Recent deep-water Cassidae of the world. A revision of *Galeodea*, *Oocorys*, *Sconsia*, *Echinophoria* and related taxa, with new genera and species (Mollusca, Gastropoda)

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ABSTRACT

Shell, radular, opercular and external anatomical characters are surveyed in world Recent deep-water Cassidae, leading to the recognition of three subfamilies: Cassinae, Oocorythinae and Phaliinae. All Recent species are revised of *Galeodea* Link, 1807 (= *Galeoocorys* Kuroda & Habe, 1957), *Microsconsia* n. gen. and *Sconsia* Gray, 1847, all included in subfamily Cassinae; of *Oocorys* Fischer, 1883 (= *Benthodolium* Verrill & Smith, 1884, = *Hadroocorys* Quinn, 1980), *Eucorys* n. gen. (including *Oocorys bartschi* Rehder, 1943 and *O. barbouri* Clench & Aguayo, 1939) and *Dalium* Dall, 1889, all included in subfamily Oocorythinae; and of *Echinophoria* Sacco, 1890, included in subfamily Phaliinae. New species named are *Galeodea plauta* n. sp. (northwestern New Zealand), *Microsconsia limpusi* n. sp. (southeastern Queensland, Australia), and *Oocorys grandis* n. sp. (central Indian Ocean, and southeastern Atlantic, off Namibia). *Galeodea bituminata* (Martin, 1933) (based on a Pliocene fossil from Buton Island, Indonesia) is an earlier name for *G. echinophorella* Habe, 1961; *G. carolimartini* Beets, 1943 is another earlier name for *G. echinophorella*. The name usually accepted for the type species of *Sconsia*, *S. striata* (Lamarck, 1816), is a junior secondary homonym of *S. striata* (J. Sowerby, 1812) and the valid name for this species is *S. grayi* (A. Adams, 1855). *Echinophoria kurodai* Abbott, 1968 was based on small specimens of *E. wyvillei* (Watson, 1886), and *E. oschei* Mühlhäusser, 1992 was based on Indian Ocean specimens of *E. wyvillei*. *Echinophoria carnosa* Kuroda & Habe, 1961 is limited to southern Japan to the Philippine Islands.

RÉSUMÉ

Les casques (Gastropoda : Cassidae) de grande profondeur de l'Océan mondial. Révision des genres *Galeodea*, *Oocorys*, *Sconsia*, *Echinophoria* et taxons apparentés, et description de nouveaux genres et espèces.

Les casques actuels de grande profondeur de l'Océan mondial sont réexaminés sur la base des caractères de la coquille, de la radula, de l'opercule et de la morphologie externe, ce qui conduit à reconnaitre trois sous-familles : Cassinae, Oocorythinae et Phaliinae.

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Toutes les espèces actuelles sont révisées dans les genres *Galeodea* Link, 1807 (= *Galeoocorys* Kuroda & Habe, 1957), *Microsconsia* n. gen. et *Sconsia* Gray, 1847, tous les trois dans les Cassinae; dans les genres *Oocorys* Fischer, 1883 (= *Benthodolium* Verrill & Smith, 1884, = *Hadroocorys* Quinn, 1980), *Eucorys* n. gen. (comprenant *Oocorys bartschi* Rehder, 1943 et *O. barbouri* Clench & Aguayo, 1939) et *Dalium* Dall, 1889, tous les trois dans les Oocorythinae; et enfin dans le genre *Echinophoria* Sacco, 1890, dans les Phaliinae. Les nouvelles espèces suivantes sont décrites : *Galeodea plauta* n. sp. (nord-ouest de la Nouvelle-Zélande), *Microsconsia limpusi* n. sp. (sud-est du Queensland, Australie) et *Oocorys grandis* n. sp. (Océan Indien central et sud-est de l'Atlantique au large de la Namibie). *Galeodea bituminata* (Martin, 1933), fondé sur un fossile du Pliocène de Buton en Indonésie, est un synonyme plus ancien de *G. echinophorella* Habe, 1961, et *G. carolimartini* Beets, 1943 est également synonyme. *Sconsia striata* (Lamarck, 1816) est un homonyme secondaire plus récent de *S. striata* (J. Sowerby, 1812) et le nom valide de l'espèce type du genre *Sconsia* est *S. grayi* (A. Adams, 1855). *Echinophoria kurodai* Abbott, 1968 s'avère avoir été fondé sur des exemplaires de petite taille d'*E. wyvillei* (Watson, 1886), et *E. oschei* Mühlhäusser, 1992 s'avère avoir été fondé sur des exemplaires de l'Océan Indien de la même espèce. La distribution d'*Echinophoria carnosa* Kuroda & Habe, 1961 est limitée du sud du Japon aux Philippines.

INTRODUCTION

Cassidae are usually known as "helmet shells" in English, or the equivalent "casques" in French. They are moderately to very large, mostly shallow-water caenogastropods with oval to subspherical, brightly coloured shells and predominantly spiral sculpture. Most are characterised by a heavily callused apertural shield or columellar collar on the apertural face of the shell, much more prominently developed than in almost all other gastropods, by a short spire and capacious last whorl enveloping most of the rest of the shell, and by a short, quite weakly to very strongly twisted anterior siphonal canal. Most species prey on echinoderms (predominantly on echinoids and starfish) on shallow, sandy substrates throughout much of the world's tropical and temperate oceans. The shallow-water species are highly variable, with few landmark characters that allow clear-cut specific distinction, and their taxonomy has presented many problems at both the specific and the generic level. Taxonomists have debated at length the taxonomic decisions in the major monograph by Abbott (1968). Many aspects of the species-level taxonomy (particularly in *Casmaria* H. & A. Adams, 1853 and *Semicassis* Mörch, 1853) still have not reached a general consensus and probably are not resolvable without recourse to genetic techniques. The excellent book by Kreipl (1997) in my opinion presents a greatly improved taxonomy over that of Abbott (1968). But continuing arguments about the taxonomy of the shallow-water taxa are nothing compared with the poor state of knowledge of the deep-water members of the family. Discussion continues even about such fundamental points as whether *Oocorys* Fischer, 1883 belongs in Cassidae or in a separate family. Much of the debate has the underlying cause of insufficient material for understanding the variation of the species, and so the large collections of deep-water cassids gathered in recent years by MNHN and IRD have a useful contribution to make to the understanding of this family. I offer here some opinions and conclusions on the Recent deep-water members of the family, revising as well as the information allows all the Recent species of *Galeodea* Link 1907, *Oocorys*, *Sconsia* Gray, 1847, *Echinophoria* Sacco, 1890 and related, more minor genera that occur mainly in water deeper than about 150-200 m.

The MUSORSTOM and other deep-sea cruise collections in MNHN from off Madagascar, the Philippine Islands, Indonesia, Fiji and the New Caledonia-Vanuatu region include much material of species of *Galeodea*, *Oocorys* and *Echinophoria*. (For the context and narratives of these expeditions, see the introductory chapter by Bouchet *et al.* (2008), this volume). With MNHN collections from the Atlantic, they provide a lot of material on which to base a reassessment of the relationships of *Oocorys* and similar genera, as well as allowing the revision of the species of these deep-sea genera. Much comparative material trawled from the far northwestern shelf of Western Australia was examined in the Western Australian Museum, and helpful comparative material was loaned by several other museums. A study of the gross external anatomy, the opercula and the radulae of as many species as possible was undertaken to try to resolve the generic relationships of *Galeodea* and *Oocorys*, along with comparison of the type specimens of nearly all of the nominal species. *Sconsia* also is included here, as some species occur in deep water, and there has been considerable debate about the species-level taxonomy of this genus. The material of the deeper-water genus of Tonnidae, *Eudolium* Dall, 1889, from the MNHN collections was included in Marshall's (1992) and Vos's (2007) revisions of *Eudolium*, and I have nothing to add on Recent species of this genus.

Oocorys is distributed almost continuously and quite commonly in deep water (about 600-4000 m, with some records down to nearly 5000 m) throughout all the areas that have been sampled in detail during deep-sea cruises. This presumably indicates that it occurs throughout the world's temperate and tropical oceans. Some species of *Oocorys*, particuarly *O. sulcata* Fischer, 1883 and *O. verrillii* (Dall, 1889), also occur more-or-less continuously throughout the area studied to date. This is in marked contrast to the geographic ranges of shallow-water benthic species, in which even the most widely distributed species, such as *Cymatium parthenopeum* (von Salis Marschlins, 1793), have widely disjunct adult populations, kept in genetic continuity by their continuously distributed planktotrophic larvae (Scheltema 1966; Pechenik *et al.*, 1984). This strengthens the recognition of the widespread, almost continuous distribution of these abyssal species that has been pointed out already by Bouchet & Warén (1993: 801).

Repositories

AMS: Australian Museum, Sydney
BMNH: The Natural History Museum, London
IRD: Institut de Recherche pour le Développement (formerly ORSTOM)
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge
MHNG: Musée d'Histoire Naturelle de Genève
MNHN: Muséum national d'Histoire naturelle, Paris [NOTE: all material listed here is in MNHN, unless otherwise stated]
MOM: Musée Océanographique, Monaco
NMNZ: Museum of New Zealand Te Papa Tongarewa, Wellington
NMP: Natal Museum, Pietermaritzburg
NSMT: National Science Museum, Tokyo
NZGS: GNS Science, Lower Hutt [formerly New Zealand Geological Survey]; paleontological collection numbers prefixed GS; non-New Zealand Mollusca prefixed WM
ORSTOM: Office de la Recherche Scientifique et Technique d'Outre Mer [now IRD, see above]
PRI: Paleontological Research Institute, Ithaca, New York
RGM: Nationaal Naturhistorisch Museum, Leiden, paleontological collections [formerly in Rijksmuseum van Geologie en Mineralogie]
RMNH: Nationaal Naturhistorisch Museum, Leiden, Recent collections [formerly in Rijksmuseum van natuurlijke Historie]
SMF: Senckenberg Museum, Frankfurt-am-Main
UMML: University of Miami Marine Laboratory, Miami
USNM: National Museum of Natural History, Washington, DC
WAM: Western Australian Museum, Perth
ZMA: Zoological Museum, University of Amsterdam
ZSM: Zoologische Staatsammlung München.

Other conventions and abbreviations

Dimensions of specimens are stated in the order H (= height), D (= maximum diameter).

Specimens with the preserved or dried animal or with the operculum retained are identified in the lists of material examined by the abbreviation "lv", whereas empty shells are identified by the abbreviation "dd".

Unless otherwise stated, all types listed under "Type material" have been examined by me.

SYSTEMATIC ACCOUNT

Superfamily TONNOIDEA Suter, 1913 (1825)

Dolioidea Latreille, 1825: 196 (as Doliaria). Type genus *Dolium* Lamarck, 1801 (junior synonym of *Tonna* Brunnich, 1772).

Family CASSIDAE Latreille, 1825

NOMENCLATURE. – Beu (1998b) used the family-group names Tonnoidea and Tonnidae rather than Cassoidea and Cassidae, which were preferred by Bandel & Riedel (1994) and Riedel (1995; 2000). Suter (1913) placed *Dolium* Lamarck, 1801 in synonymy of *Tonna* Brünnich, 1772, and replaced Doliidae Latreille, 1825 with the new name Tonnidae. Tonnidae is in prevailing usage and is to be maintained, with the precedence of Doliidae. The action of Thiele (1929) in placing both families Tonnidae and Cassidae under "Stirps Tonnacea" counts as the first reviser's action under the *Code* (ICZN 1999: Article 24) and is much earlier than those of Bandel & Riedel (1994) and Riedel (1995; 2000). Tonnoidea and Tonnidae therefore remain the valid names for the superfamily and family (see Bouchet & Rocroi 2005). Cassidae is used as a distinct family here.

CLASSIFICATION. – The gastropod Superfamily Tonnoidea traditionally has been thought of, since the influential classifications by Thiele (1929) and Wenz (1938-1944), as including the families Tonnidae Suter, 1913 (1825), Ficidae Meek, 1864 (1840), Cassidae Latreille, 1825, Bursidae Thiele, 1925 and Ranellidae Gray, 1854. Some authors have recognised an additional family Oocorythidae Fischer, 1883, to include *Oocorys* Fischer, 1883 and related genera (e.g., Thiele 1929; Quinn 1980). Beu (1988) began to change the traditional classification by recognising the additional family Personidae Gray, 1854 for *Distorsio* Röding, 1798 and related genera. The most significant change of recent times came, however, when Warén & Bouchet (1990) increased the content of the superfamily by transferring to it the genera *Pisanianura* Rovereto, 1899 and *Akibumia* Kuroda & Habe, 1958, proposed the new genus *Laubierina*, and erected the new family-group taxa Pisanianurinae (within Ranellidae) and Laubierinidae. They also questioned whether family Ficidae was correctly placed in this superfamily. Bandel & Riedel (1994) separated the Laubierinidae from the Tonnoidea (for which they used the name Cassoidea) in its own superfamily, Laubierinoidea. Riedel (1994; 1995; 2000) recognised superfamily Ficoidea to include Ficidae and the new family Thalassocyonidae Riedel, 1995, and altered the traditional classification of the remaining families of Tonnoidea by including subfamily Bursinae in family Ranellidae, and including subfamilies Cassinae, Oocorythinae, Phaliinae and Tonninae in family Tonnidae. Beu (1998a) suggested that Pisanianuridae would be better treated as a family separate from Ranellidae. Most recently, Kantor & Harasewych (2000) have added significantly to the diversity of the Ranellidae by describing the new abyssal Antarctic genus and species *Obscuranella papyrodes*.

The classification adopted here differs from that of Riedel (1995) in that the taxa of Tonnoidea with weakly and essentially spirally sculptured, strongly inflated, subspherical shells he included in four subfamilies within the one family, Tonnidae, are included here in two families, Tonnidae and Cassidae. Three subfamilies of Cassidae also are recognised here, to include combinations of different parts of the formerly recognised families Cassidae and Oocorythidae; *Oocorys* Fischer, 1883, the closely related genus *Dalium* Dall, 1889 and *Eucorys* n. gen. are included in subfamily Oocorythinae.

Riedel (1995, 2000) seems to have regarded teleoconch form alone as the prime criterion for familial classification in the Tonnoidea. The very distinctive Personidae, with their eccentric shell growth, were maintained as a separate family. However, the Ranellidae and Bursidae of previous classifications (e.g., Beu 1998a), with similar, relatively generalised, elongate, coarsely sculptured, muriciform shells, were ranked as subfamilies of Ranellidae. Similarly, the Cassidae (including Oocorythidae) and Tonnidae of previous classifications, with relatively short, subspherical, weakly sculptured shells, very short anterior siphonal canals and predominantly spiral sculpture, all were included in family Tonnidae (as Cassidae). This appears to be a superficial approach to poorly understood relationships; as Beu (1998b: 142) commented, "the phylogenetic relationships of tonnoidean families are to a large degree obscured by their specialisation for markedly different prey". Andrews *et al.* (1999) pointed out evidence for quite different relationships from those suggested by Riedel (1995; 2000). They indicated distinct types of salivary glands in several different tonnoidean families and, in particular, commented on the distinctive foregut glands of *Tonna*, concluding: "All these facts support the idea that the ranellids are the most primitive [tonnoideans] [but note that they were not considering the Laubierinidae], and that *Tonna* is further removed from the cassids than Riedel's (1995) classification implies" (Andrews *et al.* 1999: 13). I therefore retain here the "traditional" tonnoidean families as recognised by Thiele (1929), and modified by Warén & Bouchet (1990) and Beu (1988, 1998a): Ranellidae, Bursidae, Personidae, Laubierinidae (= Pisanianurinae), Tonnidae and Cassidae (within which I include subfamilies Cassinae, Oocorythinae and Phaliinae). The inclusion of Ficidae and Thalassocyonidae in a separate superfamily Ficoidea seems well justified, although Bouchet & Rocroi (2005: 250) synonymised Thalassocyonidae with Ficidae. The relationships of Laubierinidae and Pisanianuridae are considered by Beu & Bouchet (in progress).

There has been much debate since the proposal of *Oocorys* (Fischer, 1883) about the relationships of such tonnoidean genera as *Galeodea* Link, 1807 and *Oocorys*, and whether they belong in the Cassidae or Tonnidae, or in a separate family Oocorythidae. Dall (1909: 67), in an important review of the genera of Cassidae, stated that he could see no reason why *Oocorys* should not simply be regarded as a normal genus of the Cassidae related to *Galeodea*, and this view was supported by Warén & Bouchet (1990) and Beu (1998a). Other authors from Fischer (1883) and Thiele (1929) to Quinn (1980) have regarded *Oocorys* and related genera, such as *Dalium* Dall, 1889 and *Hadroocorys* Quinn, 1980, as constituting a distinct tonnoidean family, Oocorythidae, and Quinn (1980) went so far as to include the genus *Galeodea* in family Oocorythidae. A third view was promoted by Turner (1948) in her revision of western Atlantic Tonnidae, in which she included *Oocorys* in subfamily Oocorythinae in the Tonnidae, implying a closer phylogenetic relationship to *Tonna* and *Eudolium* than to other tonnoideans such as *Cassis* Scopoli, 1777 and *Galeodea*.

The fossil record of Cassidae suggests that *Galeodea* was the ancestor of at least most and probably all of the later members of the family. Possible Cretaceous *Galeodea* species were listed by Riedel (1995: 123). A species I refer to *Galeodea* occurs in Danian (Early Paleocene) rocks of New Zealand (*G. allani* Finlay & Marwick, 1937, type species of *Taieria* Finlay & Marwick, 1937, synonymised here with *Galeodea* as its sole distinguishing character is the lack of a thickened outer lip, and the sole known complete specimen might well be immature). *Galeodea* was almost cosmopolitan by Early to Middle Eocene time, and has suitably plesiomorphic anatomical, radular, opercular and shell characters to be the ancestor of all the other Cassinae. *Echinophoria*, the presumed ancestor of all the other members of subfamily Phaliinae, also was widely distributed by Eocene time, and it is feasible that *Echinophoria* could have evolved from *Galeodea* during Late Cretaceous or Paleocene time by developing a more strongly twisted, deeply notched siphonal canal and a fan-shaped operculum (the most distinctive character of subfamily Phaliinae is the operculum with its nucleus against the centre of the columellar margin). However, the very distinct radulae of *Galeodea* and *Echinophoria* suggest that it is equally feasible that *Echinophoria* developed from a completely different ancestor, and that its teleoconch merely is convergent on that of *Galeodea*. Of course, the fossil record of deep-water taxa such as *Oocorys* and *Dalium* is inadequate to be able to judge their appearance time relative to that of *Galeodea*, and Riedel's (1995) suggestion that *Oocorys* was the ancestral genus of the Tonnidae and the rest of the Cassidae remains feasible. *Oocorys* is the only cassid to retain the plesiomorphic tonnoidean protoconch (multispiral and turbiniform, with reticulate sculpture; Warén & Bouchet 1990), supporting a position near the basal stock of the family. It possibly also might reflect a retreat to very deep water and the consequent retention of plesiomorphic shell characters.

CHARACTERS OF THE SIPHONAL CANAL. — A significant point in the descriptions and taxonomic decisions in this revision is the shape of the flexure in and the length of the anterior (abapical) margin of the aperture, at its junction with the columella. The flexure in many caenogastropods is extended into a semitubular to almost tubular, anterior extension of the shell that protects and perhaps in part supports the siphon. The siphon is the anteriormost part of a creeping aquatic gastropod, a simple fold in the mantle edge that functions as a tube to draw water into the mantle cavity, to enable the animal to sense its environment chemically and to extract oxygen. The corresponding anteriorly prolonged flexure in the shell usually is known as either the siphonal canal or, better, the anterior siphonal canal (as a few tonnoideans, notably all Bursidae, also have a siphonal canal at the posterior end of the aperture). The definition of and description of the length and shape of the anterior siphonal canal is important in this work, and the spectrum of conditions in the various taxa is considered here. Some examples of anterior siphonal canals of Cassidae and Tonnidae are illustrated in Fig. 1, arranged in order from least to most strongly notched and twisted.

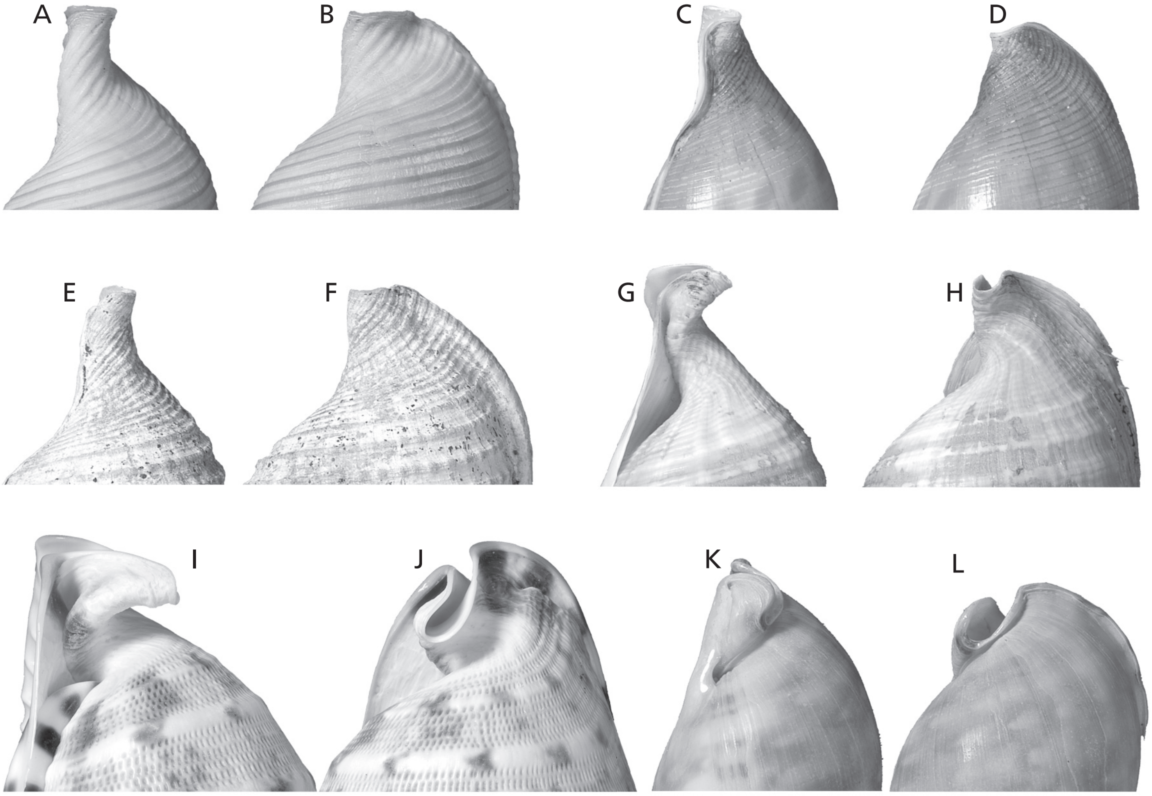


FIG. 1. Anterior siphonal canals of Cassidae and Tonnidae, left and dorsal views in all cases, with anterior to top. Tonnidae. **A**, **B**, *Eudolium bairdii* (Verrill & Smith in Verrill, 1881), 180 m, off Mikawa, Aichi Prefecture, Japan; natural size (NZGS WM12439). Cassidae Cassinae. **C**, **D**, *Sconsia grayi* (A. Adams, 1855), type species of *Sconsia* Gray, 1847; 300 m, off Basse Terre, Guadeloupe, Western Atlantic; natural size (NZGS WM17191). **E**, **F**, *Galeodea leucodoma* Dall, 1907, type species of *Galeoocorys* Kuroda & Habe, 1957, off Tosa Bay, Shikoku, Japan; natural size (NZGS WM8522). **G**, **H**, *Galeodea echinophora* (Linné, 1758), type species of *Galeodea* Link, 1807, 12-15 m, off Cuma, Naples, Mediterranean Sea; natural size (NZGS WM14138). **I**, **J**, *Cassis cornuta* (Linné, 1758), type species of *Cassis* Scopoli, 1777, 15 m, Agat Bay, Guam, Marianas Islands, western Pacific; immature specimen, reduced to X 0.75 (NZGS WM17254). Cassidae Phaliinae. **K**, **L**, *Semicassis labiata* (Perry, 1811), intertidal, point between Middle and North Harbours, Sydney Harbour, New South Wales, Australia, enlarged X 1.25 (NZGS WM12482).

The term “siphonal canal” usually is used for a structure that protrudes anteriorly (abapically) in front of the anterior end of the outer lip; in conventional spire-up apertural view it extends below the base of the outer lip. In some strongly siphonostomatous taxa such as *Murex* (*sensu stricto*), *Haustellum* and *Fusinus* the canal is a long, simple, straight tube extended anteriorly parallel to the axis of coiling of the teleoconch, ending at a simple circle in the dorsoventral plane (normal to the axis of coiling), without a dorsal notch. In these taxa, the exterior shape and sculpture of the anteriormost area of the teleoconch is not interrupted by the growth of the anterior end of the canal. Many other taxa have a siphonal canal that deviates away from the coiling axis - towards the dorsum and a little to the left, in the majority of taxa, so that the siphon can be held more-or-less vertically up in front of the creeping animal. The deviated canals of most taxa end in a dorsal siphonal notch that is more nearly, or in many examples entirely, in the antero-posterior plane than in the dorso-ventral one, i.e., notched into the canal margin behind its anterior end, and lying parallel to the coiling axis rather than normal to it. In these taxa, growth of the anterior end of the canal generates a prominent siphonal fasciole at the anterior end of the main outer wall of the shell. In most taxa the fasciole is distinctively sculptured and in many taxa a prominent, narrow bounding ridge and deep groove on the right side separate it from the shell wall of the last whorl.

A useful taxonomic character in the Cassidae is the shape of the canal and whether or not it is notched, i.e., generates a fasciole as it grows. In *Oocorys* most species lack a siphonal canal, but they retain a deep and, in some species, wide anterior notch at the junction of the outer lip with the columella. The notch is in the dorso-ventral plane, and does not generate a fasciole. In species with a wide notch and an unthickened outer lip, such as *O. grandis* n. sp., the siphonal notch is simple and thin-edged, merely an embayment in the peristome, lying in the vertical plane as the animal progresses. Although they undoubtedly have a siphon, provision of a notch for the extrusion of the siphon in such taxa makes very little impression on the form of the shell. In most other genera included here in subfamilies Cassinae (*Galeodea*, Figs 1E-H; *Sconsia*, Figs 1C, D; *Microsconsia* n. gen.) and Oocorythinae (*Dalium*, *Eucorys* n. gen.) the anterior end of the shell is produced a little and envelopes the siphon slightly to moderately, the resulting canal is only slightly deviated towards the dorsum, and the anterior end is unnotched and still in the vertical (dorso-ventral) plane and does not generate a fasciole. In many species of these genera, a short, open, simple, straight siphonal canal extends below the anterior end of the outer lip in apertural view, although in others (particularly in those species with a widely expanded outer lip) a clearly constricted canal is present but it does not extend below (in front of) the outer lip. Some species of *Galeodea*, particularly Eocene-Oligocene ones, have a long siphonal canal deviated strongly towards the dorsum and/or to the left, and extending well in front of the outer lip (although this has probably developed independently in several groups of *Galeodea* species, i.e., they form a grade rather than a clade). In *Cassis* (Figs 1I, J), the siphonal canal is twisted strongly towards the dorsum, its now anterior-posteriorly aligned anterior end is still unnotched, but the degree of twisting of the canal is great enough to generate a rounded but not distinctively sculptured fasciole that is well separated from the previous whorl.

A marked contrast with the usual condition in the Cassinae is seen in the genera of subfamily Phaliinae and in *Cypraecassis* Stutchbury, 1837 in the Cassinae, in which the siphonal canal is deviated and twisted extremely towards the dorsum, curling up above the anterior end of the shell, and notched deeply in the antero-posterior plane (e.g., *Semicassis*, Figs 1K, L). It is separated from the wall of the last whorl only by a narrow ridge and a deep groove or, in a few species, is fused to the wall of the last whorl. This allows the siphon to be extended more directly vertically than in most Cassinae, or even behind the vertical. The siphonal notch in these taxa generates a prominent, distinctively sculptured fasciole bounded on its posterior (adapical) side by a sharp, narrow ridge in most species; the fasciole of many species is sculptured with prominent spiral cords or, in many species, prominent transverse ridges. A significant point here is that, although these taxa are strongly and prominently siphonostomatous, the siphonal canal does not extend below (in front of) the anterior end of the outer lip; indeed, in some species the canal is not visible in apertural view. Whether the canal extends in front of the aperture or not therefore is of little significance in taxonomic descriptions; some cassid species have a prominent but strongly twisted canal visible only from the dorsum or from the left side, other species have a moderately long canal that extends below (in front of) the aperture, others have a short but definite canal that does not extend as far anteriorly as the anterior end of the outer lip, and others again have no canal at all, only an anterior embayment in the apertural margin, lying in the vertical plane as the animal progresses.

The length and degree of twisting of the anterior siphonal canal are important, also, for providing the means of distinguishing relatively coarsely sculptured fossil Tonnidae (species of *Eudolium* Dall, 1889a; Figs 1A, B) from similarly sculptured fossil species of the cassine genus *Galeodea* Link, 1807. Species referred to *Galeodea* all have at least slight twisting of the anterior siphonal canal, and if relatively long, the canal is quite strongly twisted towards the dorsum and, in most species, towards the left. In contrast, species with a completely straight, obvious anterior siphonal canal (i.e., untwisted, and protruding at least slightly below the base of the outer lip) are all referred to *Eudolium*. This classification means that many species are referred to *Eudolium* (Tonnidae) that previously have been included in *Galeodea* (Cassidae) [e.g., "*Galeodaria*" *shubutensis* (Aldrich, 1885) (MacNeil & Dockery 1984: 107, pl. 4, figs 1, 2; pl. 49, figs 9, 10), *G. shubutensis gardnerae* MacNeil & Dockery (1984: 108, pl. 17, figs 1-4) and *G. tricarinata* (Conrad, 1860) (MacNeil & Dockery 1984: 108, pl. 29, figs 20-22; pl. 49, figs 11-13), from the Oligocene of the southeastern USA; *Cassidaria javana* Martin (1879: 46, pl. 8, figs 9, 9a, 10) from the Miocene of Java – a synonym of *E. crosseanum* (Monterosato, 1869); Vos 2007); and *Cassidaria erbi* Haanstra & Spiker (1932: 1321, figs 16-18) and the closely similar *Galeodea errabunda* Beets (1943a: 439, figs 7-9), both from the Miocene of Indonesia]. This implies a rather longer and more complex fossil history for the Tonnidae than previously had seemed the case. However, the type species of *Galeodaria* Conrad, 1865, *Morio petersoni* Conrad *in* Wailes, 1854, is a species of *Galeodea* (Schenck 1926: pl. 14, figs 3, 4; Dockery 1977: pl. 8, figs 1A, B), so *Galeodaria* is a synonym of *Galeodea* rather than an earlier name for *Eudolium* Dall, 1889.

PROTOCONCH FAMILIAL CHARACTERS. — The very large protoconch of Tonnidae, with a prominent, superficially smooth periostracum, is another useful familial character distinguishing such genera as *Eudolium* from almost all cassids including *Galeodea*. However, a note of warning is called for about confusion with *Cypraecassis* in the Cassinae. Abbott (1968: pl. 42) illustrated the enormous protoconch of *C. rufa* (Linné, 1758) and related species. Observation of a small juvenile specimen of *C. rufa* (MNHN, MUSORSTOM 9 stn CP 1227, off Hiva Oa, Marquesas Islands, 84-85 m, protoconch plus 0.75 teleoconch whorls; H 12.0, D 8.2 mm, protoconch H 6.83, D 5.46 mm) demonstrated that at this size, the very shallowly notched anterior end and the unusual, bucciniform shape make recognition as a cassid difficult. The lightly shouldered outline, tapering very gradually to an only slightly constricted anterior end, resembles neither a tonnid nor any other cassid. However, the already well-developed, long, buccinid-like siphonal fasciole and the deep, long false umbilicus are unique characters that make recognition easy. Other very distinctive characters are the sculpture, which is entirely of very low, wide, closely spaced spiral bands (or very narrow spiral grooves), the simple aperture with lightly thickened inner and outer lips, and the faintly but evenly maculated external coloration, of spiral rows of pale, almost white spots on a pale red-brown ground. This largest of all tonnoidean protoconchs shows the care needed in familial assignment, as well as the great ontogenetic change undergone by *Cypraecassis* species. The very strongly twisted, dorsally directed, notched anterior siphonal canal of adult specimens of *C. rufa* develops through gradual ontogenetic change, and it is important to note that the juvenile teleoconch starts life with an anterior siphonal canal in a similar condition to that of adult specimens of species of *Cassis* and *Sconsia*. However, all other taxa I am aware of with large, superficially smooth protoconchs belong in the Tonnidae, so this is a useful familial character, keeping in mind the even larger protoconch of some species of *Cypraecassis*.

RADULAR SUPPORT AND LINKING STRUCTURES. — Cassids have typical taenioglossan radulae, with seven teeth in each row (one central tooth, and one lateral and two marginal teeth on each side), attached to a basal membrane in long columns of identical teeth. For this project radulae were examined of most of the nominal *Galeodea* species, most *Oocorys* species, *Eucorys bartschi* (Rehder, 1943) and *Echinophoria wyvillei* (and the nominal species, here regarded as a synonym, *E. kurodai*). The radulae of *Sconsia grayi* A. Adams, 1855 (= *S. striata* (Lamarck, 1816)) and *Dalium solidum* Dall, 1889 also were illustrated by Bayer (1971) and that of *D. solidum* by Okutani (1983: 268). Along with the laubierinid radulae examined by Beu & Bouchet (in progress), these demonstrate a range of structures for

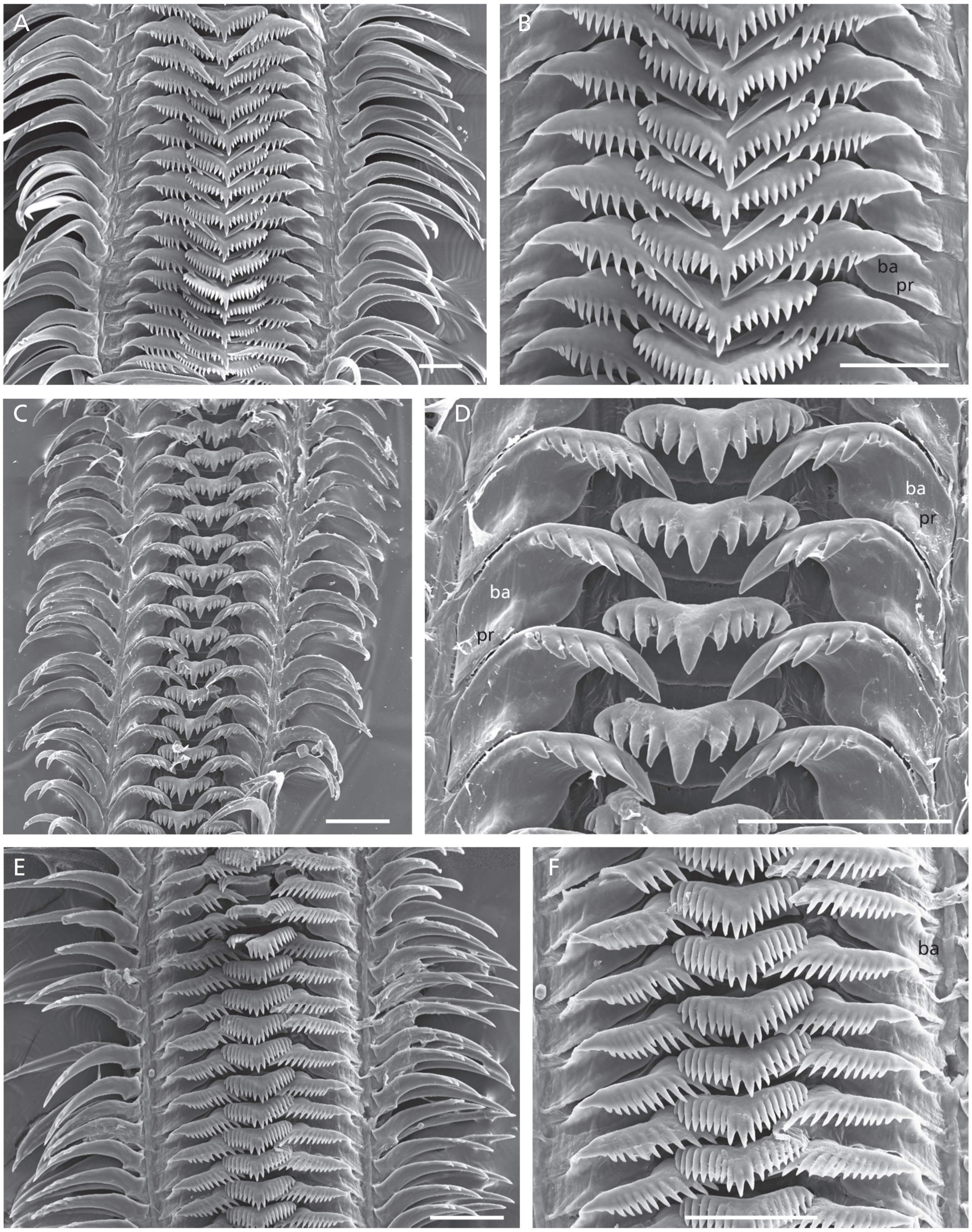


FIG. 2. Radulae of *Galeodea* species (all sale bars = 100 μm). **A**, **B**, *G. alcocki* (E. A. Smith, 1906), MUSORSTOM 3 stn CP 118, 448-466 m, Manila Bay, Philippines; part of whole radula (**A**) and central and lateral teeth enlarged (**B**). **C**, **D**, *G. echinophora* (Linné, 1758), *LOPHELIA* MILLENNIUM '99 stn 93, 320 m, between Capraia and Gorgona Islands, Tyrrhenian Sea, Mediterranean; part of whole radula (**C**) and central and lateral teeth enlarged (**D**). **E**, **F**, *G. keyteri* (Kilburn, 1975), crevettière stn 78, 530 m, off Madagascar; part of whole radula (**E**) and central and lateral teeth enlarged (**F**). Linking structures discussed in text are labelled: ba – bevelled, concave area on outer edge of lateral tooth, receiving base of inner marginal tooth; pr – pushing ridge on base of lateral tooth.

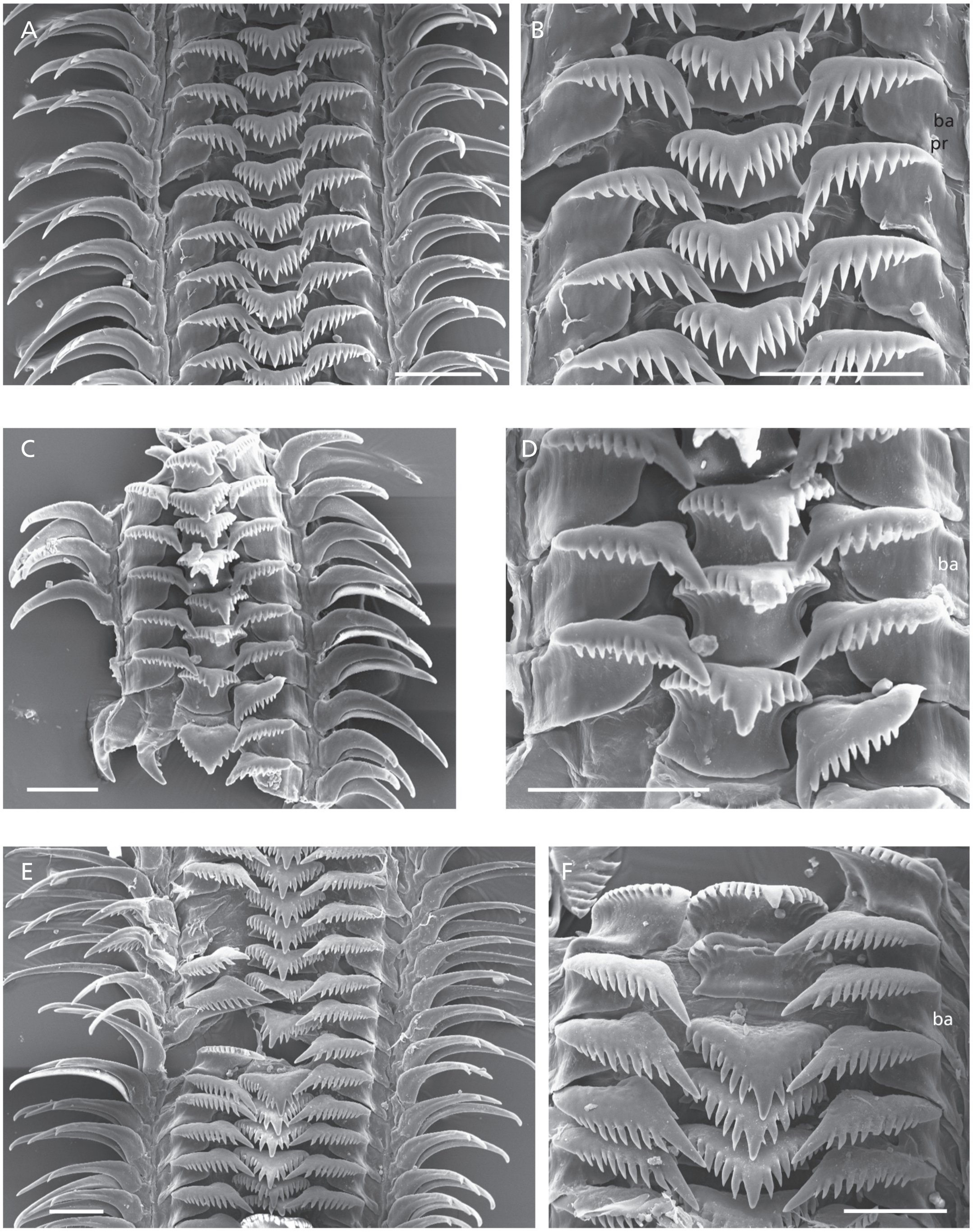


FIG. 3. Radulae of *Galeodea* and *Eucorys* species (all scale bars = 100 μm). **A**, **B**, *G. leucodoma* Dall, 1907, KARUBAR stn CP 54, 836-869 m, Tanimbar Islands, Indonesia; part of whole radula (**A**) and central and lateral teeth enlarged (**B**). **C**, **D**, *G. triganceae* Dell, 1953, NMNZ, NZOI stn R119, off Mayor Island, New Zealand; part of whole radula (**C**) and central and lateral teeth enlarged (**D**). **E**, **F**, *Eucorys bartschi* (Rehder, 1943), stn 71A7-11, 636 m, Gulf of Mexico; part of whole radula (**E**) and central and lateral teeth enlarged (**F**). Linking structures discussed in text are labelled: ba – bevelled, concave area on outer edge of lateral tooth, receiving base of inner marginal tooth; pr – pushing ridge on base of lateral tooth.

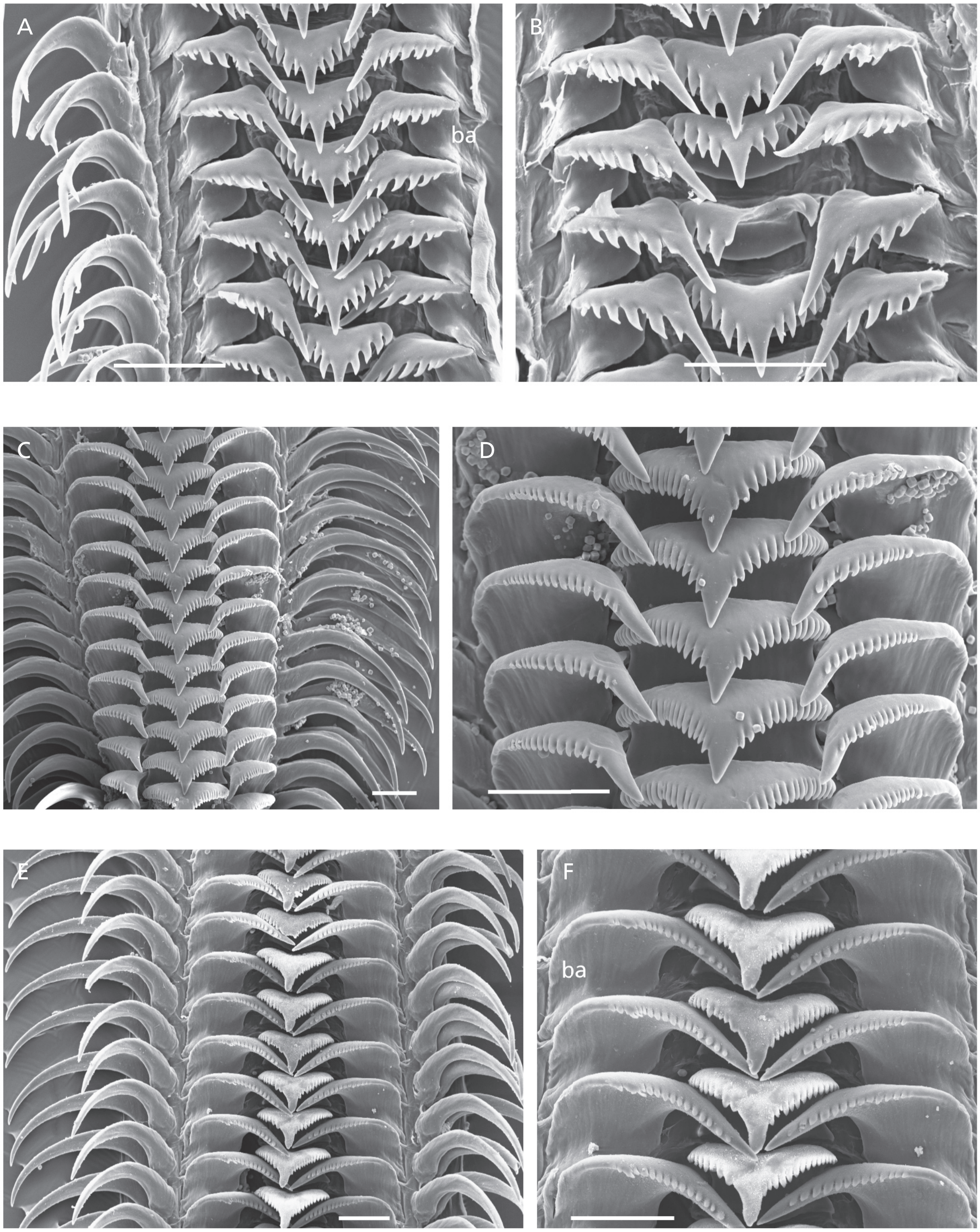


FIG. 4. Radulae of *Oocorys* species (all scale bars = 100 µm). **A**, **B**, *O. clericus* Quinn, 1980, LGL Cruise 3.MMS.C3, 764-841 m, Gulf of Mexico, part of whole radula (**A**) and central and lateral teeth enlarged (**B**). **C-F**, *O. grandis* n. sp.; **C**, **D**, paratype MNHN 20183, Safari 2 stn CP 2, 3625 m, central Indian Ocean, part of whole radula (**C**) and central and lateral teeth enlarged (**D**). **E**, **F**, WALDA stn CY 05, 2953 m, SE Atlantic Ocean off Namibia, part of whole radula (**E**) and central and lateral teeth enlarged (**F**). Linking structures discussed in text are labelled: ba - bevelled, concave area on outer edge of lateral tooth, receiving base of inner marginal tooth.

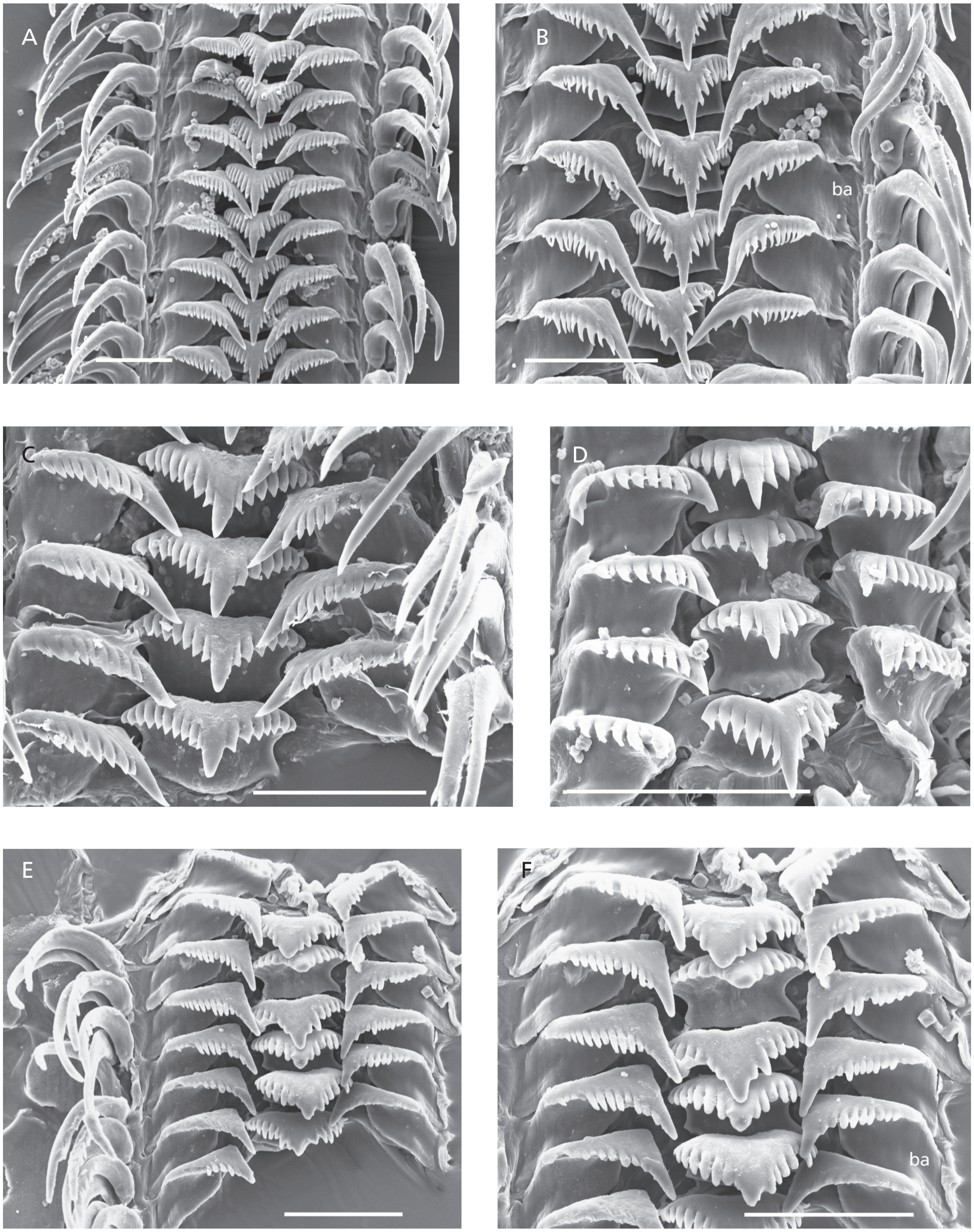


FIG. 5. Radulae of *Oocorys* species (all scale bars = 100 µm). **A-D**, *O. sulcata* (Fischer, 1883); **A**, **B**, "*abyssorum* form", DEMERABY stn CP 06, off northern Brazil, 4450 m, part of whole radula (**A**) and central and lateral teeth enlarged (**B**); **C**, "typical" form, DEMERABY stn CP 03, 4430 m, off Brazil, central and lateral teeth; **D**, thick-shelled specimen, BIOGEOCAL stn CP 226, 1990-2100 m, Loyalty Basin, New Caledonia, central and lateral teeth. **E**, **F**, *O. verrillii* (Dall, 1889), MUSORSTOM 6 stn CP 427, 800 m, New Caledonia, part of whole radula (**E**) and central and lateral teeth enlarged (**F**). Linking structures discussed in text are labelled: ba - bevelled, concave area on outer edge of lateral tooth, receiving base of inner marginal tooth.

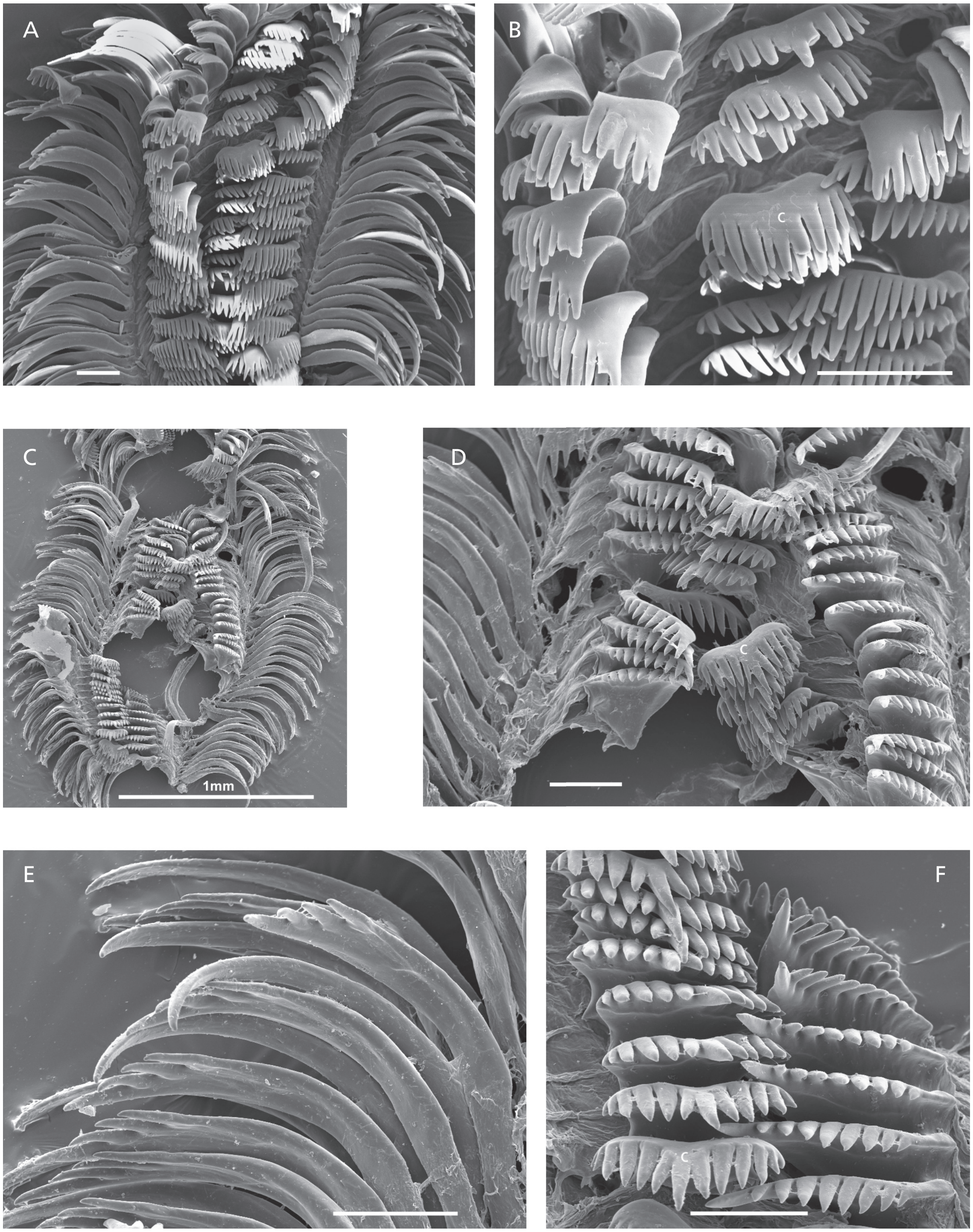


FIG. 6. Radulae of *Echinophoria wyvillei* (Watson, 1886) (all scale bars = 100 µm, except Fig. 6C, scale bar = 1 mm). **A**, **B**, "*kurodai* form", MUSORSTOM 4 stn CP 170, 480 m, New Caledonia; part of whole radula (**A**) and central and lateral teeth enlarged (**B**). **C**-**F**, "typical *wyvillei* form", Soela stn S1/84/76, 348-350 m, NW of Augustus Island, northern Western Australia (WAM 880-84); part of whole radula (**C**), central and lateral teeth enlarged (**D**, **F**) and left lateral teeth enlarged (**E**). Abbreviation: c - central tooth.

linking and supporting the teeth within one column and row, and so strengthening the whole operation of the radula as a food-gathering apparatus. The most obvious structure is the hooks on the posterior edge of the basal plate of the central teeth, quite obviously seen in some preparations (Beu & Bouchet in progress; particularly in *Pisanianura breviaxis* (Kuroda & Habe, 1961)) to hang over the succeeding tooth in the column in some Laubierinidae. Very similar, larger, interlocking hooks are present in all Bursidae and Tonnidae, but have not been observed or reported in any of the other tonnoidean families.

A range of more subtle structures was observed in cassids during the present research. Perhaps the most obvious is the relationship in undisturbed radulae (i.e., undisturbed other than having the inward-bent lateral and marginal teeth folded out for SEM examination) between the lateral and central teeth in one row. The inner edge of the head (large, inward-directed, main cutting portion) of each lateral tooth fits neatly into the waist-like embayment in the side of each central tooth in most radulae examined (Figs 3D; 5C, D), and this close fit appears to be general in the Cassidae, at least. The waist presumably is primarily a necessity when linking a flat, horizontal (in the plane of the radular membrane) basal plate to a strongly elevated, down-curved cutting head of triangular section. In most of the taxa studied here, the cutting head of the central tooth is supported by a major, deep, but relatively narrow central ridge beneath the head. It appears likely that the fit of the heads of the lateral teeth into the waisted sides of the central teeth provides lateral linkage across one radular row between the three main cutting teeth.

In some of the radulae examined (most obviously in *Galeodea echinophora* (Linné, 1758), Fig. 2D) a prominent ridge is obvious on the side of each basal plate of the lateral teeth, closely parallel to the upper edge of the succeeding lateral tooth in each column. This ridge apparently provides a support structure (labeled a pushing ridge here) to maintain the spacing and position of the lateral teeth during operation. This pushing ridge therefore functions in a similar way to the basal hooks on the central teeth of laubierinids, bursids and tonnids – keeping all the teeth in the column in a fixed position, so they essentially function as one unit during feeding.

A third type of linking structure that is obvious in most cassid radulae takes the form of a bevelled, weakly concave area on the outer edge of each lateral tooth, evidently receiving and supporting the inner edge of the base of the inner marginal tooth in the same row. This portion of the lateral tooth outside the obvious cutting head is particularly obvious in *Galeodea alcocki* (Smith, 1906), *G. keyteri* (Kilburn, 1975), *G. leucodoma* Dall, 1907 and *G. triganceae* Dell, 1953 (Figs 2B, E; 3B, D) but occurs also in all *Oocorys* species and in *Eucorys bartschi*. The lower edge of this linking embayment forms the pushing ridge in *G. echinophora*, and a similar but much lower pushing ridge is present in many of the other radulae examined. In *Oocorys grandis* n. sp., a short linking embayment occurs in the outermost edge of the radula of the smaller specimen examined (Fig. 4F) but is scarcely discernible in the large, adult radula (Fig. 4D), although the inner edges of the lateral teeth clearly fit into the waisted sides of the central teeth in this species. In *Echinophoria wyvillei* (Figs 6A-D, F), all such structures are less easily visible because of the complex teeth, with many long, narrow denticles confusing the field of view, and it is unclear whether such linking structures are present. A range of structures seems to exist in most cassid radulae to provide some rigidity to the teeth during their operation by linking the teeth in one column and between neighbouring rows.

EXTERNAL ANATOMY. — External anatomical characters were examined of alcohol-fixed specimens of all available species, in order to compare the exteriors and the mantle organs of taxa in the three supposed subfamilies. Stylised sketches are provided here (Figs 7-10) of most of the animals examined. These allow some conclusions to be made about similarities and differences between the subfamilies. However, animals were available for only several species of *Galeodea*, most species of *Oocorys* and one species of *Echinophoria* (the *kurodai* and *wyvillei* forms attributed here to one species, *Echinophoria wyvillei*). It would be useful to include further taxa in future comparisons.

