Fig. 64G, H) bears a close resemblance to some shells in the *E. leucosticta* group (e.g. *E. leucosticta*, Fig. 40; *E. biangulata*, Fig. 44; *E. philippinensis*, Fig. 46; *E. tricincta*, Fig. 48), and the range of *E. cinerea* overlaps with that of *E. tricincta* at the margin of the western Pacific Ocean. Shells of *E. tricincta* have a narrower aperture, a rounded inner lip with adjacent eroded area, less strongly carinate ribs, and sharper nodules.

Echinolittorina hawaiiensis (Rosewater & Kadolsky, 1981)

(Figures 23, 66C, D, 67, 68)

Littorina picta Philippi, 1846b: 139 (ad insulas Sandwich [Hawaiian Islands]; neotype (here designated) BMNH 1968324/1 (Fig. 67A; this specimen formerly lectotype of *L. picta*, Rosewater 1970, here rejected) + 2 additional specimens BMNH 1968324/2, 1968324/3 (formerly paralectotypes), seen; not *Litorina obtusata picta* Menke, 1845). Reeve, 1857: sp. 80, pl. 15, figs 80a, b, 81. Whipple, 1965: 155–166, fig. 2E–H (radula), fig. 3B (penis), pl. 25, fig. 2a–d, pl. 26, fig. 2 (egg capsules). Struhsaker, 1966: 137–166, figs 9C, D (egg capsule), 10B, C (veliger). Struhsaker, 1968: 459–480, fig. 8 (larval shell). Struhsaker & Costlow, 1968: 153–160, fig. 1 (veliger, larval shell).

Litorina picta—von Martens & Langkavel, 1871: 40. Weinkauff, 1882: 70, pl. 9, fig. 7 (in part; includes *E. melanacme*, *Littoraria intermedia*).

Nodilittorina picta—Oyama & Takemura, 1963: *Nodilittorina* fig. 2 (as *pictus*; in part, includes *E. vidua*). Habe & Kosuge, 1966a: 20, pl. 6, fig. 12. Cernohorsky, 1978: 43, pl. 11, fig. 4. Kay, 1979: 73–74, figs 22C (radula), 23C, D (egg capsule), 24B, C.

Nodilittorina (Granulilittorina) picta—Rosewater, 1970: 503–504, pl. 382 (map), 386, figs 7–12.

Littorina (Melaraphe) planaxis—Tryon, 1887: 248, pl. 44, fig. 57 (in part, includes *Littoraria intermedia*, *L. keenae*; not Philippi, 1847 = *L. keenae* Rosewater, 1978).

Littorina picta var. *marmorata*—Whipple, 1965: 155–166, pl. 25, fig. 2e–h (not Philippi, 1847 = *E. melanacme*).

Nodilittorina (Granulilittorina) hawaiiensis Rosewater & Kadolsky, 1981: 1234-1235 (new name for *Littorina picta* Philippi, 1846, not *Litorina obtusata picta* Menke, 1845).

Nodilittorina (Nodilittorina) hawaiiensis—Reid, 1989a: 99.

Nodilittorina hawaiiensis—Reid, 2002a: 259–281, fig. 1J, K.

Echinolittorina hawaiiensis—Williams *et al*., 2003: 63, 83. Williams & Reid, 2004: 2227–2251.

Taxonomic history: The problematic identity of *Littorina picta* Philippi, 1846 has been discussed in the Taxonomic History of *E. melanacme*. Briefly, the description suggests *E. melanacme* while the locality indicates *E. hawaiiensis*. The lectotype designated by Rosewater (1970) is a specimen of *E. hawaiiensis*, but was not a syntype, because the shell does not match the original description, and therefore loses its status (ICZN 1999: Art. 74.2). No other potential syntypes can be found in BMNH. Subsequently, it was noticed that *Littorina picta* is a junior homonym of *Litorina obtusata picta* Menke, 1845, so the replacement name *N. hawaiiensis* was introduced by Rosewater & Kadolsky (1981). (This homonymy is correct, despite the combination of the name *picta* with alternative spellings of the generic name; *Litorina* Menke, 1828 is an emendation of *Littorina* Férussac, 1822, see Reid 1996: 39; but, for purposes of homonymy, identical species names are deemed to have been combined with the generic name in its original form, see ICZN 1999: Art. 57.5). A replacement name is an objective synonym of the name it replaces, and has the same type (ICZN 1999: Art. 72.7). Therefore, if *L. picta* were determined to be *E. melanacme*, the replacement name *N. hawaiiensis* would fall into synonymy of the latter. It is clearly desirable to retain currect usage of the familiar name *hawaiiensis*. This can best be achieved by rejecting Rosewater's lectotype of *L. picta*, and redesignating the same specimen as the neotype of that species, as formally done herein.

Until renamed by Rosewater & Kadolsky (1981), this species was familiar as *L. picta* (Reeve 1857; von Martens & Langkavel 1871; Habe & Kosuge 1966a; Rosewater 1970; Cernohorsky 1978; Kay 1979). Whipple (1965; Struhsaker (née Whipple) 1969) applied Philippi's names *Littorina picta* and *Litorina picta* var. *marmorata* to the sculptured and smooth forms of this species respectively; in fact there is no suggestion that Philippi (1846b, 1847a) recognized the variability of this species, and his var. *marmorata* applies to *E. melanacme*. The inclusion of *Littoraria intermedia* in some authors' concepts of this species (Weinkauff 1882; Tryon 1887) is a consequence of their listing of *Litorina ambigua* Philippi, 1848 in the synonymy.

Diagnosis: Shell high turbinate; sculpture variable, from smooth with numerous (26–47) fine incised lines to 2–4 granulose ribs; colour variable, grey-white with coarse irregular axial flames, or black with white marks from suture to shoulder and on base, or finely marbled. Penial glandular disc and penial gland small; filament long, strap-shaped, rounded tip. Hawaiian Is. COI: GenBank AJ488613, AJ623007. AJ623008.

Material examined: 36 lots (including 6 penes, 2 sperm samples, 7 pallial oviducts, 3 radulae).

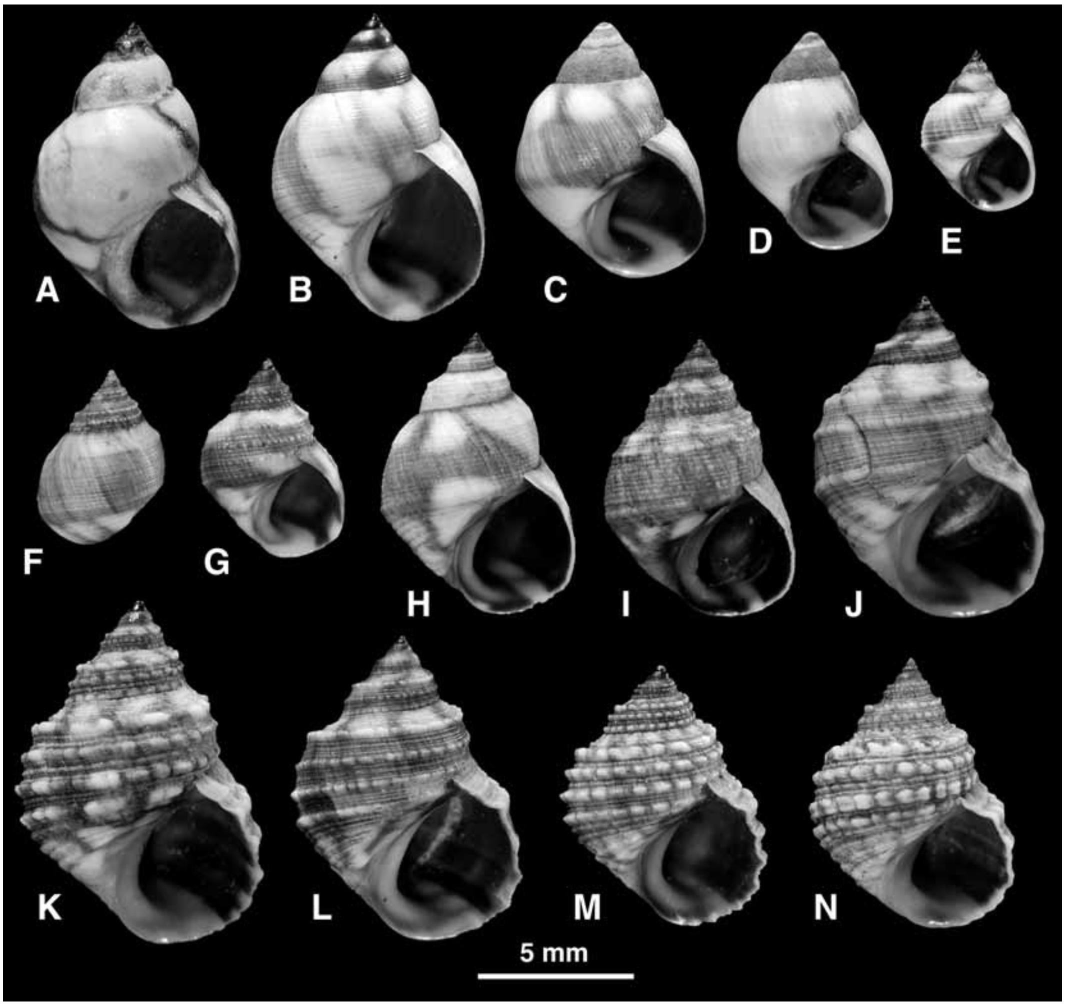

FIGURE 67. *Echinolittorina hawaiiensis*. **A,** *Littorina picta* Philippi, 1846, neotype, Sandwich Is [Hawaiian Is] (BMNH 1968324/1). **B,** Launiupoko, Maui, Hawaiian Is (USNM 339414). **C–F,** Keaau, Hawaii, Hawaiian Is (BMNH 20050540). **G, M, K,** Mokuoloe I., Oahu, Hawaiian Is (BMNH 346411). **H, I, N,** Kuilima, Oahu, Hawaiian Is (BMNH 20050541). **J, L,** Hilo, Hawaiian Is (USNM 339413).

Shell (Fig. 67): Mature shell height 2.5 mm (Struhsaker 1966)–13.0 mm (Whipple 1965). Shape turbinate to high turbinate or slightly pupoidal (H/B = 1.26–1.54, SH = 1.60–1.78); spire whorls rounded or slightly shouldered, suture distinct; spire profile slightly convex, concave at apex; periphery of last whorl rounded, sometimes slightly shouldered and angled at periphery. Columella concave, slightly hollowed at base; eroded parietal area small or absent. Sculpture of last whorl highly variable: smooth shells with 26–47 fine, incised lines or threads (Fig. 67B–E), becoming weak or worn on last whorl (Fig. 67A); peripheral rib and 1–2 ribs at shoulder may be enlarged (Fig. 67F–J); strongly sculptured shells with 4 enlarged granulose ribs at and above periphery separated by 1–3 threads, 4-6 enlarged ribs on base (Fig. 67K–N); spiral microstriae only in grooves. Protoconch 0.28–0.29 mm diameter, 2.8–2.9 whorls. Colour highly variable: grey-white with coarse pattern of 1–10 black irregular or oblique axial flames, sometimes fusing to make peripheral band (Fig. 67A–H); darkest shells with last whorl largely black, with white marks between suture and shoulder, and on base (Fig. 67I); sometimes finely marbled with brown and white, paler at suture and on base, granules white (Fig. 67M, N); apex black with white marks; aperture dark brown with pale band at base; columella purple-brown.

