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Architectonicidae of the Indo-Pacific

(Mollusca, Gastropoda)

By
Rüdiger Bieler, Chicago
With 286 Figures and 3 Plates

Schriftleitung: Prof. Dr. Otto Kraus, Hamburg 1993

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To Joe

RICHARD S. HOUBRICK

1937–1993

Abstract

A systematic monograph of the Recent Indo-Pacific species of the marine family Architectonicidae (Gastropoda: Heterostropha) is presented, based on new field studies, a large part (more than 22,000 specimens in over 50 collections) of the world-wide available collection material, as well as all available type material and original publications.

A general introduction to the family is given, concentrating on morphology and anatomy, reproductive biology, habitat and diet, phylogeny and fossil record. The group has a world-wide distribution in warm-temperate to tropical waters and is the only gastropod family possessing heterostrophic ("sinistral") protoconchs in combination with broadly conical, umbilicate, dextral teleoconchs. Architectonicids prey on various groups of zoantharian coelenterates. All members for which data are available have long-range planktotrophic veliger larvae enabling dispersal over great distances, and large areas of distribution (often ranging from Africa to the Central Pacific, sometimes even reaching the western coast of America) have been recognized for many species.

A discussion of taxonomic characters emphasizes a "finger-print" pattern of recognized homologous teleoconch spiral ribs, and species-typical size range and shape (and occasionally, sculpture) of the protoconch.

Over 250 previously introduced architectonicid species-group names are discussed. Of these, 88 are accepted as valid Indo-Pacific architectonicid species-group taxa, and 83 names are placed in their synonymies. Many others are rejected as unjustified emendations, erroneous subsequent spellings, or non-binominal names. Twenty Indo-Pacific species are described as new to science: *Architectonica arcana*, *A. consobrina*, *A. gualtierii*, *Granosolarium excavatum*, *G. gemmiferum*, *Heliacus geminus*, *H. hyperionis*, *H. nereidis*, *H. oceanitis*, *H. proteus*, *Pseudotorinia armillata*, *P. sestertius*, *P. yaroni*, *Solatisonax kilburni*, *S.? orba*, *S. propinqua*, *S. rehderi*, *Spirolaxis argonauta*, *Sp. cornuarietis*, and *Sp. exornatus*. Eight additional "forms" are recognized that demand further study and remain unnamed.

Each recognized taxon is redescribed in detail, with special emphasis on homologous features of the teleoconch and protoconch dimensions. The descriptions are illustrated with 470 light and SEM photographs of type and other relevant specimens, and 150 other illustrations such as distribution maps, histograms and line drawings. Available data on anatomy, reproductive biology, larval development, ecology, and geographical distribution are summarized.

The Indo-Pacific Architectonicidae are arranged in 11 genera: *Architectonica* RÖDING, 1798 (= *Solarium* LAMARCK, 1799, *Verticillus* JOUSSEAUME, 1888), with 16 species and 2 "forms"; *Adelphotectonica* BIELER, 1987, with 3 species; *Philippia* GRAY, 1847, with 2 species (one of which of doubtful status); *Psilaxis* WOODRING, 1928, with 2 species; *Discotectonica* MARWICK, 1931 (= *Acutitectonica* HABE, 1961, *Russetia* GARRARD, 1961), with 4 species; *Granosolarium* SACCO, 1892 (= *Solariaxis* DALL, 1892, *Claraxis* IREDALE, 1936), with 5 species; *Solatisonax* IREDALE, 1931, with 9 species and 1 "form" (two of which tentatively placed or of doubtful locality); *Heliacus* ORBIGNY, 1842 (= *Torinia* GRAY, 1842), with 28 species, 1 geographic subspecies and several "forms" of undetermined status, arranged in 6 subgenera: *Heliacus* s.s., *Pyrgoheliacus* BIELER, 1987, *Torinista* IREDALE, 1936 (= *Astronacus* WOODRING, 1959), *Grandeliacus* IREDALE, 1957, *Teretropoma* ROCHEBRUNE, 1881, and *Gyriscus* TIBERI, 1867; *Pseudotorinia* SACCO, 1892 (= *Awarua* MESTAYER, 1930, *Calodisculus* REHDER, 1935), with 12 species and 4 "forms"; *Pseudomalaxis* FISCHER, 1885 (= *Discosolis* DALL, 1892, *Mangonuia* MESTAYER, 1930), with 2 species; and *Spirolaxis* MONTEROSATO, 1913 (= *Paurodiscus* REHDER, 1935, *Aguayodiscus* JAUME & BORRO, 1946), with 5 species.

Lectotypes are selected for *Architectonica nobilis* RÖDING, 1798; *Architectonica valenciennesii* MÖRCH, 1859; *Solarium admirandum* MELVILL & STANDEN, 1903; *Solarium bicanaliculatum* VALENCIENNES, 1832; *Solarium dilectum* DESHAYES, 1863; *Solarium dunkeri* HANLEY, 1862; *Solarium enoshimense* MELVILL, 1891; *Solarium*

granulatum LAMARCK, 1816; *Solarium japonicum* PILSBRY & STEARNS, 1895; *Solarium placentale* HINDS, 1844; *Torinia aequatorialis* THIELE, 1925; *Torinia costata* SCHEPMAN, 1909; *Torinia densegranosa* PILSBRY, 1905; *Torinia discoidea* PEASE, 1868; and *Torinia gemmulata* THIELE, 1925.

A taxon index and a complete bibliography (comprising almost 800 titles) are provided.

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A. Introduction

The marine gastropod family Architectonicidae (= Solariidae), commonly known as "sundials," is a group of worldwide distribution, mainly in subtropical and tropical waters. It is the only family of gastropods possessing heterostrophic, "sinistral" protoconchs and broadly conical, umbilicate, dextrally coiled teleoconchs (Figs. 1, 2; heterostrophy explained below). Over fifty genus-group names, of which twelve are here employed for Recent species, and close to 1,000 species-group taxa have been introduced for Recent and fossil forms of this family. Most of the Recent nominal species have been described from the Indo-Pacific region, often based on single, empty shells. There are few published data on the actual morphological variability within single species and even less on their anatomy and biology.

It has been known for some time that architectonicids have an extended veliger stage enabling larvae to live in the plankton for relatively long periods and thus to cover great distances with the ocean currents, ensuring wide distributional ranges. Nevertheless, new "endemic species" are being described in considerable numbers. Local architectonicid "faunas" are firmly entrenched in the literature for Japan, Australia and many other regions. Another taxonomic problem in Architectonicidae is the chronological dimension of species. Some authors apply names given for Recent forms also to Miocene fossils, while others separate "chronospecies" by newly naming Pleistocene material that is well within the range of variability of Recent populations.

In recent years, the family has attracted much attention by malacologists analyzing the systematic position of this group when it was realized that the Architectonicidae did not fit into the long-established classification of Prosobranchia and Opisthobranchia (see section 'Phylogeny'). Other authors have focused on aspects of the biology, zoogeography, anatomy or sperm morphology in members of this group. Genus-group systematics has recently been revised by the author (BIELER, 1984b, 1985a, b, 1987, 1988). At the species level, however, identification has been hampered by the fact that the last illustrated monograph comprehensively treating the family was published more than 100 years ago (MARSHALL, 1887), covering only a very small fraction of the nominal species known today. Since then, the family has received only cursory treatment in general works, in publications dealing only with particular geographic regions (e.g., MARCHE-MARCHAD, 1969; GARRARD, 1977), or in studies of limited species-groups (e.g., BIELER, 1984d). It is the intention of this monograph to fill this gap for the Indo-Pacific (here also including the Eastern Pacific), where most of the approximately 140 worldwide living species occur. The genus *Zerotula* FINLAY, 1927, warrants further study and was excluded from this work; it is currently a catch-all for numerous minute species belonging to various families (pers. obs.).

B. Abbreviations, Definitions, Text Conventions

Institutions (for private collections, see 'Acknowledgments'):

AIM	Auckland Institute and Museum, New Zealand
AMNH	American Museum of Natural History, New York, U.S.A.
AMS	Australian Museum, Sydney, Australia
ANSP	Academy of Natural Sciences of Philadelphia, U.S.A.
BGU	Ben Gurion University, Beer-Sheva, Israel
BLIHT	Biological Laboratory, Imperial Household, Tokyo, Japan
BMNH	The Natural History Museum, London, U.K.
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, U.S.A.
CAS	California Academy of Sciences, San Francisco, U.S.A.
DMNH	Delaware Museum of Natural History, Wilmington, U.S.A.
ELM	East London Museum, Republic of South Africa
FLMNH	Florida Museum of Natural History, Gainesville, U.S.A.
FMNH	Field Museum of Natural History, Chicago, U.S.A.
HBOM	Harbor Branch Oceanographic Museum, Fort Pierce, U.S.A.
HUJ	Zoological Museum, Hebrew University, Jerusalem, Israel
IMT	Institute of Malacology, Tokyo, Japan
IRSNB	Institut Royal des Sciences Naturelles, Brussels, Belgium
KPM	Kanagawa Prefectural Museum, Yokohama National University, Japan
LACM	Natural Museum of Los Angeles County, Los Angeles, U.S.A.
LC	Linnean Collection, Linnean Society, London, U.K.
LMA	Löbbecke Museum und Aquarium, Düsseldorf, Germany
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A.
MHNG	Muséum d'Histoire Naturelle, Geneve, Switzerland
MNHNP	Muséum National d'Histoire Naturelle, Paris, France
MNHU	Museum für Naturkunde an der Humboldt-Universität, Berlin, Germany
MRAC	Musée Royal d'Afrique Centrale, Tervuren, Belgium
MZB	Zoological Museum, Università degli Studi di Bologna, Italy
NMB	Naturhistorisches Museum Basel, Switzerland
NMNZ	National Museum of New Zealand, Wellington
NMP	Natal Museum, Pietermaritzburg, Republic of South Africa
NMV	National Museum and Science Museum of Victoria, Melbourne, Australia
NMW	National Museum of Wales, Cardiff, U.K.
NSMT	National Science Museum, Tokyo, Japan
OUM	Oxford University Museum (Zoological Collections), U.K.
PRI	Paleontological Research Institution, Ithaca, U.S.A.
RGM	Rijksmuseum van Geologie en Mineralogie, Leiden, The Netherlands
RNHL	Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands
SAM	South African Museum, Cape Town, Republic of South Africa
SAusM	South Australian Museum, Adelaide, Australia
SMF	Senckenberg-Museum, Frankfurt am Main, Germany
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
UCMP	Museum of Paleontology, University of California, Berkeley, U.S.A.
UMT	University Museum, Tokyo, Japan
UMZC	University Museum of Zoology, Cambridge, U.K.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, U.S.A.
WAM	Western Australian Museum, Perth, Australia
ZIMH	Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Germany
ZMA	Zoologisch Museum, Amsterdam, The Netherlands

ZMK	Zoologisk Museum, Copenhagen, Denmark
ZMUM	Zoological Museum, University of Moskow, Russia
ZSM	Zoologische Staatssammlung, München, Germany

Abbreviations used in descriptive section

Measurements (in mm where applicable):

H	shell height
PD	protoconch diameter
SD	shell diameter [= largest teleoconch diameter]
Tw	number of teleoconch whorls [with accuracy of 1/8 whorl or better (indicated by "+" or "-")]
UD	umbilical diameter

Sculptural elements (see also diagram, last page):

BF	basal field
IPR	infraperipheral rib
LMR	lower midrib
LPR	lower peripheral rib
MR	midrib(s)
PR	peripheral rib(s)
PUR	proxumbilical rib
SSR	subsutural rib
UC	umbilical crenae
UMR	upper midrib
UPR	upper peripheral rib

Statistical terms:

n	number of specimens in sample
sd	standard deviation
$\bar{x}$	arithmetic mean of sample

The abbreviations "Fig." and "Pl." (upper case) refer to illustrations and color plates in this work; "fig." and "pl." refer to those in other publications. The symbol "±" is used in the descriptive sections to abbreviate the phrase "more or less." The acronym "SEM" in figure captions stands for "scanning electron microscope."

A source of confusion in the description of architectonicid shells has been the great variety of sculptural terms inconsistently used for spiral elevations and depressions of the shell. Instead of "cingulae," "vittae," "laminae" and "cords," the terms **spiral ribs** (for major spiral elevations as part of the species-specific sculpture) and **spiral threads** for weaker, additional spiral elevations (usually in addition to the "ground plan" and appearing only on later whorls) are used (see diagram, last page).

The systematic treatment of the species-group taxa within each genus follows the same format. Each species is illustrated by several photographs (usually showing apical, apertural and basal aspects of a type specimen and, frequently, of other conspecific shells). True synonyms in the extensive listings of synonyms and citations are identified by a preceding asterisk (*). All synonymies are critical, *i.e.*, entries from the literature were only made if the record had been verified by either a re-examination of the material in question, or if the published figure and description allowed positive identification. **Type measurements**, unless stated otherwise, are new measurements taken for this study and often differ considerably from the dimensions given in the original descriptions. The section **type localities** cites statements of the original description in quotes (" "); data in brackets ([ ]) are additional. Wherever possible, the **etymology** of the species name is given. **Material studied** lists in short form (see 'Materials and Methods') the collections in which specimens were located during this study. Collections and catalog numbers for located type material follows thereafter. The descriptive part provides a shorter **diagnosis** and an extensive **description.** The latter consists, for species with full data available, of a description of **teleoconch, protoconch, periostracum, operculum, radula, jaws, anatomy,** and the **soft-body coloration** of the living animal. Color descriptions refer to material in fresh condition unless otherwise stated. **Geographical distribution** provides a summary of the known range and is usually accompanied by a distribution map. Data to be included in the distribution maps have been selected conservatively. Rather than copying unverified literature data, the map entries are based on studied specimens with good locality data or, rarely, on literature data that are well-documented by illustrations. Single records outside the established range of distribution and otherwise "suspicious" but interesting locality data are marked by question marks (?) on the maps. Whenever possible, information is also supplied on **reproduction and larval development** and on **habits and feeding behavior.** Finally, the **discussion** first compares the species with similar forms and describes typical features, then discusses the synonymy and other taxonomic questions.

Size classes employed in descriptions:

Protoconch (mm)
very small < 0.6 > **small** < 0.9 > **medium-sized** < 1.2 > **large** < 1.5 > **very large**

Teleoconch (mm)
very small < 5 > **small** < 10 > **medium-sized** < 20 > **large** < 40 > **very large** < 60 > **extremely large**

Umbilical diameter (as percentage [%] of shell diameter)
very narrow < 10 > **narrow** < 15 > **moderately wide** <25 > **wide** < 35 > **very wide** < 45 > **extremely wide**

C. Materials and Methods

The present study is based on material from two major sources. The first are specimens from the many institutions and private collections listed in the 'Abbreviations' and 'Acknowledgments' sections. This study, based mainly on empty shells and some alcohol-preserved animals, allowed for an analysis of geographical distribution and morphological variation. Depending on the rarity of the species (or its representation in collections), only single examples could be obtained for some, while others were represented by thousands. In total more than 22,000 Recent Indo-Pacific specimens (plus several thousand Atlantic and fossil specimens for comparison) have been studied from more than 50 institutional and private collections, which probably represents the majority of Indo-Pacific architectonicid collection holdings worldwide. Most of the new and unexpected findings came from a study of the large holdings of previously unstudied architectonicids of the U.S. Fish Commission Steamer 'ALBATROSS' Expeditions in Washington (USNM), and from material supplied by the museums in Sydney (AMS), Los Angeles (LACM), Paris (MNHNP), Wellington (NMNZ), and Pietermaritzburg (NMP), gathered during recent deep-water dredgings. All available type material was studied; only in cases when the holding institution was not willing to loan type material and a visit could not be arranged (Imperial Household, Tokyo), were studies based on available photographs. The fossil record older than Pleistocene has in most cases not been studied in detail; inclusion of the many hundred described nominal fossil species was beyond the scope of this work. However, type material of type species of nominal architectonicid genera was investigated, as well as many additional type specimens of fossil European, African, Austral-Asian, and American architectonicids. In all cases of homonymy or suspected synonymy of Recent and fossil forms, the fossil type specimens (if available) were studied. Whenever a fossil form in all its protoconch and teleoconch characters fell within the established range of variation of a Recent form, the two were considered conspecific.

All type material of species newly described in this work has been deposited in collections of established research institutions.

Throughout this monograph, catalog numbers are cited only for type material, figured specimens or other pertinent voucher material, not for material studied in general. To keep the volume of this publication within limits, only the collections that are holding such material are listed for each species. However, the data for the largest single architectonicid collection studied (USNM), with representatives of most species discussed, have been computerized during this project, and a printed listing has been deposited in the library of the Division of Mollusks of that institution. Other collections for which listings are available are Delaware Museum of Natural History (computerized) and National Museum of Wales (published listing; see BIELER *in* TREW, 1986).

The second main source of data and material came from personal field studies in South Africa and Panama, as well as from comparative studies in Bermuda in the Atlantic Ocean. These studies, conducted in 1980–1981 (South Africa) and 1983 (Panama, Bermuda), concentrated on observations of the living animals, anatomy, ecology, and variability within and between populations, mainly of members of the genus *Heliacus*.[1]

In the laboratory, living snails were maintained in aquaria or finger bowls of seawater at room temperature. For gross dissections, shells were cracked and animals subsequently relaxed using magnesium chloride in distilled water or magnesium sulfate crystals ("epsom salts"). Specimens that had been preserved in formalin and/or alcohol without prior cracking of the shell were found to be unusable for anatomical studies beyond the headfoot area, because the tightly sealing operculum had prevented the preservative from entering the mantle cavity. Radulae and jaws were extracted by dissolving the surrounding tissue in a solution of 10% sodium hydroxide. Air dried shells, protoconchs, jaws and opercula were coated, and observed and photographed with a scanning electron microscope (SEM, coating method and machine model depending on the electron microscope unit used). "Charging" of uncoated specimens (e.g., examined type material)

[1] Unfortunately, most of the photographs taken from living animals as well many of the scanning electron micrographs of radulae and jaw plates were later lost and could not be included in this work (see 'Acknowledgments').

frequently was avoided by providing a conductor between the specimen and the SEM carrier stub in the form of a gold or silver wire, a thin line of silver paint, or use of a thin coat of commercially available "anti-static" spray.

One problem in working with Architectonicidae is that only a few species, usually from shallow water, are frequently obtained alive or are at least represented as alcohol-preserved material in collections. Anatomical data derived from the study of this material to date serves taxonomically mainly at the generic level. Most species are known only from empty shells and comparative systematic work at the species level thus had to concentrate on shell characters. An advantage, however, is that this largely shell-based system can be applied to fossil specimens.

For the majority of the specimens studied, the following characters were observed and recorded (using calipers and a dissecting microscope with a calibrated eyepiece at 50-80x magnification; mm accuracy given in parentheses): teleoconch diameter (0.1), shell height (0.1), protoconch diameter (0.02), length (0.02) and other features of the anal keel if present, number of teleoconch whorls (1/8 of a whorl or better, indicated by trailing "+" or "-"), position of the upper point of whorl attachment (and thus the depth of the suture), umbilical diameter (0.1); apical, peripheral, basal, and umbilical sculpture (usually as number of axial grooves on third or fourth whorl; number, size and position of spiral ribs, and number of umbilical and proxumbical crenae); coloration of proto- and teleoconch (for the latter divided into ground color and pattern on the various sculptural elements, the size of color flecks given in numbers of nodules involved). In addition, notes were compiled on characters of the periostracum and operculum, and on the shape and degree of heterostrophy of the protoconch (viewed from above and, if possible, through the umbilicus; often aided by sketches made with drawing tube at 50x). In groups with numerous similar forms (e.g., *Architectonica*), simple statistical tests were performed (see Bieler, 1984d).

Teleoconch diameter (= shell diameter) was recorded as the greatest dimension perpendicular to the columellar axis. Protoconch diameter was the largest protoconch dimension perpendicular to the columellar axis visible on the teleoconch (thus reflecting slightly less than the actual larval shell diameter in tightly coiled specimens), measured from the outer corner of the varix (see Fig.2). Shell height was the greatest dimension parallel to the columellar axis, measured from the apex to the base of the aperture. Umbilical diameter was (in ventral view) the greatest distance between the columellar lip and the far side of the umbilicus, measured to the most distant tip of an umbilical crena. Teleoconch whorls were counted from the outer corner of the varix demarcating the border between proto- and teleoconch to the farthest extent of the periphery (= the point of the outer lip utilized to measure greatest shell diameter). The varix area, often colored dark brown, is usually recognizable even in eroded specimens. In badly eroded but important specimens, such as type material, the protoconch measurements and some characters could often be collected by viewing the protoconch through the teleoconch umbilicus. The number of protoconch whorls was determined by the method of Taylor (1975: 10; summarized by Jablonski & Lutz, 1980: 332, fig.4). Aberrant specimens with obviously distorted or repaired shells were measured but the results were not used in descriptions or statistics.

The terminology used for teleoconch characters, especially the various names for elements of the spiral sculpture, is based on a system originally used by Bayer (1940: fig.1) for species of *Architectonica*, and later modified by Bieler (1984d: fig.1, 1988: fig.1) for use in the entire family. For explanations see diagram, last page.

D. General Part

I. Shell and Operculum

Teleoconch

The shell size of architectonicids ranges from only a few millimeters (*Spirolaxis*, *Pseudotorinia*) to several centimeters (*Architectonica*, *Discotectonica*). The shell shape is usually roundly cone-shaped, but occasionally coin- or disk-shaped. The umbilicus is always open, ranging from very wide to very narrow (Fig. 1). The periphery is rounded or furnished with one or two major keels. The sculpture consists of more or less finely gemmate or nodose spiral ribs. The nodules are produced by the intersection of usually weaker axial grooves with the deeper grooves between the spiral ribs. In some forms (especially *Philippia* and *Psilaxis*) the spiral ribs and grooves are secondarily reduced. Relatively smooth forms, especially members of *Architectonica* and *Psilaxis*, often have a glossy shell surface and the nodules of the remaining spiral ribs are usually flattened. Only occasionally is stronger axial sculpture present. The diagram (last page) shows a generalized sculptural pattern in this family. This ground plan is developed, at least initially, in all members of the family and provides excellent taxonomic characters (see below). A number of major ribs and areas have been homologized throughout the family (upper, lower and infra-peripheral ribs, see diagram (last page) and illustrations in sections on genus-group taxa), based on their relative position in early postlarval ontogeny and on specific qualities such as size, sculpture and coloration (Bieler, 1984a, d, 1985a, b, 1987, 1988).

All architectonicids show a noticeable growth mark in the initial third of the first teleoconch whorl, marking the end of the early postlarval phase (see Fig.2). In some specimens, especially of the genus *Heliacus*, internal septa were noted (Fig.3).

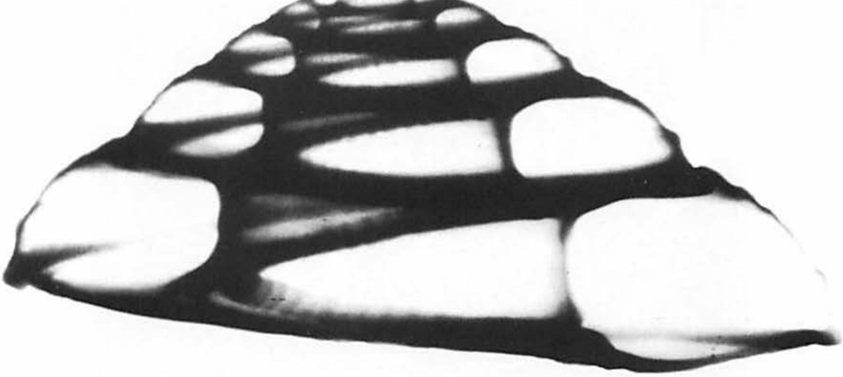


Fig. 1. X-ray photograph of the shell of *Architectonica maxima* (Philippi, 1849) [USNM 820577, courtesy M.G. Harasewych]. Note widely open umbilicus.

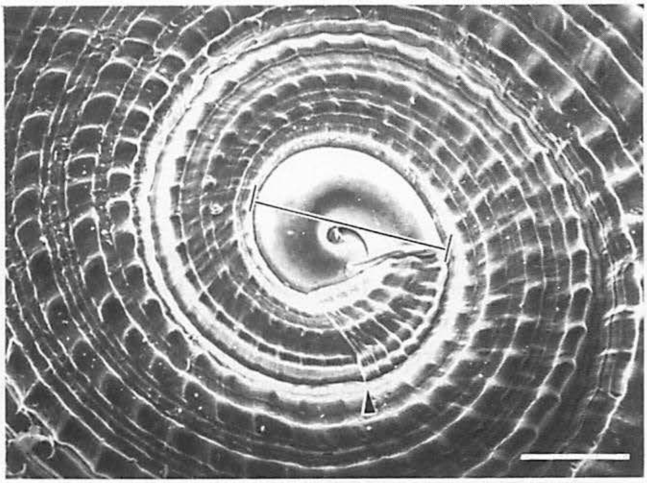


Fig. 2. Protoconch and early teleoconch whorls of *Heliacus infundibuliformis* (Gmelin, 1791). Arrow marks "stage of arrested growth"; line indicates measured protoconch size. Scale bar = 500 µm (SEM).

Most architectonicid shells have a color pattern of more or less well-defined brown flecks at least on the peripheral ribs. Especially in forms from shallow water, lively color markings are present, frequently forming regular patterns, flames or bands in various shades of brown. The pigment patterns, generated by the coordinated activities of secretory cells along the length of the mantle organ, are often disturbed after repaired shell damage. Especially in the genus *Architectonica*, a number of nominal species have been based on such "unique" specimens (see Bieler, 1984d, 1985a, 1989, and discussion under *Architectonica perspectiva*).

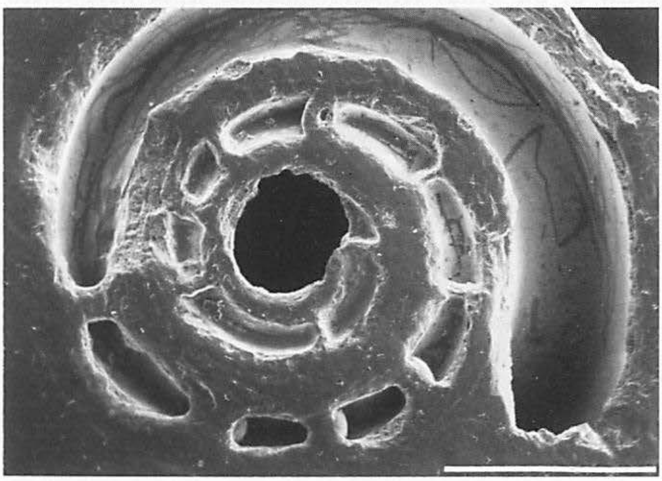


Fig. 3. Teleoconch septation in *Heliacus implexus* (Mighels, 1845). Specimen cut and ground to plane of penultimate whorl. Scale bar = 1 mm (SEM).

Protoconch

The typical architectonicid protoconch consists of a planispirally coiled embryonic (primary) shell and a usually low-trochispiral, sinistrally coiled larval shell (e.g., BANDEL et al., 1984: 97). It is smooth, glossy, often transparent and occasionally has a white or yellowish- to dark-brown pattern of blotches. A varix-forming peritreme always separates the protoconch from the first teleoconch whorl. Its lower side (visible on the *upper* side of the teleoconch) has strongly bulging, inflated whorls. Several species display a more or less distinct sculpture of axial folds in the protoconch suture (Figs.4–6, 8), which is caused by a later change in shape of the still-elastic larval shell before calcification (BANDEL, in litt.). A distinct sculpture of axial ribs, known from some Tertiary architectonicids (BIELER, 1984b: pl. 5), has not been found in Recent species. Some groups also have a distinct ridge on the protoconch, situated in the anal region of the larva. The ridge is referred to as the "anal keel" (ROBERTSON, 1963: 12). A few species, especially of *Philippia*, have a callous thickening partly or wholly overlapping the anal keel and the false umbilicus. The functional significance of the anal keel and callus is not known.

All architectonicid protoconchs are positioned at an oblique angle to the teleoconch (heterostrophy, see below) and are multispiral. Almost planispiral protoconchs occur only in *Pseudomalaxis* and *Spirolaxis*, while some species of *Pseudotorinia* have small, almost paucispiral protoconchs; larval development in these groups is still unknown.

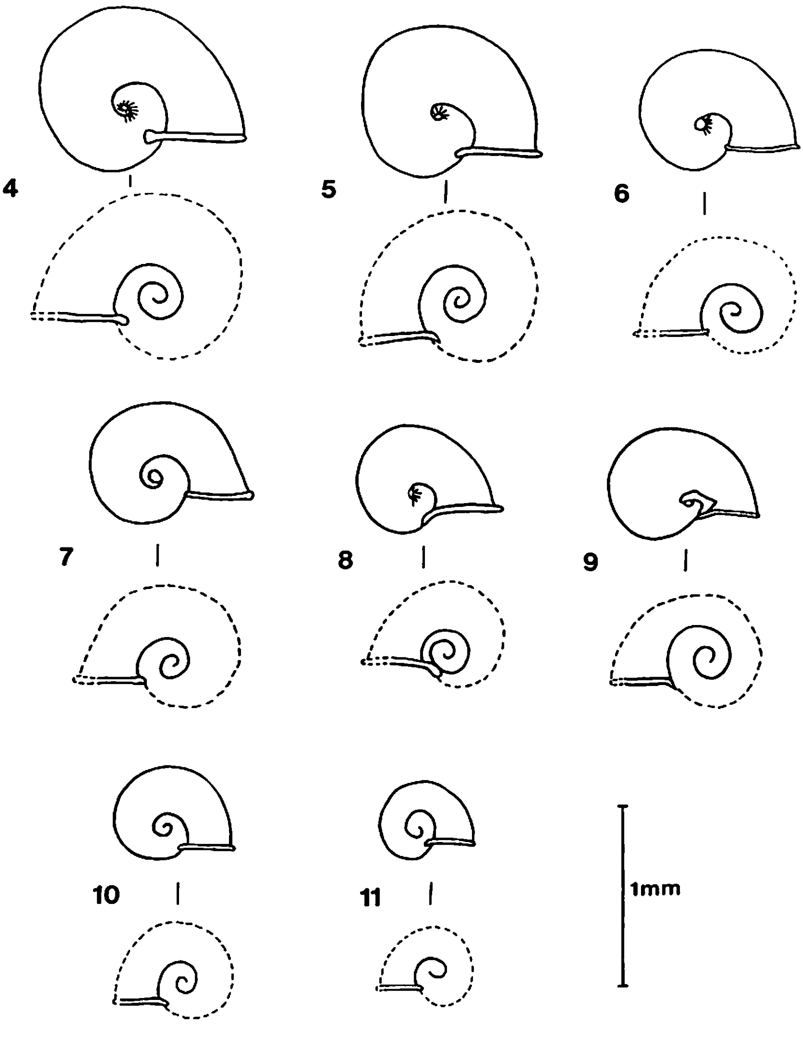
The measured protoconch size range of an architectonicid species usually displays a pattern of normal statistical distribution. In some species there is a yet unexplained bimodality of size distribution, either throughout its range or in the peripheral zones of the distributional range (ROBERTSON, 1970; BIELER, 1984d; and see species *Architectonica maxima*, *Psilaxis radiatus*, below). This phenomenon might be linked to bimodal egg size [MINNITI et al. (1988) describe bimodal size distribution of oocytes within the ovary for Mediterranean-Atlantic *Philippia hybrida* (LINNÉ, 1758)].

Periostracum

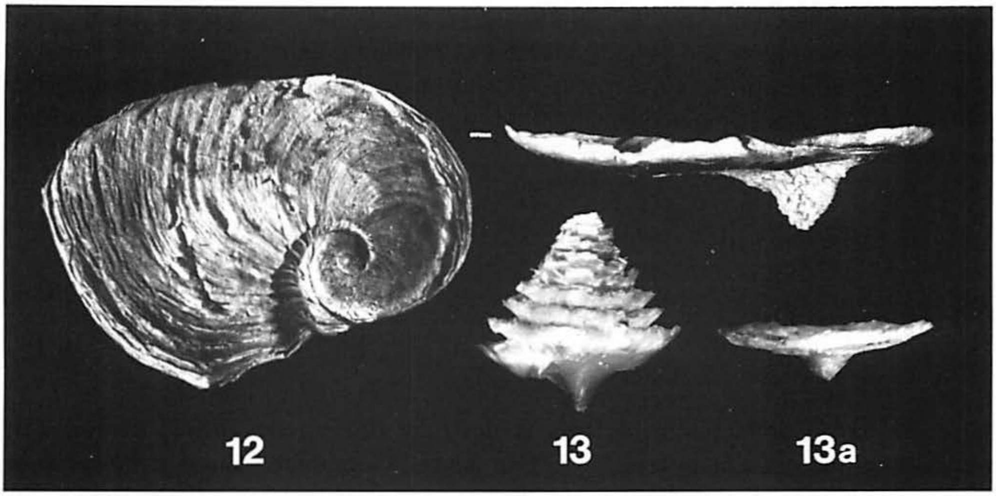
The periostracum consists of a relatively thin yellowish or transparent conchiolin layer, which swells strongly when wet. In dried condition it shrinks and flakes off in whitish or brownish scales. It overlays the teleoconch sculpture, frequently enhancing sculptural elements such as spiral ribs and nodules by its uneven thickness. While hiding weaker sculptural elements of the teleoconch such as axial and spiral threads, the periostracum adds its own sculpture to the overall appearance of the shell in the form of microscopic spiral sculpture. In sand-dwelling forms, the periostracum is usually worn off and remnants of it are only found in the spiral grooves and on the umbilical wall. In the "polyp-dwelling" *Heliacus* species, even fully grown specimens usually retain the periostracum, most prominently developed in *H. infundibuliformis* (see, e.g., photographs of living animal of *H.* [*infundibuliformis*] *perrieri* in HASZPRUNAR, 1985b: 35, figs. 9–12).

Operculum

The operculum is corneous in all Recent members of the family. Calcareous opercula have been reported for fossil forms (e.g., FISCHER, 1885: 714, after DESHAYES) but need further investigation. In species with relatively small, round apertures the multispiral operculum is of circular outline; tight closure is achieved by a flexible



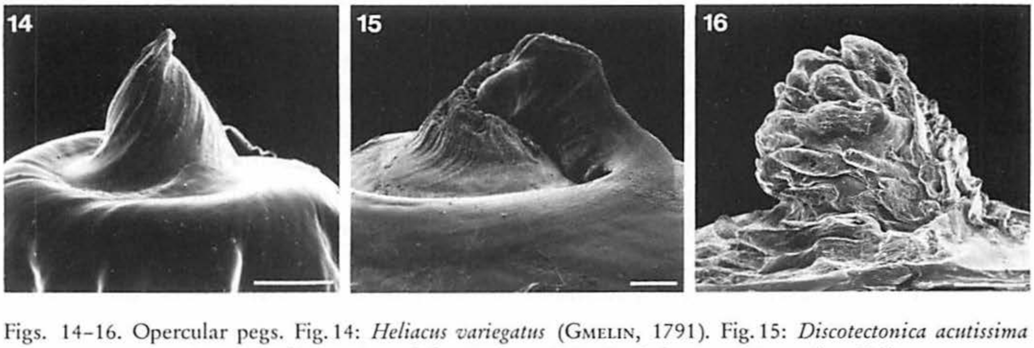
Figs. 4–11. Examples of architectonicid protoconch morphology, sketched perpendicular to teleoconch axis. Above: as visible on shell apex; below: as visible through teleoconch umbilicus, with outline of apical aspect superimposed (stippled line). Fig. 4: *Heliacus (Grandeliacus) stramineus* (GMELIN, 1791), Mocambique, NMP H7965. Fig. 5: *Heliacus (Torinista) implexus* (MIGHELS, 1845), holotype of *Solarium homalaxis* MELVILL, 1893, see Fig. 171. Fig. 6: *Heliacus (Heliacus) variegatus* (GMELIN, 1791), see Fig. 156. Fig. 7: Granosolarium asperum (HINDS, 1844), lectotype of *Solarium admirandum* MELVILL & STANDEN, 1903, see Fig. 116. Fig. 8: *Heliacus (Torinista) rotula* KILBURN, 1975, larger of two paratypes in NMP A1569/T1850. Fig. 9: *Heliacus (Torinista) corallinus*, holotype, see Fig. 188. Fig. 10: *Pseudotorinia numulus* (BARNARD, 1963), holotype, see Fig. 248. Fig. 11: *Pseudotorinia kraussi* (J.E. GRAY *in* M.E. GRAY, 1850), see Fig. 254.



Figs. 12–13a. Architectonicid opercula. Fig. 12: *Architectonica perspectiva* (LINNÉ, 1758), Mocambique (NMP). Fig. 13: *Heliacus variegatus* (GMELIN, 1791), Natal, South Africa (SMF 256388). Fig. 13a: *Pseudomalaxis zanclaeus zanclaeus* (PHILIPPI, 1844), western Atlantic (from holotype of *Omalaxis nobilis* VERRILL, 1885; USNM 203250).

fringe (Figs. 13, 13a). In larger forms (*Architectonica*, *Adelphotectonica*, *Discotectonica*) the operculum ontogenetically develops an oval, paucispiral shape (Fig. 12). All architectonicid opercula share a construction of spirally arranged lamellae, and a peg-like process on the body side, by which it is anchored to the foot muscle. The peg can be variously shaped and in some groups (e.g., *Architectonica*, *Psilaxis*, *Discotectonica*, *Solatisonax*) is frequently strengthened by a callous overlay (Figs. 14–16).

The spiral lamellae of opercula are often compressed, resulting in a flat or even overall concave shape (Figs. 12, 13a). In some groups (e.g., *Heliacus*, *Pseudotorinia*, *Spirolaxis*) the pagoda-like spacing of the lamellae results in a cone-shaped operculum (Fig. 13). The functional significance of this shape, which may be present or absent in closely related forms (e.g., *Heliacus infundibuliformis* with cone-shaped, *H. mighelsi* with flat



Figs. 14–16. Opercular pegs. Fig. 14: *Heliacus variegatus* (GMELIN, 1791). Fig. 15: *Discotectonica acutissima* (SOWERBY, 1914). Fig. 16: *Architectonica nobilis* RÖDING, 1798. Scale bar = 500 μm for all figures.

operculum), is not yet known. Similar opercular shapes are known from several not-closely related gastropod families, such as Vermetidae (*Dendropoma*), Hydrobiidae (*Gocea*) and Siliquariidae (*Tenagodus*). All of these groups also convergently share the feature of a partly uncoiled shell in some or all members; the cone-shaped operculum may be linked to that trait.

II. Heterostrophy

The body of an architectonicid larva is dextrally organized. This is demonstrated externally by the operculum (see Fig.17). In dextrally organized animals the spiral line on the outside of the operculum is directed counterclockwise (PELSENEER, 1893; ROBERTSON & MERRILL, 1963; BIELER 1984d). Despite its dextral organization, however, the larval shell appears to be sinistrally coiled. The condition of having a dextrally organized body in an apparently sinistral shell, often called "hyperstrophy", occurs in several gastropod groups, e.g., in the genus *Lanistes* of Ampullariidae. In Architectonicidae the postlarval shell, by repositioning of the mantle tissue, commences growth in a "normal" (orthostrophic) direction, resulting in a dextral teleoconch carrying an "up-side down," hyperstrophically-coiled protoconch. The protoconch apex accordingly is visible within the umbilicus of the teleoconch. The axes of proto- and teleoconch diverge by less than 10° (see also ROBERTSON, 1963). For this specific condition of the architectonicid protoconch, which was first pointed out by JOUSSEAUME (1882: 159), DAUTZENBERG & FISCHER (1896: 451) introduced the term "anastrophy". Since the difference between architectonicid "anastrophy" and the "heterostrophy" of other families (e.g., Pyramidellidae, Mathildidae) with similarly hyperstrophic coiling of the protoconchs is merely the degree of oblique attachment, the term heterostrophy is here used for all cases, as was suggested by ROBERTSON (1985).