The first obvious point is that the external anatomy, including mantle organs, of all species attributed here to *Galeodea* is strikingly similar. Drawings are provided of *G. bituminata* (Martin, 1933) (Figs 7A, B), *G. keyteri* (Figs 7C, D), *G. leucodoma* (Fig. 7E) (type species of *Galeoocorys* Kuroda & Habe, 1957) and *G. alcocki* (Fig. 8A), although animals also were examined of *G. echinophora* and *G. triganceae*. All have similar proportions, obvious black eyes,

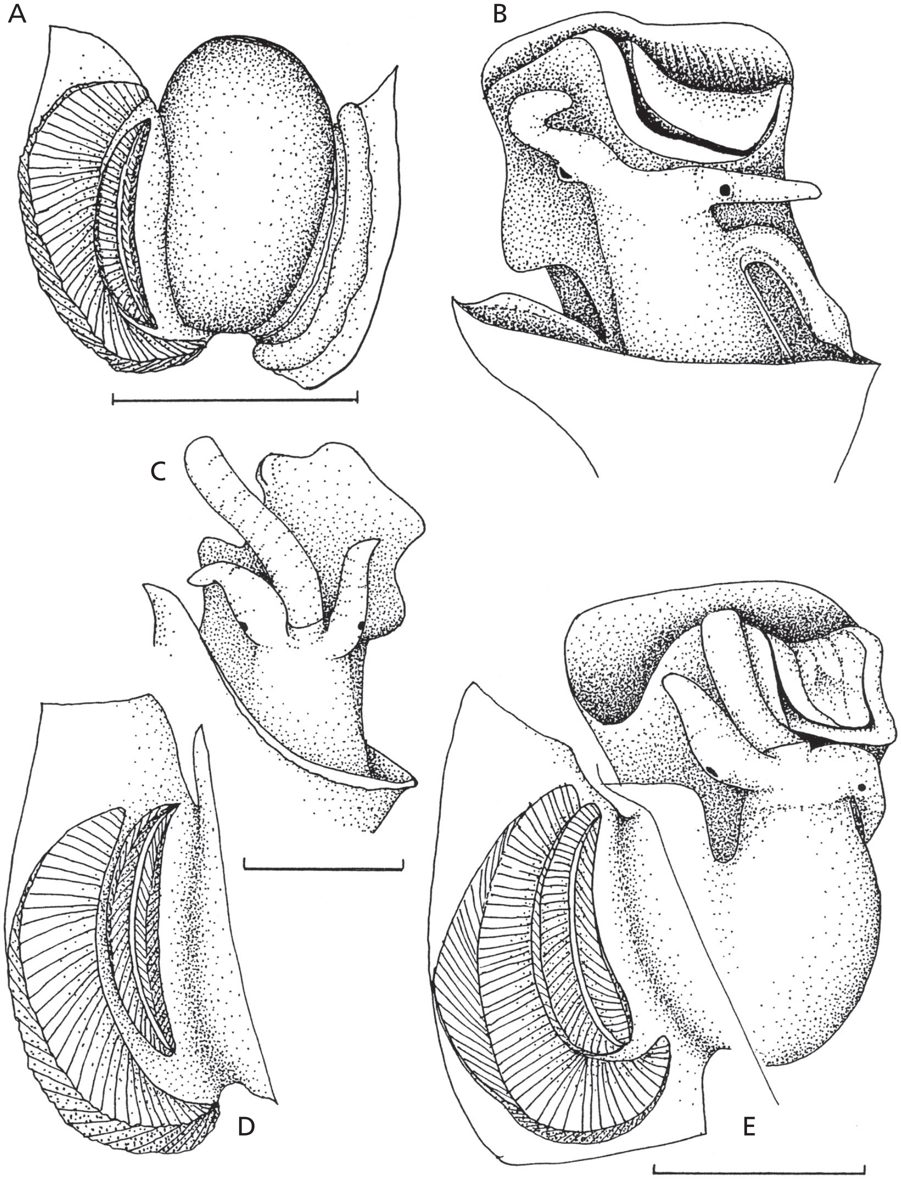


FIG. 7. *Galeodea* species, sketches of external anatomy, with mantle opened by mid-dorsal incision (all scale bars = 10 mm). **A**, **B**, *Galeodea bituminata* (Martin, 1933), male, MUSORSTOM 8 stn CP 1051, off Vanuatu, 555-558 m; **A**, mantle organs, with head rotated forwards; **B**, head-foot; proboscis retracted. **C**, **D**, *Galeodea keyteri* (Kilburn, 1975), crevettière stn 78, off Madagascar, 530 m; **C**, head-foot, proboscis partly everted; **D**, mantle organs of left side. **E**, *Galeodea leucodoma* Dall, 1907, KARUBAR stn CP 54, off Tanimbar Islands, Indonesia, 836-869 m; head-foot, proboscis partly everted (right mantle skirt not shown), and mantleorgans of left side.

similar narrow cephalic tentacles, a long, narrow, cylindrical proboscis and a weakly curved osphradium that is markedly smaller and narrower than the ctenidium. The left leaflets of the osphradium are slightly longer than the right ones. The few in which a penis has been seen have a small, simple, cylindrical one with an open seminal groove and an obvious terminal papilla, apart from *G. alcocki*, in which the distal half of the penis is slightly flattened. Most species examined had a simple inhalant siphon, but it was considerably more complicated in *G. alcocki* than in the other species examined. This highly contractile organ is difficult to study in preserved material, however. The radula and the external appearance of the animal of *Sconsia grayi* (Bayer 1971: figs 17A, 20D) seem to be essentially identical to those of *Galeodea* species.

In contrast, the external anatomy of *Oocorys* species (most illustrated in Figs 8B, 9) is consistently different from that of *Galeodea* and *Sconsia*. All have similar proportions, shorter and wider than animals of *Galeodea* species. All completely lack obvious, pigmented eyes. The cephalic tentacles are more narrowly pointed and bear more obvious contraction ridges and grooves than in *Galeodea* species, indicating that the tentacles are more extensible and contractile than those of *Galeodea*. The proboscis is narrow and cylindrical, but seems to be much shorter than that of *Galeodea* species in all animals examined. The osphradium is strongly curved or even, in *O. clericus* Quinn, 1980, recurved (weakly S-shaped), and markedly larger in relation to the ctenidium than in *Galeodea* species, although it is similar in having the left leaflets slightly to significantly longer than the right ones. Male specimens have been seen of several species; the penis is shorter, wider and more flattened than in *Galeodea*, and weakly to strongly triangular in outline. The seminal groove is open throughout the mantle cavity and penis as in *Galeodea* and all other cassids I am aware of. Almost all specimens examined had a thickened, obvious, permanent inhalant siphon in the mantle edge. The overall appearance that results from all these relatively minor differences is quite markedly different from that of *Galeodea* and *Sconsia*, and with the radular and opercular differences, supports the recognition of a separate subfamily, Oocorythinae, for *Oocorys* and the closely related genera *Eucorys* and *Dalium*.

Too few animals of species of Phaliinae have been available to be able to reach many conclusions about the distinctiveness of this subfamily. One alcohol-fixed male was examined of each of the *kurodai* and *wyvillei* forms of *Echinophoria wyvillei* (Fig. 10), but preservational differences made them hard to evaluate. Both were hardened through preservation in ethanol and had strongly retracted into their shells, producing numerous folds that would not be present in life. No obvious differences could be detected between them, except for the much larger penis of the *kurodai* than

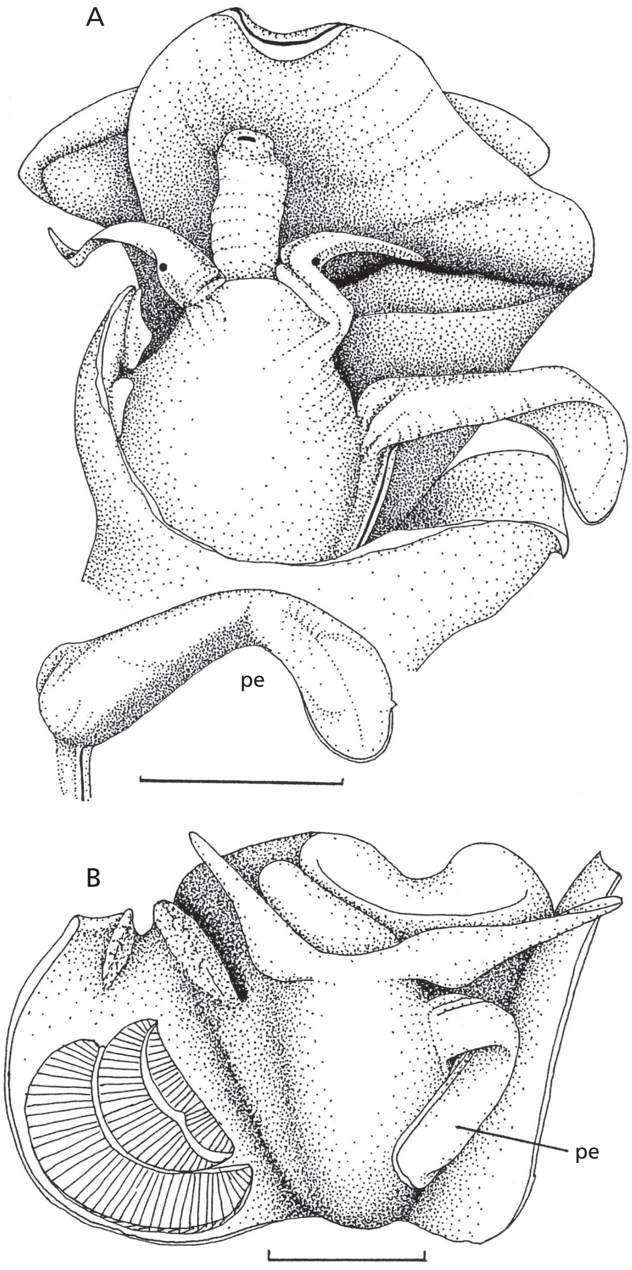


FIG. 8. *Galeodea* and *Oocorys* species, sketches of external anatomy of males. **A**, *Galeodea alcocki* (E. A. Smith, 1906), *Soela* stn S1/84/70, NW of Collier Bay, northern Western Australia, 496-494 m; head-foot, proboscis partly everted, and penis turned to left to show flattened extremity (WAM 1077-84; scale bar = 10 mm). **B**, *Oocorys sulcata* Fischer, 1883, BIOGEOCAL stn CP 266, Loyalty Basin, off New Caledonia, 1990-2100 m; mantle opened by mid-dorsal incision, proboscis fully everted (scale bar = 5 mm). Abbreviation: pe – penis.

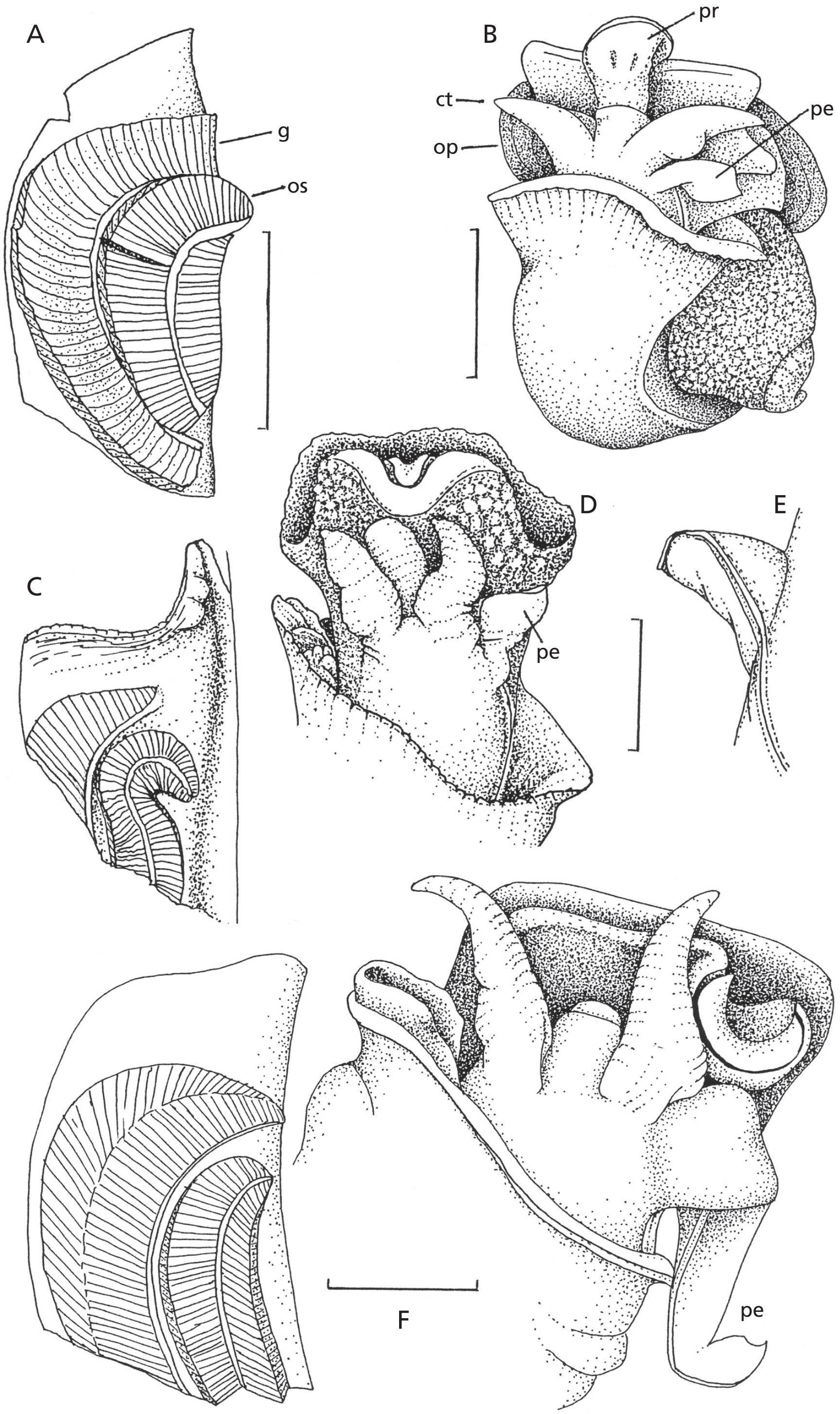


FIG. 9. *Oocorys* species, sketches of external anatomy of males. **A**, **B**, *Oocorys verrillii* (Dall, 1889), BIOCAL stn CP 72, New Caledonia, 2100-2110 m (both scale bars = 5 mm); **A**, mantle organs of left side, reflected after mid-dorsal incision; **B**, entire animal, dorsal view; proboscis fully everted. **C**-**E**, *Oocorys clericus* Quinn, 1980, LGL Cruise MMS-C3, Gulf of Mexico, 764-841 m (scale bar = 10 mm); incomplete specimen, broken through ctenidium and osphradium during removal from shell; **C**, mantle organs of left side, reflected after mid-dorsal incision; **D**, head-foot, proboscis everted; **E**, penis turned back to display seminal groove (enlarged X 1.5 compared with other drawings). **F**, *Oocorys grandis* n. sp., paratype MNHN 20183, SAFARI 2 stn CP 2, central Indian Ocean, 3625 m (scale bar = 10 mm); head-foot; proboscis partly everted, with buccal mass protruding; and mantle organs of incomplete left side, reflected after mid-dorsal incision (ctenidium has leaflets folded at half their length). Abbreviations: ct – cephalic tentacle; g – ctenidium; os – osphradium; op – operculum; pe – penis; pr – proboscis.

of the *wyvillei* form, perhaps merely reflecting the collecting time in relation to breeding season. They both have obvious, black eyes (as do all other species of Phaliinae I am aware of), and cephalic tentacles with longer, more narrowly pointed extremities than in *Galeodea* species, but without the prominent contraction ridges and grooves of *Oocorys* species. An obvious but simple, permanent inhalant siphon in the mantle edge and the proportions of the osphradium to the ctenidium seem to be very similar to those of *Galeodea* species. The two penes seen are long, regularly tapering rather than cylindrical, and as in all other cassids seen, have a widely open seminal groove. The two forms of *E. wyvillei* examined also are inseparable on the grounds of opercular and radular characters (see below). These characters indicate a closer similarity in gross external characters between Cassinae and Phaliinae than between either of them and Oocorythinae, clearly indicating that Oocorythinae is a distinctive subfamily of Cassidae. However, the radula of *Echinophoria wyvillei*, with its very much more numerous, long, brush-like denticles than in *Galeodea* or *Oocorys* on all except the outer marginal teeth, is the most distinctive of the radulae of these three subfamilies, supporting the separation of Phaliinae.

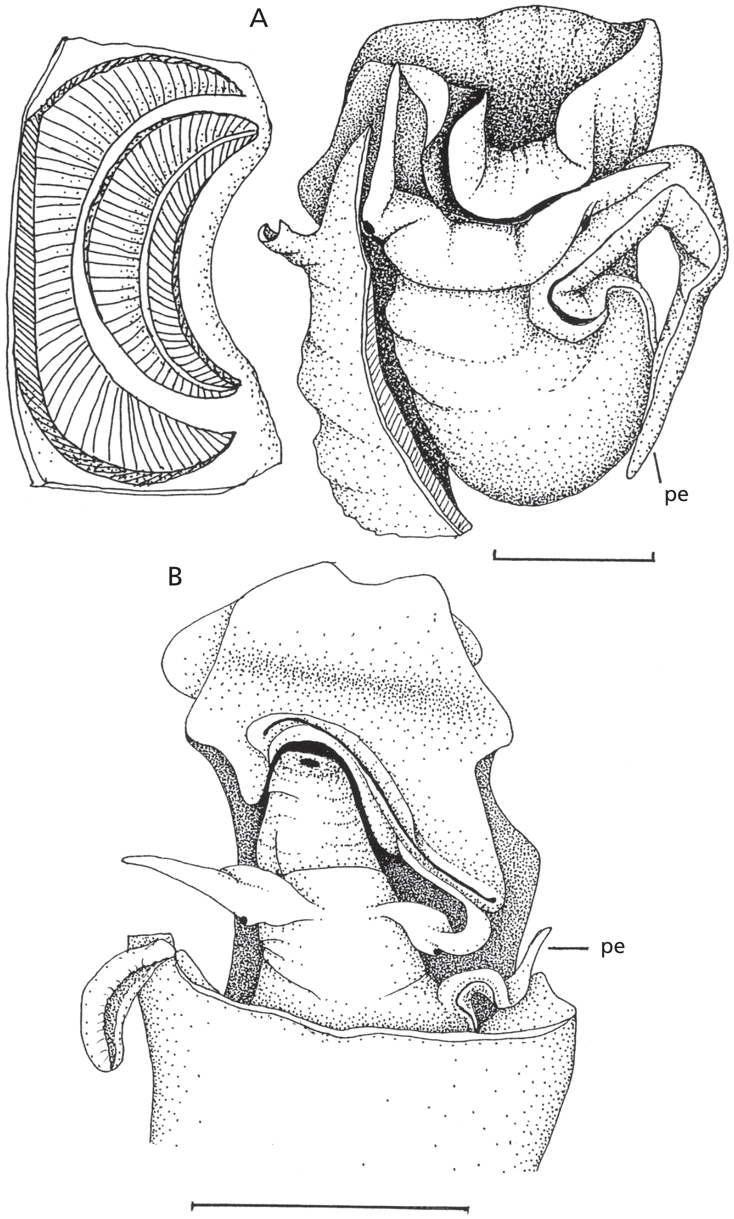


FIG. 10. *Echinophoria wyvillei* (Watson, 1886), sketches of external anatomy of males (of animals hardened by preservation in ethanol). **A**, smaller "*kurodai* form", MUSORSTOM 4 stn CP 170, New Caledonia, 480 m; head-foot, proboscis retracted, mantle opened by mid-dorsal incision (right mantle skirt not shown), and mantle organs of left side (scale bar = 10 mm). **B**, larger *wyvillei* form, WAM 880-84, *Soela* stn 01-84-076, trawled NW of Augustus Island, N Western Australia, 348-350 m; head-foot, proboscis partly everted (scale bar = 20 mm). Abbreviation: pe – penis.

Subfamily CASSINAE Latreille, 1825

DEFINITION. — Subfamily Cassinae is considered here to include the taxa of Cassidae with an oval operculum having its nucleus subcentral or near the anterior end, and situated abaxially, i.e., towards the outer lip of the shell aperture, rather than against the centre of the inner lip as in all Phaliinae; without an initial spiral area of growth lines on the operculum, as in Oocorythinae; with a relatively long proboscis, rather than the relatively short, wide proboscis of Oocorythinae; with obvious large black eyes; with a narrowly cylindrical to weakly compressed penis; with a relatively small, weakly curved rather than larger, strongly curved to weakly S-shaped osphradium; and with a subspherical to moderately elongate shell of which the anterior siphonal canal is straight or at most moderately twisted and without an anterior dorsal notch, except for the strongly twisted and notched anterior canal of adult specimens of species of *Cypraecassis*.

REMARKS. — This definition includes in subfamily Cassinae the genera *Cassis* Scopoli, 1777, *Cypraecassis* Stutchbury, 1837, *Galeodea* Link, 1807, *Sconsia* Gray, 1847 and *Microsconsia* n. gen., but excludes the genera *Dalium* Dall, 1889, *Eucorys* n. gen., and *Oocorys* Fischer, 1883, placed below in subfamily Oocorythinae. In this order, these genera provide a more-or-less continuous series of decreasing complexity of shell sculpture and of decreasing elaboration of the apertural lips and ventral callus shield. It probably is no accident that this also is a series of increasing depth of habitat; the taxa inhabiting the shallowest water presumably require the greatest armouring of the aperture to prevent predation by shell-peeling crabs, such as *Calappa* (Zipser & Vermeij 1978; Vermeij 1978: 40-46; Vermeij 1987: 104-107, the deep sea discussed as a refuge). The shallow-water genera *Cassis* and *Cypraecassis* also have the most strongly twisted anterior siphonal canals of these genera. This indicates that these genera independently have acquired a moderately strongly twisted anterior canal from an ancestral genus (apparently *Galeodea*), whereas the still more strongly twisted anterior canal present in all members of subfamily Phaliinae seem likely to have been inherited from the apparently ancestral genus *Echinophoria*.

Although a detailed phylogeny of the Tonnoidea has not been determined, Riedel (1995: fig. 43) published a generalised one for the tonnoidean families, based on all possible teleoconch, protoconch, radular, opercular and anatomical characters. As he pointed out (Riedel 1995: 124, fig. 42), it agrees closely with the times of appearance of taxa in the fossil record, providing support for the validity of his phylogeny. Riedel (1995) considered Oocorythinae to be the stem group of the Cassidae, probably evolving during Campanian (Late Cretaceous) time. He depicted both Cassinae and Phaliinae branching off Oocorythinae during Early to Middle Eocene time (Riedel 1995: figs 42, 43) and referred to Late Cretaceous and Paleocene species of *Galeodea* (Riedel 1995: 123). However, this branching date is based on the inclusion of *Galeodea* in Oocorythinae. The present work demonstrates conclusively that *Galeodea* belongs in the Cassinae, rather than in the Oocoythinae where it was placed by Quinn (1980) and Riedel (1995), so the earliest fossils of Cassidae actually belong in Cassinae. Possibly this merely means that an offshore habitat had already been adopted by Oocorythinae by early Cenozoic time. The simple phylogenetic hypothesis followed here is that the similar, coarsely sculptured teleoconchs of *Galeodea* and *Echinophoria*, along with an at least Middle Eocene time of appearance of both genera, indicates that these genera were the stem groups of the Cassinae and Phaliinae, respectively. They differ primarily in the more strongly twisted anterior canal of *Echinophoria* than of *Galeodea*, and in their distinct opercula. The other genera of Cassinae and Phaliinae are assumed to have evolved from these stem groups simply through loss of teleoconch sculptural complexity. This informal phylogeny agrees with Riedel's (1995) in paralleling the fossil record of first appearances, and is followed in assessing relationships in the present paper.

The supposed cassid genus *Microcassis* Paulmier (1997: 738; type species: *Microcassis colettae* Paulmier, 1997; Recent, Martinique) was thought by Paulmier (1997) to be related to *Cypraecassis* Stutchbury, 1837. However, Wakefield *et al.* (2002) demonstrated that this nominal species is a synonym of *Pachybathron cassidiforme* Gaskoin, 1853, and that *Pachybathron* is a close relative of *Persicula* Schumacher, 1817 (Cystiscidae, Neogastropoda).

Genus ***GALEODEA*** Link, 1807

Galeodea Link, 1807: 133. Type species (by monotypy): *Galeodea echinophora* (Linné, 1758) (= *Buccinum echinophorum* Linné, 1758), Pliocene-Recent, southern Europe-Mediterranean.

Synonyms:
Morio Montfort, 1810: 479. Type species (by monotypy): *Morio echinophora* Linné, 1758 (= *Buccinum echinophorum* Linné, 1758).

Cassidaria Lamarck, 1816: 3. Type species (by subsequent designation, Woodward, 1851: 115): *Cassidaria echinophora* Linné, 1758 (= *Buccinum echinophorum* Linné, 1758).

Echinora Schumacher, 1817: 75, 249. Type species (by monotypy): *Echinora tuberculosa* Schumacher, 1817 (= *Buccinum echinophorum* Linné, 1758).

Echinophora Latreille, 1825: 194 (?emendation of *Echinora* Schumacher, 1817; the reason for the introduction of this name is not stated by Latreille).

Galeodaria Conrad, 1865: 26. Type species (by monotypy): *Morio petersoni* Conrad *in* Wailes, 1854, Late Eocene, southeastern USA (**new synonym**).

Doliopsis Conrad, 1865: 141. Type species (by monotypy): *Doliopsis quinquecosta* Conrad, 1865 (= internal mould of *Morio petersoni* Conrad *in* Wailes, 1854; MacNeil & Dockery 1984: 123), Late Eocene, southeastern USA (junior primary homonym of *Doliopsis* Vogt, 1852 (Tunicata); senior primary homonym of *Doliopsis* Monterosato, 1872) (**new synonym**).

Taieria Finlay & Marwick, 1937: 67. Type species (by original designation): *Taieria allani* Finlay & Marwick, 1937, Early Paleocene, New Zealand (**new synonym**).

Mambrinia Gardner, 1939: 23. Type species (by original designation): *Cassidaria planotecta* Meyer & Aldrich, 1886, Middle Eocene, southeastern USA (**new synonym**).

Gomphopages Gardner, 1939: 25. Type species (by original designation): *Galeodea* (*Gomphopages*) *turneri* Gardner, 1939, Middle Eocene, Texas, USA (**new synonym**).

Caliagaleodea Clark, 1942: 118. Type species (by original designation): *Galeodea* (*Caliagaleodea*) *californica* Clark, 1942, Eocene, western USA (**new synonym**).

Galeoocorys Kuroda & Habe, 1957: 27. Type species (by original designation): *Galeodea leucodoma* Dall, 1907, Recent, western Pacific [not available from Kira (1955: 43), not accompanied by a statement "purporting to differentiate the taxon" (ICZN 1999: Article 13.1] (**new synonym**).

DEFINITION. — *Galeodea* is a highly speciose, almost cosmopolitan genus (taking the many fossil species into account) recognisable by its sculpture of many narrow, rather widely spaced, prominent spiral cords, strengthened or grouped into wider cords at the nodule rows in many species, and raised into 1-5 or more rows of narrowly rounded, small to quite large nodules on the last whorl of most species; by its moderately long, narrow, slightly twisted, unnotched anterior siphonal canal, rather than the very strongly twisted, deeply notched, fasciolate, dorsally directed anterior canal of the superficially similar phaliine genus *Echinophoria*; by its weakly thickened and slightly flared to prominently varicate outer lip, with ridges or nodules on the inner edge in many species; and by its narrowly oval operculum (with the upper left margin weakly to moderately deeply embayed to accommodate the parietel bulge in most species) with its nucleus at or near the anterior third to half of the height near the right (abaxial) opercular margin.

SYNONYMY. — The apertural characters show quite a wide range of variation in *Galeodea*, and several of those that I regard as merely species-level characters within one genus previously have been used to distinguish several supposed genera. In particular, whether the inner lip is widened into a raised, thickened collar, or ventral shield, free from the previous whorl over the neck, or is merely a thin glaze adherent to the previous whorl, and whether the outer lip is strongly thickened, nodulose and reflected or is merely smooth and slightly reflected have been used by Kuroda & Habe (1957) to separate *Galeoocorys* from *Galeodea*. Kuroda & Habe (1957) also regarded *Galeoocorys* as an "oocoryid", i.e., more closely related to *Oocorys* than to *Galeodea*. However, specimens of *G. leucodoma* with preserved animals studied here demonstrate that this species has the elongate operculum (without a spiral initial area), prominent black eyes, and all other external anatomical characters of *Galeodea,* and so Dall's (1907) original position in *Galeodea* was correct. Even the species of this group with no outer lip thickening at all, such as *G. allani* (Finlay & Marwick, 1937), Early Paleocene of New Zealand (Beu & Maxwell 1991: pl. 2l s) (type species of *Taieria*), seem best regarded as falling within the one genus *Galeodea*. Most specimens of the Recent New Zealand species *Galeodea triganceae* Dell, 1953 have only a weakly thickened outer lip that is scarcely reflected at all, and yet this species is closely similar to the other Recent species in opercular, radular and all other characters, and clearly belongs in *Galeodea*, despite its thin outer lip. Possible Late Cretaceous species of *Galeodea* were discussed by Dall (1909), Finlay & Marwick (1937: 67) and Riedel (1995: 123). *Galeodea* (*Caliagaleodea*) was proposed for a Californian Eocene species with an unusually low spire and smooth spiral cords, but again it is similar to some southeastern North American, English and Paris Basin Eocene species and seems to be merely another synonym of *Galeodea*. Some other Early Cenozoic groups are more distinctive, and at first sight seem worthy of subgeneric rank within *Galeodea*, particularly *Mambrinia* Gardner (1939: 23), proposed for *Cassidaria planotecta* Meyer & Aldrich, 1886, a US Gulf Coast Eocene species with a greatly elongated siphonal canal. Some European Eocene *Galeodea* species have long, weakly twisted siphonal canals and might also be placed in *G.* (*Mambrinia*) (e.g., Paris Basin and English Eocene species; Cossmann & Pissarro 1911, in 1907-1913, pl. 34; Wrigley 1934). However, it seems likely that at least some of these species independently have developed a long anterior canal from distinct ancestors, and including them all in *G.* (*Mambrinia*) would make it polyphyletic. *Mambrinia* then is probably a further synonym of *Galeodea*, but this requires much more research, and the taxonomy of Eocene *Galeodea* species is beyond the scope of this paper. The additional subgenus *Gomphopages* Gardner (1939: 25) is very similar to *Mambrinia* and presents the same difficulties. However, if restricted to US Gulf Coast species, both *Mambrinia* and *Gomphopages* might well prove to be minor monophyletic groups within *Galeodea*.

The genus *Pseudogaleodea* Nagao (1932: 46) was based on a Senonian (Late Cretaceous) species, *P. tricarinata* Nagao, 1932, originally recorded from Sakhalin, and since recorded from eastern Russia (Blank 1980). The strongly tricarinate shape and the thickened outer lip give *P. tricarinata* a superficial resemblance to *Galeodea*, particularly to some of the Paris Basin Eocene species with prominent, smooth spiral cords, but Squires & Saul (2003: 54) pointed out that it has a rather long, completely untwisted anterior siphonal canal; they suggested that it belongs in the Ficidae. However, Nagao (1932: 46) described the shell as “all over encrusted with a thin film of deposit so as to obliterate the sutures and minor ornamentation”. A thin surface callus hiding the suture is clearly visible in some of Nagao’s (1932: pl. 8, figs 2, 7) illustrations. There is therefore little doubt that *Pseudogaleodea* belongs in the Apporrhaidae near *Pugnellus* Conrad, 1860 and *Conchothyra* Hutton, 1877. It may be noted that *Bulbificopsis garza* Squires & Saul (2003: 54) also clearly is not a ficid. The thick shell and coarse sculpture show that this species belongs among the “neogastropods”, in the Buccinoidea, *sensu lato*, near *Melongena* Schumacher, 1817, *Hemifusus* Swainson, 1840 and *Busycon* Röding, 1798.

The genus *Coalingodea* Durham (1942: 186) has been used only for the type species, the Californian Eocene species *Galeodea tuberculiformis* Hanna, 1924. This species (Vokes 1939: 149, pl. 19, figs 19, 21, 23-27; Durham 1942: pl. 29, figs 5, 9) retains all varices throughout ontogeny, has fine, beaded spiral cords and two or three widely spaced rows of rounded nodules on the last whorl, and has fine honeycomb sculpture on the spire whorls. It closely resembles some Paris Basin and English Eocene species of *Cassis*, and appears to be a normal Eocene species of *Cassis*, *sensu stricto*, rather than related to *Galeodea*.

PROTOCONCH. — The protoconchs of all the Recent *Galeodea* species I have examined (abraded or corroded in some specimens) demonstrate almost no specific characters, unlike almost all other tonnoidean genera. The very small, blunt, paucispiral protoconchs of less than one whorl in *G. echinophora* (Warén & Bouchet, 1990: fig. 120) and *G. rugosa* (Linné, 1771) (Bouchet & Warén 1993: figs 1930, 1932) are almost identical to those of all the other species I have examined, the only character varying slightly being the height (the degree of protrusion of the nucleus). The protoconch of a specimen of *G. echinophora* is illustrated here (Figs 11A, C, E) for comparison with that of *Microsconsia limpusi* n. gen., n. sp. (Figs 11B, D, F). The one exception I have noted in protoconch characters is in the colour; almost all species have a uniform white or cream protoconch, whereas that of some specimens of *G. maccamleyi* Ponder, 1983 is deep reddish or purplish brown (Kreipl 1997: pl. 9, fig. 20). Solsona I Masana (1999: figs 14, 15) illustrated a different protoconch for a Pliocene specimen attributed to *Galeodea echinophora*. It has about 1.25 whorls, with a narrower, much lower initiation than that of *Galeodea*, and evidently is an abraded protoconch of *Echinophoria intermedia* (Brocchi, 1814). Hughes (1986a) demonstrated that, as might be expected from the very small, few-whorled protoconch, *G. echinophora* has intracapsular development. However, Hughes (1986b: 200) also demonstrated that newly hatched young of *G. echinophora* "secrete mucous strings that serve as drogues, carrying the tiny snails along in water currents". Thus both planktotrophy and intracapsular development can allow dispersal, and

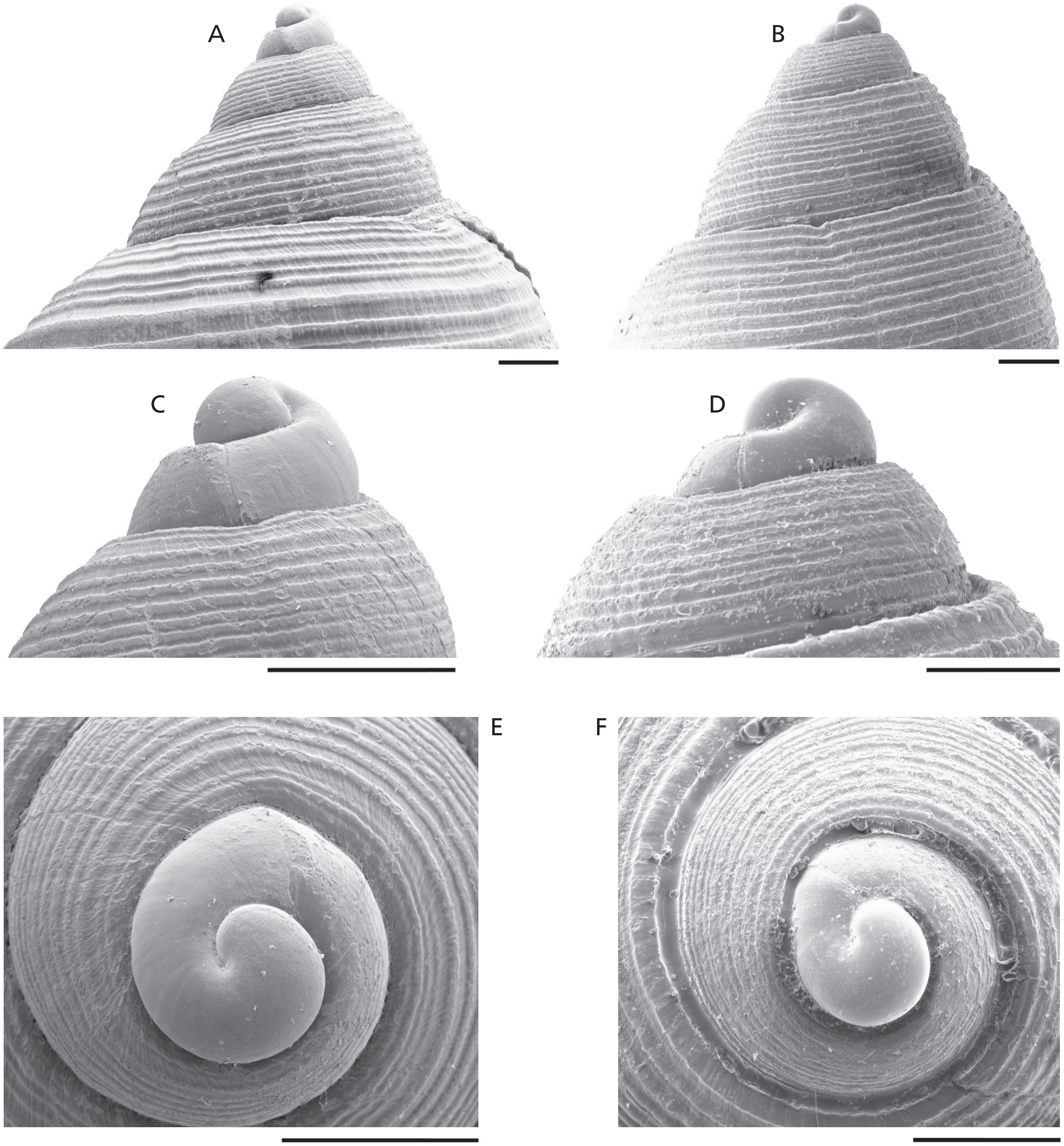


FIG. 11. Protoconchs of *Galeodea* and *Microsconsia* (all scale bars = 1 mm). **A**, **C**, **E**, *Galeodea echinophora* (Linné, 1758), *LOPHELIA* MILLENNIUM '99 stn 93, 320 m, between Capraia and Gorgona Islands, Tyrrhenian Sea, Mediterranean; lateral views X 7 (**A**) and X 20 (**C**), apical view X 20 (**E**). **B**, **D**, **F**, *Microsconsia limpusi* n. gen., n. sp., paratype, trawled in 190-192 m, SE of the Swain Reefs, southeastern Queensland, Australia (MNHN 20181); lateral views X 7 (**B**) and X 18 (**D**), apical view X 18 (**F**).

this “drogue” mechanism presumably explains the wide distribution of such western Pacific species as *G. bituminata* and *G. alcocki*, which occur throughout the western Pacific archipelagos from southern Japan to northern Western Australia.

The Recent species recognised in Galeodea, with their main synonyms, are:

Galeodea alcocki (Smith, 1906) (= *nipponica* Sakurai & Habe, 1961, = *beui* Kreipl & Alf, 2002), western Pacific.
G. bituminata (Martin, 1933) (= *carolimartini* Beets, 1943, = *echinophorella* Habe, 1961, = *marginalba* Yamamoto & Sakurai, 1977, = *noharai* Noda, 1980, = *echinophorella suzumai* Sakurai, 1984), Miocene-Recent, western Pacific.
G. echinophora (Linné, 1758), Mediterranean.
G. hoaraui Drivas & Jay, 1989, Réunion.
G. keyteri (Kilburn, 1975) (= *ferrarioi* Bozzetti, 1989), western Indian Ocean.
G. leucodoma (Dall, 1907) (= *granulosa* Schepman, 1909), western Pacific.
G. maccamleyi Ponder, 1983, southeast Queensland, Australia.
G. plauta n. sp., northwest North Island, New Zealand.
G. rugosa (Linné, 1771) (= *tyrrhena* Gmelin, 1791), western Mediterranean and Ibero-Moroccan Gulf.
G. triganceae Dell, 1953, eastern New Zealand.

Assuming that the synonymies suggested above are correct, only six species of *Galeodea* live in the tropical Indo-West Pacific, and the total living fauna consists of only 10 species - 2 further species around New Zealand and 2 in the Mediterranean Sea.

Galeodea alcocki (Smith, 1906)

Figs 2A, B; 8A; 12; 13A; 21C

Morio alcocki Smith, 1906: 170.

Synonyms:
Galeoocorys nipponica Sakurai & Habe *in* Habe, 1961: 43, pl. 20, fig. 1, appendix p. 15.
Galeodea beui Kreipl & Alf, 2002: 83, figs 1, 2.

Other references:
Morio alcocki - Schepman 1909: 124, pl.10, fig. 6.
Oocorys alcocki - Turner 1948: 189. – Kreipl 1997: 69, unnumbered fig. (copy of Schepman 1909). – Kosuge & Dan 1983: 122, pl. 40, figs 1, 2.
Galeoocorys nipponica - Habe 1964: 67, pl. 20, fig. 1. – Kosuge 1985: 59, pl. 22, fig. 5. – Romagna-Manoja 1989: 28, 4 unnumbered figs. — Hasegawa & Saito 1995: 32, pl. 4, fig. 3.
Galeodea (*Galeoocorys*) *nipponica* - Wilson 1993: 231, pl. 38, figs 7a, b. – Kreipl 1997: 29, pl. 10, fig. 24. – Okutani 2000: 273, pl. 135, fig. 3.
Galeodea nipponica - Higo *et al.* 2001: 46, fig. G1541.

TYPE MATERIAL. – *Morio alcocki*: holotype presumably in Zoological Survey of India, Calcutta (not seen); from *Investigator* stn 280, 11°29’45”N, 80°02’30”E, off the Coromandel coast, India, in 446 fathoms (802 m). – *Galeoocorys nipponica*: holotype NSMT Mo. 70275 (Figs 12E, H), *c.* 200 m, off Cape Ashizuri, Kochi Prefecture, Shikoku, Japan. – *Galeodea beui*: holotype MNHN 4137, from off northwest Panglao, Philippine Islands, lv in tangle nets in 450-550 m.

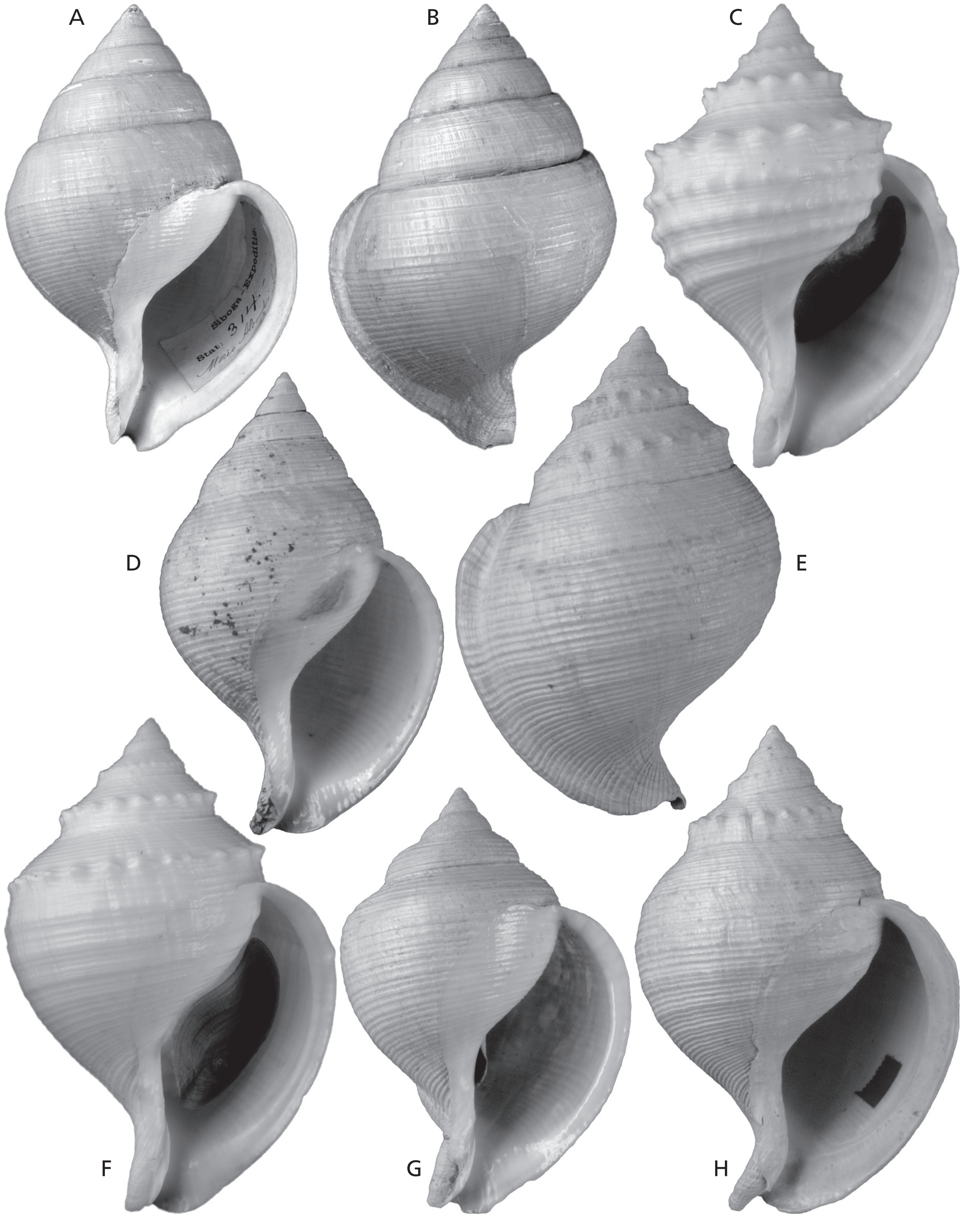


FIG. 12. *Galeodea alcocki* (E. A. Smith, 1906). **A**, **B**, specimen with narrowly channelled suture, *Siboga* stn 314, eastern Flores Sea, Indonesia, 694 m (ZMA; H 104.8 mm; X 0.67); **C**, **F**, between Mermaid and Scott Reefs, N of Broome, northern Western Australia, 470-520 m (young specimens, both at natural size; C, H 73.4 mm; F, H 78.0 mm); **D**, MUSORSTOM 3 stn CP 118, Manila Bay, Philippines, 448-466 m (H 107.4 mm; X 0.67). **E**, **H**, *Galeodea nipponica* (Sakurai & Habe in Habe, 1961), holotype off Cape Ashizuri, Kochi Prefecture, Japan, 200 m (NSMT Mo.70275; H 105.1 mm; X 0.67); **G**, specimen with second varix on dorsum, KARUBAR stn CC 10, Tanimbar Islands, Indonesia, 229-289 m (H 99.0 mm; X 0.67).

OTHER MATERIAL EXAMINED. – **Philippine Islands.** MUSORSTOM 3: sta CP 118, Manila Bay, 11°58'N, 121°06'E, 448-466 m (1 lv). – PANGLAO 2005: stn CP 2389, Bohol Sea, 9°28'S, 123°38'E, 784-786 m (1 large lv, no axial sculpture at all) ; stn CP 2405, Maribojoc Bay, Bohol Sea, 387-453 m, 9°39'S, 123°46'E (2 lv).

Indonesia. Specimen illustrated by Schepman (1909: 124, pl. 10, fig. 6), from *Siboga* stn 314, in 694 m, eastern Flores Sea, Indonesia, 7°36'S, 117°38.8'E (ZMA). – KARUBAR: stn CC 10, Tanimbar Islands, eastern Indonesia, 5°21'S, 132°30'E, 229-289 m (1 lv); stn CC 57, 8°19'S, 131°53'E, 603-620 m (1 dd); stn CP 69, 8°42'S, 131°53'E, 356-368 m, (1 lv); stn CP 75, 8°46'S, 131°36'E, 452-451 m (1 lv).

Northwestern Australia. Between Mermaid and Scott Reefs, N of Broome, 470-520 m (2 lv); 450 m, off Broome (1 lv, coll. G. Kronenberg, no. 1967); 500 m, off Dampier, *ex* W. G. Buick coll. (1 dd, WAM); F/V *Soela* cruise, Feb. 1984, coll. S. Slack-Smith stn 01-84-052, WNW of Lacépède Archipelago, 15°46.4'S, 12°39.9'E to 15°43.8'S, 120°39.8'E, 446-450 m (2 dd, WAM 1559-84); stn 01-84-070, NW of Collier Bay, 13°44.0'S, 122°13.3'E to 13°22.3'S, 122°14.7'E, 496-494 m (3 dd, WAM 1840-84; 1 dd, WAM 1841-84; 3 lv, WAM 1077-84); stn 01-84-094, W of Lacépède Archipelago, 16°55.8'S, 119°53.9'E to 17°01.8'S, 119°51.3'E, 426 m (1 dd, WAM 810-84; 1 lv, WAM 887-84); stn 01-84-106-112, W of Lacépède Archipelago, 16°57.4'S, 119°52.0'E to 16°55.5'S, 119°56.0'E, 434-432 m (3 dd, WAM 1918-84); stn 01-84-089, W of Lacépède Archipelago, 16°55.1'S, 119°54.6'E to 16°56.0'S, 119°51.5'E, 432-434 m (1 dd, second varix retained, WAM 808-84); stn 01-84-116, W of Lacépède Archipelago, 16°55.4'S, 119°52.3'E to 16°57.4'S, 119°46.4'E, 436-438 m (2 dd, WAM 1856-84; 5 lv, WAM 897-84; 1 dd, WAM 1857-84); stn 01-84-082A, NNW of Cape Leveque, 14°35.8'S, 121°49.4'E to 14°37.2'S, 121°47.4'E, 300-304 m (1 dd, WAM 812-84); stn 01-84-085, NW of Cape Leveque, 14°52.2'S, 121°41.7'E to 14°53.7'S, 121°39.9'E, 224-220 m (1 dd, WAM); stn 01-84-067, NW of Bathurst Island, 14°21.5'S, 122°02.4'E to 14°22.3'S, 122°01.0'E, 348-350 m (1 dd, WAM 1646-84); stn 01-84-075, NW of Augustus Island, 13°51.4'S, 123°01.8'E to 13°52.8'S, 122°59.0'S, 308-306 m (1 dd, WAM); stn 01-84-066, NW of Augustus Island, 14°29.4'S, 122°01.4'E to 14°28.4'S, 122°03.2'E, 296-304 m, (1 dd, WAM); stn 01-84-059, NW of Beagle Bay, 15°12.8'S, 122°05.9'E to 15°10.1'S, 121°09.2'E, 410-404 m (1 dd, WAM 803-84); stn 01-84-117, 16°57'S, 119°48'E to 16°52'S, 119°51'E, 452-450 m (1 dd, WAM 1888-84; 7 lv, small to large, WAM 898-84); stn 01-84-113, W of Lacépède Archipelago, 16°57'S, 119°51'E to 16°55'S, 119°54'E, 436 m (1 dd, WAM 1872-84; 1 dd, WAM 1870-84); stn 01-84-05, W of Lacépède Archipelago, 16°56.9'S, 119°52.0'E to 16°55.8'S, 119°53.8'E, 432 m (1 dd, WAM 815-84); stn 01-84-095, W of Lacépède Archipelago, 16°55.1'S, 119°55.0'E to 16°56.8'S, 119°51.1'E, 432-434 m (1 dd, WAM 807-84); stn 01-84-054, WNW of Lacépède Archipelago, 15°51.25'S, 120°44.3'E to 15°54.38'S, 120°45.3'E, 350-348 m (1 dd, WAM); stn 01-84-118, W of Lacépède Archipelago, 16°54'S, 119°52'E to 16°59'S, 119°47'E, 440 m (2 lv, WAM 819-84); stn 01-84-079, NNW of Augustus Island, 13°17.0'S, 122°37.4'E to 13°18.0'S, 122°35.8'E, 494-484 m (9 lv plus 1 lv *G. leucodoma*, WAM 910-84); stn 01-84-060, NW of Beagle Bay, 15°08.6'S, 121°03.4'E to 15°06.0'S, 121°06.6'E, 504-500 m (1 lv, WAM 1087-84); stn 01-84-081, NW of York Sound, 12°54.4'S, 123°00.2'E to 12°50.6'S, 123°00.4'E, 452-462 m (1 lv, WAM 963-84); stn 01-84-058, NW of Beagle Bay, 15°12.8'S, 121°15.9'E to 15°10.4'S, 121°09.2'E, 410-404 m (1 lv, WAM 895-84); stn 01-84-098, W of Lacépède Archipelago, 16°56.7'S, 119°51.2'E to 16°55.1'S, 119°55.1'E, 432 m (1 lv, WAM 884-84); stn 01-84-076, NW of Augustus Island, 13°44.5'S, 122°56.5'E to 13°40.8'S, 122°59.3'E, 348-350 m (1 lv, WAM 888-84); stn 01-84-120, W of Broome, 17°59'S, 118°11'E to 18°01'S, 118°08'E, 530-560 m (1 lv, WAM 889-84); stn 01-84-057, NW of Beagle Bay, 15°13.5'S, 121°08.9'E to 15°15'S, 121°06.5'E, 352 m (1 lv, WAM 890-84); stn 01-84-121, W of Roebuck Bay, 18°04'S, 118°14'E to 18°00'S, 118°19'E, 400-396 m (1 lv, WAM 892-84); F/V *Courageous*, prawn trawler, cruise Aug. 1983, coll. P. Berry & N. Sinclair stn 023, SW of Imperieuse Reef, Rowley Shoals, 17°51'S, 118°19'E, 431-433 m, (1 dd, WAM); stn 026, as above, 18°05'S, 118°08'E, 440-442 m (1 lv, WAM 3296-83); stn 028, as above, 18°15'S, 118°02'E, 410-414 m (1 lv, WAM 3306-83); stn 029, NW of Karratha, 18°44'S, 116°59'E, 404-406 m (1 lv, WAM 3311-83); stn 099, Rowley Shoals area, 276-497 m (2 lv plus 1 lv *G. leucodoma,* WAM 3248-83) (72 specimens).

DISTRIBUTION. – *Galeodea alcocki* is recorded from southern Japan, the Philippine Islands, the Bay of Bengal, Indonesia and northwestern Australia, and presumably occurs throughout the western Pacific archipelagos between these extremes, in depths of about 200-500 m. It seems to be rather rare in the northwestern Pacific but is common on the far northwestern shelf of Western Australia (72 specimens examined in WAM) and in the adjacent area of Indonesia.

DIMENSIONS. – *Galeodea alcocki*, holotype: H 99, D 61 mm; *Galeoocorys nipponica*, holotype: H 105.1, D 70.5 mm; *Galeodea beui*, holotype MNHN 4137: H 81.2, D 52.4 mm; *Siboga* stn 314: H 104.8, D 69.2 mm; MUSORSTOM 3 stn CP 118, Philippines: H 107.4, D 66.3 mm, MNHN; northwestern Australia: H 78.0, D 52.0 mm; H 73.4 mm, D 49.5 mm. Kreipl (1997: 29) recorded specimens 60-110 mm high.

REMARKS. — Unfortunately, the holotype of *Galeodea alcocki* has not been illustrated, despite Schepman's (1909: 124) statement that it would appear in the "Illustrations of the Zoology of the *Investigator*" (Schepman's illustration, the only published one even though not of the holotype, was copied by Kreipl 1997: 69). Presumably, the lack of its inclusion in "Illustrations of the ... *Investigator*" implies that the authors of that work considered that Schepman's (1909: pl. 10, fig. 6) illustration adequately conveyed the characters of this species. Based on the *Siboga* specimen, *G. alcocki* is recognised easily by its tall spire for the genus, with unusually straight outlines, its strongly rounded periphery and rapidly contracted base, producing a relatively short last whorl and a relatively long, narrow, weakly twisted anterior canal, the lack of a raised inner lip collar over the neck, the complete lack of nodules or, indeed, of any axial sculpture other than growth lines, the lightly flared, almost smooth and only weakly thickened outer lip, the sculpture of rather wide and low, irregular, rather widely spaced, smooth, rounded spiral cords, and its narrowly but obviously channelled suture. Most of the surface of the *Siboga* specimen bears a pale yellowish olive, smooth and lightly polished periostracum; the periostracum bears low, narrow spiral and axial ridges in the sutural channel. Smith (1906: 170) clearly distinguished this species from *G. rugosa* by the following characters: "with a rather longer spire, a broader aperture, finer liration, and a more deeply channelled suture" [than in *G. rugosa*]. There is little doubt, then, that the *Siboga* specimen represents the real *G. alcocki*, as it is the one Recent *Galeodea* specimen I have seen with an obviously channelled suture.

The main differences between the supposedly distinct species *Galeodea alcocki* and *G. nipponica* are the taller spire and the more sharply contracted base of *G. alcocki* and its unique, narrowly channelled suture, but the spiral sculpture also is weaker, smoother and less regular in *G. alcocki*, and *G. alcocki* lacks the small, sharp peripheral nodules present on most specimens of *G. nipponica*. Most specimens identified as *G. nipponica*, particularly young ones, also have one to several lower rows of small, sharp nodules below the peripheral one, although these fade out down the shell in most large specimens. However, a few specimens have no nodules at all. One Philippines specimen (Fig. 12D) is very similar to the *Siboga* specimen of *G. alcocki* in all characters except for its less sharply contracted base and the lack of the narrow sutural channel. Dr Tilo Eggeling (Braunschweig, Germany) has pointed out that several other specimens are known (in private collections) that are similar to the *Siboga* specimen in most characters (tall, narrow shape, weak spiral sculpture, lack of obvious nodules) but that lack the sutural channel, and several have very small nodules on early spire whorls. These were collected in deep water off the Philippine Islands, and it seems likely that the extreme "*alcocki* form" is conspecific with *G. nipponica*, and is based on deep-water specimens that are taller, narrower and more weakly sculptured than the usual trawled shells. It therefore is concluded that *G. nipponica* is part of the variation of the single species *G. alcocki*.

Galeodea beui was distinguished by its thin shell, its unusually elongate shape for a *Galeodea* species, its tall, narrow spire, its long, very straight anterior siphonal canal, the four rows of small, sharp, closely spaced nodules around the last whorl, and the narrowly raised collar on the inner lip. It is unusual in having no nodules at all on spire whorls, but small, well-developed nodules on the last whorl. The teleoconch is stark white, and there seem to be no characters distinguishing the single known specimen from *G. alcocki*.

ANATOMY. — The toughened animal (preserved in ethanol) was extracted from a Western Australian specimen (WAM1077-84) of the "*nipponica* form" of *Galeodea alcocki* (Fig. 8A; shell in Fig. 13A). The relatively large size and preservational artefacts make the external anatomy and mantle organs difficult to compare in the species examined, but *G. alcocki* shows no marked distinctions from other *Galeodea* species. The bipectinate osphradium is slightly asymmetrical, and markedly shorter than the ctenidium. The penis is relatively large for *Galeodea*, and is unique among the *Galeodea* penes examined in having a flattened and slightly laterally extended outer half (shown in two sketches in Fig. 8A).The seminal groove is clearly open throughout the mantle and along the penis, as in all cassid animals examined in this study. The proboscis was partially extended, and is cream, and much longer than in *Oocorys* species. Relatively small, obvious black eyes are present. A thick, complex, permament inhalant siphon is present in the mantle edge against the left side of the head-foot, but no permanent exhalent siphon was apparent, although the mantle margin was unusually thick in the exhalent area in the specimen examined.

The operculum is typical of *Galeodea*, with its nucleus near the right edge at a third of the opercular height from the anterior end. It has a weak furrow parallel to the right margin above and below the nucleus, as in *G. rugosa,* but its left posterior margin is more strongly embayed than in most other species.

RADULA. — The radula was examined from two specimens of *Galeodea alcocki* (Figs 2A, B), from the Philippine Islands (MUSORSTOM 3 stn CP 118) and from northern Western Australia (WAM1077-84). It is similar to those of other *Galeodea* species, but the cutting portions (heads) of the central and lateral teeth are markedly wider and bear more numerous, longer denticles than in all other species examined. The central teeth have 10-12 long, narrow denticles on each side of the central cusp, and the central cusp protrudes strongly in an unusual manner. The lateral teeth each have 6-9 long, narrow, lightly curved, sharp-pointed denticles outside the unusually long, narrow, prominent main cusp; the long main cusps are unusual in reaching almost to the centre-line of the radula. The inner marginal teeth each bear two small denticles on the inner edge, whereas the outer marginal teeth are smooth. While this is the most extremely wide, multicuspate radula I have seen in *Galeodea*, it is connected through a continuum of radular characters of such species as *G. keyteri*, *G. leucodoma* and *G. echinophora* with the narrow-headed central and lateral teeth of the smaller *Galeodea* species such as *G. triganceae*, in which these teeth bear fewer denticles than in *G. alcocki* and *G. keyteri.*

Galeodea bituminata (Martin, 1933)

Figs 7A, B; 13B-K; 14A-F

Cassidea (*Semicassis*) *bituminata* Martin, 1933: 28, pl. 4, fig. 28.

Synonyms:
Galeodea carolimartini Beets, 1943b: 437, fig. 1-3 (**new synonym**).
Galeodea echinophorella Habe, 1961: 44, pl. 21, fig. 2 (**new synonym**).
Galeodea marginalba Yamamoto & Sakurai, 1977: 103, text-fig. 1 (**new synonym**).
Galeodea noharai Noda, 1980: 17, pl. 6, fig. 17a, b, pl. 11, fig. 19 (**new synonym**).
Galeodea echinophorella suzumai Sakurai, 1984: 129, fig. 2 (**new synonym**).
Purpura mancinella (?) Martin, 1879: 42, pl. 8, fig. 11 (*non Purpura mancinella* Lamarck, 1822).

Other references:
Morio spec. - Martin 1899: 158.
Morio echinophora - Smith 1910: 329 (same specimen as next entry; *non Buccinum echinophorum* Linné, 1758).
Cassidaria echinophora? - Smith 1913: 263, pl. 4, fig. 5 (*non Buccinum echinophorum* Linné, 1758).
Cassidaria spec. indet. - Martin 1919: 89. — van der Vlerk 1931: 241.
Galeodea echinophorella - Hirase 1934: 1, frontispiece, fig. 10 (*nomen nudum*). — Kuroda & Habe 1952: 58 (*nomen nudum*). - Hirase & Taki 1954: pl. 130, fig. 10 (*nomen nudum*). — Azuma 1960: 29 (*nomen nudum*). - Oyama & Takemura 1961: pl. *Morum* (2) – *Galeodea*, fig. 6-8. — Lan 1979: 101, pl. 44, figs 102, 102a. — Springsteen & Leobrera 1986: 102, pl. 27, fig. 12. — Lai 1990: fig. 11 (upper) (copy of Lan's (1979) figures). — Wilson 1993: 231, pl. 38, figs 6a, b. — Kreipl 1997: 25, pl. 8, fig. 16. — Okutani 2000: 273, pl. 135, fig. 2. — Higo *et al.* 2001: 46, fig. G1543.
Phalium (*Semicassis*) *bituminatum* - Beets 1943a: 277, pl. 28, fig. 58.
Galeodea carolimartini - Skwarko & Sufiati 1994: k5.
Semicassis bituminata - Skwarko & Sufiati 1994: k9.
Galeodea marginalba - Hasegawa & Saito 1995: 31, pl. 4, fig. 2. — Higo *et al.* 2001: 47, fig. G1544.
Galeodea echinophorella suzumai - Hasegawa & Saito 1995: 33, pl. 4, fig. 1. — Higo *et al.* 2000: 47, fig. G1543s.
Morio pamotanensis - Noda 2002: 106, figs 17-10 (*non Morio pamotanensis* Martin, 1899).
Not *Galeodea echinophorella* - Springsteen & Leobrera 1986: 102, pl. 27, fig. 12.