Animal (Fig. 68): Head black, sometimes a narrow unpigmented stripe across snout, tentacle unpigmented with black base, unpigmented around eye and across base; sides of foot black. Opercular ratio 0.35–0.44. Penis (Fig. 68A–E): filament long, strap-shaped, smooth, usually rounded at tip, about 0.8–0.9 total length of penis, sperm groove extends to tip; small mamilliform gland and small glandular disc borne together on short projection of base; penis unpigmented or slightly pigmented at base. Euspermatozoa not known; paraspermatozoa (Fig. 68H, I) oval, to 20 µm, filled with small granules, rod-pieces single, narrowly fusiform, often with one or both tapering ends slightly recurved, usually projecting from cell, to 30 µm long. Pallial oviduct (Fig. 68F): bursa opening at one third length of straight section (from anterior) and extending back to albumen gland; seminal receptacle small, some sperm stored in albumen gland. Spawn (Fig. 68G) an asymmetrically biconvex pelagic capsule 180 µm, cupola-shaped upper side sculptured by 6 concentric rings, containing single ovum 75–80 µm diameter (Struhsaker 1966). Development planktotrophic (Struhsaker 1966; Struhsaker & Costlow 1968).

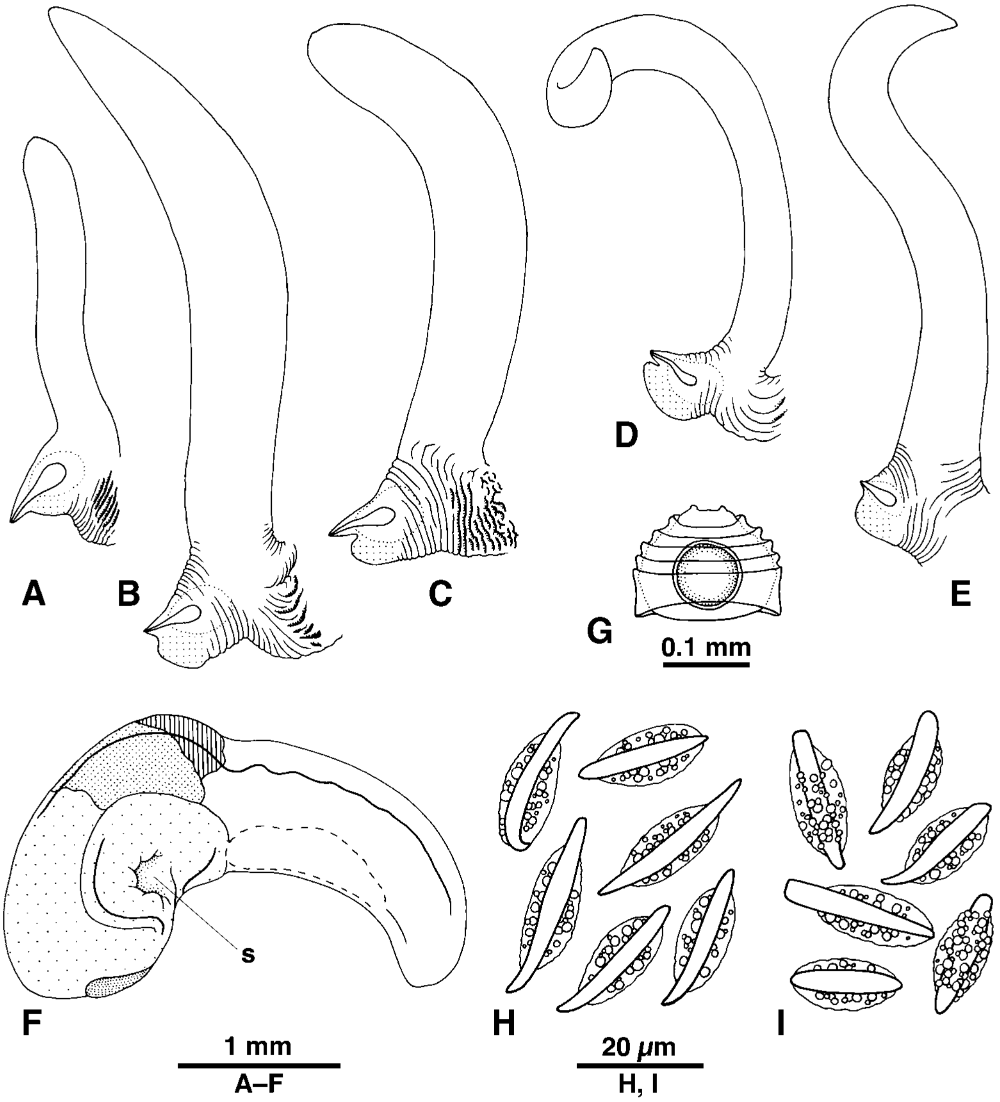

FIGURE 68. *Echinolittorina hawaiiensis*. **A–E,** penes. **F,** pallial oviduct. **G,** pelagic egg capsule (after Struhsaker 1966). **H, I,** paraspermatozoa. **A, H, I,** Mokuoloe (Coconut) I., Oahu, Hawaiian Is (BMNH 20050542; shell H **A** = 6.0 mm). **B, C,** Kuilima, Oahu, Hawaiian Is (BMNH 20050541; shell H **B** = 8.3 mm, **C** = 7.2 mm). **D, F,** Keaau, Hawaii, Hawaiian Is (BMNH 20050540; shell H **D** = 5.7 mm, **F** = 8.2 mm). **E,** Diamond Head, Oahu, Hawaiian Is (BMNH 20050543; shell H = 7.2 mm). Abbreviation: s, sperm storage area in albumen gland. Shading conventions as in Figure 3.

Radula (Fig. 66C, D): Relative radula length 1.94–4.19. Rachidian: length/width 1.24–1.39; tip of major cusp rounded to slightly pointed. Lateral and inner marginal: major cusp on each of similar size, tips rounded. Outer marginal: 6–8 cusps.

Range (Fig. 23): Hawaiian Is. Range limits: Eastern I., Midway Is (USNM 639035); Laysan I.; La Perouse Rock, French Frigate Shoals; Nihoa I. (all Rosewater 1970); Hanalei Bay, Kauai (USNM 346410); Mokuoloe I., Kaneohe Bay, Oahu (BMNH 20050542; USNM 346411); Kuilima, Oahu (BMNH 20050541); Lahaina, Maui (USNM 767305); Hilo, Hawaii (BMNH; USNM 339413); Keei, Kona Coast, Hawaii (USNM 767605).

Habitat and ecology: Upper eulittoral and littoral fringe, on wave-exposed and sheltered shores; found on basalt, coral limestone and concrete; an oceanic species. Struhsaker (1968) noted that it is rare in sheltered areas and recorded it on volcanic tuff; breeding occurs throughout the year.

Remarks: Most populations contain a range of shell sculpture types, but either smooth or sculptured types usually predominate. Available collections and personal observation suggest that shells from limestone platforms and cliffs, and from sea walls composed of limestone and concrete, are strongly sculptured, whereas those from basalt substrates are smooth or only weakly ribbed. Similar correlation between strong sculpture and limestone substrates has been observed in other species (e.g. *E. natalensis*, *E. pascua*, *E. malaccana*, *E. melanacme*), but is not clear in *E. cinerea*.

Struhsaker (1968) carried out a detailed study of the causes of shell variation in this species. Although noting that strong shell sculpture was correlated with calcium availability from the substrate, she reported the full range of shell forms on a limestone shore and therefore emphasized the importance of topography and wave action. Extreme sculptured forms were found at high tidal levels on dry benches subject to spray and in areas of low wave action, whereas smooth forms predominated on lower benches subject to heavy horizontal wave swash. In the latter environment densities were greater, shells smaller and both feeding time and food availability judged to be more favourable. Laboratory rearing suggested that the degree of sculpture of the larval shell before settlement was correlated with that of the adult parents, and that the sculptured larvae of sculptured parents grew more rapidly and were more resistant to high salinity and temperature (see also Struhsaker & Costlow 1969). Transfer experiments showed differential survival of adults on the shore and laboratory experiments indicated that sculptured adults were more resistant to desiccation. Consequently, it was suggested that the natural distribution of smooth and sculptured shells is a result of natural selection by wave action and desiccation acting on genotypes of both larvae and adults.

There are some similarities with reports on the variation of *E. australis* (Johnson & Black 1999; Yeap *et al*. 2001). In both cases, nodulose or granulose forms were found in open, sunny situations, whereas smooth forms were found in wetter areas with stronger wave action. Scuptured forms of *E. australis* dissipated heat more rapidly, and those of *E. hawaiiensis* were more resistant to desiccation. In mixed populations bimodal distributions of sculptural types were reported in both studies. There are also some contrasts. Sculptured adults of *E. hawaiiensis* were larger and their sculptured larvae grew more rapidly than those of smooth forms, whereas in *E. australis* nodulose sculpture was associated with slow growth and small adult size. In both species, however, smooth shells occurred in damper areas judged more favourable for feeding and growth. Most significantly, transfer experiments with *E. australis* demonstrated an ecophenotypic response of shell sculpture to habitat, whereas Struhsaker (1968) commented only on survival, not sculptural change, of transferred snails, and noted that the larval progeny of sculptured and smooth forms resembled their parents. Nevertheless, some rare shells do change their sculpture, from granulose to smooth (Fig. 67F), i.e. in the same direction as the majority of transformations observed in *E. australis*. Furthermore, the claim of heritability of shell sculpture is open to question (see below). Among other littorinid species, correlation between shell morphology and microhabitat within shores is known to have a strong genetic component in nonplanktotrophic species with restricted gene flow, but has generally been interpreted as the result of plasticity in planktotrophic species (review by Reid 1996; Yeap *et al*. 2001), and Struhsaker's (1968) study has been widely quoted as an exception. The question of the relative importance of genotypic and ecophenotypic control of shell sculpture in *E. hawaiiensis* should be reexamined.

The breeding, spawning and early development of this species were described by Struhsaker (1966). She noted slight sexual dimorphism (females about 1 mm larger), breeding throughout the year, spawning at the time of the highest high tide of the day and estimated release of 1900 eggs by each female once a month. So far, this is the only *Echinolittorina* species for which rearing has been accomplished in the laboratory (Struhsaker & Costlow 1968). At 25°C hatching occurred at day 3 and settlement after an average of 24 days (range 3–4 weeks depending upon temperature); at settlement the shell consisted of 3-4 whorls with a diameter of 250 µm. Struhsaker & Costlow (1968) reported finding some much larger 'post-veligers' with shells of 4-5 whorls and up to 1000 µm in size on the shore, and suggested that this indicated that the time of metamorphosis can be extended under natural conditions if suitable substrate is not available; larvae with 5 whorls were also 'rarely' found in plankton tows (Struhsaker 1968). However, in all *Echinolittorina* species studied here the range of protoconch size is narrow and reaches only one third of this figure, so either these very large larvae may have been misidentified, or there has been a confusion of terminology. Struhsaker (1968) and Struhsaker & Costlow (1968, 1969) described a correlation between the shell sculpture of adults and their larvae. The larvae of sculptured adults bore shells with about 10 undulating spiral ribs, whereas in the larval shells of smooth parents the initial small nodes of calcification remained discrete (i.e. did not connect as ribs) and grew more slowly. Shell growth of the teleoconch after metamorphosis was not described. Mortality at all stages of larval development was high, despite the use of antibiotics, and various developmental abnormalities occurred (Struhsaker & Costlow 1969). In the present study the protoconchs of all *Echinolittorina* species correspond to the 'sculptured' type (Fig. 37H; see also Bandel & Kadolsky 1982: fig. 12; Kowalke 1998: textfig. 8, pl. 9, fig. 4; Reid 2002b: fig. 22G), and it must be considered that the 'smooth' type (with slower growth and less complete calcification) may have been an abnormality induced by the experimental rearing conditions. If this is the case, there is no evidence for the genotypic control of shell sculpture in this species.