Several reports of sinistral architectonicids can be found in the literature (e.g., LAGODA, 1868; ITO, 1988). While sinistrality is a frequent phenomenon in the Gastropoda, with the regular or occasional occurrence of sinistral animals in a number of families (e.g., ANCEY, 1906), it has not yet been verified for the Architectonicidae. All records of "sinistral" architectonicids were found to refer to abnormal dextral hyperstrophy, whereby the teleoconch retains the hyperstrophic coiling of the protoconch. Shifting of the mantle, resulting in a change from hyperstrophic protoconch to orthostrophic teleoconch in a "normal" architectonicid, is apparently blocked in these animals. ROBERTSON & MERRILL (1963) described such abnormal conditions for *Heliacus* [*areola*] *bicanaliculatus* and *H. cylindricus*. Other cases known are specimens of *H. infundibuliformis* and *H. implexus* found in South Africa (NMP, pers. obs.), ITO's (1988) "sinistral" specimen of *Pseudotorinia* sp. [as *Torinista enoshimensis*] and EKAWA's (1991) "sinistral" *Heliacus* shell from Japan (see also ROBERTSON & BIELER, 1989).

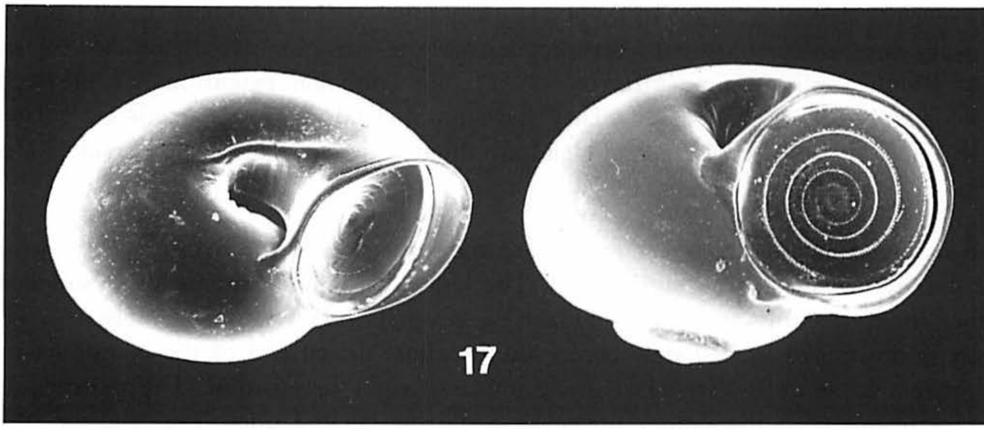


Fig. 17. Larval shells (unidentified Atlantic architectonicid larvae).

III. Anatomy and Biology

Anatomy

Previous anatomical studies on Architectonicidae have been published by IHERING (1877), BOUVIER (1886a, b, 1887)[2] , RISBEC (1955), MERRILL (1970), CLIMO (1975), and especially, HASZPRUNAR (1985 a,b,c). ROBERTSON (1974a, 1985) discussed the anatomical characters of the family in their relationships to other groups. The following summarizes the published information, augmented by personal observations (mainly on species of *Architectonica* and *Heliacus* s.s).

The anterior portion of the foot is produced into two pointed, very mobile lobes. The sole has two gland openings, one immediately behind the anterior margin, and a much smaller one in the center region. The long, tapering, very slender (in living condition) cephalic tentacles carry black, lens-equipped eyes at their outer bases. The "false mouth" (opening of the proboscis sheath) opens at the tip of a short snout. The mantle cavity comprises about half of the body whorl of the shell; the animal is able to fully retract and tightly close the aperture with its operculum. The mantle cavity is longitudinally divided by a dorsal crest, built up by the posterior pedal gland, the large arterial vessel, so-called chordoid tissue[3], long salivary glands, and a ciliary tract at its outer edge. This ventral ciliary tract, together with an opposing dorsal strip of ciliated tissue, produces a water current leading from left to right. The strongly developed osphradium, with its semi-circularly arranged lamellae above a large osphradial ganglion, is situated anteriorly on the left, incurrent side. Its morphology

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[2] It should be noted that the specimens studied by BOUVIER were not "*Solarium trochleare* HINDS, 1844," as stated by the author, but the closely related *Architectonica perspectiva* (LINNÉ, 1758). The shells of the material on which the anatomical studies were based (Zanzibar, ROSSEAU Coll.) were located in the Paris Museum during this study (MNHNP, unnumbered).

[3] See STARMÜHLNER (1952: 575), for similar conditions in *Viviparus*.

was recently described in detail by HASZPRUNAR (1985a). The foliobranch gill lamellae (ROBERTSON, 1974a) are not homologues of the prosobranch ctenidium or the opisthobranch plicatidium (MORTON, 1972), but epithelial extensions of the well-developed hypobranchial gland. They have no skeletal supporting rods or ciliated bands. The gill and hypobranchial gland are situated to the right of the dorsal ciliated strip, in the excurrent chamber.

The rectum and gonoducts are located on the right side of the mantle cavity, while the kidney occupies the posterior roof. The kidney is pallially situated and supplied, rather than viscerally as in "prosobranch" gastropods (HASZPRUNAR, 1985b: 33). The heart is positioned immediately before the proximal dorsal end of the mantle cavity. Its atrium is anterior-left, its ventricle posterior-right in position. The pericardium communicates with the kidney lumen by a narrow ciliated duct. The anterior right corner of the mantle cavity is occupied by the massive, glandular oviduct and the pallial vas deferens. The male has no penis. In hermaphroditic forms (see below), male, female and sperm-receptive structures are almost completely separate with independent openings.

The nervous system is distinctly streptoneurous, epiathroid, without zygoneury, and has (as in the "prosobranchs") only three ganglia (supra-, subintestinal-, and visceral) on the long visceral loop. The highly specialized buccal apparatus shows two main types within the family. In most groups (e.g., *Architectonica*, *Adelphotectonica*, *Philippia*, *Heliacus*, *Pseudomalaxis*, *Spirolaxis*), the proboscis is acrembolic. The connectives between buccal and cerebral ganglia run within the paired proboscis protractors which in retracted condition do not pass through the cerebropedal nerve ring. *Discotectonica* and *Granosolarium* have a short proboscis sheath, behind which the proboscis divides into a ventral part, containing a large rod-like structure (see below), and a dorsal part, the esophagus proper. Both types were described in detail by HASZPRUNAR (1985b). Proboscis retractors are absent, their function apparently taken over by the strong longitudinal musculature of the esophagus. In all genera the esophagus is cuticularized, the stomach large and unspecialized, and the short intestine is separated from the rectum by a strong sphincter. A dark glandular area next to the anus, close to the anterior right mantle margin, appears to represent an anal gland. The visceral mass contains the stomach, receptaculum seminis, the unpaired digestive gland as well as testis and ovary. The columellar muscle is ventral in position and extends about three quarters of the body whorl.

The soft-body coloration results from a combination of black (in preservative brownish) pigment in the epidermal cells, white bodies embedded in the tissue, and (to a lesser extent and only in small forms) from internal organ coloration discernible through the tissue. Species with dark shell colors usually also have darker body pigmentation. Relative to the coloration of the remaining body, the tentacles and the anterior part of the foot (the body regions exposed during normal activities) are most strongly pigmented; the sole and the upper head-foot areas are less strongly or not pigmented.

Radula and Jaw

The architectonicid radula is, compared to body size, small. This and the fact that in resting position the buccal mass is considerably withdrawn, caused early workers to believe that a radula was missing in this group (resulting in classifications of the Architectonicidae as an "aglossate" or "gymnoglossate" group, e.g., GRAY, 1853a; MÖRCH, 1867). Two main radular types are realized in the family: a five-toothed "taenioglossate-like" radula and a "ptenoglossate-like" radula with numerous marginal teeth (Figs. 18, 19). The first is thought to be derived from a typical taenioglossate caenogastropod radula with seven teeth per row, by loss of the pair of laterals (BIELER, 1988). It is the most common radular type in the family, present in all genera but *Architectonica*, *Adelphotectonica*, *Discotectonica* and *Granosolarium*. The "ptenoglossate-like" radula, present in *Architectonica* and *Adelphotectonica*, is considered secondarily derived from the five-toothed one, by multiplication of the marginals (see 'Phylogeny and Fossil Record,' below). For an extensive treatment and illustrations of architectonicid radulae, see BOSS & MERRILL (1984b) and BIELER (1988). Instead of a true radula, *Discotectonica* and *Granosolarium* have an extremely long (up to one-third of the shell diameter), toothed, rod-like cuticularized structure inside a large muscular blind sac (see, e.g., MELONE, 1975: 168, pl.1 figs. 5, 6; MELONE & TAVIANI, 1985: 155, figs. 4–10, and HASZPRUNAR, 1985b: 30, fig.2). Homology and function of this structure are unclear.

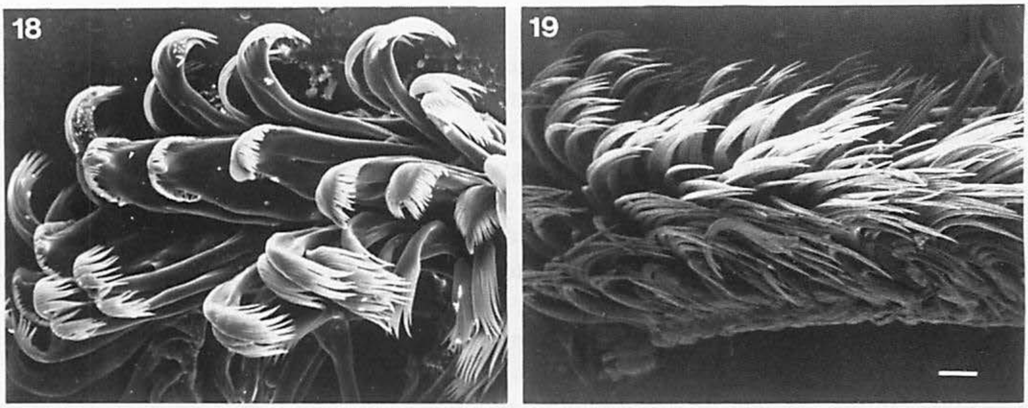
The jaws are long and narrow, consisting of numerous small elements arranged in mosaic-like fashion. The shapes of the generally prong-like elements range from very pointed (*Philippia lutea*) or rounded (Atlantic *Psilaxis krebsii*), to very blunt (Atlantic *Discotectonica discus*). The length of the jaws ranges from 0.38 to 0.75 mm, depending on the species and size of the individual. The length of the elements is about 25 µm (BOSS & MERRILL, 1984b).

Sex distribution

Sex distribution is very variable within the family. While sexes in the Mediterranean-Atlantic species *Philippia hybrida* (LINNÉ, 1758) are strictly separate (MINNITI et al., 1988), *Heliacus* was found to be protandric to simultaneously hermaphroditic [HASZPRUNAR (1985b), based on Indo-Pacific *H. variegatus* (GMELIN, 1791) and Atlantic *H. infundibuliformis perrieri* (ROCHEBRUNE, 1881); ROBERTSON (1989), based on Atlantic *H. cylindricus* (GMELIN, 1791) and *H. i. perrieri*].

Sperm and Spermatophores

HEALY described the spermiogenesis of *Psilaxis oxytropis* (1982) and the morphology of the mature sperm of *Heliacus variegatus* (1988), and MINNITI & D'ANDREA (1989) described spermiogenesis of Mediterranean-Atlantic *Philippia hybrida*. The single type of architectonicid sperm was shown to differ greatly from the "prosobranch" type. It shares several features with the Euthyneura (structure of mature and developing acrosome, periodically-banded coarse fibers, modified midpiece development, pattern of nuclear condensation), while other characters separate it from that group (e.g., the



Figs. 18, 19. Architectonicid radulae (SEM). Fig. 18: Five-toothed taenioglossate type; *Heliacus variegatus* (Gmelin, 1791) [SMF 256388]. Fig. 19: Ptenoglossate type, *Architectonica laevigata* (Lamarck, 1816). Scale bar = 200 µm for both figures.

form of the mature midpiece and the persistence of thick coarse fibers throughout the midpiece). Healy (1988) and Healy & Jamieson (1991) observed a transversely banded helix in the spermatozoan midpiece of *Heliacus variegatus*, which is also reported from *Granosolarium* (Healy, 1991: 63; citing unpubl. data by Healy & Jamieson). A probably homologous structure, a long, transversely banded column interpolated between the base of the spermatozoan nucleus and the acrosome of the midpiece, was described for *Architectonica perpectiva* by Healy (1991). Neither of these structures was found in *Psilaxis oxytropis* (see Healy, 1982).

Architectonicid spermatophores have been described from *Heliacus*. They consist of long (10–25 mm), coiled tubes, and are handled and possibly molded by a spermatophore groove extending onto part of the proboscis (Robertson, 1989).

Eggs and larval development

Spawn masses are known from species of the genera *Architectonica* and *Heliacus*. They consist of soft, gelatinous, sausage-shaped masses, usually (depending on animal-size) several centimeters long and about three millimeters in diameter. The masses are irregularly coiled, and whitish, yellowish or greenish in color (Pl.2 Fig.E). They are anchored to the substrate by sticky mucus. Within the mass, ten-thousands of eggs are arranged in irregular spiral lines, interconnected by chalazae (Pl.3 Fig.A). The length of the mass varies greatly; individuals can either produce one long continuous mass within several hours or several shorter pieces over a period of days (pers. obs., *Heliacus trochoides*). The "U-shaped jelly mass" as described by Robertson (1967: 247) as a typical egg mass of *H. cylindricus* only occurs when relatively short pieces are laid. The weakly oval eggs (about 0.1 x 0.13 mm in *Heliacus*) are still in the single-cell stage when laid. Within the almost transparent, viscous, mucous mass, the egg strings are covered by a closely-adhering mucous sheath. Development to the hatching veliger larva took 12–20 days in *Heliacus* (at 20° and 25°C, *H. variegatus* [n= 18], *H. trochoides* [n= 8]; pers. obs., South Africa). The first cleavages occured rapidly, with embryos in the slightly older end of the egg mass considerably farther along in their development. After 15 hours an early trochophore stage was reached (20°C, *H. variegatus*). After three days the chalazae were largely dissolved, but the egg strings still interconnected by the inner mucous sheath. After eight days the veliger stage was reached. At this point about 15% of the up to 30,000 embryos per mass had aborted development. After 18 days the first veligers hatched by actively working through the now partly-desintegrated mucous sheath and mass. Their size was still equivalent to the original egg size as no external food source such as nurse eggs was utilized. After 20 days the former egg mass was more or less completely dissolved, and all veligers were free. At this stage each larva had two small velar lobes, a flat operculum, a large dark "larval organ," and a transparent, thin shell corresponding to the nucleus of the later protoconch. Further laboratory maintenance was not successful; the larvae lived for another 20 days, without intake of the single-cell algae offered.

Planktic development of an architectonicid was described by Robertson et al. (1970: 61–62) for Atlantic *Psilaxis krebsii*. It is apparently very similar in Indo-Pacific *Psilaxis* species, here illustrated in Plate 3, Figures B-E. The velum develops into four elongated lobes as the feeding larva grows in the plankton. Consumption of single-celled algae is assumed, but Richter (1987: 156) also demonstrated a large number of dinoflagellate protozoans (genus *Prorocentrum*) as food items in the stomach and digestive gland of larval *Psilaxis krebsii*. There are paired eyes but no tentacles until metamorphosis. Robertson et al. (1970) observed that if the larvae were fully developed at the time of capture, they lost their vela within a few days. In *Psilaxis oxytropis*, the elongate velar lobes are ingested and appear red-orange in the digestive gland (Taylor, 1975: 62). According to Robertson et al. (1970), settlement of *Psilaxis krebsii* in the laboratory occurred in the absence of corals and was thought to be induced by substrate contact. Studies by Bonar on *Psilaxis radiatus* (reported by Hadfield, 1976: 135), however, showed that the subsequent teleoconch growth was strictly dependent on the presence of coral. Robertson et al. (1970: 63) further observed, that "[a]bout a week after capture, the teleoconch suddenly begins to grow, and the animal then actively crawls about on its broad foot ... After developing from between one-sixth to about one-half a whorl in one or two days, growth of the teleoconch stops. Animals remained alive in this state of arrested growth without further changes for several months." This stage of early postlarval arrested growth is present in all members of the family as can be demostrated by a distinct growth mark in the first or, rarely, the second quarter of the first teleoconch whorl (Fig.3 and Pl.3 Fig.F). Occasionally two or even three such marks can be seen. Robertson et al. (1970: 63) thus concluded that "at this stage the animals presumably crawl in search of their hosts. Many architectonicids die at this stage: the Recent and fossil shells are common in museum collections ... We suggest that this high mortality is caused mainly by the spatial problems in finding hosts at this critical stage in the life cycle." Architectonicid larvae have a very long planktic stage. From the localities of occurrence and the maximum current velocities from the nearest potential spawning areas, Robertson et al. (1970: 60) deduced a maximum pelagic larval stage of six or more months (see section 'Zoogeography').

Habitat and Diet

Data on habits and habitats are available for several architectonicid species. All members of the family feed on coelenterates, and their radulae (frequently ptenoglossate-like as in other coelenterate feeders such as Epitoniidae) and alimentary system (with cuticularization) show several specializations. *Architectonica nobilis* preys on actinarians. The snail rasps a hole in the base of a large actinarian polyp, extends the proboscis into the coelenterate and continues feeding until the prey dies (BANDEL, 1976; see 'Habits and feeding behavior' under *A. nobilis*). *Psilaxis radiatus* feeds on coral polyps (ROBERTSON et al., 1970; Fig.20), while juveniles of *Psilaxis oxytropis* are known to accept polyps of the sea anemone *Aiptasia* in laboratory experiments (TAYLOR, 1975: 62). Members of *Heliacus* feed on zoanthinarians ("colonial sea anemones," Pl.2 Figs.C-E; ROBERTSON, 1967; and accounts in 'Taxonomy' section below).

The habitat type of an architectonicid is well reflected in its shell shape; species can be grouped roughly into dwellers of sandy and those of hard substrates. The sand-dweller, like the "sand dollar" sea urchin of similar habitats, is characterized by a depressed, shield-like shell, usually without distinct color pattern. Large architecton-

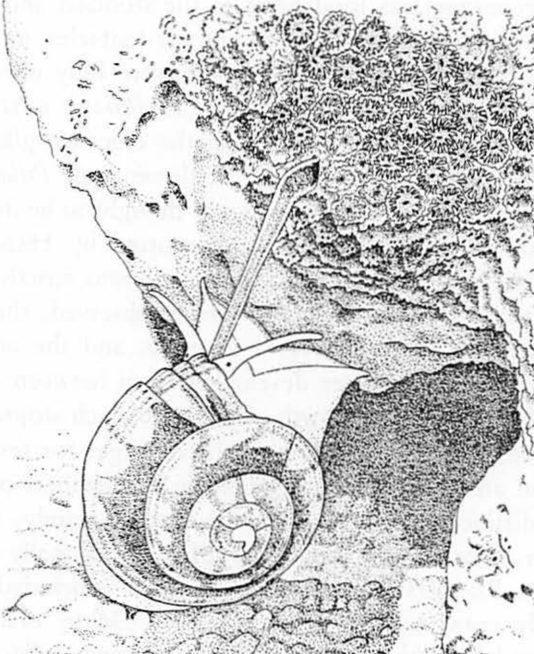


Fig. 20. Postlarval *Psilaxis radiatus* (RÖDING, 1798) feeding on the polyps of hermatypic coral *Porites lobata* DANA (from ROBERTSON et al., 1970; with permission of *Pacific Science*).

icids of various genera develop a more or less sharp peripheral shell keel that allows easier burrowing in the sand. In this group belong members of the genera *Discotectonica* and *Granosolarium*. The other morphotype is the dweller of hard substrates such as rocks, corals and zoanthinarian polyp colonies. It is characterized by a more or less rounded shell allowing for good maneuverability, and in shallow-water forms frequently has a camouflaging pattern. In this group belong most species of *Heliacus* and *Philippia*. Architectonicids who spend resting periods in the sand, but move onto various substrates to search for food (*Architectonica* and *Psilaxis*) possess an intermediate condition, a rounded shell with a single keel.

Among the predators of architectonicids are certain species of fish (see, e.g., MATTHEWS, 1968) and predatory gastropods. At the South African shoreline of Natal, the common muricid species *Morula granulata* (DUCLOS, 1832), accounts for most of the predation on intertidal *Heliacus* species. It is well adapted with its relatively small rounded shell to enter the sheltered areas in crevices and between zoanthid polyps where *Heliacus* lives (Pl.2 Fig.B). The muricid drills a hole in the upper part of the *Heliacus* shell. The reason for the internal septation found in some architectonicid shells (Fig.3) is unknown. However, several *Heliacus implexus* individuals were found in Natal who had survived one or two such muricid attacks because the drill holes had led into empty chambers (pers. obs.). Recently, LUZ (1990: 5) reported that the naticid *Tectonatica filosa* (PHILIPPI, 1844) is a regular predator of the architectonicid *Basisulcata lepida* (BAYER, 1942) in the Mediterranean.

IV. Zoogeography

The family is distributed worldwide, mainly in tropical and subtropical waters. The distributional limits are approximately 40° N and S. Only a few species, especially of *Basisulcata* and *Philippia*, occur also outside this area, for instance southwest of Ireland (warmed by the Gulf Stream, at 50° and 51° N) and off Tasmania.

Authors have described many local architectonicid "faunas," with different sets of nominal species, inhabiting Japan, Australia, and the African east coast. However, as demonstrated by the maps in the 'Taxonomy' section, most Indo-Pacific species are very widely distributed, often ranging from the African east coast to the Central or even East Pacific, and many nominal species have proven to be synonyms. For example, the "Hawaiian" species *Heliacus implexus* (MIGHELS, 1845) is known as *Heliacus codoceoae* REHDER, 1980, in the Easter Islands, as *Torinista popula* IREDALE, 1936, in Australia, as *Heliacus maorianus* POWELL, 1934, in New Zealand, as *Heliacus homalaxis* (MELVILL, 1893) in India, and under its two synonyms *Heliacus africanus* BARTSCH, 1915, and *H. alfredensis* (TURTON, 1932) in South Africa.

Apparently all architectonicids have planktic veliger larvae able to drift in near-surface currents and thus to cover great distances (e.g., ROBERTSON, 1964; SCHELTEMA, 1968, 1971, 1979; SCHELTEMA & WILLIAMS, 1983). In a study of plankton samples from the tropical Atlantic, SCHELTEMA (1979) found architectonicid larvae in approximately 70 percent of all samples. The ability to delay metamorphosis allows some species even to cross the East Pacific: several species apparently extend from the Indo-West and Central Pacific to the American west coast (e.g., *Heliacus trochoides*, *Psilaxis radiatus*; see also ROBERTSON, 1976b, 1979; EMERSON, 1983, 1984). The probability of geographic differentiation (leading to speciation) is restricted, and the wide ranges of distribution found for most architectonicids are thus explainable (see, e.g., distribution maps for *Architectonica perspectiva* and *Heliacus implexus*).

The eastern Pacific fauna deserves special mention. The architectonicid species here encountered fall into three groups: (1) Indo-Pacific forms as mentioned above, (2) forms morphologically inseparable from Atlantic populations and probably isolated from them by the closure of the Isthmus of Panama in the early Pleistocene, and (3) forms that have evolved as endemic species, from either Tethys-Atlantic or Indo-Pacific stock. Examples of amphi-American species are *Architectonica nobilis* and *A. karsteni* (the latter apparently no longer extant in the Atlantic), and probably *Pseudotorinia* sp. aff. *architae*. Some species are only known from the eastern Pacific. Among these are *Discotectonica placentalis*, *Solatisonax propinqua* n.sp. and *S. orba* n.sp., *Heliacus mazatlanicus* and *H. planispira*, as well as *Pseudotorinia panamensis*. However, a few species previously assumed to be endemic species to the American west coast or to have closest relationship to Atlantic forms (ROBERTSON, 1976a; KEEN, 1971), were found to be of Indo-Pacific ancestry. *Solatisonax radialis*, described from Panama, is now known from numerous localities throughout the Indo-Pacific, and eastern Pacific *Heliacus bicanaliculatus* is here regarded as a form of Indo-Pacific *Heliacus areola*, with intermediate morphs in the Marquesas and Galapagos Islands.

While most architectonicid species show little geographic variation (specimens of the same species from South Africa and Hawaii, for instance, are usually indistinguishable), some local forms have developed, apparently in relatively isolated areas at the fringe of the main population. *Heliacus infundibuliformis* (Africa to Central Pacific) and *H. mighelsi* (known from Hawaiian Islands and eastern Australia) seem to be separated by a number of shell and opercular characters and are generally regarded as two species. However, *Heliacus discoideus*, another locally restricted form (Tuamotu Archipelago and Society Islands) shows intermediate features. Forms with characters otherwise unusual for the species are also found in the Marquesas (e.g., of *Psilaxis radiata*); and some locally restricted "species" (e.g., *Philippia japonica* and *Architectonica* sp. aff. *grandiosa*) might prove to be locally restricted forms of widely distributed species.

The disjunct distributional patterns of some, however, do not reflect biological reality. Especially in cases of species living in great depths, they are often merely a result of the small number of localities sampled. Some species have only been collected by deep-water dredgings; the distribution maps will thus reflect the stations of certain expeditions working in deeper water, such as the 'ALBATROSS,' 'SIBOGA,' and 'VALDIVIA' cruises (e.g., *Solatisonax radialis*).

The term "subspecies" is here employed without availability of genetic data. This is used for widely geographically isolated populations believed to belong to the same species whose members are distinguished by differences in radular or teleoconch characters and for which separate names are already known in the literature (e.g., *Pseudomalaxis zanclaeus* s.s. and *Heliacus infundibuliformis perrieri* in the Atlantic, and *P. zanclaeus meridionalis* and *Heliacus infundibuliformis* s.s. in the Indo-Pacific).

At present, it is unclear whether an exchange of genetic information exists between Indo-Pacific and Atlantic architectonicid populations. This would explain the morphological similarity of some Atlantic and Indo-Pacific forms, which are here provisionally classified as subspecies. Through climatic reasons, the only possible connection allowing for larval passage is seen off the southern cape of Africa. Following the direction of the warm Agulhas Current, the direction of larval transport here is east to west. Indo-Pacific architectonicid larvae have been found in the waters southeast of the Cape of Good Hope (SCHELTEMA, in litt.) and their passage around the Cape appears possible. Under present climatic conditions, however, there seems to be an ecological barrier: Indo-Pacific architectonicid veliger larvae can round the Cape with the Agulhas Current, but then do not find suitable habitat conditions in the South Atlantic, where the southwestern African coast is influenced by the cold Benguela Current.

The distribution of architectonicid species for which food requirements are known seems to be limited by the temperature requirements of their coelenterate prey. In South Africa, the range of *Heliacus infundibuliformis*, which prefers polyps of the zoanthid genus *Isaurus*, extends into the southern Natal, the southernmost area where this zoanthid genus occurs. Adults of the less specialized *H. areola*, *H. trochoides* and *H. sterkii* were found farther south in the Transkei; the ubiquitous *H. variegatus* even occurs on the southernmost intertidal *Palythoa* zoanthid colonies located in South Africa (Haven, near the mouth of Bashee River, Transkei; pers. obs.). ROBERTSON (1964: 22) found that the 17°C (62°F) February isotherm delimits the northern boundary of the known range of *Psilaxis* species on both sides of the Atlantic. The 17°C winter isothermal line in South Africa lies in the Transkei, again marking the approximate border of non-deep-sea architectonicid distribution. Architectonicid larvae have been collected at water temperatures as low as 13.5°C (SCHELTEMA, 1971: 296), while adults of deep-water species were collected alive at temperatures as low as 2.4°C (*Solatisonax radialis*; type locality, off Panama).

V. Phylogeny and Fossil Record

Architectonicidae has recently attracted much attention by malacologists analyzing the systematic position of this group within the Gastropoda. The family was classically grouped in the superfamily Cerithioidea, although MACDONALD (1860) had early pointed out the "special" position of the Architectonicidae. Together with their presumed sister group, the family Mathildidae, they were subsequently considered an

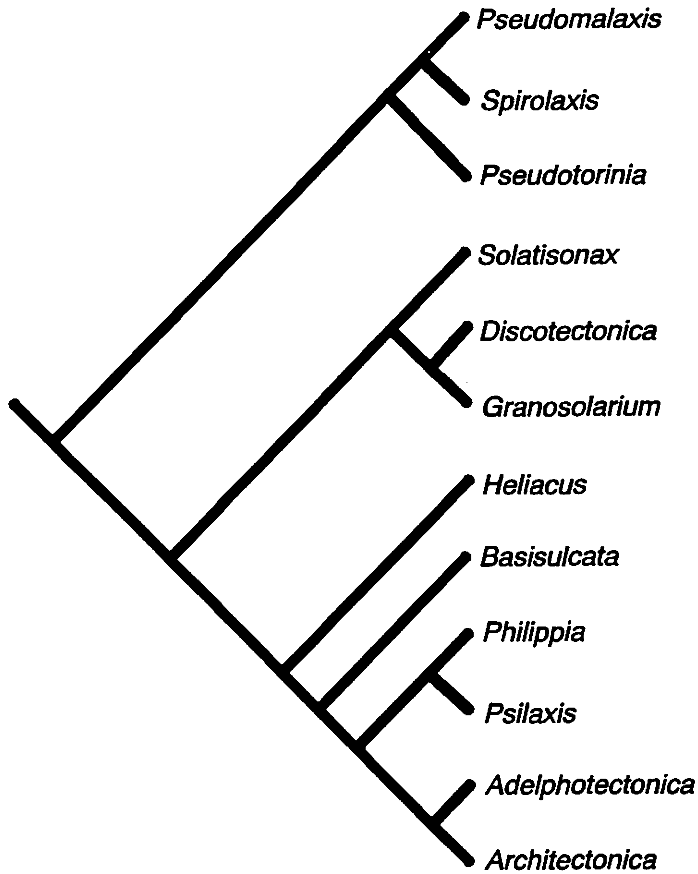


Fig. 21. Cladogram of Recent architectonicid genera (modified from BIELER, 1988: fig.22).

independent superfamily, and the group (combined with several other families) was eventually raised to ordinal rank under various names (Heterogastropoda KOSUGE, 1966; Allogastropoda HASZPRUNAR, 1985; Heterostropha FISCHER, 1885; Architectonicoida MINICHEV & STAROBOGATOV, 1979; etc.). This was based on the peculiar combination of "prosobranch-like" and "opisthobranch-like" characters displayed by members of this group. [For a discussion of prosobranch and opisthobranch traits in Architectonicidae, see MERRILL (1970: 271), ROBERTSON (1974a, 1985) and BIELER (1988); for opisthobranch-like characters of shell-matrix and spermiogenesis, see GHISELIN et al. (1967: 13), HEALY (1982: 197, 1988: 261) and MINNITI & D'ANDREA (1989).]

The family Mathildidae is considered the sister group of the Architectonicidae, based on shared characters of the protoconch, radula, and operculum (see THIELE, 1925a: 113), and a number of anatomical features (e.g, two juxtaposed ciliary tracts on the left side of the mantle cavity; fused salivary glands; a longitudinal crest at the ventral surface of the mantle cavity, built up by the anterior arterial vessel; a posterior pedal gland; HASZPRUNAR, 1985b, c). The similar five-toothed-taenioglossate radulae, however, might have evolved differently in these two groups, by independent reduction of the outer marginal (Mathildidae) or lateral teeth (Architectonicidae) (BIELER, 1988).

A recent cladistic analysis (BIELER, 1988) for 12 genus-group taxa of the Architectonicidae, covered all such taxa included in this monograph. Using the mathildid genus *Gegania* JEFFREYS, 1884, as an outgroup, the family Architectonicidae was shown to be a monophyletic group that is defined by several synapomorphies in anatomical, radular, opercular, and shell characters (see 'Family Architectonicidae,' below). The most parsimonious cladogram (the one that involves the fewest "ad hoc" hypotheses of homoplasy), here modified in Fig.21, shows three distinct, well-supported clades: (1) *Pseudomalaxis*, *Spirolaxis*, *Pseudotorinia*, (2) *Solatisonax*, *Discotectonica*, *Granosolarium*, and (3) *Basisulcata* (only known from the Atlantic Ocean), *Philippia*, *Psilaxis*, *Adelphotectonica*, *Architectonica*. The position of *Heliacus* was found to be weakly supported, the genus being mainly defined by unique derived characters and retained symplesiomorphies. The relative branching sequence in the cladogram is supported by fossil and ontogenetic evidence (BIELER, 1988). The published subdivisions of the Architectonicidae into subfamilies were found to be incongruent with recognized monophyletic groups (BIELER, 1988: 229), and were abandoned. These previously recognized subfamilies (Architectonicinae, Philippiinae, Heliacinae, Pseudomalaxinae) consisted of one or two nominal genera each, while other clades remained unassigned. Subsequently, HEALY (1991: 64) stated that studies of spermatozoa support the subfamilial division. However, his small sample (one species studied each of *Architectonica*, *Psilaxis*, *Heliacus*, and *Granosolarium*), representing one species of nominal Architectonicinae, one of Philippiinae, one of Heliacinae, one previously unassigned, none of Pseudomalaxinae, can obviously not resolve relationships at that taxonomic level. It is nevertheless noteworthy that recent studies suggested that spermatozoa of *Psilaxis oxytropis* "conceivably represent a basic or ancestral sperm type" (HEALY, 1991: 64) within the family, a conclusion that does not support the branching sequence of the cladogram in Fig. 21.

Architectonicid-like shells with heterostrophic protoconchs are known from as early as the Triassic (*Amphitomaria* KOKEN, 1897, *Rinaldoconchus* BANDEL, 1988; see BANDEL, 1988). Of the extant groups, *Pseudomalaxis*- and *Heliacus*-like shells appear earliest in the fossil record and are known from the Cretaceous, while other genera such as *Granosolarium*, *Discotectonica*, *Architectonicia*, and *Philippia* appear later, in the Eocene.

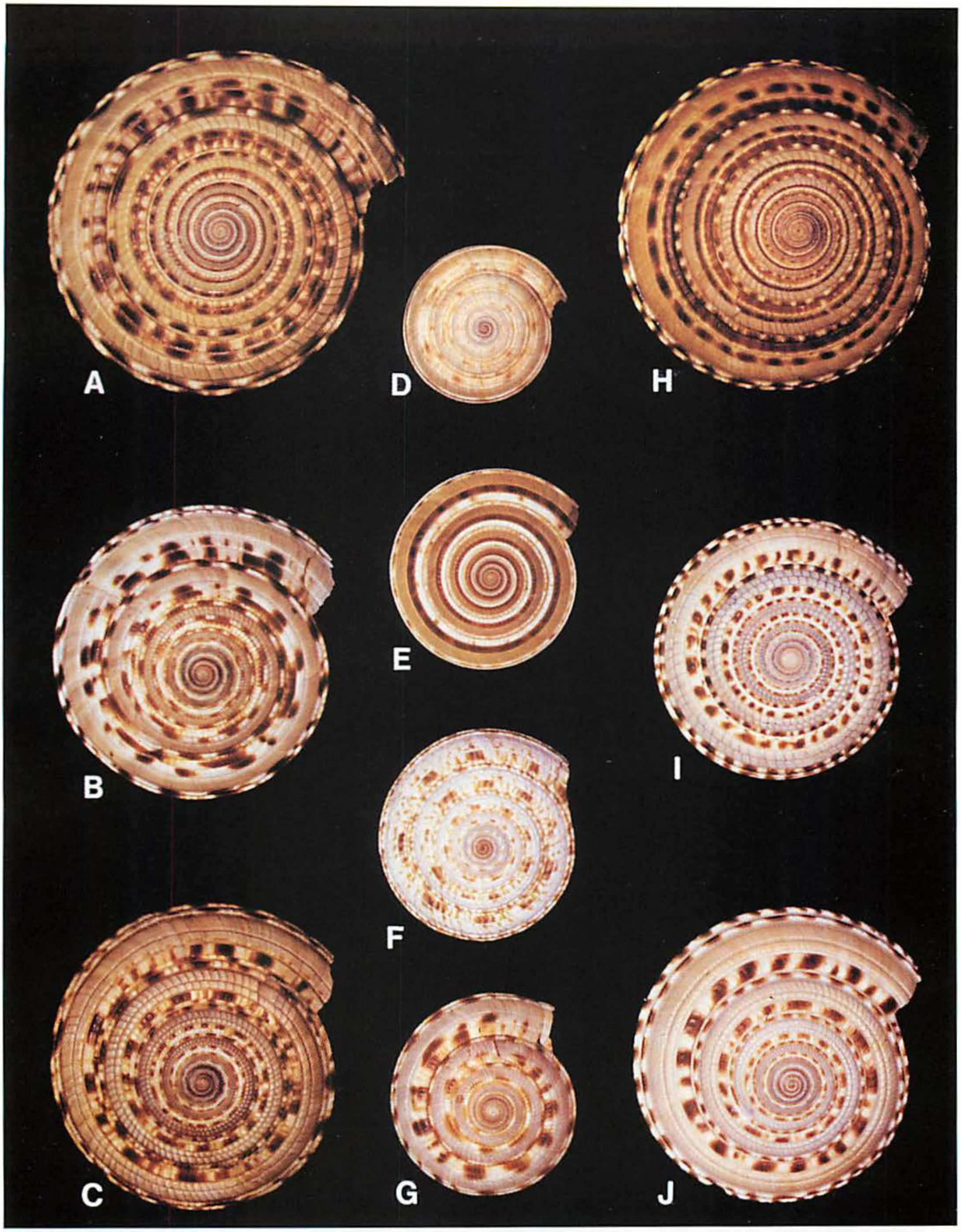
A brief overview of the sequence of appearance of architectonicid genera in time, based on fossil evidence, was given by MERRILL (1970: pl.42, modified by BIELER, 1988: 227, fig.24). Some groups with few extant members, such as *Granosolarium* and *Pseudomalaxis*, apparently had their major radiation in the Paleocene and Eocene. The family is a slowly evolving group, presumably due to ongoing communication within the gene pool through teleplanic larvae (see 'Zoogeography'), inhibiting geographic speciation. From protoconch morphology and from the wide distribution of many forms also in the fossil record, it can be inferred that individual species also had a wide range of distribution also in (at least) the Cretaceous and Tertiary. Comparison with the presumed sister group Mathildidae, with similar protoconch morphology, indicates that this trait was present even in their common ancestor. Several extant species can be traced back as 'morphospecies' into the Pliocene, some (e.g., *Architectonica nobilis*) even into the Miocene.

An additional indicator for age and stability of architectonicids is the similarity of many species in the Indo-Pacific and Atlantic regions. Genetic exchange apparently ceased in the early Pleistocene, since the existence of the Panamic isthmus, after the Atlantic and Pacific had been connected in this region for millions of years. In the probably most conservative groups, *Pseudomalaxis* and *Heliacus*, forms can be found in either ocean that belong to the same morphospecies (see *Pseudomalaxis nobilis* and *Heliacus infundibuliformis*). A number of pairs of very similar, corresponding species were found in the Indo-Pacific and Atlantic. For instance, Mediterranean *Heliacus subvariegatus* (= *fallaciosus*, *siculus* of authors) and Indo-Pacific *Heliacus stramineus* are very close; the two oceans were last connected in the Tertiary.