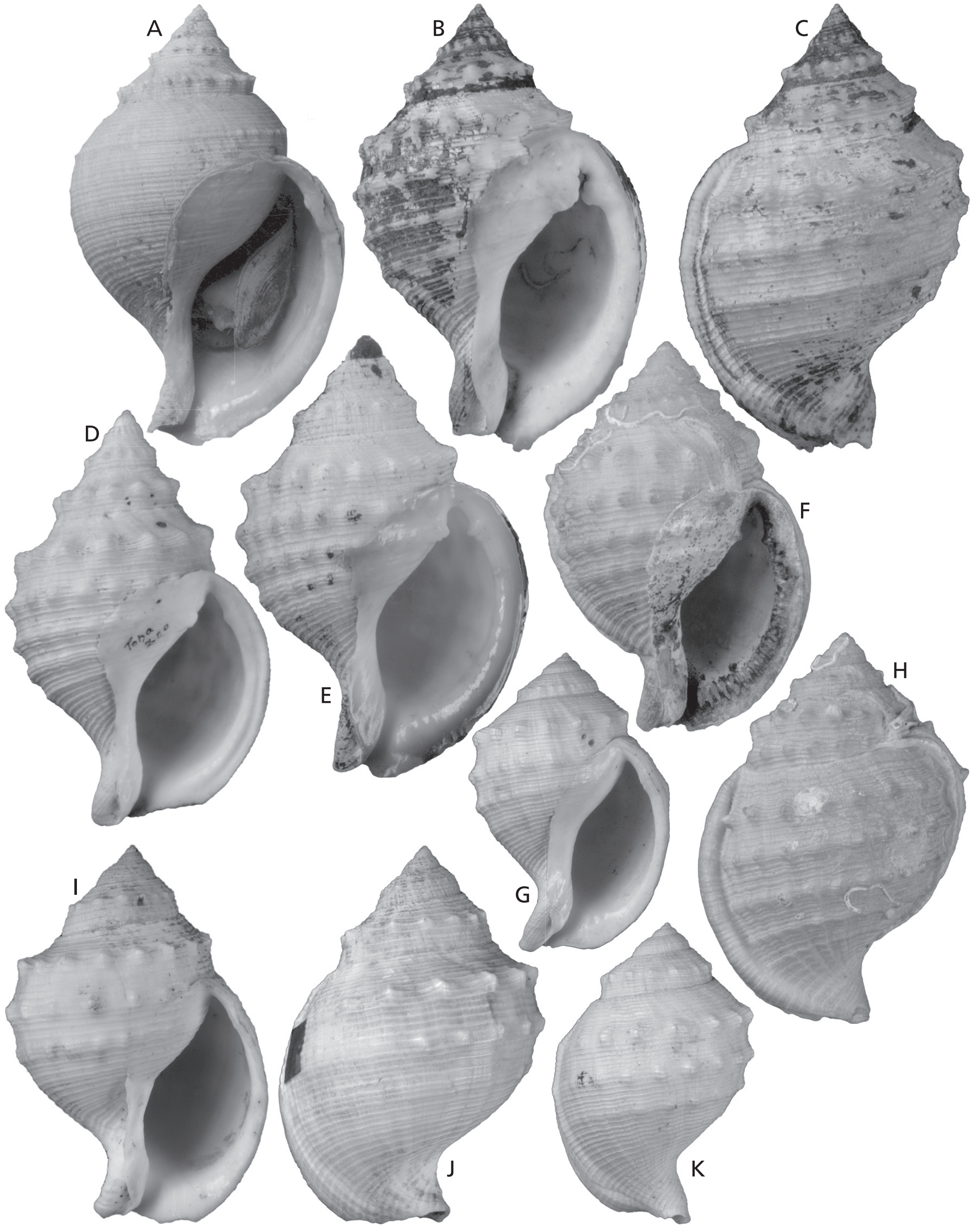


FIG. 13. *Galeodea alcocki* (E. A. Smith, 1906). **A**, *Soela* stn S1/84/70, 496-494 m, NW of Collier Bay, N Western Australia (WAM 1077-84, H 102.8 mm; X 0.67). **B**-**K**, *Galeodea bituminata* (Martin, 1933); **B**, **C**, *G. marginalba* Yamamoto & Sakurai, 1977, holotype, 360 m, East China Sea (NSMT Mo.70271; H 69.8 mm; natural size); **D**, Tosa Bay, Shikoku, Japan, 360 m (NSMT Mo.71557; H 65.0 mm; natural size); **E**, MUSORSTOM 10 stn CP 1331, Fiji, 694-703 m (H 54.5 mm; X 1.25); **F**, **H**, specimen with second varix, MUSORTOM 4 stn CP 242, New Caledonia, 500-550 m (H 48.3 mm; X 1.25). **G**, **K**, *G. echinophorella* Habe, 1961, holotype, Tosa Province, Shikoku, Japan (NSMT Mo.44913; H 31.2 mm; X 1.5). **I**, **J**, *G. echinophorella suzumai* Sakurai, 1984, holotype, off Kuriya, Fukui Prefecture, Sea of Japan (NSMT Mo.70228; H 38.9 mm; X 1.5).

TYPE MATERIAL. — *Cassidea* (*Semicassis*) *bituminata*: holotype RGM 456182, from Late Miocene bituminous shale, Waisiu, Buton Island, Indonesia. This specimen is very incomplete (anterior end and outer lip missing) and the complete specimen from the type locality illustrated by Beets (1943a: 277, pl. 28, fig. 58) is important to confirm the generic position and identity of the species. — *Galeodea carolimartini*: holotype (Figs 14E, F) RGM 456183, from "Tji. Guleh, Tangkulirang", northern Kutei, Kalimantan (eastern Borneo), of Late Miocene age (Beets 1943b: 436). — The status of the name *Galeodea echinophorella* is discussed below. The specimen illustrated by Hirase (1934) has no significance as a type. The specimen figured by Habe (1961: pl. 21, fig. 2; NSMT Mo. 44913; Figs 13G, K) is labelled "type", and is accepted as the holotype of *Galeodea echinophorella* Habe, 1961. It is labelled "Tosa Province, Kochi Prefecture, Shikoku". — *Galeodea marginalba*: holotype NSMT Mo. 70271 (Figs 13B, C); from the East China Sea, in 360 m, 27°-28°50'N, 125°50'-126°E (Yamamoto & Sakurai 1977). — *Galeodea noharai*: holotype (not seen) in Institute of Geoscience, University of Tsukuba, no. IGUT 10156, from Shinzato Formation (Pliocene), locality 415, southern cliff of Shore Golf Links, 1 km NW of Kuteken, Chinen-mura, Shimajiri-gun, Okinawa, Japan. — *Galeodea echinophorella suzumai*: holotype NSMT Mo. 70288 (Figs 13I, J), with one paratype, NSMT Mo. 70289 (Hasegawa & Saito 1995: 33), from off Kuriya, Fukui Prefecture, Sea of Japan.

OTHER MATERIAL EXAMINED — **Recent. Japan**. 200 fathoms (370 m), Tosa Bay, Shikoku (1 dd, NSMT Mo. 71557); off Noto, Sea of Japan (2 dd, NSMT Mo. 71556).

Philippine Islands. MUSORSTOM 2: stn CP 71, off Lubang Island, 14°00'N, 120°18'E, Luzon, 189-197 m (1 dd; Figs 14B, C). — MUSORSTOM 3: stn CP 86, locality as above, 14°00'N, 120°18'E, 187-192 m, (1 dd, Fig. 14A).

Indonesia. KARUBAR: stn CP 09, 5°23'S, 132°29'E, 368-389 m, (1 lv).

Northwestern Australia. Trawled off NW coast of Western Australia at *c.* 500 m (2 lv, coll. G. Kronenberg, no. 3872); 110-170 km NW of Port Hedland, 18°35'S, 117°05'E, 370-480 m (1 dd, AMS C384446); FV *Courageous* stn 005, SW of Imperieuse Reef, Rowley Shoals, 18°08'S, 188°13'E, 350-354 m (1 lv, WAM 3281-83); F/V *Soela* stn 02-82-43, NW of Port Hedland, 18°40'S, 117°13'E to 18°40'S, 117°11'E, 396-398 m, L. Marsh (1 dd, WAM); F/V Soela cruise, Feb. 1984, coll. S. Slack-Smith: stn 01-89-122, W of Broome, 17°59'S, 118°23'E, 389-390 m (1 dd, WAM 809-84); stn 01-84-055, WNW of Lacépède Archipelago, 15°47.2'S, 120°48.2'E to 15°59.05'S, 120°44.6'E, 350-348 m (2 dd, plus 2 *Echinophoria wyvillei*, WAM); stn 01-84-074, NW of Collier Bay, 14°16.5'S, 122°34.4'E to 14°13.6'S, 122°38.3'E, 302 m (1 dd, WAM 1774-84); stn 01-84-088, NW of Cape Leveque, 14°51.9'S, 121°40.6'E to 14°54.0'S, 121°39.1'E, 256-260 m (1dd, WAM 822-84); stn 01-84-066, NW of Augustus Island, 14°29.4'S, 122°01.4'E to 14°28.4'S, 122°03.2'E, 296-304 m (1 lv, WAM 900-84).

New Caledonia. MUSORSTOM 4: stn CP 242, 500-550 m, 22°06'S, 167°10'E (1 dd). — NORFOLK 2: stn CP 2153, 22°48'S, 167°12'E, 395-400 m (1 dd). — EBISCO: stn DW 2602, Chesterfield Plateau, 19°38'S, 158°44'E, 547 m (1 dd spire, with 1 dd *Echinophoria wyvillei*).

Vanuatu. MUSORSTOM 8: stn DW 986, 602-648 m, 19°21'S, 169°31'E (1 dd); stn CP 1051, 555-558 m, 16°37'S, 168°00'E (1 lv, 1 dd).

Tonga. BORDAU 1: stn CP 1396, 16°39'S, 175°57'W, 591-596 m (1 lv); stn CP 1397, 16°33'S, 175°52'W, 674-688 m (1 lv).

Fiji. MUSORSTOM 10: stn CP 1316, Bligh Water, 17°15'S, 178°22'E, 478-491 m, (2 lv, 3 dd); stn CP 1317, Bligh Water, 17°12'S, 178°14'E, 471-475 m, (1 lv); stn CP 1331, Bligh Water, 17°02'S, 178°02'E, 694-703 m (1 lv, with 1 *G. leucodoma*).

Fossils. Late Miocene (Tortonian-Messinian; Janssen 1999) bituminous shale, Waisiu, Buton Island, Indonesia (RGM, one slightly incomplete specimen); locality "Ando 6", Pliocene mudstone below Bolinao Limestone, coastal cliff section in front of Ando, Carrabuyan Island, Pangasinan, Philippine Islands, 16°14.41'N, 119°56.19'E, coll. A. W. Janssen (RGM, one); Ba Volcanic Group, Piacenzian (Pliocene), private driveway in Tababa, *c.* 8 km S of Ba, Viti Levu, Fiji (AG5786, one specimen in collection of A. Grebneff, Dunedin, New Zealand).

DISTRIBUTION. — *Galeodea bituminata*, as construed here, ranges from southern Japan, including Okinawa (Noda 2002: 106, figs 17-13), and Taiwan to the Philippine Islands, Indonesia, northwestern Australia, New Caledonia, Vanuatu and Fiji. It seems likely that Recent specimens occur throughout the western Pacific, in *c.* 200-700 m.

Late Miocene (and perhaps in part Pliocene) fossils are recorded from a road cut between Laoag and Bacarra, Ilocos Norte, Luzon, Philippine Islands (Smith 1913: 263) and from Cikarang, Java, and northern Kutei, Kalimantan (Beets 1943b: 436). A Pliocene fossil specimen is recorded above from Viti Levu, Fiji. A beautifully preserved specimen in RGM has been collected recently from Ando, Carrabuyan Island, Philippines (Pliocene). Noda (1980: 17, pl. 6, figs 17a, b; pl. 11, fig. 19) described and illustrated a normal, if small, specimen from the Pliocene Shinzato Formation of Okinawa, under the name *Galeodea noharai*. The final fossil record is of the holotype of *G. bituminata* and several other specimens, from the Late Miocene (Janssen 1999) deep-water fauna in bituminous sandstone and shale at Waisiu, Buton Island, Indonesia (the locality for *Butonius* Martin, 1933, a synonym of the deep-water volute genus *Calliotectum* Dall, 1890; Bouchet & Poppe 1995).

DIMENSIONS. — Holotype of *Galeodea echinophorella*: H 31.2, D 21.2 mm; specimen figured by Hirase (1934: 1): H 45.5, D 30.0 mm; holotype of *G. marginalba*: H 69.8, D 42.0 mm; holotype of *G. echinophorella suzumai*: H 38.9, D 25.1 mm; holotype of *G. carolimartini*: H 33.1, D 22.4 mm; Tosa Bay, Japan, NSMT Mo. 71557: H 64.9, D 41.3 mm; MUSORSTOM 2 stn CP71: H 44.5, D 28.1 mm; MUSORSTOM 3 stn CP86: H 44.6, D 31.7 mm; AMS C384446, NW of Port Hedland, Western Australia: H 28.8, D 19.9 mm.

NOMENCLATURE. — Ponder (1983: 93) commented on the confusion over the authorship of *Galeodea echinophorella*. Hirase (1934: frontispiece, fig. 10) published a coloured photograph of this species, with the name "*Galeodea echinophorella* Hirase" in the caption (Hirase 1934: 1), but this is a *nomen nudum*, having been published after 1930 without "a description or definition that states in words characters that are purported to differentiate the taxon" (ICZN 1999: Article 13.1). The name was not made available by later Japanese usages (Kuroda & Habe 1952: 58), as was also pointed out by Higo *et al.* (2001: 46, footnote 2), or in later editions of Hirase's book, including the last edition (Hirase & Taki 1954: pl. 130, fig. 10). A brief description was provided by Habe (1961: 44, pl. 21, fig. 2), thereby making the name available with Habe as the author (ICZN 1999: Article 50.1). As noted above, the specimen illustrated by Habe (1961) also is labelled as the holotype, and was accepted as the holotype by Higo *et al.* (2001: 46, footnote 2).

SYNONYMY. — The holotype of *Galeodea marginalba* is more than twice the size of that of *G. echinophorella* and has an unusually heavily thickened aperture and, consequently, a much more narrowly constricted posterior siphonal notch at the posterior end of the aperture than in the holotype of *G. echinophorella*. However, other Japanese and western Pacific specimens are intermediate in size and degree of apertural thickening between these extremes, notably the large but weakly inflated, tall-spired Japanese shell listed above (NSMT Mo.71557, Tosa Bay, 370 m). There appear to be no consistent characters distinguishing *G. marginalba* from *G. bituminata*, despite Yamamoto & Sakurai's (1977: 104) statement that *G. bituminata* (which they identified as *G. echinophorella*) differs from *G. marginalba* in having a less inflated shell and in having a less sinuous canal. The holotype was figured excellently in colour by Hasegawa & Saito (1995: pl. 4, fig. 2). The form named *G. echinophorella suzumai* does not differ in any significant characters from *G. bituminata*, apart from bearing a wider and more elevated collar on the inner lip, which is present but less obvious on most of the other specimens seen; this name seems to be based merely on a small, thin-shelled specimen of *G. bituminata* with a well developed collar.

Examination in RGM of collections of Neogene fossil Mollusca from Indonesia showed that the holotypes of *Cassidea bituminata* Martin and *Galeodea carolimartini* Beets, and the critical, complete specimen of *C. bituminata* from Buton illustrated by Beets (1943a: 277, pl. 28, fig. 58) share all significant characters with Recent western Pacific specimens. They have 3-4 rows of small, prominent nodules on the last whorl, and a moderately long canal. They also retain three varices before the terminal one, as in the Philippines Recent specimens, and have a groove behind the terminal varix that is intermediate in depth between those of Philippines and other Recent specimens. The fossil specimen from Luzon, Philippines, illustrated in an excellent drawing by Smith (1913: pl. 4, fig. 5) and a recently collected

Pliocene specimen from Ando, Carrabuyan Island, Philippines (in RGM), are almost identical to the holotype of *G. carolimartini*, with three rows of small, prominent nodules. Smith's (1910: 329) record of "*Morio echinophora*" as a Philippines fossil apparently refers to the same Luzon specimen. Although this species was not named as a fossil in Indonesia until 1933, Martin (1899: 158; 1919: 89) recognised that his record of "*Purpura mancinella*(?)" from Junghuhn's locality R, Java (Martin 1879: 42, pl. 8, fig. 11) (presumably the locality recorded as "Tjikarang" by Beets 1943b) is based on a *Galeodea* species (Martin used the synonyms *Morio* and *Cassidaria*). Beets (1943b) provided the name *Galeodea carolimartini* for the species figured as "*Purpura mancinella*" by Martin, although Martin's figure shows a very incomplete specimen partly enclosed in matrix, whereas Beets's (1943b) specimen is complete and clean. As the name *G. echinophorella* was not made available until 1961, *G. bituminata* is the earliest name for this species. *G. echinophorella* does not satisfy the requirements of the *Code* (ICZN 1999: Article 23.9.1) to be treated as a *nomen protectum*, as *G. bituminata* has been listed as a valid name in several catalogues of Indonesian fossils since 1899, and the name *G. echinophorella* has been used in many fewer than 25 publications during the past 50 years. *Galeodea noharai* Noda (1980: 17, pl. 6, figs 17a, b) is a further synonym of *G. bituminata*, and was based on a small specimen from the Pliocene Shinzato Formation of Okinawa.

VARIATION. — The published illustrations and the material examined indicate that this is a highly variable species. Most specimens of *Galeodea bituminata* are relatively small (H 35-50 mm), although the holotype of *G. marginalba* is 69.8 mm high. It is therefore among the smallest Recent species of *Galeodea*, and most specimens quite closely resemble the equally small New Zealand species *G. triganceae*. Both also quite closely resemble small specimens of *G. echinophora* in shape, in the length and degree of flexure of the anterior canal, and in most specimens having 3-5 rows of small nodules on the last whorl, with one or, in a few specimens, two rows on spire whorls. However, both species consistently are narrower than *G. echinophora*. A distinctive character of *G. bituminata* is its prominent, narrow, rather widely spaced spiral cords. It also has a conspicuously thickened, reflected and weakly nodulose terminal varix, a character distinguishing it readily from *G. triganceae*. The inner lip is well thickened in most specimens, but in most specimens is elevated into a much lower and narrower free collar than in *G. echinophora*. I am aware of only one specimen, other than the holotype, that has been referred to *G. marginalba*. This specimen was recorded by Segers & Terryn (2003) from 120 m in the Taiwan Channel, and identified as *G. marginalba*; it is 68.6 mm high with four prominent rows of nodules. As with the holotype of *G. marginalba*, this appears to be merely a large specimen of *G. bituminata*.

The specimen from Taiwan illustrated by Lan (1979: pl. 44, figs 102, 102a; operculum inverted) has four prominent rows of nodules and a weak fifth ridge on the last whorl, and closely resembles the specimen from New Caledonia (MUSORSTOM 4 stn CP 242), although the New Caledonian specimen (Figs 13F, H) appears wider because of a second varix retained on the left side of the last whorl. The MNHN specimens from Vanuatu and Fiji have 4 or 5 rows of nodules on the last whorl (although the lower two are weak on all specimens) and a narrow, well raised but unchannelled terminal varix, and appear to be small, rather weakly callused specimens of the form from New Caledonia and that illustrated by Lan (1979) from Taiwan. The MUSORSTOM 2 and 3 Philippine Islands Recent specimens are unique in retaining 3-4 varices before the terminal one, in the obvious, deep groove behind each varix, in the varix of unusual section with a narrowly and prominently rounded abapertural face but a long, gently sloping adapertural face, in the unusually clearly defined, square-edged spiral cords, in the unusually strongly armoured aperture with a thick outer lip flared markedly more widely towards the anterior than higher up, and in the many very prominent, narrow transverse ridges on both lips inside the aperture. However, the Indonesian Neogene fossils are intermediate in these characters, and I interpret these Philippines Recent specimens as merely more heavily callused than the other specimens referred here.

The Italian Miocene species *Galeodea taurinensis* (Sacco, 1890) is relatively small (specimens examined do not exceed 35 mm in height) and closely resembles *G. bituminata* in all characters, so it seems likely that the real relationships of *G. bituminata* are with *G. taurinensis* rather than *G. echinophora* (specimens examined in Dipartimento di Biologia

Evoluzionistica Sperimentale, Università di Bologna: Rio Tetti Civera, Torino, Burdigalian (late Early Miocene), collected and presented by S. Schiaparelli, 2 specimens; Valle Ceppi, Torino, Helvetian (Late Miocene), collected and presented by M. Rocca, 3 specimens).

The relatively large Philippines specimen (H 64.7 mm) illustrated by Springsteen & Leobrera (1986: pl. 27, fig. 12) under the name *Galeodea echinophorella* is unique among Indo-Pacific *Galeodea* specimens known to me in having both a wide, raised inner lip collar and only one row of prominent nodules, at the shoulder angle. Springsteen & Leobrera (1986) stated that it has 2 to 3 lower rows of nodules, fading out over the last whorl. This specimen also has a widely reflected outer lip with a weakly ridged inner margin. It much more nearly resembles *G. echinophora* than do the other specimens of *G. bituminata* available to me. More material is needed to be sure of the status of this specimen, but it is so similar to *G. echinophora* in most characters that it is possibly a wrongly localised specimen of *G. echinophora*.

ANATOMY. — The animal was examined of one specimen from Vanuatu (MUSORSTOM 8 stn CP 1051; Figs 7A, B). The operculum is evenly oval, with the nucleus against the right edge at a third of the opercular height from the anterior end of the operculum. The gross anatomy of the exterior, mantle cavity and proboscis are closely similar to those of all other species of *Galeodea* examined here; the specimen has obvious black eyes and short, stout (contracted) cephalic tentacles. The specimen is male, and has a small, cylindrical penis with a terminal papilla, and a clearly open seminal groove extending the length of the mantle cavity and penis. The osphradium is slightly asymmetrically bipectinate, as in all other *Galeodea* species examined, with the right leaflets slightly longer than the left ones.

RADULA. – The radula was examined from the same specimen from Vanuatu as is described above, but is not illustrated, as it is closely similar to that of *G. triganceae* (Figs 3C, D).

Galeodea echinophora (Linné, 1758)

Figs 1G, H; 6C, D; 11A, C, E; 14G-J; 21B

Buccinum echinophorum Linné, 1758: 735.

Synonyms:
Buccinum nodosum Solander *in* Brander, 1766: 43.
Buccinum strigosum Gmelin, 1791: 3476.
Buccinum ochroleucum Gmelin, 1791: 3477.
Buccinum diadema Brocchi, 1814: 326, pl. 4, figs 13 a, b.
Echinora tuberculata Schumacher, 1817: 75, 249.
Cassidaria scilla Risso, 1826: 185 (**new synonym**).
Cassidaria tuberculata Risso, 1826: 186 (**new synonym**).
Cassidaria echinophora var. *tuberculata* Scacchi, 1836: 11.
Pyrula provincialis Martin, 1851: 249, pl. 8, figs 4-4'.

FIG. 14. *Galeodea bituminata* (Martin, 1933). **A**-**C**, 2 specimens, off Lubang Island, Luzon, Philippines, both X 1.25; **A**, MUSORSTOM 3 stn CP 86 (H 44.6 mm); **B**, **C**, MUSORSTOM 2 stn CP 71 (H 44.5 mm); **D**, *Soela* stn S1/84/66, NW of Augustus Island, N Western Australia, 296-304 m (WAM 900-84; H 36.4 mm; X 1.5). **E**, **F**, *Galeodea carolimartini* Beets, 1943, holotype from "Tji. Guleh, Tangkulirang", northern Kutei, Kalimantan (eastern Borneo), Late Miocene (RGM 456183; H 33.1 mm; X 1.5). **G**-**J**, *Galeodea echinophora* (Linné, 1758), type species of *Galeodea*, two specimens in Linné's collection, Mediterranean Sea (Linnean Society of London collection; X 0.9); **G**, **H**, *Buccinum echinophorum* Linné, 1758, lectotype (designated here); **I**, **J**, paralectotype (Natural History Museum photographs). **K**-**O**, *Galeodea hoaraui* Drivas & Jay, 1989, Réunion, Indian Ocean; **K**, **M**, off St Gilles, 700m, in collection of J. C. Martin (H 52.7 mm); **L**, immature specimen, off St Gilles, 700 m (H 42.4 mm; X 1.25); **N**, **O**, holotype, MNHN 4157, shrimp pots in 700 m, off Saint-Pierre (H 62.8 mm; natural size).


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O

Cassidaria echinophora var. *mutica* Tiberi, 1863: 154 (junior primary homonym of *Cassidaria mutica* Michelotti, 1861).
Cassidaria echinophora vars. *subnodulosa*, *solida*, *globosa* and *obsoleta* Bucquoy, Dautzenberg & Dollfus, 1882: 69, 70, pl. 8, figs 1-5; pl. 9, figs 1, 2.
Cassidaria echinophora var. *adriatica* Mascarini, 1884: 191.
Cassidaria bucquoyi Locard, 1886: 150.
Cassidaria dautzenbergi Locard, 1886: 150.
Morio echinophora vars. *tufa*, *cassidula*, *ovalis*, *tuber* and *tenuis* Coen, 1920: 180-182, pl. 5, figs 1-8.
Morio echinophora var. *gigantea* Coen, 1920: 182, pl. 6, fig. 1.
Morio adriatica var. *aequistriata* Coen, 1920: 133, pl. 6, fig. 4.
Morio echinophora var. *chiamentii* Coen, 1929: 277, pl. 11 ("variété anormale"; not available).
Morio echinophora vars. *major*, *polycingulata*, *bonanni*, *intermediata* and *bivaricosa* Coen, 1933: 48, 163, pl. 3, figs 29-31.
Morio echinophora var. *lactea* Coen, 1933: 48, 163.
Cassidaria pliocenica Settepassi, 1970: *Cassidaria* xv, pl. 14, figs 1A-B (**new synonym**).
Cassidaria pseudobistriata Settepassi, 1970: *Cassidaria* xv, pl. 15, figs 5A-B (**new synonym**).
Cassidaria bistriata Settepassi, 1970: *Cassidaria* xiv, pl. 14, fig. 2A-B (**new synonym**).
Cassidaria echinophora vars. *quadrinodosa*, *rarituberculata*, *densetuberculata*, *globosocordonata*, *dilatata*, *dentata*, *ingens*, *subdiadema*, *multituberculata* and *minima* Settepassi, 1970: *Cassidaria* i-xv, pls. 1-9G (**new synonyms**).
Oocorys alboranensis Settepassi, 1970, appendix: vi, fig. a, b.

Other references:
Buccinum echinophorum - Linné 1767: 1198.
Buccinum nodosum - Dillwyn 1817: 586.
Cassidarie echinophora - Reeve 1849: pl. 1, figs 3 a, b.
Cassidaria provincialis - Bernardi 1861: 345.
Cassidaria mutica - Locard 1886: 150.
Morio adriatica - Coen 1914: 26, pl. 3, fig. 12.
Buccinum diadema - Rossi Ronchetti 1952: 6. — Pinna & Spezia 1978: 129, pl. 8, figs 1, 1a.
Morio echinophora var. *lactea* - Settepassi 1970: appendix, p. vi.
Cassidaria scilla - Arnaud 1978: 134.
Cassidaria tuberculata - Arnaud 1978: 138.
Galeodea echinophora - Giannuzzi-Savelli *et al.* 1996: 208-215, figs 839-860. — Kreipl 1997: 24, pl. 8, figs 15-15c. — Solsona I Masana 1999: 80, figs 8, 9 [not figs 14, 15].

TYPE MATERIAL. — Two syntypes of *Buccinum echinophorum* (Figs 14G-J) remain in Linné's collection, housed at the Linnean Society of London; their identity with *Galeodea echinophora* of all authors is confirmed, and the larger and more coarsely nodulose is here designated the lectotype of *Buccinum echinophorum* Linné, 1758 (Figs 14G, H). This lectotype designation is necessary because Linné (1758) also cited for *Buccinum echinophorum* figures by Buonanni (1681: pls 18, 19), Rumphius (1705: pl. 27, fig. I) and Dezallier d'Argenville (1742: pl. 20, fig. P). All the figured specimens therefore are further syntypes of *Buccinum echinophorum*, and not all are conspecific with *Galeodea echinophora* (Linné). Buonanni's (1681: pl. 19) and Dezallier d'Argenville's (1742: pl. 20, fig. P) drawings are recognisable as *G. echinophora*, but Buonanni's (1681: pl. 18) other cited figure is a poorly drawn, unrecognisable, sinistral view (i.e., the draftsman did not reverse the image, to ensure that it reproduced correctly). The situation regarding Rumphius's (1705: pl. 27, fig. I) figure is unusual, as there are two figures labelled "I" on the plate; the upper, central one shows an ellobiid, apparently *Pythia scarabeus* (Linné, 1758), whereas the lower one, at the start of the next row of figures, shows *G. echinophora*. Without this lectotype designation, even *Pythia scarabeus* would be eligible to bear the name *Buccinum echinophorum*! Linné (1758) gave the locality for *Buccinum echinophorum* as the Mediterranean Sea.

As it is possible that syntypes of Gmelin's nominal species *Buccinum strigosum* and *B. ochroleucum* remain in the University Zoological Museum, Copenhagen or the Zoological Institute, St Petersburg (among material illustrated by Martini & Chemnitz (1769-1795) and cited by Gmelin (1791), or material purchased for Peter the Great; Martynov 2002), no type designations are made here for these names. – No type material is known today from the work by Schumacher (1817) (Dance 1966), so no type material exists for *Echinora tuberculata*. – *Buccinum diadema* Brocchi, 1814: holotype in Museo Civico di Storia Naturale di Milano (Pinna & Spezia 1978: 129, pl. 8, figs 1, 1a); said by Brocchi (1814) to occur "fossile nel Piacentino" in northern Italy. – *Cassidaria scilla* and *C. tuberculata* of Risso (1826): type material "presumed lost" (Arnaud 1978: 134, 138). Arnaud (1978: pl. 11, figs 182, 183) reproduced Risso's figures of *C. scilla* and *C. tuberculata*, demonstrating that they are synonyms of *G. echinophora*. Both are based on Late Neogene fossils, *C. scilla* from la Trinité, and *C. tuberculata* from Magnan, both near Nice. Risso's usage of the name *C. tuberculata* might well be a usage of Schumacher's (1817) name *Echinora tuberculata* rather than being intended as a new name. – The apparent *nomen nudum* by Scacchi (1836), *Cassidaria echinophora* var. *tuberculata*, therefore possibly merely is a usage of Risso's name, and in turn of Schumacher's, and I do not know of any type material for Scacchi's name. – *Cassidaria bucquoyi* Locard, 1886: nine syntypes in MNHN 4138-4145, all small Recent Mediterranean specimens of the normal tuberculate form of *G. echinophora* (one each from Roussillon, Paulilles, Aigues-Mortes, Marseille, Bandol, Cannes (mainland France), Ajaccio, l'Ile Rousse (Corsica), and one without locality). – *Cassidaria dautzenbergi* Locard, 1886: one syntype MNHN 4149, a Recent specimen from Aigues-Mortes, close to the *adriatica* form, with strap-like spiral cords. – *Oocorys alboranensis* Settepassi, 1970: holotype (presumably along with the type material of all the other varieties of *G. echinophora* proposed by Settepassi, 1970) in Museo di Zoologia, Roma (Bouchet & Warén 1993: 800), not seen; from the Alboran Sea, western Mediterranean, in 200 m. I do not know the location of any type material of the other synonyms.

OTHER MATERIAL EXAMINED. – The MNHN collection contains many lots of this common, well known, relatively shallow-water Mediterranean species, and these need not be listed here; specimens can be purchased in any market in Spain or Italy. Specimens preserved with animals have been examined from a sample trawled in *c.* 320 m in the Tyrrhenian Sea, Mediterranean, between the Capraia and Gorgona Islands, during the "*Lophelia* Millennium '99 Cruise" (stn 93), led by Marco Taviani (Istituto di Geologia Marina, CNR, Bologna).

Martinique. Martinique, Lesser Antillies, 500 m, in lobster trap (1 specimen, in collection of R. Delannoye).

DISTRIBUTION. – *Galeodea echinophora* is limited to the Mediterranean Sea, where it is common in most areas in depths from about 30 m to over 300 m. Specimens are less common to the east of Cyprus than further west, and the holotype of *Oocorys alboranensis* is one of few specimens recorded from as far west as the Alboran Sea. Gaillard (1987: 555) reported that *G. echinophora* is sold regularly for food in the markets of Liguria, Sicily and Cyprus, and occasionally around the Adriatic Sea and in Turkey. Fossils are common throughout the Miocene, Pliocene and Pleistocene rocks of the Mediterranean region, particularly in Italy. The variation of Italian fossil specimens was demonstrated most clearly by Vinassa de Regny (1902: 197, pl. 2, figs 1-49).

Dominique Lamy (Guadeloupe) recently showed me a specimen of *Galeodea* from off Martinique, Western Atlantic, in 500 m, in the collection of R. Delannoye. It appears to be a small, very narrow, elongate specimen of *G. echinophora*. Although it is narrow, only 52.9 mm high, and has a taller spire than any specimens of *G. echinophora* I have seen, it agrees well with *G. echinophora* in all other characters. The specimen closely resembles *G. echinophora* as illustrated by Kreipl (1997: pl. 8, fig. 15a). Only the collection of more specimens from the Lesser Antillies will make it clear whether this first record of a Recent specimen of *Galeodea* from the Americas represents an accidentally dropped Mediterranean specimen or an Antillean population of *G. echinophora*.

DIMENSIONS. – Lectotype of *Galeodea echinophora*: H 61.1, D 44.4 mm; Linné's paralectotype: H 53.8, D 36.6 mm; adult specimens reach a height of 50-110 mm.

REMARKS. — *Galeodea echinophora* occurs in relatively shallow water, and is included here because it is the type species of *Galeodea*, to make coverage of the Recent species of the genus complete, and for comparison with the deep-water species revised here. Excellent coloured figures by Giannuzzi-Savelli *et al.* (1996: figs 839-860) give a good idea of the range of variation of this species. *Galeodea echinophora* is a relatively wide species of *Galeodea*, of average size for the genus. Most specimens have prominent sculpture of wide spiral cords and 3-5 rows of moderately large nodules, of which the one peripheral row is present on spire whorls. The anterior siphonal canal is moderately long to very long (at least for a Recent species; some Early Cenozoic fossil *Galeodea* species have much longer canals) and is obviously but, in most specimens, rather weakly twisted. A constant character is the prominent, wide, relatively thick, but nearly smooth inner lip collar, which is raised well above the previous whorl over the neck. The operculum, as in other species referred here to the genus, is narrowly oval, with the left posterior margin weakly embayed to accommodate the parietal area, and with its nucleus at the anterior third of the height, against the abaxial (right) edge of the operculum; a weak furrow extends parallel to the right margin above and below the nucleus, and is present also on the operculum of some of the other relatively large species of *Galeodea*, such as *G. alcocki* and *G. rugosa.* The protoconch (Figs 11A, C, E) is standard for Recent species of *Galeodea*, and is 1.3 mm in diameter.

The form *adriatica* of *Galeodea echinophora*, having smooth, strap-like cords instead of nodules, has been thought by some authors to be a distinct species limited to the Adriatic Sea. However, this form is far from limited to the Adriatic, and intergrades completely with *G. echinophora*, as was concluded also by Bouchet & Warén (1993: 800). The name *adriatica* has generally been attributed to Coen (1914), but was published first by Mascarini (1884). One of the most extreme variants I know of (other than teratalogical ones such as *Pyrula provincialis* Martin, 1851) is the short-spired, strongly inflated, very weakly sculptured specimen illustrated by Settepassi (1970, appendix: 6) under the name *Oocorys alboranensis.* This specimen has a relatively long, weakly twisted canal and a wide inner lip collar. These characters are unknown in *Oocorys* but, along with the low spire and wide spiral cords, are diagnostic of *G. echinophora.* There is no doubt that *O. alboranensis* is merely another synonym of *G. echinophora*, as also was concluded by Bouchet & Warén (1993: 800) after examination of the holotype.

ANATOMY. — The animal of *Galeodea echinophora* has the same external appearance as those of the other species studied here, with obvious black eyes, a slightly asymmetrically bipectinate osphradium, and a relatively long, narrow proboscis compared with that of *Oocorys.* Male specimens have not been seen; only females were present in the sample of about 20 specimens I examined. The operculum (Fig. 21B) is standard for *Galeodea*, with the nucleus near the right margin, at about a third of the height of the operculum.

RADULA. — The radula (Figs 2C, D) was studied from a specimen from "*Lophelia* Millennium '99 Cruise" stn 93, Tyrrhenian Sea, 320 m. It is very similar to those of the other medium-sized to small *Galeodea* species studied here, with a relatively narrow central tooth bearing 4-6 denticles on each side of the central cusp and with small, triangular protrusions at the lower corners of the basal plate, with relatively short-headed lateral teeth bearing 4-7 denticles outside the main cusp, and with lightly curved marginal teeth. The lateral teeth have a prominent, narrow ridge on the basal plate parallel to the head of the next tooth below it in the column, apparently providing support and rigidity to the column of teeth. Most marginal teeth are completely smooth, but some inner marginal teeth have 1-3 narrow denticles on the inner edge near the tip.

Galeodea hoaraui Drivas & Jay, 1989

Figs 14K-O

Galeodea hoaraui Drivas & Jay, 1989: 246, fig. 3.

Other reference:
Galeodea hoaraui - Kreipl 1997: 26, pl. 8, fig. 18.

TYPE MATERIAL. — Holotype of *Galeodea hoaraui* MNHN 4157 (Figs 14N, O); one paratype in the private collection of Drivas & Jay; from shrimp pots in 700 m off Saint-Pierre, south coast of Réunion Island, Indian Ocean.

OTHER MATERIAL EXAMINED. — **Réunion**. Off St Gilles, W coast of Réunion, 700 m, presented to MNHN by J. C. Martin (1 dd immature; Fig. 14L); off St Gilles, 600-700 m, photographs examined of specimens in collection of J. C. Martin, Nice (2 dd; Figs 14K, M).

DISTRIBUTION. — Known only from Réunion Island.

DIMENSIONS. — Holotype: H 62.8, D 34.9 mm; off St Gilles, 600-700 m: H 56.2, D 32.5 mm; H 58.7, D 34.4 mm; H 42.4, D 25.9 mm.

REMARKS. — The holotype of *Galeodea hoaraui*, two adult specimens of which photographs were sent by J. C. Martin (Nice), and a fresh immature specimen in MNHN differ from all other *Galeodea* species in their more elongate shape, brought about by the more steeply sloping sutural ramp, the much less inflated last whorl, and the much more gradually drawn out and more weakly contracted base than in other *Galeodea* species. This produces a much longer, wider and more weakly twisted anterior canal than in other *Galeodea* species, and an overall appearance close to that of species of *Sconsia*. Most specimens have a single row of small, sharp, closely spaced nodules around the periphery down the entire shell, but on the smaller of J. C. Martin's 2 adult specimens (H 56.2 mm) the periphery bears only a narrow keel, without nodules, on the last half-whorl. The holotype differs further from all other material of *Galeodea* that I have seen in having a more prominent parietal nodule and a matching enlarged nodule on the outer lip, the two together constricting an unusually well marked, large posterior apertural notch, in having a more strongly thickened and much more widely reflected lower half of the outer lip, and in having much more prominent, long, transverse ridges along the full length of both the inner and outer lips. However, the specimens from off St Gilles have much weaker apertural armature than the holotype, and it appears that the holotype is an unusually heavily calcified specimen. The base of the inner lip, over the neck, is well thickened and has a narrow free edge, elevated slightly above the previous whorl. The exterior of the holotype seems to have been white (now stained dark brown) and the other three specimens seen are stark white to pale cream. Both the holotype and the immature specimen have abraded protoconchs, but the remains of their apices and a fairly complete protoconch on one of J. C. Martin's specimens (seen only in a photograph) suggest that *G. hoaraui* has a small but turbiniform (multiwhorled) protoconch with more whorls than seen on all other Recent *Galeodea* species.

The generic position of this species will not be certain until the animal can be examined, but it brings into question the distinction between *Galeodea* and *Sconsia*. The very elongate shape, with the last whorl relatively narrow, drawn out and merging very gradually with an only weakly twisted anterior canal, and with a protoconch that seems to have been small but turbiniform, suggest that *Galeodea hoaraui* possibly belongs in *Sconsia* rather than *Galeodea*. However, the angled shoulder, with a row of peripheral nodules situated on the angulation in most specimens, is not present in any Neogene or Recent species referred to *Sconsia*, and gives the teleoconch more the appearance of *Galeodea* than of *Sconsia*. I therefore retain this species in *Galeodea*. The essential characters of *Sconsia* therefore are taken to be the relatively tall, narrow shape for a cassine cassid, without a shoulder angulation, the fine, even spiral sculpture over the entire exterior, the last whorl being drawn out anteriorly into a relatively long, weakly twisted but rather poorly defined anterior siphonal canal, and the moderately thickened outer lip. The protoconch and radula also might provide characters distinguishing these genera, but need further study.

Galeodea keyteri (Kilburn, 1975)

Figs 2E, F; 7C, D; 15; 21D

Oocorys keyteri Kilburn 1975: 582, fig. 4

Synonym:
Oocorys ferrarioi Bozzetti, 1989: 24, unnumbered figs.

Other references:
Oocorys keyteri - Romagna-Manoja 1989: 27, 28, 2 unnumbered figs.
Galeodea ferrarioi - Bozzetti 1990a: 64; 1997: 64, illus. p. 65.
Galeodea keyteri - Bozzetti 1997: 64, illus. p. 65.
Galeodea (*Galeodea*) *keyteri* - Kreipl 1997: 26, pl. 9, fig. 19.
Galeodea (*Galeodea*) *ferrarioi* - Kreipl 1997: 25, pl. 8, figs 17, 17a.

TYPE MATERIAL. – *Oocorys keyteri*: holotype NMP, G.2184 (T1841), 50 km SE of Limpopo River mouth, southern Mozambique, in *c.* 425 m (Figs 15F, G); paratype from the same area in collection of C. P. Fernandes (Kilburn 1975). – *Oocorys ferrarioi*: holotype (Figs 15A, B) MNHN 4153; off Mogadishu, Somalia, in 150-200 m.

OTHER MATERIAL EXAMINED. – **Somalia**. Trawled in 150-200 m off Mogadishu, Somalia; presented by L. Bozzetti (2 dd, NMP K6326; 1 dd, MNHN; 1 dd, WM 15232, NZGS); off Somalia (1 dd, G. Kronenberg collection, no. 1968); dredged at 200-300 m, off Cape Hafun (3 dd, G. Kronenberg collection, no. 5119); off Somalia, presented by M. Parth (2 dd, NMP K6821,); offshore, from fishermen, presented by B. Briano (5, Institute of Zoology, University of Bologna).
Madagascar. Chalutage 46, 15°59'S, 46°12'E, 400 m, collected by A. Crosnier (1 dd); chalutage 88, 18°54'S, 43°55'E, 280-310 m (1 lv); chalutage 91, 22°26'S, 43°15'E, 425-550 m (1 dd); chalutage 104, 22°16'S, 43°02'E, 750-810 m (1 lv). – MASCAREIGNES III: stn 12, 22°24'S, 43°05'E, 400-425 m, (2 lv); stn 42, 22°17'S, 43°05'E, 395-425 m (1 lv); stn 45, 22°26'S, 43°05'E, 475-510 m (1 lv); stn 56, 22°26'S, 43°05'E, 435 m (1 dd); stn 63, 22°27'S, 43°05'E, 530 m (1 lv); stn 67, 530 m, 22°26'E, 43°06'E (3 lv); stn 69, 350-420 m, 22°22'S, 43°05'E (1 dd); stn 70, 530 m, 22°25'S, 43°05'E (1 lv, 1 dd); stn 71, 525 m, 22°14'S, 43°04'E (1 lv); stn 72, 540 m, 22°11'S, 43°03'S (1 lv); stn 74, 540 m, 22°26'S, 43°03'E (1 dd); stn 76, 530 m, 22°22'S, 43°03'E (3 lv); stn 78, 530 m, 22°21'S, 43°03'E (1 lv); stn 81, 525 m, 22°23'S, 43°03'E (2 lv); stn 84, 535 m, 22°21'S, 43°04'E (1 lv); stn 96, 550 m, 22°10'S, 43°05'E (1 lv); stn 111, 610 m, 22°17'S, 43°02'E (1 lv); stn 122, 600 m, 22°17'S, 43°03'E (2 dd); stn 126, 590 m, 22°18'S, 43°02'E (1 lv) (31 specimens); Mozambique Channel, off Morondava, Madagascar, shrimp trawlers, 800m, presented by B. Briano (Institute of Zoology, University of Bologna, 1).
Mozambique. Shrimp boats, 150 m, off Cabo das Corrientes, Sofala (1 lv, collection of G. Kronenberg, no. 3842); trawled off Mozambique (1 dd, NMP H7331).

DISTRIBUTION. – *Galeodea ferrarioi* is recorded from the northwestern Indian Ocean, offshore from Somalia, in depths of about 150-300 m. *Galeodea keyteri* is recorded from the southwestern Indian Ocean, offshore from Madagascar and Mozambique, in depths of about 150-650 m. I suspect that these forms intergrade clinally, although specimens from intermediate localities in the Indian Ocean are needed to confirm this. *Galeodea keyteri* is interpreted as a single species that ranges throughout the western Indian Ocean.

DIMENSIONS. – *Oocorys keyteri*, holotype: H 70.2, D 47.8 mm; *O. keyteri*, paratype: H 89.3, D 56.6 mm (Kilburn, 1975); MASCAREIGNES III stn 78, anatomy examined: H 73.0, D 48.1 mm; MASCAREIGNES III stn 122: H 66.0, D 46.3 mm; H 64.5, D 40.4 mm; off Cabo das Corrientes, Kronenberg coll.: H 90.0, D 57.9 mm; *Oocorys ferrarioi*, holotype: H 84.4, D 59.6 mm; MNHN specimen, off Mogadishu: H 57.8, D 39.8 mm.

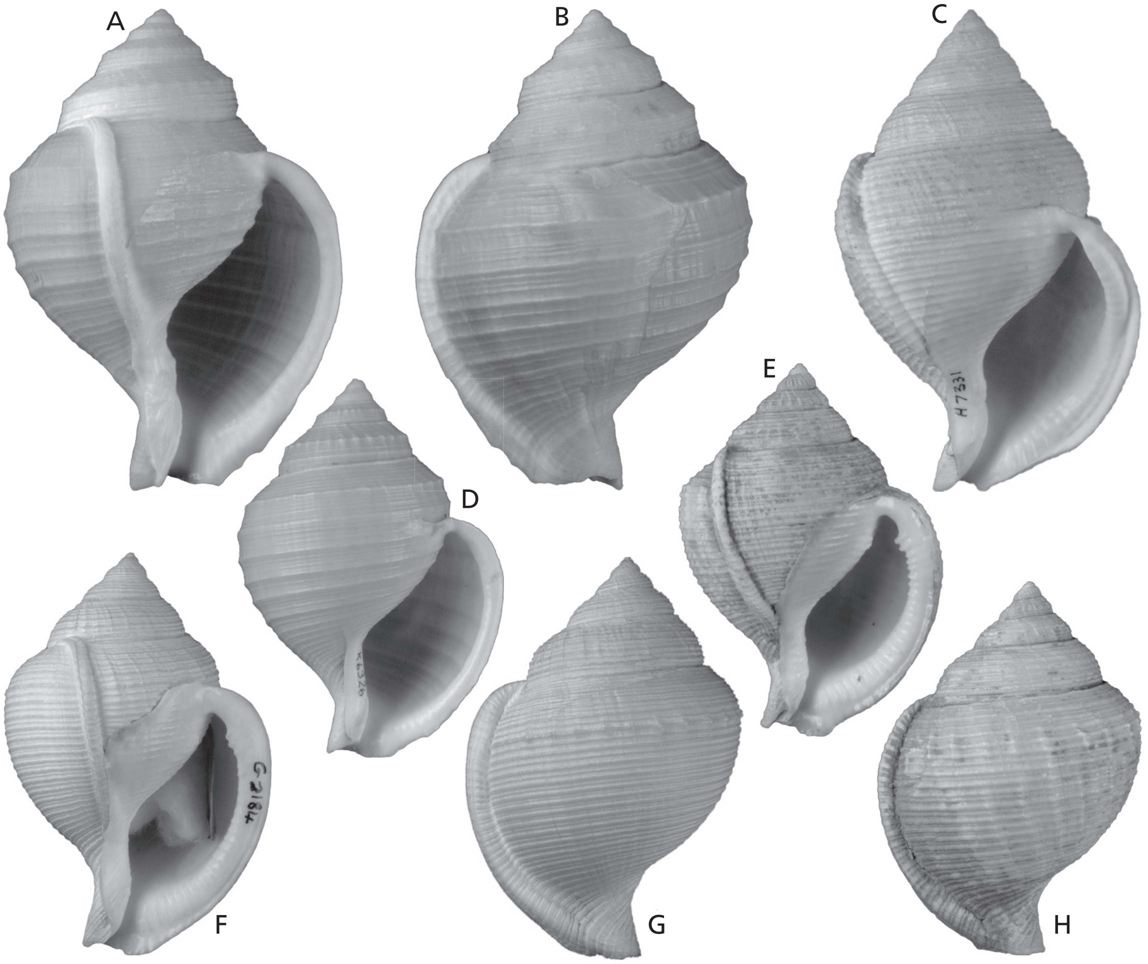


FIG. 15. *Galeodea keyteri* (Kilburn, 1975), all X 0.75. **A**, **B**, **D**, northern "*ferrarioi* form"; **A**, **B**, *Oocorys ferrarioi* Bozzetti, 1989, holotype MNHN 4153, trawled off Mogadishu, Somalia, 150-200 m (H 84.4 mm); **D**, trawled off Mogadishu, Somalia, 150-200 m (NMP K6326; H 66.8 mm); **C**, **E**-**H**, southern *keyteri* form; **C**, trawled off Mozambique (NMP H7331; H 85.0 mm); **E**, **H**, weakly nodulose specimen, MASCAREIGNES III stn 122, 200m, off SW Madagascar (H 66.0 mm); **F**, **G**, *Oocorys keyteri* Kilburn, 1975, holotype, trawled 50 km SE of Limpopo River mouth, Mozambique (NMP G2184, T1841; H 70.2 mm).

REMARKS. — A large amount of material of *Galeodea keyteri* in MNHN from off Madagascar is reasonably consistent in its characters. It is a moderate-sized species of *Galeodea* (height of most specimens 65-90 mm, although Kreipl (1997: 26) reported specimens up to 105 mm high) with a thick but weakly sculptured shell, the sculpture greatly dominated by many narrow, prominent, closely spaced spiral cords, smooth except for low, angular nodules on the peripheral cord of some specimens, not large enough to angulate the whorl profile on all but a few specimens. The anterior canal is moderately long and narrow, although only weakly twisted, and all specimens I have seen have a thick but narrow inner lip, without a free collar extended to the left of the aperture. The varix of typical Madagascan specimens is wide and prominently thickened, with a narrow but consistent abapertural channel separating it from the whorl surface, and bears many low ridges on the inner edge; the uppermost (adapical) of these ridges is raised slightly to moderately above the others, and is situated opposite a matching parietal callus pad that bears 3-5 short transverse ridges, so the two together constrict a posterior apertural notch weakly to quite prominently. The inner lip in the lower columellar area is crossed by many low, weak, weakly anastomosing transverse ridges. Several of the specimens from Madagascar retain one or two extra varices on the spire, at a much higher frequency (about 30% of specimens) than I have observed in other *Galeodea* species. The exterior is pale to quite dark brownish cream through to dull salmon-orange, with a white aperture. Specimens from Mozambique have a shallowly but obviously channelled suture on spire whorls, but the channel becomes weaker over the last whorl; it is not so obvious on the material from Madagascar.

The forms named *Galeodea ferrarioi* and *G. keyteri* are very similar in size, in shape, in their unusually high incidence of retained varices before the terminal one, and in their dark brownish cream to dull salmon-orange colour, and it seems likely that these forms constitute one western Indian Ocean species. Specimens identified as *G. ferrarioi* from off Somalia differ fairly consistently from specimens from off Madagascar and Mozambique in lacking nodules on the peripheral angulation (nodules occur on a small proportion of specimens of Madagascan specimens), in having the major spiral cords elevated into numerous low, narrow angulations of the whorl surface, i.e., the cords are more prominent than in Madagascan and Mozambique specimens, and in having a markedly thinner terminal varix and inner lip, lacking the prominent, short transverse ridges inside the outer lip of most adult specimens from Madagascar and Mozambique. The differences between them are subtle when a range of specimens is compared, and in my opinion they are conspecific, and apparently intergrade clinally in the western Indian Ocean.

ANATOMY. — The animal was examined of a female specimen from *Mascareignes III* stn 78, 530 m, off southwestern Madagascar (Figs 7C, D). No live-collected material of the "*ferrarioi* form" was available. The gross external anatomy and the mantle cavity and proboscis are as in all other species of *Galeodea* studied here. The short, stout (contracted) cephalic tentacles bear obvious, deeply pigmented, though rather small, eyes at their bases. The osphradium is rather more strongly asymmetrically bipectinate than in most other species (but not as strongly so as in *G. bituminata*), with its right leaflets significantly longer than the left ones. The operculum (Fig. 21D) is standard for *Galeodea*, with its nucleus at the anterior third of the opercular height, against the right edge of the operculum.

RADULA. — The radula (Figs 2E, F) is relatively small, but standard for *Galeodea*, with projecting lower corners of the basal plate of the central tooth. *Galeodea keyteri* (like some of the other relatively large species, notably *G. alcocki*, Figs 2A, B) has a radula much like that of *G. echinophora*, but with wider cutting areas and more numerous cusps on the heads of the central and lateral teeth than in *G. echinophora* and smaller species such as *G. triganceae*. *Galeodea keyteri* has 9-11 relatively long, narrow denticles on each side of the main cusp of the central tooth, and 9-12 long, narrow denticles outside the main cusp of the lateral teeth. Each inner marginal tooth has 2-3 relatively large denticles on its inner edge, whereas the outer marginal teeth are smooth. The radula of *G. leucodoma* (Figs 3A, B) is intermediate in the number of denticles and the width of the heads of the central and lateral teeth between the larger species, such as *G. keyteri* and *G. alcocki*, on the one hand, and *G. echinophora* and smaller species, such as *G. triganceae*, on the other. There seems no reason not to accept these slightly different tooth shapes and ranges of denticle numbers as the range within one genus; the larger species of *Galeodea* merely seem to have wider teeth with more numerous denticles than in the smaller species.

Galeodea leucodoma Dall, 1907

Figs 1E, F; 3A, B; 7E; 16; 21E

Galeodea leucodoma Dall, 1907: 166.

Synonym:
Morio granulosa Schepman, 1909: 123, pl. 10, fig. 4 (**new synonym**).

Other references:

Galeodea leucodoma - Dall 1925: 17, pl. 34, fig. 4. – Kuroda & Habe 1952: 58. – Kosuge 1972: pl. 6, fig. 9. – Okutani 2000: 273, pl. 135, fig. 1.

Galeoocorys leucodoma - Kira 1955: 43, pl. 21, fig. 2. – Kuroda & Habe 1957: 215, figs 1, 3. – Azuma 1960: 29. – Kira 1961: 54, pl. 22, fig. 2. – Shikama & Horikoshi 1964: pl. 62, fig. 1. – Matsumoto 1979: 37. – Okutani 1986: 117, first fig. second row.

Galeoocorys leucodon [*sic*] - Okutani *et al.* 1988: 72, illus. – Romagna-Manoja 1989: 27, 4 unnumbered figs.

Galeodea (*Galeoocorys*) *leucodoma* - Kreipl 1997: 29, pl. 10, figs 23, 23a.

Oocorys granulosa - Kreipl 1997: 71-72, unnumbered fig.

TYPE MATERIAL. – *Galeodea leucodoma*: holotype USNM 110503, from *Albatross* stn 4912, off Kagoshima, Honshu, Japan, in 391 fathoms (715 m) (Figs 16A, B). – *Morio granulosa*: holotype ZMA 3.09.007, from *Siboga* stn 316, 538 m, Indonesia, 7°19.4'S, 116°49.5'E (Figs 16G, H).

OTHER MATERIAL EXAMINED. – **Southern Japan**. Tosa Bay, Shikoku, in *c.* 200 m (3 lv, MNHN; 1 dd, WM 8522 NZGS); off Mie Prefecture, Honshu, 200-250 m, (1 lv, WM 14309 NZGS); off Tanegashima Islands, Kyushu (2 lv, WM 14308 NZGS); 130 m, off Cape Shiono, Wakayama Prefecture (1 lv, collection of G. Kronenberg, no. 1961); Tosa Bay, Shikoku (2 lv, NSMT Mo.7155); off Tosa Bay, Shikoku (1 lv, MCZ 282883); 130 m, Tosa Bay, Shikoku (1 dd, MCZ 233231); off Tosa Bay, 180 m, Shikoku (1 lv, NMNZ M267544,).

Taiwan. TAIWAN 2002: stn CP 166, 22°24'N, 120°15'E, 200 m (1 dd).

Philippine Islands. MUSORSTOM 1: stn CP 40, off Lubang Island, 13°58'N, 120°29'E, 265-287 m (1 dd). – MUSORSTOM 2: stn CP 55, off Lubang Island, 13°54'N, 119°58'E, 865 m (1 lv). — PANGLAO 2005 : stn CP 2335, Bohol Sea, 9°34'S, 123°38'E, 729-733 m (1 lv); stn CP 2336, off Balicasag I, 9°32'S, 123°39'E, 757-760 m (1 small lv); stn CP 2352, Bohol Sea, 9°27'S, 124°03'E, 923-1260 m (3 dd); stn CP 2385, Bohol/Sulu Sea sill, 8°51'S, 123°10'E, 982-989 m (2 small dd); stn CP 2388, Bohol Sea, 9°27'S, 123°35'E, 762-786 m (14 dd, 1 lv); stn CP 2389, Bohol Sea, 9°28'S, 123°38'E, 784-786 m (9 dd); stn CP 2390, Bohol Sea, 9°27'S, 123°43'E, 627-645 m (1 small dd).

Indonesia. KARUBAR: stn CP 20, Tanimbar Islands, 5°15'S, 132°59'E, 769-809 m, (1 lv, 1 dd juvenile); stn CC21, 5°14'S, 133°00'E, 688-694 m (1 dd); stn CP54, 8°21'S, 131°43'E , 836-869 m (2 lv, 45 dd); stn CC56, 8°16'S, 131°59'E, 552-549 m (1 dd); stn CC57, 8°19'S, 131°53'E, 603-620 m (1 dd); stn CP70, 8°41'S, 131°47'E, 413-410 m (1 dd); stn CP72, 8°36'S, 131°33'E , 699-676 m (9 dd); stn CP73, 8°29'S, 131°33'E, 855-840 m (8 dd); stn CP87, 8°47'S, 130°49'E, 1017-1024 m (1 dd); stn CP89, 8°39'S, 131°08'E, 1084-1058 m (4 dd); stn CP91, 8°44'S, 131°05'E, 884-891 m (40 dd).

Northwestern Australia. *Courageous* prawn trawler, cruise Aug. 1983, stn 099, Rowley Shoals area, 276-497 m (1 lv, with 2 lv *G. alcocki*, WAM 3248-83). – F/V *Soela* cruise, Feb. 1984, coll. S. Slack-Smith, stn 01-84-058, NW of Beagle Bay, 15°12'S, 121°05'E to 15°10'S, 121°09'E, 410-404 m (1 dd, WAM 814-84); stn 01-84-054, WNW of Lacépède Archipelago, 15°51.25'S, 120°44.3'E to 15°54.38'S, 120°45.3'E, 350-348 m (2 dd, WAM); stns 01-84-106 to 112, W of Lacépède Archipelago, 16°57.4'S, 119°52.0'E to 16°55.5'S, 119°56.0'E, 434-432 m (2 dd, WAM 1929-84); stn 01-84-091, W of Cape Leveque, 16°18'S, 120°19.5'E to 16°06.4'S, 120°20.5'E, 550-544 m (1 lv, WAM 899-84); stn 01-84-060, NW of Beagle Bay, 15°08.6'S, 121°03.4'E to 15°06.0'S, 121°06.6'E, 504-500 m (1 lv, WAM 1090-84); stn 01-84-070, NW of Collier Bay, 13°44'S, 122°13.3'E to 13°22.3'S, 122°14.7'E, 496-494 m (2 lv, WAM 1076-84); stn 01-84-061, NW of Cape Leveque, 14°39.5'S, 121°28.5'E to 14°41.9'S, 121°29.9'E, 500-506 m (1 lv, WAM 1093-84); stn 01-84-079, NW of Augustus Island, 13°17.0'S, 122°37.4'E to 13°18'S, 122°35.8'E, 494-484 m (1 lv, with 9 lv *G. alcocki*), WAM 910-84).

Fiji. MUSORSTOM 10: stn CP 1309, Bligh Water, 17°32'S, 178°53'E, 843-887 m (1 lv); stn CP 1331, Bligh Water, 17°02'S, 178°02'E, 694-703 m (1 dd, with 1 *G. bituminata*); stn CC 1336, Bligh Water, 16°58'S, 177°58'E, 797-799 m (1 lv); stn CP 1353, SE of Viti Levu, 17°31'S, 178°53'E, 897-899 m (2 lv, 2 dd); stn CP 1354, SE of Viti Levu, 17°43'S, 178°55'E, 959-963 m (2 dd). – BORDAU 1: stn CP 1396, 16°39'S, 179°57'W, 591-596 m (1 lv, 1 dd); stn CP 1397, 16°33'S, 179°52'W, 674-688 m (1 lv); stn CP 1401, 16°35'S, 179°41'W, 600-648 m (1 dd); stn CP 1502, 18°21'S, 178°27'W, 640-660 m (1 lv).