This species shows an unusual modification of the pallial oviduct, in which sperm are stored not only in the seminal receptacle, but also in an area that appears to be part of the first whorl of the albumen gland (Fig. 68F). Various sites of sperm storage have been recorded in other littorinids (Reid 1989a).

Molecular data clearly place *E. hawaiiensis* in a clade together with *E. cinerea* and the pair *E. millegrana* and *E. reticulata*, but do not resolve these relationships further (Williams & Reid 2004). This species is not sympatric with any others in the genus. The striking, irregular, black and white coloration is unique among its IWP congeners, and makes identification of shells with this typical pattern straightforward. Confusion of both smooth and sculptured shell forms could occur with the equally variable *E. cinerea* (Fig. 64; see Remarks on that species). Shells with two or three prominent ribs bear a superficial similarity to some examples of *E. biangulata* (Fig. 44), *E. philippinensis* (Fig. 46) and *E. tricincta* (Fig. 48); in *E. hawaiiensis* the striae between the major ribs are more numerous, and the inner apertural lip is sharp.

***Echinolittorina reticulata* (Anton, 1838)**

(Figures 37H, 66E, F, 69–71)

Litorina reticulata Anton, 1838: 53 (no locality; holotype SNSD MTD 1590 (Fig. 69A), seen). Philippi, 1847a: vol. 2: 199, *Litorina* pl. 4, fig. 12. von Martens, 1880: 283. Weinkauff, 1882: 66, pl. 8, fig. 13. Weinkauff, 1883: 218. Schniebs, 1995: 170, pl. 2a, b.

Littorina (Melaraphe) reticulata—H. Adams & A. Adams, 1854: 314.

Littorina reticulata—Nevill, 1885: 153. von Martens, 1903: 117, pl. 4, fig. 14.

Nodilittorina reticulata—Reid, 2001a: 441–442, figs 1E, 3E (penis). Reid, 2002a: 259–281.

Echinolittorina reticulata—Williams *et al*., 2003: 83. Williams & Reid, 2004: 2227–2251. Willan, 2005: 58, figs 1, 2.

Littorina granocostata Reeve, 1857: *Littorina* sp. 79, pl. 15, fig. 79 (Brisbane Water, Australia [in error]; lectotype (Rosewater 1970) BMNH 1968318/1, 2 paralectotypes BMNH 1968318/2, seen). Liénard, 1877: 45. Taylor, 1971: 197, pl. 15, fig. 13.

Litorina granocostata—Weinkauff, 1882: 96, pl. 14, fig. 1.

Litorina (Tectaria) granocostata—Weinkauff, 1883: 226.

Littorina millegrana var. *cinerea*—Nevill, 1885: 153–154 (in part, includes *E. cinerea*; not Pease, 1869).

Littorina granicostata E.A. Smith, 1887: 519, fig. 2 (Christmas Island, Indian Ocean; lectotype (here designated) BMNH

1968358/1, 11.5 mm, no locality, E.A. Smith 1887: fig. 2, upper shell; 2 paralectotypes BMNH 1968358/2; 1 paralectotype BMNH 1887.4.30.1, Christmas I.; all seen).

Tectarius miliaris—Tryon, 1887: 259, pl. 48, figs 71, 82 (in part, includes *E. miliaris*, *E. feejeensis*; not *L. miliaris* Quoy & Gaimard, 1833). Dautzenberg, 1929: 496 (not Quoy & Gaimard, 1833).

Littorina insularis E.A. Smith, 1889: 536 (new name for *L. granicostata* E.A. Smith, 1887, not *L. granocostata* Reeve, 1857).

Tectarius granularis—Adam & Leloup, 1938: 80 (in part, includes *E. melanacme*, *E. vidua*; not *L. granularis* Gray, 1839 = *E. miliaris*). Maes, 1967: 109 (not Gray, 1839).

Tectarius ventricosus—Kuroda & Habe, 1952: 89 (not Philippi, 1847 = *E. vidua*).

Nodilittorina ventricosus—Habe & Kosuge, 1966a: 19, pl. 6, fig. 7 (not Philippi, 1847).

Granulilittorina ventricosus—Higo, 1973: 47 (not Philippi, 1847).

Nodilittorina ventricosa—Fukuda, 1993: 39, pl. 12, fig. 178 (not Philippi, 1847). Higo *et al*., 1999: 91 (not Philippi, 1847).

Tectarius granosus—Barnard, 1963: 191, fig. 37d (not *Litorina granosa* Philippi, 1848 = *E. granosa*). Kensley, 1973: 66, fig. 201 (not Philippi, 1848).

Nodilittorina (Granulilittorina) millegrana—Rosewater, 1970: 491–494, pl. 378, figs 13, 14, pl. 380, figs 8, 9, 11, 12, pl. 382 (map) (in part, includes *E. radiata*, *E. melanacme*, *E. feejeensis*, *E. vidua*, *E. novaezelandiae*, *E. millegrana*; not Philippi, 1848). Kilburn, 1972: 405 (not Philippi, 1848). Fujioka & Kurozumi, 1980: 52, 54, fig. 1D (not Philippi, 1848).

Nodilittorina millegrana—Vermeij *et al*., 1984: 40 (not Philippi, 1848). Wells *et al*., 1990: 26, pl. 8, fig. 35 (not Philippi, 1848). Ohgaki, 1998: 157–161 (not Philippi, 1848). Ma, 2004: 33, pl. 14, fig. E (left) (in part, includes *E. melanacme*; not Philippi, 1848).

Nodilittorina (Nodilittorina) millegrana—Reid, 1989a: 99 (in part, includes *E. millegrana*; not Philippi, 1848).

Nodilittorina australis—Willan, 1993: 65, 111 (not Gray, 1826).

Nodilittorina (Granulilittorina) sp. A—Kurozumi, 1994: 366, pl. 2, fig. 3.

Nodilittorina (Granulilittorina) sp. B—Kurozumi & Asakura, 1994: 135–136.

Nodilittorina sp.—Hasegawa, 2000: 141, pl. 70, fig. 24.

Taxonomic history: *Echinolittorina reticulata* and *E. millegrana* are closely similar in shell characters. After Rosewater (1970) used the latter specific name, it became the more familiar. Nevertheless, for most of their history the former was the better known, and there has been remarkably little confusion between them.

Rosewater (1970) considered *Litorina reticulata* Anton, 1838 to be unrecognizable because of its brief description, lack of locality, and unknown type material. Nevertheless, Anton's (1838) description does mention the diagnostic axial and spiral alignment of the granules, dark apex and 'reddish white' colour. Furthermore, the holotype is preserved in Anton's collection in SNSD (Schniebs 1995), so the identity of this species is not in doubt. Anton did not record a locality; a later label by Thiele reads 'Mauritius' (K. Schniebs pers. comm.). The type locality 'Brisbane Water' given by Reeve (1857) for his *L. granocostata* is in error, because this species has not been recorded from the east coast of Australia. Despite the one-letter difference, *L. granicostata* described by E.A. Smith (1887) is a primary homonym of Reeve's (1857) *L. granocostata* (ICZN 1999: Art. 58.12). Rosewater (1970) cited the 'holotype' of *L. granicostata* E.A. Smith, 1887, but this does not constitute a valid lectotype designation (ICZN 1999: Art. 74.5). A lectotype is necessary, however, because of the existence of syntypes in two separate samples, only one with locality, and because of possible confusion with the similar, but allopatric, species *E. millegrana*.

After its early description, *L. reticulata* became a well known species. A specimen supplied by Anton was figured by Philippi (1847a) and both he (Philippi 1848) and others (Weinkauff 1882, 1883; Nevill 1885) distinguished it from *L. millegrana*. It was first recognized as originating from the Indian Ocean by von Martens (1880, 1903). Reeve (1857) redescribed the species as *L. granocostata*, but still recognized *L. millegrana* as a separate species (Reeve 1858). Reeve's name was used again by Taylor (1971). The species was redescribed once again by E.A. Smith (1887, 1889). Tryon (1887) promoted a broader species concept and identified this species as *T. miliaris*, grouping it with other strongly granulose species (*E. miliaris* and *E. feejeensis*). There were also misidentifications as *T. granularis* (Adam & Leloup 1838; Maes 1937) a synonym of *E. miliaris*, and *T. granosus* (Barnard 1963). Meanwhile, in the Japanese literature the name *ventricosus* (a synonym of *E. vidua*) was used for many years (e.g. Kuroda & Habe 1952; Habe & Kosuge 1966a; Higo 1973; Fukuda 1993;

Higo *et al*. 1999). In his IWP monograph, Rosewater (1970) employed the name *N. millegrana* for all granulose species, and this identification was widely followed (e.g. Kilburn 1972; Fujioka & Kurozumi 1980; Reid 1989a; Wells *et al*. 1990; Ma 2004). The only specimen so far recorded from Australian waters was initially misidentified as *N. australis* (Willan 1993, 2005). In recent times this species was noted as distinct from sympatric congeners in the *E. millegrana* group by Japanese workers, although not identified (Kurozumi 1994; Kurozumi & Asakura 1994; Hasegawa 2000). It was first distinguished from *E. millegrana* on the basis of penial anatomy and shell sculpture (Reid 2001a), and subsequently confirmed as distinct by DNA analysis (Williams & Reid 2004; Reid *et al*. 2006).

Diagnosis: Shell turbinate to high turbinate; sculpture variable, from smooth with fine spiral striae to 11–15 granulose ribs at and above periphery, granules aligned in distinct axial series; colour white, often with axial black lines between aligned series of granules. Penial glandular disc absent; filament thickened and wrinkled at base, tip pointed. Indian and western Pacific Oceans. COI: GenBank AJ623041, AJ623042.

Material examined: 115 lots (including 21 penes, 4 sperm samples, 8 pallial oviducts, 5 radulae).