A question remains concerning the driving forces behind speciation into many similar, sympatric species (especially in *Heliacus* and *Architectonica*). The investigation of South African *Heliacus* populations, for instance, showed no differences in microhabitat, activity period, food or reproductive biology between the common, almost equally-sized *Heliacus variegatus*, *H. areola* and *H. trochoides*.

Plate 1. *Architectonica*, apical aspects. A: *A. taylori* (Hanley, 1962); Taiwan (ZMA unnumbered); 59.8 mm. B: *A. picta* (Philippi, 1849); Mozambique (NMP H4734); 50.2 mm. C: *A. gualtierii* n.sp. [Paratype 5]; Mozambique (NMP H8282); 51.6 mm. D: *A. arcana* n.sp. [Paratype 3]; Pakistan (BMNH 198183); 27.7 mm. E: *A. modesta* (Philippi, 1849); Mozambique (NMP H5628). F: *A. laevigata* (Lamarck, 1816); Mozambique (NMP H4685); 35.6 mm. G: *A. purpurata* (Hinds, 1844); India (SMF 256456); 34.2 mm. H: *A. trochlearis* (Hinds, 1844); Taiwan (ZMA unnumbered); 55.4 mm. I: *A. grandiosa* Iredale, 1931; Australia (MNHNP unnumbered); 44.8 mm. J: *A. maxima* (Philippi, 1849); Japan (RNHL 56656); 50.8 mm. (Page 31)

Plate 2. A: *Architectonica perspectiva* (Linné, 1758) [© National Geographic Society; N.G.S. photographer Paul A. Zahl]. B: *Heliacus* habitat. Zoanthid zone on the South African east coast (Sinkwazi, Natal, at extreme low tide. Note several species of zoanthid "soft coral." C: *Heliacus variegatus* (Gmelin, 1791) *in situ* between polyps of *Palythoa nelliae* Pax (Reunion Rocks, N. of Isipingo, Natal, South Africa). D: *Heliacus implexus* (Mighels, 1845) feeding on *Palythoa natalensis* Carlgren (Sinkwazi, Natal, South Africa). Note large cone-shaped operculum. E: *Heliacus trochoides* (Deshayes, 1830) in feeding position on polyp of *Palythoa nelliae* (from Reunion Rocks, N. of Isipingo, Natal, South Africa; some zoanthid polyps removed for photograph). Note egg mass in lower left. (Page 32)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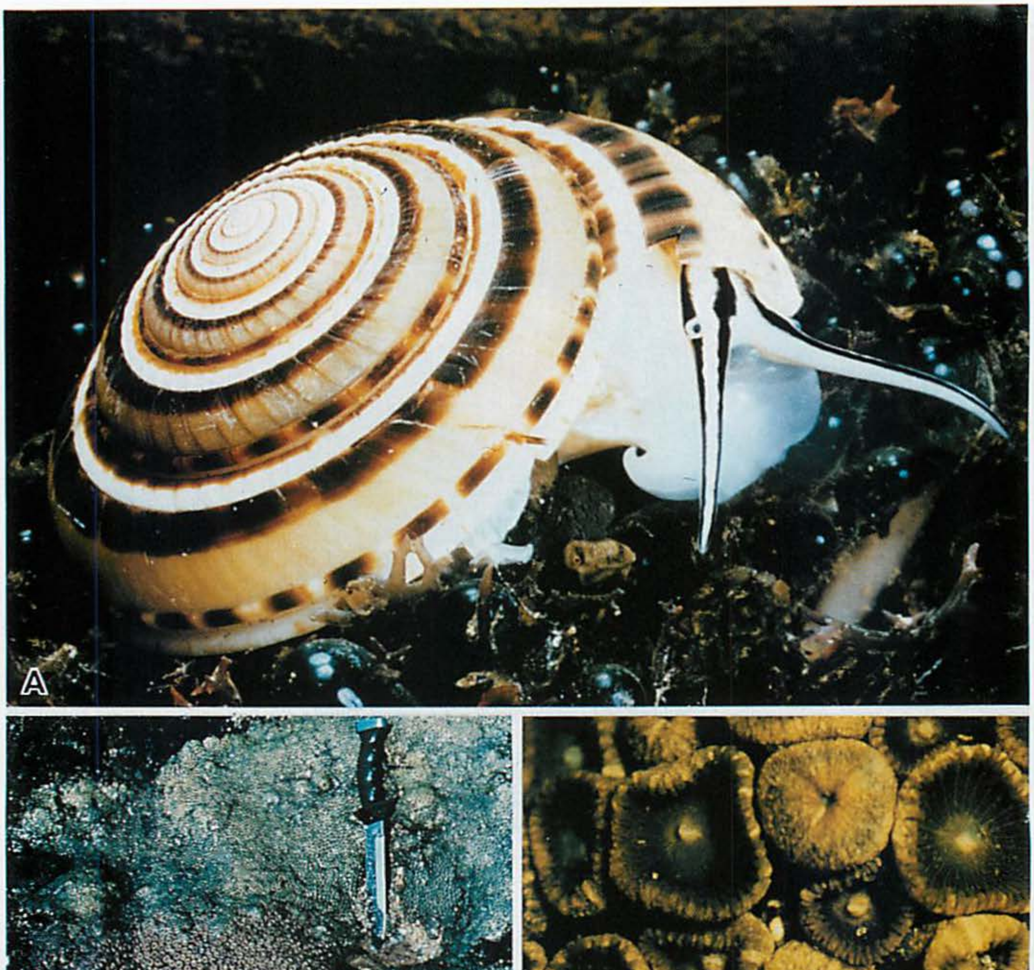
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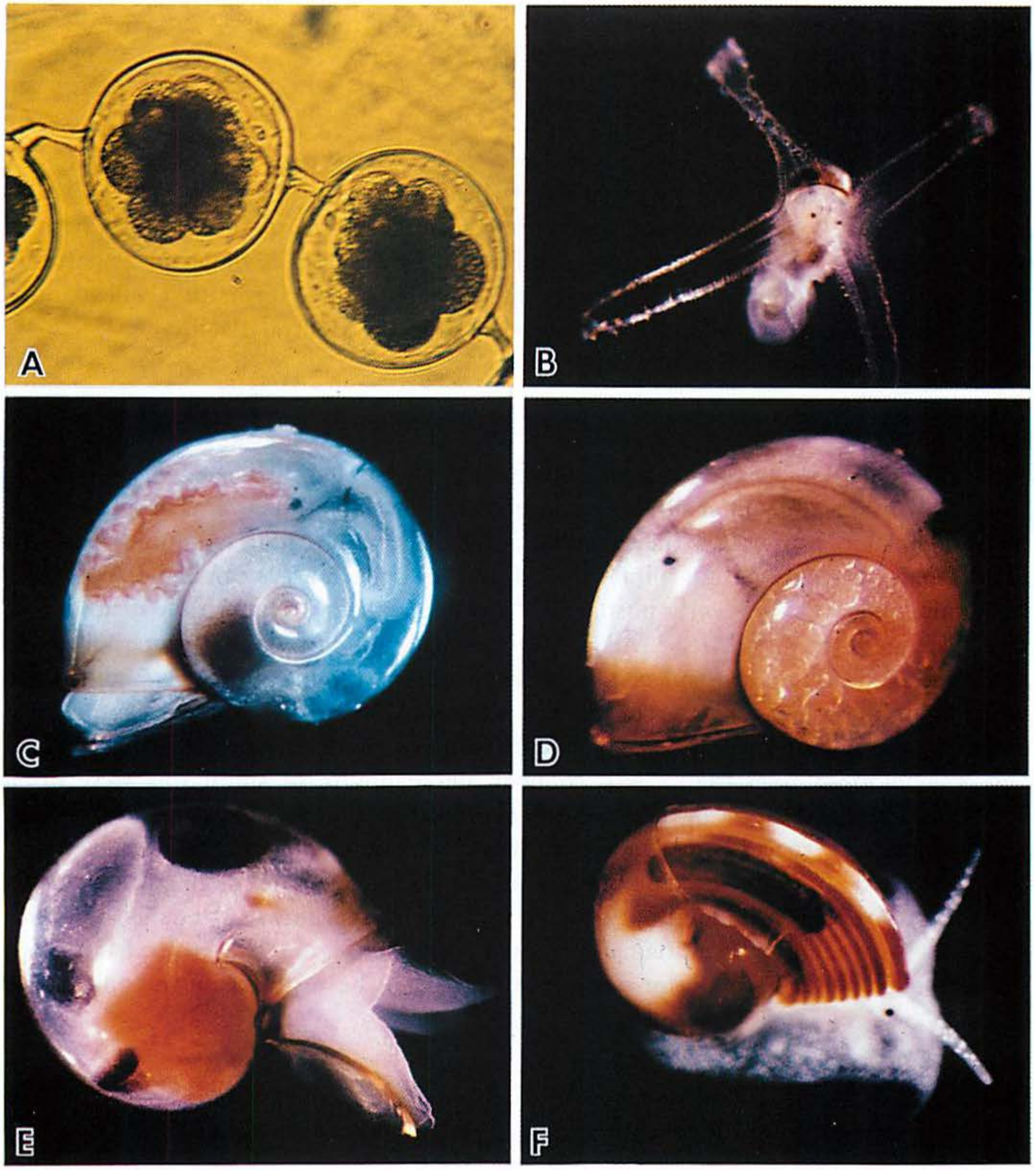


Plate 3. Architectonicid development. A: Early cleavage stage in egg mass of *Heliacus variegatus* (GMELIN, 1791), 30 minutes after deposition. Note chalazae connecting eggs. B-F: *Psilaxis oxytropis* (A. ADAMS, 1855); off Waikiki, Oahu, Hawaiian Islands [courtesy Dr. DALE B. BONAR]. B: Fully-developed, four-lobed veliger stage. C: Veliger withdrawn into shell. Note position of head (black eye spot) and velum in front of it. D: Newly metamorphosed juvenile. Note position of head (eye spot) now closer to aperture. E: Newly metamorphosed juvenile. Note anal keel on shell and black "larval organ." This side will form the apex of the adult shell. F: Stage of arrested growth. Note color pattern and first part of teleoconch whorl.

E. Systematic Part

I. Characters used in Classification

Architectonicids, and especially members of *Architectonica*, display very little variation in sculpture (such as the number and arrangement of spiral ribs) and color pattern within a species. The spiral sculpture can be used to develop a "finger-print pattern" for each species within a group of many superficially similar forms that will identify a specimen from Africa as well as a specimen from the Central Pacific.

Teleoconch

The teleoconch shape alone has no taxonomic value. Sharply keeled, coin-shaped, roundish or cone-shaped shells were convergently developed in several groups of this family. Of value, however, is the combination of shape with certain sculptural elements. In all architectonicids certain spiral ribs and thus teleoconch areas can be homologized. As a rule, at least in the early postlarval ("arrested growth") phase, four distinct ribs are developed (SSR, UMR, LMR, IPR; see diagram, last page), which differ in strength, shape, sculpture and coloration from other, secondary ribs. A study of the position of these ribs on later teleoconch whorls show marked differences between superficially similar forms (see, e.g., construction of marginal shell keel in *Heliacus* and *Pseudotorinia*, Figs.152, 224a). Number and sculpture of spiral ribs were often found to be species-typical. The coloration of the teleoconch proved to be a very stable character, especially in groups with regular color patterns such as *Architectonica*, *Philippia*, and *Heliacus* s.s. Special care needs to be taken to distinguish between normal (fresh) coloration and that of worn or aberrant specimens. After shell fractures with extensive mantle tissue damage (caused by wave action, fish or crab attacks), the normal sculptural and color pattern can often not be restored by the animal.

Protoconch

The size range of the protoconch is species-specific, and can, in connection with other characters, be used as a taxonomic character. It was found to be an ideal character to complement teleoconch characters, as it is not correlated with teleoconch size, not subject to pre-selection by the collector and easily measurable even in eroded specimens. Closely related species with similar teleoconchs were frequently found to differ considerably in protoconch size. The degree of heterostrophy, the color pattern, shape and number of whorls, presence, absence, or degree of development of umbilical folds, anal keel and callus were additional protoconch characters used in this study. A weak edge on the protoconch appears commonly, with intraspecific variability (e.g., in members of *Architectonica*) and has no taxonomic value. However, a distinct anal keel, often strengthened by a callus, was found to be a stable species-specific character in members of *Psilaxis*, *Philippia* and *Heliacus*.

Operculum

The operculum, with excellent characters at the generic level, was not found to be of use at the species level. Exceptions are *Heliacus mighelsi* and *H. discoideus*, members of the problematic *H. infundibuliformis*-complex.

Radula

At the generic and subgeneric levels, differences can be found in the number of flanking cusps on the rachidian (two or more in *Heliacus*, *Pseudotorinia* and *Pseudomalaxis*, one in *Adelphotectonica*, *Philippia* and *Psilaxis*, and absent in *Architectonica* and *Basisulcata*), and in the number of cusps on the outer marginal (three or more in all but *Architectonica* and *Adelphotectonica*). At the species level, data are still scarce, but radular formulae have occasionally been used as additional characters to distinguish between species-group taxa (see Bieler, 1988).

Data on anatomical characters, sperm, spematophores and egg masses are still too incomplete to be useful at the species level. There is an indication that the soft-body coloration in *Architectonica* (see Pl.2 Fig.A) might prove to be a valuable species-specific character.

II. Taxonomy

Class Gastropoda Cuvier, 1797
Order Heterostropha Fischer, 1885
[= Allogastropoda Haszprunar, 1985][4]

Superfamily Architectonicoidea Gray, 1840

Family Architectonicidae Gray, 1840

[as "Architectomidae," based on *Architectonica* Röding, 1798]. Includes: Solariidae Chenu, 1859 [based on *Solarium* Lamarck, 1799 = *Architectonica*]; Toriniidae Troschel, 1875 [as family "Toriniacea," based on *Torinia* Gray, 1842 = *Heliacus* Orbigny, 1842]; Teretropomidae Rochebrune, 1881 [as a family of land snails, based on *Teretropoma* Rochebrune, 1881 = *Heliacus* (*Teretropoma*)]; Heliacidae Cotton & Godfrey, 1933 [based on *Heliacus*]; Mangonuidae Iredale, 1936 [based on *Mangonuia* Mestayer, 1930 = *Pseudomalaxis* Fischer, 1885]; Pseudomalaxinae Garrard, 1977 [based on *Pseudomalaxis*]; Philippiinae Boss, 1982 [based on *Philippia* Gray, 1847].

1. Architectonicidae (Diagnosis)

Members of the Heterostropha; cone-shaped shell usually wider than high, with open umbilicus surrounded by a nodule-bearing spiral rib, sculpture of very regular spiral rings intersected by axial grooves or growth lines and, in most cases, a regular color pattern; shell circumference usually with 1 or 2 keels; columellar wall of shell aperture

[4] for other synonyms see Ponder & Warén, 1988: 308.

("inner lip") with grooves; smooth protoconch separated from the teleoconch by distinct peritreme, heterostrophic (placed "up-side-down," with the axes of proto- and teleoconch diverging by less than 10°); first part of the initial teleoconch whorls with distinct growth mark; operculum corneous, built by spirally arranged lamellae, concave, flat or cone-shaped, always with peg-like projection on body side; radula small, five-toothed taenioglossate-like, or ptenoglossate-like with numerous marginal teeth, or replaced by large rod-like structure; mantle cavity divided by dorsal crest; foliobranch gill lamellae as epithelial extensions of hypobranchial gland; osphradium with semi-circularly arranged lamellae; gonochoristic, or protrandric to simultaneous hermaphrodites; in hermaphroditic forms, male, female and sperm-receptive parts with independent openings; modified sperm type with or without helically shaped para-crystalline component; planktic development with long-range veliger; eggs interconnected by chalazae; predators on coelenterates.

2. Generic Classification

In this work, the established usage of subgeneric divisions in the genera *Architectonica, Philippia* and *Pseudomalaxis* has been abandoned. I previously (Bieler, 1988) demonstrated the pairs *Architectonica* s.s. and *Architectonica* (*Adelphotectonica*), *Philippia* s.s. and *Philippia (Psilaxis)*, as well as *Pseudomalaxis* s.s. and *Pseudomalaxis (Spirolaxis)* to form monophyletic groups. Based on currently available data, the respective members of the pairs seem to be more closely related to each other than to other members in the family. However, in order not to hamper future phylogenetic analyses by entrenching a pre-conceived hierarchy, and seeing that each of the taxa is well defined by autapomorphies, *Architectonica*, *Adelphotectonica*, *Philippia*, *Psilaxis*, *Pseudomalaxis* and *Spirolaxis* are here treated as of equal, generic rank. For the last two mentioned, Boss & Merrill (1984b) had already advocated separation at the generic level.

For *Heliacus*, the situation is different. The six subgenera here employed (*Heliacus* s.s., *Torinista*, *Grandeliacus*, *Pyrgoheliacus*, *Teretropoma*, *Gyriscus*) describe fairly well-defined species groups, the phylogenetic roots and interrelationships of which are unresolved. *Heliacus* s.l. is a problematic group, defined by a combination of autapomorphies and retained symplesiomorphies. Further research may render it necessary to remove or synonymize some of its nominal subgenera, which currently are based mainly on shell characters.

3. Indo-Pacific Species

Genus *Architectonica* Röding, 1798

Architectonica Röding, 1798: 78. Type species by subsequent designation (J.E. Gray, 1847: 151, using the incorrect secondary spelling "Architectoma"): *Trochus perspectivus* Linné, 1758; Recent, Indo-Pacific.

Synonyms:

Solarium LAMARCK, 1799: 74. Type species by monotypy: *Trochus perspectivus* LINNÉ, 1758.

Verticillus JOUSSEAUME, 1888: 194. Type species by monotypy: *Solarium formosum* HINDS, 1844 [= *Architectonica perspectiva*; not *Solarium formosum* CRISTOFORI & JAN, 1832]; not *Verticillus* MOQUIN-TANDON, 1848 (Gastropoda: Zonitidae).

Incorrect subsequent spellings:

"Architectoma" J.E. GRAY, 1847; "Architeconica" STEWART, 1927; "Architectonia" MÖRCH, 1875; "Architectonium" HAAS, 1952; "Soralium" SHUTO, 1969.

Description (Fig.22):

Teleoconch: shell usually large to extremely large, usually strong-walled, low to tall cone-shaped; umbilicus always open, moderately wide to wide (16–35% of shell diameter); upper point of whorl attachment above peripheral keel of preceding whorl, resulting in formation of distinct suture; whorls on upper (apical) side somewhat bulging; apical side with weak axial grooves; spiral ribbing either lacking except for subsutural rib (*perspectiva*-group), or distinctly developed (*maxima*-group); base usually smooth except for infraperipheral rib and two nodose ribs surrounding umbilicus (= PUR and UC) [some juveniles and *A. nobilis* have additional basal sculpture]; umbilical wall without spiral ribs; usually very regular, lively color pattern of flecks or bands in various shades of brown, fresh specimens with purplish hue in interior of aperture. *Protoconch:* small to very large (ca. 0.66–1.8), distinctly heterostrophic, with weak ridge in anal keel area, occasionally with distinct anal keel. *Radula:* ptenoglossate-like; rachidian (if present) smooth, without additional cusps, flanked by 7–14 marginals on either side; outer marginals with 2 long processes each. *Operculum:* horny, ear-shaped with very broad last whorl, flat with often callously thickened peg-like projection on body side.

The species in this genus can be sorted into two groups, based on the sculpture of the mid-field, a part of the upper-side shell-sculpture. The two resulting groups, here termed "*perspectiva*-group" and "*maxima*-group," are not considered to comprise monophyletic units, but such a division merely facilitates identification. Specimens of the "*perspectiva*-group" have mid-rib (MR) areas that are undivided, while members of the "*maxima*-group" have mid-rib areas that are divided by a distinct groove into an upper (UMR) and a lower (LMR) mid-rib.

For a more extensive description and discussion of this genus see BIELER (1985a: 233–236, 1987: 210).

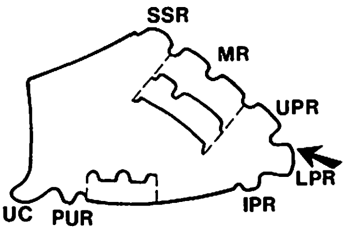


Fig. 22. Schematic representation of placement of major spiral ribs in *Architectonica*, apertural aspect. Arrow shows point of attachment of next whorl, intrageneric variation indicated by dotted lines.

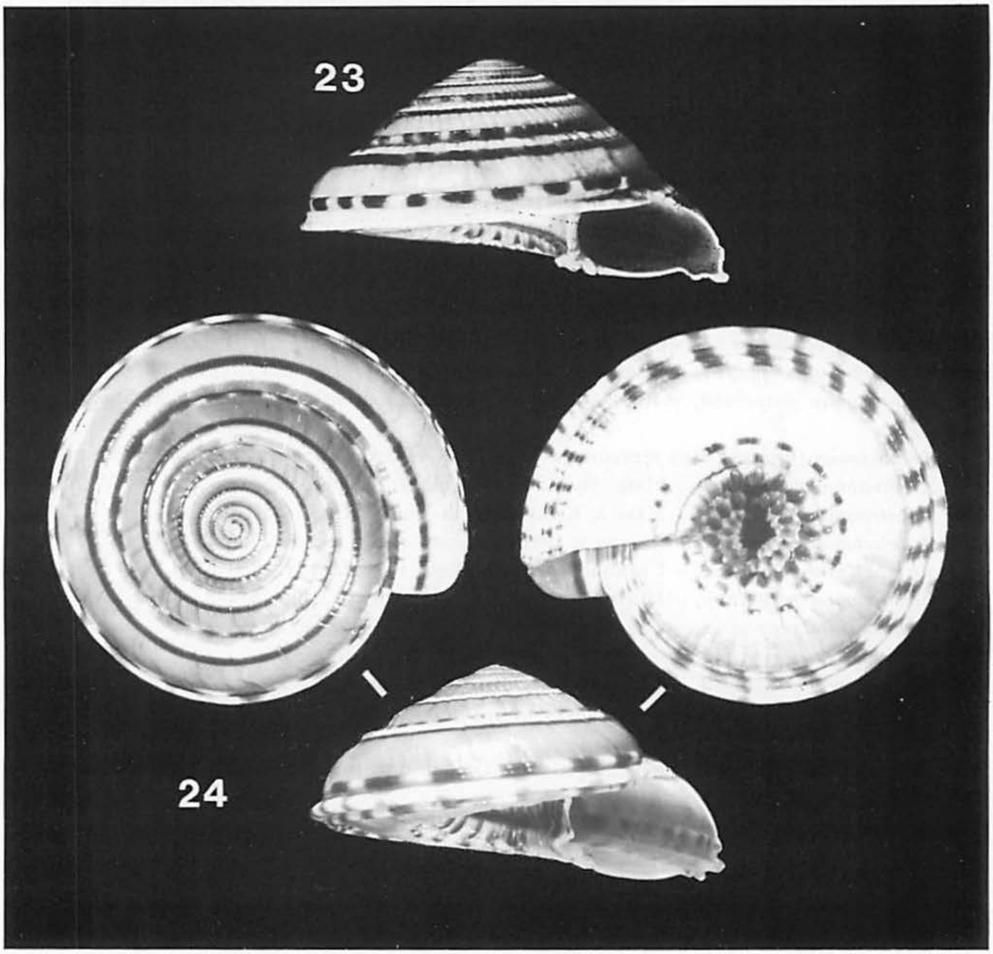
Architectonica perspectiva-group (members have shells with undivided mid-rib area):

Architectonica perspectiva (LINNÉ, 1758)
Pl.2 Fig.A; Figs.23-31

*1758 *Trochus perspectivus* LINNÉ, Syst. nat. (10. ed.), *1*: 757.
1781 "Trochus perspectivus seu opticus", - CHEMNITZ [in part], Conch. Cab., *5*: 121, pl.172 fig.1693 [not binominal].
1817 *Trochus perspectivus*, - DILLWYN, Descr. cat. Rec. shells, *2*: 784 [synonymy].
1830 *Solarium perspectivum*, - DESHAYES, 1830a, Encycl. méth., *2*(1): 157.
1832 *Solarium perspectivum*, - SOWERBY (I), Gen. Rec. foss. shells, *38*: 2 pp., 1 pl.
1834 *Solarium perspectivum*, - QUOY & GAIMARD, Voy. l'ASTROLABE, *3*: 281, pl.62 figs.20-22 [fig.21 = live animal (poor)].
1838-1839 *Solarium perspectivum*, - KIENER, Spéc. gén. icon. coqu., *10*: 3, pl.1 fig.1.
1842 *Solarium perspectivum*, - REEVE, Conch. Syst., *2*: 158, pl.213 [after SOWERBY (I), 1832].
1842 *Solarium perspectivum*, - REICHENBACH, Land-, Süsswasser-, See-Conch.: 40, pl.10 figs.262a-b.
1843 *Solarium perspectivum*, - DESHAYES, Hist. nat. [2. ed.], *9*: 97.
*1844 *Solarium fuliginosum* HINDS, 1844a, Proc. zool. Soc. Lond., *1843*: 158.
*1844 *Solarium formosum* HINDS, 1844b, Proc. zool. Soc. Lond., *1844*: 22 [non *S. formosum* CRISTOFORI & JAN, 1832, nec *S. formosum* TERQUEM & JOURDY, 1869].
1844 *Solarium formosum*, - HINDS, 1844d, Ann. Mag. nat. Hist., *14*: 437.
1846-1852 *Solarium perspectivum*, - EYDOUX & SOULEYET, Voy. 'LA BONITE', Zool., *2* [SOULEYET]: 587, pl.37 figs.10-12.
*1848 *Solarium maculatum* REEVE, Elem. conch., *1*(9): 144; *1*(4)[1846]: pl.13 fig.62 [objective synonym of *S. fuliginosum*; non *Solarium maculatum* LINK, 1807].
*1849 *Solarium australe* PHILIPPI, Z. Malakozool., *5*(11): 168.
*1849 *Solarium incisum* PHILIPPI, Z. Malakozool., *5*(11): 169.
1849 *Solarium perspectivum*, - PHILIPPI, Z. Malakozool., *5*(11): 170.
*1849 *Solarium zonatum* PHILIPPI, Z. Malakozool., *5*(11): 173.
*1850 *Solarium striatum* GRAY, J.E., Fig. moll. anim., *4*: 28; *2* [GRAY, M.E.]: pl.126 fig.6 [modified after KIENER], pl.126 figs.2-2a [after EYDOUX & SOULEYET].
1853 *Solarium formosum*, - PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 9, 28, pl.2 fig.3 [after CHEMNITZ], pl.4 fig.7.
1853 *Solarium incisum*, - PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 27, pl.4 fig.6.
1853 *Solarium australe*, - PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 29, pl.4 fig.8.
1853 *Solarium fuliginosum*, - PHILIPPI, 1853b, Syst. Conch.-Cab., II, *7*: 38.
*1862 *Solarium cumingii* HANLEY, Proc. zool. Soc. Lond., *1862*(2): 204.
1863 *Solarium (Architectonica) perspectivum*, - HANLEY, Thes. conch., *3*: 228, pl.253 figs.36-38.
1863 *Solarium (Architectonica) perspectivum* var. *incisum*, - HANLEY, Thes. conch., *3*: 228.
1863 *Solarium (Architectonica) perspectivum* var. *australe*, - HANLEY, Thes. conch., *3*: 228.
1863 *Solarium (Architectonica) Cumingii*, - HANLEY, Thes. conch., *3*: 232, pl.253 figs.44-45.
1863 *Solarium (Architectonica) fuliginosum*, - HANLEY, Thes. conch., *3*: 234, pl.251 figs.13-14.
*1863 *Solarium (Architectonica) Hanleyi* SOWERBY in HANLEY, Thes. conch., *3*: 234, pl.251 figs.15-16.
1864 *Solarium Cumingii*, - REEVE, Conch. icon, *15*: no.3, pl.1 fig.3.
1864 *Solarium fuliginosum*, - REEVE, Conch. icon., *15*: no.6, pl.1 figs.6a-b.
1864 *Solarium perspectivum*, - REEVE, Conch. icon., *15*: no.11, pl.2 figs.11a-b.
*1876 *Solarium trisulcatum* JOUSSEAUME, Bull. Soc. zool. Fr., *1*: 270, pl.5 figs.14-15.
1886 *Solarium (Architectonica) perspectivum*, - WATSON, Rep. sci. Res. Voy. CHALLENGER, *15*(42)(2): 135.
1887 *Solarium (Solarium) perspectivum* var. *australis*, - MARSHALL, Man. conch., *9*: 8, pl.2 figs.20-21 [after PHILIPPI, 1853b].
1887 *Solarium (Solarium) fuliginosum*, - MARSHALL, Man. conch., *9*: 13, pl.4 figs.47-48 [after HANLEY, 1863].

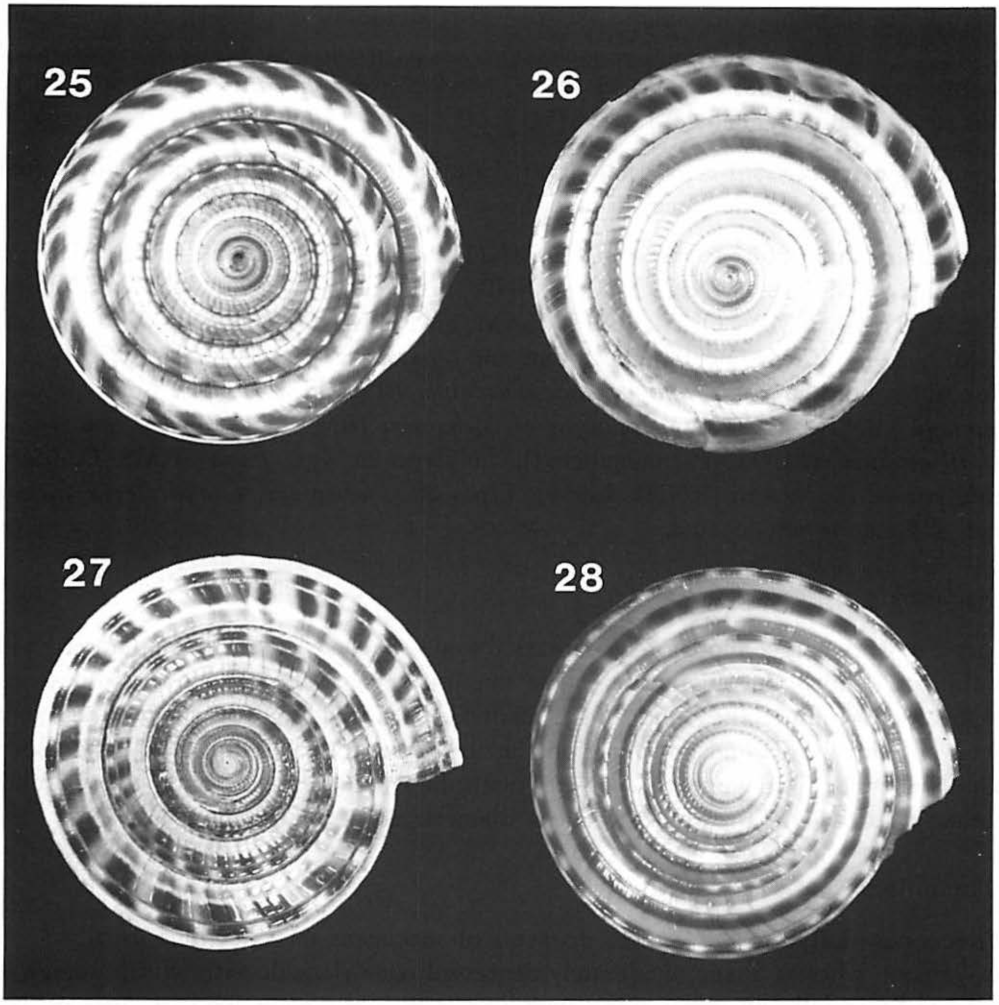
1887 *Solarium (Solarium) Cumingii*, - Marshall, Man. conch., *9*: 13, pl.5 figs.57-58 [after Hanley, 1863].
1909 *Solarium perspectivum*, - Schepman, Monogr. Res. Siboga Exped., *49*(1b): 218.
1933 *Architectonica perspectiva*, - Edmondson, Bernice P. Bishop Mus. Spec. Publ., *22*: 136, fig.60a.
*1936 *Architectonica perspectiva fressa* Iredale, Rec. Austr. Mus., *19*(5): 325, pl.23 fig.20.
1939 *Architectonica (Architectonica) perspectiva*, - Wenz, Handb. Paläozool., *6*(3): 670, fig.1912 [after Hanley, 1863].
1940 *Solarium cumingii*, - Bayer, Zool. Meded., *22*: 224 [synonymy].
1940 *Solarium fuliginosum*, - Bayer, Zool. Meded., *22*: 226 [synonymy].
1940 *Solarium fuliginosum* var. or monstr. *hanleyi*, - Bayer, Zool. Meded., *22*: 226 [synonymy].
1940 *Solarium perspectivum*, - Bayer, Zool. Meded., *22*: 233ff., figs.2-3 [synonymy].
1940 *Solarium perspectivum* var. *australis*, - Bayer, Zool. Meded., *22*: 242 [synonymy].
1940 *Solarium perspectivum* var. *formosa*, - Bayer, Zool. Meded., *22*: 243 [synonymy].
*1940 *Solarium perspectivum* var. *heurni* Bayer, Zool. Meded., *22*: 243, figs.4a-c.
1940 *Solarium perspectivum* var. ex colore, Bayer, Zool. Meded., *22*: 247.
1940 *Solarium* species, aberratio, Bayer, Zool. Meded., *22*: 253.
1941 *Architectonica perspectiva*, - Hatai, Bull. trop. indust. Inst. Palau, *7B*: 158, pl.17 figs.7-8.
1942 *Solarium perspectivum*, - Abrard, Arch. Mus. natl. Hist. nat., (6)*18*: 56, pl.6 fig.14 [Pleistocene].
1952 *Architectonica perspectiva*, - Satyamurti, Bull. Madras Gov. Mus., *1*(2)(6): 72, pl.4 figs.10a-b.
1952 *Architectonica perspectiva*, - Benthem Jutting, Shells Malay. Seas: 10, pl.8.
1960 *Solarium perspectivum*, - Franca, Mem. Jta. Invest. Ultramar, *15*: 59, pl.3 fig.4.
1960 *Solarium perspectivum*, - Franca, Mem. Jta. Invest. Ultramar, *15*: 59, pl.3 fig.4.
1961 *Architectonica perspectiva*, - Habe, Col. illus. shells Japan (*II*): 30, pl.13 fig.19.
1961 *Architectonica perspectiva*, - Rippingale & McMichael, Queensld. Gr. Barr. Reef Shells: 63, pl.6 fig.23.
1963 *Architectonica (Architectonica) perspectiva*, - Shikama & Horikoshi, Select. shells world: 30, pl.22 fig.1.
1964 *Architectonica perspectiva*, - Habe, Shells w. Pac. col., *2*: 45, pl.13 fig.19.
1966 *Architectonica perspectiva*, - Habe & Kosuge, Shells world col., *II*: 101, pl.40 fig.5.
1971 *Architectonica perspectiva*, - Wilson & Gillett, Austr. shells: 34, pl.13 figs.11, 11a-b.
1972 *Architectonica perspectiva*, - Cernohorsky, Mar. shells Pac., *II*: 194, pl.3 fig.9.
1972 *Architectonica perspectiva*, - Hinton, Shells New Guinea: 4, pl.2 figs.26-27.
1973 *Architectonica perspectiva*, - Garrard, Austr. Shell News, *3*: 9, fig.
1973 *Architectonica perspectivum*, - Kensley, Sea-shells s. Afr.: 76, fig.249.
1977 *Architectonica perspectiva*, - Garrard [in part], Rec. Austr. Mus., *31*(13): 509, fig.1 [operculum]; 510, pl.1, figs.1-6 [figs.4-6 = holotype of ssp. *fressa*; not pl.2 figs.1-3 = *A. trochlearis* (Hinds, 1844)].
1978 *Architectonica perspectiva*, - Hinton [in part], Guide Austr. shells: pl.10 fig.2 right [left and bottom = *A. trochlearis*].
1978 *Architectonica perspectiva*, - Kirtisinghe, Sea shells Sri Lanka: pl.29 fig.6.
1979 *Architectonica perspectiva*, - Kay, Hawaii. mar. shells: 97, figs.35D-E.
1980 *Architectonica perdix*, - Collins, Austr. Shell News, *28/29*: 3, fig. "bottom right" [non *Solarium perdix* Hinds, 1844].
1980 *Architectonica perspectiva*, - Shirai, Ecol. Encycl. Ryukyu Ids.: 277, fig.
1982 *Architectonica perspectiva*, - Abbott & Dance, Compend. seashells: 61, fig.
1982 *Architectonica perspectiva*, - Bosch & Bosch, Seashells Oman: 43, fig.
1982 *Architectonica perspectiva*, - Smythe, Seashells Arab. Gulf: pl.2 fig.a.
1984 *Architectonica perspectiva*, - Bieler, 1984c, Arch. Moll., *115*(1/3): pl.1 fig.1 [operculum].
1984 *Architectonica perspectiva*, - Sharabati, Red Sea shells: pl.5 figs.4-4a.
1984 *Architectonica perspectiva*, - Boss & Merrill, 1984b, Occas. Pap. Moll., *4*(66): 358, pl.56 fig.1, pl.63 fig.2, pl.64 figs.1-3 [radula, jaws].
1985 *Architectonica perspectiva*, - Bieler, 1985a, Arch. Moll., *115*(4/6): 233ff. [lectotype designation], pl.1 fig.1, fig.2 [holotype of *S. fuliginosum/maculatum*], fig.3 [holotype of *S. cumingii*], fig.4 [holotype of *S. hanleyi*], fig.5 [holotype of ssp. *fressa*], fig.6 [holotype of var. *heurni*], fig.7; [synonymy].

1985 *Architectonica perspectiva*, - DRIVAS & JAY, La Conchiglia, *17*(190–191): 8, fig.2, cover page [live animal].
1986 *Architectonica (Architectonica) fuliginosum*, - SPRINGSTEEN & LEOBRERA, Shells Philippines: 26, pl.2 fig.8.
1986 *Architectonica perspectiva*, - LAI, Mar. gastr. Taiwan, *1*: 38 fig.3.
1989 *Architectonica perspectiva*, - BOSCH & BOSCH, Seashells s. Arabia: 35, text-fig.
1989 *Architectonica perspectiva*, - BIELER, Amer. Conch., *17*(1): 21, figs.1–5 [aberrant specimens].
1991 *Architectonica perspectiva*, - ABBOTT, Seashells S.E. Asia: 27, pl.10 fig.2.



Figs. 23, 24. *Architectonica perspectica* (LINNÉ, 1758). Fig. 23: lectotype of *Trochus perspectivus*; LC (photograph courtesy BMNH); SD = 51.6. Fig. 24 (three aspects): holotype of *Solarium trisulcatum* JOUSSEAUME, 1876; MNHNP unnumbered; SD = 27.3.