Solomon Islands. SALOMON 1: stn CP 1749, 9°21'S, 159°56'E, 582-594 m (1 dd); stn CP 1750, 9°16'S, 159°55'E, 693-696 m (2 dd); stn CP 1751, 9°10'S, 159°53'E, 749-799 m (1 lv); stn CP 1752, 9°07'S, 159°53'E, 896-912 m (1 dd); stn 1794, 9°16'S, 160°08'E, 494-504 m (1 dd); stn CP 1800, 9°21'S, 160°24'E, 357-359 m (1 dd); stn CP 1808, 9°46'S, 160°53'E, 611-636 m (1 lv, 1 dd). — SALOMON 2: stn CP 2215, SW of Choiseul I, 7°44'S, 157°42'E, 718-880 m (1 lv?); stn CP 2216, New Georgia Strait, SW of Choiseul I, 7°45'S, 157°39'E, 930-877 m (1 dd).

DISTRIBUTION. — *Galeodea leucodoma* occurs quite commonly throughout the western Pacific archipelagos in *c.* 200-900 m, at least as far east as the Solomon Islands, but there are no specimens in MNHN collections from the New Caledonian region or Vanuatu. Small specimens are abundant in depths of about 400-900 m in eastern Indonesia. It

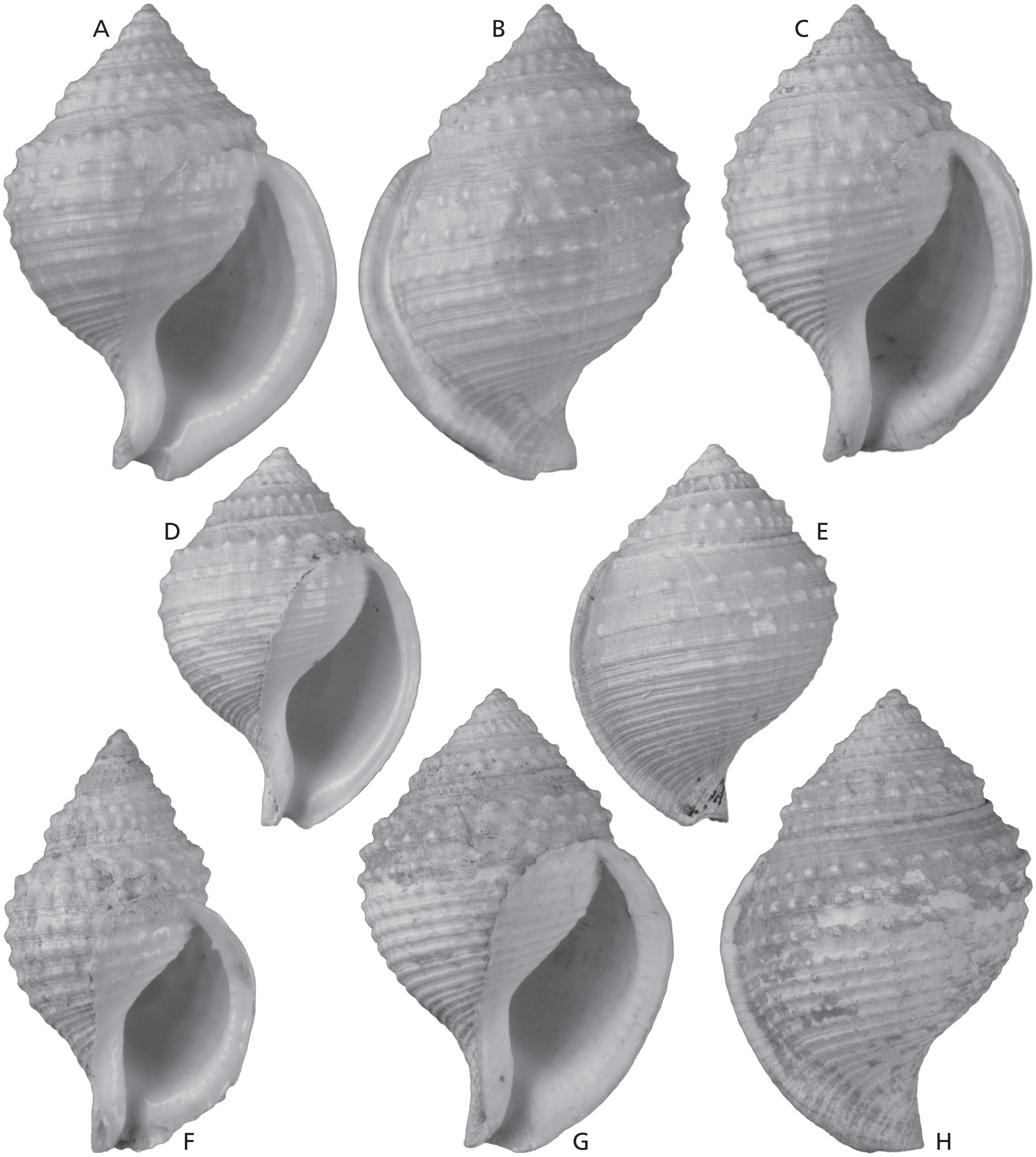


FIG. 16. *Galeodea leucodoma* Dall, 1907. **A**, **B**, holotype, off Kagoshima, Japan, 750 m (USNM 110503; H 70.2 mm; natural size); **C**, Tosa Bay, Japan, 200 m (H 53.5 mm; X 1.25); **D**, **E**, KARUBAR stn CP 54, 836-869 m, Tanimbar Islands, Indonesia (H 44.3 mm; X 1.25); **F**, MUSORSTOM 10 stn CP 1331, Fiji, 694-703 m (H 49 mm; X 1.25). **G**, **H**, *Morio granulosa* Schepman, 1909, holotype, *Siboga* stn 316, Indonesia, 538 m (ZMA 3.09.007; H 54.0 mm; X 1.25).

occurs also in small numbers off northwestern Australia where, however, it is much less common in prawn trawls than *G. alcocki* and *Echinophoria wyvillei*. Fossils have not been reported, although it seems likely to occur fossil in Indonesia. No other species of *Galeodea* were collected as far east as the Solomon Islands during the cruise SALOMON 1.

DIMENSIONS. — Holotype of *Galeodea leucodoma*: H 70.2, D 48.6 mm; holotype of *Morio granulosa*: H 54.0, D 36.7 mm; Tosa Bay, Shikoku, MNHN: H 69.9, D 46.8 mm; MUSORSTOM 1 stn 40: H 50.6, D 35.5 mm.

SYNONYMY. — The holotype of *Morio granulosa* (Figs 16G, H) agrees closely with some of the smaller Indonesian specimens in shape and number of nodule rows, but has much fewer fine interstitial spiral threads than typical large Japanese specimens. However, most of the abundant, relatively small specimens from Indonesia, Fiji and northwestern Australia have numerous fine spiral threads between the spiral cords as in Japanese specimens, and there is no doubt that the holotype of *Morio granulosa* is a small specimen of *G. leucodoma.*

VARIATION. — *Galeodea leucodoma* is of small to average size for a species of *Galeodea*, and quite typical of the genus in most characters. However, it is more evenly rounded than most other species, as the whorls are not angled at the periphery, a row of small nodules is present above the peripheral row of largest nodules (a unique character), and because most large specimens have 4-8 rows of small, even nodules below the peripheral row on the last whorl, i.e., more rows than in all the other Recent species of *Galeodea.* Some small adult specimens (e.g., some of those from Indonesia studied here; Figs 16D, E) have only 3-4 nodule rows, at and below the periphery, i.e., not including the row on the ramp, but the number of rows is highly variable. The Indonesian and Fijian specimens also are highly variable in spire height, in the width and prominence of the major spiral cords, and in overall shell shape; many are markedly taller and narrower than specimens from Japan, although the taller Japanese ones almost intergrade with Indonesian and Fijian ones. Several tonnoideans are recorded around southern Japan from shallower environments than anywhere else, and the shallow-water specimens have thicker shells, coarser sculpture and a shorter, wider shape than specimens from further offshore (particularly obvious in *Bursa ranelloides* (Reeve, 1844) and *Turritriton tenuiliratus* (Lischke, 1873)) and it seems possible that the differences merely reflect the shallower habitat of the Japanese than of the Indonesian and Fijian material. Like most other Recent Indo-West Pacific *Galeodea* species, *G. leucodoma* has only a narrow, closely adherent inner lip callus and a sharply flared but narrow terminal varix; the interior of the outer lip bears low, rounded nodules on only some specimens. Most specimens are white to pale cream with a white aperture, but some specimens collected live have a pale olive green periostracum adhering closely to the entire exterior.

Specimens taken in relatively deep water in the Bohol Sea, northern Philippines, during PANGLAO 2005 (7 stations, in 627-1260 m, listed above) are unusually thin-shelled and have relatively tall spires and very narrow, smooth, widely separated spiral cords, forming several low, narrow carinae around the shell. The interstitial sculpture consists only of low, narrow, widely spaced threads. At first, they were assumed to be an unnamed species. However, they all have a nodulose spiral cord in the centre of the convex sutural ramp, and comparison with other material of *Galeodea leucodoma* demonstrated that they intergrade with shallower-water material of that species. Most shallow-water specimens have relatively wide spiral cords, each bearing 2-3 narrow, raised spiral threads on their crests, and the interstitial spiral threads are relatively prominent and wide. A specimen in MUSORSTOM 2 stn CP 55, taken in 865 m off Lubang Island, Philippines, is neatly intermediate between the typical shallow-water specimens and the PANGLAO 2005 specimens in the width of its spiral cords and in having only very small nodules on the cords. There is little doubt that the PANGLAO 2005 specimens are merely extremely finely sculptured specimens of *G. leucodoma*, perhaps reflecting the relatively great depth at which they were collected.

Because of its evenly oval shape, narrow inner lip, narrow terminal varix and untwisted anterior siphonal canal, Kuroda & Habe (1957) regarded *Galeodea leucodoma* as more closely related to *Oocorys* than to *Galeodea*, and proposed the genus *Galeoocorys* for it. However, the shell characters are not significantly different from those of *Galeodea* *echinophora*, except for the unique character of a spiral row of nodules on the sutural ramp, and the anatomical and radular characters are standard for species of *Galeodea*. In my opinion Dall's (1907) original generic assignment was correct.

ANATOMY. – The animal was examined from a female specimen from KARUBAR stn CP 54, eastern Indonesia (Fig. 7E). The exterior appearance of the animal is standard for *Galeodea*, with small black eyes clearly visible at the bases of the short, wide (contracted) tentacles. The mantle cavity organs and their positions also are standard for *Galeodea*, with a moderately long, narrow proboscis; the osphradium is slightly asymmetrically bipectinate, with the right leaflets a little longer than the left ones. The operculum (Fig. 21E) is standard for *Galeodea,* with its nucleus against the right margin, at a third of the opercular height from the anterior end, and with no sign of the initially spiral growth that is characteristic of the *Oocorys* operculum.

RADULA. – The radula of *Galeodea leucodoma* (Figs 3A, B) is typical of *Galeodea*, with projecting basal corners on the basal plate of the central teeth, with 6-9 long, narrow denticles on each side of the main cusp of the central teeth, and with 7-9 long, narrow denticles outside the main cusp of each lateral tooth. This is one of the few *Galeodea* species in which a single small, narrow denticle also is visible on the inner edge of each lateral tooth or, on a few teeth, two denticles. The inner marginal teeth are more strongly hooked than in most other *Galeodea* species, and each bears 2 (rarely 3) large, elongate denticles on its inner edge, whereas the outer marginal teeth are smooth. The shape of the heads of the central and lateral teeth is intermediate between those of the larger *Galeodea* species I have examined that formerly were included in *Galeoocorys* (*G. keyteri* and *G. alcocki*) and the smaller *Galeodea* species such as *G. echinophora* and *G. triganceae*.

Galeodea maccamleyi Ponder, 1983

Figs 17C, D, F

Galeodea maccamleyi Ponder, 1983: 92, pl. 1, figs 1-4.

Other references:
Galeodea maccamleyi - Wilson 1993: 231, pl. 38, figs 5a, b. – Kreipl 1997: 27, pl. 9, fig. 20.

TYPE MATERIAL. – Holotype AMS C137654, with 2 paratypes, AMS C137655a, b, from 238 m, 23°52'S, 152°42'E, off Lady Musgrave Island, Capricorn Channel, Queensland, Australia; one paratype, AMS C132221, from 220 m, 24°05'S, 152°45'E, off Lady Elliot Island, Capricorn Channel, Queensland; 3 paratypes, Queensland Museum, Mo. 12609, from 220 m, between Lady Musgrave Island and Lady Elliot Island, Capricorn Channel, Queensland (Ponder 1983: 93).

OTHER MATERIAL EXAMINED. – **Southern Queensland, Australia**. *c.* 260 m, near Lady Musgrave Island, Capricorn Channel (1 dd, collection of G. Kronenberg, no. 2233,); off Hixson Cay, 22°33'S, 153°26'E, Swain Reefs, SE Queensland, 216-227 m (5 dd, AMS C383090); Lady Musgrave-Lady Elliot Island area, "deep water" (1 dd, NMP J.5923); off Lady Musgrave Island, 256 m, (1 dd, ZMA); off Lady Musgrave Island, 180 m, (1 lv, NMNZ M41042); MV *Capricorni*, E of Swain Reefs (22°S), 210 m, (1 lv, NZGS WM 16959); Capricorn Channel off Lady Musgrave Island (2 dd, NZGS WM 17338).

DISTRIBUTION. – Specimens were recorded also by Ponder (1983: 93) from northeast of Lady Musgrave Island, Capricorn Channel, in 365 m. All records are therefore from the Capricorn Channel area and the Swain Reefs in southern Queensland, in 180-365 m.

DIMENSIONS. — Holotype: H 30.1, D 22.8 mm; largest paratype (AMS, C137655a): H 37.1, D 26.3 mm; next-largest paratype (in collection of F. McCamley): H 34.0, D 24.0 mm; smallest (subadult?) specimen (AMS C137656): H 18.6, D 13.3 mm (Ponder 1983: 92). The largest (incomplete) specimen seen, AMS C383090 (off Hixson Cay, Swain Reefs) is 38.5 mm high.

REMARKS. — *Galeodea maccamleyi* is an unusually small (18-38 mm high), short and squat species, with an equally unusual colour pattern of four consistent rows of small white nodules on a uniform reddish brown to pale orange-brown background. The protoconch also is unique among Recent species in being deep reddish to purplish brown, at least on some specimens, rather than cream to white. The last teleoconch whorl is shorter and more strongly inflated than in any of the other Recent species, with a short and unusually rapidly contracted base and canal. The aperture is correspondingly wide and short, with a lightly flared outer lip that is well thickened within, and bears weak, low nodules on the inner edge; the inner lip is narrow, but is raised into a narrow, prominent, free collar over the neck. The entire exterior bears the standard *Galeodea* sculpture of prominent, narrow spiral cords. *Galeodea maccamleyi* does not closely resemble any other Recent species of *Galeodea* in detail, with its short shape and unique, bright colour pattern, although it resembles the smaller species such as *G. bituminata* and *G. triganceae* in general appearance. Rather, it appears to be a member of a species group that has evolved in Australia through much of Cenozoic time. The fossil specimens from southern Australia will be reported elsewhere (Beu & Darragh, research in progress).

ANATOMY. — Ponder (1983) described the anatomy, radula and operculum, which are typical of *Galeodea*; black eyes are present, and the osphradium was described as “bipectinate”. The operculum (Ponder 1983: pl. 2, figs. 1, 2) is reasonably typical of the genus, with the nucleus near the right edge (abaxial), but the nucleus is further towards the anterior (lower down) than on other species studied (perhaps because of the unusually wide aperture), at the lower quarter of the opercular height or lower, and is lower on small specimens than on large ones. The smaller operculum illustrated by Ponder (1983: pl. 2, fig. 1) has its nucleus close to the anterior end, and has initial growth ridges almost as obviously spiral (rigiclaudent paucispiral, in the terminology of Checa & Jiménez-Jiménez 1998) as in *Oocorys* species, but on the larger operculum, with the nucleus at about a quarter of the opercular height, growth ridges are commarginal (rigiclaudent commarginal, in the terminology of Checa & Jiménez-Jiménez 1998), and the initial weakly spiral area evidently has been abraded away.

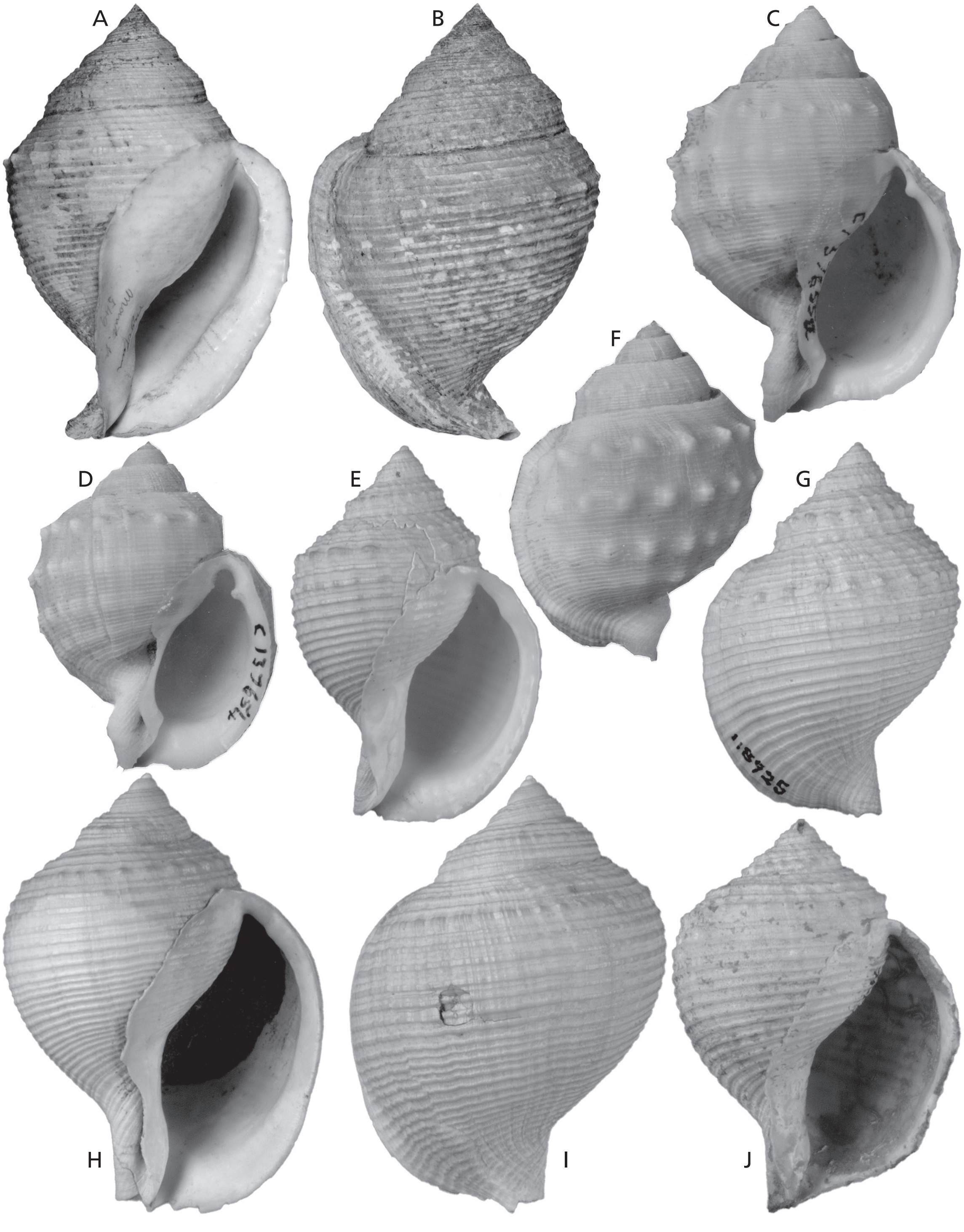
RADULA. – The radula (Ponder 1983: pl. 3, figs 1-5) is standard for *Galeodea*, with projecting corners on the basal plate of the central tooth, and 7-10 denticles on each side of the main cusp of the central tooth.

Galeodea plauta n. sp.

Figs 17E, G-J

Galeodea (*Galeoocorys*) n. sp. - Beu & Maxwell 1990: 353, pl. 48 b.

TYPE MATERIAL. — Holotype NMNZ M118925 (Figs 17E, G), off Ahipara, southern end of Ninety-Mile Beach, northwestern North Island, New Zealand, 35°00’S, 172°23’E, 500 m, F/V *Venture K*; 1 paratype, NMNZ M71974 (Fig. 17J), FRV *James Cook* stn J06-063-81, off Ninety-Mile Beach, northwestern North Island, 34°53.3’S, 172°19.2’E to 34°54.3’S, 172°20.1’E, 294-291 m; 1 paratype, NZGS TM 8196 (Figs 17H, I), locality GS 4056, New Zealand fossil record number R22/f6387, Upper Westmere Shellbed (of Abbott & Carter 1999), *c.* 1 m above Kaikokopu Shell Grit, Castlecliff coastal section W of Wanganui, New Zealand, *c.* 0.5 km E of Mowhanau Beach; age Castlecliffian New Zealand local stage, Middle Pleistocene, oxygen isotope stage 19. The age of this fossil paratype is well defined, as the Brunhes-Matuyama magnetic polarity transition, at 0.78 Ma (Bassinot *et al.* 1994), lies within the glacial-period


A
B
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C137854
118925
H
I
J

disconformity at the base of Kaikokopu Shell Grit (Turner & Kamp 1990), 1 m below the horizon where the fossil specimens of *Galeodea plauta* were collected.

OTHER MATERIAL EXAMINED. — **Recent**. NZOI stn P65, off Ahipara, 35°05'S, 172°26.6'E, 302-417 m, R/V *Tangaroa* (1 dd, incomplete, NMNZ); BS 821 (NZOI stn O.566), SW of Manukau Harbour, west Auckland, 37°32.5'S, 174°05.3'E, 502 m, R/V *Tangaroa* (1 dd, incomplete, NMNZ). **Fossils** (all from same unit and age as fossil paratype listed above): GS 4056, collected with paratype listed above (NZGS, 1 incomplete); GS 4056, at site where Kaikokopu Shell Grit descends to beach level, *c.* 400 m E of Mowhanau Beach (NZGS, 2 incomplete).

DISTRIBUTION. — *Galeodea plauta* is known so far in the Recent fauna only from the northwesternmost North Island, New Zealand, from off Ninety-Mile Beach south to west of Auckland (from 35°00'S to 37°32'S), in 290-500 m. It is not sympatric with the other New Zealand Recent species, *G. triganceae*, which lives only off the eastern coast of New Zealand.

Also, several specimens (four in NZGS, and one in the Geology Department, University of Auckland) have been collected as young fossils, about 750 000 years old, from Upper Westmere Shellbed in the Castlecliff section, on the coast west of Wanganui, southwestern North Island.

DIMENSIONS. — Holotype: H 46.7, D 31.9 mm; paratype NMNZ M71974: H 48.7, D 36.2 mm; paratype TM 8196: H 54.3, D 39.4 mm.

DESCRIPTION. — Shell rather small for genus (height 46-55 mm), unusually wide for genus, thin. Teleoconch of 4-4.25 whorls, with low, conical spire, an unusually wide, gently sloping, weakly convex sutural ramp, weakly angled shoulder and well inflated last whorl contracting gradually to short, open, almost straight anterior siphonal canal with no siphonal fasciole; canal inclined slightly towards dorsum at anterior end. Sculpture of many narrow, well raised, flat-crested, widely spaced spiral cords, 1 primary one at centre of sutural ramp, 1 more prominent than others at peripheral angle, and *c.* 20-25 primary ones on last whorl below periphery; interspaces on sutural ramp each with 1 or 2 narrow secondary spiral cords, upper 3-4 spiral interspaces below periphery each with 1 narrow secondary cord; interspaces on anterior part of last whorl each with 1 narrow secondary cord, commencing higher up last whorl on larger than on smaller specimens, strengthening progressively down shell to equal primary cords on siphonal canal; many narrow, weakly defined, somewhat irregular growth ridges cross sutural ramp and peripheral area of last whorl, fading out over base, forming low, rounded to weakly axially elongated nodules where they cross peripheral spiral cord and, on a few specimens, forming very low, weakly defined nodules also on mid-ramp primary cord and uppermost 2-3 primary cords below periphery; 19 nodules on last and 20 on penultimate whorls of holotype, on which nodules become larger and more widely spaced around last whorl than higher up; 22 on penultimate whorl of paratype M71974, nodules fading out altogether on last whorl of this specimen; 31 on last and 25 on penultimate whorls of paratype TM 8196, on which nodules become weak and indistinct over last quarter-whorl. Aperture large, oval, wide anteriorly, more constricted posteriorly; outer lip only slightly thickened, weakly flared, interior smooth or bearing numerous very low, indistinct ridges; inner lip smooth apart from spiral cords of previous whorl revealed through thin parietal callus, weakly spreading onto previous whorl in parietal area, somewhat thicker anteriorly and extended from columella into narrow, raised collar over neck; lower left edge of collar curving slightly to right

FIG. 17. *Galeodea rugosa* (Linné, 1771). **A**, **B**, lectotype, Mediterranean Sea (Linnean Society of London collection; X 0.6) (Natural History Museum photographs). **C**, **D**, **F**, *Galeodea maccamleyi* Ponder, 1983, all X 1.5; **C**, largest paratype, Capricorn Channel, off Lady Musgrave Island, southern Queensland, Australia (AMS C137655a; H 37.1 mm); **D**, **F**, holotype, same locality as paratype (AMS C137654; H 30.1 mm). **E**, **G**-**J**, *Galeodea plauta* n. sp., New Zealand, all X 1.25; **E**, **G**, holotype, off Ahipara, NW North Island, 500 m (NMNZ, M118925; H 46.7 mm); **H**, **I**, fossil paratype, locality GS4056, Upper Westmere Shellbed, Castlecliff coastal section, 500 m E of Mowhanau Beach, Wanganui, SW North Island; Middle Pleistocene (Castlecliffian New Zealand local stage), oxygen isotope stage 19 (NZGS, TM 8196; H 54.3 mm); **J**, Recent paratype, off Ninety-Mile Beach, NW North Island, 294-291 m (NMNZ, M71974; H 48.7 mm).

anteriorly to join canal, revealing narrow umbilical chink on most specimens. Protoconch standard for genus, very small, of 0.7-0.8 smooth whorls, with a protruding apex. Animals not available.

REMARKS. — The new species is most closely similar to the New Zealand Late Miocene (Kapitean New Zealand local stage) species *Galeodea sulcata* (Hutton, 1873) (see Fleming (1966) for this and closely related Late Miocene-Early Pliocene species from New Zealand). *Galeodea sulcata* has a thicker shell and a more thickened and slightly more flared outer lip than *G. plauta* n. sp., and also differs in having wider spiral cords, and obvious small nodules on 3-4 spiral cords below the periphery, as well as those that are at the periphery on *G. plauta*. I know of a single specimen from mid-Pliocene rocks (Ohawe Beach, Hawera, South Taranaki coast 45 km west of Wanganui, Waipipian New Zealand local stage, in collection of F. Chambers; plaster cast in NZGS). This specimen has still more prominent spiral cords than either *G. sulcata* or *G. plauta*, and has almost no nodules at all, but possibly belongs in a lineage that evolved from *G. sulcata* to *G. plauta*. At least two other fossil species of this type are known from New Zealand; *G. wylliei* Marwick, 1931 (see Maxwell 1978: figs 31, 32, for illustrations of the holotype) from Early Miocene rocks (Altonian New Zealand local stage) in the Gisborne district is astonishingly similar to *G. leucodoma* in most characters, i.e., it has wider spiral cords and many more rows of larger nodules than *G. plauta*, although it is otherwise similar. An undescribed species from the Mount Messenger Formation (early Late Miocene, Tongaporutuan New Zealand local stage) in North Taranaki is similar to *G. wylliei* and *G. sulcata* in most characters, but is much larger (height up to *c.* 100 mm). *Galeodea plauta* belongs in a lineage or species group that has been separate from that of *G. triganceae* for most or all of Neogene time.

The other New Zealand Recent species, *Galeodea triganceae*, is highly variable in most characters, although almost all specimens are markedly narrower and taller-spired than *G. plauta*. The major difference between these two species is the markedly wider and more complexly sculptured sutural ramp of *G. plauta* than of *G. triganceae*; the ramp bears only 5-7 very low, narrow spiral threads (as on the remainder of the teleoconch surface) in *G. triganceae*, whereas it bears a median primary spiral cord and at least 3 other secondary spiral cords in *G. plauta*, much more prominent than the sculpture on the ramp of *G. triganceae*. This character also distinguishes *G. plauta* from all other Recent *Galeodea* species other than *G. leucodoma*. *Galeodea leucodoma* differs from *G. plauta* in its markedly more numerous, wider and more prominent spiral cords, of which the cord above the main peripheral one is wide, coarsely nodulose and not distinguishable from the other primary cords, and many more cords below the periphery bear relatively larger, more obvious nodules than in *G. plauta*.

The occurrence of fossil specimens in Upper Westmere Shellbed is surprising, in view of the modern depth range of *Galeodea plauta*. The molluscan fauna of Upper Westmere Shellbed otherwise consists of inner to mid-continental shelf species, and the shellbed was deposited in no more than 50-80 m of water. The apparently ancestral species *G. sulcata* and the intermediate Ohawe Beach specimen also inhabited mid- to outer shelf soft substrates, indicating that the 290-500 m depth range of *G. plauta* is new for this species group. Evidently the retreat from central New Zealand to the northwesternmost North Island, presumably the result of glacial-period cooling of the New Zealand region, was accompanied by a retreat to deeper water than *G. plauta* had occupied previously.

A long history of geographical separation of the two species groups of *Galeodea* in New Zealand seems to be implied by their Late Miocene and younger records. *Galeodea triganceae* lives now all along the eastern coast, from the northeastern North Island to the Campbell Plateau, and is recorded as a Pliocene fossil at several eastern localities, listed below. In contrast, all Late Miocene and younger records of the *G. sulcata*-*G. plauta* species group are from western New Zealand (*Galeodea* n. sp., Late Miocene, North Taranaki; *G. sulcata*, Late Miocene-Early Pliocene, northern Westland, South Island; *G.* cf. *sulcata*, Hawera, South Taranaki; *G. plauta*, Middle Pleistocene, Wanganui, and living off northwestern North Island). It seems feasible that currents and water masses around New Zealand, after the axial mountains began significant uplift *c.* 5 my ago, have maintained these two species groups on separate coasts of New Zealand.

ETYMOLOGY. — The specific name (Latin, *plauta* = broad) is intended to indicate that the new species is the wider of the two New Zealand Recent species of *Galeodea*.

Galeodea rugosa (Linné, 1771)

Figs 17A, B; 21A

Buccinum rugosum Linné, 1771: 549.

Synonyms:
Buccinum tyrrhenum Gmelin, 1791: 3478.
Cassidaria depressa Philippi, 1844: 186, pl. 27, fig. 3.
Cassidaria echinophora var. *dubia* Cerulli-Irelli, 1911: 318, pl. 43, figs 4a-b.
Morio tyrrhena var. *globosior* Coen, 1920: 135, pl. 6, fig. 2.
Morio simplex Coen, 1920: 133, pl. 6, fig. 5.
Morio cylindrica Coen, 1920: 134, pl. 6, fig. 6.
Cassidaria deperdita Settepassi, 1970: *Cassidaria* xv, pl. 15, fig. 3 (**new synonym**).
Cassidaria tyrrhena fossilis Settepassi, 1970: *Cassidaria* xv, pl. 15, fig. 4 (**new synonym**).
Cassidaria uniseriata Settepassi, 1970: *Cassidaria* xv, pl. 16, figs 6A-B (**new synonym**).
Cassidaria pseudotyhhrena [*sic*] *dentata* Settepassi, 1970: *Cassidaria* xv, pl. 16, fig. 17 (**new synonym**).
Cassidaria obesostriolata Settepassi, 1970: *Cassidaria* xv, pl. 16, fig. 8 (**new synonym**).
Cassidaria tyrrhena vars. *major*, *minor*, *atlantica*, *dentata*, *varicosa*, *elongata*, *carenata* and *soluta* Settepassi, 1970: *Cassidaria* xviii-xix, pls 15-17 (**new synonyms**).

Other references:
Cassidaria tyrrhena - Reeve 1849: pl. 1, fig. 1.
Galeodea rugosa - Clarke 1962: 22. — Bouchet & Warén 1993: 805, figs 1945-1947. — Giannuzzi-Savelli *et al.* 1997: 216, figs 861-862. — Kreipl 1997: 27, pl. 9, figs 21-21a.

TYPE MATERIAL. — *Buccinum rugosum* Linné: lectotype selected by Bouchet & Warén (1993: 805), the one specimen remaining in Linné's collection, housed at the Linnean Society of London (Figs 17A, B). — *Buccinum tyrrhenum* Gmelin: lectotype selected by Bouchet & Warén (1993: 805), the specimen illustrated by Chemnitz (1788: figs 1461-1462), in University Zoological Museum, Copenhagen; from "Mari Tyrrheno". — The type material of the many minor varieties proposed by Settepassi (1970) presumably is in the Museo di Zoologia, Roma (not seen). — The type material of Coen's taxa is in the Hebrew University of Jerusalem (not seen). I am not aware of the location of the type material of the remaining synonyms.

OTHER MATERIAL EXAMINED. — Many lots in MNHN from the western Mediterranean and the eastern Atlantic; it is not necessary to list material of this well known species. Bouchet & Warén (1993: 805) listed the 75 lots they had examined, from depths of 178-1350 m.

DISTRIBUTION. — *Galeodea rugosa* occurs in the western Mediterranean, and in the eastern Atlantic from west of Ireland to southern Morocco (southernmost record 22°52'N). Bouchet & Warén (1993) considered that the few records from the western part of the eastern Mediterranean require confirmation. It is common in the Ibero-Moroccan Gulf, and fishermen net large numbers off southern Portugal (Beu, personal observation). Fossils occur not uncommonly in the Pliocene and Pleistocene of Italy and along the French Mediterranean coast.

DIMENSIONS. — Celtic Sea, PROCELT 1 stn K 210, 630-632 m, 49°57'N, 11°17'W (MNHN): H 107.4, D 69.7 mm; fishermen's nets, between Sagres & Faro, Algarve, Portugal, collected by S. Gofas, May 1986 (MNHN): H 122.0, D 71.1 mm. Kreipl (1997) recorded specimens reaching 140 mm high.

REMARKS. — *Galeodea rugosa* is a large, elongate species resembling *G. alcocki* in most characters, although most specimens have a shorter spire and more inflated spire whorls than *G. alcocki*, so that it is not so smoothly, narrowly and evenly fusiform as *G. alcocki*. Also, all specimens examined have a wide, prominent, rather thin, smooth inner lip collar raised above the previous whorl over the neck, extending to the left from the inner lip; a free collar is not present in the specimens of *G. alcocki* I have seen. The outer lip is much more strongly flared outwards and thickened and ridged on the interior than in *G. alcocki*, producing a much wider and more obvious terminal varix than in *G. alcocki,* and rendering the aperture unusually narrow. The smooth, even, round-topped, rather widely spaced spiral cords and the moderately long, weakly twisted siphonal canal are similar in the two species. *Galeodea rugosa* differs from the partly sympatric species *G. echinophora* in its much larger size, its more elongate shape, its more prominent spiral cords, and in most specimens lacking peripheral nodules, whereas several rows of peripheral nodules are present in most specimens of *G. echinophora*.

Although an unusually dark brown, the operculum of *Galeodea rugosa* (Fig. 21A) is typical of *Galeodea*, with its nucleus near the right edge at a third to almost half of the opercular height from the anterior end of the operculum, and with a weak furrow near and parallel to the right margin, above and below the nucleus. I have not examined an animal, but the anatomy was described by Reynell (1905, 1906) and agrees with that of all the other species studied here; Reynell (1905) recorded and illustrated obvious, deeply pigmented eyes.

Galeodea triganceae Dell, 1953

Figs 3C, D; 18

Galeodea triganceae Dell, 1953: 51, figs 1-4.

Other references:

Galeodea triganceae - Dell 1956: 85, pl. 12, figs 116-118; 1963: 210, pl. 1, fig. 7. — Powell 1979: 161, pl. 33, fig. 13. — Beu 1979: 91. — Campbell *et al.* 1993: 143, table 4.30. — Spencer & Willan 1996: 22. — Kreipl 1997: 28, pl. 9, fig. 22.

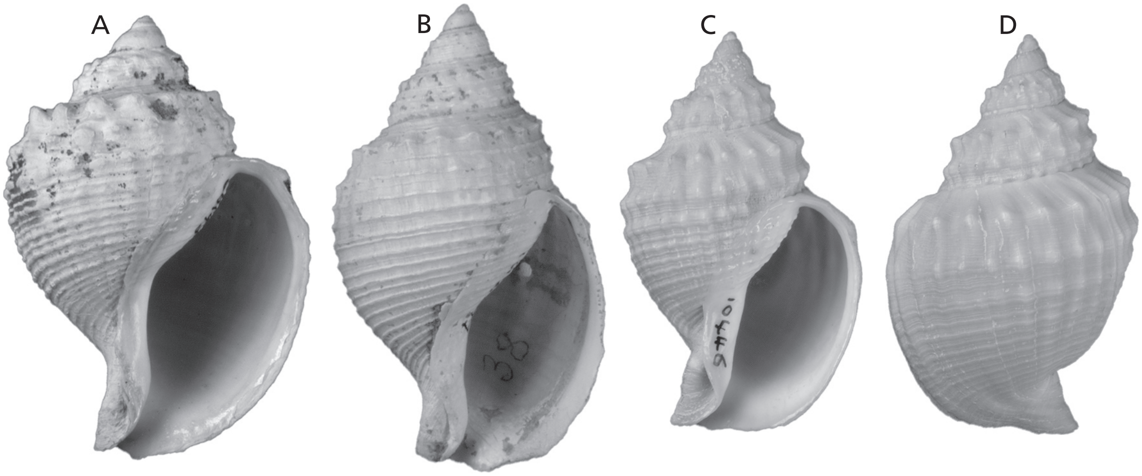


FIG. 18. *Galeodea triganceae* Dell 1953, New Zealand, all X 1.25. **A**, 37 km E of Mayor Island, NE North Island, 616-666 m (NMNZ, M60193; H 47.0 mm); **B**, 30 km N of Poor Knights Islands, NE North Island, 620-640 m (NMNZ, M102077; H 48.8 mm); **C**, **D**, Chatham Islands Exped. stn 41, SE of Pitt Island, Chatham Islands, 650 m (NMNZ, M10446; H 42.4 mm).

TYPE MATERIAL. — Holotype (M5717) and two paratypes (M5718-9) in NMNZ, 1 paratype in the private collection of S. Trigance, 1 paratype in the private collection of Mr and Mrs N. Gardner, all trawled in *c.* 120-140 m, off Timaru, eastern South Island, New Zealand (Dell 1953).

OTHER MATERIAL EXAMINED. — **New Zealand**. **Recent**. Chatham Islands Expedition (CIE) stn 41, *c.* 650 m, SE of Pitt Island, Chatham Islands, 44°35.5'S, 176°04'W (1 dd, figured by Dell 1956: pl. 12, fig. 116, NMNZ M10446); NZ Marine Dept. prawn survey, haul 28, 30 km N of the Poor Knights Islands, northeastern North Island, 620-640 m (1 lv, NMNZ M102077); BS 761, 616-666 m, 37 km E of Mayor Island, Bay of Plenty, eastern North Island, 37°22.0'S, 176°40'E to 37°22.4'S, 176°37.2'E, RV *Tangaroa* (3 lv, NMNZ M60193); BS 668, 454-424 m, 43 km SE of Cape Campbell, northeastern South Island, 41°55.9'S, 174°43.2'E, RV *Tangaroa* (6 lv, NMNZ M59673); trawled, 450 m, Chatham Rise, E of South Island, 42°20'S, 175°30'E (1 lv & 1 dd, coll. of G. Kronenberg nos., 3704, 3803); CIE stn 41, SE of Pitt I., Chatham Islands, 44°35.5'S, 176°04'W, 604 m (3 dd, NMNZ M10449); CIE stn 6, Chatham Rise, 43°40'S, 179°28'E, 402 m (2 lv, NMNZ M10447); BS 300, Turakirae Trench, Cook Strait, 41°30.5'S, 174°54'E, 640-658 m, R/V *Acheron* (2 dd, NMNZ M20124); prawn trawls off Alderman Islands, NE North Island, 400 m (3 lv, NMNZ M91709); RV *Eltanin* stn 1403, 41°42'S, 175°29'E, 946-951 m (1 dd, NMNZ M23622); FRV *James Cook* stn J01-012-77, Cathedral Banks, 51°20'S, 166°34'E to 51°18'S, 166°29'E, 646-670 m (1 lv, NMNZ M58400); BS 546, 39 km off Waiau River mouth, 42°55'S, 173°43'E, 549-586 m, R/V *Acheron* (1 dd, NMNZ M50871); BS 424, Turakirae Trench, Cook Strait, 41°30.2'S, 174°52'E to 41°28.2'S, 174°52'E, R/V *Acheron* (1 dd, NMNZ M35044); Taiaroa Trench, off eastern Otago, 722-768 m, R/V *Acheron* (1 dd, NMNZ M33602); FRV *James Cook* stn J03-101, between Auckland and Campbell Islands (1 dd, NMNZ M30971); BS 672, off Turakirae Head, Wellington, 41°31.4'S, 174°52.6'E, 533-225 m, R/V *Tangaroa* (2 dd, NMNZ M64924); BS 643 (NZOI stn R1), Palliser slope, southern North Island, 41°42.0'S, 174°15'E, 461 m, R/V *Tangaroa* (3 lv + 1 juvenile, NMNZ M59649); 60-80 m, trawled off Timaru, eastern South Island (2 dd, NMNZ M11333); BS 559, up steep wall of Pegasus Canyon, North Canterbury, 43°14'S, 173°39'E, 1006-512 m, R/V *Acheron* (2 lv, NMNZ M52763); BS 560, 15 km S of Kaikoura light, Marlborough, 42°35'S, 173°41'E, 640 m (1 dd, NMNZ M53681); Victoria University of Wellington Zoology Dept. stn 54, off Cape Palliser, SE North Island, 41°39.5'S, 175°17.0'E, 100-360 m (1 dd, NMNZ M9738); CIE stn 40, SE of Pitt I., Chatham Islands, 44°32'S, 176°05'W, 283 m (2 lv, NMNZ M10448); BS 669 (NZOI stn R27), 41 km S of Cape Campbell, NE South Island, 41°55.8'S, 174°40.7'E, 434-446 m, R/V *Tangaroa* (4 lv NMNZ, M60403); prawn trawler *Normandy*, off Mayor I., Bay of Plenty, 400 m (1 lv, NMNZ M70001); BS 752 (NZOI stn R110), 15 km NNW of Mayor Island, Bay of Plenty, 37°08.7'S, 176°14.2'E to 37°08.3'S, 176°15.5'E, 356-380 m, R/V *Tangaroa* (1 dd, NMNZ M61038); FRV *James Cook* stn J9-4-89, 41°21.5'S, 176°10.3'E, 830-710 m (3 lv, NMNZ M100343); off the Auckland Islands, 51°10.0'S, 166°40.0'E, 360-390 m, F/V *Venture K* (5 lv, NMNZ M117118); E of Mernoo Bank, Chatham Rise, 43°40'S, 176°26'E, 390 m, F/V *Venture K* (1 lv, NMNZ M117029); stn 1087-36, off the Auckland Islands, 50°54'S, 166°47'E, 430 m (2 dd); stn 1087-12, off the Auckland Islands, 50°57'S, 167°12'E, 485 m (1 dd, NMNZ M147015); BS 740 (NZOI stn R98), 45 km E of Mayor Island, Bay of Plenty, 37°23.5'S, 176°45.0'E, 631-666 m, R/V *Tangaroa* (1 dd, NMNZ M60180); stn 1087-34, off the Auckland Islands, 50°53'S, 166°46'E (2 dd, NMNZ, M147030); off eastern Otago, 360 m, R/V *Munida* (1 dd, NMNZ M132593); off the Auckland Islands, 51°10'S, 166°37'E, 490-510 m, F/V *Peterson* (7 dd, NMNZ M119014); Campbell Plateau, 49°09.6'S, 171°23.8'E, 310-370 m, F/V *Aragonit* (trip 367, haul 246) (1 dd, NMNZ M100584); stn 1022-44, off the Auckland Islands, 51°08.7'S, 166°23.9'E, 505 m (1 dd, NMNZ M144943); BS 878 (NZOI stn O.624), E of North Cape, 34°25.7'S, 173°12.8'E, 222-207 m, R/V *Tangaroa* (1 dd, NMNZ); stn 1087-21, off the Auckland Islands, 50°50'S, 166°57'S, 435 m (6 dd, NMNZ M147021); stn 1087-22, off the Auckland Islands, 50°44.7'S, 167°02.2'E, 408 m (3 dd, NMNZ M147027); off Taiaroa Head, Otago, 55 m, R/V *Munida* (2 dd, NMNZ M132594); NE slope of Mernoo Bank, Chatham Rise, 43°10'S, 175°44'E, 450 m, F/V *Peterson* (4 dd, NMNZ M127033); CIE stn 40, SE of Pitt Island, Chatham Islands, 44°32'S, 176°05'W, 283 m, M/V *Alert* (1 dd, NZGS RM 2857); stn Mu 70-45, Papanui Canyon, off Otago Peninsula, 540-490 m, R/V *Munida*, 22 Oct. 1970 (1 dd, NZGS RM 4733) (96 specimens).

Fossils. Locality GS11872, shellbed in Stace Stream, tributary of Blind River, Marlborough, Opoitian (Early Pliocene), 1 specimen; locality GS12161, Whenuataru Tuff, cliff near "The Point" homestead, Pitt Island, Chatham Islands, Waipipian (mid-Pliocene), 1 specimen (Campbell *et al.* 1993: 143, table 4.30); locality GS10337, Bourne Siltstone, hill above Glenstrae Station woolshed, Oaro, Southern Marlborough, 4 small, fragmentary specimens (Beu 1979: 91), early Nukumaruan (latest Pliocene); Palliser Bay coast, southernmost North Island, 1 specimen in NMNZ and several fragments in Geology Dept., Victoria University of Wellington (Beu 1967: 100), early Nukumaruan (latest Pliocene).

DISTRIBUTION. — *Galeodea triganceae* occurs throughout the eastern New Zealand area from North Cape (north to at least 34°25'S) south to the Campbell Plateau (to at least 51°10'S), and around the Chatham Islands, in depths of *c.* 200-710 m (the type material, from *c.* 120-140 m, was occupied by hermit crabs, as is all other material collected in less than about 200 m). All material is from the eastern side of New Zealand; there are no records from off the western coasts, and the new species *G. plauta* replaces *G. triganceae* off the northwestern North Island. Fossils are recorded from several Early to Late Pliocene localities of bathyal facies in eastern central New Zealand and at one mid-Pliocene locality on the Chatham Islands.

DIMENSIONS. — Holotype: H 42.6, D 27.5 mm; paratype: H 46.3, D 31.2 mm (Dell 1953); NMNZ M 102077, 30 km N of Poor Knights Islands: H 48.8, D 28.2 (Dell 1963).

REMARKS. — *Galeodea triganceae* is one of the smallest of the Recent species of *Galeodea*, similar in size to the smaller to medium-sized specimens of *G. bituminata*, and has an unusually thin, light-weight and, in most specimens, elongate shell, with a moderately tall spire, and with a rather long, strongly twisted anterior canal for a Recent *Galeodea* species (although shorter than in *G. bituminata*), directed quite strongly towards the dorsum. The sutural ramp slopes quite gently, forming a strongly gradate spire, and the whorl profile is weakly inflated below the shoulder angle. Most specimens bear 2-4 rows of narrowly rounded, closely spaced nodules at and below the periphery, although these are quite small on some specimens and completely absent from a few; the peripheral row is visible on spire whorls. Most specimens have a few low, narrow, widely spaced spiral cords on the sutural ramp, but none has any prominent, primary spiral cords on the ramp. This provides an important difference from *G. plauta*, in which there is one major spiral cord in the centre of the sutural ramp (rivalling the primary cords below the periphery in prominence) and one or two narrower, but still relatively prominent, cords on either side of the largest one. The ramp is correspondingly narrow in *G. triganceae* and wide in *G. plauta*, and this provides most of the difference in shape between the two species. The outer lip of *G. triganceae* is unusually thin for a Recent *Galeodea* species, with only a very light outward flare in most specimens, and not flared at all in a few; it is lightly thickened and smooth on the interior in most specimens. The inner lip is thin and narrow for most of its height, but is raised into a moderately thick, well elevated, smooth but quite narrow collar over the neck, extended ventrally and to the left at a marked angle to the plane of the aperture rather than more nearly parallel to the plane of the aperture as in the other species with an inner lip collar. The sum of its characters makes *G. triganceae* one of the more distinctive of the Recent *Galeodea* species. However, it is likely that it descended from the New Zealand Early Miocene species *G. apodometes* Marwick, 1934 (Beu & Maxwell 1990: 193, pl. 20 q). *Galeodea apodometes* is a more standard species of *Galeodea*, resembling *G. bituminata*, with larger nodules and a much thicker outer lip than in *G. triganceae. Galeodea apodometes* and *G. triganceae* are otherwise similar in size, shape and sculpture.

ANATOMY. — The animal was examined of two specimens from BS761, 37 km east of Mayor Island, Bay of Plenty, New Zealand, in 616-666 m (NMNZ M60193). Both are male, with a relatively small cylindrical penis, and with the widely open seminal groove clearly visible throughout the length of the mantle cavity and along the penis. The short, thick (contracted) cephalic tentacles have unusually large, obvious black eyes on their outer bases, larger in proportion to the size of the animal than in any other *Galeodea* species examined. The osphradium is short and wide, widening backwards into the mantle cavity to be half the width of the ctenidum towards the rear, and is slightly asymmetrically bipectinate. The proboscis was almost completely everted in both specimens, and is long and narrowly cylindrical compared with that of *Oocorys*. The operculum is the simplest one seen in *Galeodea*, evenly oval, flat and with regularly commarginal growth lines, with its nucleus against the right (abaxial) margin and a third of the opercular height from the anterior end.

RADULA. — The radula (Figs 3C, D) is standard for the smaller species of *Galeodea*, with small projecting triangular corners on the basal plates of the central teeth, with the width of the head of the central tooth only slightly greater than the height of the tooth, and with 5-7 denticles on each side of the main cusp of each central tooth. The denticles are narrow and very closely spaced, and are highly variable in number, height and width, even between the two sides of one tooth. The cutting heads of the lateral teeth are relatively wide (i.e., a little wider then the head of a central tooth) with a large main cusp, and each bears 7-9 denticles outside the main cusp; the denticles are again highly variable, and are a little further apart than on the central tooth. The inner marginal teeth each bear a single small, blunt denticle on the inner side, near the tip of the tooth, whereas the outer marginal teeth are smooth.

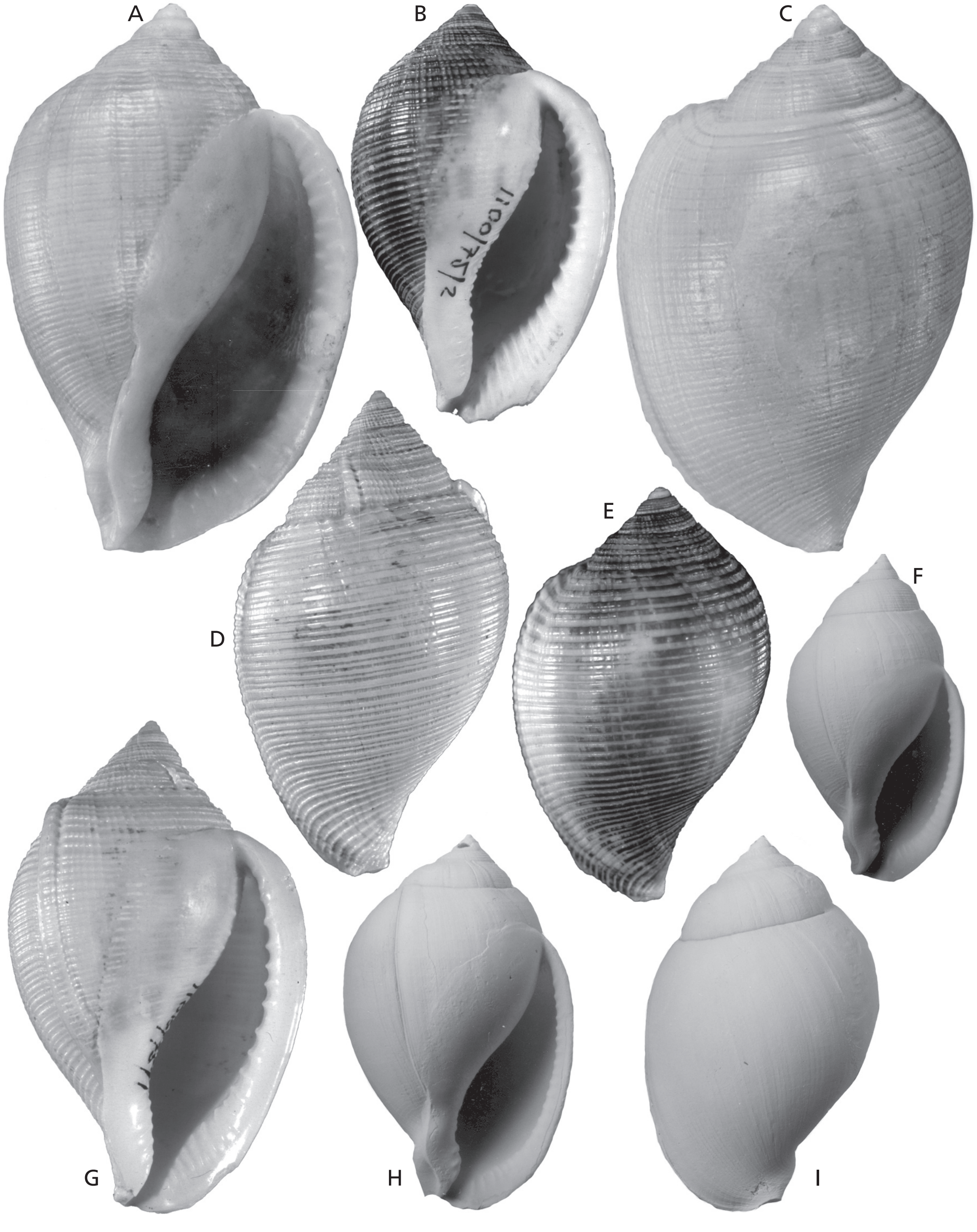
Genus ***SCONSIA*** Gray, 1847

Sconsia Gray, 1847: 137. Type species (by original designation): *Cassidaria striata* Lamarck, 1816 (junior secondary homonym of *Cassis striata* J. Sowerby, 1812, which subsequently has been referred to *Cassidaria* and *Sconsia*; see synonymy below), = *Sconsia grayi* A. Adams, 1855), late Pliocene to Recent, Caribbean Sea.

Synonyms:
?*Morionassa* Sacco, 1890a: 74. Type species (by original designation): *Morionassa amplectens* Sacco, 1890, Miocene, Italy (teratalogical form?).
Galeodosconsia Sacco, 1890a: 69. Type species (by original designation): *Cassidaria striatula* "Bonelli, 1825", an unpublished catalogue, = *C. striatula* Bellardi & Michelotti, 1840, Miocene, Italy.

DEFINITION. — *Sconsia* is recognisable by its elongate, graceful shape with a short spire and a long, gradually tapered last whorl, without a shoulder angulation (at least in Neogene and Recent species; several Paleogene species have a marked shoulder angulation), by its sculpture almost solely of fine spiral cords with smooth crests, by the presence of varices on the spire of several species, and by its long, drawn out anterior end, merging imperceptibly into a completely untwisted siphonal canal, with no fasciole. The protoconch (in *S. grayi*) is very small, of only one whorl, simple and smooth, similar to that of *Galeodea* but a little taller. Bayer (1971: fig. 17A) illustrated the operculum of *Sconsia grayi* - which is closely similar to that of *Galeodea* species - and also (Bayer 1971: fig. 20D) illustrated the radula. The radula is very distinct from those of *Galeodea* species, and from any of the other taxa studied here, in having 5 large denticles on the free end of each inner marginal tooth, the second denticle as long as the main cusp of the tooth. The central and lateral teeth also have rather long, narrow denticles. The unusually numerous, brush-like denticles on the inner marginal tooth seem likely to be a generic character that would help determine whether *Galeodea hoaraui* should be referred to *Sconsia*.

REMARKS. — Dall (1909) pointed out that Early Cenozoic species of *Sconsia* and *Galeodea* are similar in shell morphology, i.e., they diverged quite early in Early Cenozoic time. *Sconsia* is a major Cenozoic genus in the western Atlantic area, including the southern USA, the Central American area and islands, and northern South America. The well-known type species, *S. grayi* (A. Adams) (= *S. striata* (Lamarck, 1816), preoccupied), also is moderately common along the southern coast of the Caribbean Sea at present, and occurs also in the Lesser Antilles. This has therefore been thought of as largely a western Atlantic genus, and certainly is limited to this area at present. Parth (1994) added significantly to the known diversity of the genus by describing the almost completely smooth species *S. alexarthuri* from the Lesser Antilles, where it lives in deeper water (300-400+ m) than *S. grayi* (*c.* 15-200+ m). However, *Sconsia* has a long fossil record in Europe and the Mediterranean area and in the tropical Indo-West Pacific (van Regteren Altena 1942) as well as the Americas. The Neogene fossil species of the tropical Central American region (Costa Rica, Panama, the Dominican Republic and Venezuela) will be revised by Beu (in prep., "Revison of Central American Neogene tonnoidean gastropods"), and the Recent species are revised here.


A
B
C
D
E
F
G
H
I
1100/75/2

Probably, the only two Recent species of *Sconsia* are *S. grayi* (A. Adams, 1855) and *S. alexarthuri* Parth, 1994, but *S. nephele* Bayer, 1971 tentatively is retained here as a species separate from *S. grayi*. All species are limited to the western Atlantic Ocean.

Sconsia alexarthuri Parth, 1994

Figs 19F, H, I

Sconsia alexarthuri Parth, 1994: 175, illus.

Other reference:
Sconsia alexarthuri - Kreipl 1997: 30, pl. 10, fig. 25.

TYPE MATERIAL. — Holotype, ZSM 1881; dredged in 305 m, Virgin Islands, Caribbean (not seen).

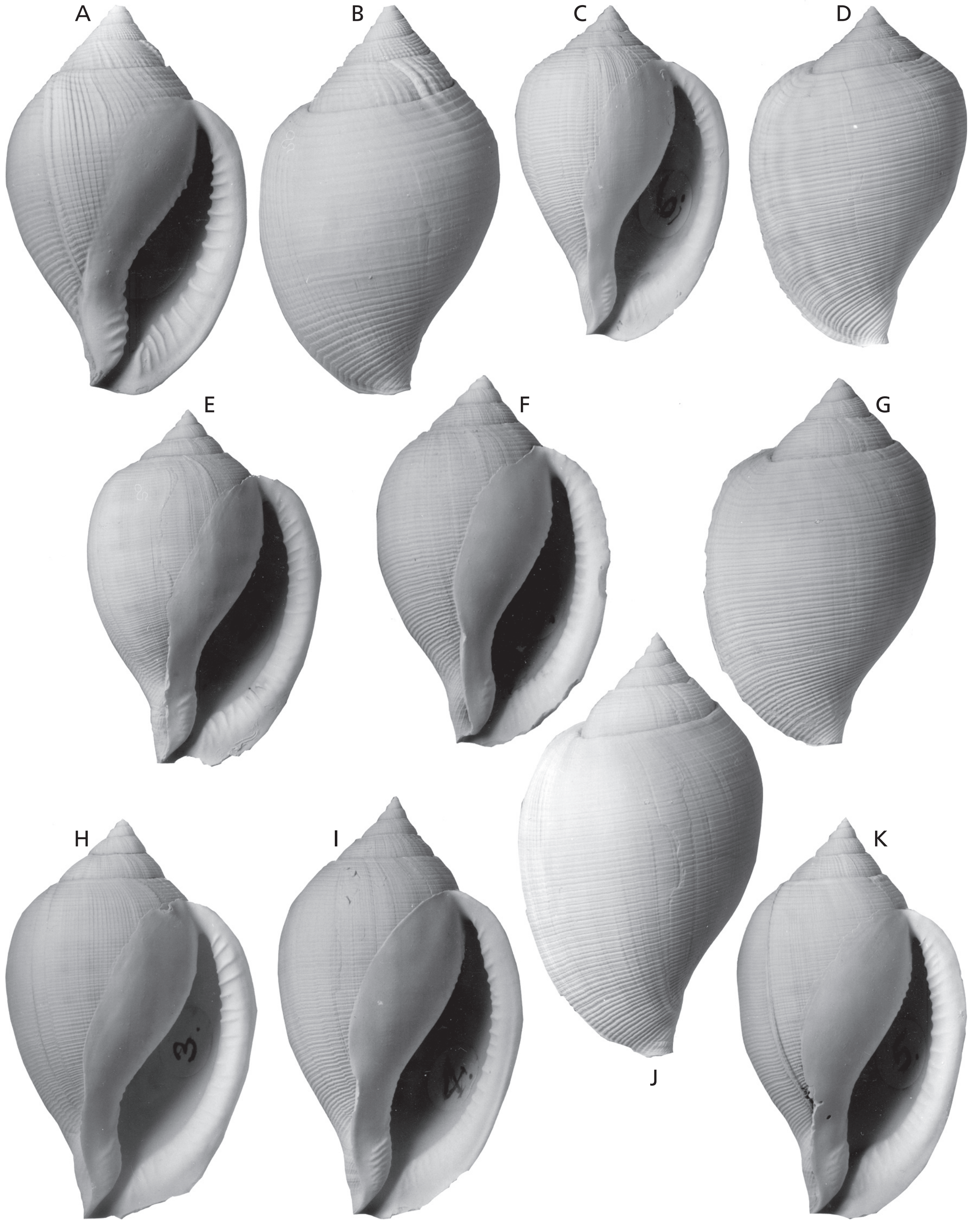
OTHER MATERIAL EXAMINED. — **Caribbean**. Racket Bank, off Guadeloupe, Lesser Antilles, from fish traps in 200 m (3 dd, D. Lamy collection; 1 dd, NZGS WM 17014); taken in baited trap in 170 m, Virgin Islands, Lesser Antilles (1 specimen, in collection of L. Sunderland, Florida).