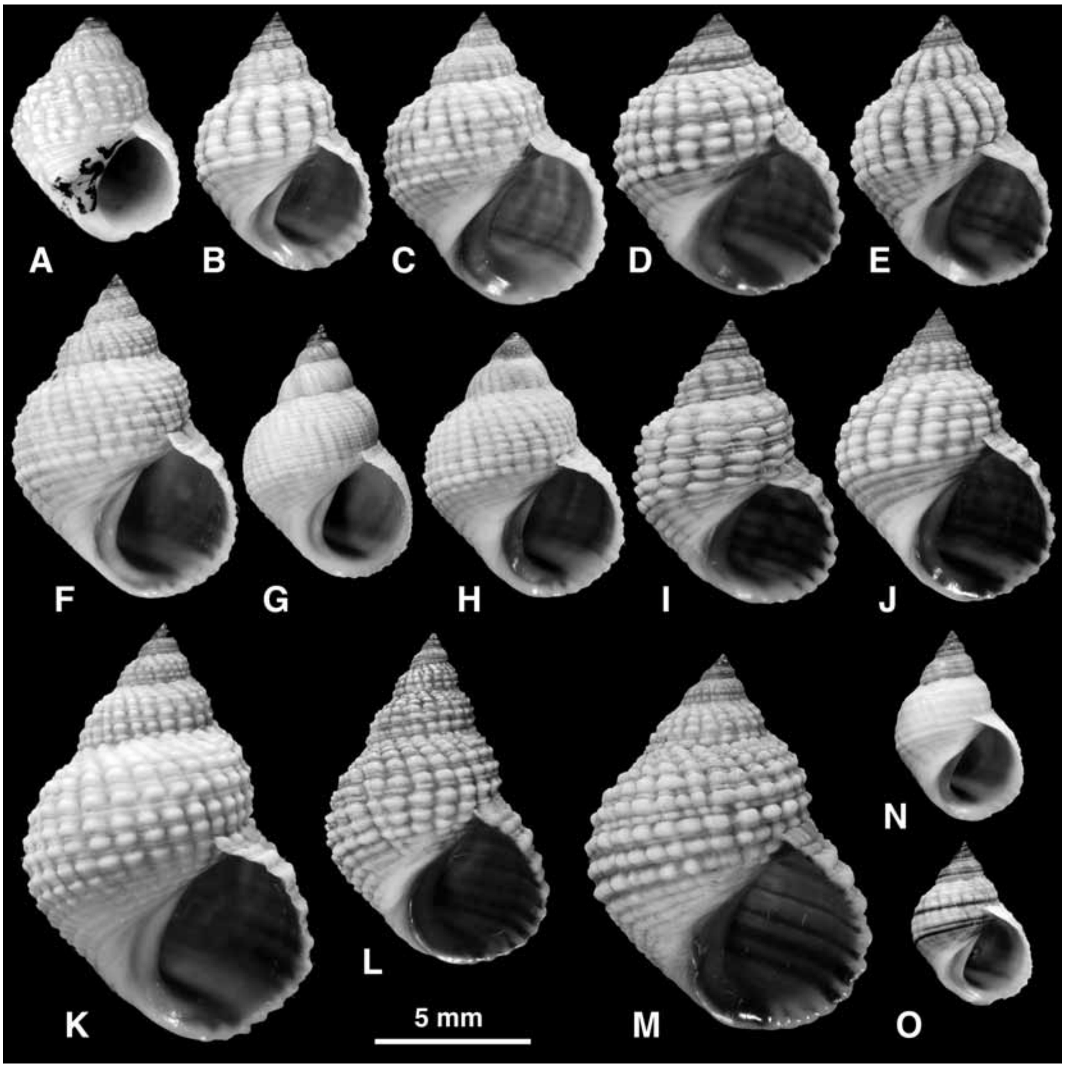

FIGURE 69. *Echinolittorina reticulata*. **A,** *Litorina reticulata* Anton, 1838, holotype, no locality (MTD 1590). **B, N, O,** Senggigi, Lombok, Indonesia (BMNH 20050555). **C, D, J, L, M,** Guintungauan I., Bacuit Archipelago, Palawan, Philippines (BMNH 20050556). **E, I,** Chialoshui, SE Taiwan (BMNH 20050557). **F,** Pointe des Trois Bassins, Réunion (BMNH 20050558). **G,** Pointe au Sel, Réunion (BMNH 20050559). **H,** Anakena, Île Ste Marie, Madagascar (BMNH 20030678). **K,** Bras Panon, Réunion (BMNH 20050560).

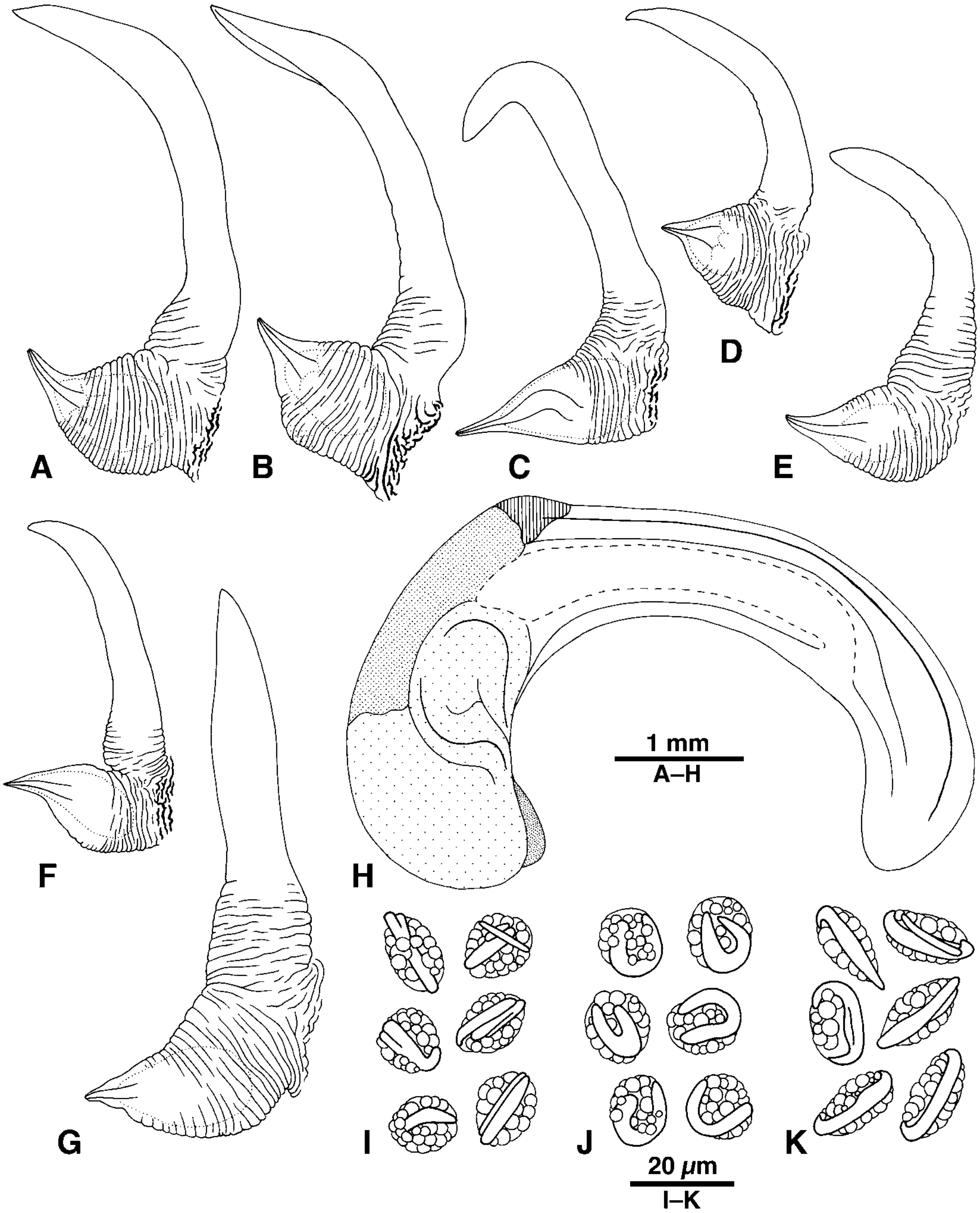

FIGURE 70. *Echinolittorina reticulata*. **A–G,** penes. **H,** pallial oviduct. **I–K,** paraspermatozoa. **A, B, H,** Anakena, Île Ste Marie, Madagascar (BMNH 20030678; shell H **A** = 8.3 mm, **B** = 8.9 mm, **H** = 10.6 mm). **C,** St Leu, Réunion (BMNH 20050561; shell H = 6.2 mm). **D, E, I,** Mirissa, Weligama, Sri Lanka (BMNH 20050562; shell H **D** = 4.7 mm, **E** = 5.6 mm). **F,** Senggigi, Lombok, Indonesia (BMNH 20050555; shell H = 5.8 mm). **G, J, K,** Guintungauan I., Bacuit Archipelago, Palawan, Philippines (BMNH 20050556; shell H **G** = 7.8 mm). Shading conventions as in Figure 3.

Shell (Fig. 69): Mature shell height 4.7–13.4 mm. Shape turbinate to high turbinate (H/B = 1.26–1.55, SH = 1.39–1.82); spire whorls rounded, suture distinct; spire profile straight; periphery of last whorl rounded. Columella straight, hollowed at base; eroded parietal area small or absent. Sculpture of last whorl variable: 4–6 ribs on base, 6–20 at and above periphery, ribs remaining small in smooth shells (Fig. 69G, N); usually 6–9 ribs at and above periphery are enlarged and strongly granulose, separated by single threads, basal ribs also becoming granulose (Fig. 69A–E, I–M); in large shells granules may become obsolete at end of last whorl; granules almost always conspicuously aligned (especially on spire whorls) into axial series or fusing to form axial ribs, 13–23 on last whorl (more numerous in Mascarene Is and Madagascar, 24–38, Fig. 69F, G, H, K); spiral microstriae only in grooves. Protoconch (Fig. 37H) 0.28–0.31 mm diameter, 2.8–3.1 whorls. Colour white; usually brown marks or black axial lines in spaces between axially aligned granules (Fig. 69B–E); first 1–2 whorls of teleoconch with single brown spiral line, rarely continuing to last whorl (Fig. 69O); rarely all spiral grooves pale brown (Fig. 69D); aperture orange brown with brown spiral lines showing through, pale band at base; columella purple-brown.

Animal (Fig. 70): Head grey to black, narrow unpigmented stripe across snout, tentacle unpigmented with black base, unpigmented around eye and across base; sides of foot grey to black. Opercular ratio 0.36–0.48. Penis (Fig. 70A–G): filament smooth with thickened wrinkled base, pointed at tip, about 0.7–0.8 total length of penis, sperm groove extends to tip; base short; large mamilliform gland on short projection of base; glandular disc apparently absent, may be represented by slightly thickened area adjacent to mamilliform gland, but never projects as a lobe; penis unpigmented or slightly pigmented at base. Euspermatozoa 75–82 µm; paraspermatozoa (Fig. 70I–K) oval, 12–20 µm, filled with round granules, 1–2 rod-pieces, straight, recurved at tips or U-shaped, with rounded ends, not or only slightly projecting from cell. Pallial oviduct (Fig. 70H): bursa large, opening at one quarter to one third length of straight section (from anterior) and extending back between albumen and capsule gland. Development predicted to be planktotrophic.

Radula (Fig. 66E, F): Relative radula length 1.72–3.70. Rachidian: length/width 1.12–1.46; tip of major cusp rounded to pointed. Lateral and inner marginal: major cusp on each of similar size, tips rounded. Outer marginal: 6–7 cusps.

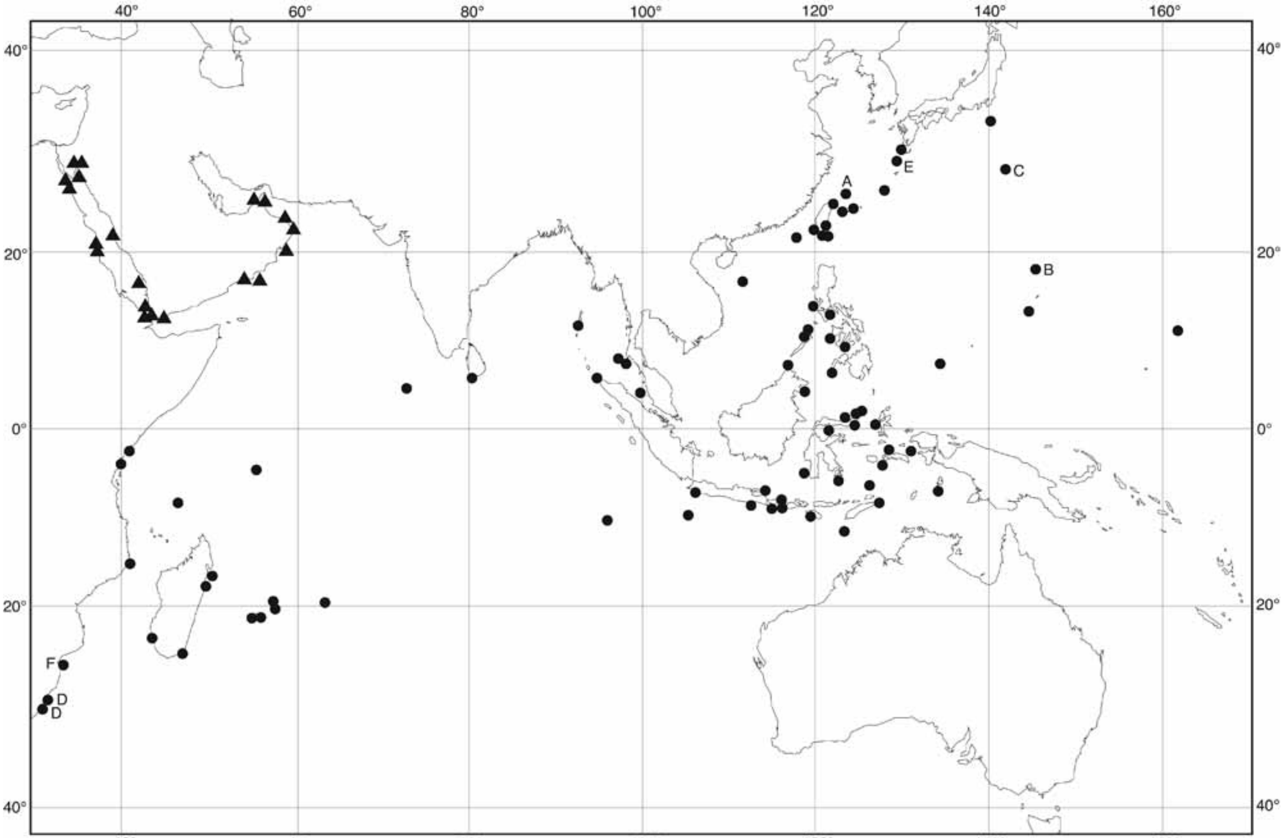

FIGURE 71. Distribution of *Echinolittorina millegrana* (solid triangles) and *E. reticulata* (solid circles). Literature records: A, Fujioka & Kurozumi (1980); B, Vermeij *et al*. (1984); C, Fukuda (1993); D, Kilburn (1972); E, Kurozumi (1994); F, Kensley (1973).