Type measurements: Lectotype of *S. perspectivum*: SD= 51.6, H= 24.6 [apex damaged], UD= 12.6. Holotype of *S. fuliginosum / maculatum*: SD= 47.8, H= 27.4 [apex damaged], UD= 13.5. Holotype of *S. cumingii*: SD= 35.1, H=21.9, PD= 0.9, Tw= 7 1/4, UD= 8.5. Holotype of *S. hanleyi*: SD= 36.0, H= 17.4, PD= 0.98, Tw= 7



Figs. 25–28. Aberrant shells of *Architectonica perspectica* (LINNÉ, 1758). Fig. 25: holotype of *Solarium fuliginosum* HINDS, 1844, and of *Solarium maculatum* REEVE, 1848; BMNH 1970026; SD = 47.8. Fig. 26: holotype of *Solarium cumingii* HANLEY, 1862; BMNH 1981157; SD = 35.1. Fig. 27: holotype of *Solarium hanleyi* SOWERBY *in* HANLEY, 1863; BMNH 1980126; SD = 36.0. Fig. 28: holotype of *Architectonica perspectiva fressa* IREDALE, 1936; AMS C.60679; SD = 38.7.

3/8, UD= 11.5. Holotype of *S. trisulcatum*: SD= 27.3, H= 14.5, PD= 0.68, Tw= 6 3/4–, UD= 6.8. Holotype of ssp. *fressa*: SD= 38.7, H= 19.0, PD= 0.86, Tw= 7 3/8–, UD= 10.2. Holotype of var. *heurni*: SD= 27.7, H= 12.1, PD= 0.74, Tw= 6 3/4+, UD= 7.7.

Type localities: *S. perspectivum*: "Habitat ad O. Asiae littora"; *S. formosum*: "Amboina"; *S. fuliginosum/maculatum*: "Hab.: --- ?"/not given; *S. australe*: "Nova Zeelandia, Taiti etc."; *S. incisum*: "Patria ..."; [PHILIPPI, 1853b, p.28: "das Indische Meer (Zanzibar, [...]), das Chinesische Meer (Manila, [...])]; *S. zonatum*: not given; *S.*

striatum: not given; *S. cumingii*: "Hab.---?" ["Moluccas" on label]; *S. hanleyi*: not given; *S. trisulcatum*: "Nouvelle Calédonie"; ssp. *fressa*: "at Dundas" [IREDALE & McMICHAEL, 1962: 68: "Sydney Harbour, N.S.W."]; var. *heurni*: "Laboehan Deli (E. Sumatra)" [Labunhandeli; 3°45'N, 98°41'E].

Etymology: *perspectivus-a-um* [adjective]; Late Latin: being transparent, evident (past participle from *perspicio*, "see through").

Material studied: 2000+ specimens (AMNH, AMS, ANSP, BMNH, BPBM, CAS, DMNH, FLMNH, FMNH, HUJ, IRSNB, LACM, LC, LMA, MCZ, MNHNP, MRAC, NMP, NMW, OUM, RNHL, SAM, SMF, SMNS, UCMP, UMZC, USNM, ZIMH, ZMA, ZSM); including lectotype and 6 paralectotypes of *S. perspectivum* (LC, Box 497), holotype of *S. fuliginosum/maculatum* (BMNH 1970026), holotype of *S. cumingii* (BMNH 1981157), holotype of *S. hanleyi* (BMNH 1980126), holotype of *S. trisulcatum* (MNHNP unnumbered), holotype of ssp. *fressa* (AMS C.60679), holotype of var. *heurni* (RNHL 56654). Types of *S. formosum*, *S. australe*, *S. incisum* and *S. zonatum* not located.

Diagnosis:

Large to very large, moderately depressed cone-shaped shell with moderately wide umbilicus; whorls on upper side rather smooth, somewhat inflated; only one spiral groove below suture (i.e., midrib-area undivided); no wide groove below the axially grooved midrib-area and upper peripheral rib. Subsutural rib white with brown spiral band on upper half, upper midrib-area with dark-brown spiral band, and umbilical crenae colored dark-brown. Protoconch diameter ≤ 1.00 mm.

Description:

Teleoconch: Large to very large, diameter of specimens in collections usually 35–59 at 7 to 9+ whorls. Shape: moderately depressed cone-shaped, with whorls somewhat inflated (especially on upper side); umbilicus moderately wide (UD ca. 24% of SD). Sculpture: Upper side: SSR distinctly separated; MR-area not separated into individual ribs; Periphery: UPR and LPR strong, with LPR less wide and somewhat more prominent; in most specimens one additional narrow spiral rib between UPR and LPR; upper point of whorl attachment usually between UPR and LPR, thereby forming a shallow suture; upper side and periphery crossed by deeply incised oblique axial grooves, resulting in formation of many elongate oblique segments, becoming smooth on MR-area of body whorl of larger specimens; Base: IPR strong; usually one additional narrow spiral rib between LPR and IPR; BF without spiral ribs; with radiating plications (especially in younger specimens), stronger towards umbilicus; two distinctly separated nodulose spiral ribs (PUR and UC) surrounding umbilicus, with umbilical crenae wide and strongly nodulose; columellar wall forming almost straight inner lip with plications for support of the columellar muscle, with deepest groove in umbilical crenae overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration (see Pl.2 Fig.A): SSR white with ± distinctly separated brown spiral band on upper half; upper 1/4 to 1/3 of MR-area with dark-brown spiral band (dissolving

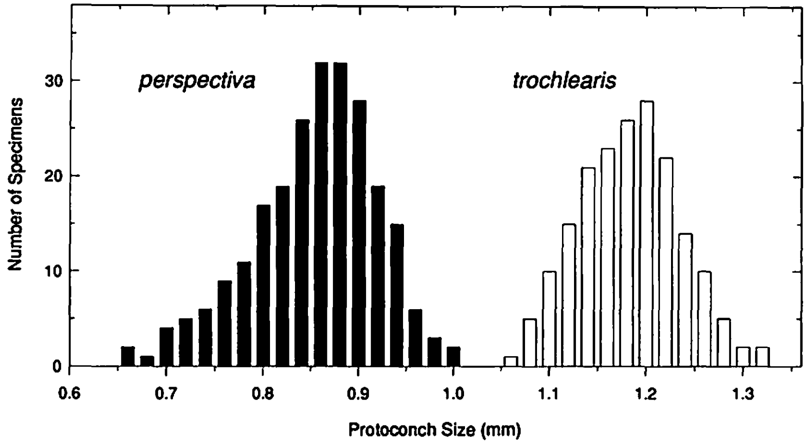


Fig. 29. Histogram of measured protoconch size. *Architectonica perspectiva* (n = 237, x̄ = 0.85, sd = 0.06), and *A. trochlearis* (n = 184, x̄ = 1.18, sd = 0.05).

into irregularly light- and dark-brown variegated band on body whorl of larger specimens); remaining MR-area greyish-brown; UPR, LPR and IPR white with ± sharply outlined, rectangular dark-brown pattern (with LPR lighter colored); BF greyish; a spiral band of small brown blotches in front of PUR; PUR white, sometimes with light-brown marks; UC dark-brown. - Protoconch [5] (see Fig.29): small to medium-sized (0.66–1.0, x̄ = 0.85); distinctly heterostrophic; anal-keel weak to well-developed; whitish to light-brown, with brown outer corner in front of varix and usually with short central brown band, starting shortly before varix (and continuing on teleoconch as brown spiral of upper MR-area).- Operculum: as described for genus. - Radula: "ptenoglossate," with 28 long, recurved, prong-like teeth per row (14–0–14), with the outer ones being shorter and forked with long tapering subequal cusps [see, e.g., Boss & Merrill, 1984b: 386, pl.56 fig.1 (not pls.63–64)]. - Jaws: consisting of numerous pointed rods (Boss & Merrill, 1984b: 359, pl.56 fig.1b). - Anatomy: extensively described by Bouvier (1886a: 94 ff., pl.4 fig.3 [6], nervous system; pl.5 figs.1–2, gross anatomy; 1887: 156 ff.) [7] and by Risbec (1955: 70,fig.8, gross anatomy; as "*Solarium trisulcatum*"). - Soft-body coloration of living animal: white tentacles with two black longitudinal stripes each, running from their tips to the upper part of the head (see Pl.2 Fig.A); remaining anterior body white with sparse brown pigment in lateral foot region. Figures and descriptions of living animals of this species in Quoy & Gaimard (1834: 282), Kiener (1838–1839: 4, fig.1) [8] and Eydoux & Souleyet (1846–1852: 587, pl.37 figs.10–12) show additional black stripes in the anterior foot

[5] The architectonicid larva described and figured as "cf. *Architectonica perspectiva*" by Scheltema & Williams (1983: 553, figs.3 E, F) does not belong to this species, the given larval shell diameter (1.26) being much too large.

[6] With figure caption of "Fig.2"; printer error (see Thiele, 1928: 82).

[7] As "*Solarium trochleare*," but based on *A. perspectiva* specimens (shells in MNHNP, unnumbered; vidi).

[8] re-figured by Chenu, 1847: 265, fig. 988; by M.E. Gray, 1850: pl.126 fig.6 [with shell sculpture modified!], and by Philippi, 1853b: pl.1 fig.1.

region. - Spermatozoa: with long, transversely banded column between the the base of the nucleus and the axonome of the midpiece (described in detail by HEALY, 1991).

Geographical distribution (see Fig.30): Continous range throughout subtropical and tropical Indo-West and Central Pacific.

Habitat: Sublittoral (most depth records between 10 and 120 m), live records from 10-65 m, sandy and muddy substrates.

Discussion:

Architectonica perspectiva is one of the most widespread and probably the most commonly collected species of its genus. The only other species with a similar color pattern and a likewise undivided midrib-area is *A. trochlearis* (see below; Fig. 31).

With thirteen names introduced for this species, *A. perspectiva* holds a record within the family Architectonicidae. Members of this species are variable in shell coloration, and a number of local and individual forms have been described as nominal species (e.g., *S. formosum* HINDS, 1844; *S. australe* PHILIPPI, 1849). Six additional names were based on individual shells, where shell coloration, and in some cases shell shape, show aberrant patterns after a repaired break in the teleoconch (i.e., *S. fuliginosum* HINDS, 1844; *S. maculatum* REEVE, 1848; *S. cumingii* HANLEY, 1862; *S. hanleyi* SOWERBY in HANLEY, 1863; *A. perspectiva fressa* IREDALE, 1936, and *S. perspectivum* var. *heurni* BAYER, 1940; see Figs.25-28). For a more extensive discussion of aberrant forms, see BIELER (1985a: 233 ff., pl.1, and 1989).

The identity of *Trochus perspectivus* LINNÉ, 1758, has been a matter of dispute in the literature, since LINNÉ (1758: 757) gave only a very short description of his species, together with references to illustrations in ARGENVILLE (1742), BUONANNI (1684), GREW (1681), GUALTIERI (1742), LISTER (1688), PETIVER (1702-1712), REGENFUSS (1758) and RUMPHIUS (1705). Not all of these figures [and those of additional references in LINNÉ's subsequent publications, the 12th edition of his 'Systema naturae' (1767:1227)

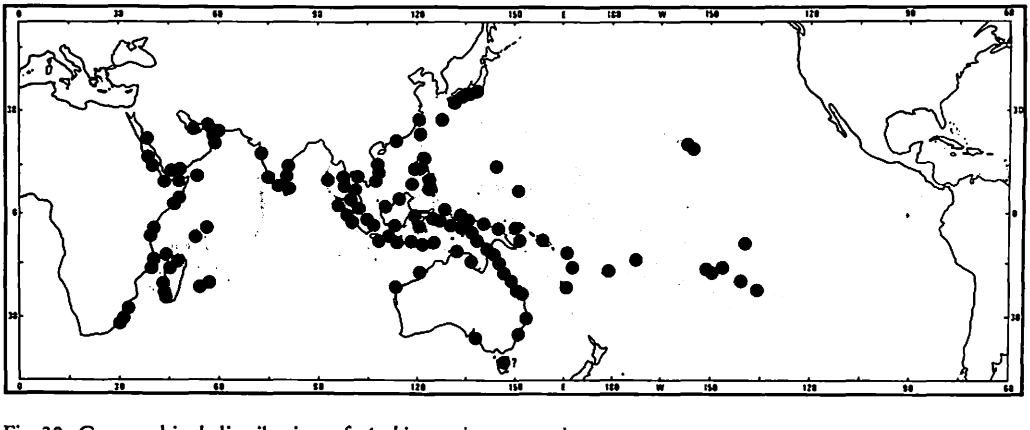
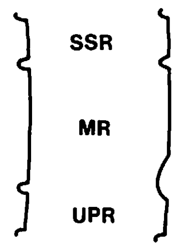


Fig. 30. Geographical distribution of *Architectonica perspectiva*.

Fig. 31. Difference in teleoconch midrib sculpture between *Architectonica perspectiva* (LINNÉ, 1758) [left] and *A. trochlearis* (HINDS, 1844) [right].



and the 'Museum Ulricae' (1764: 646)] referred to the species here considered. PHILIPPI (1853b: 6) suggested to solve the problem by dropping the "Trivialname" *Trochus perspectivus* completely. Several authors (e.g., HANLEY, 1855: 314 ff.; BAYER, 1940: 233 ff.,; DODGE, 1958: 165 ff.) attempted to restrict the use of LINNÉ's name to a single form, and the figure of "*Solarium perspectivum*" in SOWERBY (1832), reproduced by REEVE (1842: pl.208) and BAYER (1940: 240, fig.2), was declared a "good example" of this species (a "holotype," erroneously cited by GARRARD, 1977: 511, does not exist). *Solarium perspectivum* sensu SOWERBY is the only form of this species complex that has been found in the Linnean Collection in London (see also HANLEY, 1855: 314). The largest of seven specimens in that collection (LC, Box 497) was selected as lectotype (BIELER, 1985a: 235) and is here figured for the first time (Fig.23). The whorls of the type specimen are somewhat less inflated than in most specimens, here exemplified by a figure of the holotype of *Solarium trisulcatum* JOUSSEAUME, 1876 (Fig.24).

Architectonica trochlearis (HINDS, 1844)
Pl.1 Fig.H; Figs.29, 31–34

*1844 *Solarium trochleare* HINDS, 1844b, Proc. zool. Soc. Lond., *1844*: 25 [not *Solarium trochleare* SORGENFREI, 1958].
1844 *Solarium trochleare*, – HINDS, 1844d, Ann. Mag. nat. Hist., *14*: 440.
1863 *Solarium (Architectonica) trochleare*, – HANLEY, Thes. conch., *3*: 228, pl.251 figs.19–20.
1864 *Solarium trochleare*, – REEVE, Conch. icon., *15*: no.10, pl.2 fig.10.
1887 *Solarium (Solarium) perspectivum*, – MARSHALL [in part], Man. conch., *9*: 8, pl.2 figs.18–19 [after HANLEY; non *Trochus perspectivus* LINNÉ, 1758].
1940 *Solarium perspectivum* var. *trochlearis*, – BAYER, Zool. Meded., *22*: 245, fig.5a [synonymy].
1952 *Architectonica perspectiva*, – TINKER, Pac. sea shells: 176, pl. p.178, upper row.
1954 *Architectonica trochlearis*, – KIRA, Col. illus. shells Jap.: 24, pl.12 fig.6.
1962 *Architectonica trochlearis*, – KIRA, Shells w. Pac. col., *I*: 24, pl.13 fig.6.
1966 *Architectonica trochlearis*, – HABE & KOSUGE, Shells world col., *II*: 102, pl.40 fig.9.
1971 *Architectonica maxima*, – KURODA et al., Sea shells Sagami Bay: (418), 261, pl.61 fig.28 [non *Solarium maximum* PHILIPPI, 1849].
1972 *Architectonica trochlearis*, – ANGELETTI, Sea shells: 20, fig.14.
1974 *Architectonica maxima*, – DANCE, Coll. encycl. shells: 62, fig.
1974 *Architectonica perspectiva*, – MORRIS [in part], Field guide Pac. coast shells: 223, pl.7 fig.1, pl.67 fig.7 "above" [not "below, left and right" = *A. nobilis* RÖDING, 1798].
1977 *Architectonica (Architectonica) perspectiva*, – GARRARD [in part], Rec. Austr. Mus., *31*(13): 510, pl.2 figs.1–3 [not pl.1 figs.1–6 = *A. perspectiva*].

1978 *Architectonica perspectiva*, - HINTON [in part], Guide Austr. shells: pl.10 figs.2 left and bottom [right = *A. perspectiva*].
1979 *Architectonica perspectiva*, - HINTON, Guide shells Papua: pl.1 figs.7-7a.
1984 *Architectonica nobilis*, - SENDERS & SENDERS, Shells - coll. col. guide: fig.20 (left) [non *A. nobilis* RÖDING, 1798].
1986 *Architectonica (Architectonica) perspectiva*, - SPRINGSTEEN & LEOBRERA, Shells Philippines: 24, pl.2 fig.5.
1986 *Architectonica trochlearis*, - LAI, Mar. gastr. Taiwan, *1*: 38, fig.2.
1989 *Architectonica maxima*, - WYE, Shells world: 40, fig.1.

Original measurements: SD= ca. 61.2, UD= ca. 16.9 [after HINDS, 1844b].

Type locality: "Indian Seas ... It is no doubt an Indian species, but the locality is not known."

Etymology: *trochlearis-e* [adjective]; Late Latin: shaped like a pulley.

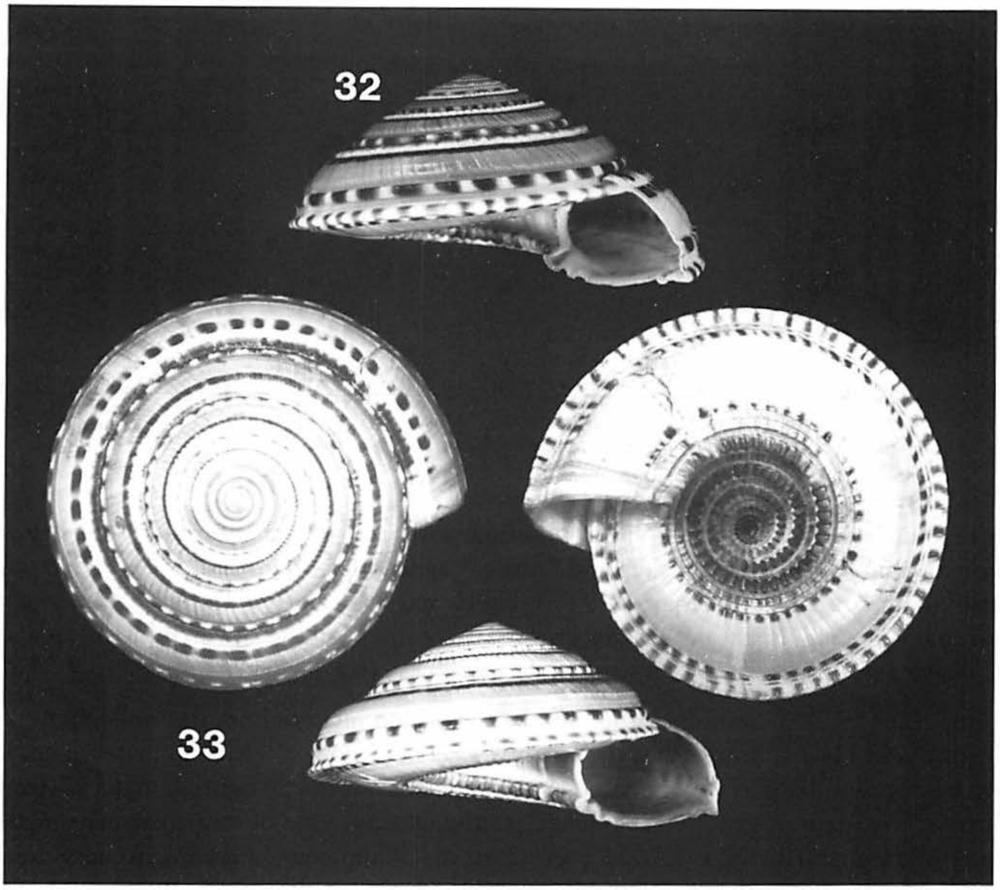
Material studied: 390 specimens (AMNH, ANSP, BMNH, BPBM, CAS, DMNH, FLMNH, FMNH, HUJ, IRSNB, LACM, MNHNP, MRAC, NMP, NMW, OUM, RNHL, SMF, UCMP, UMZC, USNM, ZMA, ZMK, ZSM, COLL. ALF). Type material not located (BMNH).

Diagnosis:

Very large to extremely large, depressed cone-shaped shell with widely open umbilicus; whorls on upper side rather smooth, somewhat inflated; only one spiral groove below suture (i.e., midrib-area undivided), and with ± wide groove below axially grooved midrib-area and upper peripheral rib. Subsutural rib white with variegated brown spiral band on upper part, upper midrib-area with dark-brown spiral band, and umbilical crenae dark-brown. Protoconch diameter ≥ 1.00 mm.

Description:

Teleoconch: Very large to extremely large; diameter of specimens in collections usually 45–65 at 7 1/2 to 9 whorls. Shape: depressed (rarely moderately high-spired) cone-shaped; umbilicus wide (UD ca. 30% of SD); whorls on upper side weakly convex. Sculpture: as in *A. perspectiva*, but with finer axial sculpture and with a ± wide, shallow groove (Fig.31) between MR-area and UPR (often with one additional fine rib in this groove). Coloration (see Pl.1 Fig.H): SSR white with variegated brown spiral band on upper part; MR-area bluish-grey on early whorls, grey on later whorls, upper 1/5 with dark-brown spiral band (dissolving into ± regular brown blotches on body whorl of larger specimens; coloration of periphery and base as in *A. perspectiva*, with blotches often finer and more numerous and PUR usually flecked with brown. - Protoconch (see Fig.29): medium-sized to large (1.06–1.32, $\bar{x}$ = 1.18); distinctly heterostrophic; anal keel weak to well-developed; yellowish with brown outer corner in front of varix, or completely brown.- Operculum: as described for genus. - Radula and Anatomy: not known. The anatomical observations published by BOUVIER (1886a,b, 1887) for "*Solarium trochleare* HINDS, 1844" are based on specimens of *A. perspectiva* [shells in MNHNP, unnumbered; vidi].



Figs. 32, 33. *Architectonica trochlearis* (HINDS, 1844). Fig. 32: specimen from Tosa, Japan; USNM 711428; SD = 54.2. Fig. 33 (three aspects): specimen from the Philippines; BMNH 1970027; SD = 68.7.

Geographical distribution (see Fig.34): Apparently less common in the Indian Ocean than in the western to central Pacific.

Habitat: Sublittoral (most depth records between 30 and 200 m, rarely to 400 m), live records from 30–90 m, sandy and muddy substrates.

Discussion:

Architectonica trochlearis is one of the largest forms of its genus, which might account for its frequent confusion with *A. maxima* (PHILIPPI, 1849). The most obvious feature to distinguish the two is the midrib-area, which in *A. maxima* is divided into two distinct spiral ribs (see Figs.39, 40).

Architectonica trochlearis is very close to *A. perspectiva*. It attains a much larger adult size and has a distinctly larger protoconch (Fig.29). *A. trochlearis* shells are usually

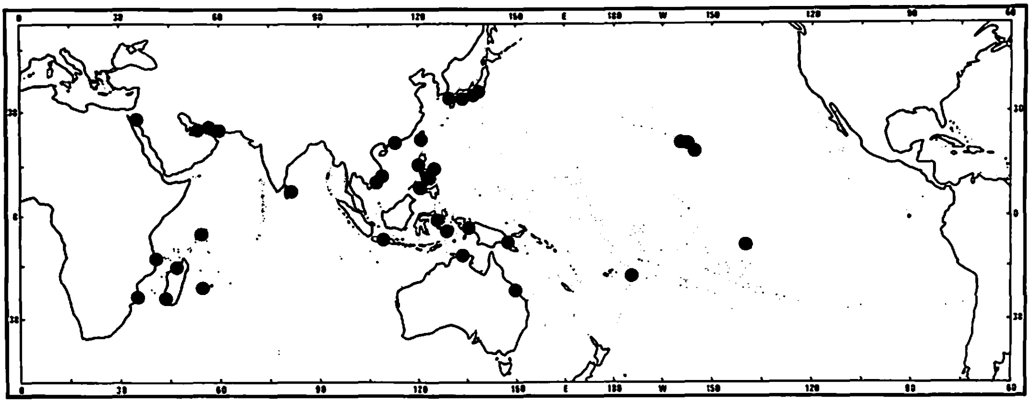


Fig. 34. Geographical distribution of *Architectonica trochlearis*.

more bluish in color, which, in connection with the firmly attached olive-brown periostracum, results in a darker and "dirtier" appearance than that of *A. perspectiva* shells (compare color photographs, Pl.1 Fig.H and Pl.2 Fig.A). The two species can be readily distinguished by a wide groove at the base of the lower mid-rib area in *A. trochlearis*, which is not present in *A. perspectiva* (see Fig.31).

HINDS (1844b: 25) described this species based on material in the collections of CUMING and HINDS, noting that the locality was "not known." Original material could not be located (BMNH). HANLEY (1863) and REEVE (1864) figured material from CUMING's collection, giving "Philippines" as the locality. One of two specimens in the British Museum (BMNH 1970027; ex CUMING; Philippines) that might have been used for those illustrations is figured here (Fig.33).

Architectonica perdix (HINDS, 1844)
Figs.35–38

*1844 *Solarium perdix* HINDS, 1844b, Proc. zool. Soc. Lond., *1844*: 22.
1844–1845 *Solarium perdix*, - HINDS, 1844c–1845, Zool. voy. SULPHUR, *3*: 50, *2*: pl.14 figs.3–4.
1844 *Solarium perdix*, - HINDS, 1844d, Ann. Mag. nat. Hist., *14*: 438.
1853 *Solarium perdix*, - PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 8, pl.1 figs.8–9 [after HINDS, 1844c].
*1862 *Solarium dunkeri* HANLEY, Proc. zool. Soc. Lond., *1862*(2): 204.
1863 *Solarium (Architectonica) Dunkeri*, - HANLEY, Thes. conch., *3*: 233, pl.252 figs.29–30.
1863 *Solarium (Architectonica) perdix*, - HANLEY, Thes. conch., *3*: 233, pl.251 figs.17–18.
1864 *Solarium perdix*, - REEVE, Conch. icon., *15*: no.1, pl.1 fig.1.
1864 *Solarium Dunkeri*, - REEVE, Conch. icon., *15*: no.17, pl.3 fig.17.
1887 *Solarium (Solarium) perdix*, - MARSHALL, Man. conch., *9*: 9, pl.2 figs.24–25 [after HINDS, 1844c]
1887 *Solarium (Solarium) Dunkeri*, - MARSHALL, Man. conch., *9*: 9, pl.2 figs.26–27 [after HANLEY, 1863].
1940 *Solarium dunkeri*, - BAYER, Zool. Meded., *22*: 225 [synonymy].
1940 *Solarium perdix*, - BAYER, Zool. Meded., *22*: 233 [synonymy].
1961 *Architectonica perdix*, - RIPPINGALE & MCMICHAEL, Queensld. Gr. Barr. Reef shells: 63, pl.6 fig.25.
1961 *Architectonica perdix*, - CHUANG, Malayan shores: 153, pl.59 fig.2.
1966 *Architectonica perdix*, - HABE & KOSUGE, Shells world col., *II*: 102, pl.40 fig.6.

1971 *Architectonica perdix*, - WILSON & GILLETT, Austr. shells: 34, pl.13 figs.9-9a.
1973 *Architectonica perdix*, - GARRARD, Austr. Shell News, *3*: 9, fig.
1977 *Architectonica (Architectonica) perdix*, - GARRARD, Rec. Austr. Mus., *31*(13): 509, fig.3 [operculum]; 514, pl.1 figs.13-15.
1978 *Architectonica perdix*, - HINTON, Guide Austr. shells: pl.10 fig.3.
1979 *Architectonica perdix*, - HINTON, Guide shells Papua: pl.1 figs.6-6a.
1980 *Architectonica* sp., - COLLINS, Austr. Shell News, *28/29*: 3, fig. "bottom left".
1982 *Architectonica perdix*, - ROBERTS et al., Shallow wat. mar. moll. NW Java: 28, pl.6 fig.1.

Type measurements (lectotype of *Solarium dunkeri*, here designated): SD= 31.0, H= 20.0, PD= ca. 0.84, Tw= ca. 7 1/10, UD= 6.7.

Type localities: *S. perdix*: "Ceylon; north-west coast of Australia"; *S. dunkeri*: "Hab. Insulas Indiae orientalis."

Etymology: *perdix* [noun in apposition]; Latin: partridge.

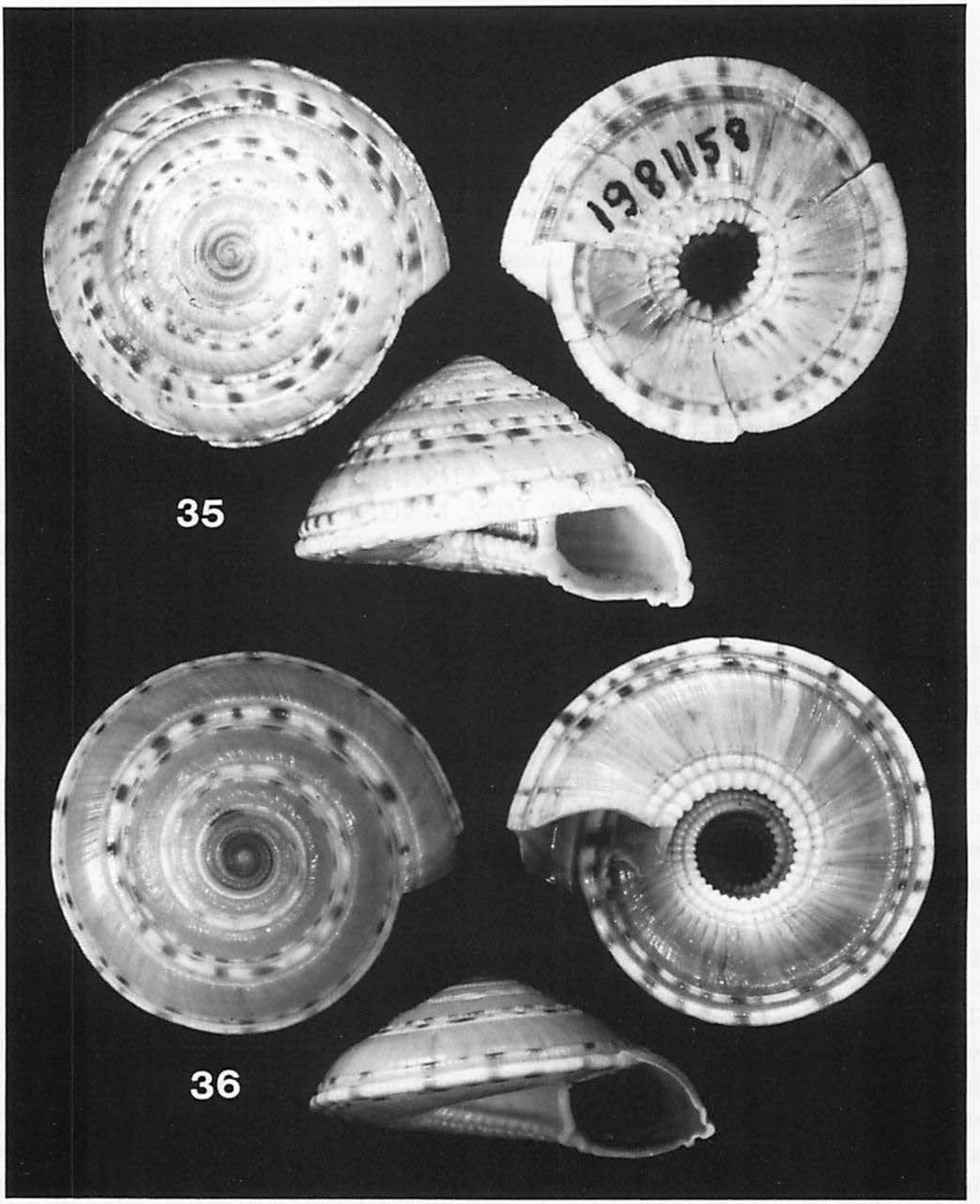
Material studied: 855 specimens (AMNH, ANSP, BMNH, CAS, DMNH, FLMNH, FMNH, HUJ, IRSNB, LACM, LMA, MCZ, MNHNP, NMP, NMW, RNHL, SMF, SMNS, UCMP, UMZC, USNM, ZIMH, ZMA, ZSM); including lectotype of *S. dunkeri* (BMNH 1981158). Type specimen of *S. perdix* not found (BMNH).

Diagnosis:

Large, moderately depressed to high-spired cone-shaped shell with moderately wide umbilicus; whorls on upper side rather smooth, inflated; only one spiral groove below the suture (i.e., midrib-area undivided); no wide groove below the axially grooved midrib-area and upper peripheral rib. Subsutural rib whitish with brown pattern, midrib-area plain light-brown (rarely with brown spiral band on upper edge); and umbilical crenae light-brown. Protoconch diameter < 1.00 mm.

Description:

Teleoconch: Large, diameter of specimens in collections usually 25-35 at 6 to 7 1/2 whorls; ranging from thin- to thick-walled. Shape: moderately depressed to fairly high-spired cone-shaped, with whorls somewhat inflated (especially on upper side); umbilicus moderately wide (UD ca. 24% of SD). Sculpture: Upper side: with fine and closely-spaced axial growth lines; SSR distinctly separated; MR-area not separated into individual ribs (rarely with faint spiral grooves); Periphery: UPR and LPR strong, of approximately equal strength, without additional spiral ribs; upper point of whorl attachment usually on upper edge of LPR, thereby forming a narrow suture; upper side and periphery crossed by narrow-spaced, ± weakly incised oblique axial grooves, resulting in formation of many elongate oblique segments, becoming smooth on MR-area of body whorl of larger specimens; Base: IPR strong; rarely one additional narrow spiral rib between LPR and IPR; BF without spiral ribs; with radiating plications (especially in younger specimens), stronger towards umbilicus; two distinctly separated nodulose spiral ribs (PUR and UC) surrounding umbilicus, with umbilical crenae wider and with uniformly shaped nodules; columellar wall forming an almost



Figs. 35, 36. *Architectonica perdix* (HINDS, 1844). Fig. 35: lectotype of *Solarium dunkeri* HANLEY, 1862; BMNH 1981158; SD = 31.0. Fig. 36: specimen from N. Borneo; USNM 632389; SD = 30.8.

straight inner lip with plications for support of the columellar muscle, with deepest groove in umbilical crenae overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration: SSR, UPR, LPR and IPR whitish, with ± regular brown pattern (LPR lightest colored); MR-area light-brown (some specimens with diffuse brown spiral band on upper edge); BF and PUR marbled with shades of mauve; PUR

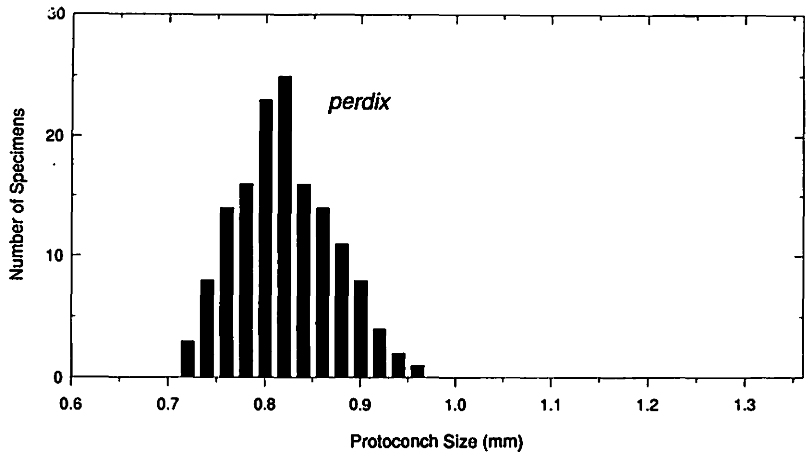


Fig. 37. Histogram of measured protoconch size. *Architectonica perdix* (n = 145, x̄ = 0.82, sd = 0.05).

often with additional blotches of light-brown; UC light-brown. - Protoconch (see Fig.37): small to medium-sized (0.72–0.96, x̄ = 0.82); distinctly heterostrophic; often with ridge in anal-keel area; yellowish to light-brown, with short central brown band in some specimens, starting shortly before varix (and continuing on teleoconch as brown spiral of upper MR-area on early whorls). - Operculum: as described for genus. - Radula and Anatomy: not known.

Geographical distribution (Fig.38): Common in subtropical and tropical eastern Indian Ocean and West- to Central Pacific. Records from western Indian Ocean and northern Central Pacific still questionable.

Habitat: Sublittoral (most depth records between 10 and 60m), live records from 15–50 m, sandy substrates.

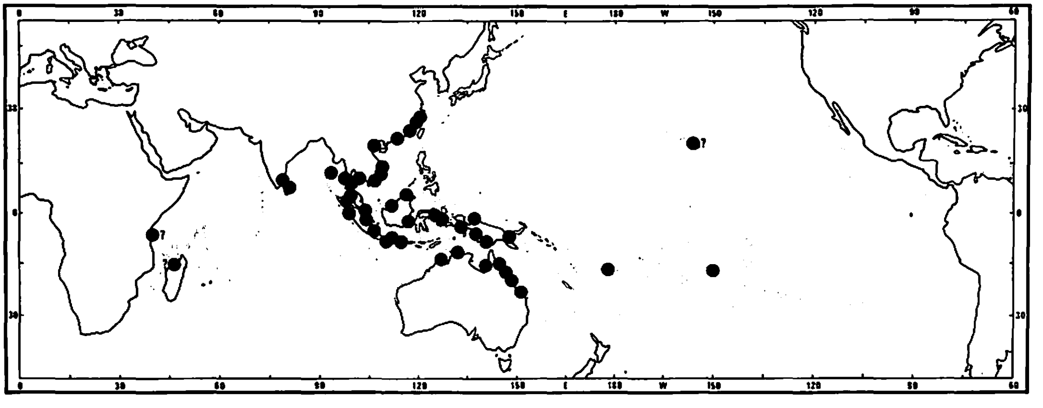


Fig. 38. Geographical distribution of *Architectonica perdix*.

Discussion:

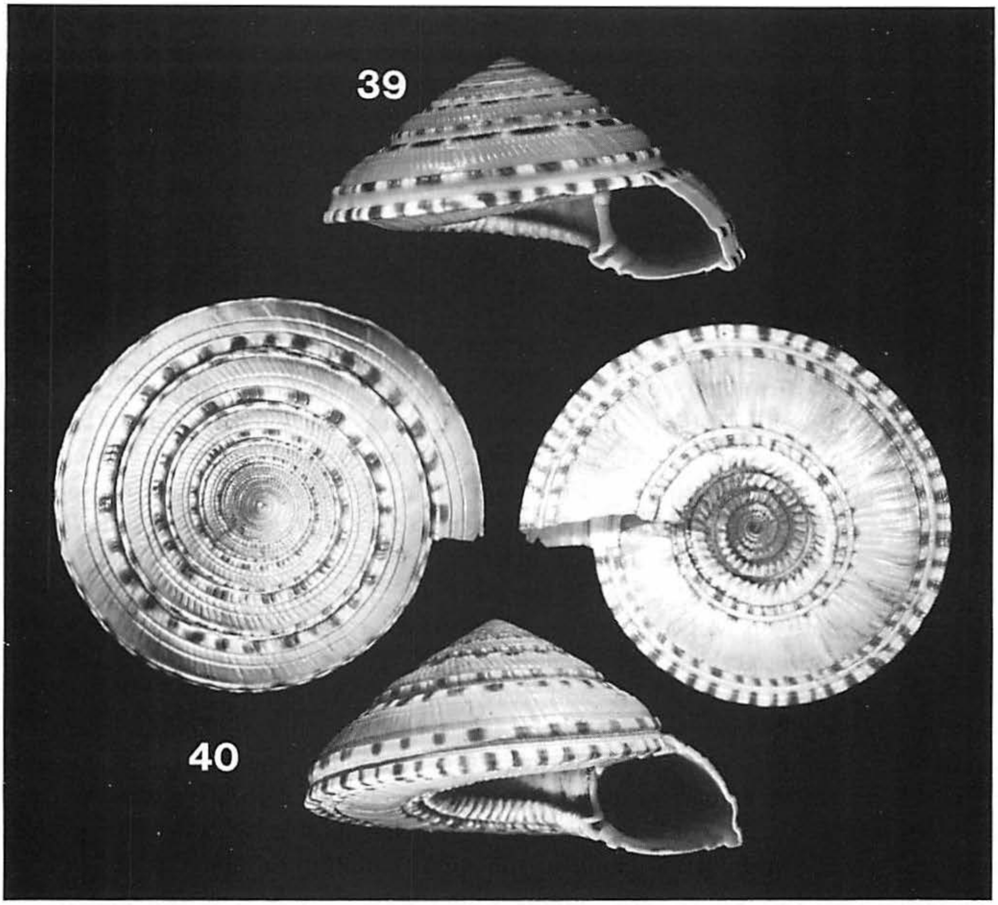
Architectonica perdix is often confused with *Adelphotectonica reevei* (HANLEY, 1862), because of its relatively small size, the often fairly high-spired shell shape, the more or less fine axial sculpture, and the light-brown shell coloration. Characters that allow easy distinction between the two are the position of the upper point of attachment of the whorls (much lower in *A. reevei*, making the lower peripheral rib part of the upper-side sculpture), and the protoconch, which is much larger and dark-brown in *A. reevei*.