DISTRIBUTION. — *Sconsia alexarthuri* is recorded only from the Virgin Islands and Guadeloupe, in the Lesser Antilles. It possibly is limited to the northern Lesser Antilles, but its range is very poorly known as yet.

DIMENSIONS. — Holotype: H 46.4 mm, D not stated; NZGS WM 17014: H 44.9, D 25.4 mm; Racket Bank, in collection of D. Lamy: H 47.0, D 29.5 mm; H 45.0, D 25.0 mm.

REMARKS. — *Sconsia alexarthuri* is one of the most distinctive of all Cassidae, because of its inflated but elongate shape, with a markedly taller spire than that of *S. grayi*, and its smooth, polished surface without obvious sculpture on the last whorl. However, all specimens examined have low, narrow, closely spaced spiral cords on spire whorls, fading out over the penultimate whorl, although on one specimen the spiral cords are faintly visible on the early part of the last whorl. A few faint growth lines are present on some specimens, and the inside of the outer lip has several low denticles. The holotype, illustrated in colour by Kreipl (1997: pl. 10, fig. 25) is a pale cream, almost white specimen, shaped much like *S. grayi* but with a slightly taller spire and markedly more deeply impressed sutures. Four specimens collected by Dominique Lamy (3 in D. Lamy's collection and 1 in NZGS) from fish traps off Guadeloupe show that fresh specimens are a darker cream than the holotype, shading to pale brown at the suture and to a darker brown along the outer edge of the outer lip, and particularly at the base of the last whorl, around the margin of the siphonal canal. They also vary a great deal in width, from short-spired, wide specimens to tall-spired, narrow specimens. Although the lack of sculpture on the last whorl is an almost unique, unexpected character in the Cassinae, seen otherwise only in "*Cassis*" *abbotti* Bouchet, 1988 (p 11) (Kreipl 1997: 18, pl. 5, fig. 7), the general similarity to *S. grayi* and the fine, even spiral sculpture on spire whorls show that, at least on the basis of teleoconch characters, *S. alexarthuri* is correctly referred to *Sconsia*. *Sconsia alexarthuri* is distinctive enough that it could conceivably be a convergent shell form superficially resembling other species of *Sconsia*, and only examination of its radula, operculum and anatomy will confirm the generic position.

FIG. 19. *Sconsia grayi* (A. Adams, 1855). **A**, **C**, holotype, locality unknown (designated here as off Punta Allegre, Cuba) (BMNH 1967664; H 43.0 mm; X 2.0) (Natural History Museum photographs); **B**, **D**, **E**, **G**, *Cassidaria striata* Lamarck, the two syntypes without locality (Clench & Abbott (1943) designated the type locality as off Punta Allegre, Cuba), from colour transparencies, MHNG photographs; **B**, **E**, dark syntype, illustrated by Lamarck (1816: pl. 405, fig. 2) (MHNG 1100/75/2; H 43 mm; X 1.5); **D**, **G**, pale syntype, illustrated by Kiener (1835: pl. 2, fig. 3) (MHNG 1100/75/1; H 51 mm; X 1.5). **F**, **H**, **I**, *Sconsia alexarthuri* Parth, fish traps, 250 m, Racket Bank, off Guadeloupe, French West Indies (2 specimens in collection of D. Lamy; H 45 mm (**F**) and 47 mm (**H**, **I**; X 1.25).


A
B
C
D
E
F
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H
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J
K

The specimen listed above from the Virgin Islands has a complete protoconch (photograph sent by Linda Sunderland, Florida), showing that it is small, blunt and paucispiral, of less than one whorl, with a protruding apex, as in *Galeodea* species. The lecithotrophic larval type that this protoconch demonstrates presumably explains the very limited distribution of this species.

Sconsia grayi (A. Adams, 1855)

Figs 1C, D; 19A-E, G; 20

Cassidaria striata Lamarck, 1816: pl. 405, figs 2a, b; "*Liste des objets*" p. 3. Junior secondary homonym of *Cassis striata* J. Sowerby, 1812 (p 24), which was referred to *Cassidaria* by Brown (1839, in 1838-1849: 53) and to *Sconsia* by Glibert (1963: 109) and Tracey (1992: 161).
Sconsia grayi A. Adams, 1855: 136, pl. 28, fig. 6.

Synonyms:
Sconsia barbudensis Higgins & Marrat, 1877: 411, pl. 1, fig. 1.
Sconsia bocasensis Olsson, 1922: 137, pl. 12, figs 12, 13 (**new synonym**).
Sconsia laevigata var. *gabbi* Olsson, 1922: 308, pl. 12, fig. 3 (**new synonym**).
Sconsia lindae Petuch, 1987: 96, pl. 15, figs 7, 8 (**new synonym**).

Other references:
Cassidaria striata - Lamarck 1822: 216. – Kiener 1835: 6, pl. 2, fig. 3. – Deshayes 1844: 10. – Reeve 1849: pl. 1, fig. 2.
Sconsia striata - Gray 1847: 137. – Clench & Abbott 1943: 6, pl. 4, figs 1-4. – Morretes 1949: 91. – Warmke & Abbott 1961: 97, pl. 28 g. – Bayer 1971: 138, figs 14, 17 A, 20 D. – Matthews & Coelho 1972: 13, fig. 8. – Abbott 1974: 160, pl. 6, fig. 1730. – Rios 1985: 73, pl. 26, fig. 320. – Lipe & Abbott 1991: 8, illus. – Rios 1994: 85, pl. 28, fig. 332. – Kreipl 1997: 31, pl. 10, figs 28, 28a.
Cassidaria (*Sconsia*) *striata* - Chenu 1859: 208, fig. 1138. – Watson 1886: 410.
Sconsia grayi - Trew 1992: 34.
Sconsia barbudensis - Clench 1959: 329, pl. 172.
Sconsia laevigata - Petuch 1981: 321 (*non Sconsia laevigata* G. B. Sowerby II, 1850).
Sconsia lindae - Robinson 1991: 305, pl. 13, fig. 14. – Diaz & Puyana 1994: 171, fig. 637. – Kreipl 1997: 30, pl. 10, fig. 27.

TYPE MATERIAL. – *Cassidaria striata*: 2 syntypes MHNG 1100/75/1-2, without locality. The paler syntype, MHNG 1100/75/1, H 51 mm (Figs 19D, G), is the specimen illustrated by Kiener (1835: pl. 2, fig. 3), whereas the smaller, darker syntype, MHNG 1100/75/2, H 43 mm (Figs 19B, E), is the specimen illustrated by Lamarck (1816: pl. 405, fig. 2). The two specimens are conspecific, and represent the Caribbean species universally known as *Sconsia striata*. Clench & Abbott (1943: 8) designated the type locality as *Atlantis* stn 2981A, off Punta Allegre, Cuba. – *Sconsia grayi*: holotype BMNH 1967664 (Figs 19A, C), without locality. The type locality is here designated as off Punta Allegre, Cuba, the locality designated by Clench & Abbott (1943) as the type locality for *C. striata*. – *Sconsia barbudensis* Higgins & Marrat: holotype in City of Liverpool Public Museum (not seen; illustrated by Clench 1959: pl. 172), from

FIG. 20. *Sconsia grayi* (A. Adams, 1855), range of variation of specimens in R. von Cosel's material trawled off the north coast of Colombia (all in SMF; whitened with MgO). **A**, **B**, *Choco* stn 621, c. 200 m (X 1.5); **C**-**K**, specimens taken in shallow-water shrimp trawls, demonstrating intergradation between short, low-spired "*striata*" form (**C**-**E**) and narrow, tall-spired "*lindae*" form (**I**-**K**) (all at natural size); **C**, **D**, *Heroica* haul 12, 30-50 m, off Mendiguaca-Buritaca, E of Santa Marta (H 52.5 mm); **E**, westernmost specimen, *Sagitario* haul 17, 50 m, off Acandi-Napu, Gulf of Uraba, near Panama-Colombia border (H 54.1 mm); **F**, **G**, *Esperanza* haul 17, 30-50 m, off Punta Espada, easternmost Colombia (H 57.5 mm); **H**, *Acuario* haul 34, 50 m, off Acandi, Gulf of Uraba, western Colombia (H 62.1 mm); **I**, **J**, *Heroica* haul 0, 50 m, off Cartagena-Bocachica, central Colombia (H 65.9 mm); **K**, *Tortuga*, 15-20 m, off El Rodadero, central Colombia (H 63.1 mm).

30 m, off Barbuda I., Lesser Antilles. – *Sconsia bocasensis* Olsson: holotype PRI 21083, a late Pliocene fossil from Bocas del Toro, NE Panama. – *Sconsia laevigata* var. *gabbi* Olsson: holotype PRI 21074, a late Pliocene fossil from "Toro Cay" (i.e., also Bocas del Toro), NE Panama. – *Sconsia lindae* Petuch, 1987: holotype USNM 784457 (not seen), trawled by commercial shrimpers from 35 m, off Cartagena, Colombia, 1976; 3 paratypes from Gulf of Urabia, Colombia (Petuch 1987: 96).

OTHER MATERIAL EXAMINED. – **Colombia**. R. von Cosel's material in SMF: *Choco* stn 621, off Guajira Peninsula, *c.* 200 m (3); dredged off El Rododero, near Santa Marta, by Santa Marta Institute's R/V *Tortuga*, 30 m (2); as last, 15-20 m, in 23-m shrimp trawl (1); as last, 80 m (1); dredged, R/V *Melongena* 35-40 m, Bahia Santa Marta, 28 April 1971 (1); shrimp trawler *Sagitario* off westernmost Colombia near Panama border: haul 6, 17-20 m, S of Isla Fuerte, SW of Cartagena (2); as last, haul 17, off Acandi to Napu, Gulf of Uraba, 50 m (2); as last, haul 31, off Trigana to Titumate, Gulf of Uraba, 50-55 m (1); as last, haul 34, off Acandi, Gulf of Uraba, 55 m (1, with 1 trawled by shrimper *Acuario* at same site); as last, haul 35, Gulf of Uraba, 50 m (1, with 2 trawled by *Acuario* at same site); as last, haul 43, off Acandi to Napu, Gulf of Uraba, 50 m (1); second voyage on shrimp trawler *Sagitario*, off north-central coast of Colombia between Mendiguaca and Buritaca, E of Santa Marta, in 30-35 m: haul 2 (6); haul 3 (3); haul 4 (1); haul 5 (1); haul 6 (1); haul 7 (1); haul 8 (4); haul on last night (7); shrimp trawler *Esperanza*, voyage to Punta Espada, off the extreme eastern tip of Guajira Peninsula, easternmost Colombia, in *c.* 30 m: haul 7, ESE of Punta Esperanza (1); haul 9, as last (1); haul 17, off Punta Esperanza (1); haul 36, as last (1); last sample, off Dibulla (1); shrimp trawler *Heroica*, off north-central coast of Colombia, between Mendiguaca and Dibulla-Camarones, in *c.* 50 m; trial before voyage, off Cartagena to Bocachica (1); haul 11, off Mendiguaca to Buritaca (3); haul 12, as last (9); haul 13, as last (2); haul 14, as last (2); haul 15, off Buritaca (2); haul 16, off Buritaca (5); haul 18, off Dibulla (1); haul 20, off Pedregal, just W of Dibulla (7); haul 22, of Pedregal to Dibulla (5); haul 23, as last (2); haul 24, off Dibulla (2); haul 25, off Buritaca (1); haul 27, off Buritaca (9); haul 28, off Mendiguaca to Buritaca (5); haul 29, as last (1); haul 30, as last (3); haul 31, as last (3); haul 32, as last (7); haul 33, as last (5); haul 39, just W of Dibulla (1); no haul no., off Pedregal to Dibulla (1) (48 samples containing 124 specimens).

Small numbers of other specimens have been examined also from a wide range of western Atlantic localities in NZGS, MNHN, and many other museums.

DISTRIBUTION. – *Sconsia grayi* lives now throughout the tropical western Atlantic from southern Florida and the Bahamas (Clench & Abbott 1943) south to Bahia, Brazil (Rios 1994: 85). However, it seems to be more common along the coastline of northern South America than elsewhere. Fossil specimens are common in latest Pliocene and Pleistocene rocks along the Atlantic coast of Panama and at Limon, Costa Rica (Beu in prep., "Revison of Central American Neogene tonnoidean gastropods"). Robinson (1991) recorded 98 specimens in Tulane University collections from the area around Limon on the Atlantic coast of Costa Rica.

DIMENSIONS. – Syntypes of *Cassidaria striata*: H 51.0, D 31.5 mm; H 43 mm, D not known; holotype of *Sconsia grayi*: H 43.0, D 27.8 mm; holotype of *S. barbudensis*: H 67, D 38 mm (Clench 1959: 330); holotype of *S. bocasensis* (very incomplete): H 35.9, D 24.5 mm; holotype of *S. laevigata* var. *gabbi*: H 46.2, D 29.7 mm.

NOMENCLATURE. – This species has long been known under the name *Sconsia striata* (Lamarck, 1816). However, as Tracey (1992: 162) pointed out, Sacco (1890a: 69) placed the English Eocene species *Cassis striata* J. Sowerby, 1812: 24 in *Galeodosconsia*, and all later authors (e.g., Cossmann 1903: 133; Dall 1909: 66; Wrigley 1934: 117; Glibert 1963: 109) have considered *Galeodosconsia* Sacco, 1890 to be a synonym of *Sconsia* Gray, 1847. Glibert (1963) and Tracey (1992) took the logical step of referring *Cassis striata* J. Sowerby to *Sconsia*. *Sconsia striata* (Lamarck, 1816) is therefore a junior secondary homonym of *S. striata* (J. Sowerby, 1812), and the next available name, *Sconsia grayi* A. Adams, 1855, must be used for the Recent species. According to Sherborn (1931: 6178), Lamarck's species name also was at one time a junior secondary homonym of *Cassidaria striata* (J. Sowerby), as Sowerby's taxon was referred to *Cassidaria* by Brown (1839: 53).

REMARKS. – *Sconsia grayi* is recognised easily by its graceful, oval shape, by the base being drawn out very gradually into a short, completely straight siphonal canal without an anterior notch, by bearing sculpture of many high, narrow spiral cords with interspaces of varying width, from less than one cord to equal to one cord in width, crossed by fine axial ridgelets in a narrow zone behind the terminal varix, by lacking varices before the terminal one in all except a few individuals, and by its well thickened aperture with a thick terminal varix, many short, prominent transverse ridges inside the outer lip, and a thick, nearly smooth inner lip bearing very faint transverse ridges over most of its height and a row of 8-10 shorter and more prominent ones on the base of the columella.

SYNONYMY. — The range of variation of this species and whether such nominal species as *Sconsia lindae* Petuch and *S. nephele* Bayer are distinct from *S. grayi* has been difficult to assess previously, as material of this species group is uncommon. Fortunately, for this study I was able to examine the suite of 124 specimens collected along the northern coast of Colombia by Dr Rudo von Cosel (MNHN), now stored in SMF. Three of these specimens were immature, tall-spired ones collected from a depth of *c.* 200 m at *Choco* stn 621, but all the others were collected in *c.* 15-50 m in 23 m-wide Gulf of Mexico semiballoon shrimp trawls, from localities along the entire Colombian coastline, encompassing the type locality of *Sconsia lindae* Petuch. These specimens range from coarsely sculptured, moderately short-spired ones of the type usually regarded as typical *S. grayi*, and even more short-spired specimens with a weakly angled periphery, through to tall and narrow, tall-spired specimens with relatively weak spiral sculpture, of the type named *S. lindae* by Petuch (1987), and through to even more extreme, tall-spired specimens than Petuch's type material. Occurrence of the "*S. lindae*" form is not correlated with depth or geographic location; the tallest and most weakly sculptured specimens were collected near the centre of the Colombian coastline, where they intergrade completely with the shorter and more coarsely sculptured specimens collected to the east and west. It is therefore clear that the Recent *S. grayi* population is quite variable in the characters that have been used to distinguish species, and the fossil populations, in particular, need to be reinterpreted with this variation in mind. The three small (immature) specimens collected at *Choco* stn 621 are all rather more different from the shallow-water ones than are the specimens of the "*S. lindae*" form. They have a more biconic shape, with a taller, more conical spire than shallow-water specimens, and have significantly weaker sculpture than shallow-water ones. They also have a more zigzag, axially banded colour pattern, not the evenly banded pattern of shallow-water specimens, in which a combination of axial and spiral bands produces a vaguely defined pattern of squares. The *Choco* specimens therefore more nearly resemble the Pliocene fossil species *S. sublaevigata* (Guppy, 1866) than they do the shallow-water specimens of *S. grayi*, and indicate that the depth of the habitat affects the interpretation of the taxonomy of the Caribbean-Central American fossil species.

RELATIONSHIPS. – The relatively elongate, evenly spirally sculptured species *Sconsia grayi* contrasts strongly with the Miocene-Early Pliocene species *S. laevigata* (G. B. Sowerby II, 1850: 47, pl. 10, fig. 2), from the Dominican Republic and from Cantaure, Paraguana Peninsula, northern Venezuela. *Sconsia laevigata* is considerably larger than *S. grayi*, adult specimens are completely smooth around the central area of the last whorl (although with fine spiral threads on the spire and base), the shape is markedly wider, shorter and more biconical, with a weakly shouldered periphery and a weakly humped shape produced by a low, wide swelling on the dorsum of the last whorl, and all varices are retained throughout ontogeny. This is about as different from *S. grayi* as is achieved within the genus, and yet *S. laevigata* seems to have been the ancestor of *S. grayi* (Beu in prep., "revision of Central American Neogene tonnoidean gastropods"), as was pointed out long ago by Gabb (1875). *Sconsia lindae* Petuch, 1987: 96, pl. 15, figs 7, 8 originally was identified by Petuch (1981: 321) as *S. laevigata*, but its elongate, subcylindrical shape and the presence of spiral sculpture over the entire exterior show that this is incorrect, and Petuch (1987) later named it as a separate Recent species. *Sconsia bocasensis* Olsson, 1922: 137 was proposed for relatively coarsely sculptured Late Pliocene or Pleistocene fossil specimens from the Bocas del Toro area, northeastern Panama, but specimens examined during a revision of Central American Neogene tonnoideans (Beu in prep.) show they are indistinguishable from *S. grayi*. Olsson (1922) thought that this and *S. sublaevigata* var. *gabbi* Olsson, from the same area and age of rocks, were Miocene in age, and did not compare them with *S. grayi*, but they actually are Late Pliocene or Pleistocene, and in my opinion these two forms simply intergrade completely with *S. grayi*.

Sconsia nephele Bayer, 1971

Sconsia nephele Bayer, 1971: 139, fig. 15.

Other references:
Sconsia nephele - Abbott 1974: 160. – Kreipl 1997: 27, unnumbered text fig.

TYPE MATERIAL. – Holotype USNM 700004, from *Pillsbury* stn P-851, SW of Grenada, Caribbean, 11°52.8'N, 61°53.3'W, in 18 m (not seen).

OTHER MATERIAL EXAMINED. – Shrimp trawl, 100 m, off Guyana, January 1977 (tentatively identified specimen in collection of Linda Sunderland, Florida).

DISTRIBUTION. – Known only by the holotype, from off Grenada Island, and one other possible specimen from off Guyana.

DIMENSIONS. – H 37.8 mm, diameter not stated (Bayer 1971: 139).

REMARKS. – This small species was differentiated from *Sconsia grayi* by Bayer (1971) on the basis of its low spire and wide shape, its low, wide spiral cords, and its better-developed "checkerboard" colour pattern consisting of alternating brown and white maculations, in 8 relatively wide spiral bands of dark brown interrupted regularly by "squarish spots of white" (Bayer 1971). The wide, short-spired shape is matched by some of the shortest specimens of *S. grayi* in Rudo von Cosel's material from Colombia listed above (Figs 20C, D). A second specimen with the shape, sculpture and colour pattern of *Sconsia nephele* (height 41.5 mm) has been shown to me recently. It seems likely that *S. nephele* is part of the range of variation of *S. grayi*, especially as the holotype is still apparently one of only two known specimens, but more material is required from near the type locality before this species can be evaluated adequately.

Genus ***MICROSCONSIA*** n. gen.

Type species. *Microsconsia limpusi* n. sp., Recent, Swain Reefs, southeastern Queensland, Australia.

DIAGNOSIS. – Cassinae with a very small shell for the family (height up to 22 mm), moderately inflated, with moderately tall, conical spire, last whorl moderately elongate but with a short, wide, weakly twisted anterior siphonal canal deflected strongly to left (in conventional apertural view) through truncation and leftward deflection of columellar base, so anteriormost part of outer lip extends slightly below anterior end of siphonal canal; suture narrowly but quite deeply channelled; teleoconch exterior sculptured with fine, low, close spiral ridges only; aperture with lightly callused, transversely ridged lower area on inner lip (crossing neck) and narrow, internally thickened, but only weakly varicate outer lip bearing numerous short, narrow, relatively prominent, internal transverse ridges. Protoconch (Figs 11B, D, F) small, paucispiral, agreeing with that of all Recent species of *Galeodea*.

REMARKS. – The new genus *Microsconsia* is proposed for a strange little shell that could be said to combine the overall shape (other than a relatively taller spire), the fine spiral sculpture and some of the apertural characters of *Sconsia* with a much shorter and less graceful anterior end, a protoconch identical to that of all the Recent species of *Galeodea*, and with the curiously twisted and truncated columellar base and very short anterior canal of *Pisanianura,* in the tonnoidean family Laubierinidae (see Warén & Bouchet 1990; Beu & Bouchet in progress). Apart from being the smallest adult Recent cassid I am aware of, the new genus and species adds an uncommon character (for cassids) to this unusual combination: a narrowly but obviously channelled suture, produced by a narrow contraction to an inverted-V-shaped notch at the posterior end of the aperture. While it seems very likely that this genus belongs in the Cassinae, and is closely related to *Galeodea* and *Sconsia*, the taxonomic position will remain uncertain until the operculum and radula are described.

ETYMOLOGY. — The generic name (*micro-*, small, plus *Sconsia*) is intended to indicate that the type species of this genus resembles a diminutive species of *Sconsia*. Gender feminine.

Microsconsia limpusi n. sp.

Figs 11B, D, F; 22A-C

TYPE MATERIAL. — Holotype AMS C382770, trawled in 183 m, N of Halfmoon Reef, Swain Reefs, southeastern Queensland, Australia (Figs 22A, B); one paratype MNHN 20181, trawled in 190-192 m, 22°35'S, 153°16'E, SE of the Swain Reefs, southeastern Queensland (Fig. 22C). Both specimens were trawled by commercial fishermen, and were collected and presented to me by Allan Limpus.

DISTRIBUTION. — Known only by the type material.

DIMENSIONS. — Holotype: H 21.5, D 12.7 mm; paratype: H 20.8, D 12.1 mm.

DESCRIPTION. — Shell very small, up to 21.5 mm high (the smallest Recent adult cassid I am aware of), thin and slightly translucent. Teleoconch of 4 whorls, of standard inflated cassine-phaliine shape, with moderately tall, conical spire (significantly shorter in paratype than in holotype), large last whorl enveloping most of rest of shell, and short, wide anterior siphonal canal deflected slightly dorsally and to left in conventional apertural orientation, produced by truncation and deflection of columellar base so canal does not extend as far anteriorly as base of outer lip. Suture narrowly but deeply and obviously channelled, narrow outer margin of channel formed by one narrowly rounded spiral cord. External sculpture of numerous low, narrow, rounded, smooth, closely spaced spiral cords, *c.* 20 on spire whorls and *c.* 40 on last whorl, with one interstitial thread filling each interspace, thread low and narrow on posterior part of last whorl but increasing in prominence and width anteriorly, rivalling primary cords in prominence over siphonal canal. Axial sculpture absent other than faint growth lines. Aperture elongate, pear-shaped, rounded anteriorly, drawn up posteriorly into narrow v-shaped posterior notch margining sutural channel, notch weakly constricted by one short, low, narrow parietal ridge situated opposite short posteriormost ridge inside outer lip; inner lip weakly callused posteriorly, weakly spreading onto previous whorl over parietal area, narrow but more thickened anteriorly, raised into a narrow, thin, sharp-edged free collar over neck, abruptly truncated at *c.* 100-110° to columellar base by edge of siphonal canal slightly posterior to (above, in apertural view) inner edge of thickening inside outer lip, forming left siphonal canal margin inclined at *c.* 45° to coiling axis; lower (anterior) third of lip bearing *c.* 12-15 low, narrow, rounded, weakly anastomosing transverse ridges, remainder smooth apart from parietal ridge. Outer lip raised into very low, wide, inconspicuous external varix (only terminal varix present on both specimens), lip extending into thin, sharp margin in front of varix; interior thickened into rounded ridge markedly more prominent than external varix, markedly wider over anterior half than posteriorly, bearing *c.* 20 low, narrow, short transverse ridges, ridges single posteriorly, tending to be arranged in pairs over central area of lip, becoming progressively lower, weaker and more closely spaced anteriorly. Protoconch small, smooth, of *c.* 0.7 whorls, 1.1 mm in diameter, with apex protruding, as in *Galeodea*, but smaller than that of any *Galeodea* species. Animals not available.

REMARKS. — At first sight, the truncated and deflected columellar base gives the impression that *Microsconsia limpusi* is more closely related to *Pisanianura* Rovereto, 1899 (Family Laubierinidae) than to *Sconsia* or any other Cassinae, and it is still possible that the radula and operculum will demonstrate that its correct position is alongside *Pisanianura* in the Laubierinidae. However, it seems more likely that it is most nearly related to *Galeodea* and *Sconsia*. The very small size for a Recent cassid, the narrowly but deeply channelled suture, the fine spiral sculpture similar to that of *Sconsia* and the protoconch closely similar to those of the Recent *Galeodea* species, along with the truncated columellar base, make this a species that cannot be confused with any other. The very small protoconch suggests that *M. limpusi* has lecithotrophic (and probably direct, intracapsular) development, as in *Galeodea*, and so it is probably limited to the Swain Reefs and the neighbouring area of southeastern Queensland.

Microsconsia limpusi bears a striking resemblance to *Cassis nupera* Conrad, 1833 [Nov.] (Eocene, Alabama, USA), type species of *Doliocassis* Dall (1909: 62; designated as the synonym *Buccinum sowerbii* Lea, 1833 [Dec.]; Palmer 1937: 253, pl. 31, figs 12, 18; pl. 83, figs 7, 11), a genus regarded by Abbott (1968: 123) as a synonym of *Galeodosconsia* Sacco, 1890 (material of *Doliocassis nupera* examined in the Cossmann Collection (Palaeontology Collections, MNHN J08924, MNHN J08983). The resemblance is caused by similarity in size (most specimens of *C. nupera* are 15-20 mm high), shape and sculpture, although the spiral cords are much lower and less obvious in *C. nupera* than in *M. limpusi*, giving the shell a very smoothly oval appearance. However, profound differences between these species in the shape and orientation of the anterior siphonal canal demonstrate that this resemblance is entirely superficial. The canal is little more than a simple anterior notch in *C. nupera*, with a low, smooth siphonal fasciole separated from the previous whorl by a very weak groove, and without any truncation or deviation of the columellar base. (The character of the siphonal canal also suggests that *C. nupera* might not be correctly referred to *Sconsia,* i.e., that *Doliocassis* is a useful genus). Rather than a modern representative of a genus otherwise recorded only from the North American Eocene, *Microsconsia* seems likely to be a relatively recent Pacific derivative from *Galeodea*.

ETYMOLOGY. — The new species is named for Allan Limpus, of Bundaberg, Queensland, who generously provided the type material, along with many other interesting specimens from Queensland waters.

Subfamily OOCORYTHINAE

Oocorythinae Fischer, 1883: 392 (as Oocorythidae). Type genus *Oocorys* Fischer, 1883.

DIAGNOSIS. — Subfamily Oocorythinae includes the taxa of Cassidae with a thin, light-weight, pale shell; with predominantly spiral sculpture, with very little of the axial sculpture that is prominent in most Cassinae and Phaliinae, and without peripheral nodules; with a thin, narrow terminal callus or with no outer lip thickening at all, and with no varices retained before the terminal one, other than in a few individuals; with an anterior siphonal notch but no siphonal canal in most taxa and at most a very short, widely open canal in a few species, made still more widely open by the truncation of the base of the columella and its deviation to the left in many species; with an operculum similar to that of *Galeodea* but with a more anterior nucleus, causing a spiral initial area of growth (rigiclaudent paucispiral, in the terminology of Checa & Jiménez-Jiménez 1998); without obvious, darkly pigmented eyes; with a short, wide proboscis (length about twice the width in most taxa); with a curved or shallowly S-shaped osphradium; and with a relatively wide, thin, flat penis of triangular shape.

REMARKS. — This definition unites *Oocorys* Fischer, 1883, *Dalium* Dall, 1889 and *Eucorys* n. gen., and separates them from the taxa I include in Cassinae and Phaliinae. Oocorythinae was concluded by Riedel (2005: 124) to be a monophyletic group that has been distinct from the other Cassidae for a long period, probably at least all of Cenozoic time (although as noted above, this was based partly on inclusion of *Galeodea*, with its many early fossils, in Oocorythinae). The history of recognition of this subfamily and the significance of the characters of the anterior siphonal canal are discussed above, while opercular characters are discussed below, under *Oocorys*.

Among differences noted between *Galeodea* and *Oocorys* in anatomy, the most striking is the lack of obvious, deeply pigmented eyes in all animals of *Oocorys* I have examined (as well as in the animal of *Dalium solidum* (Dall, 1889) illustrated by Bayer 1971); eyes are obvious in all specimens of *Galeodea* and, indeed, all other Cassidae I have examined. The dried, reconstituted animal of *Eucorys bartschi* also lacked obvious eyes, but this needs to be checked from better-preserved material. Another difference is in the length and proportions of the proboscis, which is relatively long and narrow in *Galeodea*, but relatively short and wide (about a third to half the length of that of a similar-sized *Galeodea* specimen) in *Oocorys*. The penis of the few male specimens of *Oocorys* I have examined (most examined specimens were female) is as shown by Quinn (1980: fig. 3): relatively short, wide and flattened, weakly to obviously triangular in outline, with a subquadrate termination, in contrast to the narrower, almost cylindrical penis of most *Galeodea* species (it is wider in a few species). The penis is quite short in *O. verrillii* (Dall, 1889) (Fig. 9B) and *O. clericus* (Figs 9D, E) but moderately long in *O. sulcata* Fischer, 1883 (Fig. 8B) and consideralbly elongated in *O. grandis* n. sp. (Fig. 9F), but the apparent length is partly a preservational artefact. Large, weakly translucent (i.e., thin-walled), complex secondary salivary glands are present in all the *Oocorys* animals examined, filling most of the cephalo-pedal cavity as in *Galeodea* and all other tonnoideans. The external appearance and mantle cavity configuration of all specimens of *Oocorys* and related genera studied below were exactly as shown by Bayer (1971: fig. 19), with minor variation in the relative width of the two sides of the osphradium; i.e., the osphradium of the different species differs in its degree of asymmetry, the left leaflets being shorter in some species than in others, and the right leaflets varying from almost equal to the left ones in some species, to up to twice as long as the left ones in others, as in *Galeodea*. Another apparently unique character of the *Oocorys* osphradium is that it is more strongly curved than in *Galeodea* and other genera of Cassinae, and in a few species is weakly S-shaped. Osphradia and most other anatomical features have not been examined for *Eucorys*. Few of the *Oocorys* specimens studied here had a well-preserved protoconch; it is corroded or abraded in almost all specimens. However, the rather better-preserved protoconchs of *O. sulcata* and (I assume) *O. clericus* illustrated by Warén & Bouchet (1990: figs 118-119) and the excellent, complete larval shell and well preserved protoconch illustrated by Bouchet & Warén (1993: figs 1920, 1930) demonstrate that at least most species of *Oocorys* have a very different protoconch from the paucispiral, smooth one of less than one whorl of all *Galeodea* species, as the protoconch of *Oocorys* species is larger, turbiniform and of about 2.3-3 whorls, with the fine, prominent, cancellate sculpture characteristic of planktotrophic tonnoidean protoconchs. However, the two species I transfer here to the new genus *Eucorys*, *E. bartschi* (Rehder, 1943) and *E. barbouri* (Clench & Aguayo, 1939), have very small cap-shaped protoconchs of only 0.7-0.8 whorls, as in *Galeodea*. These apparently are geographically limited species, each having been reported only from part of the Caribbean Sea, and this difference in protoconch type reflects a difference in developmental type. The paucispiral protoconch of *Eucorys* implies intracapsular development (to judge from that of *Galeodea*; Hughes 1986a, b) whereas the larger, turbiniform, cancellate protoconch of *Oocorys* implies planktotrophic development (Warén & Bouchet 1990). The animal of *Dalium*, illustrated by Bayer (1971), is closely similar in all visible characters to that of *Oocorys*, but the protoconch of *Dalium* has not been described.

The question must be considered of whether *Oocorys* and its relatives should be placed in a subfamily of their own, or merely included in Cassinae. Three genera are recognised here, but the distinction of *Dalium* is uncertain; should a subfamily be recognised that contains only two or at most three genera? I suggest that the unusually simple shell, along with its unusually simple animal, lacking obvious eyes, and its distinctive operculum, initially rigiclaudent paucispiral but later rigiclaudent commarginal, indicate that this is a remnant of an early, originally primitive cassid group that is now largely extinct, but has adapted to conditions in the deep sea. These characters are a combination of primitive and highly specialised ones, and it seems likely that the group identified by them is paraphyletic rather than monophyletic. Whether Oocorythinae should be recognised will best be determined once a phylogeny has been developed. Here, Oocorythinae is recognised tentatively.

Genus ***OOCORYS*** Fischer, 1883

Oocorys Fischer, 1883: 392. Type species (by monotypy): *Oocorys sulcata* Fischer, 1883, Atlantic and Indo-West Pacific oceans.

Synonyms:
Benthodolium Verrill & Smith *in* Verrill, 1884: 177. Type species (by monotypy): *Benthodolium abyssorum* Verrill & Smith *in* Verrill, 1884 (= *Oocorys sulcata* Fischer, 1883).
Hadroocorys Quinn, 1980: 156. Type species (by original designation): *Dolium* (*Eudolium*) *verrillii* Dall, 1889, western Atlantic (**new synonym**).

DIAGNOSIS. — Oocorythinae with a thin shell, sculptured predominantly with low spiral cords (although weak axial ridgelets are present in some species); most species with flat-crested cords and flat-bottomed interspaces; aperture weakly to moderately callused, terminal varix moderately prominent in many species, completely lacking in a few; anterior siphonal canal very short or represented only by a dorso-ventrally oriented notch in the apertural margin (normal to the coiling axis of the teleoconch), accommodated at the base of the columella by its shortening and deviation to the left. Protoconch relatively large, turbiniform, of about 2.3-3 whorls, with prominent cancellate sculpture. Animal with no obvious, pigmented eyes; proboscis short and wide, length *c.* twice width; males with a short, wide, dorsoventrally flattened penis with a triangular outline and subquadrate termination. Osphradium curved to weakly S-shaped. Operculum with its nucleus at the anterior end (base) of the right (abaxial) margin, producing spiral initial growth lines (rigiclaudent paucispiral, in the terminology of Checa & Jiménez-Jiménez 1998) that become more obviously commarginal as the operculum grows (rigiclaudent commarginal, in the terminology of Checa & Jiménez- Jiménez 1998). Radula essentially as in *Galeodea*; the larger species with shorter, more numerous and more closely spaced denticles on the central and lateral teeth (up to 14-20 in the larger species) than in *Galeodea* (in which the maximum is about 12 denticles).

REMARKS. — Almost everything about *Oocorys* has been contentious since Fischer (1883) first named it: its family position, how many species it contains, their distribution, and their range of variation. The concept that the Atlantic bathyal species *O. sulcata* might be living in the Indo-West Pacific first arose when Smith (1906) named *O. sulcata* var. *indica* from the RIS *Investigator* collections off India. The concept of a distinct family Oocorythidae continued to rear its head up until the time of Quinn (1980). Only when Warén & Bouchet (1990) studied the gross anatomy of *Oocorys* and Bouchet & Warén (1993) studied much larger collections of material than previous investigators had was the real situation in this genus made clear: it closely resembles *Galeodea* in many characters, and it contains

FIG. 21. Opercula of *Galeodea*, *Eucorys* and *Oocorys* species. **A**-**I**, X 2; **J**-**M**, X 3. **A**, *Galeodea rugosa* (Linné, 1771), off Tangier, Morocco (operculum H 32.5 mm). **B**, *Galeodea echinophora* (Linné, 1758), type species of *Galeodea*, Adriatic Sea (H 30 mm). **C**, *Galeodea alcocki* (E. A. Smith, 1906), NW Western Australia, 420-520 m (H 30.5 mm). **D**, *Galeodea keyteri* (Kilburn, 1975), holotype, 50 km SE of Limpopo River mouth, Mozambique (NMP G2184, T1841; H 26.5 mm). **E**, *Galeodea leucodoma* Dall, 1907, holotype, off Kagoshima, Japan, c. 750 m (USNM 110503; H 24.5 mm). **F**, *Eucorys bartschi* (Rehder, 1943), Gulf of Mexico, 430 m (MCZ 198513; H 40 mm). **G**, *Oocorys grandis* n. sp., WALDA stn CY 05, off NE Namibia, 2953 m (H 23 mm). **H**, *Oocorys grandis* n. sp., paratype MNHN 20183, SAFARI 2 stn CP 2, central Indian Ocean, 3625 m (H 25 mm). **I**, *Oocorys elevata* Dall, 1908, holotype, between Galapagos Islands and Sechura Bay, Peru, 4023 m (USNM 110569; H 28 mm). **J**, *Oocorys sulcata* Fischer, 1883, holotype of *Oocorys rotunda* Dall, 1908, Gulf of Panama, 3009 m (USNM 123029; H 17 mm). **K**, *Oocorys sulcata* Fischer, type species of *Oocorys*, DEMERABY stn CP 06, off northern Brazil, 4450 m (H 16 mm). **L**, *Oocorys verrillii* (Dall, 1889), holotype of *Benthodolium pacificum* Dall, 1896, Gulf of Panama, 4162 m (USNM 123021; H 12.5 mm). **M**, *Oocorys verrillii* (Dall, 1889), MUSORSTOM 6 stn CP 427, Loyalty Ridge, New Caledonia, 800 m (H 13.5 mm).


A
B
C
D
E
G
F
I
H
J
K
L
M

only a few, quite variable species, some (but by no means all) of which have enormous geographic ranges; *O. sulcata* and *O. verrillii* seem to be common in the deep sea (*c.* 600-5000 m) in the Atlantic, Indian and Pacific Oceans wherever intensive sampling has been carried out. The differences from *Galeodea* seem great enough to justify the recognition of subfamily Oocorythinae for *Oocorys* and the closely related genera *Dalium* and *Eucorys*. The more extensive collections now available in MNHN have enabled a fuller assessment than previously of the number of species, their anatomical characters and, in some cases, their geographical ranges. In the central and, in particular, the eastern Pacific, so little deep-sea sampling has been carried out (indeed, records of *Oocorys* in the eastern Pacific still have not increased from those of Dall in 1896 and 1908) that I have nothing new to add to the knowledge of these molluscs in this area.

The anatomical examinations carried out while studying the *Oocorys* species revised below allow a new concept of the genus, and also allow the separation of the new genus *Eucorys* (below) for two Caribbean species with thicker, more colourful shells and longer anterior siphonal canals than *Oocorys* species. *Oocorys* differs from *Galeodea* in having a thinner, simpler shell with still more predominantly spiral sculpture than *Galeodea*, with a less well developed anterior canal than that in *Galeodea* which, instead, is little more than a notch (normal to the coiling axis, i.e., oriented in the dorso-ventral plane rather than the antero-posterior plane) in the anterior shell margin, accommodated at the base of the columella by a shortening and deviation to the left of the columellar base, producing a cut off appearance. Most species have a thinner and less well-developed terminal varix than that of most *Galeodea* species, and some mature specimens of some *Oocorys* species completely lack a terminal varix. As noted first by Dall (1909), the weakly spiral nuclear area of the operculum also is an important character of *Oocorys*.

OPERCULA. — Opercula of *Galeodea*, *Eucorys* and *Oocorys* species are compared in Fig. 21. The operculum of *Oocorys* has been described as spiral, but does not grow by adding on a narrow, truly spiral strip around the exterior margin as does, e.g., *Trochus* (flexiclaudent, in the terminology of Checa & Jiménez-Jiménez 1998). Rather, in young specimens the narrowly triangular, radially aligned area of new growth (wider at the margin of the operculum than at the nucleus) subtends such a large angle at the margin of the small, almost circular operculum that the whole operculum must rotate slightly to accommodate each increment (rigiclaudent paucispiral, in the terminology of Checa & Jiménez-Jiménez 1998). As the aperture grows larger, and the operculum grows correspondingly taller, the angle subtended by each new increment becomes smaller, and the operculum needs to rotate by a progressively smaller amount as it grows. The later growth lines therefore appear more nearly commarginal than the earlier ones (rigiclaudent commarginal, in the terminology of Checa & Jiménez-Jiménez 1998). That this mode of growth is not very fundamentally different from that of *Galeodea* is demonstrated by the operculum of a young specimen of *G. maccamleyi* illustrated by Ponder (1983: pl. 2, fig. 1), in which the same growth rotation as in *Oocorys* species is demonstrated by early growth lines, although regular commarginal growth replaces it rapidly. Probably, then, the apparently different mode of size increase between the opercula of *Oocorys* and *Eucorys* and those of the Cassinae results merely from the strongly anterior position of the opercular nucleus in *Oocorys* and *Eucorys*. It is at or near the anterior end of the operculum in *Oocorys* (certainly at less than a quarter of the opercular height in all material examined), whereas it is higher up the operculum in *Galeodea* (at a third to half the opercular height) and in *G. maccamleyi*, which has an unusually short, wide aperture for a *Galeodea* species, the nucleus is close to the anterior end of the operculum in juvenile specimens. The operculum of *Eucorys bartschi* (Fig. 21F) differs from those of either *Galeodea* or *Oocorys* in having a more weakly developed spiral initial area than in *Oocorys*, in having an unusual, pointed anterior end, in being taller and narrower than in *Oocorys* and resembling that of *Galeodea* in shape, and in being thicker than in either *Oocorys* or *Galeodea*.

STATUS OF *HADROOCORYS* QUINN, 1980. — I am aware of only about 5 specimens that would be referable to *Hadroocorys*, as defined by Quinn (1980): (1) the holotype of *Dolium* (*Eudolium*) *verrillii* (Figs 27A, B), type species of *Hadroocorys*; (2) the holotype of *Oocorys tosaensis* Habe & Azuma (1959: 116, pl. 12, fig. 3; Habe 1961: pl. 20, fig. 2;

1964: pl. 20, fig. 2; Figs 26C, G), the second species referred to *Hadroocorys* by Quinn (1980); (3) a single specimen from the Norfolk Ridge, New Caledonia (BATHUS 3 stn CP 811, 383-408 m, 23°41'S, 168°15'E; Figs 26E, F); and (4 & 5) photographs of two specimens from fish traps in 600-700 m, off St Gilles, Réunion (Figs 27C, D), sent by J. C. Martin (Nice). ["*Hadroocorys*" *dorae* Kreipl & Mühlhäusser (1996: 305; Kreipl 1997: 75) from 120 m, off northern Sri Lanka, has a long, prominently twisted anterior canal, and despite its very elaborately sculptured aperture, clearly belongs in *Semicassis*, a position agreed with by Kreipl (1998)]. In view of the large amount of Atlantic *Oocorys* material available to Bouchet & Warén (1993), and of the large amount of western Pacific material available to me, the first obvious question about *Hadroocorys* is, why is it still apparently so exceedingly rare? The 5 specimens listed here are so similar that the next obvious question is, are they all conspecific? It seems likely that the answer to these questions is that "*Hadroocorys* species" are extreme variants of another, widespread *Oocorys* species. The specimen from New Caledonia occurs with a large number of specimens of the species identified by Bouchet & Warén (1993) as *Oocorys cancellata* (= *O. verrillii* herein), which is a little more common than *O. sulcata* in the New Caledonia-Vanuatu region. Some of these specimens of *O. cancellata* have a prominent, widely flared, thickly callused varix, with low transverse ridges on the adapertural face, a moderately developed parietal callus pad with several transverse ridges, opposite the top of the strongly thickened part of the outer lip, and an external shell sculpture of relatively few, coarse spiral cords, lightly cancellated by the fine axial ridgelets. It is only a short step from these to a slightly more heavily callused, coarsely spirally sculptured specimen that would be identified as *Hadroocorys verrillii*. In my opinion, the holotype of *Hadroocorys verrillii*, the holotype of *H. tosaensis* and the New Caledonian and Réunion specimens all are heavily callused and coarsely sculptured specimens of *Oocorys cancellata*, for which the earliest name is therefore *O. verrillii*, and this is a wide-ranging species occurring from the Caribbean, throughout the Indian and western Pacific Oceans to New Caledonia and Japan - even, probably, to the eastern Pacific. An indication that *O. cancellata* (= *O. verrillii*) occurs in Japan is provided, despite the few records of *Oocorys* from Japan, by the illustration of "*Oocorys japonica*" (*nomen nudum*) by Matsumoto (1979: pl. 7, fig. 8); the specimen has a strongly thickened outer lip, and in my opinion is a specimen of *O. cancellata* (= *O. verrillii*).

A final observation about the "*Hadroocorys*" specimens is that they are all from quite shallow water for a species of *Oocorys*. The holotype of *D. verrillii* is from only 133 m, that of *O. tosaensis* is from 200 m, the New Caledonian specimen is from 383-408 m, and the Réunion specimens are from 600-700 m. All five also are similarly poor, abraded and corroded specimens, and in my opinion the specimens assigned to "*Hadroocorys*" are unusually robust specimens of *Oocorys cancellata* that have survived abrasion in a relatively high-energy, shallow-water habitat. I conclude that *Hadroocorys* is a synonym of *Oocorys*. The proposed taxonomy has a nomenclatural implication: *Dolium* (*Eudolium*) *verrillii* Dall, 1889 is an earlier name than *O. sulcata* var. *cancellata* Dautzenberg & Fischer, 1897, so *O. verrillii* (Dall) is the valid name for this species.

A further species recently proposed in *Oocorys* is *O. donghaiensis* Xu (1989: 514, fig. 1a-c) from 900 m in the East China Sea. Beu & Bouchet (in progress) transfer this species to *Pisanianura* Rovereto, 1899 (Laubierinidae), and it will not be considered further here.

The Recent species recognised here in *Oocorys,* with their main synonyms, are:

Oocorys clericus Quinn, 1980, Bahamas, Caribbean Sea and Gulf of Mexico.
O. elevata Dall, 1908, eastern Pacific.
O. grandis n. sp., central Indian Ocean and southeastern Atlantic.
O. sulcata Fischer, 1883 (= *Benthodolium abyssorum* Verrill & Smith, 1884, *O. watsoni* Locard, 1897, *O. fischeri* Locard, 1897, *O. sulcata* var. *indica* E. A. Smith, 1906, *O. rotunda* Dall, 1908, *O. elongata* Schepman, 1909, *O. weberi* Schepman, 1909, *Eudolium aulacodes* Tomlin, 1927, *O. schepmani* Turner, 1948, *O. umbilicata* Quinn, 1980), cosmopolitan.
O. verrillii (Dall, 1889) (= *Benthodolium pacificum* Dall, 1896, *O. sulcata* var. *cancellata* Dautzenberg & Fischer, 1897, *O. sulcata caribbaea* Clench & Aguayo, 1939, *O. tosaensis* Habe & Azuma, 1959, *O. lussii* Bozzetti, 1990, *O. morrisoni* Kreipl & Alf, 2001), cosmopolitan.

Oocorys clericus Quinn, 1980

Figs 4A, B; 9C-E; 22E, F

Oocorys bartschi clericus Quinn, 1980: 156, figs 1A, 2C, D, 7.

Other references:
Oocorys bartschi clericus - Kreipl 1997: 70, unnumbered fig.
Oocorys sulcatus - Okutani 1983: 266, illus.
Oocorys bartschi - Warén & Bouchet 1990: 80, 92, 101, fig. 119 (*non O. bartschi* Rehder, 1943).

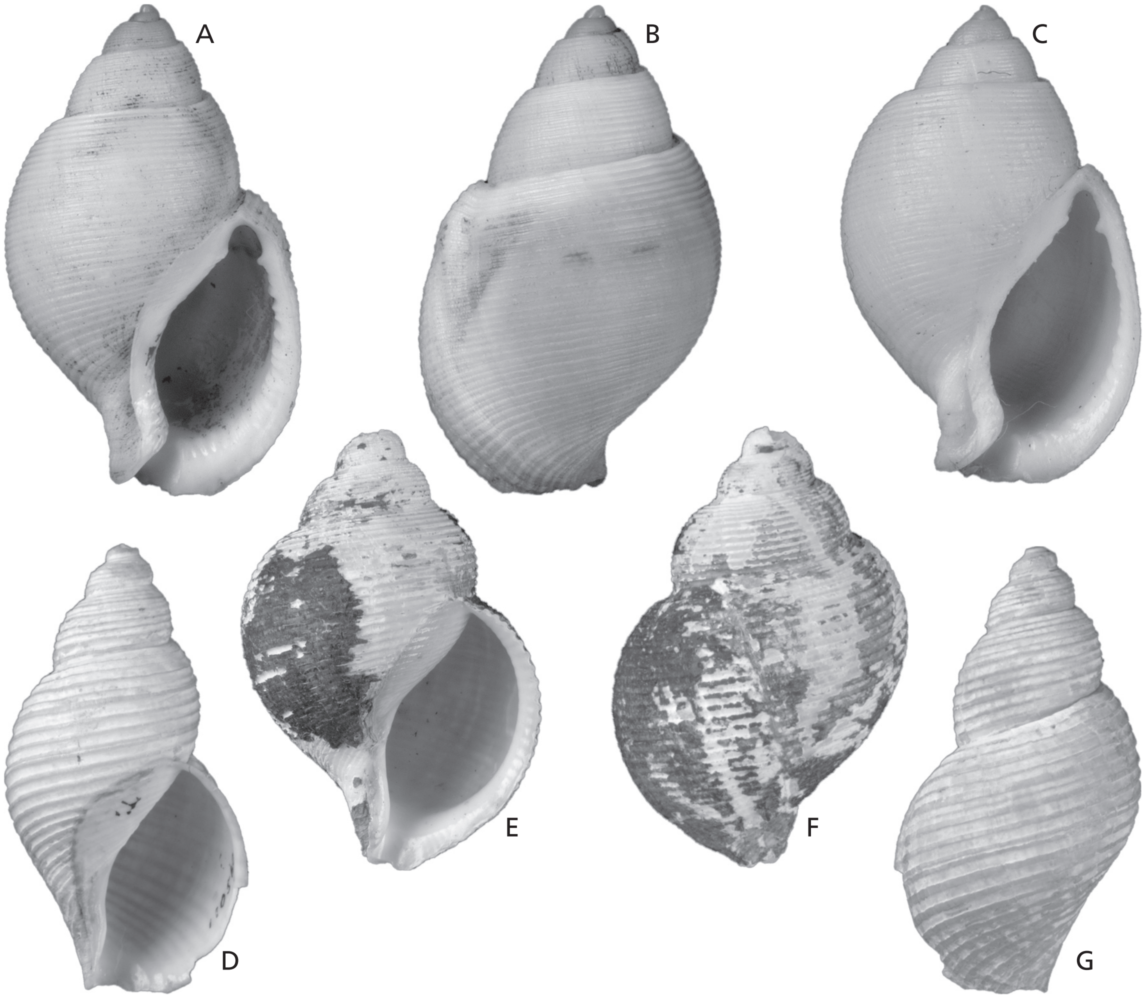


FIG. 22. *Microsconsia* and *Oocorys* species. **A-C**, *Microsconsia limpusi* n. gen., n. sp., Swain Reefs, SE Queensland, Australia, X 3; **A**, **B**, holotype, trawled in 180 m, N of Halfmoon Reef (AMS, C382770; H 21.5 mm); **C**, paratype, trawled in c. 190 m, SE of Swain Reefs (MNHN 20181; H 20.8 mm). **D**, **G**, *Oocorys elevata* Dall, 1908, holotype, between the Galapagos Islands and Sechura Bay, Peru, 4023 m (USNM 110569; H 58.5 mm; natural size). **E**, **F**, *Oocorys clericus* Quinn, 1980, LGL cruise 3.MMS.C3, Gulf of Mexico, 764-841 m (H 58.3 mm; natural size).

TYPE MATERIAL. — Holotype, USNM 751953, from *Oregon* stn 3601, off Santa Catalina, Atlantic coast of Panama, 731 m, 9°07'N, 81°10'W; 4 paratypes from Tongue of the Ocean, Bahamas, in 732-1554 m, in UMML; 21 paratypes from the southwestern Caribbean Sea, from off Santa Marta, Colombia, westwards to Golfo de los Mosquitos, Panama, in 329-548 m, in UMML (Quinn 1980: 156).

OTHER MATERIAL EXAMINED. — **Gulf of Mexico.** LGL Cruise 3.MMS.C3, 764-841 m, 27°49'N, 90°08'W (1 lv; Figs 22E, F).

DISTRIBUTION. — *Oocorys clericus* is recorded from off the Bahamas and throughout the Caribbean Sea and the Gulf of Mexico.

DIMENSIONS. — Holotype: H 69.3, D 43.4 mm; MNHN specimen, LGL Cruise 3.MMS.C3: H 58.3 (spire apex incomplete), D 39.2 mm; Quinn (1980: 156) recorded specimens up to 91.9 mm high.

REMARKS. — Quinn (1980) spelled the "subspecies" name *clericus*. As *Oocorys* is feminine, the masculine ending implies that the subspecies name was intended to be a noun, and is indeclinable.

Oocorys clericus resembles *O. sulcata* in general appearance, apart from its rather larger size and its markedly taller and narrower shape than all specimens of *O. sulcata*. The exterior sculpture is of very simple, even, smooth, prominent, flat-topped, widely spaced, very regularly arranged spiral cords, similar to but a little coarser than those of *Eucorys bartschi*. The anterior end is produced into a slight anterior canal, a little more obvious than that of *O. sulcata*, although shorter than that of *Eucorys* species. A narrow, smooth subsutural band, or collar, is not otherwise distinguished from the rest of the shell surface, e.g., not strongly concave, as in *Eucorys*. A unique character is the outer lip, which is not reflected at all externally, but bears a prominent, thick, smooth internal callus ridge of semicircular cross-section.

Quinn (1980) proposed *Oocorys clericus* as a subspecies of *Eucorys bartschi*, although he realised they might prove to be distinct species. *Eucorys bartschi* is much larger than *O. clericus* (up to more than 130 mm high, compared with up to 92 mm, and most specimens around 60-70 mm, in *O. clericus*), and *E. bartschi* has a rather thin but strongly reflected, transversely ribbed outer lip and a polished exterior, which give it more the appearance of the tonnid genus *Eudolium* than of *Oocorys* species. *Oocorys clericus* has a chalky white exterior (on the specimen examined, and in Quinn's (1980: fig. 7) illustration of the holotype), and resembles tall specimens of *Oocorys sulcata* much more closely than it does *E. bartschi*. The most important distinction between these species, though, is in the protoconch. Presumably the cancellate, multiwhorled protoconch illustrated as that of *E. bartschi* by Warén & Bouchet (1990: fig. 119) actually is that of *O. clericus*, as that of *E. bartschi* is very small, smooth and paucispiral, as in *Galeodea* (see below).

ANATOMY. — The single MNHN specimen (Figs 4A, B; 9C-E; 22E, F) was preserved with the animal intact, and is male. The penis is short and wide, with a widely open seminal groove, exactly as illustrated by Quinn (1980: fig. 3) for *Oocorys umbilicata* (= *O. sulcata*). The external appearance of the head-foot and the arrangement and position of the mantle cavity organs are precisely as illustrated by Bayer (1971) for *O. sulcata*. The osphradium is symmetrically bipectinate, but is unusual in being S-shaped, curled to the right at the anterior end. It is a little more strongly curved in *Oocorys* species than in *Galeodea*, but the *O. clericus* osphradium is unique among species examined here in the degree of curvature to the right. The operculum (shown also by Quinn 1980: figs 2C, D) is standard for *Oocorys*, with its nucleus almost at the base of the right edge, and with weakly spiral initial growth lines, followed by commarginal ones, but in *O. clericus* the nucleus is slightly above the base of the right edge, and the area of spiral growth lines is less obvious than in other *Oocorys* species (possibly this character is less developed than in other species because of the longer aperture and anterior canal in *O. clericus* than in other *Oocorys* species).

RADULA. — The radula (Figs 4A, B; shown also by Quinn 1980: fig. 1A) is standard for *Oocorys*, with triangular basal extremities on the basal plate of the central teeth, and with 4-7 denticles on each side of the main cusp of each central tooth, and 5-7 denticles outside the main cusp of each lateral tooth (8-9 on the specimen studied by Quinn 1980). The radula studied here also has one unusually long denticle on the inner edge of each inner marginal tooth, the largest on any *Oocorys* species I have examined. The radula of *E. bartschi* (Figs 3E, F) is similar to that of *O. clericus*, but has slightly more antero-posteriorly elongate (i.e., more strongly triangular) cutting heads on the central and lateral teeth, more numerous and longer denticles on both these teeth (8-9 on centrals and 8-10 on laterals), a smaller denticle on the inner edge of each inner marginal tooth, and a small denticle on the inner edge of each lateral tooth that I have not observed in *O. clericus*. The basal plate of the central teeth also is much lower and wider than in all other radulae examined in this work. It is clear that these are distinct species, here considered to belong in different genera.

Oocorys elevata Dall, 1908

Figs 21I; 22D, G

Oocorys elevata Dall, 1908: 322, pl. 8, fig. 9.

Other references:
Oocorys elevata - Turner 1948: 190. – Clarke 1962: 22. – Keen 1971: 500, fig. 943. – Kabat 1996: 11. – Kreipl 1997: 71, unnumbered fig.

TYPE MATERIAL. – Holotype, USNM 110569, from *Albatross* stn 4649, between the Galapagos Islands and Sechura Bay, Peru, 4023 m, 5°17'S, 85°19'30"W (SE of the Galapagos Islands; Kabat 1996: 11, 31).

DISTRIBUTION. – Only the holotype has been recorded.

DIMENSIONS. – Holotype: H 58.5, D 32 mm; height of aperture 32.3 mm.

REMARKS. – *Oocorys elevata* is one of the most distinctive species of the Cassidae, because of its very tall, elongate shape, its thin, fragile shell and its particularly tall spire. The holotype (the only known specimen) is quite large, considering the depth at which it was collected (4023 m). It has gently but quite evenly convex whorls, and sculpture of low, flat-topped, widely spaced spiral cords, 6 on the antepenultimate whorl, 10 on the penultimate whorl (with the eleventh showing in places) and 23 on the last whorl and base. Extremely fine, close axial threads weakly corrugate the flat crests of the spiral cords, but are not discernible in the interspaces, which are flat and chalky. Some cords, particularly those on the base but also a few higher ones at apparently random positions, are much wider than the others, and a few of these are subdivided by a median groove along their crests. The spiral cords are visible from the interior because the spiral interspaces are relatively thin and translucent, but the interior is smooth, i.e., there is no sculpture on the interior equivalent to the exterior cords. The outer lip is reflected narrowly over the posterior third of the aperture height, but is incomplete below this; the lip is smooth and unthickened. The inner lip is moderately thickened, with a clearly defined margin, but is smooth and closely adherent to the previous whorl. The lower half of the columella is lightly excavated, and its anterior end is truncated at a low angle well above (*c.* 9 mm above) the anterior end of the shell, producing a very slightly contracted, wide anterior notch (in the dorso-ventral plane) at the same position as the anterior end of the outer lip. The operculum (Fig. 21I) is a standard, relatively short and wide *Oocorys* operculum, with the nucleus slightly above the centre of the base, and with a small spiral area of growth lines around the nucleus. Despite its very tall, narrow shape, there is little to suggest that this is any more than a very tall species of *Oocorys*.

Beu (in prep. “Revison of Central American Neogene tonnoidean gastropods”; fauna summarised by Beu 2001) records a new species similar to but shorter than *Oocorys elevata* from the late Early Miocene Cantaure Formation of the Paraguana Peninsula, northern Venezuela. The new species has flatter whorl sides and base and a weak peribasal angulation that is absent from *O. elevata*. A closely similar form was illustrated by Nielsen (2003: 92, pl. 16, figs 23, 24) from the Lacui Formation (Miocene), west coast south of Cucao, Chiloé Island, Chile.

Oocorys grandis n. sp.

Figs 4C-F; 9F; 21G, H; 23

TYPE MATERIAL. — Holotype MNHN 20182 (Figs 23C, D) and one paratype MNHN 20183, from central Indian Ocean, 05°42’N, 78°56’E, 3625 m, collected live [SAFARI 2: stn CP 2].

OTHER MATERIAL EXAMINED. — **Southeastern Atlantic**. WALDA: stn CY 05, off the coast of northern Namibia, southeastern Atlantic Ocean, 21°46’S, 11°08’E, in 2953 m (4 lv; Figs 23A, B, E). — WALVIS 1978-79: stn CP 12, 27°38’05”S, 0°51’3”E, in 4660 m (1 lv; referred tentatively).