Range (Fig. 71): East Africa, Madagascar, islands of Indian Ocean, Indonesia, western Pacific islands including Ryukyu Is, Taiwan, Philippines to Marshall Is, but excluding Java Sea, South China Sea and mainland of Asia and Japan. Range limits: Lamu, Kenya (BMNH); Conducia Bay, Mozambique (NM H240); Delagoa Bay, Mozambique (Kensley 1973); Illovo, Natal, South Africa (Kilburn 1972); Aldabra (BMNH); Anakena, Île Ste Marie, Madagascar (BMNH 20030678); Tolagnaro, Madagascar (BMNH; USNM 678834); Toliara, Madagascar (IRSNB); Mahé, Seychelles (BMNH; USNM 749630); Pointe au Sel, Réunion (BMNH 20050559); Souillac, Mauritius (BMNH; USNM 637365); Rodrigues (NMW); Dunidu I., Male Atoll, Maldives (USNM 672390); Mirissa, Weligama, Sri Lanka (BMNH 20050562); Andaman Is (BMNH 1907.8.30.97); Surin Beach, Phuket I., Thailand (BMNH); Pulau Jarak, W of Sembilan Is, Malaysia (USNM 661049); Pulau Weh, Sumatra, Indonesia (NNML); Direction I., Cocos Keeling Is (AMS C380521); Christmas I., Indian O. (AMS); Cartier Reef, Australia (Willan 1993, 2005; NTM); Pelabuan Ratu, Java, Indonesia (IRSNB); S coast Madura, Indonesia (NNML); Tanah Lot, Bali, Indonesia (BMNH); Senggigi, Lombok, Indonesia (BMNH 20050555); Pantai Marosi, Sumba, Indonesia (H. Kool); Jaco I., East Timor (BMNH); S Trangan I., Aru, Indonesia (WAM S10898; USNM 747519); Pisang Is, Irian Jaya, Indonesia (IRSNB); Lae-Lae I., Makassar, Sulawesi, Indonesia (BMNH); Manado Bay, Sulawesi, Indonesia (BMNH); Kudat, Sabah, Malaysia (BMNH); Zamboanga, Mindanao, Philippines (USNM 233411); Santo Domingo, Batan I., Philippines (USNM 233279); Paracel Is (ZMB); Pratas I., Taiwan (National Museum of Marine Biology, Checheng); Kaohsiung, Taiwan (BMNH); Tali, 20 km SE Keelung, Taiwan (BMNH); Senkaku Is, Japan (Fujioka & Kurozumi 1980); Nago City, Okinawa, Japan (BMNH); Katae, Kuro-shima, Kagoshima Pref., Japan (BMNH); Mitsune, Hachijo-jima, Japan (BMNH); Chichijima, Ogasawara Is, Japan (Fukuda 1993); Babelthuap, Palau, Caroline Is (USNM 599173); Tagachan, Guam, Mariana Is (G.J. Vermeij Colln); Pagan, Mariana Is (Vermeij *et al*. 1984); Eniwetak, Marshall Is (USNM 679731).

This species is restricted to oceanic habitats, and the absence from the continental shores of India, Australia, Southeast Asia, Japan, the southern South China Sea and the Java Sea is undoubtedly genuine. The distributional area therefore includes a wide area of the Indian Ocean and also of the western Pacific, but these two parts of the range are only narrowly connected in eastern Indonesia by the oceanic ‘eastern Indonesian corridor’ through the Lesser Sunda Islands (Reid *et al*. 2006). It is rare in the Ogasawara Islands (Fukuda 1993) and northern Mariana Islands (Vermeij *et al*. 1984; Kurozumi & Asakura 1994), and was not recorded in Guam by B.D. Smith (2003). The distribution in the islands of Micronesia, western Philippines, western Sumatra and Irian Jaya is poorly known, but it is to be expected in all these regions. There are only two records from South Africa (Kilburn 1972).

Habitat: This species is found only in oceanic situations where the water is clear, and usually on oceanic islands, or on peninsulas and promontories on large land masses. It is most abundant under conditions of moderate wave exposure, but can be found on both strongly wave-exposed and sheltered shores. Recorded substrates include basalt, coral limestone, granite, sandstone, shale and concrete, and it occupies the uppermost eulittoral and lower littoral fringe. In the Tokara Islands it is found mainly on exposed volcanic rocks (Kurozumi 1994) and on Ishigaki it was recorded only on the open coast, and not within a sheltered cove (Ohgaki 1998). Restriction to wave-exposed rocks was noted both in Madagascar (Plante 1964) and Mauritius (Baissac *et al*. 1962).

Remarks: This species is closely similar to its sister, *E. millegrana* (Fig. 72), likewise with a white, granulose shell. However, the granules on the shell of *E. reticulata* are always (at least on the spire) arranged in conspicuous axial alignment, sometimes forming axial ribs (Fig. 69E, J) that are further enhanced by dark axial bands between them. Although there are no differences in head pigmentation, pallial oviduct or paraspermatozoa, the penis of each is diagnostic; that of *E. reticulata* has a pointed filament, large mamilliform penial gland, and no glandular disc (Fig. 70A–G), whereas that of *E. millegrana* has a vermiform filament, smaller penial gland, and a glandular disc forming a distinct (although sometimes small) lobe (Fig. 73A–D, G, H). The close relationship between these two was shown by DNA-sequence analysis (Williams & Reid 2004);

haplotypes of the mitochondrial genes COI and 12S rRNA did not segregate, whereas sequences of the nuclear 28S rRNA sorted according to species. This was confirmed by a more detailed study of the two species, showing intermixing of COI haplotypes in phylogenetic trees, but well supported segregation of 28S rRNA sequences (Reid *et al*. 2006). This is the only pair of IWP *Echinolittorina* species that are not separated by their COI sequences. Their species status is confirmed by the 28S rRNA data, penial differences and shell characters. The mitochondrial data are unlikely to be a result of introgression at the present time, because no shared haplotypes were found and the distributions of the two species are separated by a gap of about 2000 km, but historical introgression is a possibility (Reid *et al*. 2006).

Among the mitochondrial haplotypes of *E. reticulata* there was no evidence of phylogeographic structure, nor of a genetic break between Indian and Pacific Oceans, perhaps because during low sea-level stands of the Pleistocene glaciations the populations of the two oceans remained in genetic contact (Reid *et al*. 2006) There is, however, some regional variation in the shells, because the axial series of granules are more numerous in specimens from the Mascarene Islands and Madagascar (Fig. 69F, G, H, K).

The geographical distribution of this species is the clearest example of a typically oceanic distribution, on a large scale across the Indian and Pacific Oceans. The species is absent from mainland shores with broad continental shelves, as in Australia, New Guinea, all of Asia, Japan and most of Borneo, where oceanic primary productivity is high; it is also absent from the west coast of India and Somalia where high productivity is the result of seasonal upwelling (Rutgers University Primary Productivity Study; Reid *et al*. 2006). At a local scale, the species is common only where water is clear. As an example, on the north coast of Sulawesi it is absent in the muddy location of Molantadu (W of Kwandang); proceeding eastward it is very rare at Mariri Baru, uncommon in Manado Bay, and frequent on the island of Sangihe 200 km out in the Celebes Sea (pers. obs., and F. Boneka pers. comm.); this is a sequence of localities with increasingly clear-water, oceanic conditions. As a result of this geographical distribution, the Indian Ocean and Pacific Ocean populations of this species are in contact only through the narrow, oceanic ‘eastern Indonesian corridor’ through the Lesser Sunda Islands (Reid *et al*. 2006).

Echinolittorina reticulata can be found in sympatry with *E. melanacme* (Fig. 53) and *E. vidua* (Fig. 59); both have patterned shells and generally finer granulation. Other similar species that are sometimes sympatric are *E. cinerea* in the western Pacific (Fig. 64), and *E. philippinensis* in the Philippines (Fig. 46); although shells of both these can be white and granulose, neither shows the axial alignment of granules so distinctive of *E. reticulata*.

Echinolittorina millegrana **(Philippi, 1848)**

(Figures 66G, H, 71–73)

Litorina millegrana Philippi, 1848: vol. 3: 65–66, *Litorina* pl. 7, fig. 15 (Mare Rubrum [Red Sea]; lectotype (Rosewater 1970) Philippi, 1848, *Litorina* pl. 7, fig. 15; this figured specimen ZMB 112.713 becomes lectotype (Fig. 72J), seen). Weinkauff, 1882: 98, pl. 14, figs 5, 8.

Tectarius millegrana—H. Adams & A. Adams, 1854: 315.

Littorina millegrana—Reeve, 1858: sp. 99, pl. 17, fig. 99. Issel, 1869: 192. Nevill, 1885: 153.

Litorina (Tectaria) millegrana—Weinkauff, 1883: 226.

Nodilittorina (Granulilittorina) millegrana—Rosewater, 1970: 491–494, pl. 379, fig. A (radula), pl. 380, figs 1, 10, pl. 382 (map) (in part, includes *E. radiata*, *E. melanacme*, *E. feejeensis*, *E. vidua*, *E. novaezelandiae*, *E. reticulata*). Sabelli & Taviani, 1984: 95–100, pl. 1 (radula, penis).

Nodilittorina (Nodilittorina) millegrana—Bandel & Kadolsky, 1982: fig. 12 (protoconch). Reid, 1989a: 99 (in part, includes *E. reticulata*). Bosch *et al*., 1995: 46, fig. 116.

Nodilittorina millegrana—Sharabati, 1984: pl. 6, figs 3, 3a–c. Kowalke, 1998: 67, textfig. 8, pl. 9, fig. 4 (protoconch). Reid, 2001a: 441–442. Reid, 2002a: 259–281, fig. 2D (penis). Verbinnen & Dirkx, 2005: 111, fig. 3.

Echinolittorina millegrana—Williams *et al*., 2003: 83. Williams & Reid, 2004: 2227–2251.