Shell wall thickness is very variable in *A. perdix*. The two extremes of the continuum have been named as separate species, *Solarium perdix* HINDS, 1844, and *Solarium dunkeri* HANLEY, 1862, which are here synonymized. *Solarium perdix* was described by HINDS (1844b: 22) based on specimens from the collections of CUMING and HINDS. Original material was not located (BMNH), but HIND's figures (1844c: pl.14 figs.3–4) allow positive identification. HANLEY's *S. dunkeri* was based on specimens in the collections of CUMING and HANLEY (1862: 204). One specimen (Coll. CUMING) was later figured by HANLEY (1863: pl.252 figs.29–30). One syntype (ex Coll. CUMING) is in the British Museum (BMNH 1981158) and is here selected as a lectotype of *Solarium dunkeri* (see Fig.35).

***Architectonica maxima*-group** (members have shells with mid-rib area divided into upper and lower mid-rib):

Architectonica maxima (PHILIPPI, 1849)
Pl.1 Fig.J; Figs. 1, 39–42

1795 "Trochus Perspectivus Australis", - CHEMNITZ, Conch.-Cab., *11*: 162, pl.196 figs.1884–1885 [not binominal].
1816 *Solarium Perspectivum*, - LAMARCK, Tabl. encycl. méth.: pl.446 figs.1a-b [non *Trochus perspectivus* LINNÉ, 1758].
*1849 *Solarium maximum* PHILIPPI, Z. Malakozool., *5*(11): 170.
1853 *Solarium maximum*, - PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 6, pl.1 fig.2–3.
1859 *Solarium perspectivum*, - CHENU, Man. conch. paléont., *1*: 232, fig.1352.
1863 *Solarium (Architectonica) maximum*, - HANLEY, Thes. conch., *3*: 229, pl.250 figs.5–6.
1864 *Solarium maximum*, - REEVE, Conch. icon., *15*: no.4, pl.1 fig.4.
1887 *Solarium (Solarium) maximum*, - MARSHALL [in part], Man. conch., *9*: 9, pl.3 figs.31–32 [after HANLEY, 1863].
1954 *Architectonica maxima*, - KIRA, Col. illus. shells Jap.: 24, pl.12 fig.7.
1962 *Architectonica maxima*, - KIRA, Shells w. Pac. col., *I*: 25, pl.13 fig.7.
1971 *Architectonica trochlearis*, - KURODA, et al., Sea shells Sagami Bay: 261, pl.61 figs.26–27 [non *Solarium trochleare* HINDS, 1844].
1974 *Architectonica trochlearis*, - DANCE, Coll. encycl. shells: 63, fig.
1978 *Architectonica maxima*, - HINTON, Guide Austr. shells: pl.10 fig.1.
1979 *Architectonica maxima*, - HINTON, Guide shells Papua: pl.1 figs.5–5a.
1980 *Architectonica maxima*, - SHIRAI, Ecol. encycl. Ryukyu Islands: 277, fig.
1984 *Architectonica maxima*, - BIELER, 1984d, Verh. natw. Ver. Hamburg, (NF)*27*: 468, pl.1 figs.I–III.
1985 *Architectonica maxima*, - BIELER, 1985a, Arch. Moll., *115*(4/6): 233.
1986 *Architectonica (Architectonica) maxima*, - SPRINGSTEEN & LEOBRERA, Shells Philippines: 26, pl.2 fig.7.



Figs. 39, 40. *Architectonica maxima* (PHILIPPI, 1849). Fig. 39: specimen from Tosa Bay, Japan; USNM 820577; SD = 57.8. Fig. 40 (three aspects): specimen from "mare austr."; SMF 256454/1; SD = 70.8.

Original measurements: SD= ca. 64.0, H= ca. 29.8, UD= ca.19.6 [after PHILIPPI, 1849].

Type locality: not given; PHILIPPI (1853): "Aufenthaltsort unbekannt" [= not known].

Etymology: *maximus-a-um* [adjective]; Latin; superlative of *magnus-a-um*: large, great.

Material studied: 205 specimens (AMNH, ANSP, BMNH, CAS, DMNH, FLMNH, FMNH, HUJ, IRSNB, LACM, LMA, MCZ, MNHNP, NMP, NMW, OUM, RNHL, SMF, SMNS, UCMP, UMZC, USNM, ZIMH, ZSM, COLL. ALF). Type material not located.

Diagnosis:

Very large to extremely large, moderately depressed cone-shaped shell with widely open umbilicus; whorls on upper side gemmate, somewhat inflated; two spiral grooves below suture (midrib-area divided subequally, with upper midrib narrower), and wide groove at base of lower midrib. Subsutural rib whitish with brown pattern, midribs tan without color pattern, proxumbical rib variegated light- and dark-brown; and umbilical crenae whitish-brown with darker markings. Protoconch diameter > 1.20 mm.

Description:

Teleoconch: Very large to extremely large, diameter of specimens in collections usually 50–65 (rarely up to 75) at 7 1/2 to 8 1/2 whorls; ranging from rather thin- to thick-shelled. Shape: moderately depressed cone-shaped, with whorls somewhat inflated (especially on upper side); umbilicus wide (UD ca. 33% of SD). Sculpture: Upper side: SSR distinctly separated; LMR wider than UMR (usually ca. 2:1); ± wide groove at the base of LMR (in this groove often one additional fine spiral rib); fine nodulose sculpture of upper side due to many axial grooves (often >100 per whorl on 5th to 7th whorl); Periphery: PR strong, often with 1 additional fine spiral rib between UPR and LPR; upper point of whorl attachment usually above LPR (thereby covering it; suture narrow); upper side and periphery crossed by deeply incised oblique axial grooves, resulting in formation of many elongate oblique segments, becoming weaker or smooth on MR-areas of body whorl of larger specimens; segments of the two midribs not necessarily corresponding; Base: IPR strong; often one additional narrow spiral rib between LPR and IPR; BF without spiral ribs; with radiating plications (especially in younger specimens), stronger towards umbilicus; two distinctly separated nodulose spiral ribs (PUR and UC) surrounding umbilicus, with umbilical crenae strong and irregular on later whorls; columellar wall forming almost straight inner lip with plications for support of the columellar muscle, with deepest groove in umbilical crenae overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration (see Pl.1 Fig.J): SSR initially white, with pattern of brown blotches (ca. 12–20 per whorl, each 2–3 nodules wide), starting at about 2 1/2 Tw; UMR initially mauve-brown, turning tan as LMR after about 2 1/2 Tw; UPR, LPR and IPR whitish with brown blotches, (each about two nodules wide); BF flamed with greyish-brown; one spiral band of small brown blotches in front of PUR; PUR initially white, later variegated light- and dark-brown; UC whitish-brown with darker markings (lighter colored on body whorl of large specimens). - Protoconch (see Fig.41): large to very large (1.2–1.64, $\bar{x}$ = 1.45); distinctly heterostrophic; with weakly defined ridge or distinct anal-keel; yellowish-brown. - Operculum: as described for genus. - Radula: "ptenoglossate," with 28 long, recurved, prong-like teeth per row (14–0–14); the outer ones being shorter and forked with long, tapering subequal cusps [see Boss & Merrill, 1984b: 358, pl.63 fig.2 and pl.64 figs.1–3 (as "*Architectonica perspectiva*"; based on USNM 747000, juvenile specimen, vidi)]. - Anatomy: not known.

Geographical distribution (Fig.42): Indian Ocean to western and central Pacific (Society Islands). Records from Madagascar, Australia and New Zealand in need of verification.

Habitat: Sublittoral (most depth records between 10 and 165 m, rarely to 280 m), live records from 10–50 m, sandy and muddy substrates.

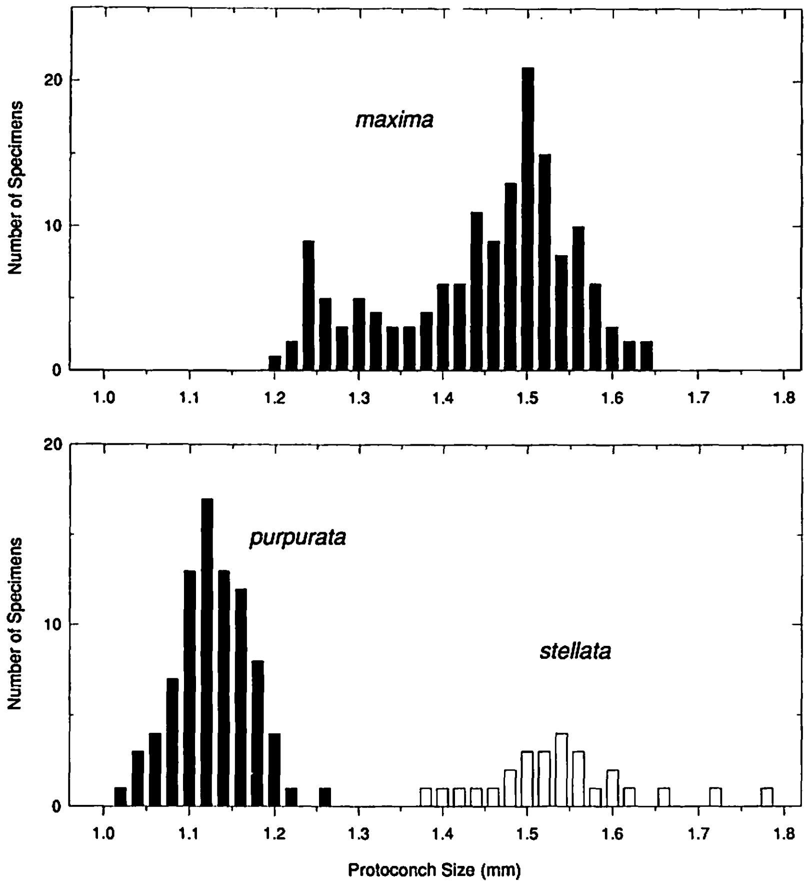


Fig. 41. Histograms of measured protoconch size. *Architectonica maxima* (n = 151, x̄ = 1.45, sd = 0.11), *A. purpurata* (n = 84, x̄ = 1.13, sd = 0.04), and *A. stellata* (n = 27, x̄ = 1.54, sd = 0.09).

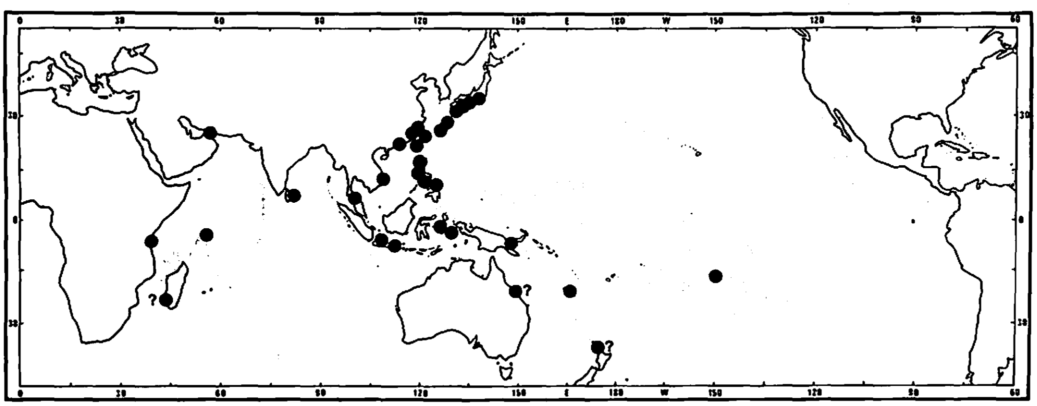


Fig. 42. Geographical distribution of *Architectonica maxima*.

Discussion:

Architectonica maxima is aptly named, since it attains (together with *A. trochlearis* and *A. taylori*) the largest shell size in this family. The species is easily recognized by its clearly subequal division of the midrib-area, which has a distinct groove at the base of the lower midrib. The closest form is *A. stellata* (see below). See additional comments under *A. trochlearis*.

Two rarely-collected forms with undivided or three-ribbed midrib-areas ("Teleoconch forms II and III" of BIELER, 1984d: 459, pl.1 figs.II–III) occur sympatrically with typical *A. maxima*. Noteworthy is the unusual bimodal pattern of protoconch-size distribution (see Fig.41) which does not reflect geographical distribution as it does in *Psilaxis radiatus* (see below).

Although type material has not been located, the original description by PHILIPPI (1849: 170) and the more extensive subsequent diagnosis and figure by the same author (1853b: 6, pl.1 figs.2–3) allow positive identification.

Architectonica purpurata (HINDS, 1844)
Pl.1 Fig.G; Figs.41, 43–45

*1844 *Solarium purpuratum* HINDS, 1844b, Proc. zool. Soc. Lond., *1844*: 25.
1844–1845 *Solarium purpuratum*, – HINDS, 1844c–1845, Zool. voy. SULPHUR, *3*: 49, *2*: pl.14 figs.1–2.
1844 *Solarium purpuratum*, – HINDS, 1844d, Ann. Mag. nat. Hist., *14*: 440.
1849 *Solarium purpureum* [sic], – PHILIPPI, Z. Malakozool., *5*(11): 172.
1853 *Solarium purpuratum*, – PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 8, pl.1 figs.6–7 [after HINDS, 1844c].
1863 *Solarium (Architectonica) purpuratum*, – HANLEY, Thes. conch., *3*: 232, pl.250 figs.7–8.
1864 *Solarium purpuratum*, – REEVE, Conch. icon., *15*: no.5, pl.1 fig.5.
1887 *Solarium (Solarium) purpuratum*, – MARSHALL, Man. conch., *9*: 11, pl.4 figs.41–42.
1940 *Solarium purpuratum*, – BAYER, Zool. Meded., *22*: 249.
1984 *Architectonica purpurata*, – BIELER, 1984d, Verh. natw. Ver. Hamburg, (NF)*27*: 470, pl.1 fig.IV.

Original measurements: SD = ca. 31.6, UD = ca. 8.4 [after HINDS, 1844b].

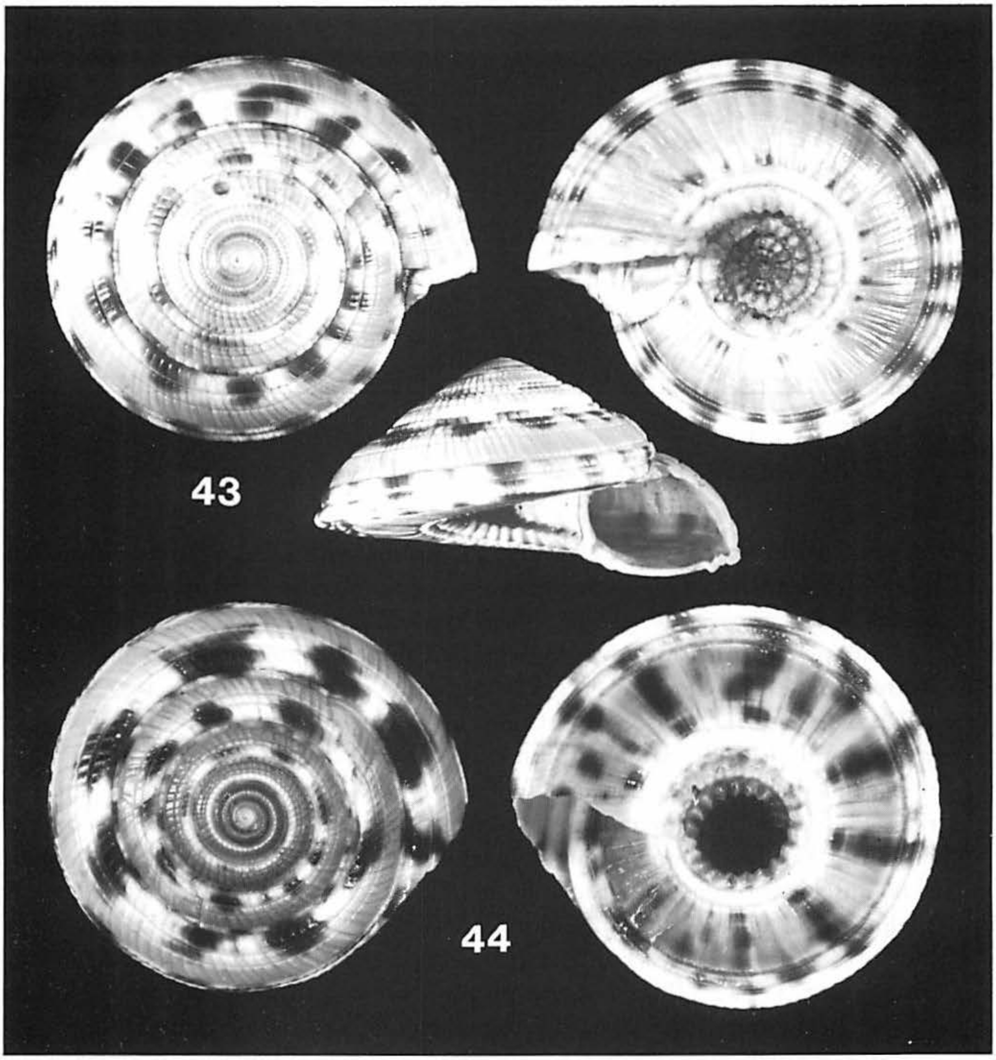
Type locality: "Hab. ---?" [not known].

Etymology: *purpuratus-a-um* [adjective]; Latin: wearing royal purple.

Material studied: 106 specimens (AMNH, ANSP, BMNH, CAS, DMNH, FLMNH, FMNH, HUJ, IRSNB, LACM, LMA, MCZ, MNHNP, NMP, NMW, OUM, RNHL, SMF, UMZC, USNM, ZIMH, ZMA, ZSM). Type material of *S. purpuratum* not found (BMNH).

Diagnosis:

Large cone-shaped shell with widely open umbilicus; whorls on upper side gemmate, somewhat inflated; two spiral grooves below suture (midrib-area divided subequally, with the upper midrib narrower); groove at the base of lower midrib. Subsutural rib white with pattern of ± large reddish-brown blotches extending onto upper midrib;



Figs. 43, 44. *Architectonica purpurata* (HINDS, 1844). Fig. 43: specimen from Madras, India; SMF 256456/1; SD = 34.2. Fig. 44 (two aspects): specimen from Moluccas, Indonesia; FMNH 223423; SD = 30.2.

most specimens with reddish-brown axial flames on basal field; proxumbical rib pure white; umbilical crenae reddish-brown (white on body whorl of larger specimens). Protoconch diameter ≤ 1.26 mm.

Description:

Teleoconch: Large, diameter of specimens in collections usually 25–35 at 6 to 7 1/2 whorls. Shape: moderately depressed to fairly high-spired cone-shaped, with whorls somewhat inflated (especially on upper side); umbilicus wide (UD ca. 26% of SD). Sculpture: Upper side: SSR distinctly separated; LMR wider than UMR (ca. 2:1, later

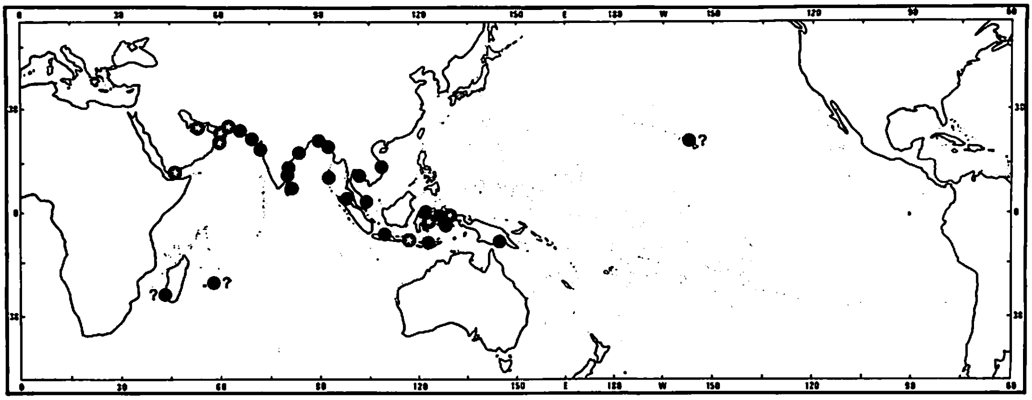


Fig. 45. Geographical distribution of *Architectonica purpurata* and *A. stellata*.

3:1); groove at the base of LMR; Periphery: PR strong, with UPR almost as prominent as LPR; upper point of whorl attachment on upper edge of LPR (thereby covering it; suture narrow); upper side and periphery crossed by deeply incised oblique axial grooves, resulting in formation of many elongate oblique segments, becoming smooth on MR-area of body whorl of larger specimens; segments of the two MR not necessarily corresponding; Base: IPR strong; always one additional narrow spiral rib between LPR and IPR; BF without spiral ribs; with radiating plications (especially in younger specimens), stronger towards umbilicus; two distinctly separated nodulose spiral ribs (PUR and UC) surrounding umbilicus, with umbilical crenae very regular; columellar wall forming almost straight inner lip with plications for support of the columellar muscle, with deepest groove in umbilical crenae overhanging umbilicus; no spiral sculpture on umbilical wall. Coloration (see Pl.1 Fig.G): SSR initially white, with pattern of reddish-brown blotches (ca. 6–9 per whorl, each 2–4 nodules wide), starting at about 3 Tw; UMR initially purplish-brown, turning tan as LMR after about 2 Tw; beginning with 4th whorl, blotches of SSR extend onto UMR; UPR, LPR and IPR whitish with reddish-brown blotches (each about 2–4 nodules wide); BF marbled in mauve and tan, often with large reddish-brown flames extending from IPR; one spiral band of small brown blotches in front of PUR; PUR pure white; UC reddish-brown, turning white on body whorl of large specimens. - Protoconch (see Fig.41): medium-sized to large (1.02–1.26, $\bar{x}$ = 1.13); distinctly heterostrophic; without anal keel; yellowish-white with brown outer corner in front of varix. - Operculum: as described for genus. - Radula and Anatomy: not known.

Geographical distribution (Fig.45): Northern Indian Ocean to New Guinea in the western Pacific. Records from eastern Indian Ocean and from Hawaiian Islands in need of verification.

Habitat: Sublittoral (no depth records available).

Discussion:

Shells of *Architectonica purpurata* resemble those of *A. maxima* in sculptural features, especially in having a similar subequal division of the midrib-area. The shell, however, is much smaller in size (compare Pl.1 Figs. G and J), has a narrower umbilicus, a smaller protoconch (Fig.41), and can be readily separated by the color pattern of large blotches that extend onto the upper midrib, and by the combination of reddish-brown umbilical crenae with a pure-white proxumbical rib. *A. stellata* is similar (see discussion under *A. stellata*, below).

Type material of could not be located, but HIND's description (1844b: 25) and figures (1844c: pl.14 figs.1-2) of *Solarium purpuratum* allow positive identification.

Architectonica stellata (PHILIPPI, 1849)

Figs.41, 45, 46

*1849 *Solarium stellatum* PHILIPPI, Z. Malakozool., *5*(11): 172.
1853 *Solarium stellatum*, - PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 16, pl.3 fig.3.
*1903 *Solarium abyssorum* MELVILL & STANDEN, Ann. Mag. nat. Hist., (7)*12*: 297, pl.21 fig.1.
1942 *Philippia abyssorum*, - BAYER, Zool. Meded., *24*(1-2): 1.
1982 *Architectonica purpurata*, - BOSCH & BOSCH, Seashells Oman: 43, fig. [non *Solarium purpuratum* HINDS, 1844].
1984 *Architectonica stellata*, - BIELER, 1984d, Verh. natw. Ver. Hamburg, (NF)*27*: 472, pl.1 figs.Va-b [lectotype designation for *S. abyssorum*].
1987 *Solarium abyssorum*, - TREW, MELVILL's new moll. names: 22.

Type measurements: *S. stellatum*: SD = ca. 26.2, H = ca. 12.0, UD = ca. 6.5 [after PHILIPPI, 1849]. Lectotype of *S. abyssorum*: SD = 5.5, H = 2.2, PD = 1.78, Tw = 1 9/10, UD = 1.9.

Type localities: *S. stellatum*: not given; PHILIPPI (1853b): "Aufenthaltsort unbekannt" [= not known]; *S. abyssorum*: "Gulf of Oman, lat. 24°58'N. long. 56°54'E., 156 fathoms."

Etymology: *stellatus-a-um* [adjective]; Latin: set with stars, glossy.

Material studied: 35 specimens (AMNH, ANSP, BMNH, DMNH, FMNH, HUJ, IRSNB, MCZ, NMW, USNM), including lectotype of *S. abyssorum* (BMNH 1903.12.15.108). Type material of *S. stellatum* not located.

Diagnosis:

Large, moderately depressed cone-shaped shell with moderately wide umbilicus; whorls on upper side gemmate, somewhat inflated; two spiral grooves below suture (midrib-area divided subequally, with upper midrib narrower); ± wide groove at base of the lower midrib. Subsutural rib whitish with pattern of ± large brown blotches (usually not extending onto midrib-area); basal field with 1-5 dotted spiral lines, proxumbical rib whitish (often with a few darker marks), umbilical crenae whitish or reddish brown. Protoconch diameter $\geq$ 1.38 mm.

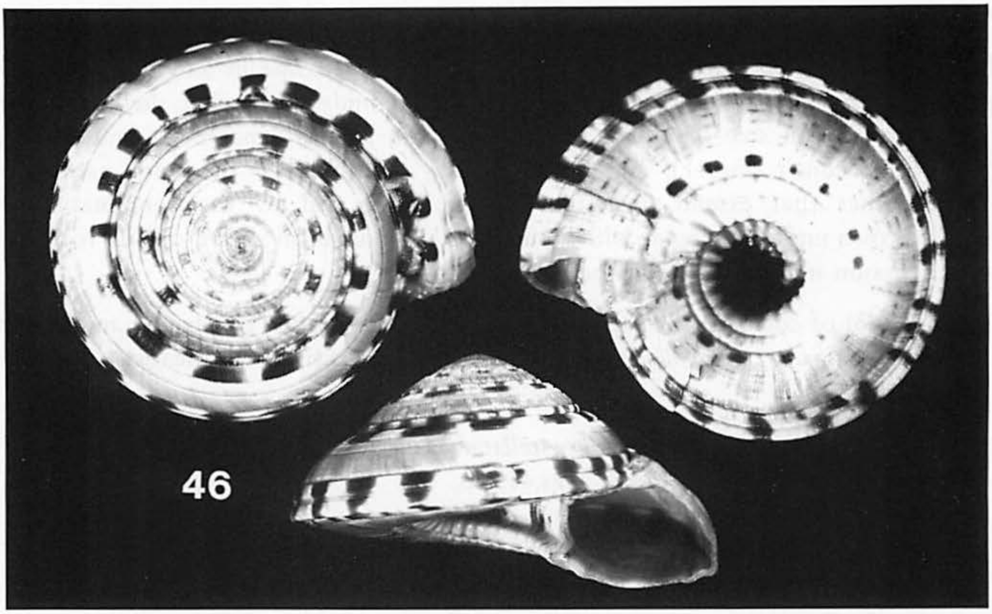


Fig. 46. *Architectonica stellata* (PHILIPPI, 1849); specimen from Muscat, Oman; AMNH 104871; SD = 43.6. Note barnacles overgrown by body whorl.

Description:

Teleoconch: Large, diameter of specimens in collections usually 30–40 (rarely over 50) at 5 1/2 to 6 1/2 (7 1/4)) whorls; ranging from rather thin- to thick-walled. Shape: moderately depressed cone-shaped, with whorls somewhat inflated (especially on upper side); umbilicus moderately wide (UD ca. 24% of SD). Sculpture: as in *A. purpurata*. Coloration: SSR initially white, with pattern of brown blotches (ca. 9–15 per whorl, each 1–4 nodules wide), starting at about 3 Tw; blotches usually not extending onto UMR; UMR initially purplish-brown, turning tan as LMR after about 3 Tw; UPR, LPR and IPR whitish with dark-brown blotches; BF flamed with shades of mauve and tan, with 1–5 spiral lines of brown blotches of various widths in front of PUR; PUR white or whitish-brown with a few darker marks; UC whitish or reddish-brown. – Protoconch (see Fig.41): large to very large (1.38–1.78, x̄ = 1.54); distinctly heterostrophic; often with ridge in anal-keel area; light- to dark-brown, with darker outer corner in front of varix. – Operculum: as described for genus. – Radula and Anatomy: not known.

Geographical distribution (Fig.45): Known from the northern Indian Ocean and Indonesia.

Habitat: Sublittoral (depth records from 45 to 285 m).

Discussion:

Shell shape and sculpture of *Architectonica stellata* agree with those of *A. purpurata*. The coloration of the midrib-area is different: in *A. stellata*, blotches of the subsutural-rib do not usually extend onto the upper midrib; if so, they are irregular in shape and do not fully correspond between the two ribs. *A. stellata* lacks the reddish-brown flames that occur on the base of most *A. purpurata* specimens. The protoconch-size is much larger than in *A. purpurata* (see Fig.41), and there are significant statistical differences between the two in relative shell height (*A. purpurata* being higher-spired) and in relative umbilical diameter (*A. purpurata* having a slightly smaller umbilicus) (see BIELER, 1984d).

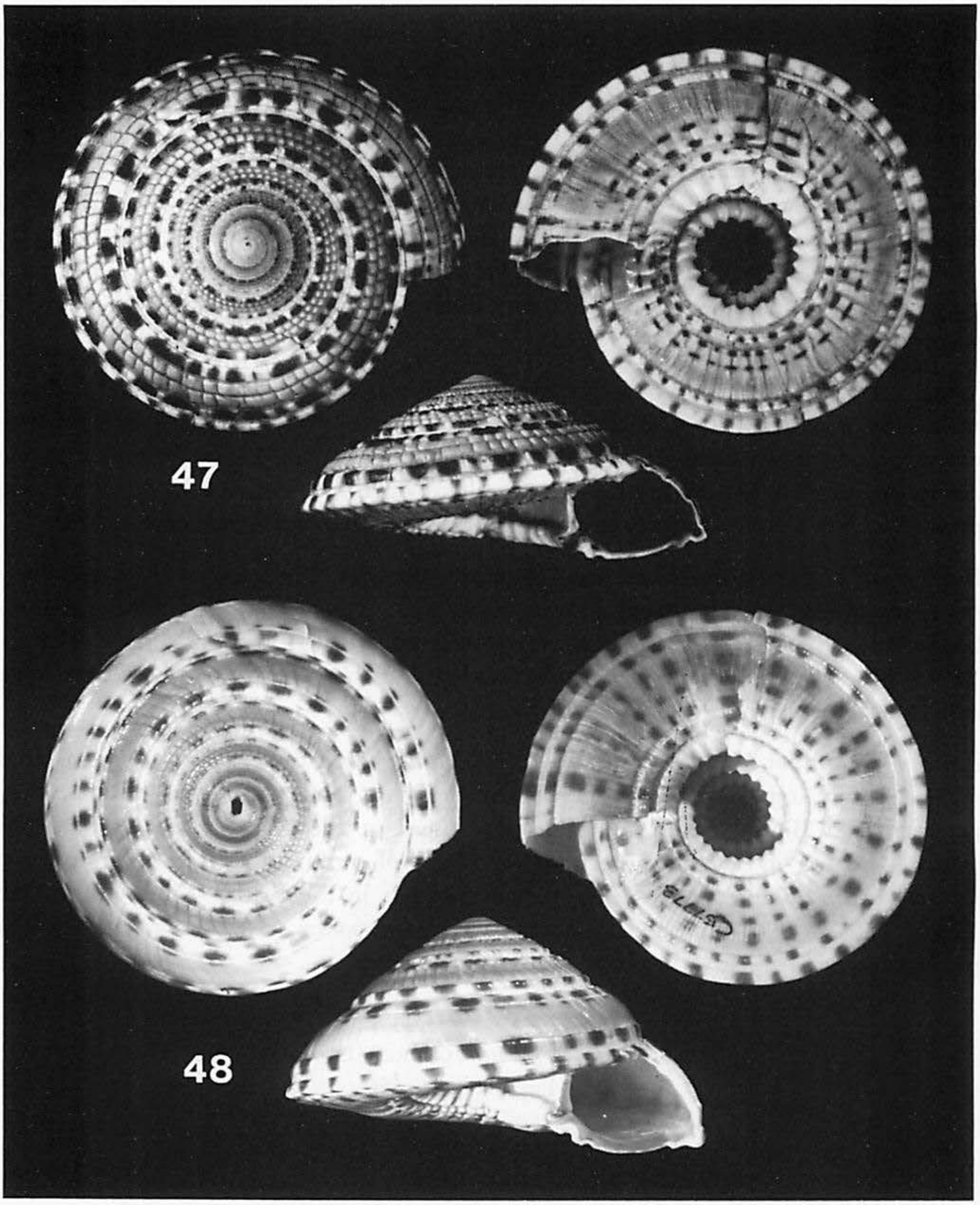
Young specimens of the much larger-shelled *Architectonica maxima* can be distinguished by a wider groove at the base of the lower midrib, and by a much darker coloration of the proxumbical rib. *Architectonica gualtierii* n.sp. (see below) is superficially similar, but has the midrib-area usually divided into two almost equally strong spiral ribs, has a much coarser sculpture and a brown-colored proxumbical rib.

Architectonica stellata, described and figured by PHILIPPI (1849: 172; 1853b: pl.3 fig.3) was synonymized by subsequent authors either with *A. purpurata* (e.g., HANLEY, 1863; REEVE, 1864; MARSHALL, 1887; BAYER, 1940) or with *A. maxima* (e.g., PAETEL, 1887–1888). Type material could not be located, but the specimens figured here agree with PHILIPPI's original diagnosis and figure.

Solarium abyssorum MELVILL & STANDEN, 1903, was based on juvenile specimens from a 156-fathom station in the Gulf of Oman. Shape and small size of the young specimens led BAYER (1942: 1) to transfer them to the genus *Philippia*. Syntypic material located in several collections consisted of a mixture of juvenile shells of various *Architectonica* species. One of two syntypes in the British Museum (BMNH 1903.12.15.108–9) was selected as lectotype of *S. abyssorum* (see BIELER, 1984d). This specimen is most likely a juvenile shell of *A. stellata*.

Architectonica grandiosa IREDALE, 1931
Pl.1 Fig.I; Figs.47–50

*1931 *Architectonica grandiosa* IREDALE, Rec. Austr. Mus., *18*(4): 228, pl.25, figs.19–20.
1940 *Solarium grandiosum*, - BAYER, Zool. Meded., *22*: 226.
1961 *Architectonica grandiosa*, - GARRARD, J. malac. Soc. Austr., *1*(5): 23.
1961 *Architectonica taylori*, - RIPPINGALE & MCMICHAEL, Queensl. Gr. Barr. Reef shells: 63, pl.6 fig.24 [non *Solarium taylori* HANLEY, 1862].
1971 *Architectonica maxima*, - WILSON & GILLETT, Austr. shells: 34, pl.13 figs.12–12a [non *Solarium maximum* PHILIPPI, 1849].
1972 *Architectonica maxima*, - HINTON, Shells New Guinea: 4, pl.2 figs.24–25.
1975 *Architectonica maxima*, - COLEMAN, What shell is that?: 261, fig.713.
1977 *Architectonica (Architectonica) maxima*, - GARRARD, Rec. Austr. Mus., *31*(13): 509, fig.2 [operculum]; 512, pl.2 figs.4–9 [figs.7–9 = holotype of *A. grandiosa*].
1984 *Architectonica grandiosa*, - BIELER, 1984d, Verh. natw. Ver. Hamburg, (NF)*27*: 473, pl.2 fig.VI [holotype].



Figs. 47, 48. *Architectonica grandiosa* IREDALE, 1931. Fig. 47: fresh specimen from Queensland, Australia; USNM 845176; SD = 38.2. Fig. 48: holotype, Sydney Harbour, Australia; AMS C.57773; SD = 43.6.

Type measurements (holotype): SD = 43.6, H = 26.2, UD = 11.7 [apex damaged].

Type locality: Sydney Harbour, N.S.W., Australia; ex 'TRITON' dredge.

Etymology: *grandiosus-a-um* [adjective]; Latinization of the English adjective "grandiose."

Material studied: 51 specimens (AMNH, AMS, ANSP, DMNH, FMNH, IRSNB, MNHNP, NMP, SMF, SMNS, USNM, ZIMH, ZMA, Coll. ALF), including holotype of *A. grandiosa* (AMS C.57773).

Diagnosis:

Large to very large, moderately depressed cone-shaped shell with widely open umbilicus; whorls on upper side gemmate, somewhat inflated; two spiral grooves below suture (midrib-area equally divided); narrow groove at base of lower midrib. Subsutural rib white with pattern of brown blotches; midribs uniformly greyish-brown; basal field with 1–3 dotted spiral lines; proxumbical rib whitish with few brown blotches; umbilical crenae pure white (rarely with single brown blotches). Protoconch diameter $\leq$ 1.18 mm.

Description

Teleoconch: Large to very large, diameter of specimens in collections usually 30–45 (rarely to 55) at 7 to 8 (8 1/8) whorls. Shape: moderately depressed cone-shaped, with whorls somewhat inflated (especially on upper side); umbilicus wide (UD ca. 29% of SD). Sculpture: Upper side: SSR distinctly separated; MR-area initially almost undivided, separating into UMR and LMR (nearly 1:1) after about 2 Tw; narrow groove at base of LMR; Periphery: PR strong, with UPR almost as prominent as LPR; upper point of whorl attachment above center of LPR (after ca. 5 1/2 Tw at upper edge of LPR), thereby displaying part of LPR as element of upper-side sculpture; upper side and periphery crossed by deeply incised oblique axial grooves, resulting in a general gemmate appearance, becoming weaker on midrib-area of body whorl of larger specimens; Base: IPR strong; BF without spiral ribs; with radiating plications (especially in younger specimens), stronger towards umbilicus; two distinctly separated nodulose spiral ribs (PUR and UC) surrounding umbilicus, with UC strong; columellar wall forming almost straight inner lip with plications for support of the columellar muscle, with deepest groove in UC overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration (see Pl.1 Fig.I): SSR white with pattern of brown blotches (each about 1–2 nodules wide), starting after about 1 Tw; UMR-area initially mauve-grey, later greyish-brown as LMR-area; UPR, LPR and IPR white with brown blotches (each of which about 1–2 nodules wide), with LPR generally lighter colored than other ribs; BF flamed with mauve and tan, with 1–3 dotted spiral lines of varying width; PUR whitish with brown blotches; UC pure white (rarely with single brown blotches. – Protoconch (see Fig.49): medium-sized (1.00–1.18, $\bar{x}$ = 1.06); distinctly heterostrophic; without anal keel; whitish, with brown outer corner in front of varix. – Operculum: as described for genus. – Radula and Anatomy: not known.