DISTRIBUTION. — Central Indian Ocean and southeastern Atlantic, in 2953-4660 m. Likely to be widespread in very deep water.

DIMENSIONS. — Holotype: H 103.0, D 73.7 mm; paratype: H 60.4, D 50.2 mm (slightly distorted during drying); WALDA stn CY 05: H 64.0, D 46.0 mm; H 61.0, D 46.5 mm; H 57.4, D 43.2 mm.

DESCRIPTION. — Holotype much the largest specimen recorded of short, wide *Oocorys* species, markedly but not greatly taller than wide, with evenly and strongly inflated whorls, well impressed suture, spire moderately low, aperture very large, wide, and base of outer lip descending well below base of columella and anterior siphonal notch. Teleoconch very flexible, with only an extremely thin, transparent calcium carbonate layer on interior of periostracum; sculptured with regular, even, narrow axial ridges on early spire whorls, ridges becoming more closely spaced and less regular over penultimate whorl, and forming closely appressed axial ridges of irregular position and height over last whorl. Spiral sculpture of low, narrow, widely spaced cords, reticulated by finer and more closely spaced axial ridges on early spire whorls; 7-9 spiral cords on early spire whorls and *c.* 25 on last whorl of smaller specimen; cords weaken over penultimate whorl, and on last whorl of holotype almost completely fade out. Over last whorl of paratype and penultimate and last whorls of holotype, suture developing marked subsutural groove, demarcating a low, narrow ridge bordering the suture. Inner lip a thin, smooth glaze over previous whorl; outer lip thin, sharp-edged, not reflected at all in holotype, lightly reflected in paratype as a result of drying. Columellar base thin and sharp-edged, descending to left and stopping well before base of outer lip, without forming anterior canal; anterior siphonal notch deep and very wide. Apex corroded in both specimens.

Animal (Fig. 9F; removed from paratype) male, with standard tonnoidean anatomy as shown by Bayer (1971: fig. 19) for *Oocorys sulcata*, with short, wide (contracted) cephalic tentacles lacking obvious eyes, and with moderately short, wide proboscis; mantle cavity organs arranged as shown by Bayer (1971: fig. 19) for *Oocorys sulcata*, with slightly asymmetrically bipectinate osphradium, right leaflets slightly longer than left ones. Penis flattened, larger and longer than in all other *Oocorys* species examined here, with open seminal groove, terminal papilla, and subparallel sides.

Operculum (Figs 21G, H) relatively small for aperture size (much more markedly so in holotype than in other material), extremely short and wide for genus, subtriangular, with spiral initial growth line area at centre of wide, nearly straight basal margin, most of operculum bearing growth lines parallel to left margin; left posterior angle bluntly

FIG. 23. *Oocorys grandis* n. sp. **A**, **B**, **E**, 2 specimens from WALDA stn CY 05, off Namibia, SE Atlantic, 2953 m; X 1.25; **A**, **B**, H 64.0 mm; **E**, H 61.0 mm; **C**, **D**, holotype MNHN 20182, SAFARI 2 stn CP 2, central Indian Ocean, 3625 m (H 103.0 mm; natural size).

rounded, left margin almost straight, right margin evenly and strongly convex, right anterior margin narrowly and evenly rounded.

Radula (Figs 4C-F) standard for *Oocorys*, but with unusually wide, low central teeth, unusually wide cutting areas on central and lateral teeth, and unusually numerous, narrow, closely spaced, neatly parallel denticles on these teeth; 14-20 denticles on each side of main cusp on each central tooth, 12-16 outside main cusp on each lateral tooth; inner edge of lateral teeth and all marginal teeth without denticles. Adult radula with thicker teeth than immature one, and without an obvious groove or embayment in lateral margin to receive base of inner marginal tooth; linking embayment in outer edge of lateral teeth obvious but very short in immature specimen.

REMARKS. — *Oocorys grandis* is a relatively short, wide species resembling *O. sulcata* in shape, and clearly differs from all other previously known short, wide species of the genus by its large size – up to 103 mm high, compared with 53 mm high for the largest specimen of *O. sulcata* – and also differs from all others in its thin, flexible shell composed almost entirely of the periostracum, in its wide aperture and long outer lip descending below the columellar base and anterior notch, in its thin, unreflected outer lip, in its very wide, rather shallow anterior notch, in its very wide operculum (presumably associated with the wide aperture), and in the fading out of the sculpture over the last whorl. *Eucorys bartschi* reaches a markedly larger size (up to 130 mm high) but is quite a different-looking shell from *O. grandis*, with its taller and narrower shape, its much taller spire, its well developed anterior siphonal canal, its much thicker aragonitic shell layer and lightly polished exterior, its markedly more prominent, more widely spaced spiral cords, and its narrowly but obviously flared outer lip that is lacking in *O. grandis*. The anatomy and radula of *O. grandis* are unremarkable for an *Oocorys* species, and there is little doubt that it is closely related to *O. sulcata*.

A single sample of four large specimens from WALDA stn CY 05, in the southeastern Atlantic, taken in 2953 m off the coast of Namibia, is referred to *Oocorys grandis*. These specimens reach a considerably larger size (up to 65 mm in height) than any specimens assigned to *O. sulcata* (up to 53 mm). They also have markedly wider shells, apertures and opercula than any specimens of *O. sulcata*, have very consistent sculpture of widely spaced, narrow, prominent spiral cords, fewer and much more widely spaced than in any specimens assigned to *O. sulcata*. Most distinctively, they have a thinner, shorter and much more strongly concave columella than in *O. sulcata*, deviated sharply to the left to end in a shallow notch (in the dorso-ventral direction, rather than the antero-posterior one) in the apertural margin at the base of the aperture, without a true siphonal canal in the sense of a semitubular structure that protrudes in front of the outer lip. They also differ from almost all other *Oocorys* species in having a straight to very weakly flared, simple, unthickened outer lip, and the inner lip merely is a thin, translucent glaze on the previous whorl, without sculpture. The aragonite teleoconch is very thin, and the periostracum correspondingly quite thick and prominent for an *Oocorys* species. In almost all these characters, and in radular characters (Figs 4E, F), these specimens are very similar to the holotype of *O. grandis*, although much smaller than it. They also have a markedly thicker aragonite teleoconch and correspondingly thinner periostracum than *O. grandis*, but this is interpreted as a consequence of the shallower depth of the collection site. The shell shape also is significantly different, as the WALDA stn CY05 specimens have rather less evenly rounded whorls, a slightly taller spire and more deeply impressed sutures than *O. grandis*. The important point is that the radula closely resembles that of the holotype of *O. grandis* in the shape and proportions of all the teeth, and in having many, unusually short, closely spaced denticles on the cutting edges of the central and lateral teeth. The radula demonstrates quite convincingly that these WALDA stn CY 05 specimens are very distinct from *O. sulcata*. These specimens from the southeastern Atlantic seem best regarded as immature specimens of *O. grandis*, indicating that it is likely to be quite widely distributed in very deep water.

The one specimen from WALVIS 1978-79 stn CP 12 is similar to the WALDA stn CY 05 material in size, in shape, in the thin shell and the particularly thin columella, in the prominent, narrow, widely spaced spiral cords, in the unthickened outer lip, and in the very wide operculum. However, the aragonitic shell material is exceedingly thin in this specimen, and the dried specimen is translucent golden brown in colour, and has distorted a little during drying.

The identification is uncertain, but it seems likely that this is a specimen of *Oocorys grandis* that has a particularly thin aragonite layer.

ETYMOLOGY. — The specific name, *grandis*, reflects the large and imposing size of this species.

Oocorys sulcata Fischer, 1883

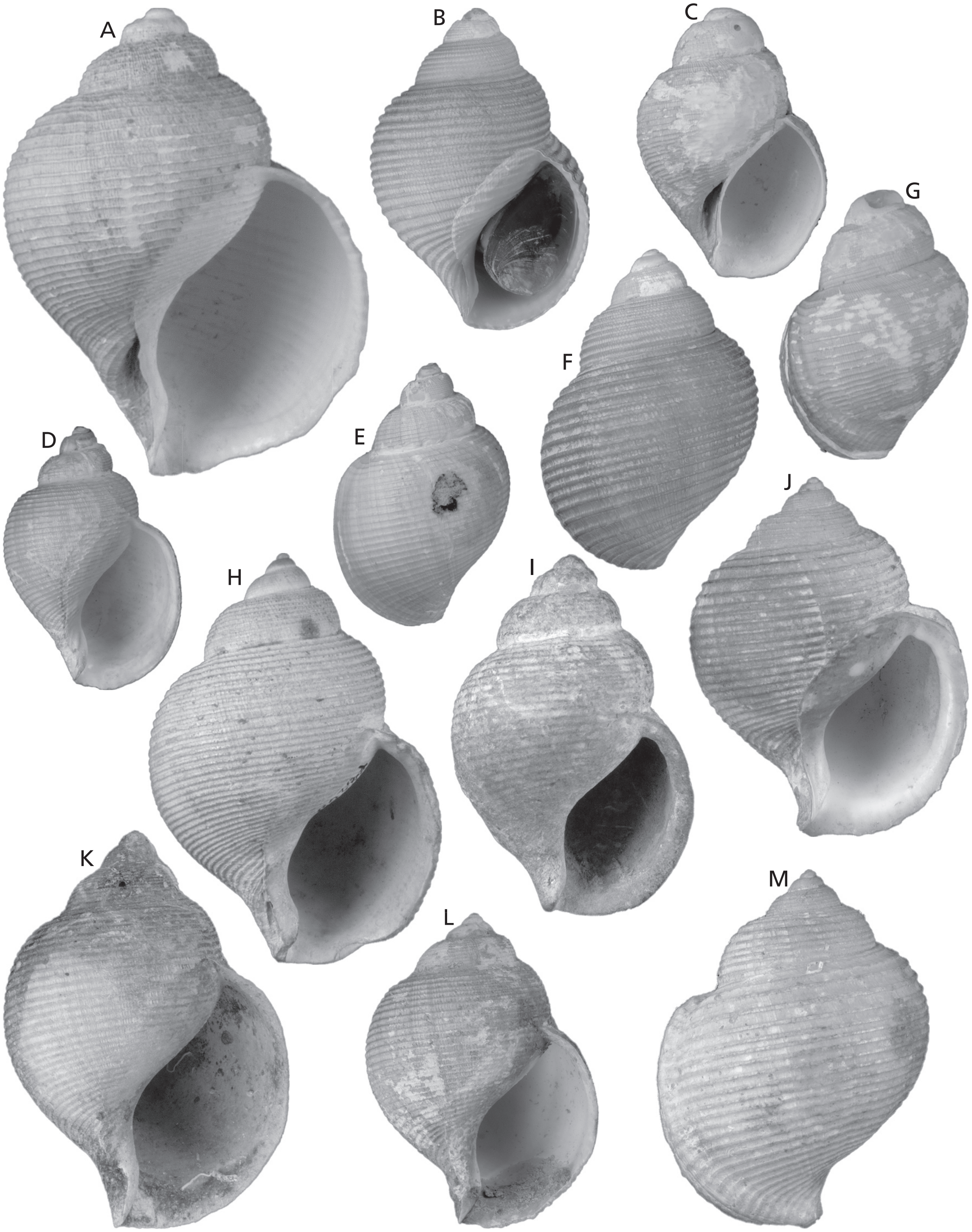
Figs 5A-D; 8B; 21J, K; 24; 25

Oocorys sulcata Fischer, 1883: 392.

Synonyms:
Benthodolium abyssorum Verrill & Smith *in* Verrill, 1884: 177, pl. 31, figs 12-12b.
Oocorys watsoni Locard, 1897: 290.
Oocorys fischeri Locard, 1897: 291, pl. 15, figs 7-9.
Oocorys sulcata var. *minor* and var. *elongata* Locard, 1897: 292.
Oocorys sulcata var. *indica* Smith, 1906: 170.
Oocorys rotunda Dall, 1908: 322, pl. 4, fig. 9.
Oocorys elongata Schepman, 1909: 121, pl. 10, fig. 3 (junior primary homonym of *O. sulcata* var. *elongata* Locard, 1897) (**new synonym**).
Oocorys weberi Schepman, 1909: 120, pl. 10, fig. 2 (**new synonym**).
Eudolium aulacodes Tomlin, 1927: 83, fig. 4a (**new synonym**).
Oocorys schepmani Turner, 1948: 190 (new name for *O. elongata* Schepman, 1909, preoccupied) (**new synonym**).
Oocorys umbilicata Quinn, 1980: 151, figs 1C, 2A-B, 3-4.

Other references:
Oocorys sulcata - Fischer 1885 (in 1880-1887): 769, fig. 536. — Tryon 1885: 267, pl. 6, figs 40-42. — Watson 1886: 412, pl. 17, fig. 11. — Dall 1889a: 228; 1889b: 132, pl. 62, figs 84-84b. — Locard 1897: 288, pl. 15, figs 4-6. — Dautzenberg & Fischer 1906: 53. — Schepman 1909: 120. — Dautzenberg 1927: 143. — Turner 1948: 186, pl. 75, fig. 8; pl. 85, figs 1-2. — Johnson 1934: 114. — Clarke 1962: 22. — Bayer 1971: 142, figs 18-19, 20B-C, 22B. — Abbott 1974: 169, fig. 1793. — Kilburn 1975: 584, fig. 5a. — Horikoshi 1989: 62, pl. 14, figs 15-16. — Warén & Bouchet 1990: 101, figs 15, 16, 24, 50, 150-152. — Bouchet & Warén 1993: 800, figs 1920, 1927, 1936-1943. — Gofas & Beu 2003: 104, figs 10A, B.
Oocorys abyssorum - Dall 1889a: 229; 1889b: 132. — Johnson 1934: 114. — Warén & Bouchet 1990: 101, fig. 66.
Oocorys fischeri - Turner 1948: 190. — Clarke 1962: 22.
Oocorys rotunda - Turner 1948: 190. — Clarke 1962: 22. — Keen 1971: 500, fig. 945. — Kabat 1996: 18. — Kreipl 1997: 73, unnumbered fig.
Oocorys watsoni - Turner 1948: 190. — Clarke 1962: 22.
Oocorys sulcata var. *indica* - Turner 1948: 190. — Clarke 1962: 22.
Oocorys weberi - Turner 1948: 190. — Clarke 1962: 22. — Okutani 1966: 18, pl. 2, fig. 3. — Kreipl 1997: 74, unnumbered fig. — Okutani 2000: 273, pl. 135, fig. 5.
Eudolium aulacodes - Turner 1948: 180. — Barnard 1963: 9.
Oocorys (*Benthodolium*) *abyssorum* - Turner 1948: 188, pl. 75, figs 6, 11-12; pl. 85, figs 3-4. — Clarke 1962: 22. — Abbott 1974: 169, fig. 1794.

FIG. 24. *Oocorys sulcata* (Fischer, 1883), all X 1.5. **A**, WALDA stn CY 15, SE Atlantic, 3413 m (H 48.7 mm); **B**, **C**, **F**, **G**, *O. elongata* Schepman, 1909, the 2 syntypes, *Siboga* stn 221, Banda Sea, Indonesia, 2798 m; **B**, **F**, ZMA 3.09.005 (H 33.5 mm); **C**, **G**, ZMA 3.09.006 (H 27.7 mm); **D**, **E**, *O. watsoni* Locard, 1897, holotype, *Challenger* stn 106, mid-Atlantic, 3367 m (BMNH 1887.2.9.1263; H 26.9 mm); **H**, off Bazaruto Island, S Mozambique, 540 m (NMP F8268, H 42.6 mm); **I**, *O. fischeri* Locard, 1897, lectotype, E Atlantic, from either *Talisman* stn 38, 2200 m, or stn 76, 2518-2638 m (MNHN 4155, H 37.2 mm); **J**, **M**, *O. sulcata* Fischer, 1883, lectotype, *Talisman* stn 130, off the Azores, 2235 m (MNHN 4160, H 36.9 mm); **K**, MUSORSTOM 10 stn CP 1361, Fiji, 1058-1091 m (H 41.0 mm); **L**, NZOI stn K873/2, off East Cape, New Zealand, 1280-1215 m (NMNZ; H 32.5 mm).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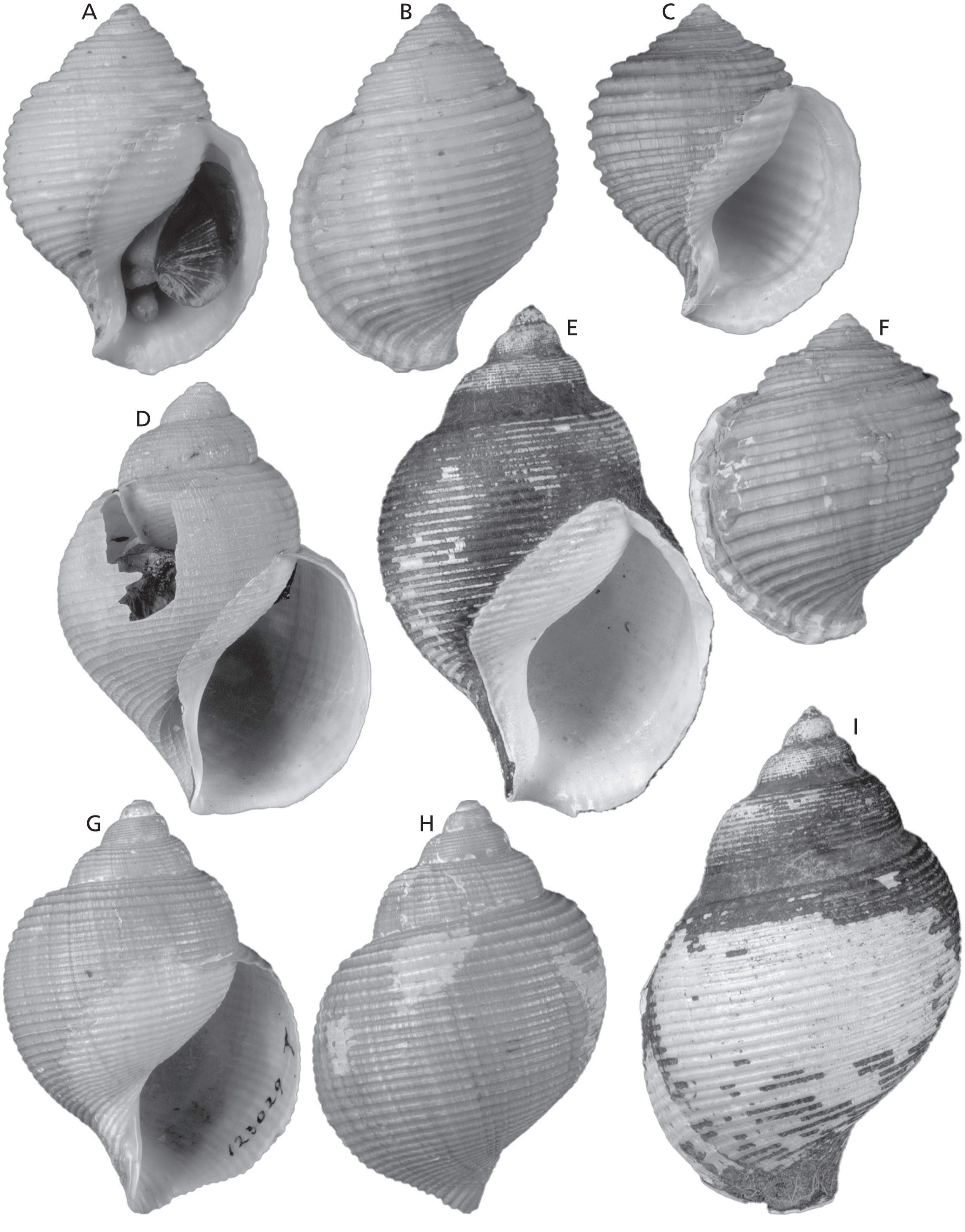


FIG. 25. *Oocorys sulcata* Fischer, 1883; all X 1.5. **A**, **B**, *O. weberi* Schepman, 1909, holotype, *Siboga* stn 175, Ceram Sea, Indonesia, 2798 m (ZMA 3.09.004; H 38.0 mm); **C**, **F**, KARUBAR stn CP 89, Tanimbar Islands, Indonesia, 1084-1058 m (H 34.8 mm); **D**, "*abyssorum* form", DEMERABY stn CP 06, northern Brazil, 4450 m (H 45.0 mm); **E**, **I**, BORDAU 1 stn CP 1400, Fiji, 1004-1012 m (H 53.7 mm); **G**, **H**, *O. rotunda* Dall, 1908, holotype, Gulf of Panama, 3009 m (USNM 123029; H 43.9 mm).

Oocorys schepmani - Clarke 1962: 22.
Oocorys elongata - Okutani 1966: 18, pl. 2, fig. 4. – Okutani 2000: 273, pl. 135, fig. 6.
Oocorys umbilicata - Warén & Bouchet 1990: 101, fig. 118.

TYPE MATERIAL. – *Oocorys sulcata*: lectotype MNHN 4160 designated by Bouchet & Warén (1993: 800), from *Talisman* stn 130, off the Azores, in 2235 m, 37°55’N, 27°02’W, the specimen illustrated by Locard (1897) (Figs 24J, M). – *Benthodolium abyssorum*: holotype USNM 35273 (not seen; illustrated by Turner 1948: pl. 85, fig. 3), paratype USNM 35364, from *Albatross* stn 2098, off Virginia, USA, in 4042 m, 37°40’N, 70°37’W. – *Oocorys fischeri*: lectotype MNHN 4155 designated by Bouchet & Warén (1993: 800), from either *Talisman* stn 38, in 2200 m, or *Talisman* stn 76, in 2518-2638 m (Fig. 24I). – *Oocorys watsoni*: holotype BMNH 1887.2.9.1263, from *Challenger* stn 106, mid-Atlantic, in 3367 m, 01°47’N, 24°26’W (Bouchet & Warén 1993: fig. 1942; Figs 24D, E). – *Oocorys sulcata* var. *indica*: type material presumably in Zoological Survey of India, Calcutta (not seen); from RIS *Investigator* stn 278, S of Sri Lanka, in 1912 fathoms (3525 m). – *Oocorys rotunda*: holotype USNM 123029 (Figs 25G, H), from *Albatross* stn 3360 [6°17’00”N, 82°5’00”W, SW of Isla Jicarón; Kabat 1996: 18, 29], Gulf of Panama, in 3009 m. – *Oocorys elongata* Schepman (= *O. schepmani* Turner): two syntypes (Figs 24B, C, F, G), ZMA 3.09.005 and 3.09.006, from *Siboga* stn 221, Banda Sea, Indonesia, in 2798 m, 6°24’S, 129°39’E. – *Oocorys weberi*: holotype ZMA 3.09.004, from *Siboga* stn 175, Ceram Sea, Indonesia, in 1914 m, 2°37.7’S, 13°33.4’E (Figs 25A, B). – *Eudolium aulacodes*: holotype in South African Museum, Cape Town (Barnard 1963: 9) (not seen); from *c.* 65 km NE of Cape Point, South Africa, in 1120-1400 m. – *Oocorys umbilicata*: holotype USNM 784592 (not seen); from *Columbus Iselin* stn CI-306, off the Bahamas in 1379-1408 m, 24°06’N, 77°18’W.

OTHER MATERIAL EXAMINED – Material from the Atlantic listed by Bouchet & Warén (1993) has been examined, but details are not repeated here.

Mozambique. Off Bazaruto Island, 600 m (1 dd, NMP F.8268); between Xai Xai and Inhaca, 300-400 m (2 dd, NMP V.2642); off Xai Xai, 400-500 m (1 dd, NMP V.2634).

Tanzania. *John Murray* Expedition stn 108, off Zanzibar I., 5°18’06”S, 39°24’12”E to 5°14’30”S, 39°25’36”E, 786 m (1 dd, BMNH); stn 118, further offshore from Zanzibar I., 4°05’54”S, 41°10’12”E to 4°17’00”S, 41°11’48”E, 1792 m (3 dd, BMNH).

Madagascar. BENTHEDI: stn 90, 11°44’S, 47°30’E, 3700 m (1lv). – SAFARI 2: stn CP 2, 05°42’N, 78°56’E, 3625 m (1 dd).

Réunion. MD32: stn CP 105, 20°47’S, 55°04’E, 1740-1850 m (1 dd).

Indonesia. KARUBAR: stn CP 52, Tanimbar Islands, 8°03’S, 131°48’E, 1244-1266 m (1 dd, coarse spiral cords); stn CP 89, 8°39’S, 131°08’E, 1084-1058 m (2 dd, very coarse spiral cords, resembling holotype of “*Eudolium” aulacodes* Tomlin; Figs 25C, F); stn CP 91, 8°44’S, 131°05’E, 884-891 m (1 dd, finely sculptured).

New Caledonia. BIOCAL: stn CP 30, 23°09’S, 166°41’E, 1140 m (1 dd); stn CP 62, 24°19’S, 167°49’E, 1395-1410 m (1 dd); stn CP 72, 22°10’S, 167°33’E, 2100-2110 m (1 dd). – BIOGEOCAL: stn CP 214, 22°43’S, 166°28’E, 1590-1665 m (1 dd); stn CP 260, 21°00’S, 166°58’E, 1820-1980 m (1 dd); stn CP 266, 21°05’S, 166°57’E, 1990-2100 m (1 lv); stn CP 272, 21°00’S, 166°57’E, 1615-1710 m (1 dd); stn CP 317, 20°48’S, 166°53’E, 1620-1630 m (1 dd). – EBISCO: stn CP 2652, SE Fairway Banks, 21°24’S, 162°37’E, 1019-1147 m (1 dd).

Wallis and Futuna. MUSORSTOM 7: stn CP 567, Tuscarora Bank, 11°48’S, 178°27’W, 1010-1020 m (1 dd, coarsely sculptured).

Vanuatu. MUSORSTOM 8: stn CP 1037, 18°04’S, 168°54’E, 1058-1086 m (1 lv).

Fiji. MUSORSTOM 10: stn CP 1354, 17°43’S, 178°55’E, 959-963 m (1 lv); stn CP 1361, SE of Viti Levu, 18°00’S, 178°54’E, 1058-1091 m (1 dd). – BORDAU 1: stn CP 1400, 16°28’S, 179°50’W, 1004-1012 m, (2 dd).

Solomon Islands. SALOMON 1: stn CP 1754, 9°00’S, 159°49’E, 1169-1203 m (2 lv); stn CP 1764, 08°37’S, 160°07’E, 1327-1598 m (1 lv, 1 dd). – SALOMON 2: stn CP 2216, New Georgia Strait, SW of Choiseul I, 7°45’S, 157°39’E, 930-977 m (2 dd); stn CP 2230, N of Choiseul I, 06°28’S, 156°24’E, 837-945 m (1 dd); stn CP 2241, Choiseul I, S of Taylor Reefs, 06°55’S, 156°21’E, 815-1000 m (1 dd); stn CP 2251, NW of Vella Lavella I, 07°28’S, 156°14’E, 1000-1050 m (2 dd); stn CP 2252, NW of Vella Lavella I, 07°28’S, 156°18’E, 1059-1109 m (7 dd); stn DW 2254, Kolombangara I, Vella Gulf, 8°28’S, 157°03’E, 150 m (3 dd); stn CP 2270, E of Vella Lavella I, 07°38’S, 156°59’E, 970-1060 m (2 dd, incl. 1 very large).

Australia (most material in AMS). SE of Newcastle, NSW, 732 m, 33°11’-09’S, 152°23’-25’E (1 dd, C108670); off Sydney, NSW, 823 m, 33°35’-32’S, 152°01’-03’E (1 dd, C108681); *Tangaroa* stn U223, off Newcastle, NSW, 1150-

951 m, 32°58.8'S, 152°41.6'E (3 dd, C155963); off St Patrick's head, E Tasmania, 940-990 m, 41°38-40'S, 148°41-40'E (1 dd, C156076); off Port Stephens, NSW, 1090-1134 m, 32°52-50'S, 152°47-50'E (1 dd, C158724); slope stn 15, off Nowra, NSW, 1750-1650 m, 34°53.40'-56.40'S, 151°23.20'-29.10'E (2 dd, Museum of Victoria).

Tasman Sea. NORFANZ: stn 71, Lord Howe Rise, S of Lord Howe Island, 1920-1934 m, 32°03.98'S, 159°52.80'E (1 dd, NMNZ M160618).

New Zealand (material in NMNZ). NZOI stn J658, NE of E Cape, 2505 m, 36°00.59'S, 179°12.80'E (1 lv); NZOI stn K873/2, off East Cape, 1280-1215 m, 37°32.6'S, 178°19.3'E (1 dd; Fig. 24L); NZOI stn U197, Lord Howe Rise, 1186 m, 34°09.8'S, 163°36.7'E (2 dd); NZOI stn U226, 2417-2421 m, Lord Howe Rise, 38°37.3'S, 165°36.0'E (3 lv); NZOI stn U601, northern Three Kings Rise, 1570-1563 m, 31°19.9'S, 173°05.1'E (1 dd, with 1 *O. verrillii*); NZOI stn O.578, SE slope of Ranfurly Bank, 37°38.5'S, 178°56.4'E, 153-143 m, R/V *Tangaroa* (1 dd apex); NZOI stn P.476, 13 km N of Great Island, Three Kings Islands, 34°01.8'S, 172°12.0'E, 508 m, R/V *Tangaroa* (1 dd, fragment); NZOI stn R.123, 31 km WNW of Orete Point, Cape Runaway, 37°33.1'S, 177°33.8'E to 37°34.2'S, 177°34.1'E, 482-353 m, R/V *Tangaroa* (1 dd).

DISTRIBUTION. — *Oocorys sulcata* seems to have a continuous distribution in about 350-5000 m throughout the Atlantic, Indian and Pacific Oceans, i.e., apparently throughout the world's temperate and tropical oceans (other than the Mediterranean). Specimens are confirmed as occurring from southwest of Ireland and off New England south to Brazil and off southern East Africa, in the Indian Ocean, in Indonesia, around Japan, around New Zealand, Australia, the New Caledonian region, Vanuatu and Fiji, i.e., wherever intensive deep-sea sampling has been carried out. The holotype of *O. rotunda* Dall, from the Gulf of Panama, eastern Pacific, is likely to be a further specimen of *O. sulcata*.

DIMENSIONS. — Lectotype of *Oocorys sulcata*: H 36.9, D 27.4 mm; holotype of *O. watsoni*: H 26.9, D 17.9 mm; lectotype of *O. fischeri*: H 37.2, D 25.0 mm; holotype of *O. weberi*: H 38, D 27 mm (Schepman 1909); syntype of *O. elongata* ZMA 3.09.005: H 33.5, D 22.5 mm (Schepman 1909); syntype of *O. elongata* ZMA 3.09.006: H 27.7, D 19.2 mm; holotype of *O rotunda*: H 43.9, D 31.1 mm; BORDAU 1 stn CP 1400: H 53.7, D 34.7 mm; H 53.2, D 36.7 mm; MUSORSTOM 10 stn CP 1354: H 52.6, D 36.4 mm; AMS, C158724, off Port Stephens, NSW: H 49.0, D 33.7 mm; WALDA stn CY 14, SW Atlantic, 3431 m: H 43.8, D 37.2 mm. Most specimens range in height from about 27 mm to 50 mm. A highly incomplete specimen from DEMERABY 1980 stn CP 05, off northern Brazil, 08°08'N, 49°02'W, from 4434 m, is 53 mm high, and appears to be an unusually tall and narrow specimen of *O. sulcata*.

REMARKS. — The name *Benthodolium abyssorum* was provided for very thin-shelled specimens with a thin, narrow inner lip (which therefore reveals a narrow false umbilicus) and a thin, only weakly flared outer lip, and with sculpture of very narrow, widely spaced spiral cords. These specimens came from deep water (holotype from 4042 m). The name *Oocorys sulcata* Fischer (1883) was based on thicker-shelled specimens with wider spiral cords, a thicker and wider inner lip that hides the umbilicus in most specimens, and a more thickened, more strongly flared outer lip forming a true varix. These specimens came from shallower water (holotype from 2235 m; but this form occurs as shallow as *c.* 350 m). All specimens have an anterior siphonal notch in the dorso-ventral plane and no anterior canal (in the sense of protruding below the base of the outer lip), the base of the columella is deviated sharply to the left, and they have a fairly uniform shape, with evenly rounded, well inflated whorls, and no axial sculpture other than growth lines. Bouchet & Warén (1993) concluded that these forms intergrade completely, and that these and many of the other nominal species proposed in *Oocorys* refer to one biological species. The larger amount of material available now makes it clear that this synonymy is correct, and that the range of variation is still greater than Bouchet & Warén (1993) thought. I have no doubt that *O. sulcata* is an extremely wide-ranging, quite variable species, forming thinner shells with much narrower spiral cords in deeper water than it does in shallower water. A large lot in MNHN from the Gulf of Mexico, LGL Cruise 3.MMS.C5, 26°57'N, 89°31'W, in 2486-2523 m (17 dried, 20 in alcohol), includes a range of shape and sculpture nicely intermediate between the *sulcata* and *abyssorum* forms. The holotype of *O. rotunda* is a little taller and narrower than most other specimens assigned to *O. sulcata*, but can be matched among the large MNHN Atlantic collections of *O. sulcata*. Larger (H 53.9 mm) specimens from Fiji in

BORDAU 1 samples closely resemble the holotype in shape, and occur with standard specimens of *O. sulcata*. There seems little doubt that *O. rotunda* is yet another synonym of *O. sulcata*, extending its range to the eastern Pacific. The type material of *O. elongata* Schepman (= *O. schepmani* Turner) does not have any characters differentiating it from *O. sulcata*. Some Indian Ocean specimens, such as the types of *O. weberi* and *Eudolium aulacodes*, have more prominent and more widely spaced spiral cords than most Atlantic and western Pacific specimens I have seen, but some of the Indian Ocean specimens identified by Bouchet & Warén (1993) as *O. sulcata* (e.g., Madagascar, chalutage 109, 1200 m, 22°17'S, 42°56'E, one specimen; MD32 REUNION stn CP 105, 1740-1850 m, 20°47'S, 55°04'E, one specimen) and a few from New Caledonia and Vanuatu (e.g., Loyalty Basin, BIOGEOCAL stn CP 214) are almost as strongly sculptured as the holotype of *O. weberi*, and in my opinion this name also was based on extreme specimens of *O. sulcata*. The holotype of *Eudolium aulacodes* also seems to be a very extreme, coarsely and sparsely sculptured specimen of *O. sulcata,* and was referred to *Oocorys* by both Kilburn (1986) and Marshall (1992).

ANATOMY. — Preserved animals were examined of a specimen of the "*Benthodolium abyssorum*" form from DEMERABY stn CP 06, off northern Brazil, in 4450 m, of another specimen from this same cruise, stn CP 03, in 4430 m, and of a thick-shelled specimen of the typical *Oocorys sulcata* form from BIOGEOCAL stn CP 266, Loyalty Basin, New Caledonia. The two Brazilian specimens are female, whereas the Loyalty Basin specimen is male (Fig. 8B), all lack obvious eyes, and all have a similar, asymmetrically bipectinate osphradium, the left leaflets being somewhat longer than the right ones. The osphradium is relatively large, more than two-thirds the area of the ctenidium, and the curvature of the mid-line suggests that it is weakly bilobate. As with most taxa studied here, a permanent incurrent siphon is present in the mantle edge to the left of the head-foot, whereas a permanent excurrent siphon is not developed. The penis of the Loyalty Basin specimen is longer and more parallel-sided than that of *O. clericus*, but is similar in being flattened and somewhat blade-shaped, with a subquadrate termination. The narrow specimen from the Loyalty Basin has a markedly narrower operculum than the other specimens (Figs 21J, K); it appears likely that the operculum becomes wider as the shell grows, as well as varying in width concomitantly with the aperture.

RADULA. — The radula was examined from the three specimens listed above: an average one with fine sculpture, similar to the holotype of *Oocorys sulcata*, from DEMERABY stn CP 03, off northern Brazil, in 4430 m (Fig. 5C); a thin-shelled specimen ("*Benthodolium abyssorum*" form) from a nearby DEMERABY station (stn CP 06, in 4450 m; Figs 5A, B); and a thick-shelled, narrow specimen from off New Caledonia (BIOGEOCAL stn CP 266, Loyalty Basin, in 1900-2100 m; Fig. 5D). Although these are quite similar in most radular characters, there are surprisingly large differences among them in others. The New Caledonian specimen (Fig. 5D) has central teeth with the width almost equal to the height, with 5-7 wide denticles on each side of the main central cusp, and with 7-8 large, rather wide, closely spaced denticles on each lateral tooth outside the main cusp. There also are two small denticles on the inner side of each inner marginal tooth. This radula is most similar to that of the DEMERABY stn CP 06 specimen (Figs 5A, B) from off Brazil, in the shape of the central teeth and in the two denticles on each inner marginal tooth, but the DEMERABY stn CP 06 radula has more numerous denticles on the central tooth (8-10 on each side, much narrower and more varied in width and length than on the New Caledonian specimen). The DEMERABY stn CP 06 radula (Figs 5A, B) also differs markedly from both the others in its much longer (antero-posteriorly) heads on the lateral teeth and their more numerous denticles (10-11) outside the main cusp, and in the denticles being highly varied in shape and size; many are hooked much more strongly than in any other *Oocorys* radula examined. The radula from the "typical" specimen from DEMERABY stn CP 03, off Brazil (Fig. 5C), differs from both the others in its significantly shorter and wider cutting head on the central teeth, which bear 9-10 considerably wider, blunter and more closely spaced denticles on each side of the main cusp than in either of the other radulae. The 8-10 denticles on the outer edge of each lateral tooth also are wider and more closely spaced than in the other radulae of this species. A single small denticle, rather than two, also is visible on the inner edge of each marginal tooth in the DEMERABY stn CP 03 radula. Much of the apparent difference in shape between these three radulae can be attributed to the differing orientation of the teeth. However, this does not explain the shorter and wider heads of the central and lateral teeth of the stn CP 03 radula than of the other two, as rotating the teeth forward to make more of the head visible has the effect of making a shorter area of the base of each tooth visible, whereas the visible area of each tooth base is longer in the other two radulae than in the one from stn CP 03. Without examining a much larger number of radulae it is difficult to know what to make of this range of variation, and it is assumed to be variation within the one species, *O. sulcata*.

Oocorys verrillii (Dall, 1889)

Figs 5E, F; 9A, B; 21L, M; 26; 27

Dolium (*Eudolium*) *verrillii* Dall, 1889a: 233, pl. 35, fig. 12.

Synonyms:
Benthodolium pacificum Dall, 1896: 11 (**new synonym**).
Oocorys sulcata var. *cancellata* Dautzenberg & Fischer, 1897: 162 (**new synonym**).
Oocorys sulcata caribbaea Clench & Aguayo, 1939: 192, pl. 29, fig. 3 (**new synonym**).
Oocorys tosaensis Habe & Azuma, 1959: 116, pl. 12, fig. 3 (**new synonym**).
Oocorys lussii Bozzetti, 1990b: 46, unnumbered fig. (**new synonym**).
Oocorys morrisoni Kreipl & Alf, 2001: 245, figs 1 a, b, 2 a, b.

Other references:
Eudolium verrillii - Dall 1889b: 134, pl. 35, fig. 12.
Oocorys (*Benthodolium*) *pacifica* - Dall 1908: 323, pl. 4, fig. 7. – Clarke 1962: 22.
Oocorys sulcata var. *cancellata* - Dautzenberg 1927: 144.
Oocorys (*Oocorys*) *caribbaea* - Turner 1948: 184, pl. 83, figs 3-4. – Abbott 1974: 169, fig. 1791.
Oocorys (*Oocorys*) *pacifica* - Turner 1948: 190. – Keen 1971: 500. – Kreipl 1997: 72, unnumbered fig.
Oocorys (*Oocorys*) *verrillii* - Turner 1948: 185, pl. 84, figs 1-2. – Abbott 1974: 169, fig. 1792.
Oocorys tosaensis - Azuma 1960: 29. – Habe 1961: 43, pl. 20, fig. 2; 1964: 67, pl. 20, fig. 2. – Okutani 2000: 273, pl. 135, fig. 4.
Oocorys japonica - Azuma 1960: 29 (*nomen nudum*). – Matsumoto 1979: 37, pl. 7, fig. 8 (*nomen nudum*).
Oocorys caribbaea - Clarke 1962: 21. – Quinn 1980: 153, figs 1B, 2 I, J, 5.
Hadroocorys verrillii - Quinn 1980: 157, fig. 8. – Kreipl 1997: 76, unnumbered fig.
Hadroocorys tosaensis - Quinn 1980: 157. – Kreipl 1997: 75, unnumbered fig.
Oocorys lussii - Kreipl 1997: 72, unnumbered fig.
Oocorys cancellata - Bouchet & Warén 1993: 803, figs 1930, 1944.
Oocorys verrillii - Gofas & Beu 2003: 105, fig. 10C, D.

TYPE MATERIAL. – *Dolium* (*Eudolium*) *verrillii*: holotype USNM 87208, from *Albatross* stn 2120, off Grenada, Lesser Antilles, 11°07'00"N, 62°14'30"W, in 133 m (Figs 27A, B). – *Benthodolium pacificum*: holotype USNM 123031, from *Albatross* stn 3375, S of Malpelo Island, Gulf of Panama, in 4162 m (Figs 26J, M). – *Oocorys sulcata* var. *cancellata*: lectotype (not seen; designated by Bouchet & Warén 1993: 803) in MOM, from Monaco Expeditions stn 703, off the Azores, in 1360 m, 39°21'N, 31°06'W. – *Oocorys sulcata caribbaea*: holotype MCZ 135072, from *Atlantis* stn 2953, off Pinar del Rio, Bahia de Corrientes, Cuba, 21°47.5'N, 85°32.5'W, 1125 m (Figs 27G, I); paratype from same station, MCZ 135053; paratype, MCZ 135052, *Atlantis* stn 2970, off SW Oriente Prov., Cuba, 19°51'N, 74°26'W, 2928-3294 m (Fig. 27H). – *Oocorys tosaensis*: holotype NSMT Mo. 38642, from *c.* 200 m, off Tosa Bay, Shikoku, Japan (Figs 26C, G). – *Oocorys lussii*: holotype NMP S.3236/T.364, off Durban, South Africa, in 550 m (Figs 26A, B). – *Oocorys morrisoni*: holotype WAM S.1365, on sand and mud in 450-500 m, 296 km W of Broome, Western Australia, from scampi trawlers; two paratypes from same locality; one in collection of Hugh Morrison, Kingsley, Western Australia, one in Meeresmuseum Öhringen, Germany, reg. no. 8400 (Kreipl & Alf 2001: 245); all collected live.

OTHER MATERIAL EXAMINED. — Atlantic Ocean material listed by Bouchet & Warén (1993) is not listed again here.

Other Atlantic material. Blake stn 111, Caribbean Sea, N of Navassa Island, 19°5'55"N, 74°49'5"W, 2196 m (1 dd, MCZ 175595). — SEAMOUNT 2: stn CP 224, central Atlantic, Irving Bank (S of the Azores), 32°12'N, 28°15'W, 1240 m (3 dd; one white but slightly chalky adult, one chalky juvenile, one black-stained fragment) (Gofas & Beu 2003: 105, figs 10C, D).

South Africa. R/V *Meiring Naudé* stn W10, off Sandy Point, Transkei coast, 32°42.9'S, 28°41.9'E, 450-498 m (1 dd, NMP C 4099).

Réunion Island. Off St Gilles, 700 m, presented to MNHN by J. C. Martin (1 dd, close to *Hadroocorys* form; and 2 dd, *Hadroocorys* form, in collection of J. C. Martin).

Coral Sea. MUSORSTOM 5: stn 323, 21°19'S, 157°58'E, 970 m (2 dd); stn 324, 21°15'S, 157°51'E, 970 m (1 dd, close to *Hadroocorys* form).

New Caledonia. BIOGEOCAL: stn CP 232, 21°34'S, 166°27'E, 760-790 m (1 dd). — MUSORSTOM 6: stn CP 438, Loyalty Ridge, 20°23'S, 166°20'E, 780 m (1 dd). — BATHUS 2: stn CP 767, southern New Caledonia, 22°11'S, 165°59'E, 1060-1450 m (1 lv). — BATHUS 3: stn CP 811, Norfolk Ridge, 23°41'S, 168°15'E, 383-408 m (1 dd, *Hadroocorys* form); stn CP 842, 23°05'S, 166°48'E, 830 m (1 dd); stn CP 844, 23°06'S, 166°46'E, 908 m (2 dd). — NORFOLK 2: stn DW 2053, 23°40'S, 168°16'E, 670-708 m (1 dd); stn DW 2144, 23°09'S, 167°27'E, 1004-1009 m (1 dd). — EBISCO: Stn CP 2557, W of Bellona Plateau, 21°07'S, 158°30'E, 800-923 m (1 dd); stn CP 2650, SE of Fairway Banks, 21°27'S, 162°33'E, 825-894 m (1 dd).

Tonga. BORDAU 2: stn CP 1539, 21°37'W, 175°19'W, 558-586 m (1 lv, 3 dd); stn CP 1621, 24°19'S, 176°23'W, 570-573 m (3 dd); stn CP 1625, 23°28'S, 176°22'W, 824 m (1 dd).

Wallis and Futuna. MUSORSTOM 7: stn DW 557, Tuscarora Bank, 11°48'S, 178°18'W, 600-608 m (1 dd); stn CP 562, 11°48'S, 178°22'W, 775-777 m (1 dd); stn CP 564, 11°46'S, 178°27'W, 1015-1020 m (5 dd); stn CP 567, 11°47'S, 178°27'W, 1010-1020 m (1 dd).

Vanuatu. MUSORSTOM 8: stn CP 990, 18°52'S, 168°51'E, 980-990 m (1 dd); stn CP 1008, 18°53'S, 168°53'E, 919-1000 m (1 dd); stn CP 1036, 18°01'S, 168°48'E, 920-950 m (1 dd); stn CP 1075, 15°53'S, 167°27'E, 944-956 m (1 dd); stn CP 1080, 15°57'S, 167°28'E, 799-850 m (2 dd); stn CP 1129, 16°01'S, 166°40'E, 1014-1050 m (1 dd).

Solomon Islands. SALOMON 1: stn CP 1781, 8°32'S, 160°37.7'E, 1036-1138 m (1 dd).

Austral Islands. BENTHAUS: stn DW 1923, Récif Neilson, 27°01'S, 146°05'W, 360-840 m (1 dd).

New Zealand. NZOI stn U601, northern Three Kings Rise, 1570-1563 m, 31°19.9'S, 173°05.1'E (1 dd, with 1 *O. sulcata*, NMNZ); RV *Kaharoa* stn 204/44, South Cavalli Seamount, ENE of North Cape, 34°15.94'S, 174°06.19'E, 850-840 m (1 dd, NMNZ M158243); NORFANZ stn 126, southern Norfolk Ridge, W of Cape Reinga, 469-526 m, 33°23.41'S, 170°11.58'E (1 dd, NMNZ M160945).

DISTRIBUTION. — A specimen from 465 m off Guadeloupe was illustrated by Paulmier (1994: fig. 17). *Oocorys verrillii* is recorded from the Caribbean Sea, only, in the western Atlantic, and at the Azores where, however, Bouchet & Warén (1993) suggested that the few old shells known represent temporary, perhaps Pleistocene pseudopopulations recruited from the western Atlantic, and the newly recorded lot from Irving Bank appears likely to have the same origin (Gofas & Beu 2003); off South Africa; three specimens are recorded here from Réunion; the type material of *O. morrisoni* is from northern Western Australia; rare in 400-1100 m around New Caledonia and not uncommon around Vanuatu (possibly a little more common than *O. sulcata* in this area) and Wallis and Futuna, off northern New Zealand, and off Japan. One specimen (holotype of *Benthodolium pacificum*) is recorded from the Gulf of Panama, eastern Pacific. *Oocorys verrillii* probably occurs throughout the Indian and Pacific Oceans, including the eastern Pacific, as well as in the western Atlantic.

DIMENSIONS. — Holotype of *Dolium* (*Eudolium*) *verrillii*: H 32.5, D 24.1 mm; holotype of *Benthodolium pacificum*: H 30.1, D 20.7 mm; holotype of *Oocorys sulcata caribbaea*: H 40.5, D 28.5 mm; paratype MCZ 135052: H 47.1, D 33.6 mm; holotype of *O. tosaensis*: H 32.4, D 23.6 mm; holotype of *O. lussii*: H 38.0, D 25.9 mm; Vanuatu, MUSORSTOM 8 stn 1008: H 37.3, D 23.7 mm; MUSORSTOM 8 stn 1075: H 43.7, D 29.8 mm; MUSORSTOM 8 stn 1080: H 42.1, D 28.6 mm; holotype of *O. morrisoni*: H 39.7, D 28.5 mm; paratypes of *O. morrisoni*: H 32.2, D 22.0 mm; H 32.5, D 20.9 mm.

REMARKS. — *Oocorys verrillii*, as construed here, is the species identified by Bouchet & Warén (1993: 803) as *O. cancellata*. These authors synonymised *O. sulcata caribbaea* Clench & Aguayo with *O. sulcata* var. *cancellata*

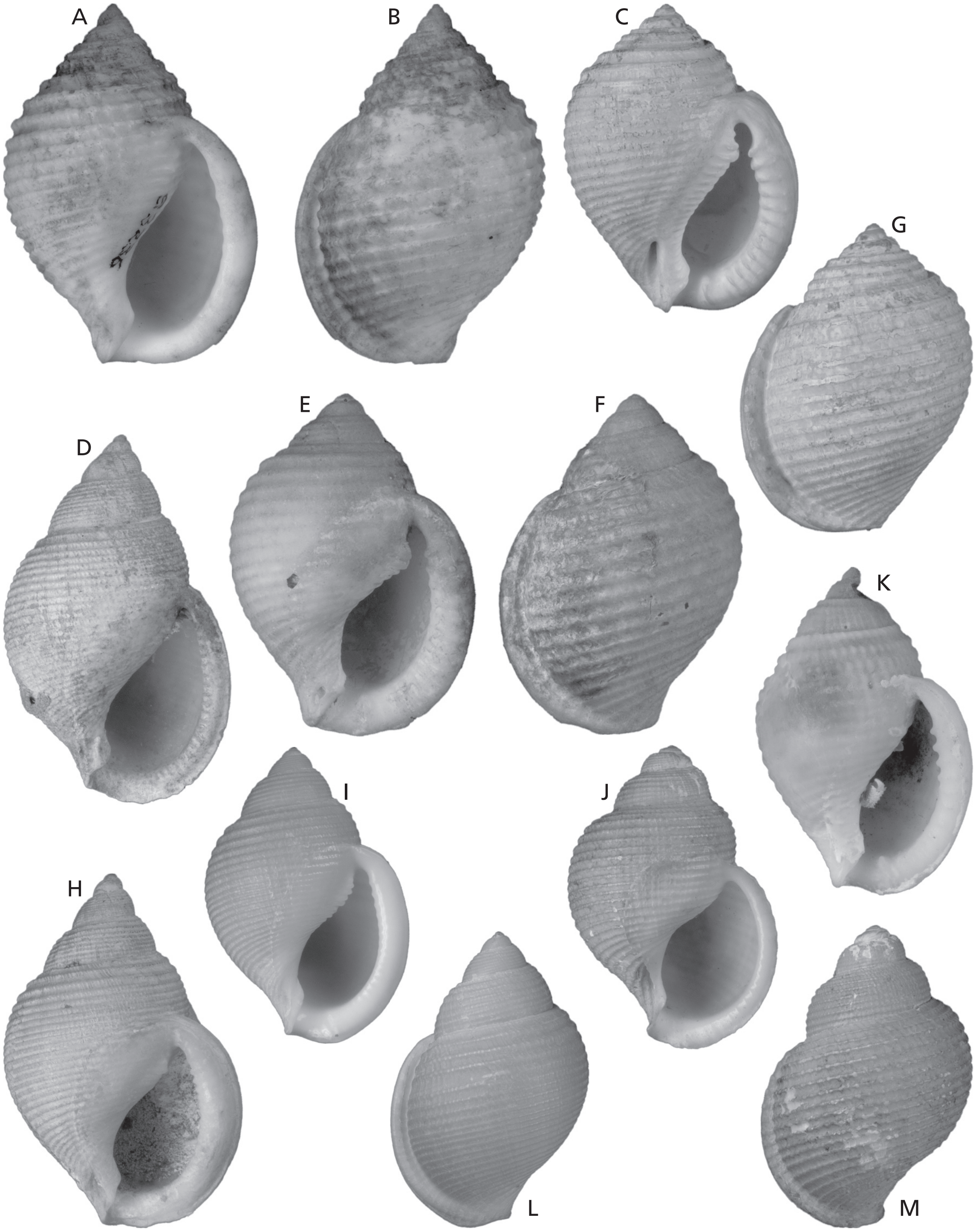


FIG. 26. *Oocorys verrillii* (Dall, 1889), all X 1.5. **A**, **B**, *O. lussii* Bozzetti, 1990, holotype, trawled off Durban, South Africa (NMP S3236, T364; H 38.0 mm). **C**, **G**, *O. tosaensis* Habe & Azuma, 1956, holotype, Tosa Bay, Japan, 200 m (NSMT Mo.38642; H 32.4 mm); **D**, tall specimen, MUSORSTOM 7 stn CP 564, Banc Tuscarora, Wallis and Futuna Islands, SW Pacific, 1015-1020 m (H 38.0 mm); **E**, **F,** BATHUS 3 stn CP 811, Norfolk Ridge, southern New Caledonia, 383-408 m (H 34.9 mm); **H**, MUSORSTOM 8 stn CP 990, Vanuatu, 980-990 m (H 36.8 mm); **I**, **L**, MUSORSTOM 6 stn CP 438, Loyalty Ridge, New Caledonia, 780 m (anatomy and radula examined; H 30.7 mm). **J**, **M**, *Benthodolium pacificum* Dall, 1896, holotype, Gulf of Panama, 4162 m (H 30.1 mm); **K**, off St Gilles, Réunion, 700 m (H 33.7 mm).

Dautzenberg & Fischer and, as noted above in the discussion on the status of *Hadroocrys verrillii*, I conclude that *O. verrillii* is simply an earlier name for the same species. *Oocorys verrillii* is distinguishable from *O. sulcata* easily by its consistently small size (up to *c.* 47 mm high, but few specimens are over 40 mm high); its consistently adherent inner lip, which is smooth in most specimens but bears weak to prominent transverse ridges in relatively few, strongly callused specimens, particularly on the parietal callus pad; its lack of an umbilicus; its strongly truncated and left-deviated columellar base; its thick to very thick, strongly reflected outer lip, which varies from smooth to bearing regular, weak to quite prominent transverse ridges; its weakly to very strongly developed parietal callus; and its

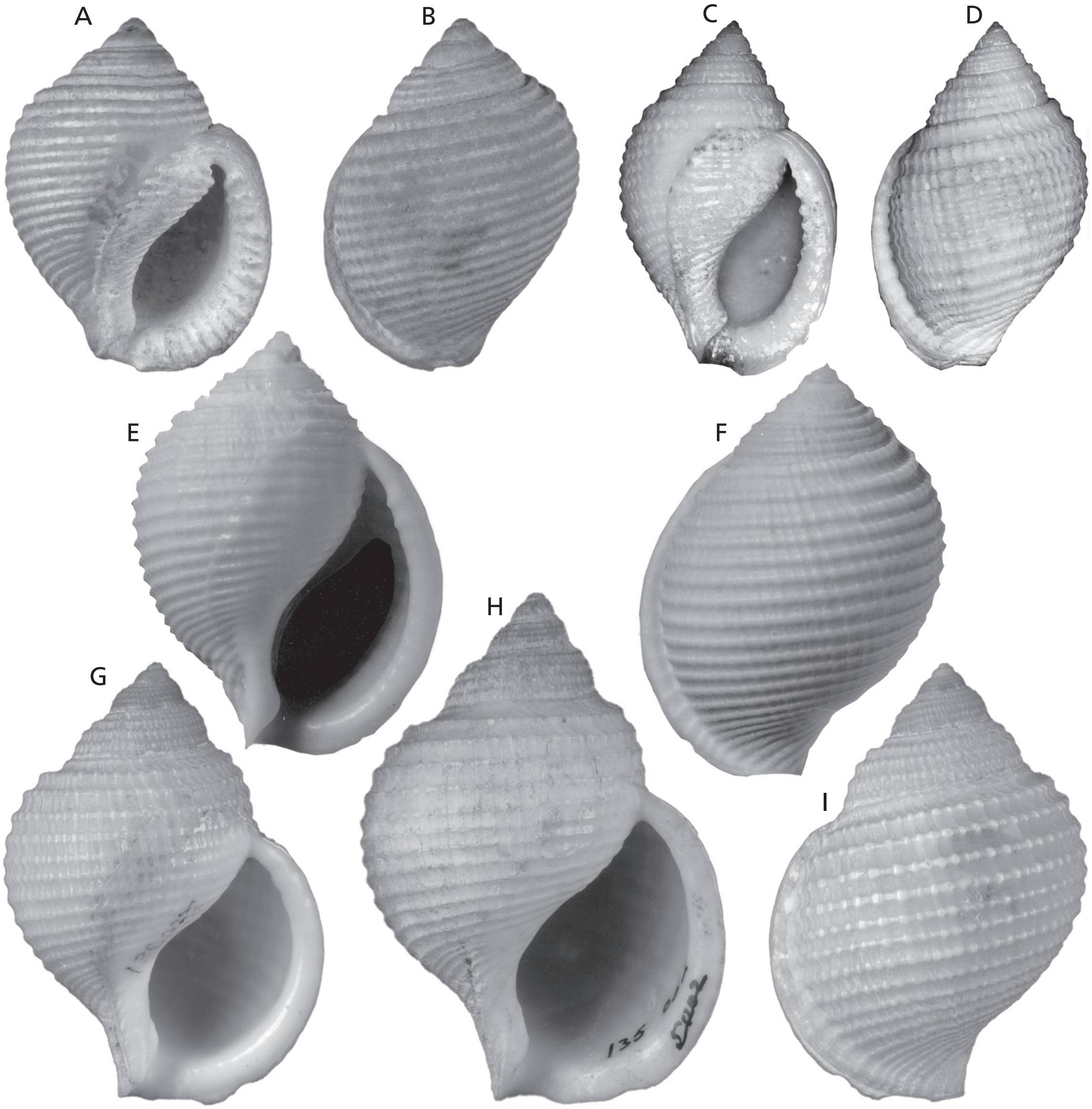


FIG. 27. *Oocorys verrillii* (Dall, 1889), all X 1.5. **A**, **B**, holotype, off Grenada, lesser Antilles, Caribbean, 133 m (USNM 87208; H 32.5 mm); **C**, **D**, off St Gilles, Réunion, 700 m, specimen in collection of J. C. Martin (from a colour print; H 32.4 mm). **E**, **F**, *O. morrisoni* Kreipl & Alf, 2001, holotype, 450-500 m, 296 km W of Broome, Western Australia, from scampi trawlers (WAM S.1365, H 39.7 mm). **G**, **I**, *O. sulcata caribbaea* Clench & Aguayo, 1939, holotype, off Pinar del Rio, Bahia de Corrientes, Cuba, 1125 m (MCZ 135072; H 40.5 mm); **H**, paratype, off SW Oriente Prov., Cuba, 2928-3294 m (MCZ 135052; H 47.1 mm).

exterior sculpture of rather widely spaced, narrow, prominent spiral cords crossed by weak to quite prominent axial ridgelets that are absent from *O. sulcata*. It seems to be less variable than *O. sulcata*, with significantly more consistent size and sculpture, although the spire height, the prominence of the spiral cords and axial ridgelets, the thickness of the parietal callus and the thickness and width of the outer lip are quite variable in the material examined. The protoconch (Bouchet & Warén 1993: fig. 1930) is like that of *O. sulcata* but smaller, turbiniform, of *c.* 2.7 whorls, with fine cancellate sculpture. Similar but slightly abraded protoconchs have been observed on several New Caledonian specimens of *O. verrillii*.

The holotype of *Benthodolium pacificum* (Figs 26J, M) seems to fall within the range of variation of *O. verrillii*. The shape, the small size, the left-deviated columellar base, the prominent, narrow spiral cords crossed by low axial ridges that form small nodules at the sculptural intersections, and the strongly flared outer lip bearing weak transverse ridges are all characters agreeing with those of *O. verrillii*. The only distinguishing character is the more deeply impressed suture than in most western Pacific specimens of *O. verrillii*. The spire of the holotype of *B. pacificum* also is taller than that of most Atlantic and western Pacific specimens assigned to *O. verrillii*. However, it is greatly exceeded by the spire of a specimen from Tuscarora Bank, Wallis & Futuna Islands (MUSORSTOM 7 stn CP 564; Fig. 26D; tallest of 5 tall-spired specimens). The record (above) of a specimen from the Austral Islands, southeastern Polynesia, helps fill a huge gap between western and eastern Pacific records of this species. I here treat *Benthodolium pacificum* as another synonym of *O. verrillii*, but the synonymy needs confirmation by study of much more material from the eastern part of its range. This record, the only one I am aware of from the eastern Pacific, is important for demonstrating that *O. verrillii* apparently occurs in deep water throughout the world's temperate and tropical oceans (other than in the eastern Atlantic and the Mediterranean).

The argument is presented in the introduction to Oocorythinae for regarding "*Hadroocorys*" *verrillii* and "*H*". *tosaensis* as part of the variation of the species previously known as *O. cancellata*. New Caledonian material ranges through to specimens almost as extreme as "*Hadroocorys*" *verrillii* (Figs 27A, B) and there is no doubt that these names are synonyms. The holotype of *Oocorys tosaensis* (Figs 26C, G) is almost indistinguishable from that of *Dolium verrillii* and the New Caledonian "*Hadroocorys*" specimen. The holotype of *O. lussii* (Figs 26A, B) clearly also is a rather short-spired, strongly cancellate specimen of *O. verrillii*. The three Réunion specimens (Figs 26K, 27C, D) also are only a little more weakly sculptured and armoured than the holotype of *D. verrillii*.