Tectarius granularis—Tryon, 1887: 260, pl. 48, fig. 85 (in part, includes *E. radiata*, *E. miliaris*, *E. cinerea*, *E. vidua*; not

L. granularis Gray, 1839 = *E. miliaris*). Melvill & Standen, 1901: 364 (not Gray, 1839).
Littorina (Melarapha) novaezelandae—Safriel & Lipkin, 1964: 187 (not *L. novaezelandiae* Reeve, 1857).
Littorina urieli Biggs, 1966: 137–139, pl. 7, figs 1, 2 (Eilat, Israel; holotype BMNH 1966121, seen; 27 paratypes BMNH (Fig. 72B), seen; paratypes in Hebrew University, Jerusalem).

Taxonomic history: Rosewater (1970) designated as lectotype the figure of Philippi (1848). A specimen in ZMB corresponds in size, shape and sculpture with this figure. It measures 12.9 x 10.6 mm (cf 6 x 5 lines, i.e. 13.1 x 10.9 mm, given by Philippi 1848) and was collected by Hemprich & Ehrenberg in the Red Sea, as also recorded by Philippi. It is labelled '*Littorina granulosa* Ph.' in Philippi's hand; this is evidently a manuscript name, suggesting that Philippi examined the shell before publication of the new species. This shell is here identified as the figured specimen and is therefore the lectotype (ICZN 1999: Art. 74.4). Smooth forms were first identified as *L. novaezelandiae* by Safriel & Lipkin (1964), which they do indeed resemble, and were later named *L. urieli* by Biggs (1966).

The name *N. millegrana* became widely familiar after Rosewater (1970) used it as the oldest available name for a taxon consisting of five members of the *E. millegrana* group (*E. melanacme*, *E. vidua*, *E. novaezelandiae*, *E. millegrana*, *E. reticulata*, besides several misidentified examples of *E. feejeensis* and *E. radiata*). However, since *E. millegrana* is restricted to the Red Sea and Arabia, there have been relatively few correct usages. The shell is extremely similar to that of *E. reticulata*, but nevertheless there was no confusion between them in the literature until synonymized by Rosewater (1970; see Taxonomic History of *E. reticulata*). The anatomical distinction between these two was pointed out by Reid (2001a) and confirmed by DNA-sequence data (Williams & Reid 2004; Reid *et al*. 2006).

Diagnosis: Shell turbinate; sculpture variable, from smooth with fine spiral striae to 11–13 granulose ribs, granules not aligned into axial series; colour white, occasionally with spiral brown lines between ribs. Penial glandular disc projects as small lobe; filament long, strap-shaped, pointed tip. Red Sea and Arabia. COI: GenBank AJ623013, AJ623014.

Material examined: 48 lots (including 21 penes, 4 sperm samples, 6 pallial oviducts, 2 radulae).

Shell (Fig. 72): Mature shell height 3.3 mm (Hulings 1986) –15.2 mm. Shape turbinate to high turbinate (H/B = 1.27–1.56, SH = 1.42–1.79); spire whorls rounded, suture distinct; spire profile slightly convex; periphery of last whorl rounded, sometimes slightly angled at periphery. Columella straight, hollowed at base; eroded parietal area small or absent. Sculpture of last whorl variable: 5–6 ribs on base, 9–23 at and above periphery, all ribs small in smooth shells (Fig. 72A, B); usually, 6–7 (rarely 11) ribs at and above periphery are enlarged and strongly granulose, separated by single threads, basal ribs also becoming granulose (Fig. 72D–L); granules may become obsolete on last whorl but ribs remain strongly raised (Fig. 72D); granules not conspicuously aligned into axial series or ribs; spiral microstriae only in grooves. Protoconch 0.28 mm diameter, 2.7 whorls. Colour white; sometimes brown spiral lines in grooves; first 1–2 whorls of teleoconch with single brown spiral line; aperture orange brown with brown lines showing through, pale band at base; columella purple-brown.

Animal (Fig. 73): Head (Fig. 73E) grey to black, sometimes a narrow unpigmented stripe across snout, tentacle unpigmented with black base, unpigmented around eye and across base; sides of foot grey to black. Opercular ratio 0.37–0.43. Penis (Fig. 73A–D, G, H): filament long, strap-shaped, smooth, pointed at tip, about 0.7–0.8 total length of penis, sperm groove extends to tip; mamilliform gland and glandular disc borne together on short projection of base; glandular disc varies from small to large but always projects as a lobe; penis unpigmented or slightly pigmented at base. Euspermatozoa 68–82 µm; paraspermatozoa (Fig. 73I, J) oval, 11–20 µm, filled with round granules, rod-pieces single, rarely two, straight or curved, often recurved at tips or S-shaped, with rounded ends, not or only slightly projecting from cell. Pallial oviduct (Fig. 73F): bursa large, opening at one third length of straight section (from anterior) and extending back between albumen and capsule glands. Spawn a pelagic capsule 190 µm diameter, 80 µm high, cupola-shaped upper side sculptured by 2 concentric rings, containing single ovum 70 µm diameter (Hulings 1986). Development planktotrophic

(Hulings 1986).

Radula (Fig. 66G, H): Relative radula length 1.95–4.95. Rachidian: length/width 1.11–1.20; tip of major cusp rounded. Lateral and inner marginal: major cusp on each of similar size, tips rounded. Outer marginal: 6–8 cusps.

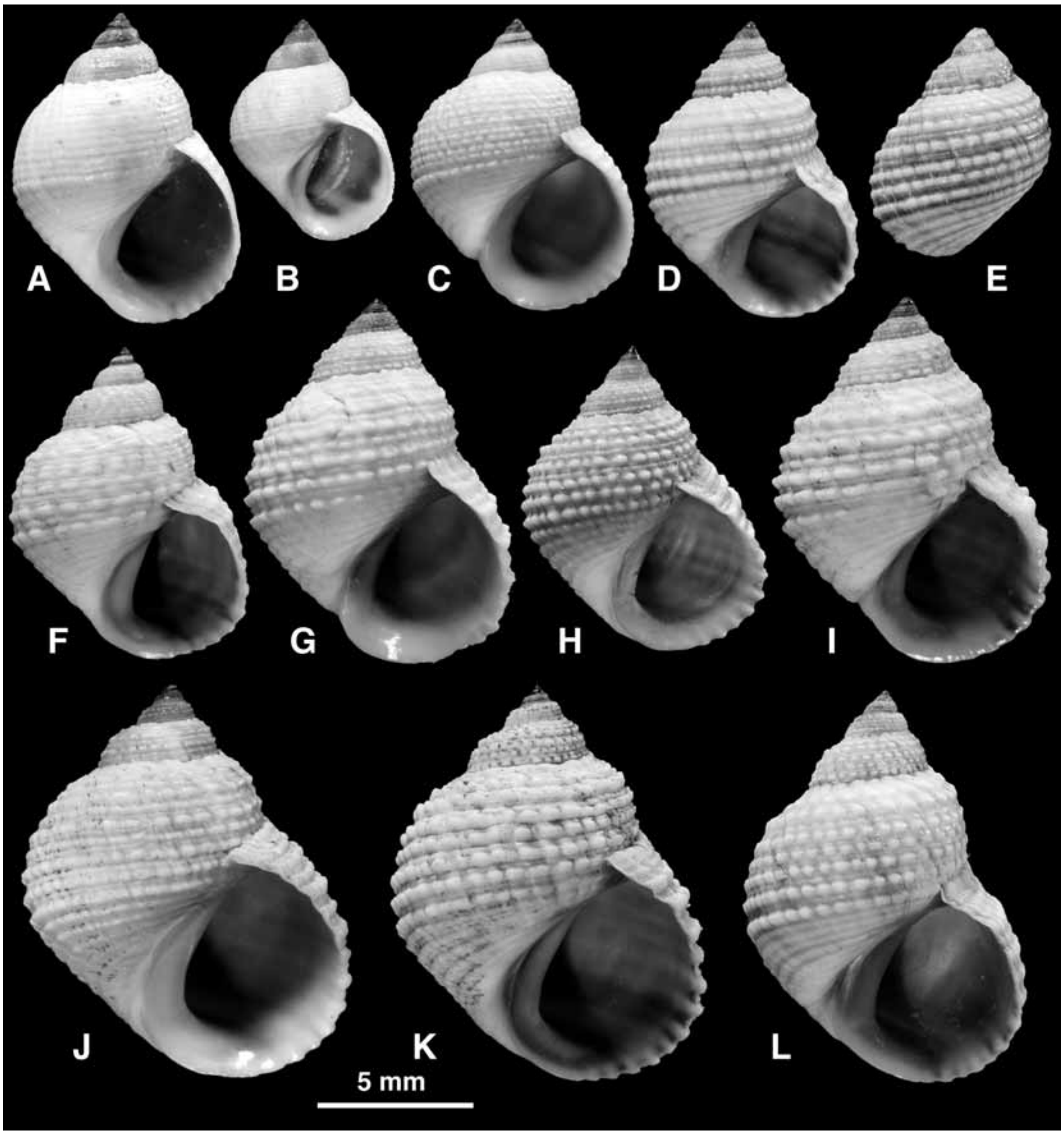

FIGURE 72. *Echinolittorina millegrana*. **A,** Red Sea, Saudi Arabia (BMNH 20050544). **B,** *Littorina urieli* Biggs, 1966, paratype, Eilat, Israel (BMNH 20050545). **C, G,** Hurghada, Egypt (BMNH 20050546). **D, E,** Fujairah, United Arab Emirates (BMNH 20050547, 20050548). **F, K, L,** Harvey Reef, 16 km S Port Sudan, Sudan (BMNH 20050549). **H,** Hamriya, Sharjah, United Arab Emirates (BMNH 20050550). **I,** El Qalawi, Egypt (BMNH 20050551). **J,** *Litorina millegrana* Philippi, 1848, lectotype, Red Sea (ZMB 112.713).

Range (Fig. 71): Red Sea, Arabia, to mouth of Persian Gulf. Range limits: Eilat, Israel (BMNH 20050554; USNM 709141); Hurghada, Egypt (BMNH 20050546); lagoon S of Port Sudan harbour, Sudan (BMNH); Tawq I., Yemen (H. Dekker Colln); Perim I., Yemen (BMNH 1891.1.31.199); Aden, Yemen (BMNH; MNHN; USNM 679341); Salalah, Dhofar, Oman (BMNH); Al Qibliyah, Kuria Muria Is, Oman (ZMA); Masirah I., Oman (BMNH); Ras al Junayz, Ras al Hadd, Oman (BMNH); Fujairah, UAE (BMNH 20050548); Hamriya, Sharjah, UAE (BMNH 20050550).

Although abundant at Aden and Ras al Hadd, this species is apparently rare on the intervening 2000 km of the Arabian coast (only 7 specimens recorded from 4 localities; compare with numerous samples of *E. oman-*

ensis in same area, Fig. 16). It is again common on the south coast of the Gulf of Oman (no information available for Iran) and 3 specimens are recorded from Sharjah just within the mouth of the Persian Gulf. A record from Kuwait (BMNH), near the northern end of the Persian Gulf, is considered unreliable.