Geographical distribution (Fig.50): Apparently restricted to Australian region (other records in need of verification).

Habitat: Sublittoral (most depth records between 45 and 125 m), live records from 45–65 m, sandy and muddy substrates.

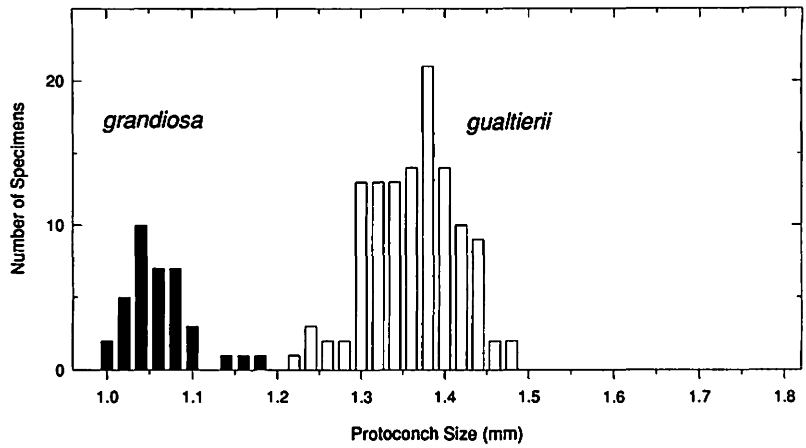


Fig. 49. Histogram of measured protoconch size. *Architectonica grandiosa* (n = 37, x̄ = 1.06, sd = 0.04), and *A. gualtierii* n.sp. (n = 119, x̄ = 1.36, sd = 0.05).

Discussion:

Architectonica grandiosa has been synonymized with *A. maxima* by most authors. It can, however, be easily distinguished by the midrib-area which is divided into two equally-strong spiral ribs, pure-white umbilical crenae, and a much smaller protoconch size (see Fig.49). The coloration of the type specimen (Fig.48) has faded; fresh specimens are much richer in contrast (see Fig.47 and Pl.1 Fig.I). *Architectonica gualtierii* n.sp. is similar (see discussion, below).

Architectonica sp. aff. *grandiosa* Iredale, 1931
Figs.50, 51

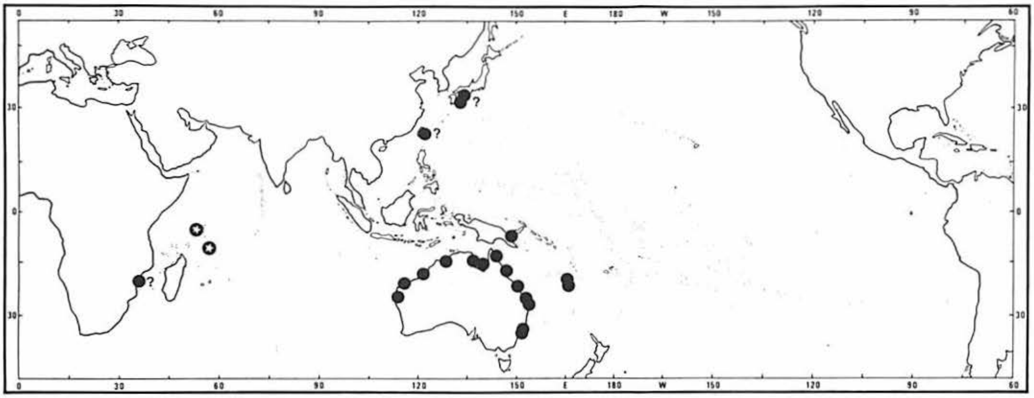
1984 *Architectonica* sp. I aff. *grandiosa*, - Bieler, 1984d, Verh. natw. Ver. Hamburg, (NF)27: 474, pl.2 fig.VII.

Measurements (largest specimen): SD = 35.1, H = 15.8, PD = 1.28, Tw = 6 5/8, UD = 11.2 [MRAC 794.201].

Material studied: 4 specimens (BMNH, MNHNP, MRAC).

Diagnosis:

Medium-sized to large, depressed cone-shaped shell with widely open umbilicus; whorls on upper side gemmate, somewhat inflated; two spiral grooves below suture (midrib-area almost equally divided, with upper midrib slightly narrower); distinctly separated groove at base of lower midrib. Subsutural rib white with pattern of brown blotches; midribs uniformly light-tan, proxumbical rib white with brown blotches; umbilical crenae pure white. Protoconch diameter 1.28–1.38 mm.



● *grandiosa* ○ sp. aff. *grandiosa*

Fig. 50. Geographical distribution of *Architectonica grandiosa* and *A.* sp. aff. *grandiosa*.

Description:

Teleoconch: Medium-sized to large, diameter of specimens in collections 12–35 at 4 1/8 to 6 5/8 whorls. Shape: depressed cone-shaped, with whorls somewhat inflated (especially on upper side); umbilicus wide (UD ca. 29% of SD). Sculpture: Upper side: SSR distinctly separated; LMR only somewhat wider than UMR (ca. 1.5:1); distinctly separated groove at base of LMR; Periphery: PR strong, upper point of whorl

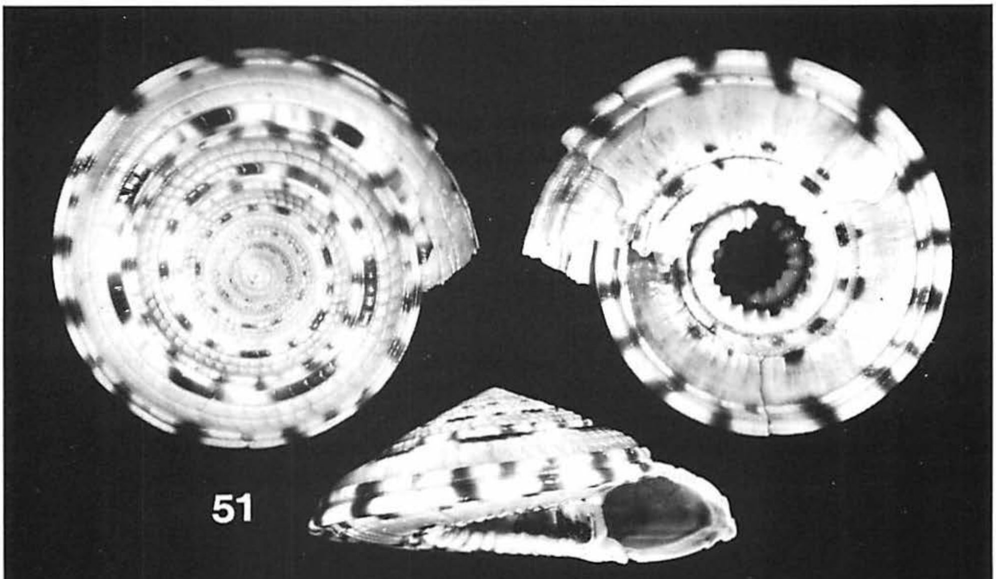


Fig. 51. *Architectonica* sp. aff. *grandiosa* IREDALE, 1931; specimen from Seychelles; MRAC 794.201; SD = 35.1.

attachment above center of LPR, thereby displaying part of LPR as element of upper-side sculpture; upper side and periphery crossed by deeply incised oblique axial grooves, resulting in a general gemmate appearance; Base: IPR strong; BF without spiral ribs; with radiating plications, stronger toward umbilicus; two distinctly separated nodulose spiral ribs (PUR and UC) surrounding umbilicus, with UC strong; columellar wall forming almost straight inner lip with plications for support of the columellar muscle, with deepest groove in UC overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration: SSR initially white, with pattern of brown blotches (5–14 per whorl, each of which 1–2, on later whorls 3–4, nodules wide), starting after about 2 Tw; MR light-tan; UPR, LPR and IPR white with pattern of brown blotches; BF marbled with greyish-brown; one dotted spiral line in front of PUR; PUR white with brown blotches; UC pure white. – Protoconch: large (1.28–1.38, $\bar{x} = 1.32$); distinctly heterostrophic; without anal keel; white, with brown outer corner in front of varix (sometimes varix itself brown). – Operculum, Radula and Anatomy: not known.

Geographical distribution (Fig.50): Only known from a small area in the western Indian Ocean (Seychelles and Saya-de-Malha Banks).

Habitat: Sublittoral (45–86 m).

Discussion:

Shell shape, sculpture and the pure-white umbilical crenae of this form resemble the conditions of *Architectonica grandiosa*, however, the protoconch is much larger and resembles that of *A. gualtierii* n.sp. (see below). Only four specimens are currently known and the taxonomic status of this form needs further study as additional material becomes available.

Architectonica gualtierii n.sp.
Pl.1 Fig.C; Figs.49, 52–54

1742 "Cochlea marina Depressa, ...", – Gualtieri, Index test. conch.: pl.65 fig.O (bottom right) [not binominal].
1781 "Trochus perspectivus seu opticus", – Chemnitz [in part], Conch.-Cab., *5*: 121, pl.172 figs.1691–1692 [not binominal].
1790 –, Geve, Belustigung: pl.25, figs.266a-b.
1838–1839 *Solarium granulatum*, – Kiener, Spéc. gén. icon. coqu., *10*: 4, pl.2 fig.2 [non *S. granulatum* Lamarck, 1816].
1849 *Solarium granulatum*, – Philippi, Z. Malakozool., *5*(11): 173.
1852 *Solarium australe*, – Mörch, Cat. conch. Yoldi: 47 [non *S. australe* Philippi, 1849].
1853 *Solarium granulatum*, – Philippi, 1853b, Syst. Conch.-Cab. II, *7*: 9, pl.2 figs. 1–2 [after Chemnitz, 1781], and p.17, pl.3 fig.5.
1863 *Solarium (Architectonica) quadriceps*, – Hanley [in part], Thes. conch., *3*: 229, pl.252 figs.25–26 [non *S. quadriceps* Hinds, 1844].
1864 *Solarium quadriceps*, – Reeve [in part], Conch. icon., *15*: no. 18, pl.3 fig.18b.
1887 *Solarium (Solarium) quadriceps*, – Marshall, Man. conch., *9*: 10, pl.4 figs. 39–40 [after Hanley, 1863].
1897 *Solarium maximum*, – Sowerby (III), Append. mar. shells S. Afr.: 15 [non *S. maximum* Philippi, 1849].
1940 *Solarium maximum*, – Bayer, Zool. Meded., *22*: 227.

1940 *Solarium quadriceps*, - BAYER [in part], Zool. Meded., *22*: 249.
1962 *Architectonica maxima*, - Anon., Hawaii. Shell News, *10*(10): 7, fig.
1963 *Solarium maximum*, - BARNARD, 1963b, Ann. S. Afr. Mus., *47*(1): 156, fig. 31a.
1973 *Architectonica maximum*, - KENSLEY, Sea-shells s. Afr.: 76, fig.248.
1974 *Solarium maximum*, - BARNARD, Ann. S. Afr. Mus., *47*(5): 711.
1979 *Architectonica maxima*, - KAY, Hawaii. mar. shells: 97, figs.35A-C.
1984 *Architectonica* sp. II aff. *grandiosa*, - BIELER, 1984d, Verh. natw. Ver. Hamburg, (NF)*27*: 474, pl.2 fig.VIII.
1984 *Architectonica* sp. III aff. *grandiosa*, - BIELER, 1984d, Verh. natw. Ver. Hamburg, (NF)*27*: 475, pl.2 fig.IX [paratype 6].
1984 *Architectonica* cf. *laevigata*, - BOSS & MERRILL, 1984b, Occas. Pap. Moll., *4*(66): 406, pl.66 figs.1-3 [radula; non *Solarium laevigatum* LAMARCK, 1816].
1985 *Architectonica maxima*, - DRIVAS & JAY, La Conchiglia, *17*(190-191): 8, fig.1.
1986 *Architectonica (Architectonica) trochlearis*, - SPRINGSTEEN & LEOBRERA, Shells Philippines: 24, pl.2 fig.6 [non *Solarium trochleare* HINDS, 1844].

Type measurements:

	SD	H	PD	Tw	UD	Locality	Collection
Holotype	51.2	28.3	1.38	7 3/8	15.1	Tosa Bay, Japan	USNM 820576
Paratype 1	35.9	18.9	1.42	6 5/8	10.5	Tosa Bay, Japan	USNM 859450
Paratype 2	30.7	15.1	1.36	6 1/4-	8.5	Tosa Bay, Japan	USNM 859450
Paratype 3	23.8	11.4	1.42	5 3/4+	6.8	Tosa Bay, Japan	USNM 859450
Paratype 4	41.5	21.8	1.36	7 1/8	12.3	Tosa Bay, Japan	USNM 859450
Paratype 5	59.5	37.7	1.40	8 1/4	17.4	Tosa Bay, Japan	FMNH 223414
Paratype 6	51.6	27.5	1.34	7 5/8	17.0	Mozambique Channel	NMP H8282/T371
Paratype 7	50.8	30.8	1.36	8-	15.5	Osaka, Japan	RNHL 56655
Paratype 8	37.7	20.2	1.38	7 1/8	12.3	Oshima, Osumi (Amami)	ANSP 227212

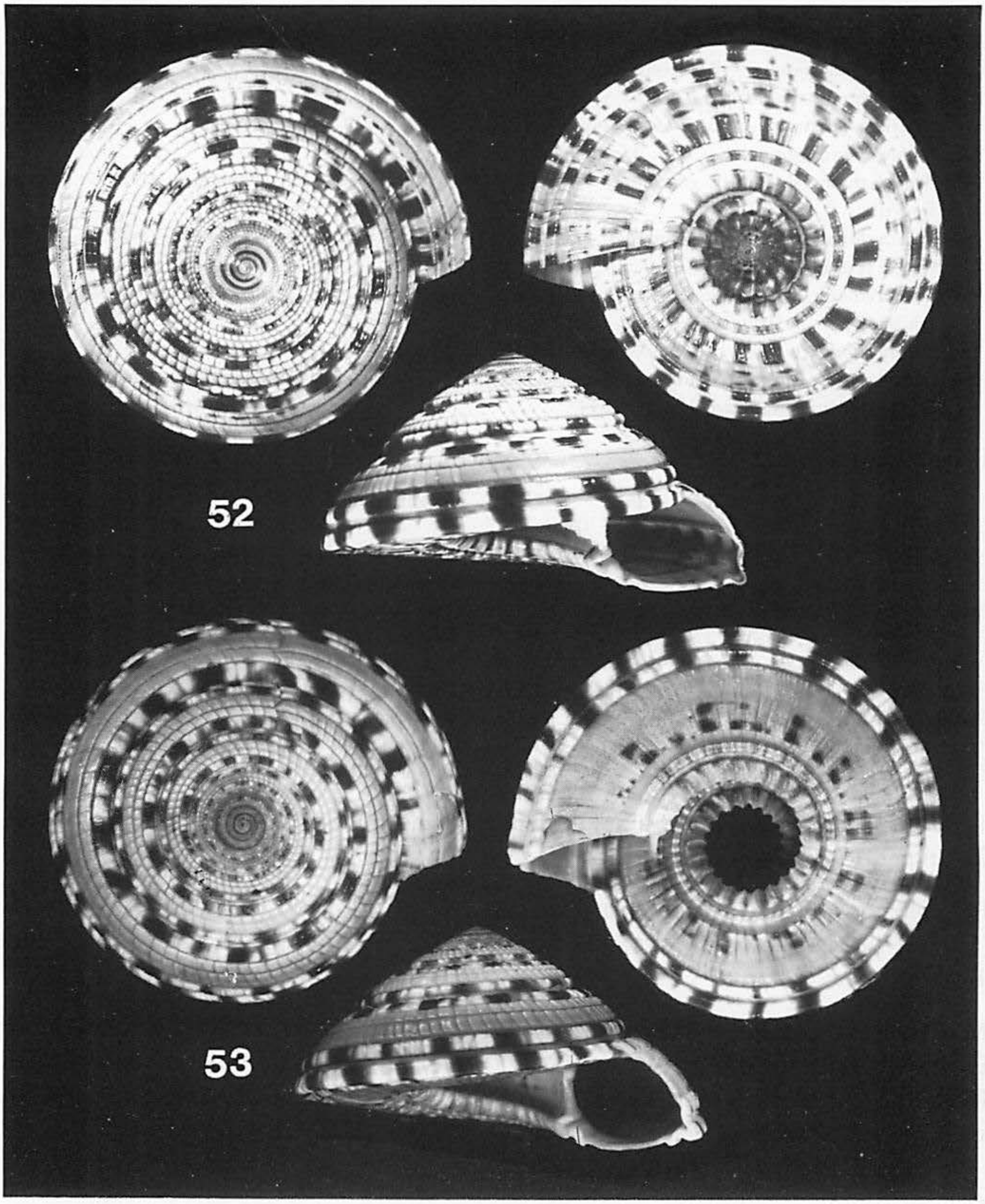
Type locality: Tosa Bay, Shikoku, Japan, 91m (50 fms) [ex WITHINGTON Coll.]. Paratypes 1-4 from holotype lot.

Etymology: *gualtierii* [genitive singular case-ending]. Named after NICCOLÓ GUALTIERI (1688-1744), physician to COSIMO III (Grand Duke of Toscany) and author of the 'Index Testarum Conchyliorum' (1742), wherein this species was figured for the first time.

Material studied: 215 specimens (AMNH, ANSP, BMNH, BPBM, CAS, DMNH, FMNH, HUJ, IRSNB, LACM, LMA, MCZ, MNHNP, NMP, NMW, OUM, RNHL, SAM, SMF, SMNS, UMZC, USNM, ZMA, ZSM, Coll. ALF); including type specimens as listed above.

Diagnosis:

Very large, moderately depressed cone-shaped shell with widely open umbilicus; whorls on upper side gemmate, somewhat inflated; two spiral grooves below suture (midrib-area initially subequally divided, with upper midrib narrower); deep, narrow groove at base of lower midrib. Subsutural rib whitish with pattern of brown blotches; midribs greyish-brown, basal field with 1-3 dotted spiral lines; proxumbical rib white with brown blotches; umbilical crenae usually light-brown with one side of each nodule dark-brown, sometimes whitish with a few brown blotches. Protoconch diameter 1.22-1.48 mm.



Figs. 52, 53. *Architectonica gualtierii* n.sp. Fig. 52: paratype 6; Osaka, Japan; RNHL 56655; SD = 50.8. Fig. 53: holotype; Tosa Bay, Japan; USNM 820576; SD = 51.2.

Description:

Teleoconch: Thick-walled, very large; diameter of specimens in collections usually 40–60 at 6 1/2 to 8 1/2 whorls. Shape: moderately depressed cone-shaped, with whorls somewhat inflated (especially on upper side); umbilicus wide (UD ca. 31% of SD). Sculpture: Upper side: SSR distinctly separated; MR-area initially divided 1:2 in UMR and LMR, some specimens later 1:1; deep and narrow groove at base of LMR; nodules in MR-area usually gemmate, sometimes (especially in small specimens from the central Pacific) slanted like roof tiles; Periphery: PR strong, larger specimens with additional fine spiral rib between UPR and LPR; upper point of whorl attachment on upper part of LPR (upper edge of LPR visible in suture up to ca. 7 Tw); upper side and periphery crossed by deeply incised oblique axial grooves, resulting in general gemmate appearance, becoming smooth on MR-area of body whorl of larger specimens; segments of the two MR not necessarily corresponding; Base: IPR strong, large specimens with additional fine spiral rib between LPR and IPR; BF without spiral ribs; with radiating plications (especially on younger specimens), stronger towards umbilicus; two distinctly separated nodulose spiral ribs (PUR and UC) surrounding umbilicus, with UC very strong, regular, and widely-spaced; columellar wall forming almost straight inner lip with plications for support of the columellar muscle, with deepest groove in UC overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration (see Pl.1 Fig.C): SSR initially white, with pattern of brown blotches (ca. 9–17 per whorl, each 1–2, rarely 3, nodules wide), starting after about 1 Tw; UMR on early whorls purplish-grey, later as LMR greyish-brown; UPR, LPR and IPR white with pattern of brown blotches (each 1–3 nodules wide); BF flamed with shades of mauve and grey; especially on large specimens 1–3 dotted spiral lines of varying width on BF; PUR white with brown blotches; UC usually light-brown with one side of each nodule dark-brown, sometimes whitish with few brown blotches (especially in small specimens from the central Pacific). – Protoconch (see Fig.49): large (1.22–1.48, $\bar{x}$ = 1.36); distinctly heterostrophic; without anal keel, some specimens with rounded ridge in anal-keel area; whitish-brown or light-brown, with brown outer corner in front of varix. – Operculum: as described for genus. – Radula: "ptenoglossate," with 15 long, prong-like teeth per row (7-1-7). Rachidian short and pointed. Marginal teeth recurved, prong-like and forked with long tapering subequal cusps; with the outer teeth being shorter (see Boss & Merrill, 1984b: 359, pl.66 figs.1–3; as "*Architectonica* c.f. *laevigata*"; based on USNM 747441, vidi). – Anatomy: not known.

Geographical distribution (Fig.54): Indian Ocean to central Pacific (excluding Australia?).

Habitat: Sublittoral (most depth records between 12 and 195 m), live records from 12–95 m, sandy and muddy substrates.

Discussion:

Architectonica gualtierii is a fairly common species. The midrib-area of its rather large shell has a much coarser sculpture than that of *A. maxima*. Compared to *A. maxima* it has a higher-spired shell, a color pattern on the peripheral ribs that consists of

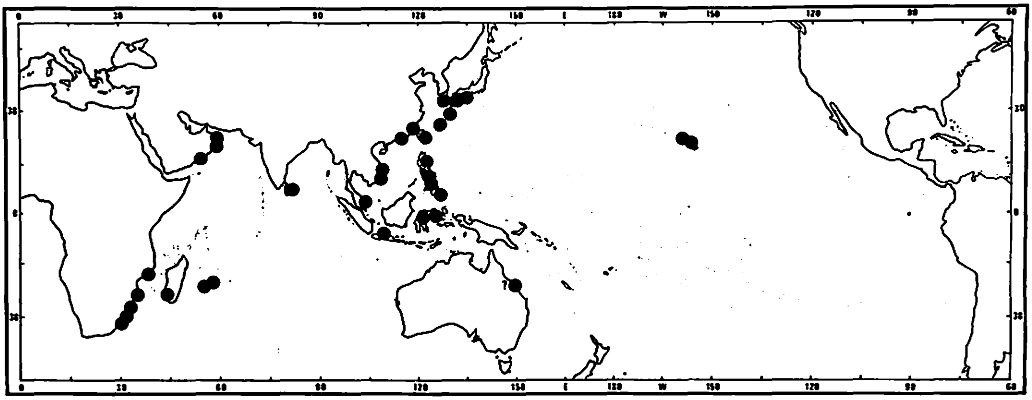


Fig. 54. Geographical distribution of *Architectonica gualtierii* n.sp.

fewer and larger blotches, and much darker colored umbilical crenae. Boss & Merrill (1984b) studied the radulae of both species, finding 14 teeth per half-row for *A. maxima* (1984b: 358, pl.63 fig.2, pl.64 figs.1–3; as "*A. perspectiva*," USNM 747000, vidi) and only 7 teeth per halfrow for *A. gualtierii* (as "*Architectonica* cf. *laevigata*"). The brown umbilical crenae and much larger protoconch-size (Fig.49) separate it readily from its closest congener, *A. grandiosa*.

Bieler (1984d: 474) recognized an additional form in this complex, "*Architectonica* sp. II aff. *grandiosa*" from the Hawaiian Islands. At that time only juvenile shells were available for "sp. II" and a morphometric analysis distinguished between the Hawaiian form and *A. gualtierii* (the latter as "sp. III aff. *grandiosa*" in that publication). Extensive material including adult shells from several Hawaiian Islands has since been studied (BPBM collections) and no significant differences to Indo-West-Pacific *A. gualtierii* were found. Specimens from the central Pacific are frequently somewhat lighter-colored (especially on the base) and the midrib sculpture of early whorls often consists of scaly, rather than gemmate, nodules. This Hawaiian form, called "*Architectonica maxima*" in the literature (e.g., Kay, 1979: 97), is here considered as belonging to *A. gualtierii* n.sp.

This species has been known to science for about 250 years, since Gualtieri (1742) published the first recognizable figure. Subsequent authors have used six different names for it (*australe*, *granulatum*, *laevigata*, *maximum*, *quadriceps* and *trochleare*), none of which is taxonomically available for this form.

The name *Solarium quadriceps* Hinds, 1844, was used by several authors. This nominal species was based on a single specimen from the Bay of Panama. The original figures (Hinds, 1844c: pl.14 figs.7–8) show a juvenile shell of the *maxima*-group, that Hinds (1845: 50) compared to *Solarium granulatum* [= *Architectonica nobilis*]. The type specimen of *S. quadriceps* is lost (BMNH), and Hinds' figure does not allow positive identification. The name *S. quadriceps* came into use for the species here considered, when Hanley (1863) and Reeve (1864) decided to illustrate "adult specimens" of that species, using Indo-Pacific shells of *A. gualtierii* for their purpose. This resulted in unusual statements of *A. quadriceps*' geographical distribution (e.g., MARSHALL, 1887, p.10: "Zanzibar, Bay of Panama"). Only two *Architectonica* species are known from the East Pacific, *A. nobilis* RÖDING, 1798, and *A. karsteni* RUTSCH, 1934 (see below). Based on the cited type locality in the East Pacific, subsequent authors (e.g., KEEN, 1971: 388; ABBOTT, 1974: 97) have synonymized *S. quadriceps* with *A. nobilis*, a procedure accepted here.

All references to *Architectonica maxima* in the South African region (BARNARD, 1963b, 1974; KENSLEY, 1973) are based on *A. gualtierii*; *A. maxima* has not been collected there to date. It is noteworthy that BAYER's treatment of "*Solarium maximum*" (1940: 227, 249ff.) was based entirely on specimens of *A. gualtierii* (RNHL, vidi).

Architectonica taylori (HANLEY, 1862)
Pl.1 Fig.A; Figs.55–58

*1862 *Solarium taylori* HANLEY, Proc. zool. Soc. Lond., *1862*(2): 205.
1863 *Solarium (Architectonica) Taylori*, - HANLEY, Thes. conch., *3*: 230, pl.252 figs.31-32.
1887 *Solarium (Solarium) maximum*, - MARSHALL [in part], Man. conch., *9*: 10, pl.3 figs.33-34 [after HANLEY, 1863] [non *S. maximum* PHILIPPI, 1849].
1940 *Solarium taylori*, - BAYER, Zool. Meded., *22*: 252.
1982 *Architectonica maxima*, - ABBOTT & DANCE, Compend. seash.: 61, fig.
1984 *Architectonica taylori*, - BIELER, 1984d, Verh. natw. Ver. Hamburg, (NF)*27*: 477, pl.3 fig.X [holotype].
1986 *Architectonica perspectiva*, - LAI, Mar. gastr. Taiwan (1): 38 fig.4.

Type measurements (holotype): SD = 35.8, H = 20.9, PD = 1.3, Tw = 6 7/8, UD = 9.2.

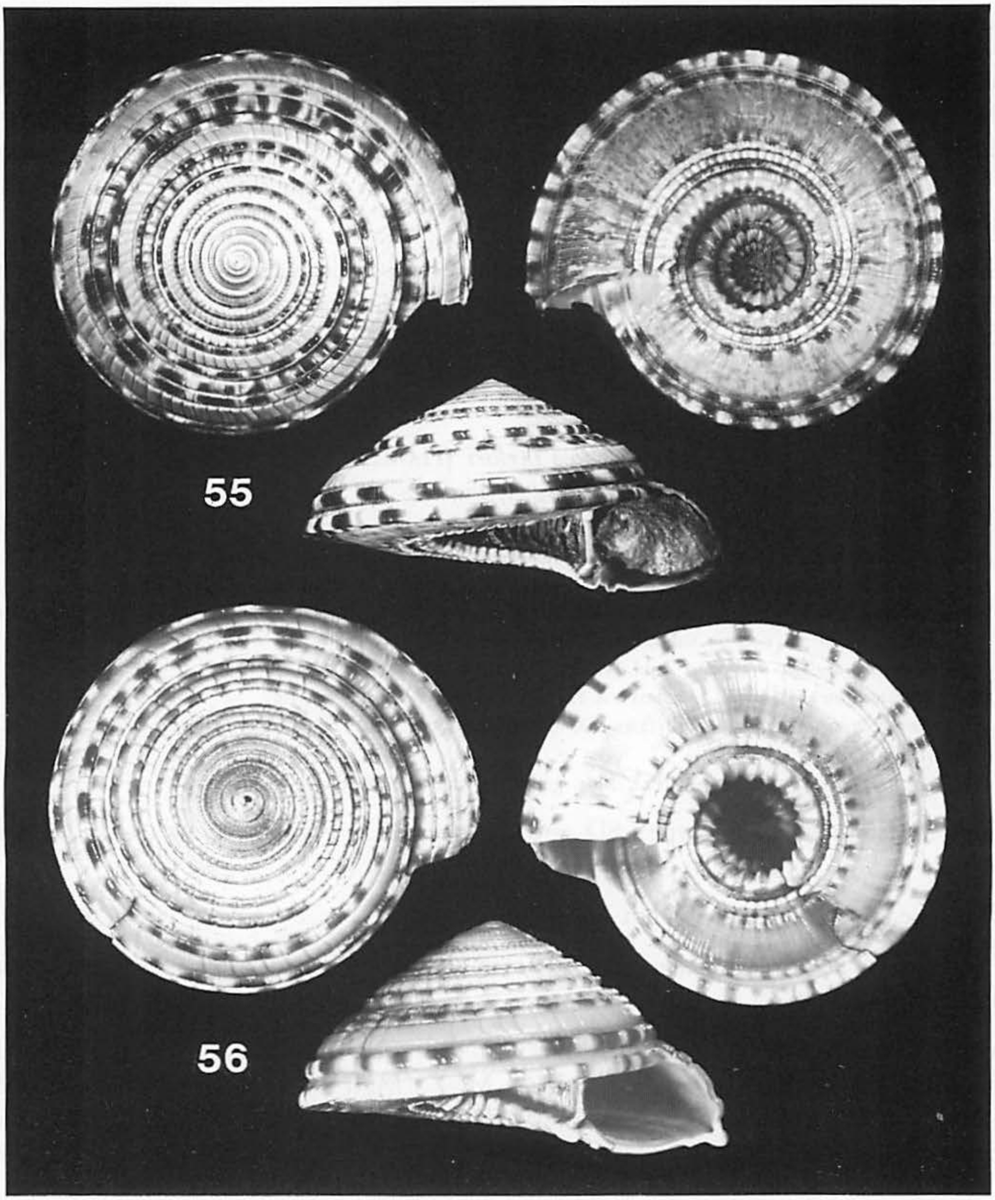
Type locality: "Hab. ---?" [not known].

Etymology: *taylori* [genitive singular case-ending]. Named after THOMAS LOMBE TAYLOR (1802–1874), British collector.

Material studied: 92 specimens (AMNH, ANSP, BMNH, CAS, DMNH, FLMNH, FMNH, HUJ, IRSNB, LACM, LMA, MCZ, MNHNP, NMP, NMW, OUM, RNHL, SMF, SMNS, UMZC, USNM, ZIMH, ZMA, ZSM, Coll. ALF), including holotype (BMNH 1907.10.28.98).

Diagnosis:

Very large to extremely large, moderately depressed cone-shaped shell with widely open umbilicus; whorls on upper side gemmate, somewhat inflated; two spiral grooves below suture (midrib-area subequally divided, with upper midrib narrower); distinctly separated groove at base of lower midrib. Subsutural rib whitish with pattern of brown blotches starting after about 4–5 whorls; upper midrib darker colored than subsutural rib, solid brown or dissolving into pattern of brown blotches; proxumbical rib whitish with pattern of brown blotches; umbilical crenae variegated with light- and dark-brown. Protoconch diameter 1.22–1.42 mm.



Figs. 55, 56. *Architectonica taylori* (HANLEY, 1862). Fig. 55: fresh specimen from Taiwan; ZMA unnumbered; SD = 59.8. Fig. 56: holotype of *Solarium taylori*; BMNH 1907.10.28.98; SD = 35.8.

Description:

Teleoconch: Thick-walled, very large to extremely large, diameter of specimens in collections usually 50–60 (rarely over 70) at 7 1/2 to 8 1/8 (8 1/2) whorls. Shape: moderately depressed cone-shaped, with whorls somewhat inflated (especially on upper side); umbilicus wide (UD ca. 31% of SD). Sculpture: Upper side: SSR distinctly separated; LMR wider than UMR (ca. 2:1); distinctly separated groove at base of LMR; Periphery: PR strong, even in very large specimens hardly any additional spiral ribs; upper point of whorl attachment on upper part of LPR (upper edge of LPR visible in suture of early whorls); upper side and periphery crossed by deeply incised oblique axial grooves, resulting in formation of many elongate oblique segments, becoming weaker or smooth on MR-area of body whorl of larger specimens; segments of the two MR not necessarily corresponding; Base: IPR strong; BF without spiral ribs; with radiating plications (especially in younger specimens), stronger towards umbilicus; two distinctly separated nodulose spiral ribs (PUR and UC) surrounding umbilicus, with UC strong and irregular on later whorls; columellar wall forming almost straight inner lip with plications for support of the columellar muscle, with deepest groove in UC overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration (see Pl.1 Fig.A): SSR initially white, with pattern of brown blotches starting at about 4–5 Tw (usually the lightest colored of all spiral ribs); UMR initially with brownish pattern, then solid brown for several whorls, later dissolving into pattern of brown blotches (these ± corresponding with pattern on SSR); LMR always olive-grey; UPR, LPR and IPR white with pattern of dark-brown blotches; BF flamed with shades of greyish-brown; one dotted spiral line in front of PUR, its blotches often extending outwards onto the BF; PUR whitish with brown blotches; UC variegated with light- and dark-brown. – Protoconch (see Fig.57): large (1.22–1.42, $\bar{x}$ = 1.31); distinctly heterostrophic; no anal keel (some specimens with rounded ridge in anal-keel area); yellowish, with brown outer corner in front of varix. – Operculum: as described for genus. – Radula and Anatomy: not known.

Geographical distribution (Fig.58): Known from Sri Lanka, the Philippines, Indonesia and the northwestern subtropical Pacific (record from Madagascar doubtful).

Habitat: Sublittoral (most depth records between 30 and 90 m), live records from 35–55 m, sandy substrates.

Discussion:

A distinctive character of *Architectonica taylori* is the more or less completely brown-colored upper mid-rib, which is always darker than the subsutural rib (see Pl.1 Fig.A and Fig.55). The upper midrib in *A. maxima*, with which *A. taylori* is frequently confused, has no brown pattern. Young specimens are similar to shells of *A. picta* and *A. modesta* (see below).

Architectonica picta (Philippi, 1849)

Pl.1 Fig.B; Figs.57–61

1758 "Cochlea turbinata pallide alba, ...", – Seba, Thes., *3*: 121, pl.40 figs.41–42 [not binominal].

1781 "Trochus perspectivus seu opticus", – Chemnitz [in part], Conch.-Cab., *5*: 121, pl.172 fig.1694 [not binominal].

*?1807 *Solarium maculatum* Link, Beschr. Nat.-Slg. Univ. Rost., *2/3*: 136 [referring to *Trochus maculatus* Linné, 1758? Non *Solarium maculatum* Reeve, 1848].

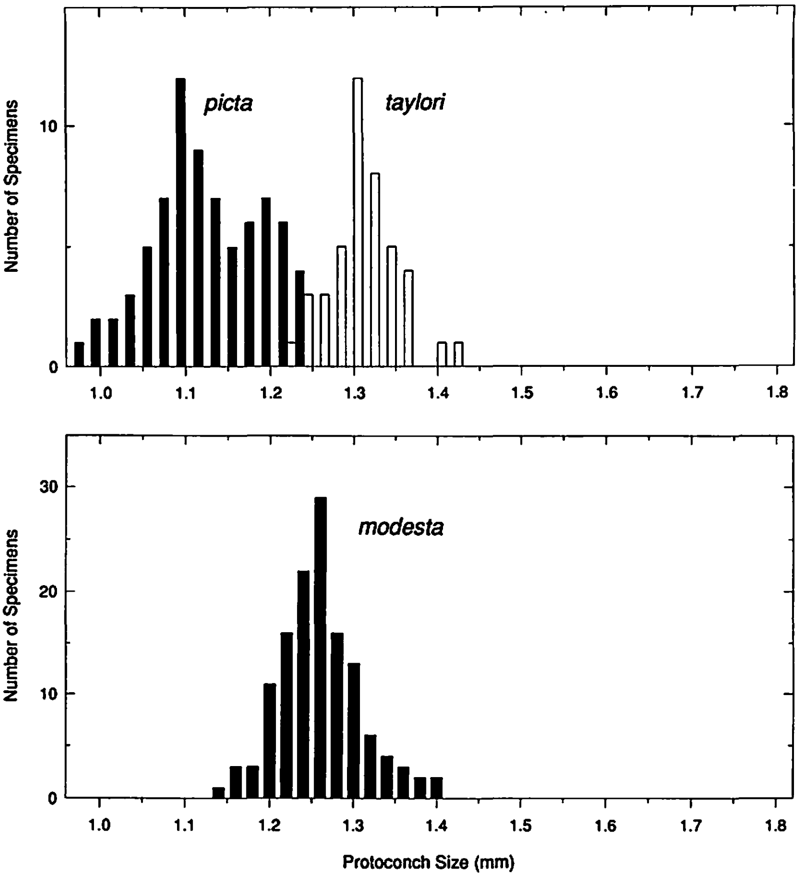


Fig. 57. Histograms of measured protoconch size. *Architectonica picta* (n = 76, x̄ = 1.13, sd = 0.06), *A. taylori* (n = 43, x̄ = 1.31, sd = 0.04), and *A. modesta* (n = 131, x̄ = 1.26, sd = 0.05).

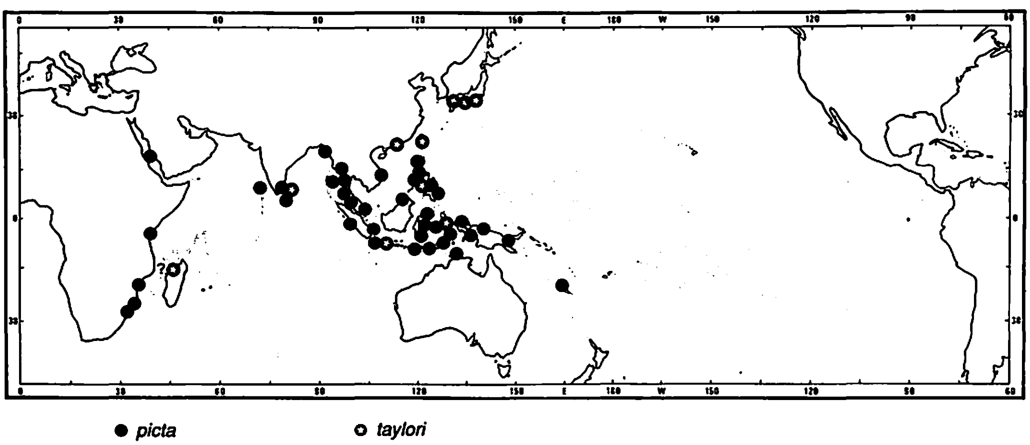


Fig. 58. Geographical distribution of *Architectonica picta* and *A. taylori*.