The overall appearance of the teleoconch of the type material of *Oocorys morrisoni* (Figs 27E, F) is very similar to that of coarsely sculptured, low-spired, rather thin-shelled specimens of *O. verrillii*, except for the rather more obvious sutural ramp of *O. morrisoni*. The sutural ramp is formed by a rather wide interspace between the two uppermost spiral cords (at the suture and just below), while the next spiral interspace below also is wider than the succeeding ones. The well-marked spiral cords are crossed by many low, narrow axial ridges, forming a finely nodulose sculpture as in normal white specimens of *O. verrillii*. The distinctive character of the teleoconch is its relatively bright coloration, "bright cream to soft orange with a moderate gloss" (Kreipl & Alf 2001: 247). The coloration is a little brighter than in all other species referred here to *Oocorys*, all of which are stark white to, at most, pale cream. The operculum (Kreipl & Alf 2001: figs 1 b, 2 b) also is distinctive in the holotype, relatively tall and narrow with a slightly embayed left posterior margin and a relatively small area of spiral growth lines, and resembles that of *Eucorys bartschi*. However, the opercula of the paratypes are shorter and wider. The protoconch was described by Kreipl & Alf (2001: 245) as "of 3 whorls", but is severely corroded and its original shape and size are not determinable. Information on the protoconch and radula might help to decide the status of this nominal species. However, it is very likely that *O. morrisoni* is merely based on unusually colourful specimens of *O. verrillii*.

ANATOMY. — The preserved animal (Figs 9A, B) was examined from a tall-spired male specimen from the Loyalty Ridge, New Caledonia (MUSORSTOM 6 stn CP 438). The external appearance and the arrangement of the mantle cavity organs are very similar to those of *O. sulcata*, and are as illustrated by Bayer (1971: fig. 19) for *Oocorys sulcata*. The specimen lacks obvious, pigmented eyes. The proboscis is relatively short for a cassid, as in *O. sulcata,* and is almost completely everted. The osphradium is only slightly asymmetrically bipectinate, with the right leaflets only a little longer than the left ones, but is more strongly curved to the right at the anterior end than in all other specimens examined, other than in *O. clericus*. The penis is similar to those of *O. clericus* and *O. sulcata* in having a subquadrate termination, with an open seminal groove and a terminal papilla, but is a little more narrowly waisted at the base than in either similar species. The jaw plates are thinner and more fragile than those of *O. sulcata*, and the radula is almost completely transparent, rather than pale brown to yellowish, as in all other material examined in this study.

RADULA. — The radula (Figs 5E, F) was examined from the same specimen as studied for anatomy, and is similar to that of *O. sulcata*, and particularly to that of the average specimen from DEMERABY stn CP 03, off northern Brazil. However, as the *O. verrillii* radula has severely abraded cusp tips the details are difficult to compare. The radula has 6-7 denticles on each side of each central tooth, 8-10 much narrower denticles on the outer edge of each lateral tooth, and 3-4 denticles on the inner side of each inner marginal tooth. The base of the basal plate of each lateral tooth bears a low ridge parallel to the tooth in front. The ridge appears to be a pushing ridge to keep the teeth in position as they function, as described above for *Galeodea* species, and it borders a shallow but obvious hollow or groove in the outer lateral margin of the tooth that receives the base of the inner marginal tooth in the same row.

Genus ***EUCORYS*** n. gen.

Type species. *Oocorys bartschi* Rehder, 1943, Recent, northern Gulf of Mexico, northern coasts of the Greater Antilles Islands, and eastern Florida.

DIAGNOSIS. — Oocorythinae with shell, radula and anatomy similar to those of *Oocorys* Fischer, 1883 (e.g., lacking obvious, pigmented eyes), but differing from *Oocorys* in having a coloured (pale pinkish brown, peach or yellow) rather than plain white teleoconch, a much thicker and more solid teleoconch, a smooth and lightly polished shell surface rather than the dull white or slightly chalky surface of *Oocorys* species, a relatively elongate shape with a tall spire compared with that of most *Oocorys* species, a short but well-developed anterior siphonal canal (better-developed than in *Oocorys* species), a deeply concave sutural ramp (wider and more deeply concave than in *Oocorys* species), a well-developed terminal varix (considerably thicker and more strongly reflected than in most *Oocorys* species except *O. verrillii*), sculpture of prominent, smooth, evenly convex-crested spiral cords separated by smooth, evenly concave grooves that give the shell quite a different appearance from the lower, flat-crested cords and flat interspaces of *Oocorys*, and a thicker, heavier operculum with the nucleus a little further above the anterior end and, consequently, less obviously developed spiral initial growth lines than in *Oocorys*. Radula similar to that of *Galeodea* and *Oocorys*, but with a longer (antero-posteriorly; i.e., more evenly triangular) cutting head and markedly shorter and wider basal plate on the central teeth than in *Galeodea* and *Oocorys* species, and with many long, narrow denticles on outer edges of the central (7-9 denticles) and lateral teeth (9-11) in *Eucorys bartschi* (no radular or anatomical characters are known for *E. barbouri*). Gender feminine.

The two included species, "*Oocorys*" *barbouri* and "*O*". *bartschi*, also are the only two species formerly assigned to *Oocorys* that have a small, smooth, cap-shaped protoconch of less than 1 whorl, closely similar to that of *Galeodea*, rather than the larger, turbiniform, cancellate-sculptured, typical tonnoidean planktotrophic protoconch of *Oocorys*. However, I do not consider this difference in developmental type to be an important generic character.

REMARKS. – "*Oocorys*" *barbouri* and "*O*". *bartschi* differ from all the species included here in *Oocorys* in a number of significant characters, listed above. Although "*O*". *bartschi* is similar to *Oocorys* species in lacking obvious pigmented eyes, and has a similar radula to that of *Oocorys sulcata* apart from the longer, more triangular cutting head on the central teeth (nothing is known of the animal of *O. barbouri*), all other external shell characters are significantly different from those of *Oocorys* species. This becomes particularly clear when the very large new species *O. grandis* and elongate species, such as *O. elevata* Dall, are compared with *Eucorys* species; the distinctions between them in shell thickness, colour and sculpture are very marked. The greatest differences in shell appearance result from the evenly and strongly convex whorl profile, particularly on spire whorls, the much more fully developed anterior siphonal canal and the more "standard" tonnoidean, varicate outer lip of *Eucorys* than of *Oocorys* species. The operculum of *Eucorys bartschi* also is a little different from those of *Oocorys* species in its thicker and less flexible nature, its more elongate shape and its less obvious spiral initial area, but the significance of these characters will not be clear until the operculum of *E. barbouri* is described. The two species *Eucorys barbouri* and *E. bartschi* are so markedly distinct from the other species assigned to *Oocorys* in shell characters that I consider them to belong in a separate genus. The precedent already exists for regarding *Dalium* as a genus distinct from *Oocorys*, even though it shares radular characters and the lack of obvious, pigmented eyes with *Oocorys*, and the status of *Eucorys* is comparable. Turner (1948) illustrated the radula of *E. bartschi* as having unusual rounded corners on the lower edge of the basal plate of the central tooth, rather than the protruding, triangular corners of *Oocorys* species, but SEM examination of a radula of *E. bartschi* (Figs 3E, F) demonstrated that the central tooth has the same small, projecting triangular corners on the base as in all other *Oocorys* and *Galeodea* species, even though the basal plate is much shorter than any observed in any *Oocorys* or *Galeodea* species.

Some correspondents have suggested to me that the species here identified as *Eucorys barbouri* is more similar in shape to *Dalium solidum* than to *E. bartschi*, and it certainly remains possible that *Dalium* would be a better position than *Eucorys* for *E. barbouri*. Knowledge is required of further taxonomically significant characters – the protoconch of *D. solidum* and, preferably, gene sequences from as many as possible of these species – before the generic position of *E. barbouri* can be considered certain.

ETYMOLOGY. — The name *Eucorys* is composed from parts of the names *Eudolium* and *Oocorys*, and is intended to reflect the unusual combination of characters of the new genus, which has external shell characters in common with *Oocorys*, *Galeodea* and *Eudolium*, and in some ways resembles *Eudolium* more closely than *Oocorys*.

Eucorys barbouri (Clench & Aguayo, 1939)

Figs 28A-D, F, H

Oocorys barbouri Clench & Aguayo, 1939: 193, pl. 29, fig. 2.

Other references:
Oocorys barbouri - Turner 1948: 183, pl. 83, figs 1, 2. — Abbott 1974: 168, fig. 1790. — Kreipl 1997: 69, unnumbered fig.

TYPE MATERIAL. — Holotype, MCZ 135055 (Figs 28D, F), from *Atlantis* stn 2987, off Sagua la Grandes, Cuba, 23°22'N, 79°53'W, 560-600 m; paratype, MCZ 135265, from *Atlantis* stn 3451, also off Sagua la Grandes, 23°20'N, 79°59'W, in 741 m; paratype, Museo Poey, Habana, Cuba, from *Atlantis* stn 3437, 23°05'N, 79°32'W, in *c.* 500 m, also from the same area as the type locality (Turner 1948: 184).

OTHER MATERIAL EXAMINED. — **Guadeloupe**. Lobster traps, off Pigeon Island, 550-600 m (in collection of D. Lamy; 2 dd, Figs 28A-C, H); lobster traps, off Pointe Noire, 450 m (2 dd; 1 in collection of D. Lamy and 1 in NZGS WM 17164); lobster traps, 450 m, off Pigeon Island, presented by D. Lamy (1 dd, NZGS WM17192).

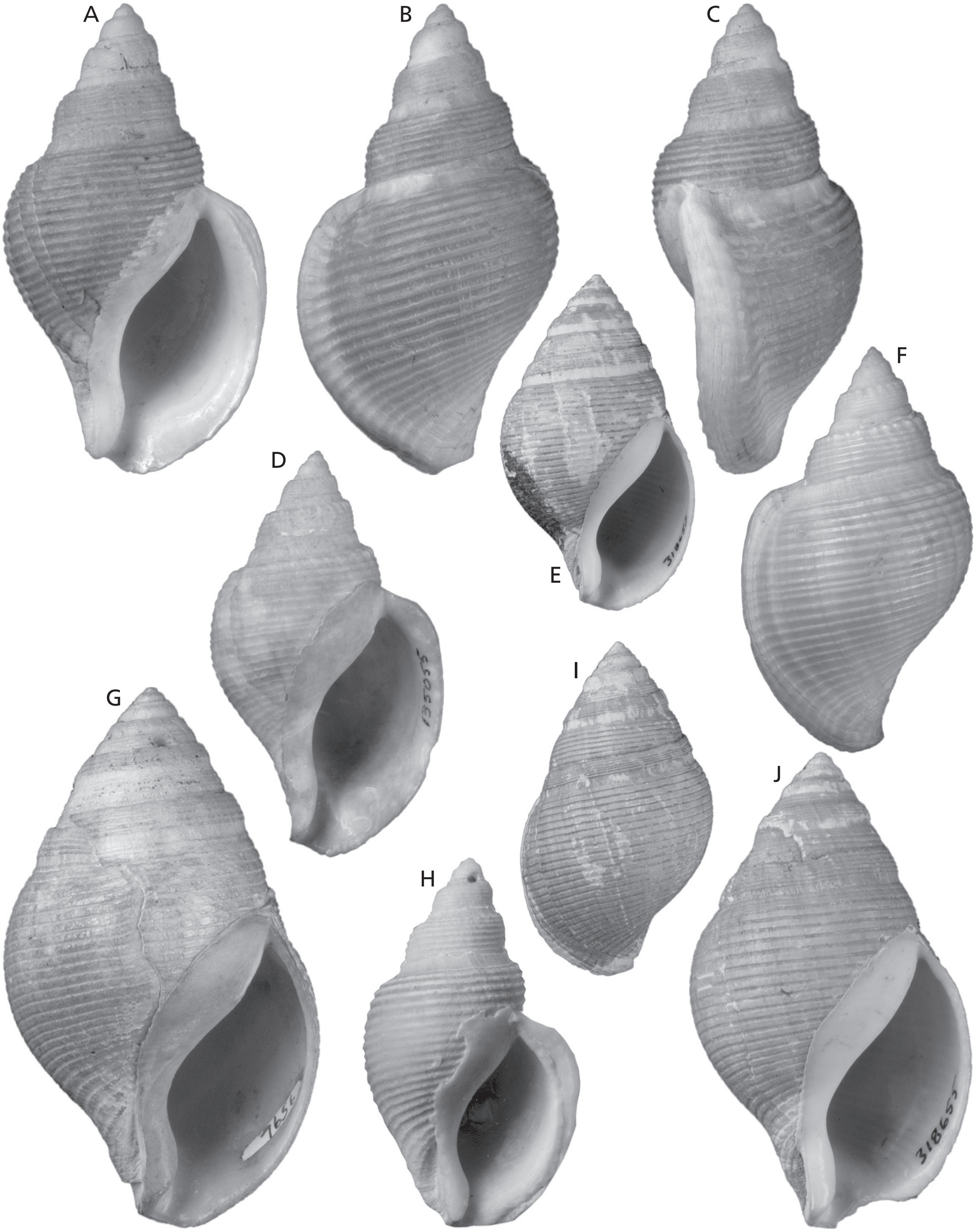


FIG. 28. A-D, **F**, **H**, *Eucorys barbouri* (Clench & Aguayo, 1939), all X 1.25. **A-C**, **H**, 2 specimens from lobster traps, off Pigeon Island, Guadeloupe, 550-600 m, in collection of D. Lamy (A-C, H 58.7 mm; H, H 45.1 mm); **D**, **F**, holotype, off Sagua la Grandes, Cuba, 560-600 m (MCZ 135055; H 50.0 mm). **E**, **G**, **I**, **J**, *Dalium solidum* Dall, 1889, Caribbean, all X 1.25; **E**, **I**, lectotype, off Grenada, 1037 m (MCZ 07656; H 41.9 mm); **G**, largest specimen seen, N of Cayenne, Guiana, 668 m (MCZ 318653; H 67.4 mm); **J**, specimen with narrowly varicate outer lip, N of Mana, Guiana, 728 m (MCZ 318655; H 59.0 mm).

DISTRIBUTION. — Turner (1948) recorded *Eucorys barbouri* from one further *Atlantis* station off Cuba, stn 3359, 20°38'N, 74°32'W, off Baracoa, in *c.* 2000 m, and Paulmier (1994: fig. 16) illustrated a specimen collected live in 425 m off Guadeloupe, Lesser Antilles. These records from Cuba and Guadeloupe are the only ones I am aware of, but *E. barbouri* probably occurs sparsely throughout at least the northern Caribbean, around the Greater Antilles and the northern Lesser Antilles.

DIMENSIONS. — Holotype: H 50.0, D 28.9 mm; paratype MCZ 135265: H 28.6, D 16.1 mm; off Pigeon I., Guadeloupe, in the collection of D. Lamy: H 58.7, D 33.4 mm (Figs 28A-C).

REMARKS. — *Eucorys barbouri* is very distinctive. It is immediately recognisable by its tall, narrow shell, with a tall spire and a deeply concave, steeply sloping sutural ramp, which lacks sculpture and thus produces a smooth subsutural collar as also occurs in *Oocorys clericus*, although it is markedly wider than that of *O. clericus*. The last whorl tapers unusually gradually into a moderately well developed anterior canal, much better developed than in any *Oocorys* species, and the outer lip is reflected and thickened to form an obvious, smooth varix. The large specimen (H 58.7 mm) in D. Lamy's collection, from Guadeloupe (Figs 28A-C), has a heavy, thick terminal varix with the outer lip flared out in front of the varix; it is much more massive than any varix I have seen in *Oocorys*. The sculpture is largely of almost smooth, widely spaced spiral cords, very similar to those of *O. bartschi*, crossed by very fine axial ridgelets in a relatively narrow zone around the periphery. The holotype has a wide, pale brownish pink band around the periphery and upper part of the base, and a white anterior canal, aperture and sutural ramp. On the large specimen from Guadeloupe the colour pattern is even better developed, most of the shell being a dark brownish pink, with a slightly paler subsutural band and a cream anterior end. Unfortunately, the operculum is not yet recorded for this species. The holotype has the protoconch well preserved. As in *E. bartschi*, it is a minute, smooth cap-shaped shell of less than one whorl, with a weakly protruding apex, closely similar to that seen on all the Recent species of *Galeodea*.

Eucorys bartschi (Rehder, 1943)

Figs 3E, F; 21F; 29

Oocorys bartschi Rehder 1943: 197, pl. 10, fig. 16.

Other references:
Oocorys bartschi - Turner 1948: 182, pl. 75, figs 7, 9-10; pl. 82, figs 1-2. — Abbott 1974: 168, fig. 1789. — Okutani 1983: 267, illus.
Oocorys bartschi bartschi - Quinn 1980: 154, figs 2E, F, 6. — Kreipl 1997: 70, unnumbered fig.
Not *Oocorys bartschi* - Warén & Bouchet 1990: 80, 92, 101, fig. 119 (= *O. clericus* Quinn).

TYPE MATERIAL. — Holotype, USNM 535689, from 144-256 m, Gulf of Mexico, off the Dry Tortugas, Florida (Figs 29D, E); one paratype, Henderson coll., USNM 417859, from Florida.

OTHER MATERIAL EXAMINED. — **Gulf of Mexico.** Trawled ESE of South Pass, mouth of Mississippi River, in *c.* 550 m (1 dd); stn 71A7-11, 26°32.3'N, 96°05'W, 636 m (5 lv); stn 71A8-29, 23°54.1'N, 97°00'W, *c.* 1000 m (6 dd); stn 69A11-64, 19°28'N, 95°58'W, 384 m (1 dd); stn 71A8-29, 23°54.7'N, 96°59.9'W, 937 m (1 dd); stn 72A13-17, 23°27.6'N, 97°12.3'W, 677 m (2 dd); stn 71A7-10, 26°32.9'N, 96°06.4'W, 937 m (2 dd); stn 72A13-39, 27°26.4'N, 94°07.6'W, 1061 m (1 dd); stn 68A13-22, 27°38'N, 95°22.5'W, 476 m (1 dd); stn 71A7-11, 26°32.3'N, 96°05'W, 636 m (1 dd) (all except the first presented to MNHN by Texas A & M University); shrimp trawl, *c.* 55 km offshore, SW of Southwest Pass, mouth of Mississippi River, Louisiana, 240 fathoms (440 m) (1 dd, MCZ 198513); R/V *Oregon II* stn 10954, NE of Tampica, Mexico, 23°14'N, 97°17'W, 677 m (2 dd, MCZ 318651).

Dominican Republic. Trap, off Cabo Rojo, Prov. Pedernales, coll. B. Vega, Dec. 1961 (1 dd, MCZ 281598).

DISTRIBUTION. — I have seen material and records of *Eucorys bartschi* only from the northern Gulf of Mexico as far west as Mexico, off the northern Dominican Republic, in the Straits of Florida and off northeastern Florida, in *c.* 150-1200 m. It apparently is limited to the northern Gulf of Mexico, Florida, and the northern coasts of the Greater Antilles. Its apparently small range is correlated with lecithotrophic (probably intracapsular) development (to judge from that of *Galeodea*; Hughes 1986a), as indicated by its very small protoconch of less than one whorl.

DIMENSIONS. — Holotype: H 112.5, D 73.6 mm; MCZ 198513, SW of Southwest Pass, Louisiana: H 115.2, D 74.5 mm; MNHN, off South Pass, Mississippi River: H 87.3, D 56.7 mm; MNHN, stn 71A7-11: H 90.3, D 59.2 mm; H 82.8, D 56.5 mm (Fig. 29F, animal examined); MNHN, stn 71A8-29: H 106.5 (incomplete), D 58.9 (incomplete) (Fig. 29C). Quinn (1980) recorded specimens over 130 mm high.

REMARKS. — Large, clean specimens of *Eucorys bartschi* are lightly polished, peach or yellowish brown shells resembling *Eudolium* in general appearance, apart from their taller spire and more strongly inflated spire whorls. The aperture, the outer lip, the subsutural band and the anterior siphonal canal are paler than the rest of the shell, white on some specimens. The sculpture is very distinctive, compared with that of *Oocorys* species, because of the coarseness of the spiral cords: moderately prominent, quite wide, each with a weakly convex crest, and with each interspace about equal in width to one cord; there are about 9-12 on spire whorls (varying with the spire height) and 32-34 on the last whorl and canal; they tend to become a little wider and more closely spaced over the base and canal than higher up. A subsutural band is defined weakly by bearing 2-3 lower, narrower spiral cords than on the rest of the teleoconch surface, and by its paler colour on most fresh specimens. The spire height is greatly variable, as pointed out by Quinn (1980), and I illustrate one of the Gulf of Mexico specimens with a spire about twice as tall as that of the other material I have seen (Fig. 29C). The one protoconch I have seen (MNHN, stn 69A11-64) is translucent white, very small, smooth, and of less than one whorl, with a protruding apex, as in *Galeodea* species and *E. barbouri*. This specimen also bears a thin, pale straw yellow periostracum, which tends to peel off in narrow commarginal strips.

ANATOMY. — I reconstituted the dried female animal from one of the five specimens in stn 71A7-11, Gulf of Mexico (Fig. 29F). The animal appears to have no obvious, pigmented eyes (as in *Oocorys* species), and the gross external anatomy and arrangement of the mantle cavity organs appear to be as in *Oocorys* species. However, this needs to be checked from better-preserved material. The operculum (Fig. 21F) also is not greatly different from that of *Oocorys* species, with a weakly developed, small, spiral initial growth area almost at the anterior end of the operculum, but it differs from those of *Oocorys* species in being significantly wider at the anterior than at the posterior end, tapering posteriorly, in having the nucleus further from the anterior end, in having less obviously spiral (rigiclaudent paucispiral) initial growth lines, and in having a rather pointed, triangular anterior end. Turner (1948) and Quinn (1980) illustrated the large attachment scar of the operculum; the operculum is larger and markedly thicker than I have seen in any species of *Oocorys*.

RADULA. — The radula (Figs 3E, F) is similar to that of *Oocorys* species in most characters, but differs in having the cutting area of the central teeth a longer and narrower triangle than in *Oocorys* species, and in the basal plate of the central teeth being much shorter than in any *Oocorys* or *Galeodea* species I have examined. There are 7-9 long, narrow denticles on each side of the central tooth, 8-12 on the outer edge of each lateral tooth, rather unusually one long, narrow denticle on the inner edge of each lateral tooth, and one long, narrow denticle on the inner edge of each inner marginal tooth. The very short, wide basal plate and longer triangular cutting head of the central tooth may well prove to be generic characters of *Eucorys*, but the radula of *E. barbouri* requires examination before the significance of radular characters is clear.

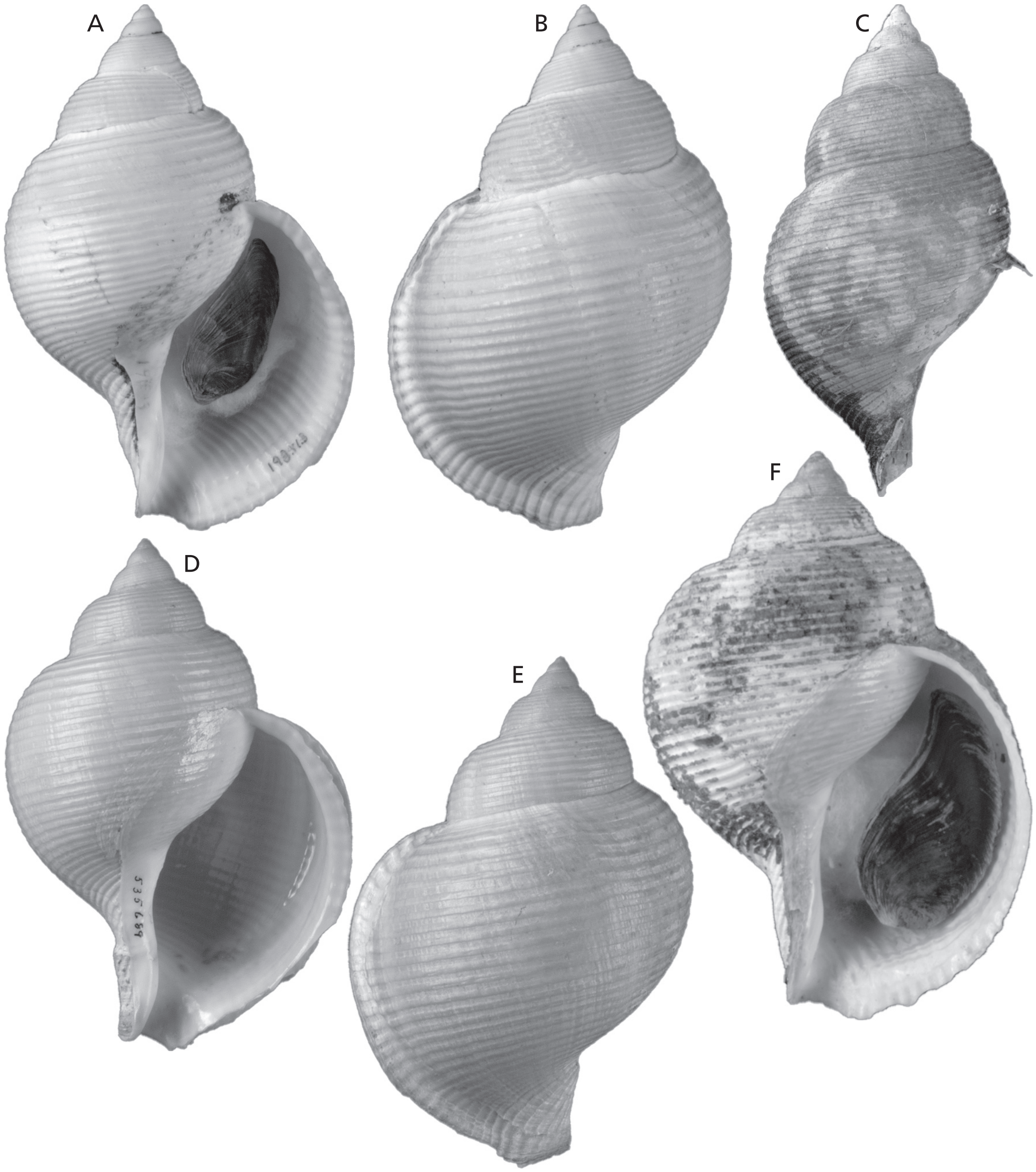


FIG. 29. *Eucorys bartschi* (Rehder, 1943), type species of Eucorys n. gen. **A**, **B**, off Southwest Pass, Mississippi River (MCZ 198513; H 115.0 mm; X 0.67); **C**, stn 71A8-29, Gulf of Mexico, 1000 m (H 106.5 mm; X 0.67); **D**, **E**, holotype, off the Dry Tortugas, Florida, 144-256 m (USNM 535689; H 112.5 mm; X 0.67); **F**, stn 71A7-11, Gulf of Mexico, 636 m; anatomy and radula examined (H 82.8 mm; natural size).

Genus ***DALIUM*** Dall, 1889

Dalium Dall, 1889a: 230. Type species (by original designation): *Dalium solidum* Dall, 1889, deep water (more than 1000 m), Caribbean Sea.

REMARKS. — The shell of *Dalium solidum* differs from those of all species assigned here to *Oocorys* in a number of subtle characters, discussed in more detail under *D. solidum*, below. The main differences are the very much thicker and more solid shell and the more exert, straight-sided spire than those of *Oocorys* species. However, none of the shell characters is very fundamental. There also are no anatomical or radular differences from species assigned to *Oocorys*. It seems quite feasible that *D. solidum* is merely the youngest of a presumed lineage of tall-spired *Oocorys* species (apparently containing also the Miocene-Early Pliocene *D. dalli* (Böse, 1906) and the Pliocene *D. ecuadorianum* Olsson, 1942) that lives in rather shallower water than most other species of the genus, and so has a thicker shell than other species assigned here. However, differences from *Eucorys* are almost as subtle as those from *Oocorys*, and *Dalium* might prove to be an earlier name for the genus here named *Eucorys*, rather than a synonym of *Oocorys*. It would be helpful for the generic position to know whether the protoconch of *D. solidum* (unknown at present) is relatively large, turbiniform and cancellate, as in *Oocorys* species, or small, few-whorled, smooth and cap-shaped, as in *Eucorys* species. In the mean time, *Dalium* tentatively is retained as a genus distinct from *Oocorys*.

Sven Nielsen (University of Hamburg) has sent me SEM micrographs of the protoconch of an apparently unnamed species of *Dalium* similar to *D. dalli*, from the Middle Miocene Ranquil Formation of Punta el Fraile, near Arauco, south of Concepcion, Chile. The protoconch (seen in dorsal view only) seems to be much like that of *Oocorys sulcata*, turbiniform and of several inflated whorls, but lacks the reticulate sculpture seen on all *Oocorys* protoconchs. Much greater knowledge of *Dalium* protoconchs is needed to tell whether this is a protoconch like that of *Oocorys* that merely has lost its sculpture through abrasion, or *Dalium* has a distinctive protoconch lacking reticulate sculpture.

Dalium solidum Dall, 1889

Figs 28E, G, I, J

Dalium solidum Dall, 1889a: 230, pl. 19, fig. 10 d.

Other references:

Dalium solidum - Dall, 1889b: 132. — Clench & Abbott 1943: 8, pl. 4, figs 6-7. — Bayer 1971: 145, figs 20A, 21, 22A. — Abbott 1974: 169, fig. 1795. — Okutani 1983: 268, illus. — Horikoshi 1989: 62, pl. 14, fig. 17. — Kreipl 1997: 77, unnumbered fig.

TYPE MATERIAL. — Lectotype, designated here, MCZ 007656 (Figs 28E, I), from *Blake* stn 265, off Grenada, Lesser Antilles, Caribbean, in 1037 m.

Dall (1889a: 231, pl; 19, figs 10 d) clearly referred to “specimens” in his description, without using the words “type” or “holotype” either in the description and comments or in the figure caption. His specimens therefore all are construed as syntypes. Clench & Abbott (1943: 8) stated that the “holotype” is MCZ 007656 (the specimen illustrated by Dall, as demonstrated by the small size and by the healed break to the left of the aperture, shown clearly in both Dall’s (1889a: pl. 19, fig. 10 b) and Clench & Abbott’s (1943: pl. 4, fig. 6) illustrations). Under the *Code* (ICZN 1999: Article 74.5) this “holotype” statement does not constitute designation of the illustrated syntype as the lectotype, as Clench & Abbott merely thought the illustrated specimen was the holotype, and did not explicitly indicate that they were intending to select this specimen from the type series to serve as the name-bearing type, so the illustrated syntype is formally designated as the lectotype here. Dall’s (1889a: pl. 19, fig. 10 d) original illustration showed the specimen as shorter and wider than it actually is.

OTHER MATERIAL EXAMINED. – **French Guiana**. R/V *Oregon II* stn 10802, N of Mana, 7°26'N, 53°16'W, 619 m (1dd, MCZ 318652); R/V *Oregon II* stn 10799, N of Mana, 7°31'N, 53°11'W, 728 m (2 dd, MCZ 318655); R/V *Oregon II* stn 10800, N of Mana, 7°29'N, 53°04'W, 692 m (3 dd, MCZ 318654); R/V *Oregon II* stn 10614, N of Cayenne, 7°06'N, 52°44'W, 668 m (2 lv, MCZ 318653); dredged, 800 m, off French Guiana, presented by D. Lamy (4 lv?, NZGS WM 17392).

DISTRIBUTION. – Bayer (1971: 145) recorded a further 54 specimens from R/V *Pillsbury* stations in the southern Caribbean off Panama, Colombia, Venezuela and Suriname, in 604-1867 m, and Okutani (1983: 268) illustrated the shell, operculum and radula of a specimen dredged off Suriname. *Dalium solidum* seems to be moderately common throughout the southern Caribbean Sea, along the northern coast of South America, but has not been reported from elsewhere. This suggests that it is likely to have direct development and a small, cap-shaped protoconch, rather than planktotrophic development and a large, cancellate protoconch as in *Oocorys* species.

DIMENSIONS. – Lectotype: H 41.9, D 24.1 mm; MCZ 318652: H 60.5, D 34.9 mm; MCZ 318653: H 67.4, D 39.0 mm; Bayer (1971: 147) recorded specimens ranging from H 64.0, D 37.1 mm to H 23.1, D 15.0 mm.

REMARKS. – The shell of *Dalium solidum* differs from that of *Oocorys* and *Eucorys* species in several rather subtle characters. The most important one is the very much thicker, heavier shell than in *Oocorys* species; the shell has a solid, heavy feel definitely unlike any specimens of *Oocorys* species I have examined. The tall, almost straight-sided spire does not resemble the gradate one of *Oocorys*, and is much shorter in most *Oocorys* species, although those of *Eucorys barbouri* and *Oocorys elevata* are not very different in height from that of *D. solidum*. The straight spire outlines are produced by the succeeding whorl covering the preceding whorl up to the base of the subsutural collar, in a manner not seen in any *Oocorys* species. The aperture has a corresponding tall, narrow posterior channel, formed by the narrow posterior extension of the whorl that rides over the previous whorl, and is unique to *Dalium*. The sculpture is of low, wide, flat-topped, closely spaced spiral cords, wider than in any *Oocorys* species, separated by grooves that are much narrower (compared with the width of the cords) than in *Oocorys* species. The outer lip is thin-edged and completely without any thickening or reflection in most specimens, a character not seen in any of the *Oocorys* species that have a thick, solid shell as in *D. solidum*.

One specimen of *Dalium solidum* examined (in MCZ 318655; Fig. 28J) has a very weakly flared outer lip and a very low, flat terminal varix, up to 2 mm wide in the direction of shell coiling; I have not observed a varix on any other specimen. The anterior end is produced into a very short, weakly defined anterior canal, clearly descending a little beyond the base of the outer lip, but quite narrow and elongate on the columellar side because of the marked contraction of the whorl base. One of the most distinctive characters is the nature of the subsutural band, which is a simple, smooth, depressed subsutural zone in those *Oocorys* species that have it, but is more complex in *Dalium*, consisting of an elevated, narrowly spirally sculptured upper band, separated from the normal, sculptured whorl surface by a markedly depressed, smooth band about the same width as the raised band. The radula and operculum have been illustrated by both Bayer (1971: 145-148, figs 20A; fig. 22A) and Okutani (1983: 268) and are both closely similar to those of *Oocorys*, so there is no doubt of the taxonomic position, which is close to *Oocorys*. The shell apex is corroded on all material I have seen, and the protoconch has not been described. However, the limited distribution suggests that this species has lecithotrophic development, and therefore that it might well have a simple cap-shaped protoconch as in *Galeodea*, rather than the turbiniform, cancellate-sculptured, planktotrophic tonnoidean one of *Oocorys*. Considerable further study of anatomical and radular characters would then be necessary to determine whether *Dalium solidum* is congeneric with species here placed in *Eucorys*. However, the precedent for an *Oocorys* species that definitely has a turbiniform, cancellate protoconch but has a more limited geographical distribution than other *Oocorys* species is set by *O. clericus* Quinn, which is restricted to an area in the western Atlantic from the Caribbean Sea to off the Bahamas (although this is a poorly known species that could prove to range more widely).

Olsson (1942: 29, pl. 9, figs 2-3; 1964: 171, pl. 30, figs 7, 7a) described a second species of *Dalium*, *Dalium ecuadorianum,* from the Pliocene Esmereldas Formation near Esmereldas, on the Pacific coast of northern Ecuador. This species differs from *D. solidum* in its shorter spire and in having fewer, more widely spaced spiral cords, but is otherwise closely similar. The specimen of *D. solidum* from off Suriname illustrated by Horikoshi (1989: pl. 14, fig. 17) has an unusually short spire with convex outlines, and resembles material of *D. ecuadorianum*. A third species, *Dalium dalli* Böse (1906: 58, pl. 4, figs 7-8), was described from Pliocene rocks of the Isthmus of Tehuantepec, Mexico. This species resembles a small, thin-shelled, finely sculptured, weakly varicate specimen of *D. solidum,* and possibly was ancestral to *D. ecuadorianum*. It occurs also in Late Miocene-Early Pliocene rocks of the Dominican Republic and will be discussed by Beu (in prep., "Revison of Central American Neogene tonnoidean gastropods"). Fossils of a *Dalium* form close to *D. dalli* occur in the Miocene of Arauco, south-central Chile (Nielsen 2003: 92, pl. 16, figs 21, 22; Ranquil Formation (Middle Miocene) near Punta El Fraile, east of Arauco).

In marked contrast to *Oocorys* (of which I am aware of 1 fossil specimen, to be reported by Beu in prep., "Revison of Central American Neogene tonnoidean gastropods", other than those related to *O. elevata* reported above) and *Eucorys*, the fossil record of *Dalium* is moderately extensive. This presumably reflects the shallower depths inhabited by *Dalium* than by the other Oocorythinae, as well as its relatively in-shore habitat along the South American coast. In the past, while the Panama seaway was still open, its range extended down the west coast of South America at least as far south as central Chile. *Dalium* apparently was one of the many molluscs extinguished in the eastern Pacific after the uplift of the Isthmus of Panama.

Subfamily PHALIINAE Beu, 1981

Phaliinae Beu, 1981: 252. Type genus: *Phalium* Link, 1807.

DIAGNOSIS. — The members of subfamily Phaliinae differ from those of subfamilies Cassinae and Oocorythinae in having a radula with longer, more numerous cusps and denticles (producing an almost brush-like effect in many taxa). The most important distinguishing character of the subfamily, though, is the operculum, which resembles that of the bursid genus *Bufonaria* in being fan-shaped, with the nucleus at the centre of the left (adaxial) edge, against the angle where the parietal area of the inner lip joins the columella, with two prominent, raised, straight columellar edges meeting at a very obtuse angle and with the right (abaxial) margin of the operculum evenly and lightly curved in outline (Figs 30J, K); many species have a few to many prominent radial ridges on the operculum, radiating from the nucleus. The members of the subfamily also all have the very strongly twisted, dorsally directed, deeply notched (in the antero-posterior plane), fasciolate siphonal canal, bent back so far as almost to touch the previous whorl, that is seen only in adult specimens of species of *Cypraecassis* in the Cassinae. Although the aperture has quite well thickened lips, with a callus pad and columellar collar on the inner lip of many species and a varicate outer lip, no member of the subfamily produces a wide, thickly callused ventral shield as in *Cassis* and *Cypraecassis*. The Phaliinae were concluded by Riedel (1995: 124) to be a distinctive, monophyletic group that has been separate from the Cassinae since at least Middle Eocene time. In my opinion *Echinophoria*, with its prominent sculpture resembling that of *Galeodea*, is likely to be the stem group of the Phaliinae.

REMARKS. — Abbott (1968) used a more conservative classification than that adopted here, essentially ranking as genus *Phalium* the group that is here treated as subfamily Phaliinae, recognising only the 1 separate genus, *Casmaria*. The main genera now recognised as distinct in Phaliinae are (as also were recognised by Kreipl 1997): *Casmaria* H. & A. Adams, 1853, containing unusually elongate, largely smooth species with only the terminal varix retained, and with small, sharp nodules ("spines") around the outer edge of the anterior end of the varix; *Echinophoria* Sacco, 1890, containing evenly inflated, moderately to very large species (for the subfamily) with only the terminal varix retained, sculptured with spiral cords and one to several rows of relatively large nodules; *Phalium* Link, 1807, containing evenly inflated to quite elongate species retaining all varices down the teleoconch, sculptured with both axial and spiral ridges and grooves, and bearing spines around the outer edge of the terminal varix as in *Casmaria*; and *Semicassis* Mörch, 1852, similar to *Echinophoria* in most characters but more moderate-sized and with more prominent spiral sculpture, at least in most species, and with at most small, inconspicuous nodules around the periphery. *Kahua* Marwick (1928: 482) (= *Mauicassis* Fleming, 1943; Neogene, New Zealand) and *Liracassis* Moore (1963: 30) (Oligocene and Neogene, North Pacific) are among several genera that diverged from *Echinophoria* during Cenozoic time, but are now extinct. It also seems likely that the coarsely nodulose species grouped in *Echinophoria* at present are polyphyletic, and that losing and, possibly, gaining rows of nodules have been frequent evolutionary trends in the subfamily, but recognition of this presumed homoplasy and of the (possibly many) distinct lineages is a major research project in itself, well beyond the scope of the present paper. In a phylogenetic sense, then (rather than the strictly shell morphology sense followed here), not all the generic names listed below as synonyms of *Echinophoria* might actually be synonyms.

I take this opportunity to point out a little-known, earlier but invalid name for *Liracassis*: *Doliocassis* Kuroda (1933: 25, text-fig.); type species, by monotypy: *Galeodea japonica* Yokoyama, 1923, Miocene, Japan (renamed by Kuroda (1933) as *Tonna* (*Doliocassis*) *yokoyamai* Kuroda, 1933, because it was a secondary homonym of *Tonna japonica* (Dunker, 1867), and by Nomura & Hatai (1933) as *Phalium yokoyamai* Nomura & Hatai, 1933, because it was a secondary homonym of *Phalium* (i.e., *Semicassis*) *japonicum* Reeve, 1848; which of these homonymous replacement names has priority is unclear). Kanno (1973) listed all the Cenozoic cassids recorded from Japan, with detailed localities, and mentioned the name *Doliocassis* Kuroda, 1933 and the homonymous replacement species names. He also returned to using *Liracassis japonica* (Yokoyama) as the name for the type species of *Doliocassis* Kuroda, but this is incorrect as under the *Code* (ICZN 1999: Article 59.3) *G. japonica* is permanently invalid, as it was replaced before 1961 and the substitute name has remained in use, apart from in the publication by Kanno (1973). *Doliocassis* Kuroda, 1933 is preoccupied by *Doliocassis* Dall (1909: 62), type species *Buccinum sowerbyi* Lea, 1833 (= *Cassis nupera* Conrad, 1833), Eocene, Gulf Coast of the USA; *C. nupera* now is usually placed in *Sconsia* (see Abbott 1968: 123-124), i.e., *Doliocassis* Dall, 1909 now usually is regarded as a synonym of *Sconsia* but, as mentioned above under *Microsconsia*, it appears to me to be a useful genus. The generic name *Doliocassis* Kuroda, 1933 was listed by Kuroda (1950: 64), where it was stated to be preoccupied by *Doliocassis* Dall, 1909, but was incorrectly stated to be a synonym of *Shichiheia* Hatai & Nisiyama, 1949. *Shichiheia* is regarded here as a junior subjective synonym of *Echinophoria*, whereas the figure accompanying Kuroda's (1933) proposal of *Doliocassis* clearly shows a much more strongly spirally sculptured species belonging in *Liracassis* Moore, 1963.

The MNHN deep-water collections that are the subject of this report and material I have examined in other collections shed some light on the species to be recognised in *Echinophoria,* but I have nothing to contribute on the other genera of the subfamily, all of which inhabit shallow water (the continental shelf to shallow subtidal zones), are highly variable, and are in need of rigorous re-examination, including with molecular techniques.

Genus ***ECHINOPHORIA*** Sacco, 1890

Echinophoria Sacco, 1890a: 88 (separate), 195 (journal). Type species (by subsequent designation, Dall 1909: 62): *Buccinum intermedium* Brocchi, 1814, Oligocene-Miocene, Italy (holotype illustrated by Pinna & Spezia 1978: pl. 10, fig. 1, 1a). Marshall (1991) pointed out that *Echinophoria* was published first in Sacco (1890a: 88, 195) and only later in Sacco (1890b: 9; 1890c: 39).

Synonyms:

Trachydolium Howe, 1926: 303 (*nomen nudum*). Type species (by monotypy): "*Trachydolium dalli*" Howe, 1926 (presumably = *Galeodea dalli* Dickerson, 1917), Oligocene of Washington, USA.

Euspinacassis Finlay, 1926: 230. Type species (by original designation): *Euspinacassis pollens* Finlay, 1926, Early Miocene, New Zealand.

Shichiheia Hatai & Nisiyama, 1949: 230. Type species (by original designation): *Shichiheia etchuensis* Hatai & Nisiyama, 1949, Miocene, Japan.

Bathygalea Woodring & Olsson, 1957: 22. Type species (by original designation): *Cassis coronadoi* Crosse, 1867, Recent, western Atlantic.

Miogalea Woodring & Olsson, 1957: 22. Type species (by original designation): *Cassis* (*Phalium*) *dalli* Anderson, 1929 (junior secondary homonym of *Galeodea dalli* Dickerson, 1917, referred to *Phalium* (*Echinophoria*) by Abbott, 1968, = *Echinophoria andersoni* Abbott, 1968, = *Bathygalea* (*Miogalea*) *hadra* Woodring & Olsson, 1957), Miocene to Recent, Caribbean coast of Central and South America.

Mariacassis Petuch, 1988: 17. Type species (by original designation): *Cassis caelata* Conrad, 1830, Miocene, eastern USA (**new synonym**).

REMARKS. — Marshall (1991) pointed out that, as a result of the earlier publication by Sacco (1890a) of many more names than had been realised previously, several commonly accepted type designations are invalid, as they did not designate a species originally included by Sacco (1890a). However, *Buccinum intermedium* Brocchi, 1814 was originally included in *Echinophoria* by Sacco (1890a).

Echinophoria superficially resembles *Galeodea*, in having a short spire and a large, inflated last whorl, prominent spiral sculpture at least on the early spire whorls, a spiral row or several rows of prominent nodules at least at the periphery, and descending below the periphery on the last whorl of most specimens of some species, and in having a thickened and narrowly but prominently reflected terminal varix. However, it differs from *Galeodea* in a number of significant characters. The most obvious is in having a much more strongly twisted anterior siphonal canal, deeply notched (in the antero-posterior direction) at the dorsal anterior end so as to generate a prominent siphonal fasciole, which on all the Recent species of *Echinophoria* bears a prominent, narrow ridge on the posterior (adapical) side and is separated from the previous whorl by a narrow, deeply and evenly concave groove. The shell shape of species assigned to *Echinophoria* also is distinctive, as its consistent, even, marked inflation produces a teleoconch that is more nearly spherical than those of most *Galeodea* species. The anterior siphonal canal is scarcely visible in conventional apertural view, contrasting with the obvious canal of *Galeodea* species, and contributing further to the subspherical appearance. The protoconch of *Echinophoria* is low-turbiniform, with a well-impressed suture and about 3 strongly inflated, smooth whorls. The subfamilial character of a fan-shaped operculum, with the nucleus in the centre of the left (columellar, adaxial) edge, also distinguishes *Echinophoria* effectively from *Galeodea*, which has its opercular nucleus at about a third to half of the opercular height from the anterior end of the right (outer lip, abaxial) edge of the operculum. The animal of *E. wyvillei* investigated here also differs from that of all *Galeodea* and *Oocorys* species investigated in having the mantle cavity organs situated markedly further back in the mantle cavity. It seems quite feasible that *Echinophora*, along with the other taxa here referred to Phaliinae, evolved from quite a different early tonnoidean ancestor from that of the Cassinae, i.e., the shell shapes of *Galeodea* and *Echinophoria* might well be convergent rather than closely related phygenetically.

The protoconch, siphonal canal, apertural characters and shell shape of *Echinophoria* are closely similar to those of species of *Phalium* and *Semicassis*. *Phalium* is distinguished from *Echinophoria* by lacking the many prominent nodules, other than a peripheral row present in some species, by having axial and spiral sculpture both fine but more-or-less equally well developed (whereas axial ridges and grooves are weak in *Echinophoria*), by retaining varices at all growth pauses, unlike all other genera of the subfamily, by having a better-developed ventral apertural callus shield, by the shell shape being narrower and more elongate than in most species of *Echinophoria* or *Semicassis*, and by most species having sharp nodules or small spines around the outer edge of the anterior half of the outer lip. Such nodules around the outside of the terminal varix are present also in some of the species referred by Abbott (1968) to *Casmaria*, and low, weak nodules are present on the exterior of the lower part of the outer lip in some specimens of the *kurodai* form of *Echinophoria wyvillei* (Watson), but they are not present in the other members of the subfamily. *Semicassis* is distinguished from *Echinophoria* by having dominantly spiral sculpture, forming prominent, strap-like cords in many species, and by lacking nodules other than a peripheral row in most specimens of most species. *Semicassis* differs from *Phalium* in having a more weakly developed ventral callus shield (similar to that of *Echinophoria*), in lacking obvious axial sculpture (other than the nodules, which are axially aligned in some species), and in retaining only the terminal varix, except in a few individuals. *Semicassis* differs less obviously from *Casmaria*, as used by Abbott (1968). Several of the smaller, more elongate, more weakly sculptured species of *Semicassis*, such as *S. bulla* Kuroda *in* Habe, 1961 (Japan) and *S. glabrata* (Dunker, 1852) (western Pacific), very closely resemble some of the smaller, more weakly sculptured, and more elongate species referred by Abbott (1968) to *Casmaria*, such as *C. cernica* (Sowerby, 1888) (Mauritius), *C. nipponensis* Abbott, 1968 (Japan) and *C. perryi* (Iredale, 1912) (southwest Pacific to Easter Island; Philippines, Japan, ?western Atlantic – Parth 2000). These small, elongate species referred to *Casmaria* lack nodules on the outside of the anterior half of the terminal varix, and seem better referred to *Semicassis*. This would leave only the abundant, widespread, tropical species *C. erinaceus* (Linné, 1758) and *C. ponderosa* (Gmelin, 1791) in *Casmaria*, along with the eastern Pacific species *C. vibexmexicana* (Stearns, 1894). Anatomical and radular characters need to be compared to determine whether *Casmaria* and *Semicassis* are distinct genera.

Abbott (1968) listed *Trachydolium* in the synonymy of *Echinophoria*, but Howe (1926: 303) merely listed the name "*Trachydolium dalli*" in a table, with no description and no bibliographic indication of which species he meant. Abbott (1968) apparently assumed that Howe was referring to *Galeodea dalli* Dickerson, 1917, which occurs in Oligocene rocks in the area described by Howe. Although Abbott's interpretation is reasonable, this identification cannot be determined from Howe's (1926) paper alone. *Trachydolium* Howe, 1926 is a *nomen nudum*.

Finlay (1926: 230) proposed *Euspinacassis* with a combined description of "*Euspinacassis pollens* n. gen., n. sp.", but then went on to include two further species in the new genus. Finlay undoubtedly intended the heading to indicate that *E. pollens* is the type species, but Abbott (1968: 95) stated that the type species of *Euspinacassis* was selected by Powell's (1928: 631) subsequent designation. However, the *Code* (ICZN 1999: Article 68.2.1) states unequivocally that "the expressions "gen. n., sp. n.", "new genus and species", or an equivalent", applied before 1931 to only one of the included species, is an original type species designation "if no other type species was explicitly designated", and this clearly covers the case of *Euspinacassis*; *E. pollens* is the type species by original designation. Rutsch (1931) pointed out that, despite Finlay's (1926) statement to the contrary, the correct genus for these New Zealand species is *Echinophoria* Sacco, 1890.

The species-level taxonomy of the Recent species of *Echinophoria* has received widely differing treatment from different authors. Pain & Cox (1988) advocated the recognition of only three species, *E. coronadoi* (= *Cassis wyvillei*; = *Bathygalea pilsbryi*), *E. carnosa* and *E. kurodai*, although they later (Pain & Cox 1990) conceded that *E. bituberculosa* is a species of *Echinophoria*. In contrast, Kreipl (1997) recognised all the named Recent forms as distinct species. Abbott (1968) followed an intermediate approach, recognising the western Pacific form *Cassis wyvillei* as a geographic subspecies of *E. coronadoi*. Mühlhäusser (1992) later added the species *E. oschei*, from Mozambique, East Africa; he thought it most nearly similar to *E. bituberculosa*. Comparison of the MNHN material, including the holotype of *Cassis coronadoi*, with the illustrations by Woodring & Olsson (1957), Abbott (1968), Bayer (1971), Pain & Cox (1988, 1990), Mühlhäusser (1992) and Kreipl (1997) resulted in the recognition of most Recent taxa as distinct species, but also in the synonymy of several species recognised by Abbott (1968) and several later authors, such as Mühlhäusser (1992).

Recent species recognised here in *Echinophoria*, with some of their main synonyms, are:
Echinophoria bituberculosa (Martens, 1901), western Indian Ocean.
E. carnosa Kuroda & Habe, 1961, southern Japan.
E. coronadoi (Crosse, 1867), western Atlantic.
E. hadra (Woodring & Olsson, 1957), off Suriname and French Guiana.
E. pilsbryi (Woodring & Olsson, 1957), eastern Pacific.
E. wyvillei (Watson, 1886) (= *kurodai* Abbott, 1968, = *oschei* Mühlhäusser, 1992), Indian and western Pacific Oceans.

Echinophoria bituberculosa (Martens, 1901)

Figs 30A-H

Cassis bituberculosa Martens, 1901: 23.

Other references:
Cassis bituberculosa - Martens 1904: 111, pl. 3, fig. 11.
Phalium (*Echinophoria*) *bituberculosum* - Abbott 1968: 103, pl. 85.
Echinophoria bituberculosa - Pain & Cox 1990: 6, illus. – Mühlhäusser 1992: fig. 3 – Kreipl 1997: 39, pl. 13, figs 37-37a.
Phalium bituberculosum - Bozzetti 1997: 64, illus. p. 65.

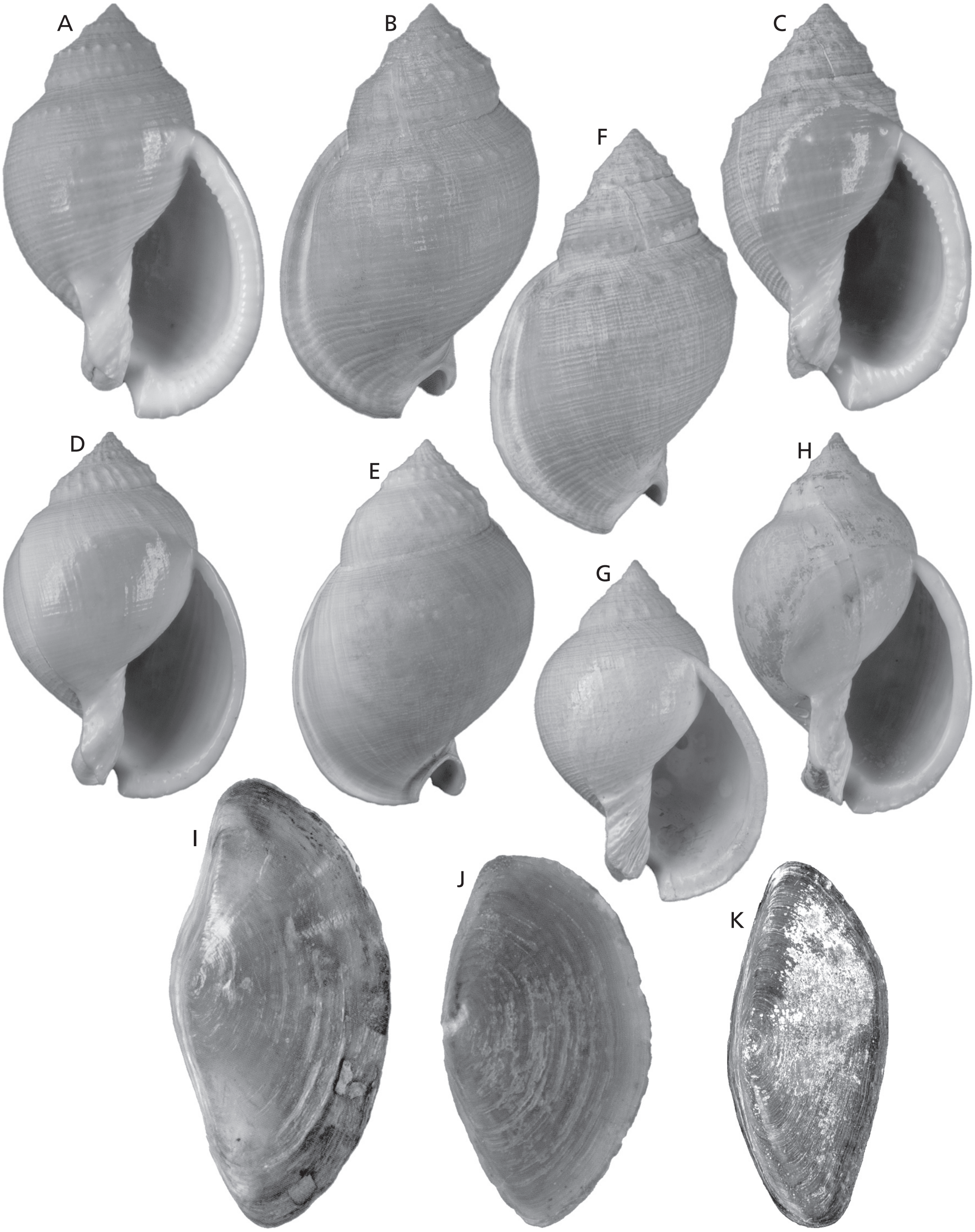
TYPE MATERIAL. – *Cassis bituberculosa*: holotype in Humboldt Museum, University of Berlin, ZMB 60052 (Abbott 1968: 103), from *Valdivia* stn 264, 1079 m, *c.* 160 km NNE of Obbia, Somalia, East Africa, 6°18'N, 49°32'E (not seen).

OTHER MATERIAL EXAMINED. – **Gulf of Aden**. Apparently dredged off Aden, purchased from shell-dealer in Aden by H. Dekker, 1996 (1 dd, ZMA; Figs 30C, F).
Seychelles Islands. Purchased in Victoria, Mahé (1 dd, Institute of Zoology, University of Bologna).
Somalia. Off Cape Hafun, Somalia (2 dd, MNHN; 2 dd, WM 15233, NZGS); Somalia (1 dd, collection of G. Kronenberg, no. 1965); 200 m, off Obbia (1 dd, collection of G. Kronenberg, no.1974); 200-300 m, off Cape Hafun (3 dd, collection of G. Kronenberg, no. 5123); off Mogadishu, Somalia, trawled 150-200 m (1 dd, NMP, K 6940); offshore, from fishermen, Somalia, presented by B. Briano (6 dd, Institute of Zoology, University of Bologna).
Madagascar. P1, chalutage 5, off Madagascar, 12°45'S, 48°10'E, 570-563 m, collected by A. Crosnier (2 dd; Figs 30D, E, H); off SW Madagascar (1 dd; Figs 30A, B).
Réunion. MD32: stn CP 181, off Réunion, 300-410 m, 20°58'S, 55°14'E (1 dd). – Off Réunion, lobster pot, 350-500 m, collected by P. Guézé (1 dd; Fig. 30G). – Off Réunion, prawn traps, 600 m, collected by Kopp (2 dd). – Off St Gilles, 700 m, collected by J. C. Martin (1 dd).

DISTRIBUTION. – *Echinophoria bituberculosa* occurs throughout the western Indian Ocean, possibly as far north as the Gulf of Aden, south to southern Mozambique, and at Madagascar and Réunion, in *c.* 200-600 m (the depth of the holotype of *E. bituberculosa* probably refers to an empty shell carried down slope). It is much less common than *Galeodea keyteri* in MNHN material from off Madagascar.

DIMENSIONS. – Holotype of *Echinophoria bituberculosa*: H 45, D 30.1 mm; MNHN, off Somalia: H 85.5, D 51.2 mm; H 52.0, D 33.6 mm; MNHN, Réunion, coll. Guézé: H 70.8, D 47.8 mm; MNHN, P1 chalutage 5, Madagascar: H 74.0, D 47.2 mm; H 70.7, D 46.7 mm.

REMARKS. – *Echinophoria bituberculosa* is very distinctive in being taller and narrower than the other Recent species of *Echinophoria*, and is intermediate in size between the larger species, *E. coronadoi* and *E. wyvillei*, and the smaller species *E. carnosa*. All specimens have a narrow but thick, clearly raised callus collar extending from the inner lip over the most constricted part of the neck, hiding the narrow false umbilicus. The degree of development of the collar and of its transverse ridges varies greatly, and some specimens with only weakly sculptured exteriors have coarse, prominent transverse ridges on the inner lip, extending across the collar (e.g., one of the 2 specimens in P1, chalutage 5, off Madagascar, 570-563 m), whereas others with or without obvious spiral sculpture have an almost completely smooth collar. The width of the shell and the strength of the spiral sculpture vary greatly in the available material, so although all specimens have many low, obvious, closely spaced spiral cords on the first one or two teleoconch whorls, the cords may remain unchanged throughout growth, may strengthen down the shell to produce the prominent cords of the typical *E. bituberculosa* form, or may fade out altogether by the end of the last whorl. Animals were not available for examination.


A
B
C
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J
K

Echinophoria carnosa Kuroda & Habe *in* Habe, 1961

Figs 30J; 31A-D

Echinophoria carnosa Kuroda & Habe *in* Habe, 1961: 44, pl. 21, fig. 11, appendix p. 16.
Echinophoria carnosa Kuroda *in* Azuma 1960: 30, pl. 3, fig. 9 (*nomen nudum*).

Other references:
Echinophoria carnosa - Oyama & Takemura 1961: *Echinophoria* pl., figs 2-3, 6-8. – Habe 1964: 70, pl. 21, fig. 11; 1968: 61. – Matsumoto 1979: 37. – Pain & Cox 1988: 21, illus. – Kreipl 1997: 39, pl. 13, fig. 38. – Okutani 2000: 277, pl. 137, fig. 22.
Phalium (*Echinophoria*) *carnosa* [*sic*] - Shikama & Horikoshi 1964: 113, fig. 192.
Phalium (*Echinophoria*) *carnosum* - Abbott 1968: 104, pl. 86.
Not *E. carnosa* - Springsteen & Leobrera 1986: 102, pl. 27, fig. 11 (= *E. wyvillei*). – Parth 2000: 93, fig. 19 (= *E. wyvillei*).

TYPE MATERIAL. – Holotype NSMT Mo. 71554, from *c*. 400 m, Tosa Bay, Kochi Prefecture, Shikoku, Japan (live-collected, with operculum; Figs 31A, B).

OTHER MATERIAL EXAMINED. – **Japan**. Unlocalised, Staadt collection (1 lv, MNHN; Figs 31C, D). – Abeno, Japan (1 lv, RMNH).