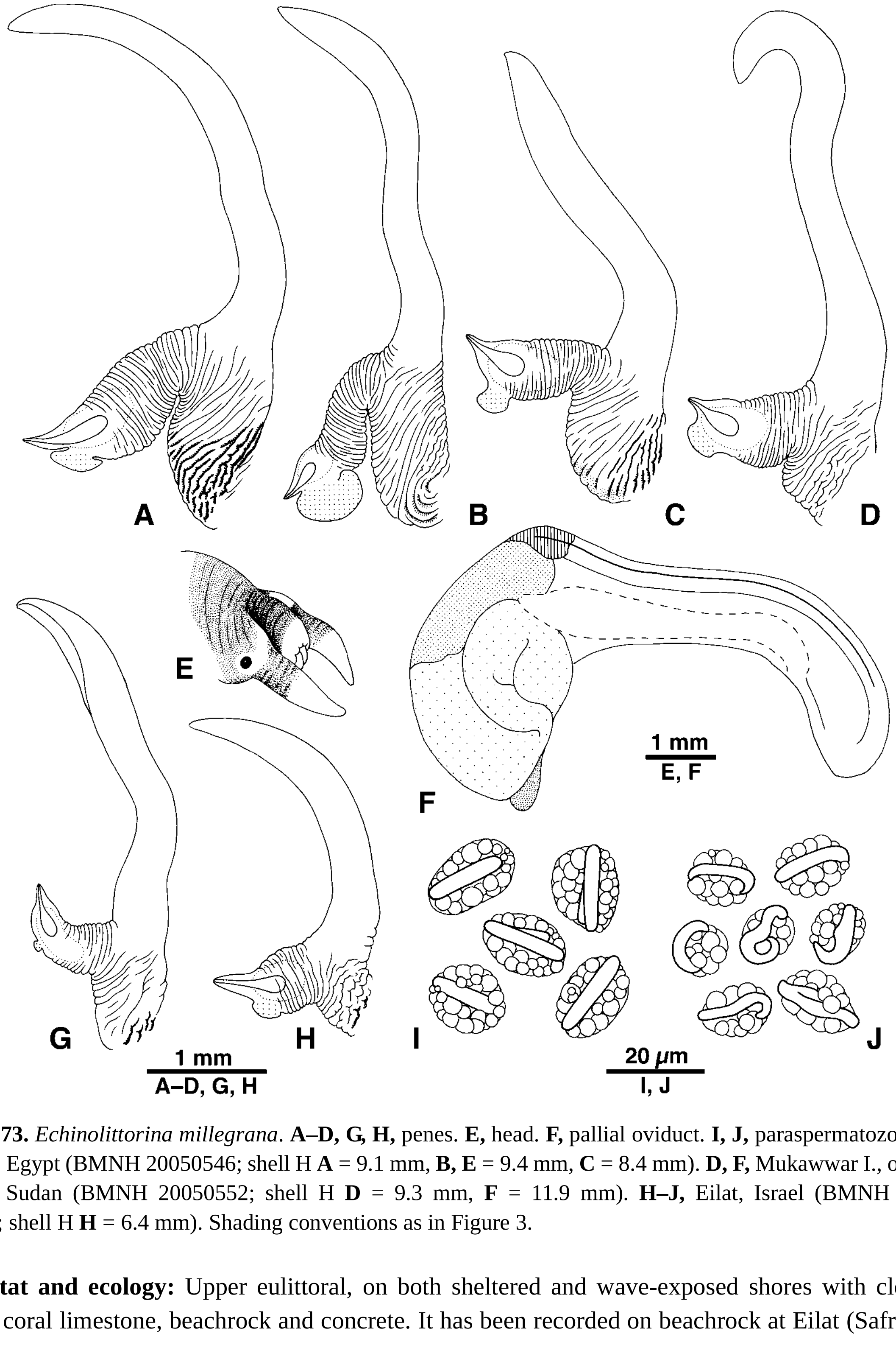

FIGURE 73. *Echinolittorina millegrana*. **A–D, G, H,** penes. **E,** head. **F,** pallial oviduct. **I, J,** paraspermatozoa. **A–C, E,** Hurghada, Egypt (BMNH 20050546; shell H **A** = 9.1 mm, **B, E** = 9.4 mm, **C** = 8.4 mm). **D, F,** Mukawwar I., off Muhammad Qol, Sudan (BMNH 20050552; shell H **D** = 9.3 mm, **F** = 11.9 mm). **H–J,** Eilat, Israel (BMNH 20050553, 20050554; shell H **H** = 6.4 mm). Shading conventions as in Figure 3.

Habitat and ecology: Upper eulittoral, on both sheltered and wave-exposed shores with clear water; found on coral limestone, beachrock and concrete. It has been recorded on beachrock at Eilat (Safriel & Lipkin 1964) and on limestone cliffs near Jeddah (Hughes 1977). In the Gulf of Aqaba Hulings (1987) found it in the lower littoral fringe, below *E. marisrubri* (also Vermeij 1973); the rate of water loss was measured, and snails survived desiccation for 12 days in the field; shells were larger on wave-exposed boulders and smaller on horizontal slabs where desiccation was more severe. Reproduction occurred throughout the year in the Gulf of Aqaba (Hulings 1986).

Remarks: Little information is available on the habitat and ecology of *E. millegrana*, but it shows an interesting distribution, being common in the Red Sea and on the south coast of the Gulf of Oman, but scarce or absent on the southeastern coastline of Arabia, and absent from all but the very mouth of the Persian Gulf. The Red Sea is an area of predominantly low productivity, with the exception of the remote southwestern part (for which records of all littorinids are scarce). The southeastern Arabian coast is subject to summer upwelling, which both reduces sea temperatures and results in seasonally high productivity (Wilson 2000). It is also exposed to strong wave action, although this does not prevent the occurrence of *E. millegrana* at other localities (e.g. Ras al Hadd). The Gulf of Oman is also highly productive, but at least for the second half of the year productivity falls to moderate levels, below those of adjacent areas including the productive Persian Gulf (Rutgers University Primary Productivity Study; Sheppard *et al*. 1992). The correlation of areas of abundance of *E. millegrana* with regions of low or moderate productivity suggests that this is likely to be a species of moderately oceanic habitats, explaining its distribution in Arabia.

The sister species of *E. millegrana* is *E. reticulata*, although this is shown only by the nuclear 28S gene; sequences of the mitochondrial COI gene do not separate the two (Williams & Reid 2004; Reid *et al*. 2006; see Remarks on *E. reticulata*). The boundary between these two species lies in the Arabian Sea (Fig. 71) and may be connected with the summer upwelling of cold, nutrient-rich water that takes place both along the coast from Somalia to Oman, and offshore through much of the northern Arabian Sea (Wilson 2000; Wilson & Klaus 2000; Luis & Kawamura 2004). The likely effectiveness of this barrier is suggested by the rarity of *E. millegrana* on the southeastern coast of Arabia as discussed above. During glacial intervals the extent of the upwelling zone was considerably reduced (Sheppard *et al*. 1992) and contact between these sister species may then have been possible, consistent with the suggestion of historical introgression of COI haplotypes (Reid *et al*. 2006).

The shell is similar to that of *E. reticulata* (Fig. 69), but they are allopatric (see Remarks on *E. reticulata* for discrimination). Of sympatric species, occasional pale, granulose shells of *E. arabica* (e.g. from Sharjah, Fig. 8A, B) are similar, but recognized by their fewer enlarged spiral ribs and more distantly spaced granules. In the Red Sea, *E. marisrubri* (Fig. 11) shows only 2–3 rows of enlarged granules. Penial anatomy also distinguishes *E. millegrana* from these congeners.

Discussion

Intraspecific variation in shells and radulae

Two striking examples of intraspecific variation in shells have previously been documented among *Echinolittorina* species in the IWP (Struhsaker 1968; Johnson & Black 1999; Yeap *et al*. 2001), and other cases are known among species from the tropical eastern Pacific (Reid 2002b). The present survey of all IWP species has shown that pronounced shell variation is a feature of almost all of them. It is usually expressed in the degree of sculpture, often ranging from smooth to strongly granulose or nodulose. In contrast to species from the Atlantic and eastern Pacific, few IWP species show strong colour patterns but, if present, patterns may also vary (e.g. *E. melanacme*, *E. vidua*, *E. cinerea*, *E. hawaiiensis*).

The basis and control of intraspecific shell variation have been extensively studied in littorinids and other intertidal gastropods (reviews by McQuaid 1996a; Reid 1996). The most striking variation is found among species with nonplanktotrophic development, in which restricted gene flow permits local genetic adaptation even over small spatial scales, sometimes resulting in differentiated ecotypes in contrasting microhabitats on the same shore. Species with planktotrophic development and wide gene flow are expected to show genetic differentiation only at spatial scales that are large relative to the dispersal distance. Where such species show shape differences between habitats at small scales, these have been interpreted as the result of ecophenotypic effects during growth (Chapman 1995; Reid 1996; Johnson & Black 1999). There is now experimental evidence for ecophenotypic effects on shell form, but in both planktotrophic and nonplanktotrophic species (Kemp & Bertness 1984; Boulding & Hay 1993; Trussell 1996, 2000; Parsons 1997).

Shell variation in *Echinolittorina* species is mainly consistent with this interpretation. Only the most widespread species show significant geographical variation (*E. natalensis*, *E. malaccana*, *E. melanacme*, *E. vidua*, *E. cinerea*, *E. reticulata*), with a likely genetic basis. At a local scale, a number of species show an association between stronger granulose or nodulose sculpture and a limestone substrate (*E. natalensis*, *E. pascua*, *E. malaccana*, *E. austrotrochoides*, *E. cecillei*, *E. wallaceana*, *E. melanacme*, *E. hawaiiensis*), although others do not (*E. cinerea*, *E. australis*). A predictable association of this kind is a possible candidate for an ecophenotypic influence on shell growth. *Echinolittorina australis* shows the most extreme intraspecific variation (Fig. 50) and occasional abrupt changes in sculpture during the growth of individuals implicate an environmental influence, but the associations with microhabitat are complex. Nevertheless, transfer experiments have clearly demonstrated the asymmetrical plasticity and canalized development of shell form in this species, and suggested a developmental constraint, because nodulose sculpture was connected with slow growth (Yeap *et al*. 2001). It may be that the dependence of shell shape and sculpture upon growth rate is the general means by which all these ecophenotypic effects are mediated (Reid 1996, 2002b). There is, however, one example of intraspecific variation in *Echinolittorina* that has been widely quoted as a case of genotypic determination of within-shore differences between smooth and granulose shell morphs. This is Struhsaker's (1968) study of the microdistribution and heritability of shell sculpture in *E. hawaiiensis*. This claim of genetic control was based on correlation between the sculpture of adults and that of the larval shells of their progeny. As discussed in the Remarks on *E. hawaiiensis*, there are concerns about the reliability of the methodology and this case should be re-examined.

Sexual dimorphism is present in many littorinid species (Reid 1986a, 1996), males being slightly smaller and with a relatively larger aperture. Among IWP *Echinolittorina* species dimorphism of this type is noticeable in only a few species (*E. melanacme*, *E. feejeensis*, *E. vidua*).

As in *Echinolittorina* species of the eastern Pacific (Reid 2002b), radulae do not show usefully diagnostic differences between species in the IWP clade. However, among western Atlantic species radular differences have in the past been used as diagnostic characters. For example, Bandel & Kadolsky (1982) discriminated *E. tuberculata* (with a narrow rachidian, massive lateral teeth with one major cusp, inner marginal with two cusps, and reduced outer marginal lacking basal flanges) from *E. dilatata* (D'Orbigny, 1842) with a typical *Echinolittorina*-type radula. Similarities of reproductive anatomy, shells, COI sequences and distribution now suggest that these forms are conspecific (Reid 2002a; Williams & Reid 2004). The intraspecific variation reported here in *E. natalensis* (and, less striking, in *E. wallaceana* and *E. australis*) is of exactly the same type (Fig. 15A–D). Environmental effects of the substrate upon radular form have been described in the littorinid genera *Lacuna* and *Littoraria* (Padilla 1998; Reid & Mak 1999; Andrade & Solferini 2006), and might also explain the intraspecific variation in *Echinolittorina*. So far, no environmental correlate has been found; the radular variation does not appear to be obviously connected with the type of rock substrate, for example.