*?1844 *Solarium fragile* HINDS, 1844b, Proc. zool. Soc. Lond., *1844*: 24.
?1844–1845 *Solarium fragile*, - HINDS, 1844c–1845, Zool. Voy. SULPHUR, *3*: 51; *2*: pl.14 figs.15–16.
?1844 *Solarium fragile*, - HINDS, 1844d, Ann. Mag. nat. Hist., *14*: 439.
*1849 *Solarium pictum* PHILIPPI, Z. Malakozool., *5*(11): 171.
1853 *Solarium pictum*, - PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 10, pl.2 fig.4 [after CHEMNITZ, 1781] & p.15, pl.3 fig.2.
?1853 *Solarium fragile*, - PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 20, pl.3 fig. 9 [after HINDS, 1844c].
1863 *Solarium (Architectonica) pictum*, - HANLEY, Thes. conch., *3*: 231, pl.252 figs.33–34.
1864 *Solarium pictum*, - REEVE, Conch. icon., *15*: no.2, pl.1 fig.2.
*1887 *Solarium (Solarium) Tryoni* MARSHALL, Man. conch., *9*: 10, pl.2 figs.28–29.
1887 *Solarium (Solarium) pictum*, - MARSHALL, Man. conch., *9*: 10, pl.3 figs.35–36 [after HANLEY, 1863].
1940 *Solarium pictum*, - BAYER, Zool. Meded., *22*: 248.
1940 *Solarium tryoni*, - BAYER, Zool. Meded., *22*: 252.
1966 *Architectonica taylori*, - HABE & KOSUGE, Shells world col., *II*: 101, pl.40 fig.2 [non *Solarium taylori* HANLEY, 1862].
1972 *Architectonica perspectiva*, - HINTON, Shells New Guinea: 4, pl.2 fig.23 [non *Trochus perspectivus* LINNÉ, 1758].
?1977 *Heliacus (Claraxis) fragilis*, - GARRARD, Rec. Austr. Mus., *31*(13): 558, pl.8 figs.1–9 [syntypes of *S. fragile*].
1984 *Architectonica picta*, - BIELER, 1984d, Verh. natw. Ver. Hamburg, (NF)*27*: 478, pl.3 fig.XIa [holotype of *S. tryoni*], XIb [lectotype of *S. fragile*] & XIc.
1986 *Architectonica (Architectonica) picta*, - SPRINGSTEEN & LEOBRERA, Shells Philippines: 26, pl.2 fig.10.
1988 *Architectonica picta*, - BIELER, Malac. Rev., Suppl. *4*: 215, fig.13 [radula].

Type measurements: *S. pictum*: SD = ca. 37.0, H = ca. 16.4, UD = almost 13 [after PHILIPPI, 1849]. Holotype of *S. tryoni*: SD = 23.0, H = 13.9, PD = 1.18, Tw = 6 1/6, UD = 5.4. Lectotype of *S. fragile*: SD = 6.9, H = 2.8, PD = 1.18, Tw = 3 1/8, UD = 2.2.

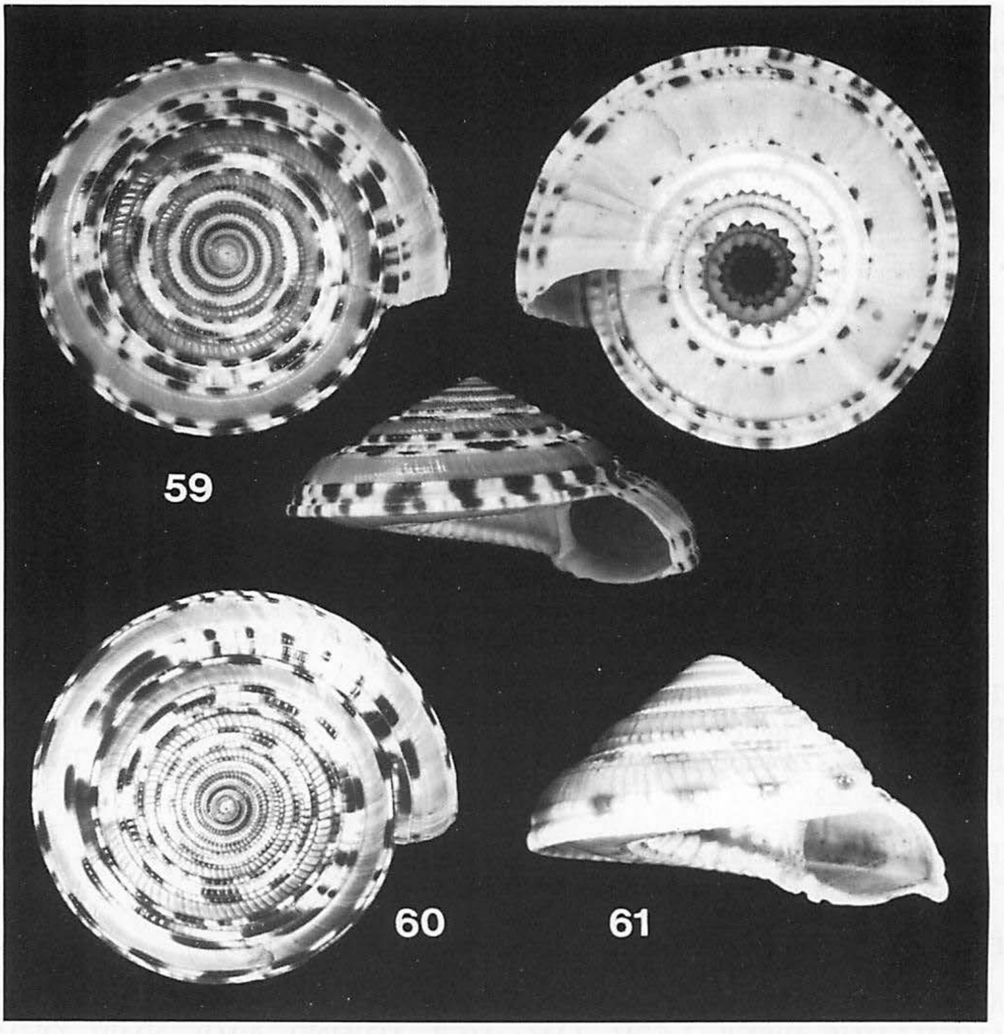
Type localities: *S. pictum*: "Patria: ..." [not known]; *S. tryoni*: "?Moluccas"; *S. fragile*: "North coast of New Guinea; in seven fathoms, sand."

Etymology: *pictus-a-um* [adjective]; Latin: decorated, colored.

Material studied: 138 specimens (AMNH, ANSP, BMNH, CAS, DMNH, FLMNH, FMNH, HUJ, IRSNB, LACM, LMA, MCZ, MNHNP, NMP, NMW, OUM, RNHL, SMF, SMNS, UCMP, UMZC, USNM, ZIMH, ZMA, ZSM, Coll. ALF), including holotype of *S. tryoni* (ANSP 38773), lectotype of *S. fragile* (BMNH 1879.2.26.160). Type specimen of *S. pictum* not located.

Diagnosis:

Large to very large, moderately depressed to fairly high-spired cone-shaped shell with widely open umbilicus; whorls on upper side gemmate, somewhat inflated; two spiral grooves below suture (midrib-area divided subequally, with upper midrib much narrower); shallow depression at base of lower midrib. Subsutural rib white with pattern of brown blotches starting after about 3 1/2 whorls; upper midrib only initially brown, dissolving into grey-brown, then white-brown pattern; proxumbical rib and umbilical crenae white with few brown blotches. Protoconch diameter 0.98–1.24 mm.



Figs. 59–61. *Architectonica picta* (PHILIPPI, 1849). Fig. 59 (three aspects): specimen from Andaman Islands; FMNH 223424; SD = 41.7. Fig. 60: specimen from Mozambique; NMP H4740; SD = 49.1. Fig. 61: holotype of *Solarium tryoni* MARSHALL, 1887; "?Moluccas"; ANSP 38773; SD = 23.0.

Description:

Teleoconch: Large to very large; diameter of specimens in collections usually 30–50 at 6 1/8 to 7 3/4 whorls. Shape: moderately depressed to fairly high-spired cone-shaped, with whorls somewhat inflated (especially on upper side); umbilicus wide (UD ca. 29% of SD). Sculpture: Upper side: SSR distinctly separated; LMR wider than UMR (2:1 to 3:1); shallow depression at base of LMR; Periphery: PR strong, with usually one additional fine spiral rib between UPR and LPR; upper point of whorl attachment on upper part of LPR (upper edge of LPR visible in suture of early whorls); upper side and periphery crossed by deeply incised oblique axial grooves, resulting in formation of many elongate oblique segments, becoming smooth on body whorl of larger specimens; Base: IPR strong; BF without spiral ribs (younger specimens with radiating plications, stronger towards umbilicus; two distinctly separated nodulose spiral ribs (PUR and UC) surrounding umbilicus, with UC rather small; columellar wall forming almost straight inner lip with plications for support of the columellar muscle, with deepest groove in UC overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration (Pl.1 Fig.B): SSR initially white, with pattern of brown blotches (ca. 3–8 per whorl, each 3–8 nodules wide), starting after about 3 1/2 Tw (blotches initially light-brown, darker brown as in UMR only after ca. 6 Tw); UMR initially ± solid brown, dissolving into a grey-brown pattern after a few whorls, and turning eventually into a white-brown variegated pattern; blotch pattern of SSR and UMR usually not corresponding; LMR marbled with mauve-grey; UPR, LPR and IPR white with pattern of brown blotches (with LPR almost white on early whorls); BF marbled with bluish-white; usually one dotted spiral line in front of PUR; PUR and UC white with a few brown blotches. – Protoconch (see Fig.57): medium-sized to large (0.98–1.24, $\bar{x}$ = 1.13); distinctly heterostrophic; weak ridge in anal-keel area; whitish, with brown outer corner in front of varix. – Operculum: as described for genus. – Radula: "ptenoglossate," with 28 long, prong-like teeth per row (14–0–14), with the outer ones being shorter and bicuspid (see Bieler, 1988: fig.13). – Anatomy: not known.

Geographical distribution (Fig.58): Subtropical and tropical Indian Ocean and West Pacific.

Habitat: Upper sublittoral (most depth records between 1 and 50 m), live records from sandy substrates in shallow water.

Discussion:

The shell sculpture of *Architectonica picta* agrees with that of *A. taylori*, but the coloration is very different (compare Pl.1 Figs.A and B). *Architectonica picta* is much thinner shelled, has a smaller protoconch than *A. taylori* (see Fig.57), and never has a solid-brown colored upper midrib as in *A. taylori* and in *A. modesta*. A useful character distinguishing between the three is the coloration of the umbilical crenae, which is pure-white in *A. modesta*, variegated with light- and dark-brown in *A. taylori*, and white with a few occasional brown spots in *A. picta*.

Type material of this species could not be located, but Philippi's original description and subsequent figures (1849: 171, 1853b: pl.2 fig.4 and pl.3 fig.2) allow positive identification. *Solarium tryoni* Marshall, 1887, was based on a faded, fairly high-spired specimen of this species (see Fig.61, and Bieler, 1984d: pl.3 fig.XIa).

The validity of the name "*Solarium maculatum* Link, 1807" is questionable. G. Fischer (1807: 210) referred to figures in Chemnitz (1781: pl.172 fig.1696 [= *Architectonica nobilis*], and figs. 1691, 1692 [= *A. gualtierii*]) as "*Trochus maculatus* Linné," while Link (1807: 136) referred to Chemnitz's (1781) figure 1694 [= *A. picta*] as "*S. maculatum*." It is likely that Link also meant *Trochus maculatus* of Linné (1758: 756), a nominal species with a complicated taxonomic history (see DODGE, *1958*: *163–165*). However, some subsequent authors (TOMLIN & WINCKWORTH, 1936: 38; DODGE, 1958: 167) credited LINK (1807) with the introduction of a new nominal species.

The syntypic series of *Solarium fragile* HINDS, 1844 [BMNH 1879.2.26.160-2; figured by GARRARD, 1977: pl.8 figs.1-9, as "*Heliacus (Claraxis) fragilis*"] contained three juvenile shells, probably belonging to more than one species of the "*A. maxima*-complex". The specimen best matching the original description was selected as lectotype (BIELER, 1984d: 480, pl.3 fig.XIb). It is most likely a young specimen of *Architectonica picta*.

Architectonica modesta (PHILIPPI, 1849)

Pl.1 Fig.E; Figs.57, 62, 63

1790 –, GEVE, Belustigung: pl.25 figs.269a-b.
*1849 *Solarium modestum* PHILIPPI, Z. Malakozool., *5*(11): 171.
1853 *Solarium modestum*, – PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 15, pl.3 fig.1.
1863 *Solarium (Architectonica) modestum*, – HANLEY, Thes. conch., *3*: 229, pl.250 figs.11-12.
1863 *Solarium (Architectonica) modestum* var., – HANLEY, Thes. conch., *3*: pl.252 figs.27-28.
1864 *Solarium modestum*, – REEVE, Conch. icon., *15*: no.12, pl.2 fig.12.
1887 *Solarium (Solarium) modestum*, – MARSHALL, Man. conch., *9*: 9, pl.2 figs.22-23 [after HANLEY, 1863].
1909 *Solarium modestum*, – SCHEPMAN, Monogr. Res. SIBOGA Exped., *49*(1b): 219.
1923 *Solarium modestum*, – OOSTINGH, Meded. Landbouwhoogesch., *26*(3): 52, fig.4.
1940 *Solarium modestum*, – BAYER, Zool. Meded., *22*: 228.
1975 *Architectonica perspectiva*, – SALVAT & RIVES, Coqu. Polyn.: 97, fig.7; 265, fig.46 bottom [non *Trochus perspectivus* LINNÉ, 1758].
1977 *Architectonica (Architectonica) modesta*, – GARRARD, Rec. Austr. Mus., *31*(13): 509, fig.5 [operculum]; 513, pl.1 figs.7-9.
1979 *Architectonica modesta*, – HINTON, Guide shells Papua: pl.1 figs.8-8a.
1980 *Architectonica (Architectonica) modesta*, – *Collins, Austr. Shell News, 28/29(1979-80): 3, fig. "top left".*
1984 *Architectonica modesta*, – BIELER, 1984d, Verh. natw. Ver. Hamburg, (NF)*27*: 480, pl.3 fig.XII.
1986 *Architectonica (Architectonica) modesta*, – SPRINGSTEEN & LEOBRERA, Shells Philippines: 26, pl.2 fig.9.

Original measurements: SD = ca. 26.2, H = 12.0, UD = ca. 7.6 [after Philippi, 1849].

Type locality: "Patria: ..." [unknown].

Etymology: *modestus-a-um* [adjective]; Latin: modest, discreet.

Material studied: 269 specimens (AMNH, ANSP, BMNH, CAS, DMNH, FLMNH, FMNH, IRSNB, LACM, LMA, MCZ, MNHNP, NMP, NMW, OUM, RNHL, SMF, SMNS, UCMP, UMZC, USNM, ZMA, ZSM, Coll. ALF). Type material of *S. modestum* not located.

Diagnosis:

Large cone-shaped shell with widely open umbilicus; whorls on upper side gemmate, somewhat inflated; two spiral grooves below suture (midrib-area divided subequally, with upper midrib much narrower), and shallow depression at base of the lower

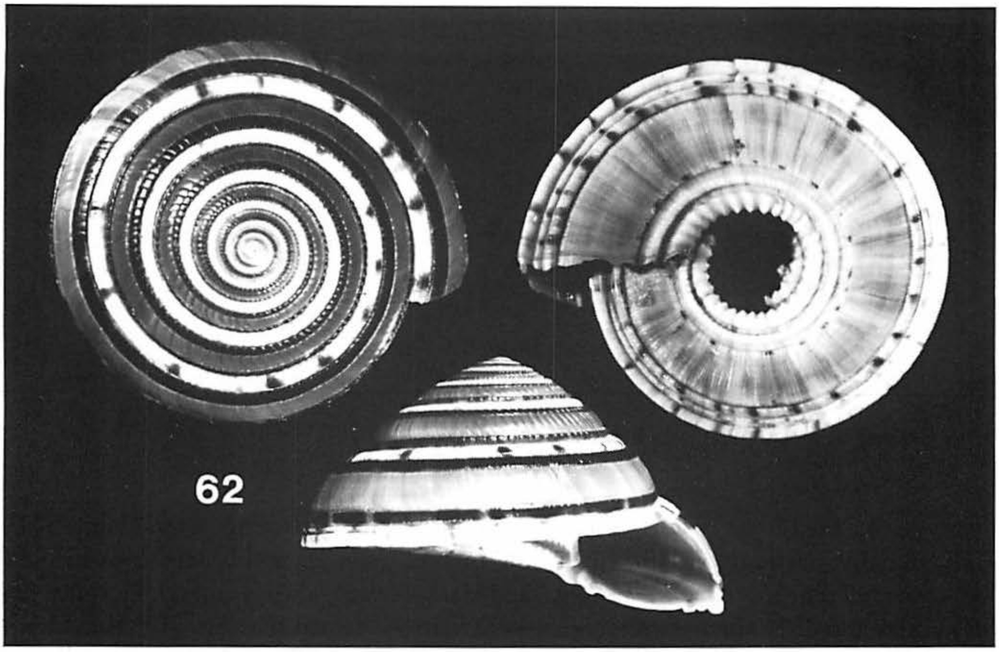


Fig. 62. *Architectonica modesta* (Philippi, 1849); specimen from Mozambique; NMP H5628; SD = 38.8.

midrib. Subsutural rib white, after about 5 whorls with pattern of roundish blotches; upper midrib nearly solid dark-brown; proxumbical rib and umbilical crenae pure white. Protoconch diameter 1.14–1.40 mm.

Description:

Teleoconch: Large, diameter of specimens in collections usually 25–40 at 5 1/2 to 7 3/8 whorls. Shape: moderately depressed to fairly high-spired cone-shaped, with whorls somewhat inflated (especially on upper side); umbilicus wide (UD ca. 29% of SD). Sculpture: Upper side: SSR distinctly separated; LMR wider than UMR (ca. 3:1); shallow depression at base of LMR; Periphery: PR strong, with UPR almost as prominent as LPR; one additional fine spiral rib between UPR and LPR; upper point of whorl attachment on upper part of LPR (upper edge of LPR visible in suture of early whorls); upper side and periphery crossed by deeply incised oblique axial grooves, resulting in formation of many elongate oblique segments, becoming smooth on body whorl of larger specimens; Base: IPR strong, with one additional spiral rib between LPR and IPR; BF without spiral ribs (smaller specimens with radiating plications, stronger towards umbilicus); two distinctly separated nodulose spiral ribs (PUR and UC) surrounding umbilicus, with UC relatively fine and regular; columellar wall forming almost straight inner lip with plications for support of the columellar muscle, with deepest groove in UC overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration (Pl.1 Fig.E): SSR initially white, with pattern of ± round brown

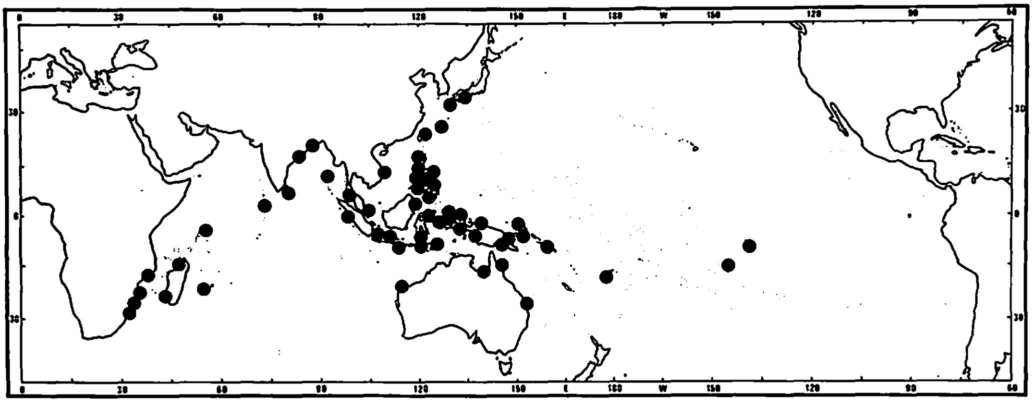


Fig. 63. Geographical distribution of *Architectonica modesta*.

blotches (ca. 10–14 per whorl, each 1–2 nodules wide), starting after about 5 Tw; UMR initially variegated with shades of brown, later ± solid dark-brown; LMR olive-brown; UPR blotched with light- and dark-brown (always lighter in color than SSR); LPR and IPR almost white, with weak narrow brown blotches; BF flamed with bluish-white; one dotted spiral line in front of PUR; PUR and UC pure white. – Protoconch (see Fig.57): medium-sized to large (1.14–1.40, $\bar{x}$ = 1.26); distinctly heterostrophic; with rounded ridge in anal-keel area; whitish, with brown outer corner in front of varix. – Operculum: as described for genus. – Radula & Anatomy: not known.

Geographical distribution (Fig.63): Subtropical and tropical Indian Ocean and West to Central Pacific.

Habitat: Upper sublittoral (most depth records between 1 and 85 m), live records from sandy substrates in shallow water.

Discussion:

The shell sculpture of *Architectonica modesta* is similar to those of *A. picta* and *A. taylori*, but the axial sculpture is weaker. This species is easily recognized by the combination of a white subsutural rib (that often has a few regularly spaced brown blotches) and a more or less solid-brown colored upper midrib (see Pl.1 Fig.E). It is frequently confused with *A. perspectiva*, which has no spiral groove in the midrib-area below the brown band and which has dark-brown umbilical crenae, while those of *A. picta* are pure white.

Type material could not be located, but PHILIPPI's description and subsequent figure (1849: 171, 1853: pl.3 fig.1) allow positive identification.

Architectonica arcana n.sp.
Pl.1 Fig.D; Figs.64–67

1940 *Solarium laevigatum*, - BAYER [in part], Zool. Meded., *22*: 227 [non *S. laevigatum* LAMARCK, 1816].
1984 *Architectonica* sp. aff. *laevigata*, - BIELER, 1984d, Verh. natw. Ver. Hamburg, (NF)*27*: 481, pl.4 fig.XIII.

Type measurements:

	SD	H	PD	Tw	UD	Locality	Collection
Holotype	33.5	19.2	1.42	5 7/8	9.0	Karachi, Pakistan	BMNH 1991002
Paratype 1	27.8	17.8	1.40	5 5/8	6.9	Karachi, Pakistan	BMNH 1991003
Paratype 2	38.7	23.8	1.36	7	10.6	Muscat, Oman [9]	BMNH 1981118
Paratype 3	27.7	17.0	1.40	5 5/8	6.8	Karachi, Pakistan	BMNH 198183
Paratype 4	31.4	20.0	1.40	5 7/8-	7.8	Karachi, Pakistan	USNM 633074
Paratype 5	35.0	23.9	1.40	6 3/8	9.5	Muscat, Oman	ANSP 321721
Paratype 6	24.1	16.2	1.38	5 3/4	5.5	Aden, South Yemen	FMNH 223413

Type locality: Karachi, Pakistan (ex Coll. F.W. TOWNSEND). Paratype 1 from holotype lot.

Etymology: *arcanus-a-um* [adjective]; Latin: secret, concealed; referring to its modest size and coloration compared to other members of its genus and to its previously hidden existence in the collections.

Material studied: 35 specimens (AMNH, ANSP, BMNH, DMNH, FMNH, MCZ, RNHL, SMF, USNM), including type material as listed above.

Diagnosis:

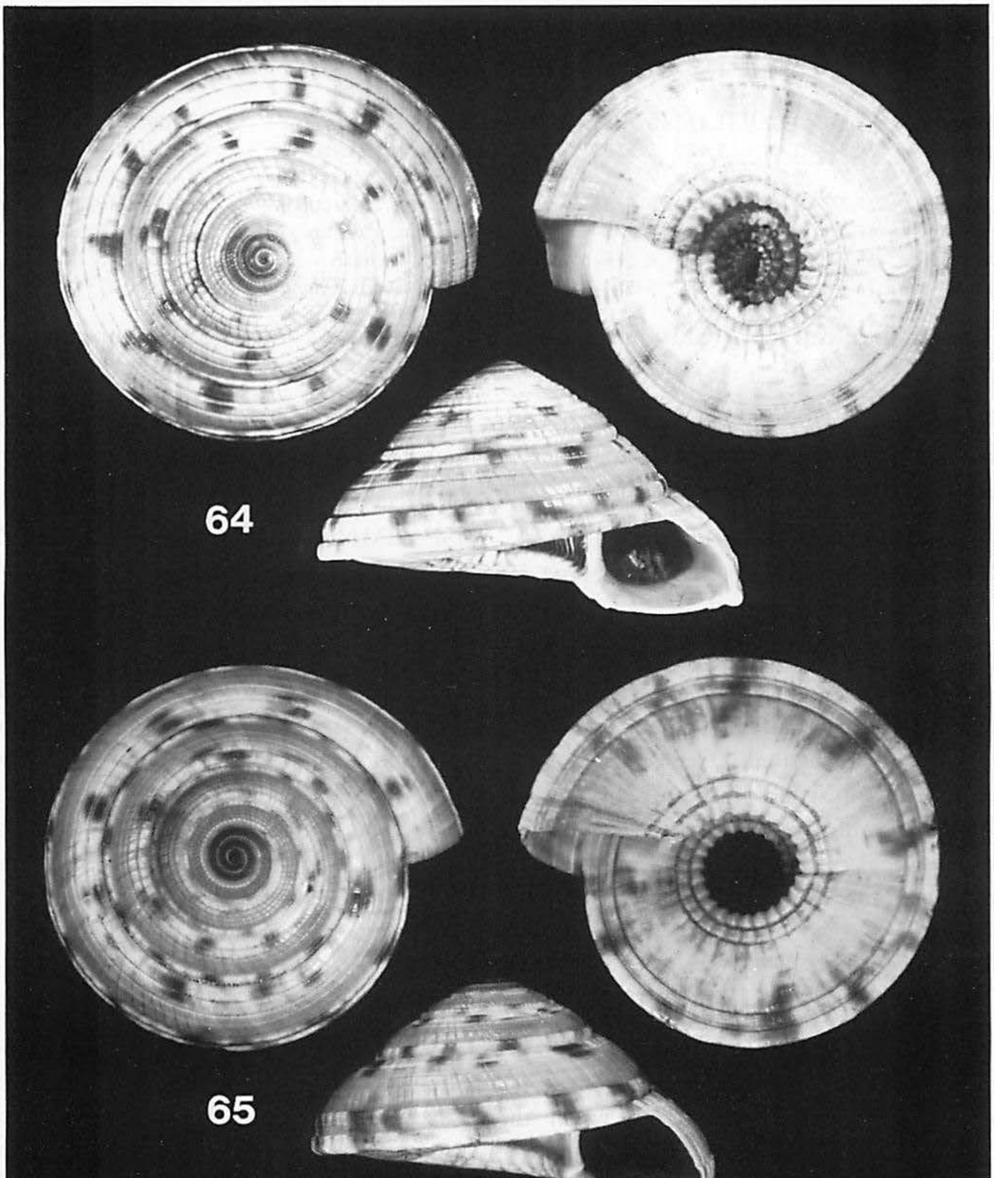
Large, fairly high-spired cone-shaped shell with moderately wide umbilicus; whorls on upper side gemmate, somewhat inflated; two spiral grooves below suture (midrib-area divided subequally, with the upper midrib much narrower); lower midrib always with some spiral sculpture and shallow depression at its base. Subsutural rib yellowish with brown blotches, blotches extending onto upper midrib after about 3 1/2 whorls; proxumbical rib and umbilical crenae pale tan, without color pattern; umbilical crenae forming lightest colored area of shell base. Protoconch diameter ≥ 1.30 mm.

Description:

Teleoconch: Large, diameter of specimens in collections usually 25–35 at 5 1/4 to 6 3/8 whorls. Shape: fairly high-spired cone-shaped, with whorls inflated (especially on upper side); umbilicus moderately wide (UD ca. 24% of SD). Sculpture: Upper side: SSR distinctly separated; LMR wider than UMR (initially ca. 2:1 to 3:1, later ca. 2:1); LMR always with some spiral sculpture, in some specimens divided by a ± faint spiral groove; shallow depression at base of LMR; Periphery: PR strong, with UPR almost as prominent as LPR; upper point of whorl attachment on upper part of LPR (upper edge of LPR visible in suture of early whorls); upper side and periphery crossed

[9] Erroneously cited with "no locality" in BIELER, 1984d: 466, pl.4 fig.XIII (3 views of paratype 2).

by ± deeply incised oblique axial grooves, resulting in a general gemmate appearance on early whorls, becoming smooth on body whorl of larger specimens; segments of the two midribs not necessarily corresponding; Base: IPR strong, already in small specimens with one additional spiral rib between LPR and IPR; BF without spiral



Figs. 64, 65. *Architectonica arcana* n.sp. Fig. 64: paratype 2; Muscat, Oman; BMNH 1981118; SD 38.7. Fig. 65: holotype; Karachi, Pakistan; BMNH 1991002; SD = 33.5.

ribs; with weak radiating plications (especially in younger specimens), stronger towards umbilicus; two distinctly separated nodulose spiral ribs (PUR and UC) surrounding umbilicus, with UC relatively fine; columellar wall forming almost straight inner lip with plications for support of the columellar muscle, with deepest groove in UC overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration (see Pl.1 Fig.D): SSR initially white, on later whorls pale tan with brown blotches (7–11 per whorl, each ca. 2 nodules wide); MR initially mauve, turning grey or purplish-grey after about 2 1/2 Tw; pattern of SSR after about 3 1/2 Tw extending onto UMR; UPR, LPR and IPR greyish, with ± large irregular brown blotches extending from the UPR around the periphery onto the base; BF marbled greyish-brown; large specimens with few brown marks in front of PUR; PUR and UC without pattern; UC forming lightest colored area of base. - Protoconch (see Fig.66): large (1.30–1.48, $\bar{x}$ = 1.39); distinctly heterostrophic; without anal keel; reddish- or greyish-brown, with outer corner in front of varix darker. - Periostracum: extremely thin and firmly attached, imparting an overall olive-brown appearance and forming dark-brown vertical scales on umbilical wall. - Operculum: as described for genus. - Radula and Anatomy: not known.

Geographical distribution (Fig.67): Apparently restricted to northwestern Indian Ocean (Arabian Peninsula to Sri Lanka).

Habitat: Sublittoral (available depth records between 67 and 103 m).

Discussion:

Architectonica arcana, compared to other members of its genus, is a relatively small species in terms of shell size (see Pl.1 Fig.D). The subequal division of the midrib-area and the corresponding brown blotches of subsutural rib and upper midrib are similar to the conditions in *A. purpurata*, from which it can be readily separated by its pale umbilical crenae (reddish-brown in *A. purpurata*). *Architectonica laevigata* (see below) appears to be the closest living relative, with which it shares widely spaced axial grooves, the fairly high-spired shell-shape and the purplish tint of the midrib-area. The wider umbilicus with finer umbilical crenae, and especially the overall olive-brown appearance (compare Pl.1 Figs. D and F), allow easy distinction between the two.

No published name was available for this species. In collections, specimens are frequently found in mixed lots with *A. laevigata*. One of the 19 shells on which Bayer (1940: 227) based his discussion of *A. laevigata*, is a specimen of *A. arcana* (RNHL, vidi).

Architectonica laevigata (Lamarck, 1816)
Pl.1 Fig.F; Figs.66–69

*1816 *Solarium laevigatum* Lamarck, Tabl. encycl. méth.: pl.446 figs.3a-b.
1822 *Solarium laevigatum*, - Lamarck, Hist. nat., *7*: 3.
1838–1839 *Solarium levigatum* [sic], - Kiener, Spéc. gén. icon. coqu., *10*: 5, pl.2 fig.3.
1843 *Solarium laevigatum*, - Deshayes, Hist. nat. [2nd ed.], *9*: 98.
1849 *Solarium laevigatum*, - Philippi, Z. Malakozool., *5*(11): 169.

1853 *Solarium laevigatum*, - PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 17, pl.3 fig.4.
1863 *Solarium (Architectonica) laevigatum*, - HANLEY, Thes. conch., *3*: 233, pl.251 figs.21-22.
1864 *Solarium laevigatum*, - REEVE, Conch. icon., *15*: no.9, pl.2 fig.9.
1887 *Solarium (Solarium) laevigatum*, - MARSHALL, Man. conch., *9*: 12, pl.4 figs.43-44 [after KIENER].
1897 *Solarium laevigatum*, - SOWERBY (III), Append. mar. shells S. Afr.: 15.
1940 *Solarium laevigatum*, - BAYER [in part], Zool. Meded., *22*: 227.
1952 *Architectonica laevigata*, - SATYAMURTI, Bull. Madras Gov. Mus., *1*(2)(6): 73, pl.4 figs.11a-b.
1963 *Solarium laevigatum*, - BARNARD, 1963b, Ann. S. Afr. Mus., *47*(1): 157.
1982 *Architectonica laevigata*, - BOSCH & BOSCH, Seashells Oman: 42, fig.
1982 *Architectonica laevigata*, - ABBOTT & DANCE, Compend. Seash.: 61, fig.
1984 *Architectonica laevigata*, - BIELER, 1984d, Verh. natw. Ver. Hamburg, (NF)*27*: 482, pl.4 fig.XIV [lectotype designation].
1989 *Architectonica laevigata*, - HORIKOSHI, Sea shells world: pl. 40 fig. 22.
1989 *Architectonica laevigata*, - BOSCH & BOSCH, Seashells s. Arabia: 34, text-fig.

Type measurements (lectotype): SD = ca. 37.5, H = ca. 25.3, UD = ca. 8.7 [from photograph].

Type locality: not given; LAMARCK (1822): "Habite ....." [unknown].

Etymology: *laevigatus-a-um* [adjective]; 19th century variant spelling of the Latin *levigatus-a-um*; smooth, slippery.

Material studied: 362 specimens (AMNH, ANSP, BMNH, CAS, DMNH, FMNH, HUJ, IRSNB, LACM, LMA, MCZ, MNHNP, NMP, NMW, RNHL, SMF, SMNS, UCMP, UMZC, USNM, ZIMH, ZMA, ZSM, Coll. ALF), and photograph of lectotype of *S. laevigatum* (MHNG 1095/37/1).

Diagnosis:

Large cone-shaped shell with moderately wide umbilicus; whorls on upper side gemmate and inflated; two spiral grooves below suture (midrib-area divided equally);

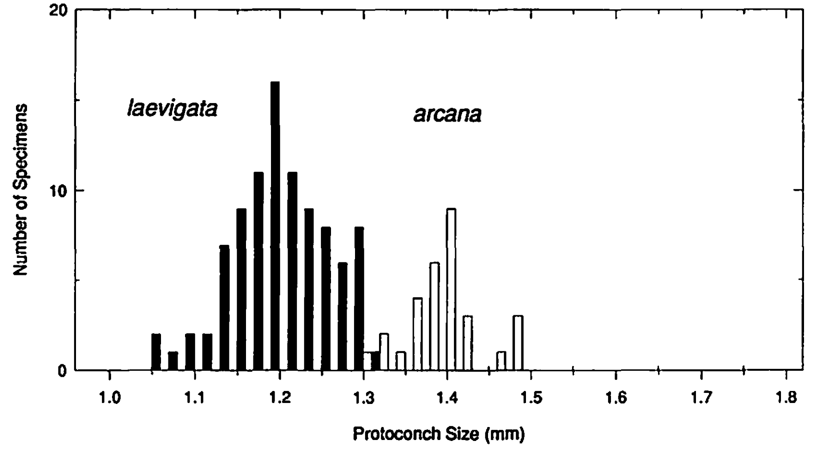


Fig. 66. Histogram of measured protoconch size. *Architectonica laevigata* (n = 93, x̄ = 1.21, sd = 0.06), and *A. arcana* (n = 30, x̄ = 1.39, sd = 0.04).

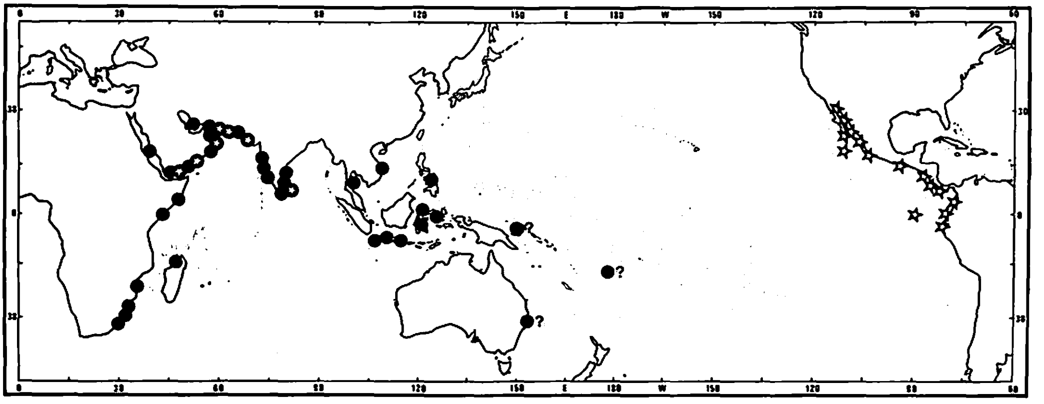
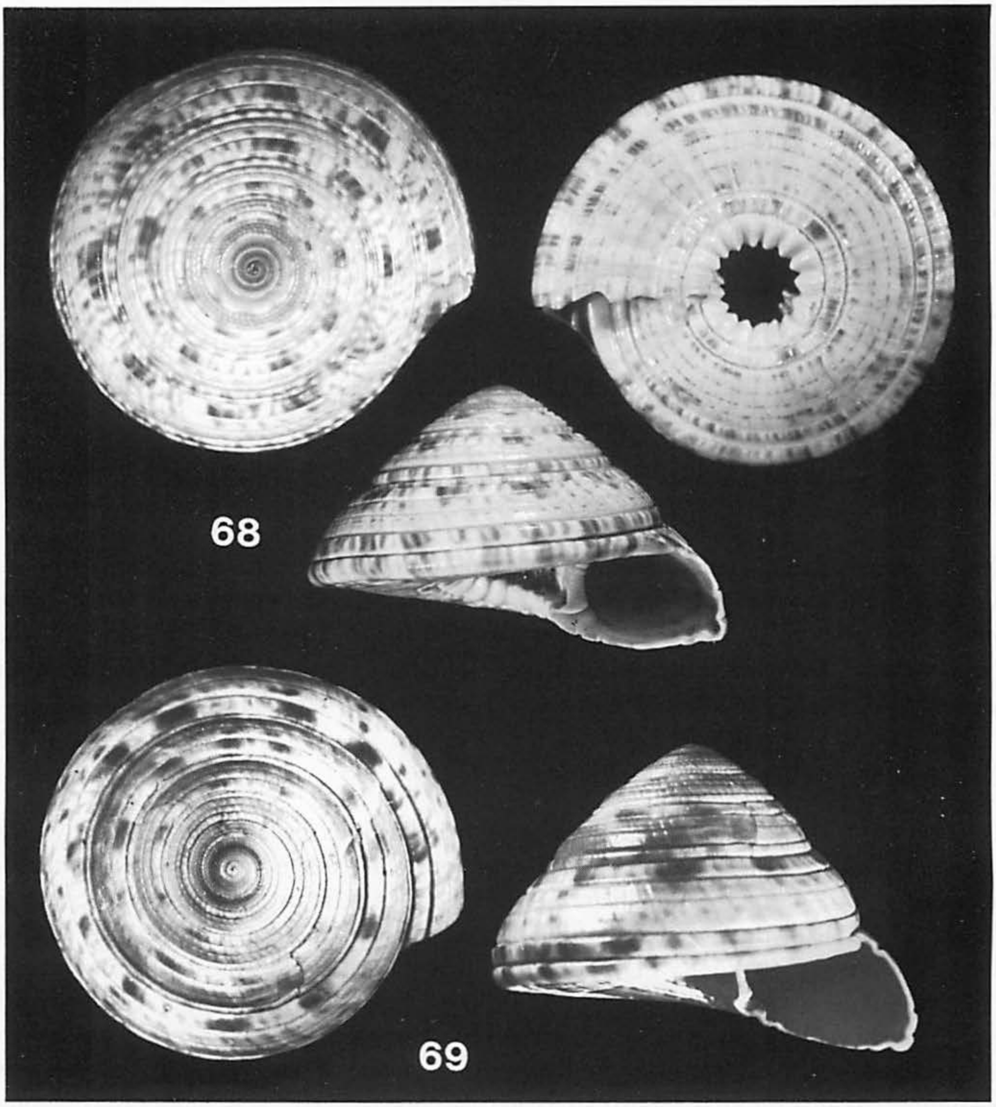


Fig. 67. Geographical distribution of *Architectonica laevigata*, *A. arcana* and *A. karsteni*.

shallow depression at base of lower midrib. Subsutural rib whitish with irregular brown blotches, midrib-area purplish or bluish-grey with diffuse pattern of small brown blotches, basal field with up to four dotted spiral lines, proxumbical rib pale greyish-brown (often with brown blotches); umbilical crenae forming lightest colored area of shell base, often white. Protoconch diameter $\leq$ 1.32 mm.