DISTRIBUTION. – *Echinophoria carnosa* has been recorded from Tosa Bay, Shikoku, southern Japan (Habe 1964; Abbott 1968), from the Philippine Islands (Springsteen & Leobrera 1986: 102) and from the northwest shelf of Western Australia (Wilson 1993; Kreipl 1997). However, the published figure of a Philippines specimen (Springsteen & Leobrera 1986) actually shows a slightly immature, coarsely nodulose specimen of *E. wyvillei*. The *Soela* prawn trawling survey carried out on the northwestern shelf of Western Australia by S. Slack-Smith (WAM) did not collect *E. carnosa*, despite collecting more than 70 specimens of *E. wyvillei*. The Western Australian specimens identified as *E. carnosa* by Wilson (1993: pl. 38, fig. 11A) and Kreipl (1997) appear to be further slightly immature, coarsely nodulose specimens of *E. wyvillei*. The Philippines and northwestern Australian specimens illustrated as *E. carnosa* by Parth (2000: fig. 19) also both are *E. wyvillei*. Little of the material from outside Japan identified as *E. carnosa* actually is that species, and *E. carnosa* possibly is restricted to southeastern Japan. Habe (1968: 61) gave the range as Tosa Bay, Shikoku to Enshu-nada, Honshu. However, Dr Tilo Eggeling (Braunschweig, Germany) has shown me an authentic specimen from the Philippine Islands.

DIMENSIONS. – Habe (1964) stated the dimensions of the holotype as H 53.2, D 34.7 mm, whereas the actual dimensions are H 81.4, D 53.2 mm; other Tosa Bay specimens recorded by Abbott (1968): H 64.5, D 44.1 mm; H 62.8, D 42.5 mm.

REMARKS. – *Echinophoria carnosa* seems to be surprisingly unvaried. It is similar to the "*kurodai* form" of *E. wyvillei* in many characters. The two are similar in size and shape, in having a white to (more commonly) pale flesh-pink exterior with a white aperture, in having numerous rows of very even-sized, regularly placed nodules

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FIG. 30. *Echinophoria bituberculosa* (Martens, 1901), western Indian Ocean; all X 0.67. **A**, **B**, A. Crosnier chalutage off SW Madagascar (H 85.6 mm); **C**, **F**, apparently dredged in Gulf of Aden, purchased in market, Aden (ZMA; H 84.2 mm); **D**, **E**, **H**, 2 specimens from A. Crosnier chalutage 5, off SW Madagascar, 570-563 m (D, E, H 75.6 mm; H, H 78.5 m); **G**, specimen with coarsely ridged columella, Réunion, 350-500 m (H 70.8 mm). **I**-**K**, opercula of *Echinophoria* species. **I**, *Echinophoria wyvillei* (Watson, 1886), "typical form", off SW Taiwan (NMP G8672; operculum H 35 mm; X 2). **J**, *Echinophoria carnosa* Kuroda & Habe, 1961, holotype, Tosa Bay, Japan (NSMT Mo. 71554; H 29 mm; X 2). **K**, *Echinophoria wyvillei* (Watson, 1886), "*kurodai* form", MUSORSTOM 4 stn CP 170, New Caledonia, 480 m (H 19 mm; X 3).

covering most of the last whorl and in having no free callus collar extending from the inner lip, the lip adhering directly to the previous whorl. The "*kurodai* form" of *E. wyvillei* differs from *E. carnosa* in having a slightly shorter spire, in having a slight shoulder angulation that is not seen on the evenly convex whorls of *E. carnosa*, in having the nodule row at the periphery (on the shoulder angle) more prominent and bearing larger nodules than in lower rows, whereas all nodule rows are similar in *E. carnosa*, in having a markedly wider spiral interspace between the uppermost two rows of nodules than lower on the shell, rather than having all the rows evenly spaced as in *E. carnosa,* and in having the suture positioned at the crest of the second row of nodules from the posterior, or in some specimens even higher on the penultimate whorl, so that little of the second nodule row is visible on spire whorls, whereas in *E. carnosa* the even spacing of the nodule rows allows the suture consistently to fall in the interspace below the second row of nodules from the posterior, and the two posterior rows of nodules both are revealed completely on spire whorls. In fresh specimens, collected live, the shell surface is glossy in the "*kurodai* form" of *E. wyvillei*, whereas it is dull (apart from the glossy inner lip) in *E. carnosa*. This difference seems to result from the many very fine, low, rather widely placed spiral threads that cover the surface of *E. carnosa*, but are absent, at least on the last whorl, on most specimens of *E. wyvillei*. Also, the terminal varix is consistently narrower in *E. wyvillei* than in *E. carnosa*, and lacks nodules on its inner edge, although many specimens have low nodules on the anterior half of the exterior of the varix, a unique character; whereas the varix is thicker, and in some specimens much thicker, in *E. carnosa*, and in some specimens bears low nodules or low but obvious transverse ridges on the lower half of the interior edge. Illustrations and the two specimens seen indicate that *E. carnosa* has a uniformly coloured, pale pinkish cream exterior, whereas in most specimens of the "*kurodai* form" of *E. wyvillei* the spiral bands are paler around the nodule rows than elsewhere, and there are pale brown spots on the abapertural (dorsal) face of the terminal varix between the paler bands, corresponding in position to the nodules along the varix edge. Also, their partial sympatry is good evidence of specific distinction. Parth (2000: 93, fig. 19) suggested that *E. kurodai* is a synonym of *E. carnosa*, but both specimens illustrated by him are typical specimens of the "*kurodai* form" of *E. wyvillei*, indicating that he probably has not examined the real *E. carnosa*, which evidently is a rare species occurring only in southern Japan and, very rarely, the Philippines. Animals have not been available for examination. The operculum of the holotype (Fig. 30J) is a little shorter and wider than those of *E. wyvillei* examined here.

It is possible that the two specimens identified here as *Echinophoria carnosa* (Figs 31A-D) are not conspecific. The larger specimen (Figs 31A, B), the holotype of *E. carnosa*, closely resembles *E. wyvillei* in most characters, particularly the relatively large size (height 81.4 mm), the elongate shape, the narrow columellar callus, the relatively weakly thickened outer lip with little sign of nodules on its inner face, and the relatively long outer lip ascending well up the previous whorl, forming a very narrow, V-shaped channel at the top (adapical end) of the aperture. The smaller specimen (Figs 31C, D) (and all other authentic Japanese specimens assigned to *E. carnosa*) is shorter, with heavier, more evenly developed nodules, a slightly more flared, more strongly convex outer lip, a thicker, shorter varix with much more obvious nodules down its entire inner face, and a shorter and more rounded channel at the top (adapical end) of the aperture. It is possible that the holotype is an unusual specimen of *E. wyvillei* with more rows of nodules than usual (although by no means outside the range of variation of other specimens of *E. wyvillei*) and with two rows of nodules exposed on the spire, but comparison of many more specimens is required before the identity of the holotype is certain, and I have seen very few specimens assigned to this species. If the holotype does prove to be a specimen of *E. wyvillei*, the smaller specimen would represent an unnamed species. The typical *E. carnosa*, as represented by the smaller specimen (Figs 31C, D), is the only one of the Recent specimens examined in this work that appears to be congeneric with the widespread, coarsely nodulose Cenozoic fossil species assigned to *Echinophoria*, in the sense of being phylogenetically related to *E. intermedia* (Brocchi), apart from the recently recognised Recent occurence of *E. hadra.*

Echinophoria coronadoi (Crosse, 1867)

Figs 31E, F

Cassis coronadoi Crosse, 1867: 64, pl. 4, fig. 1; pl. 5, fig. 1.

Other references:
Cassis (*Bezoardica*) *coronadoi* - Watson 1886: 409.
Galeodea coronadoi - Dall 1889a: 231; 1889b: 134. – Johnson 1934: 113. – Clench 1944: 4, pl. 2.
Bathygalea (*Bathygalea*) *coronadoi* - Woodring & Olsson 1957: 24, pl. 9, figs 2-3. – Bayer 1971: 135, figs 13a-d, 17c (operculum inverted).
Phalium (*Echinophoria*) *coronadoi coronadoi* - Abbott 1968: 99; 1974: 161, fig. 1740.
Phalium coronadoi - Porter 1974: 197. – Bozzetti 1997: 66, illus. p. 67.
Echinophoria coronadoi - Pain & Cox 1988: 19 (in part; no figured specimens show *E. coronadoi*). – Kreipl 1997: 40, pl. 14, fig. 39.

TYPE MATERIAL. – *Cassis coronadoi*: holotype MNHN 4147; from off Matanzas, Cuba (Figs 31E, F). Crosse (1867) stated only that the holotype was “collected at Matanzas, Cuba” by “M. le docteur Coronado”. Most subsequent records are from depths of more than 100 m, and the holotype has bryozoans in the siphonal canal, so rather than being a shallow-water (e.g., beach) specimen, it was evidently collected offshore in a fish or lobster trap.

OTHER MATERIAL EXAMINED. – **Trinidad**. Off the north coast of Trinidad, from fish traps at 100-150 m (1 dd, collection of G. Kronenberg).

Colombia. *Choco* stn 620, off La Guajira Peninsula, Caribbean coast of Colombia, 275-320 m (4 small dd, R. von Cosel’s collection in Senckenberg Museum, Frankfurt).

DISTRIBUTION. – *Echinophoria coronadoi* is recorded from the western Atlantic only. The northernmost record I am aware of is from Wimble Shoals, *c*. 40 km N of Cape Hatteras, North Carolina (Porter 1974: 197), and several specimens have been reported over the years from off Cape Fear, southern North Carolina (Dall 1889a: 231; Woodring & Olsson 1957; Porter 1974). The few other definite records are from Barbados (Bozzetti 1997; Kreipl 1997) and northeast of Caracas, Venezuela (Bayer 1971). Records are added here from Trinidad and Colombia. These records indicate a range from North Carolina to Cuba, the Lesser Antilles and throughout the Gulf of Mexico, although a wider range would not be surprising.

DIMENSIONS. – Crosse (1867) stated the dimensions of the holotype of *Cassis coronadoi* as H 99, D 85 mm, but the correct dimensions are H 110.3, D 82.0 mm. Abbott (1968: 99) recorded the specimen from off Cape Fear, North Carolina, illustrated by Woodring & Olsson (1957: pl. 9, figs 2-3), with H 117.0, D 82.0 mm; off Trinidad, Kronenberg collection: H 116.4, D 87.8 mm. Kreipl (1997: pl. 14, fig. 39) recorded a specimen from southeast of Barbados with H 120.8 mm.

REMARKS. – As the holotype of *Echinophoria coronadoi* has not been illustrated since Crosse (1867) apart from the copy of Crosse’s figure repeated by Abbott (1974), and the species was not illustrated at all by Abbott (1968), I take this opportunity to illustrate the holotype again. Crosse’s original illustration is an excellent one, and it is clear that the specimen from off Barbados, illustrated by Kreipl (1997: pl. 14, fig. 39), is a typical adult example of *E. coronadoi*, although the nodules are a little larger and the spire is slightly taller than in the holotype. A specimen more nearly resembling the holotype was illustrated by Bozzetti (1997: 67). Diagnostic characters of the species are its large size – it is the largest and widest of the Recent *Echinophoria* species, the retention of relatively prominent spiral cords down onto the last whorl, the presence of a row of moderately large, sharp nodules at the periphery over the entire

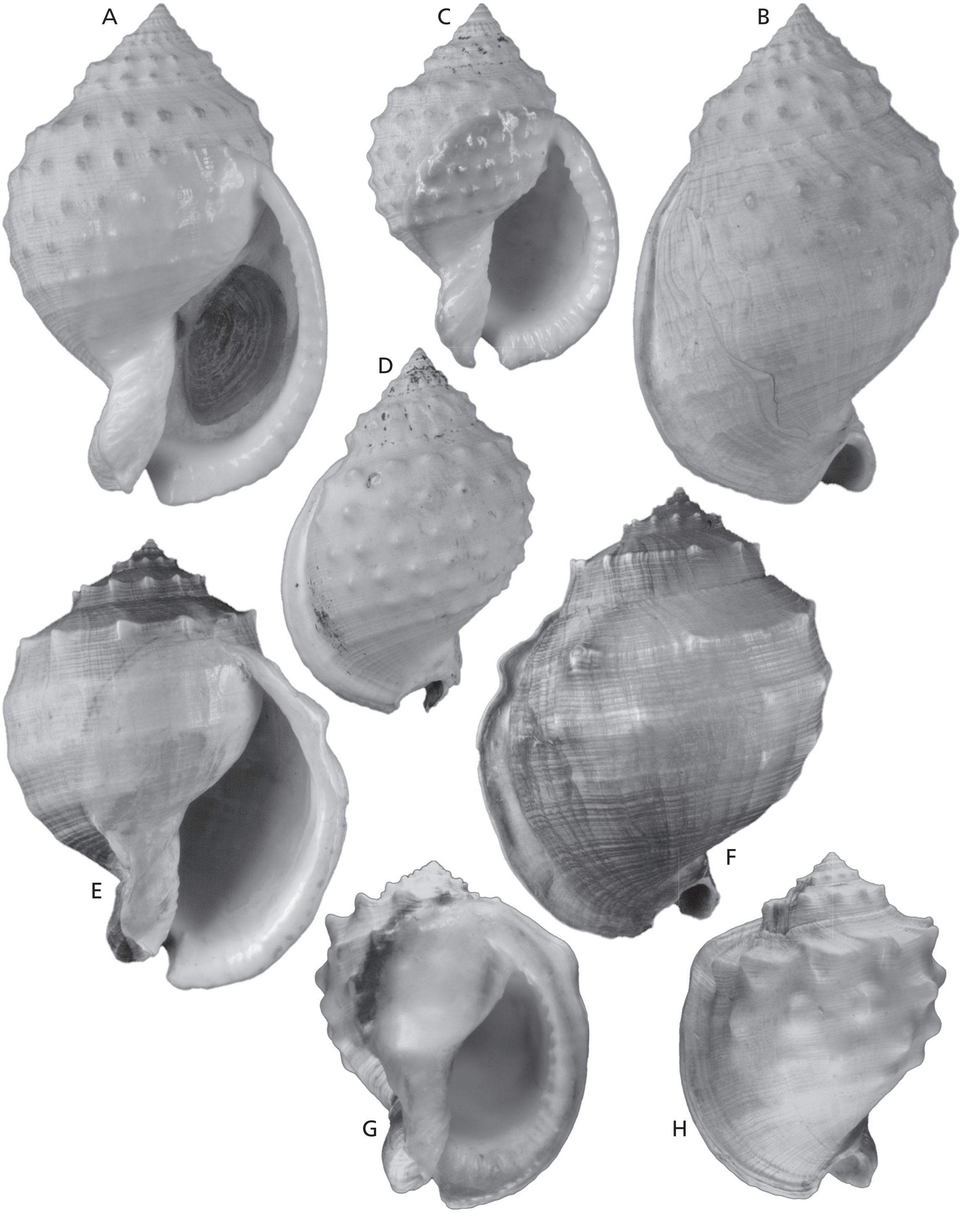

FIG. 31. *Echinophoria carnosa* Kuroda & Habe, 1961, Japan. **A**, **B**, holotype, Tosa Bay, Japan, c. 400 m (NSMT Mo.71554; H 81.4 mm); **C**, **D**, Japan, ex Staadt Collection (H 59.3 mm). **E**, **F**, *Echinophoria coronadoi* (Crosse, 1867), holotype, off Matanzas, Cuba (MNHN 4147; H 110.3 mm). **G**, **H**, *Echinophoria hadra* (Woodring & Olsson, 1957), off the coast of Suriname and French Guiana, fish traps in 70-80 m, in collection of Dominique Lamy (H 60 mm).

teleoconch, the presence of three further (and a weak fourth) wide, slightly elevated spiral bands below the peripheral nodules on the last whorl, bearing low, widely spaced nodules on most specimens, at least on the early part of the last whorl, and the presence of a relatively wide, almost smooth free callus collar over the neck, with a moderately deep indentation in its left edge at the position of the false umbilicus. The exterior is pale yellowish brown (tan), much stained with dark reddish tan on the holotype (as shown accurately by Crosse), with the nodules and spiral cords slightly paler than the rest, and the aperture white. The fine spiral cords and the rows of nodules below the periphery are both considerably more strongly developed than in the other large, thin-shelled Recent species, *E. pilsbryi* and *E. wyvillei*, although *E. pilsbryi* resembles *E. coronadoi* in the development of the inner lip collar. Animals were not available for examination.

Echinophoria hadra (Woodring & Olsson, 1957)

Figs 31G, H

Cassis (*Phalium*) *dalli* Anderson, 1929: 141, pl. 14, figs 10-13 (junior secondary homonym of *Galeodea dalli* Dickerson, 1917, referred to *Phalium* (*Echinophoria*) by Abbott 1968: 107).

Bathygalea (*Miogalea*) *hadra* Woodring & Olsson, 1957: 23, pl. 8, figs 1, 2.

Phalium (*Echinophoria*) *andersoni* Abbott, 1968: 107, pl. 89, figs 1, 2 (replacement name for *Cassis* (*Phalium*) *dalli* Anderson, 1929, junior secondary homonym of *Galeodea dalli* Dickerson, 1917).

Other references:
Bathygalea (*Miogalea*) *dalli* - Woodring & Olsson 1957: 23, pl. 7, figs 1-4; pl. 8, figs 3, 4.
Bathygalea (*Miogalea*) *hadra* - Woodring 1959: 198, pl. 37, figs 10, 13.
Phalium (*Echinophoria*) *hadrum* - Abbott 1968: 107, pl. 89, figs 3, 4.

TYPE MATERIAL. — *Cassis* (*Phalium*) *dalli* Anderson: holotype California Academy of Sciences Geology 4649, one paratype 4650, from Las Perdices Formation (Early Miocene), coast 1.6 km W of pier at Puerto Colombia, Dept Atlantico, Colombia (Woodring & Olsson 1957: 23). *Bathygalea* (*Miogalea*) *hadra* Woodring & Olsson, 1957: holotype USNM 562268, with one small damaged specimen, from Chagres Sandstone (Pliocene), Caribbean coast at mouth of Rio Indio, Colon, Panama.

OTHER MATERIAL EXAMINED. — Numerous fossils in Naturhistorisches Museum Basel from Miocene and Pliocene rocks of Atlantic Panama; Arroyo Zalaya, Río Gurabo, deep-water facies of Gurabo Formation (early Pliocene), northern Dominican Republic, in collection of Bernard Landau (1); Cantaure Shellbed, Early Miocene, Paraguaná Peninsula, Falcón, Venezuela, in collection of Bernard Landau (1 small, incomplete); Naturhistorisches Museum Basel locality 17531, Punta Gavilán Formation (Early Pliocene), Punta Gavilán, Falcón, Venezuela, J. & W. Gibson-Smith collection, Naturhistorisches Museum Basel (4); Recent, fish traps in 70-80 m, off the coast of Suriname and French Guiana, in collection of Dominique Lamy (Guadeloupe) (4).

DISTRIBUTION. — Miocene and Pliocene fossils occur throughout central America; living specimens recorded only off Suriname and French Guiana.

REMARKS. — Abbott (1968: 107) introduced the replacement name *Phalium* (*Echinophoria*) *andersoni* for *Cassis dalli* Anderson, 1929, which became a secondary homonym when Abbott (1968) also referred *Galeodea dalli* Dickerson, 1917 to *Phalium* (*Echinophoria*). *Echinophoria dalli* (Dickerson) remains an accepted species of *Echinophoria*, so a substitute name remains necessary. However, in my opinion, *Echinophoria hadra* (Woodring & Olsson, 1957) is conspecific with

E. dalli Anderson, so this name takes precedence over Abbott's replacement name. *Echinophoria hadra* has been reported previously only as a Miocene-Pliocene fossil from the Atlantic coastal area of Central America, from Panama, Colombia, Venezuela and the Dominican Republic (Abbott 1968; Beu in prep., "revision of Central American Neogene tonnoideans"). Dominique Lamy (Guadeloupe) has recently shown me specimens of *E. hadra* taken in fish traps off Suriname and French Guiana, so this species is added to the Recent Caribbean fauna. *Echinophora hadra* differs from *E. coronadoi* in its smaller size (most specimens are 50-60 mm high, compared with 100-120 mm for *E. coronadoi*), its much heavier, more solid appearance, its much more heavily thickened aperture, with a much thicker inner lip callus and a much wider, more coarsely nodulose outer lip, and its 2-4 (5 in a few specimens) more closely spaced rows of relatively large nodules around the last whorl.

Echinophoria pilsbryi (Woodring & Olsson, 1957)

Bathygalea (*Bathygalea*) *pilsbryi* Woodring & Olsson, 1957: 24, pl. 10, figs 1-2.

Other references:
Phalium (*Echinophoria*) *pilsbryi* - Abbott 1968: 101, pl. 83.
Echinophoria coronadoi - Pain & Cox 1988: 19 (in part *non B. pilsbryi* Woodring & Olsson).
Phalium pilsbryi - Skoglund 1990: 120; 1992: 47. – Finet 1994: 38. – Garcia & Marr 1998: 28, 3 figs.
Echinophoria pilsbryi - Kreipl 1997: 41, pl. 14, figs 42-42a.

TYPE MATERIAL. – *Bathygalea pilsbryi*: holotype ANSP 153618, from Seymour Bay, Indefatigable Island (Isla Santa Cruz), Galapagos Islands, picked up from the beach.

OTHER MATERIAL EXAMINED. – **Galapagos Islands** (1 dd, collection of G. Kronenberg, no. 2199).

DISTRIBUTION. – *Echinophora pilsbryi* has been reported only from the Galapagos Islands, from Playas de Villamil, Guayas Province, Ecuador (Skoglund 1990, 1992), and dredged off the southwest point of Isla Cebaco, Veraguas Province, southwest Pacific Panama, in "about 200 m" (Garcia & Marr 1998). These records suggest that it occurs rarely throughout the tropical eastern Pacific coast of the Americas. Two small specimens were illustrated by Kreipl (1997: pl. 14, figs 42-42a), from Barrington and Santa Cruz Islands, Galapagos Islands, confirming the record there, originally based only on the holotype.

DIMENSIONS. – Holotype of *Bathygalea pilsbryi*: H 66.3, D 47.0 mm (Woodring & Olsson 1957); Galapagos Islands, Kronenberg coll.: H 95.2, D 63.0 mm; specimens illustrated by Kreipl (1997): H 58 and H 41.5 mm; specimens from Panama illustrated by Garcia & Marr (1998): H 70.5, D 46.5 mm; H 76.7, D 57.0 mm; H 92.3, D 67.3 mm.

REMARKS. – The few known specimens suggest that *Echinophoria pilsbryi* is a smaller species than *E. coronadoi*, reaching a height of 95 mm rather than 120 mm. *E. pilsbryi* also has a slightly narrower inner lip callus collar than *E. coronadoi*, and on most specimens the collar lacks the indentation in the left edge at the position of the false umbilicus that is present in *E. coronadoi*. Most of the few known specimens also differ from *E. coronadoi* in having nodules only at the periphery, or at least very weak below the periphery, and some have small, sharp nodules down the entire inner margin of the outer lip that are absent from all other Recent species of *Echinophoria*. However, the 3 specimens from 200 m, off Isla Cebaco, Veraguas Province, Panama, illustrated in colour by Garcia & Marr (1998) have 2 or 3 rows of nodules below the peripheral one, and 1 specimen has a deeply indented columellar collar resembling that of *E. coronadoi*. Garcia & Marr (1998) pointed out, though, that all specimens differ from *E. coronadoi* in having a "heavier columella” (i.e., a thicker columellar callus and collar) bearing more numerous and more prominent columellar folds than *E. coronadoi*. *Echinophoria wyvillei* reaches a larger size (*c.* 120 mm, as in *E. coronadoi*) and has a much narrower inner lip collar than *E. pilsbryi*, and the teleoconch is taller and narrower than in either *E. coronadoi* or *E. pilsbryi*. *Echinophoria pilsbryi* therefore appears to be a distinct species limited to the Galapagos Islands and the eastern Pacific coast from Panama south to Ecuador, but a larger number of adult specimens is needed before the range of variation in its characters can be fully understood. Animals were not available for examination.

Echinophoria wyvillei (Watson, 1886)

Figs 6; 10; 30I, K; 32; 33

Cassis (*Bezoardica*) *wyvillei* Watson, 1886: 408, pl. 14, fig. 13.

Synonyms:
Phalium (*Echinophoria*) *kurodai* Abbott, 1968: 105, pl. 87 (**new synonym**).
Echinophoria oschei Mühlhäusser, 1992: 211, figs 1-2 (**new synonym**).
Echinophoria wyvillei dolium Kuroda *in* Azuma, 1960: 30, pl. 1, fig. 7 (*nomen nudum*).
Echinophoria galeodiformis Kuroda *in* Azuma, 1960: 30, pl. 3, fig. 10 (*nomen nudum*).

Other references:
Cassis (*Bezoardica*) *wyvillei* - Brazier 1894: 43.
Galeodea wyvillei - Clench 1944: 4.
Semicassis wyvillei - Kuroda & Habe 1952: 85.
Bathygalea (*Bathygalea*) *wyvillei* - Woodring & Olsson 1957: 24, pl. 9, figs 1, 4; pl. 10, figs 3-4.
Echinophoria wyvillei - Habe 1961: 44, pl. 21, fig. 10; 1964: 70, pl. 21, fig. 10; 1968: 61. – Garrard 1969: 9. – Matsumoto 1979: 37. – Kay 1979: 214. – Okutani 1986: 118, second fig. bottom row. – Okutani *et al.* 1988: 71, illus. – Wilson 1993: 232, pl. 38, figs 10, 11 B only. – Kreipl 1997: 42, pl. 14, figs 43-43a. – Okutani 2000: 277, pl. 137, fig. 20.
Echinophoria sp. - Oyama & Takemura 1961: *Echinophoria* pl., fig. 1.
Phalium (*Echinophoria*) *wyvillei* - Shikama & Horikoshi 1963: pl. 42, fig. 7.
Phalium (*Echinophoria*) *coronadoi wyvillei* - Abbott 1968: 100, pls 80-82.
Echinophoria kurodai - Habe 1968: 59, text-fig. 1. – Matsumoto 1979: 37. – Lan 1979: pl. 44, figs 103-104. – Okutani 1986: 118, first fig. bottom row. – Pain & Cox 1988: 21, bottom fig. – Okutani *et al.* 1988: 70, illus. – Lai 1990: fig. 11, lower (copy of Lan’s fig.). – Wilson 1993: 232, pl. 38, figs 12a-b. – Kreipl 1997: 40, pl. 14, figs 40-40a. – Okutani 2000: 277, pl. 137, fig. 21. – Higo *et al.* 2001: 47, fig. G1551.
Echinophoria carnosa - Springsteen & Leobrera 1986: 102, pl. 27, fig. 11. – Parth 2000: 93, fig. 19 (*non Echinophoria carnosa* Kuroda & Habe, 1961).
Echinophoria coronadoi - Pain & Cox 1988: 19 (in part, *non Cassis wyvillei* Watson, 1886).
Echinophoria oschei - Kreipl 1997: 41, pl. 14, figs 41-41a. – Parth 2000: 93, fig. 20.
Echinophoria coranadoi wyvillei - Higo *et al.* 2001: 47, fig. G1552.

TYPE MATERIAL. – *Cassis wyvillei*: holotype BMNH 1887.2.9.1259 (Figs 33F, G; Abbott 1968: pl. 80), from *Challenger* stn 204A, off Tablas I., Philippines, in 183-210 m, 12°43’-46’N, 122°9’-10’E. – *Echinophoria kurodai*: holotype NSMT Mo. 37139, from *c.* 240 m, Tosa Bay, off Cape Ashizuri, Kochi Prefecture, Shikoku, Japan (Figs 32A, B); 4 paratypes ANSP 231694, from the same locality, in *c.* 200 m. – *Echinophoria oschei*: holotype ZSM 1869, from “deep water” off Mozambique, East Africa; with one paratype from off southern Mozambique, trawled in 200 m (not seen).

OTHER MATERIAL EXAMINED. – **Madagascar**. Off Tuléar, “deep sea”, purchased in shell market, presented by J. C. Martin (1 dd, NZGS WM 17045, see below).

Japan. Enshu Nada Sea, Pacific coast of central Honshu (2 lv, NSMT Mo.37237; Figs 33A, C, E).

Taiwan. Off SW Taiwan (2 dd); Taiwan (1 lv, in collection of

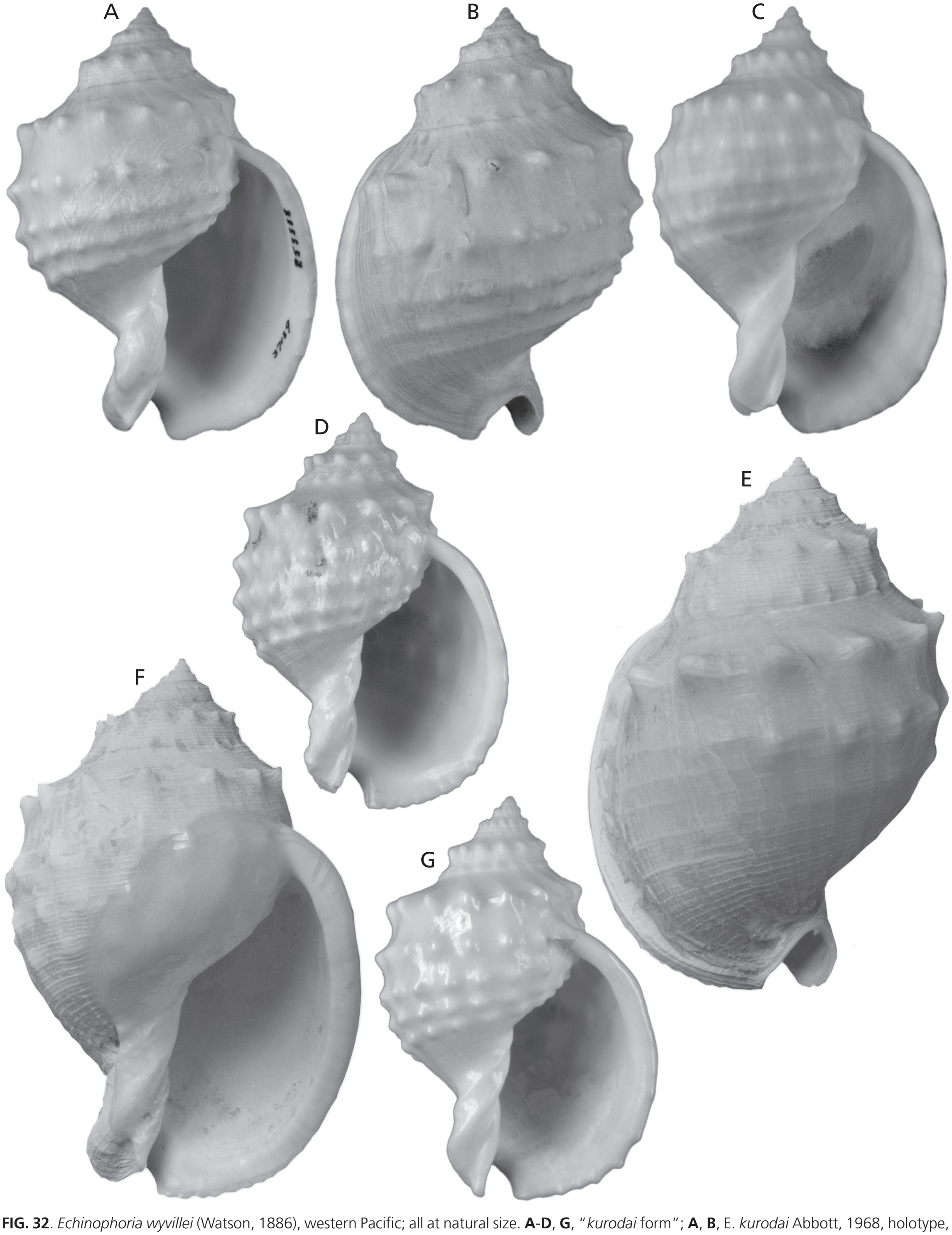

FIG. 32. *Echinophoria wyvillei* (Watson, 1886), western Pacific; all at natural size. **A**-**D**, **G**, "*kurodai* form"; **A**, **B**, E. *kurodai* Abbott, 1968, holotype, off Cape Ashizuri, Tosa, Japan, c. 240 m (NSMT Mo.37139; H 68.3 mm); **C**, between Mermaid and Scott Reefs, N of Broome, N Western Australia (H 67.4 mm); **D**, MUSORSTOM 8 stn CP 974, Vanuatu, 492-520 m (H 62.5 mm); **G**, anatomy, operculum and radula examined; MUSORSTOM 4 stn CP 170, New Caledonia, 480 m (H 63.7 mm); **E**, **F**, "typical" *wyvillei* form, anatomy and radula examined, *Soela* stn S1/84/76, NW of Augustus Island, northern Western Australia, 348-350 m (WAM 880-84; H 84.6 mm).

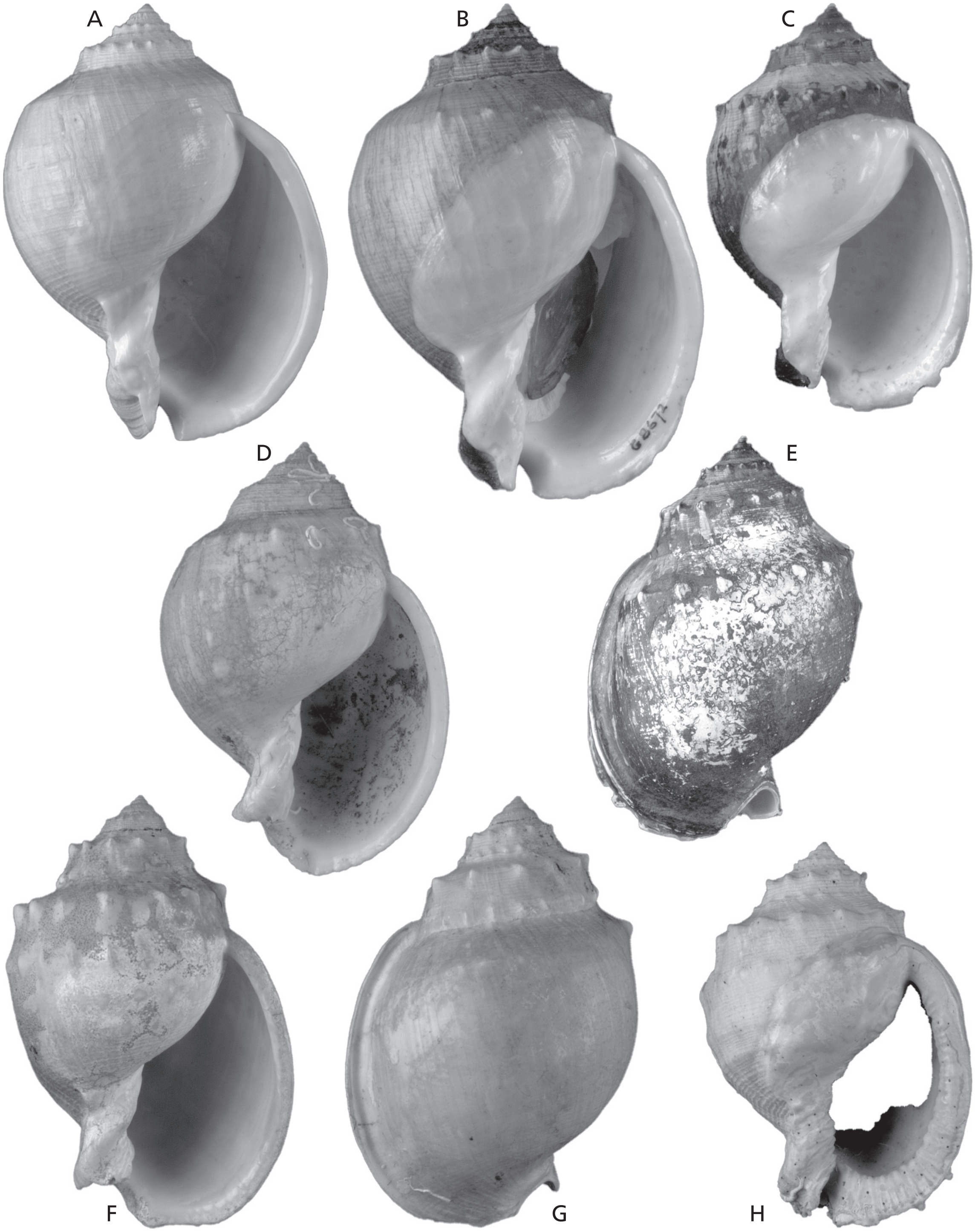

FIG. 33. *Echinophoria wyvillei* (Watson, 1886), western Pacific; all X 0.67. **A**, **C**, **E**, weakly and coarsely nodulose specimens in one lot, Enshu Nada, Pacific coast of central Honshu, Japan (NSMT Mo.37237; **A**, H 101.4 mm; **C**, **E**, H 99.2 mm); **B**, off SW Taiwan, 100-180 m (NMP G8672; H 102.9 mm); **D**, MUSORSTOM 2 stn CP 75, central Philippines, 300-330 m (H 88.6 mm); **F**, **G**, holotype, *Challenger* stn 204A, off Tablas I., Philippines, 183-210 m (BMNH 1887.2.9.1259; H 99.0 mm); **H**, coarsely sculptured, heavily callused specimen, MUSORSTOM 8 stn DW 1065, Vanuatu, 340-419 m (H 88.2 mm).

G. Kronenberg); 70-100 fathoms (130-180 m), off SW Taiwan (NMP G.8672, 1 lv, Fig. 33B); Taiwan Strait, 1971 (2 lv, RMNH). – TAIWAN 2001: stn CP 103, off Tashi, NE coast of Taiwan, 24°49'N, 122°06'E, 367-424 m (1 lv).

Philippines. MUSORSTOM 2: stn CP 75, 13°51'N, 120°30'E, 300-330 m (1 dd; Fig. 33D). – Tangle nets between Bohol and Cebu, 1986 (1 dd); off Panglao, Bohol (1 lv, collection of G. Kronenberg); Pamilacan I., off Bohol, tangle nets, 90-145 m, (2 dd, AMS C165724-5). – PANGLAO 2005: stn DW 2347, Bohol Sea, 9°29'N, 123°54'E, 198-233 m, (1 large fresh dd) ; stn CP 2361, Bohol/Sulu Sea sill, 8°53'S, 123°34'E, 516-543 m, (2 fresh dd); stn CP 2362, as last, 8°57'S, 123°33'E, 679-740 m, (1 dd); stn CP 2392, Bohol Sea off Balicasag I, 9°29'S, 123°41'E, 242-400 m, (1 large broken dd).

Indonesia. KARUBAR: stn CP 35, 6°08'S, 132°45'E, 390-502 m (1 lv); stn CP 36, 6°05'S, 132°44'E, 268-210 m (1 dd).

Coral Sea. CORAIL 2: stn DE 16, Bancs Lansdowne-Fairway, 20°48'S, 16°56'E, 500 m (1 lv).

New Caledonia. MUSORSTOM 4: stn CP 170, 18°57'S, 163°13'E, 480 m (1 lv; Fig. 32G); stn CP 179, 18°57'S, 163°14'E, 475 m (1 lv). – HALICAL 1: stn DW 01, Grand Passage, 18°56'S, 163°24'E, 380-400 m, (2 dd). – BATHUS 4: stn CP 909, 18°58'S, 163°10'E, 516-558 m (1 dd); stn CP 930, 18°51'S, 163°24'E, 520-530 m (1 dd). – NORFOLK 2: stn CP 2146, Ile des Pins, 22°50'S, 167°17'E, 518 m (1 lv *kurodai* form). – EBISCO: stn DW 2544, W of Bellona Plateau, 21°10'S, 158°39'E, 650-723 m (1 dd large); stn CP 2545, W of Bellona Plateau, 21°10'S, 158°36'E, 765-778 m (1 dd *kurodai* form); stn CP 2568, NW of Bellona Plateau, 20°23'S, 158°41'E, 411-414 m (1 dd *kurodai* form); stn DW 2602, Chesterfield Plateau, 19°38'S, 158°44'E, 547 m (1 dd spire, with 1 dd *Galeodea bituminata*); stn CP 2611, Chesterfield Plateau, 19°34'S, 158°41'E, 492-506 m (1 dd *kurodai* form).

Tonga. BORDAU 2: stn CP 1510, 21°05'S, 175°23'W, 461-497 m (2 dd, fragments); stn CP 1527, Eua, 21°16'S, 174°59'W, 483-509 m (1 lv); stn CH 1563, 19°52'S, 174°39'W, 362-388 m (2 dd, 1 small and one intermediate); stn CH 1564, 19°52'S, 174°39'W, 371-387 m (1 dd); stn CP 1590, 19°12'S, 174°13'W, 353-386 m (1 dd, small spire fragment); stn CP 1592, 19°09'S, 174°17'W, 391-426 m (1 lv); stn CH 1596, 19°06'S, 174°18'W, 371-437 m, (1 dd); stn CP 1644, NW of Tongatapu, NW of Tongatapu, 21°05'S, 175°23'W, 501 m (1 lv).

Vanuatu. MUSORSTOM 8: stn CP 974, 19°22'S, 169°28'E, 492-520 m (1 dd; Fig. 32D); stn CAS 981, 19°21'S, 169°24'E, 320 m (2 dd); stn DW 1065, 16°16'S, 167°21'E, 340-419 m (1 dd, ventral half only; Fig. 33H).

Fiji. MUSORSTOM 10: stn CP 1328, Bligh Water, 17°17'S, 177°50'E, 248-277 m (1 dd); stn CC 1336, Bligh Water, 16°58'S, 177°58'E, 797-799 m (1 dd).

Solomon Islands. Makira ("Makeira") Harbour, San Cristobal Island, from native fisherman, March 1872, *ex* J. C. Cox collection (1 specimen recorded by Brazier 1894: 43, AMS C68846). – SALOMON 2: stn CP 2260, off Kolombangara I., 8°04'S, 156°55'E, 399-427 m (1 dd large).

Eastern Australia. Trawled off Townsville, Queensland, 185-325 m (1 dd, AMS C150615); trawled off Townsville, Queensland, 185-325 m (1 lv, AMS C150614); FRV *Kapala* stn K78-17-11, off Coolangatta, Queensland, 412 m, 28°00"S, 153°58.0'E (1 lv, AMS C401159); trawled ESE of Townsville, Great Barrier Reef, Queensland, 300 m, 19°30.0'S, 150°0.0'E (1 lv, AMS C145356); recorded also by Garrard (1969: 9) from off Coff's Harbour, New South Wales (from a lobster pot, in 146 m), and off Southport and Caloundra, southern Queensland.

Northwestern Australia. **(a)** "*wyvillei* **form**". 400 m, MS *Kingfisher*, SW of Imperieuse Reef, off Rowley Shoals (1 lv, coll. of G. Kronenberg); *Soela* stn 01-84-076, NW of Augustus Island, 13°44.5'S, 122°56.5'E to 13°40.8'S, 122°59.3'E, 348-350 m (1 lv, WAM 880-84); *Soela* stn 01-84-055, WNW of Lacépède Archipelago, 15°57.2'S, 120°48.2'E to 15°59.05'S, 120°44.6'E, 296-298 m (1 dd, fragment, WAM).

(b) "*kurodai* **form**"**:** Between Mermaid and Scott Reefs, N of Broome, 470-520 m (1 lv; Fig. 32C); 450 m, off Port Hedland (1 lv, collection of G. Kronenberg, no. 1907); 400 m, off Broome (1 lv, collection of G. Kronenberg, no. 2638); 500 m, off Port Hedland (1 lv, collection of G. Kronenberg, no. 5245); trawled 100-145 km NW of Port Hedland, 370-480 m (2 lv, AMS C156259); F/V *Soela* stn 04-82-08A, off Port Hedland, 18°55'S, 116°41'E, 380 m, (1 lv, WAM 3245-83); F/V*Soela* stn 04-82-08D, off Port Hedland, 17°58'S, 118°25'E, 376 m (1 dd, WAM); F/V *Soela* cruise, February 1984, coll. S. Slack-Smith: stn 01-84-049, ENE of Mermaid Reef, Rowley Shoals, 16°58.7'S, 119°55.6'E to 16°56.6'S, 119°58.9'E, 430-432 m (2 lv, WAM 894-84); stn 01-84-050, W of Lacépède Archipelago, 16°41.8'S, 120°07.3'E to 16°40.5'S, 120°09.7'E, 434-430 m (1 lv, WAM 882-84); stn 01-84-053, WNW of Lacépède Archipelago, 15°48.0'S, 120°41.0'E to 15°50.1'S, 120°39.5'E, 400-396 m (1 lv, WAM 886-84); stn 01-84-054, WNW of Lacépède Archipelago, 15°51.25'S, 12°44.3'E to 15°54.38'S, 120°45.3'E, 350-348 m (8 dd, WAM); stn 01-84-055, WNW of Lacépède Archipelago, 15°57.2'S, 120°48.2'E to 15°59.05'S, 120°44.6'E, 296-298 m (8 dd, WAM); stn 01-84-056, NW of Beagle Bay, 15°20.0'S, 121°09.6'E to 15°18.0'S, 121°11.2'E, 300-302 m (1 dd, WAM); stn 01-84-058, NW of Beagle Bay, 15°12.8'S, 121°05.9'E to 15°10.11'S, 121°09.2'E, 410-404 m (1 dd, WAM 814-84); stn 01-84-059, NW of Beagle Bay, 15°09'S, 121°05'E to 15°11'S, 121°03'E, 450-448 m (2 dd, WAM 803-84); stn 01-84-064, NW of Cape Leveque, 14°50.2'S, 121°31.4'E to 14°48.6'S, 121°33.2'E, 356 m (2 dd, WAM); stn 01-84-065, NW of Cape Leveque, 14°49.0'S, 121°36.1'E to 14°50.8'S, 121°35.6'E, 302-300m (1 dd, WAM 1633-84); stn 01-84-067, NW of Bathurst Island, 14°21.5'S, 122°02.4'E to 14°22.3'S, 122°01.0'E, 348-350 m (2 dd, WAM); stn 01-84-073, NW of Collier Bay, 14°10.9'S, 122°35.1'E to 14°12.1'S, 122°32.1'E, 350-348 m (1 lv, WAM 883-84); stn 01-84-074, NW of Collier Bay, 14°16.5'S, 122°34.4'E to 14°13.6'S, 122°38.3'E, 302 m (1 dd, WAM); stn 01-84-077, NW of Augustus Island, 13°33.3'S, 122°54.5'E to 13°34.3'S, 122°52.3'E, 394-390 m (2 lv, WAM 885-84); stn 01-84-087, NW of Cape Leveque, 15°11.1'S, 121°26.9E to 15°12.9'S, 121°25.7'E, 258-260 m (1 dd, WAM 819-84); stn 01-84-090, W of Lacépède Archipelago, 16°53'S, 119°54'E to 16°55'S, 119°51'E, 435-434 m (1 dd, WAM 816-84); stn 01-84-094, W of Lacépède Archipelago, 16°55.8'S, 119°59.3'E to 17°01.8'S, 119°51.3'E, 426 m (1 dd, WAM; 1 lv, WAM 891-84); stn 01-84-095, W of Lacépède Archipelago, 16°55.1'S, 119°55.0'E to 16°56.8'S, 119°51.1'E, 432-434 m (1 dd, WAM 807-84); stn 01-84-096, W of Lacépède Archipelago, 16°55.4'S, 119°54.1'E to 16°56.7'S, 119°52.5'E, 431-432 m (1 dd WAM; 1 lv, WAM 881-84); stn 01-84-100, W of Lacépède Archipelago, 16°55.9'S, 119°52.5'E to 16°54.7'S, 119°55.4'E, 432-436 m (2 lv, WAM 1879-84); stn 01-84-099-102, W of Lacépède Archipelago, 16°55.2'S, 119°50.9'E to 16°56.3'S, 119°54.8'R, 430-436 m (3 dd, WAM); stn 01-84-105, W of Lacépède Archipelago, 16°56.9'S, 119°52.0'E to 16°55.8'S, 119°53.8'E, 432 m (1 dd, WAM 815-84; 1 lv, WAM 1882-84); stn 01-84-111, W of Lacépède Archipelago, 16°55.1'S, 119°54.8'E to 16°55.2'S, 119°53.8'E, 432-430 m (1 lv, WAM); stn 01-84-113, W of Lacépède Archipelago, 16°57'S, 119°51'E to 16°55'S, 119°54'E, 436 m (1 dd, WAM 1872-84); stn 01-84-116, W of Lacépède Archipelago, 16°55.4'S, 119°52.3'E to 16°57.4'S, 119°46.4'E, 436-448 m (1 dd, WAM 1857-84); stn 01-84-118, W of Lacépède Archipelago, 16°54'S, 119°52'E to 16°59'S, 119°47'E, 440 m (1 dd, WAM); stn 01-84-121, W of Roebuck Bay, 18°04'S, 118°14'E to 18°00'S, 118°19'E, 400-396 m (2 dd, WAM); stn 01-84-122, W of Broome, 17°59'S, 118°23'E to 17°54'S, 118°29'E, 389-390 m (6 dd, WAM 809-84; 2 lv, WAM 904-84); F/V *Courageous* cruise, prawn trawler, Aug. 1983: stn 010, SW of Imperieuse Reef, Rowley Shoals, 17°23'S, 118°52'E, 428-433 m (1 lv, WAM 3283-83); stn 018, NW of Mermaid Reef, Rowley Shoals, 16°56'S, 120°06'E, 431 m (2 lv, WAM 3287-83); stn 063, SW of Imperieuse Reef, 18°01'S, 118°18'E, 380 m (1 lv, WAM 3328-83); stn 091, N of Mermaid Reef, 16°25'S, 120°33'E, 400 m (1 lv, WAM 3330-83) (71 specimens).

DISTRIBUTION. — *Echinophoria wyvillei* has been recorded from off Kii Peninsula, Honshu, Tosa Bay, Shikoku, and Mikawa Bay, Ishikawa Prefecture, Honshu, Japan, from Taiwan, from the Philippine Islands, from Indonesia, from the Solomon Islands, from off North Solitary Island, Wooli, northern New South Wales, Australia (Habe 1964; Abbott 1968; Lan 1980; Lai 1990), from off Coff's Harbour, northern New South Wales, and off Southport and Caloundra, southern Queensland (Garrard 1969: 9), from Hawaii (Kay 1979: 214) and from Rowley Shoals, northwestern shelf of Western Australia off Port Hedland (Wilson 1993; Kreipl 1997; and specimens listed above). The present records extend its range to New Caledonia, Vanuatu, Tonga and Fiji. The small form identified as *E. kurodai* has been reported from southern Japan, where most material seems to be from Tosa Bay, Shikoku, from the Philippine Islands (Kreipl 1997), and from the northwestern shelf of Western Australia (Wilson 1993; and 71 specimens listed above); and specimens are recorded here from Indonesia, the Coral Sea, New Caledonia, Fiji and Vanuatu. These forms are concluded here to be conspecific. *Echinophoria wyvillei* occurs uncommonly throughout the western Pacific and the Indian Ocean, in depths of *c.* 200-600 m, from southern Japan to northern New South Wales, Australia, as far east as Hawaii, and is common off northwestern Australia and less common in East Africa. I know of fossils from Nausori, Fiji (behind Dilkusha, new road off Prince's Road, 18°0'S, 178°30'E; Nakasi Sandstone, Late Pliocene; AMS C302701, 3 specimens) and *E. vandervlerki* (Martin, 1933) from the Late Miocene (Janssen 1999) asphaltic turbidite of Buton Island, Indonesia, probably is a synonym of *E. wyvillei*.

A single white, tall-spired specimen purchased in the market in Tuléar, Madagascar (NZGS, WM 17045, presented to MNHN by J. C. Martin, Nice) resembles western Pacific specimens of *Echinophoria wyvillei* in most characters. It is a little wider than most of the specimens referred to *E. oschei* Mühlhäusser and, taken together, this material seems to confirm the suggestion by Parth (2000: 93) that *E. oschei* is based on Indian Ocean specimens of *E. wyvillei*. A further Madagascan specimen of typical *E. wyvillei* has been shown to me by Dr Tilo Eggeling (Braunschweig, Germany). Certainly, all these Indian Ocean specimens have the same very narrow inner lip collar as western Pacific specimens referred to *E. wyvillei*. Indian Ocean material has been reported so far only from Madagascar and Mozambique. *Echinophoria wyvillei* almost certainly ranges throughout the Indian and western Pacific Oceans.

DIMENSIONS. — Holotype of *Echinophoria wyvillei*: H 99.0, D 65.2 mm; holotype of *Echinophoria kurodai*: H 68.3, D 47.9 mm; Vanuatu, MUSORSTOM 8 stn DW 1065: H 88.2, D (incomplete) 60.3 mm; Philippines, MUSORSTOM 2 stn CP 75: H 88.6, D 58.3 mm; Taiwan, MNHN: H 117.9, D 67.1 mm; NMP G.8672, Taiwan: H 102.9, D 70.8 mm; holotype of *E. oschei*: H 101, D 62 mm; paratype, H 115, D 76 mm; New Caledonia, MUSORSTOM 4 stn CP 170: H 63.7, D 44.6 mm; Grand Passage, HALICAL 1 stn DW 01: H 74.6, D 51.1 mm; Vanuatu, MUSORSTOM 8 stn CAS 981: H 67.3, D 45.5 mm; NW of Port Hedland, AMS C156269: H 115.5, D 80.2 mm. Kreipl (1997) recorded specimens up to 123 mm high.

REMARKS. — *Echinophoria wyvillei* is the only species recorded at present from the Indo-West Pacific of which the large, adult form has a relatively thin, pale yellow-brown to bright tan shell with only a single row of nodules around the periphery on the last whorl of large specimens, particularly on the last half-whorl. Most large adult specimens are a dark tan (orange-brown) and much larger than any specimens of *E. carnosa.* Some small specimens and most of the Indian Ocean specimens identified as *E. oschei* have 3-4 rows of nodules on the early part of the last whorl, but all other than the peripheral row fade out before the end of the last whorl on all large specimens seen. The holotype of *E. wyvillei* (Figs 33F, G; Abbott 1968: pl. 80) is unusually narrow and elongate, but agrees with the majority of illustrations and with almost all the material listed above in having a narrow terminal varix, a moderately well elevated spire (although it is unusual in bearing two rows of nodules on the holotype), and the callus collar of the inner lip is very narrow and elevated only a little over the umbilicus - i.e., markedly narrower than in both *E. coronadoi* and *E. pilsbryi*. The excellent coloured illustrations by Kreipl (1997: pl. 14, figs 43, 43a) give a good idea of the shape and colour, and his illustrations show small nodules around the periphery that characterise large specimens − although the nodules are lacking altogether in some specimens. The very incomplete specimen from Vanuatu (MUSORSTOM 8 stn DW 1065; Fig. 33H) is unusual in having low, narrow, but prominent spiral cords on the spire, sutural ramp and base, and weak spiral cords between the rows of weak nodules on the centre of the last whorl, and has a particularly strongly ridged columellar callus and a very thick terminal varix with many prominent, closely spaced transverse ridges crossing its ventral face. This specimen probably is an unusually thick-shelled, coarsely sculptured, heavily callused specimen of *E. wyvillei*. Abbott (1968) ranked *E. wyvillei* as a subspecies of the Atlantic *E. coronadoi*, but these are distinct species, distinguished easily by the larger size and wider shape, the wider inner lip callus collar, the more prominent spiral sculpture and the more persistent rows of nodules lower on the last whorl in *E. coronadoi* than in *E. wyvillei*.

Small, pale (pink or flesh-coloured), spirally banded specimens (with paler bands around the nodule rows) of what I conclude to be specimens of *Echinophoria wyvillei* living on a relatively coarse substrate were named as the supposedly separate species *Echinophoria kurodai* by Abbott (1968). The sculpture on spire whorls is closely similar in the "*kurodai* form" to that of typical *E. wyvillei*; all specimens have quite prominent spiral cords and a row of prominent nodules at the periphery, in many with the tips of the nodules of a second row showing at the suture. In moderate-sized to large specimens identified as *E. wyvillei* that retain several rows of small nodules on the early part of the last whorl, and in particular in the holotype of *E. wyvillei*, the essential character of *E. kurodai* is clearly seen: a wider spiral interspace between the peripheral and immediately succeeding rows of nodules than between rows lower down the shell. The type material of *Echinophoria oschei* illustrated by Mühlhäusser (1992, figs 1, 2) also has nodules arranged in the same way, and closely resembles the holotype of *E. wyvillei* in being narrower than most of the other material seen. The type specimens of *E. oschei* also are unusually thickened, with relatively coarse ridges on the inner lip, but the incomplete specimen from Vanuatu (Fig. 33H) is much thicker and more coarsely sculptured than any of these. All these specimens also have identical apertural and anterior canal characters, with at most a narrow, raised collar over the neck of the previous whorl. One unusual character displayed only by specimens of the "*kurodai* form", among Recent species referred to *Echinophoria*, is small nodules down the outside edge of the outer lip in some specimens. However, this could easily be a character that changes as the shell grows. Other differences are obvious between specimens of the two forms of the same size, most notably the narrower shape and the longer, more left-directed anterior siphonal canal of the *wyvillei* than of the *kurodai* form when they are placed side-by-side in dorsal view (as pointed out by Dr Tilo Eggeling, Braunschweig, Germany, pers. comm.). However, these might still well be consistent ecological forms of one species, as to my knowledge the two have not been collected together at the same station. In my opinion *E. kurodai* was probably based on small specimens of a distinctive ecological form of *E. wyvillei*. The *kurodai* form apparently is reasonably consistent over wide areas of the western Pacific, suggesting that the consistently dimorphic species has an ecological explanation. I have seen no specimens of the *kurodai* form from the Indian Ocean, but so few specimens have been seen from there as yet that the distribution is unclear. However, if continued sampling demonstrates that the *kurodai* form does not occur in the Indian Ocean, it will throw considerable doubt on the synonymy suggested here. The suggested synonymy explains at least some of the confusion that has reigned over the identification of nodulose specimens of *E. wyvillei* of intermediate size (e.g., Kreipl 1997: pl. 13, fig. 38, identified as *E. carnosa*; Wilson 1993: pl. 38, fig. 10, identified as *E. wyvillei*, and figs 11a, b, identified as *E. carnosa*).

ANATOMY. — The preserved, intact animal of a male specimen of the "*kurodai* form" of *Echinophoria wyvillei* from MUSORSTOM 4 stn CP 170 was examined (Fig. 10A), along with a larger male of the "typical" form from northwest of Augustus Island, northern Western Australia (WAM 880-84, F/V *Soela* stn S1/84/76; Fig. 10B). Preservational artefacts (both were toughened through preservation in ethanol) make detailed comparison of the specimens difficult, although they are very similar in almost all characters. The exterior displays a much more obvious anterior siphonal fold in the mantle edge than was seen on any of the species of Cassinae and Oocorythinae examined during this study. Also, the mantle cavity organs are positioned much further back from the anterior edge of the mantle than in the Cassinae and Oocorythinae species examined – their anterior ends lie *c.* 20 mm from the mantle edge, compared with *c.* 10 mm in *Galeodea* species of comparable size. However, the overall appearance of the animal and its mantle organs, and the gross anatomy of the mantle organs and the secondary salivary glands is otherwise closely comparable in *E. wyvillei* to those of species of Cassinae and Oocorythinae. The smaller specimen bears a long, narrow, subcylindrical penis that is much larger than that of any species of Cassinae and Oocorythinae examined in this study, but with a clearly open seminal groove throughout the mantle cavity and along the penis, as in all the species of Cassinae and Oocorythinae examined. However, the larger specimen has a much smaller penis than the smaller one, even taking the animals' size difference into account, and it seems likely that penis size varies with the season. The obvious, deeply pigmented eyes at the outer bases of the cephalic tentacles are about twice the size of those of any species of Cassinae examined. The osphradium is similar to that of Cassinae and Oocorythinae species, bipectinate but weakly asymmetrical, with the right leaflets a little shorter than the left ones. Comparison of much more material is needed to understand the significance of the differences between these specimens.

The opercula (Figs 30I, K) of the two forms are similar, although that of the "*kurodai* form" is narrower than that of the "typical" form – perhaps merely reflecting their size difference.

RADULA. — The radula was examined of both the specimens studied above (Figs 6A-F). Preparation was more difficult than for the other radulae examined here. The radula is very different in appearance from that of any of the species of Cassinae and Oocorythinae studied here, because of the brush-like effect produced by the very much longer denticles on the central and lateral teeth than in any species of Cassinae and Oocorythinae, other than in the radula of *Sconsia grayi* illustrated by Bayer (1971: fig. 20D). Also, the cutting area of each tooth, bearing the denticles, is not sharply differentiated from the basal plate by an abrupt angle; each tooth curves smoothly from one area into the other. Also, an obviously larger main cusp is not differentiated on the central teeth, where instead 10-12 long, narrow denticles are arranged fairly evenly (a little irregularly on some teeth) around the front edge of the tooth, producing an only weakly triangular cutting area. The lateral teeth also have 8-10 long, narrow denticles and no obviously differentiated main cusp, but the plate area bearing the cusps is a little more clearly triangular, and more elongated towards the centre-line of the radula, than are the central teeth. Finally, the marginal teeth are a little wider and more evenly curved than in all the Cassinae and Oocorythinae examined, and each inner marginal tooth bears 3-4 relatively long denticles on its outer end. This highly distinctive radula confirms that *Echinophoria* is only distantly related to the Cassinae and Oocorythinae examined in this paper. The interlinking and supporting structures reported above in *Galeodea* and *Oocorys* radulae are not obvious in *E. wyvillei*, except that an obvious smooth, bevelled outer margin on each lateral tooth, outside the cutting head, appears to be equivalent to the linking groove or embayment to receive the bases of the inner marginal teeth, reported above for *Galeodea* and *Oocorys* species. The denticles on both central and lateral teeth are significantly longer in the specimen of the "*kurodai* form" than in the "typical" *wyvillei* form, but without comparing more radulae it is difficult to evaluate whether this might be due simply to differences in age and/or radular usage.

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