Larval development and dispersal

Only a single species of *Echinolittorina*, *E. hawaiiensis*, has yet been successfully reared in the laboratory. The total duration of planktonic development, from spawning until settlement, was 4 weeks at 25°C (Struhsaker & Costlow 1968). This is believed to be representative of the entire genus. Spawning of pelagic egg capsules has been described for many species, and the large capsule gland of the pallial oviduct indicates that all will do likewise (Reid 2002b). A similar duration of planktotrophic larval life throughout the genus can be predicted from the uniformity of the larval shells, as described here (Fig. 37G, H; see also figures by Bandel & Kadolsky 1982; Kowalke 1998; Reid 2002b).

The maximum distance of larval dispersal is an important consideration for discussion of speciation in this genus. While this can be estimated from larval duration and speed of current flows, indirect genetic evidence suggests that pelagic eggs and larvae do not always achieve their potential dispersal distance. Direct observations of dispersal are therefore valuable. Unusually, the geographical ranges of *Echinolittorina* species are known with sufficient precision that extralimital records of rare individuals (that are apparently not part of a self-sustaining population) can be used as evidence for dispersal, particularly when dispersal must have occurred across open water without intermediate landfall. The maximum distances of open-water dispersal from source populations recorded during the present study are: 1500 km (*E. austrotrochoides*), 1500 km (*E. leucosticta*), 1000 km (*E. feejeensis*) and 1300–2100 km (*E. cinerea*). Dispersal distances of 1200 km have been recorded in the eastern Pacific (Reid 2002b). Distances of this order are therefore likely to be required for allopatric speciation in this group (Williams & Reid 2004).

Distribution in oceanic, continental and upwelling areas

From detailed records of geographical distribution it is sometimes possible to infer the causes of distributional limits, for example when range limits coincide with stretches of sedimentary coastline without suitable habitat (e.g. *E. natalensis*, *E. malaccana*) with the limits of influence of warm currents (*E. radiata*, *E. natalensis*, *E. australis*), with isolating current flows (*E. marquesensis*) or when species are restricted to isolated island groups (*E. hawaiiensis*, *E. pascua*). Observations at a local scale suggest that the geological composition of the substrate does not affect distributions (see Habitat notes; Vermeij 1971).

Oceanographic conditions are an equally important, though less readily quantified, influence on distribution. As in many other molluscan groups, littorinid species can often be described as ‘oceanic’ or ‘continental’ (for detailed discussion see Reid 1986a, 1996; Williams & Reid 2004; Reid *et al*. 2006); this is not a categorical classification, but a gradient between extremes. Continental species are those restricted to nutrient-rich shores of continental land masses and large, high islands, whereas oceanic species occur on islands in water of low nutrient status. At a geographical scale, these contrasting distributions are clear from comparison with global maps of oceanic primary productivity (SeaWiFS data displayed e.g. by Rutgers University Primary Productivity Study; Reid *et al*. 2006). Typical continental species are *E. radiata*, *E. arabica*, *E. malaccana*, *E. austrotrochoides* and *E. vidua*. Typical oceanic ones are *E. subnodosa*, *E. pascua*, *E. wallaceana*, *E. cecillei*, *E. marquesensis*, *E. feejeensis*, *E. cinerea*, *E. hawaiiensis* and *E. reticulata*. At a local scale, the reality of this subjective classification is reinforced, because on coastlines of mixed or intermediate types the continental species occur where water is turbid, while oceanic species are restricted to clear-water sites (usually on open coasts, promontories or offshore islands). The fact that littorinids in the littoral fringe, where they are rarely submerged, are so affected by oceanographic conditions suggests that the effect may be mediated by requirements of tolerances of their larvae, but experimental investigation is required.

There is one category of distributions that does not clearly fit the continental/oceanic classification. These species are found on shores of moderate or seasonal productivity, on the margins of oceans where they are exposed to strong winds or currents (*E. omanensis*, *E. sundaica*, *E. leucosticta*, *E. biangulata*, *E. philippinensis*, *E. tricincta*, *E. australis*). Here it is pointed out for the first time that the areas where these species occur are all subject to seasonal upwelling of cool, nutrient-rich water. Again it seems likely that larval ecology may hold the key to understanding the reasons for this restriction. Simple tolerance of cool water temperature cannot provide the whole explanation, for these species (with the exception of *E. australis*) do not extend far outside tropical latitudes. Comparison with the molecular phylogeny (Fig. 1) suggests that the continental/oceanic character of species is evolutionarily labile, but five of the upwelling species form a single clade (the *E. leucosticta* group), and therefore show a distinct phylogenetic pattern.

Evolutionary radiation

The evolutionary radiation of *Echinolittorina* in the IWP can be described as ‘nonadaptive’ (*sensu* Gittenberger 1991) or ‘morphostatic’ (*sensu* Davis 1992), because speciation is widely allopatric (Williams & Reid

2004) and accompanied by little anatomical change or habitat diversification. There is virtually no geographical overlap between sister species (the only case involves 3 specimens of *E. vidua* from within the range of *E. novaezelandiae* in Sri Lanka), and allopatry is usually maintained through at least two or three speciation events spanning approximately 5–10 Ma. During this time, distributions must have shifted, not least because of the fluctuations in sea level during the glaciations of the Plio-Pleistocene. This suggests that there is an impediment to sympatry of close relatives.

Interspecific competition is just one of several mechanisms that may maintain allopatry following speciation (Wilke & Pfenninger 2002), and there are some indications that it may operate in *Echinolittorina*. The *E. natalensis* and *E. malaccana* groups are morphologically similar in their tall, nodulose shells, and the distributions of these two clades are entirely mutually exclusive, despite their close approach in the northern Arabian Sea. It has been suggested that the *E. natalensis* clade was formerly widespread throughout the IWP, but became extinct in the central region where it was replaced by the *E. malaccana* clade (Williams & Reid 2004); it now survives only at the periphery of the region, in the western Indian Ocean and in the far southeast of Polynesia. Of the nine species in these two clades, there is parapatric contact between only two (*E. malaccana* and *E. wallaceana*). All nine species occupy the same physical microhabitat at the highest level of the littoral fringe, but there is differentiation according to the oceanographic regime: *E. subnodosa*, *E. pascua, E. wallaceana, E. cecillei* and *E. marquesensis* are oceanic species; *E. natalensis* is tolerant of a wider range of conditions; *E. malaccana* and *E. austrotrochoides* are continental species; *E. omanensis* occupies an upwelling zone. Throughout the IWP region the number of sympatric *Echinolittorina* species seldom exceeds three or four, but reaches six at two localities (southwestern Java, northeastern Sulawesi) and seven at one (southeastern Taiwan). The highest totals are only achieved on the boundaries of biogeographic provinces and where oceanographic conditions are mixed or intermediate, and several of the species are always rare. Where two or more species are common, there is usually some segregation by tidal level. In the central IWP, for example, members of the *E. malaccana* group occupy the highest level (upper littoral fringe), followed by *E. vidua* and *E. melanacme* together, while *E. reticulata*, *E. leucosticta* and *E. tricincta* extend to the lowest levels (upper eulittoral zone) (for examples of zonation studies, see Endean *et al*. 1956a, b; Habe 1958b; Vermeij 1973; Rao & Sudaram 1974; Ohgaki 1983a; Berry 1986; Tsuchiya & Lirdwitayapasit 1986; Hulings 1987; Asakura *et al*. 1990, 1991; Black & Johnson 2001). Field manipulation experiments suggest that interactions between syntopic *Echinolittorina* species can have small effects on their zonation levels (Dudgeon & Yipp 1986), and show that the standing crop of microalgae is controlled by their grazing (Potter & Schleyer 1991; Mak & Williams 1999), so interspecific competition is a possibility and may have had some influence on their ecology.

The morphological differences among IWP *Echinolittorina* species are mainly subtle variations in shell shape, sculpture and penial form, rather than discrete characters suited to cladistic analysis. Reid (2002a) attempted a phylogenetic analysis of morphological characters of '*Nodilittorina*' and, of the 26 characters used, six show variable states within the IWP clade of *Echinolittorina*. One of these characters (length of euspermatozoa) is incompletely known and shows continuous variation among *Echinolittorina* species. The other five characters are listed in Table 2, with the addition of an extra character, the bifurcate copulatory bursa. Comparison with the molecular phylogeny (Fig. 1) and parsimonious reconstruction of character states, indicates that several of these characters have a marked phylogenetic pattern. Nodulose shell sculpture in the majority of individuals of a species is a parallel synapomorphy of the *E. natalensis* and *E. malaccana* clades, although extreme sculptural forms of a number of species outside these groups may achieve the same degree of nodulosity (e.g. *E. marisrubri*, *E. australis*, *E. biangulata*, *E. tricincta*). The basal band of the cephalic tentacles is a unique synapomorphy of the *E. leucosticta* and *E. millegrana* clades. The reduced or absent penial glandular disc is a synapomorphy (unique among IWP species, but not in the genus) of the clade *E. vidua*, *E. novaezelandiae*, *E. cinerea*, *E. hawaiiensis*, *E. reticulata* and *E. millegrana*. Curved rod-pieces of the paraspermatozoa are parallel synapomorphies of the *E. arabica* clade and the combined *E. leucosticta* and *E. millegrana* (except *E. vidua* and *E. novaezelandiae*) clades. Nevertheless, these small morphological differences gave only very limited resolution in the cladistic analysis (Reid 2002a). Notably, there is no known morphological synapomorphy for the subgenus *Granulilittorina*, nor indeed for the entire genus *Echinolittorina*.

TABLE 2. Character states in Indo-West Pacific (IWP) *Echinolittorina* species. Character definitions from Reid (2002a) with new data from present study. State 0 is the plesiomorphic condition among the IWP species, as determined by outgroup comparison with other *Echinolittorina* species (Fig. 1). Consistency index (CI) = minimum number of character state changes divided by number observed in parsimonious reconstruction of character states on topology of molecular phylogeny (Fig. 1).

Character	Character state	Distribution of apomorphic states	CI
1. Aperture	0: eroded parietal area 1: eroded area absent	1: *E. arabica* clade; *E. sundaica*	0.5
2. Shell sculpture	0: spiral grooves only 1: variably granulose 2: nodulose	0: *E. sundaica* 1: All others 2: *E. natalensis* clade, *E. malaccana* clade	0.5
3. Axial alignment of colour or nodules	0: aligned 1: not aligned	1: *E. radiata*, *E. arabica* clade, *E. subnodosa*, *E. sundaica*, *E. millegrana*	0.25
4. Coloration of cephalic tentacles	0: 2-3 longitudinal lines 1: basal transverse band	1: *E. leucosticta* clade, *E. millegrana* clade	1.0
5. Penial glandular disc	0: normal 1: small or absent	1: *E. vidua*, *E. novaezelandiae*, *E. cinerea*, *E. hawaiiensis*, *E. reticulata*, *E. millegrana*	1.0
6. Rod-pieces in paraspermatozoa	0: long, straight 1: small, irregular 2: curved	1: *E. radiata*, *E. natalensis* clade, *E. vidua*, *E. novaezelandiae* 2: *E. arabica* clade, *E. leucosticta* clade, *E. millegrana* clade (except *E. vidua*, *E. novaezelandiae*)	0.33
7. Copulatory bursa	0: normal 1: bifurcate	1: *E. malaccana* clade (except *E. wallaceana*)	0.5

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Taxonomic index

This index lists all names that appear in the synonymies of *Echinolittorina* species, as well as all genera to which these species have been assigned. Valid names of IWP *Echinolittorina* species are in upper case. Entries are in the form: specific (or subspecific) epithet, followed by author, date and original genus (and, for subspecific and varietal names, original species). For each name, the valid name, if different, follows in square brackets. Page references are to the main entries in the synonymies only. Also listed are all names that have been incorrectly applied to IWP *Echinolittorina* species (including three that are not members of the Littorinidae), although page references are only given to those misidentifications that have become widely followed or are otherwise noteworthy. Emendations are included, but incorrect subsequent spellings are not.