Description:

Teleoconch: Large, diameter of specimens in collections usually 20–30 (rarely over 40) at 5 1/2 to 6 1/2 (7 1/4) whorls. Shape: cone-shaped, with whorls inflated (especially on upper side); umbilicus moderately wide (UD ca. 17% of SD). Sculpture: Upper side: SSR distinctly separated; UMR and LMR of about equal strength; shallow depression at base of LMR; Periphery: PR strong, with UPR almost as prominent as LPR; upper point of whorl attachment on upper part of LPR (upper edge of LPR visible in suture of early whorls); upper side and periphery crossed by deeply incised oblique axial grooves, resulting in a general gemmate appearance on early whorls, becoming smooth on later whorls of larger specimens; Base: IPR moderately strong; BF without spiral ribs; with weak radiating plications (especially in younger specimens), stronger towards umbilicus; two distinctly separated nodulose spiral ribs (PUR and UC) surrounding umbilicus, with UC strong; columellar wall forming almost straight inner lip with plications for support of the columellar muscle, with deepest groove in UC overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration (see Pl.1 Fig.F): SSR initially white, after about 1 1/2 Tw with pattern of irregular brown blotches; MR purplish or bluish-grey with diffuse pattern of small brown blotches (usually not corresponding with pattern of SSR and PR); UPR, LPR and IPR whitish with irregular pattern of brown blotches; BF light bluish-brown with up to four dotted spiral lines of various widths; PUR pale grayish-brown, often with brown blotches; UC forming lightest colored area of base, often white. - Protoconch (see Fig.66): medium-sized to large (1.06–1.32, $\bar{x}$ = 1.21); distinctly heterostrophic;



Figs. 68, 69. *Architectonica laevigata* (LAMARCK, 1816). Fig. 68: specimen from Mozambique; NMP H4685; SD = 35.6. Fig. 69 (two aspects): lectotype of *Solarium laevigatum*; MHNG 1095/37/1 (photograph: G. DAJOZ, MHNG); SD = 40.7.

without anal keel; whitish to brown, with outer corner in front of varix brown. – Operculum: as described for genus. – Radula and Anatomy: not known.

Geographical distribution (Fig. 67): Indian Ocean to the Philippines (records from the Australian region in need of verification).

Habitat: Upper sublittoral (most depth records between 2 and 30 m), with live records from sandy substrates in shallow water.

Discussion:

Architectonica laevigata is readily recognized by its relatively small, high-spired and narrowly umbilicated shell and its teleoconch coloration of small, diffuse brown blotches on a bluish background (see Pl.1 Fig.F). The only other similar Recent forms are *A. arcana* n.sp. (see above) and *A. karsteni* (below).

The one of two syntypes in Geneva (MNHNG 1095/37/1; see Fig.69), that most likely served for LAMARCK's original illustrations (1816: pl.446 figs.3a-b), was selected as lectotype (BIELER, 1984d: 483, pl.4 fig.XIV).

Architectonica karsteni RUTSCH, 1934

Figs.67, 70

*1934 *Architectonica nobilis karsteni* RUTSCH, Abh. schweiz. palaeont. Ges., *54-55*: 44, pl.1 figs.8-10 [Miocene fossil].

1981 *Architectonica (Architectonica) nobilis karsteni*, - FRASSINETTI & COVACEVICH, Bol. Mus. nac. Hist. nat. Chile, *38*: 145, figs.2a-c, 4a-c [after RUTSCH] [synonymy].

1985 *Architectonica (Architectonica) karsteni*, - DEVRIES, Veliger, *27*(3): 282ff., figs.2-12, 15-16, 18, 20 [synonymy, distribution map; Miocene to Recent].

Type measurements (fossil holotype): SD = 31.4, H = 18.0, Tw = ca. 7 [protoconch damaged], UD = 4.6. Measurements of figured specimen (LACM 40-30.3, Baja California, Recent): SD = 38.4, H = 24.6, PD = 1.10, Tw = 7- [damaged, was 7+], UD = 5.7.

Type locality: "Punta Gavilan (Lok.1769)," Falcon, northern Venezuela ('Cantaure' Formation, Miocene).

Etymology: *karsteni* [genitive singular case-ending]. Named after the German geologist HERMANN GUSTAV KARL WILHELM KARSTEN (1817-1908).

Material studied: 298 specimens, of which 187 were Recent material (AMNH, ANSP, CAS, FMNH, LACM, NMB, PRI, UCMP, USNM); including fossil holotype (NMB H1836).

Diagnosis:

Medium-sized to large, fairly high-spired cone-shaped shell with moderately wide umbilicus; whorls on upper side gemmate and inflated on both sides; two spiral grooves below suture (midrib-area divided equally); basal field often with 4-6 weakly developed spiral grooves; proxumbical rib never clearly separated in larger specimens. Subsutural rib whitish with irregular brown blotches; midribs light-brown or bluish-grey and mottled with brown; basal field with 5-6 dotted lines; umbilical crenae whitish with brown pattern (darkest area of base). Protoconch diameter 1.00-1.22 mm.

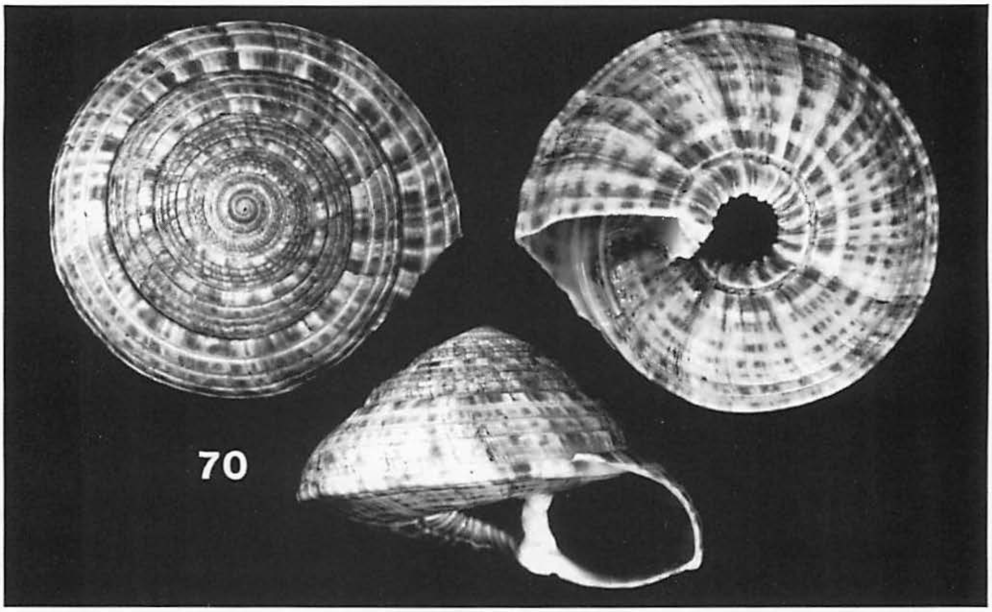


Fig. 70. *Architectonica karsteni* Rutsch, 1934; Recent specimen from Isla Angel de la Guardia, Baja California, Mexico, 99–124 m; LACM 40-30.3; SD = 38.4.

Description (Recent specimens):

Teleoconch: Medium-sized to large, diameter of specimens in collections usually 17–34 at 4 3/4 to 6 3/4 whorls. Shape: fairly high-spired cone-shaped, with whorls inflated; umbilicus moderately wide (UD ca. 16.5% of SD). Sculpture: Upper side: SSR distinctly separated; UMR and LMR of about equal strength; Periphery: PR strong, with UPR almost as prominent as LPR; UPR usually wider than LPR, similar to MR (often one ± fine additional spiral rib between the two); upper point of whorl attachment on central to upper part of LPR (therefore upper edge of LPR ± visible in suture); upper side and periphery crossed by deeply incised oblique axial grooves, resulting in a general gemmate appearance on early whorls, becoming almost smooth on body whorl of larger specimens; Base: IPR strong; BF of larger specimens without distinct spiral ribs, but often with 4–6 weakly developed spiral grooves; younger specimens with 5–6 ± smooth, faintly separated spiral ribs, crossed by radial plications, stronger towards umbilicus; wide PUR not or only weakly separated from BF; one wide, distinctly separated, irregular nodulose spiral rib (UC) surrounding umbilicus; columellar wall forming almost straight inner lip with plications for support of the columellar muscle, with deepest groove in UC overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration: SSR and PR whitish with ± irregular brown blotches (about 10–16 on 4th whorl of UPR, each 1–2 nodules wide); MR light-brown or bluish-grey, ± weakly mottled with brown; BF light-brown or bluish-grey with 5–6 dotted or ± solid spiral lines (marking the reduced spiral ribs of the BF), wider towards the umbilicus; UC whitish with light- to dark-brown pattern (darkest area of base). - Protoconch: medium-sized to large (1.00–1.22, $\bar{x}$ = 1.11, sd = 0.057, n = 43; Recent specimens only); distinctly heterostrophic, some specimens with weak anal keel; whitish to light-brown, some specimens with outer corner in front of varix brown. - Operculum: as described for genus. - Radula and Anatomy: not known.

Geographical distribution (Recent specimens only; Fig.67): Eastern Pacific, continental shelf (from Baja California to Peru) and Galapagos Islands.

Habitat: Sublittoral (depth records between 18 and 183 m), most live records from below 50 m; muddy, sandy and rocky substrates.

Discussion:

Architectonica karsteni differs from all other species in this genus by not having a distinctly separated proxumbical rib on the body whorl of the teleoconch, the umbilical crenae forming the only obvious spiral rib around the umbilicus. The single sympatric congener, *A. nobilis*, can be distinguished by its multi-ribbed basal field on the body whorl of adult specimens (only juvenile *A. karsteni* specimens show occasionally faint spiral grooves on the basal field), by midribs that are more coarsely sculptured and much narrower, and by a lower-spired shell with less inflated whorls.

Architectonica karsteni was only known as a Neogene fossil, reported from a number of localities in the western Atlantic Ocean and eastern Pacific (e.g., FRASSINETTI & COVACEVICH, 1981), until DEVRIES (1985) first reported Recent specimens from the West American coast.

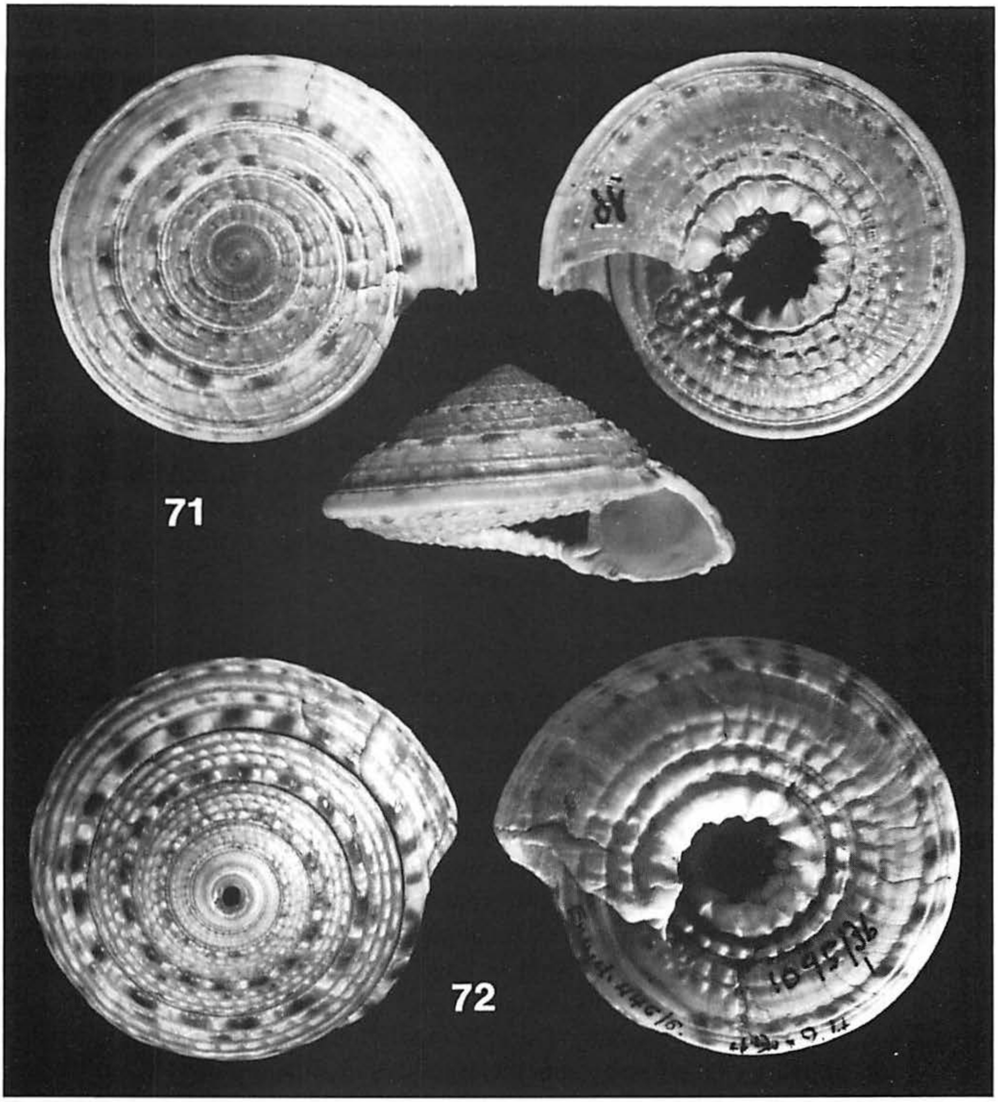
Architectonica nobilis RÖDING, 1798
Figs.71–73

1781 "Trochus perspectivus seu opticus", - CHEMNITZ [in part], Conch.-Cab., *5*: 121, 127, pl.172 figs.1695–1696 [not binominal].
*1798 *Architectonica Nobilis* RÖDING, Mus. Boltenianum: 78.
*1816 *Solarium granulatum* LAMARCK, Tabl. encycl. méth.: pl.446 [non *Solarium granulatum* LEA, 1833 (= *S. tricostatum* CONRAD, 1835, nomen novum), nec *S. nitens* var. *granulata* HAANSTRA & SPIKER, 1932].
1830 *Solarium granulatum*, - DESHAYES, 1830a, Encycl. méth., *2*(1): 158.
*1832 *Solarium granosum* VALENCIENNES, Rec. Obs. Zool. Anat. comp., *2*: 269.
1832 *Solarium granulatum*, - VALENCIENNES, Rec. Obs. Zool. Anat. comp., *2*: 269.
1843 *Solarium granulatum*, - DESHAYES, Hist. nat. (2nd ed.), *9*: 98.
1844–1845 *Solarium quadriceps*, - HINDS, 1844c–1845, Zool. voy. SULPHUR, *3*: 50; *2*: pl.14 figs.7–8.
*1844 *Solarium quadriceps* HINDS, 1844b, Proc. zool. Soc. Lond., *1844*: 23.
*1849 *Solarium verrucosum* PHILIPPI, Z. Malakozool., *5*(11): 172.
1852 *Solarium* sp. indet a, - C.B. ADAMS, Ann. Lyc. nat. Hist. New York, *5*: 190.
1852 *Solarium* sp. indet b, - C.B. ADAMS, Ann. Lyc. nat. Hist. New York, *5*: 190.
1853 *Solarium verrucosum*, - PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 10, pl.2 figs.5–6.
*1859 *Architectonica Valenciennesii* MÖRCH, Malakozool. Bl., *6*: 122.
1863 *Solarium granulatum*, - CARPENTER, Proc. zool. Soc. London, *1863*: 355.
1863 *Solarium (Architectonica) nobile*, - HANLEY, Thes. conch., *3*: 230, pl.253 fig. 35.
1863 *Solarium (Architectonica) granulatum*, - HANLEY, Thes. conch., *3*: 231, pl.250 figs.1–2.
1864 *Solarium granulatum*, - REEVE, Conch. icon., *15*: no.7, pl.2 fig.7.
1864 *Solarium verrucosum*, - REEVE, Conch. icon., *15*: no.8, pl.2 fig.8.

1875 *Architectonica nobilis*, - MÖRCH, Malakozool. Bl., *22*: 154.
*1875 *Architectonica Wroblewskyi* MÖRCH, Malakozool. Bl., *22*: 154.
1875 *Architectonica Wroblewskyi* var. α, MÖRCH, Malakozool. Bl., *22*: 154.
1875 *Architectonica Wroblewskyi* var. ß, MÖRCH, Malakozool. Bl., *22*: 154.
1887 *Solarium (Solarium) granulatum*, - MARSHALL, Man. conch., *9*: 11, pl.5 figs.53-54 [after HANLEY, 1863].
1887 *Solarium (Solarium) verrucosum*, - MARSHALL, Man. conch., *9*: 12, pl.3 figs.37-38 [after PHILIPPI, 1853b].
*1890 *Solarium ordinarium* E.A. SMITH, Proc. zool. Soc. Lond., *1890*: 281, pl.21 figs.17, 17a-b.
1909 *Architectonica granulata*, - DALL, Proc. U.S. natl. Mus., *37*(1704): 232.
1940 *Solarium nobilis*, - BAYER, Zool. Meded., *22*: 229 [synonymy].
1940 *Solarium wroblewskyi*, - BAYER, Zool. Meded, *22*: 252.
1962 *Architectonica nobilis*, - WEISBORD, Bull. Amer. Paleont., *42* (193): 152, pl.13 figs.15-16 [fossil; synonymy].
1963 *Architectonica nobilis*, - SHIKAMA & HORIKOSHI, Select. shells world: 30, pl.22 fig.3.
1964 *Architectonica nobilis*, - PARKER, Mem. mar. Geol. Gulf Calif. Symp., *3*: 345, pl.4 fig.1.
1964 *Architectonica nobilis*, - KEEN, Proc. Calif. Acad. Sci., (4)*30*(9): 198.
1966 ?*Architectonica nobilis*, - KEEN, 1966b, Occas. Pap. Calif. Acad. Sci., *59*: 22, figs.26-26a [syntypes of *A. valenciennesii*].
1969 *Architectonica nobilis*, - MARCHE-MARCHAD, Bull. Inst. franç. Afr. Noire, (A)*31*(1): 479, fig.9.
1971 *Architectonica (Architectonica) nobilis*, - KEEN, Sea shells trop. W. Amer. (2nd ed.): 388, fig.425 ["above and left" = syntypes of *A. valenciennesii*].
1974 *Architectonica nobilis*, - ABBOTT, Amer. seashells (2nd ed.): 97, fig.938.
1974 *Architectonica nobilis*, - MORRIS, Field guide Pac. coast shells: 160, pl.54 fig.7.
1974 *Architectonica perspectiva*, - MORRIS [in part], Field guide Pac. coast shells: 223, pl.67 fig.7 ("below, left and right") [not pl.67 fig.7 "above"; not pl.7 fig.1 = *A. trochlearis*] [non *A. perspectiva* (LINNÉ, 1758)].
1976 *Architectonica nobilis*, - ROBERTSON, 1976a, Bull. Amer. malac. Union, *1975*: 51.
1982 *Architectonica nobilis*, - ABBOTT & DANCE, Compend. seashells: 61, fig.
1984 *Architectonica nobilis*, - BOSS & MERRILL, 1984b, Occas. Pap. Moll., *4*(66): 358, pl.56 fig.2, pl.63 fig.1, pl.65 figs.1-2, pl.67 figs.1-2 [radula, jaws].
1985 *Architectonica nobilis*, - BIELER, 1985a, Arch. Moll., *115*(4/6): 235.
1987 *Architectonica nobilis*, - BANDEL & WEDLER, Senckenb. marit., *19*(1/2): 15.
1988 *Architectonica (Architectonica) nobilis*, - BIELER, Malac. Rev., Suppl.*4*: 235 [radula].
1989 *Architectonica nobilis*, - HORIKOSHI, Sea shells world: pl. 40 figs.23, 24.
1989 *Architectonica nobilis*, - WYE, Shells world: 40, fig.2.

Type measurements: Lectotype of *A. nobilis* [here designated]: SD = 29.6, H = 15.0 [apex damaged]. Lectotype of *S. granulatum* [here designated]: SD = 41.8, H = 25.1, UD = 9.4. *S. granosum*: SD = 20.25, H = 9.0 [after VALENCIENNES]. *S. quadriceps*: SD = ca. 29.5, H = ca. 12.7 [after HINDS, 1844c]. *S. verrucosum*: SD = ca. 32.2, H = ca. 7.6 [after PHILIPPI, 1849]. Lectotype of *A. valenciennesii* [here designated]: SD = 34.7, H = 20.5, PD = 1.18, Tw = 6 3/8, UD = 7.8. Presumed original specimen of *A. wroblewskyi* var. α: SD = 35.3, H = 20.9 [protoconch damaged]; Tw = 7 1/8+, UD = 8.6. Presumed original specimen of *A. wroblewskyi* var.ß: SD = 44.6, H = 23.5, PD = 0.98, Tw = 7 1/4, UD = 10.2. Holotype of *S. ordinarium*: SD = 13.5, H = 6.4, PD = 1.08, Tw = 4 1/2, UD = 2.2.

Type localities: *A. nobilis*: not given; *S. granulatum*: not given [LAMARCK 1822, p.3: "Habite..." (= unknown)]; *S. granosum*: "ad Acapulco Mexicanorum"; *S. quadriceps*: "Bay of Panama; in five fathoms, among mud"; *S. verrucosum*: "Patria ..." [unknown];



Figs. 71, 72. *Architectonica nobilis* Röding, 1798. Fig. 71: lectotype from Spengler coll.; ZMK unnumbered; SD = 29.6. Fig. 72: lectotype of *Solarium granulatum* Lamarck, 1816; MHNG 1095/36/1; SD = 41.8.

A. valenciennesii: "Realejo" [Real Llejos, Nicaragua]; *A. wroblewskyi*: "St.Thomas," var. α: "Portorico," var. ß: "Rio Janeiro"; *S. ordinarium*: "St. Helena".

Etymology: *nobilis-e* [adjective]; Latin: noble, famous.

Material studied: 2000+ specimens (AMNH, ANSP, BMNH, CAS, DMNH, FLMNH, FMNH, HUJ, IRSNB, LACM, LMA, MNHNP, MRAC, NMP, MNW, RNHL, SMF, SMNS, UCMP, UMZC, USNM, ZIMH, ZMA, ZMK, ZSM, Coll. Alf, Coll. von Cosel); of which 600+ were from the eastern Pacific. Lectotype of

A. nobilis (ZMK unnumbered), lectotype and 5 paralectotypes of *A. valenciennesii* (ZMK unnumbered), presumed original specimens of *A. wroblewskyi* vars. α and ß (ZMK unnumbered), holotype of *S. ordinarium* (BMNH 1889.10.1.834) and lectotype of *S. granulatum* (MHNG 1095/36/1). Original material of *S. quadriceps*, *S. verrucosum* and *A. wroblewskyi* s.s. not located; type specimen of *S. granosum* lost (MNHNP).

Diagnosis

Large, moderately depressed to fairly high-spired cone-shaped shell with moderately wide umbilicus; whorls on upper side gemmate, somewhat inflated (with nodules in midrib-area scaly and tilted); two spiral grooves below suture (midrib-area divided equally into two narrow spiral ribs); wide groove at base of the lower midrib; basal field with 1-3 nodulose ribs in front of well-separated proxumbical rib. Subsutural rib light-brown with dark-brown blotches; midrib-area and basal field bluish-brown with irregular brown markings (often with dotted spiral bands on, or in place of, basal field ribs); proxumbical rib and umbilical crenae light brown with darker blotches. Protoconch diameter 0.96–1.24 mm.

Description:

Teleoconch: Heavy, thick-walled, large, diameter of specimens in collections usually 20–40 at 5 1/2 to 7 7/8 whorls. Shape: moderately depressed to fairly high-spired cone-shaped, with whorls somewhat inflated (especially on upper side); umbilicus moderately wide (UD ca. 23% of SD). Sculpture: Upper side: SSR strong, distinctly separated; MR-area initially not clearly separated, dividing on first whorl into two narrow spiral ribs (UMR and LMR); wide groove between LMR and UPR, on later whorls also between SSR and UMR (this groove often with one additional fine spiral rib); Periphery: UPR narrow and less prominent than LPR; upper point of whorl attachment on upper part of LPR (upper edge of LPR visible in suture of early whorls); already in young specimens one additional spiral rib between UPR and LPR; upper side and periphery crossed by ± deeply incised oblique axial grooves, resulting in formation of many elongate segments (bearing scaly nodules, usually tilted like roof tiles on UMR and LMR), becoming weaker on body whorl of larger specimens; segments of the two midribs not necessarily corresponding; Base: IPR strong; already in small specimens one additional spiral rib between LPR and IPR; BF-area in front of PUR ± distinctly divided into 1-3 nodulose ribs of various strengths (smaller specimens with radiating plications, stronger towards umbilicus); PUR strong and distinctly separated from BF-ribs and UC; UC large and usually irregular; columellar wall forming almost straight inner lip with plications for support of the columellar muscle, with deepest groove in UC overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration: SSR, UPR, LPR, IPR and BF-ribs with dark-brown blotches (largest blotches on SSR; lightest coloration on LPR); MR and remaining BF bluish-brown with faint irregular brown markings, often with dotted spiral bands, on or in place of, BF-ribs; PUR and UC light brown with darker blotches. – Protoconch: medium-sized to large (0.96–1.24, $\bar{x}$ = 1.07, sd = 0.069, n = 124;

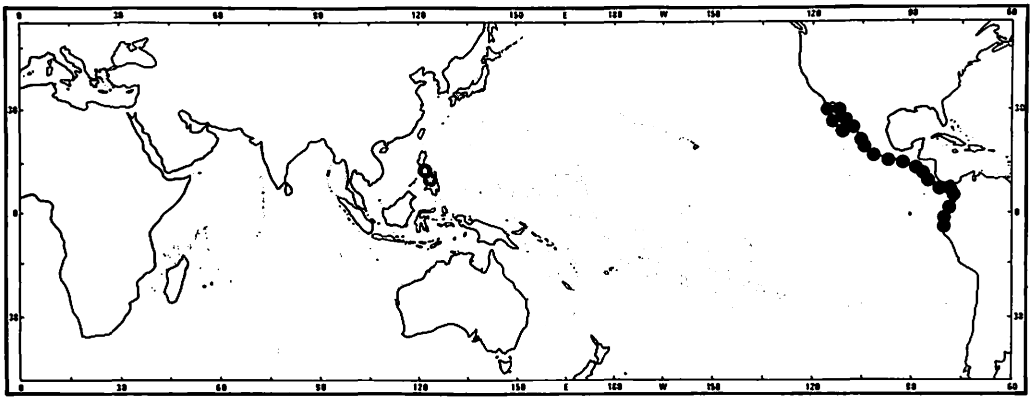
eastern Pacific specimens only); distinctly heterostrophic; anal keel present; yellowish to brown. – Operculum: as described for genus. – Radula: "ptenoglossate," with 12–16 long, recurved, prong-like teeth per row, with the outer ones shorter and forked with long, tapering subequal cusps [conflicting statements in literature; see, e.g., Boss & Merrill, 1984b: 358, pl.56 fig.2, pl.63 fig.1, pl.65 figs.1–2; Bieler, 1988: 235]. – Jaws: consisting of numerous pointed rods (Boss & Merrill, 1984b: 359, pl.56 fig.2b, pl.67 figs.1–2). – Anatomy: described by Merrill (1970a: 26) [but see corrections by Haszprunar, 1985b: 25]. – Soft-body coloration of living animal: overall flesh color, sole of foot whitish; sides of foot and head blotched with rusty pigment; tentacles a deep russet color, white at tips.

Reproduction and larval development: reported by Bandel (1976: 256–257, fig.7) for Colombian (Atlantic) populations: "In the area of occurrence of adults of this species their gelatinous egg masses may be found at all times of the year, anchored in the sand. ... The spawn consists of up to 50 cm long and 3–4 mm thick, gelatinous massive tubes, round in cross section. These are looped in such a way that every 5 to 10 cm of tube they are connected with a gelatinous anchor extending into the substrate. Thus, a spawn mass in place looks like a number of independent loops, even though it actually consists only of one long, soft, continuous tube. Within the tube the capsules are arranged in irregular spiral lines. Each of the shiny, spherical, durable capsules contains one greenish egg or embryo and is connected to the next by a string. One millimeter of egg tube contains about 300 capsules. Therefore, an average 10 cm long spawn tube of one female contains about 30,000 embryos. After 5 to 8 days of development the spawn dissolves and liberates small veligers."

Geographical distribution (Fig.73): American Pacific coast, from lower California to northern Peru, as well as subtropical and tropical eastern and western Atlantic.

Habitat: Usually in shallow water on sandy substrates (often in seagrass beds), but occurs in lower sublittoral and upper bathyal on sandy and muddy substrates (most depth records in the eastern Pacific between 1 and 100 m, in the Atlantic between 1 and 250 m).

Habits/feeding behavior: observed by Bandel (1976: 252–253) for Colombian (Atlantic) populations: "Individuals of this species are usually hidden in the sand buried shallowly, strangely with the apical part of the shell pointing into the sand. ... Only rarely may individuals of this species be seen searching for food during daylight, but at dawn or at night most animals become active. They leave their resting place in the sand and crawl over the substrate on a broad sole, the apex now pointing in the normal upward position. Their prey consists of all kinds of soft bodied actinian-type coelenterates which usually are present in large numbers on the blades of seagrass and on rock-surfaces. Large prey individuals are attacked by the gastropod close to the base. Here [the gastropod] rasps a hole and extends its proboscis into the coelenterate, feeding on it until it dies (up to a few days)." A similar description was given by Bandel & Wedler (1987: 15).



● nobilis　　　　　o consobrina

Fig. 73. Geographical distribution of *Architectonica nobilis* and *A. consobrina*. Atlantic records for *A. nobilis* omitted.

Discussion:

Architectonica nobilis shells can easily be recognized by their narrow, scaly midribs, the narrow umbilicus with coarse, irregular umbilical crenae, and, especially, by their additional spiral ribs on the shell base. Two Recent species are similar in some features of color pattern and sculpture, *A. karsteni* (above) and *A. consobrina* n.sp. (below).

The synonymy of *Architectonica nobilis* has been a matter of extensive discussion in the literature (e.g., BAYER, 1940: 230 ff.). No significant difference in proto- or teleoconch characters has been found that would justify a separation between Atlantic and Pacific populations even at the subspecific level, the difference between Atlantic populations being greater than between West Atlantic and East Pacific populations (BIELER, unpubl.). *Architectonica nobilis* has been a member of the Caribbean/Central American fauna since the Miocene (see, e.g., WEISBORD, 1962: 152 ff.). Some of the fossil forms that have been treated as "*A. nobilis*" in the paleontological literature, however, appear to be much closer to Recent Indo-Pacific species (such as *A. maxima*, *A. gualtierii* n.sp. and *A. consobrina* n.sp.) than to *A. nobilis* (see, for instance, middle to late Miocene specimens discussed and figured by WOODRING, 1959: 165, pl.29).

RÖDING (1798: 78) referred in his description of *Architectonica nobilis* to figures in CHEMNITZ (1781: pl.172 figs.1695–1696) which were based on a specimen in SPENGLER's collection (ZMK unnumbered; see Fig.71). MERRILL (1970a: 231) selected a specimen of this collection as a lectotype. This lectotype designation is here repeated, since MERRILL's work is not published and therefore not available for taxonomic purposes. The reference to "the type specimen of *A. nobilis*" by DEVRIES (1985: 284) is based on an erroneous translation of RUTSCH's (1934: 43) "Typ." RUTSCH, who considered his new taxon *karsteni* as a subspecies of *A. nobilis*, was referring to the typical form (i.e., *A. nobilis* s.s.), not to a certain specimen.

Solarium granulatum LAMARCK, 1816, is a synonym of *A. nobilis*. One of two syntypes in Geneva (MHNG 1095/36/1; see Fig.72) agrees with the original figure (1816: pl.446) and with the measurements given by LAMARCK ("19 lignes"). This specimen is here selected as a lectotype. The other former syntype (MHNG 1095/36/2) is not conspecific, but a specimen of *A. gualtierii* n.sp.

Solarium granosum VALENCIENNES, 1832, was described from a specimen from Acapulco. VALENCIENNES (1832: 269–270) compared it with *Solarium millegranum* LAMARCK (the type species of *Granosolarium* SACCO, a group without known Recent representatives in the eastern Pacific) and with *S. granulatum* (= *A. nobilis*). The specimen was never figured, the type material is considered lost (MNHNP). CARPENTER (1857a: 408) and BAYER (1948: 19) understood it as a member of the genus *Torinia* [= *Heliacus*]. Other authors (e.g., KEEN, 1971: 388; ABBOTT, 1974: 97) interpreted *S. granosum* as a synonym of *A. nobilis*. The latter approach is followed here, since most statements of the original description and the given dimensions fit juvenile specimens of *A. nobilis*.

For the reasons leading to the synonymy of *Solarium quadriceps* HINDS, 1844, with *Architectonica nobilis*, see discussion under *A. gualtierii* n.sp. (above).

MÖRCH (1859: 122) based the description of *Architectonica valenciennesii* on "6 specimina" (6 syntypes, ZMK unnumbered, vidi). KEEN illustrated two of the syntypes (1966b: 22, figs.26–26a; 1971: 387, 946, fig.425 "above," erroneously labelled as "holotype"). The left specimen in KEEN's illustration (shell diameter: 34.7 mm) matches MÖRCH's statement of "Diam. 34 [...] mm" and has a complete apex. It is here selected as lectotype.

The presumed original specimen of *Architectonica wroblewskyi* var. α of MÖRCH (1875:154) is a normal specimen of *A. nobilis*, while that of his var. ß an aberrant specimen with a repaired shell (ZMK unnumbered, vidi). The holotype of *Solarium ordinarium* E.A. SMITH, 1890, from St. Helena (BMNH 1889.10.1.834, vidi) is a subadult specimen of *A. nobilis*.

Architectonica consobrina n.sp.

Fig.73, 74

Type measurements:

	SD	H	PD	Tw	UD	Locality	Collection
Holotype	28.9	15.9	1.02	6 1/4–	6.0	Marinduque Island	LACM 2279
Paratype 1	27.6	14.5	1.00	6 1/8	6.4	Marinduque Island	LACM 2280
Paratype 2	31.7	15.4	1.00	6 3/8	7.5	Talajit Island	USNM 243599
Paratype 3	28.2	14.6	1.02	6 1/8	6.7	Sibuyan Sea	MNHNP unnumbered

Type locality: South of Gaspar Island, Marinduque, Philippines; 259–293 m on sand and coral substrates. Paratype 1 from holotype lot. Paratype 2 from Talajit Island, 14.6 mi SE of Panganalen Point, between Samar and Masbate, Philippines (12°03'30"N, 124°03'36"E); 249 m, hard sand ['ALBATROSS' Expedition USBF

Sta.5393]. Paratype 3 from N. of Panay Island, Sibyuan Sea (*11°54'N, 122°15'E*), 252–370 m [N.O. 'Coriolis' MUSORSTOM 3 Sta. CP138].

Etymology: *consobrina* [noun in apposition]; Latin: first female cousin; implying close relationship with other species of the *Architectonica maxima*-group.

Material studied: 4 type specimens as listed above.

Diagnosis

Large, moderately depressed cone-shaped shell with moderately wide umbilicus; whorls on upper side gemmate, inflated on both sides; two spiral grooves below suture (midrib-area divided into two ribs, with the lower midrib becoming narrower after 1–3 whorls); wide groove at base of lower midrib; basal field divided into 3–4 nodulose ribs; proxumbical rib strong and wider than basal-field ribs. Subsutural rib yellowish or whitish with brown blotches; midrib-area greyish to olive-brown, with pattern of brown blotches on lower midrib; proxumbical rib and umbilical crenae yellowish, without color pattern; umbilical crenae darker than basal field. Protoconch diameter 1.00–1.02 mm.

Description:

Teleoconch: Large, diameter of known specimens ca. 30 at about 6 1/2 Tw. Shape: moderately depressed cone-shaped, with whorls equally inflated on upper side and base; umbilicus moderately wide (UD ca. 22.5% of SD). Sculpture: Upper side: SSR strong, distinctly separated; MR-area initially ± equally divided into two spiral ribs (UMR and LMR), after 1–3 whorls turning into subequal division with LMR becoming much narrower; wide groove between UMR and UPR; Periphery: PR prominent but narrow, with wide space between them; upper part of whorl attachment on upper part of LPR (upper edge of LPR visible in suture); upper side of shell and periphery crossed by deeply incised oblique axial grooves, resulting in a generally gemmate appearance, becoming smooth on body whorl; segments of the two midribs not necessarily corresponding; Base: IPR strong but narrow, with one ± fine additional spiral rib between UPR and IPR; BF distinctly divided into 3–4 nodulose ribs, wider towards the umbilicus; PUR strong and usually wider than BF-ribs; UC large and ± regular; columellar wall forming almost straight inner lip with plications for support of the columellar muscle, with deepest groove in UC overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration: SSR, UPR, LPR and IPR yellowish to whitish (LPR lightest colored) with brown blotches, each of which ca. 2 nodules wide; MR and BF greyish to olive-brown, with faint to distinct pattern of brown blotches on LMR (especially on later whorls); UC and PUR without pattern; UC, partly also PUR, slightly darker colored than other basal ribs; spaces between UPR and LPR, and between LPR and IPR white, therefore suture appearing white. – Protoconch: medium-sized (1.00–1.02); distinctly heterostrophic; with rounded ridge in anal-keel area; yellowish to light-brown, with brown outer corner in front of varix. – Operculum, Radula and Anatomy: not known.

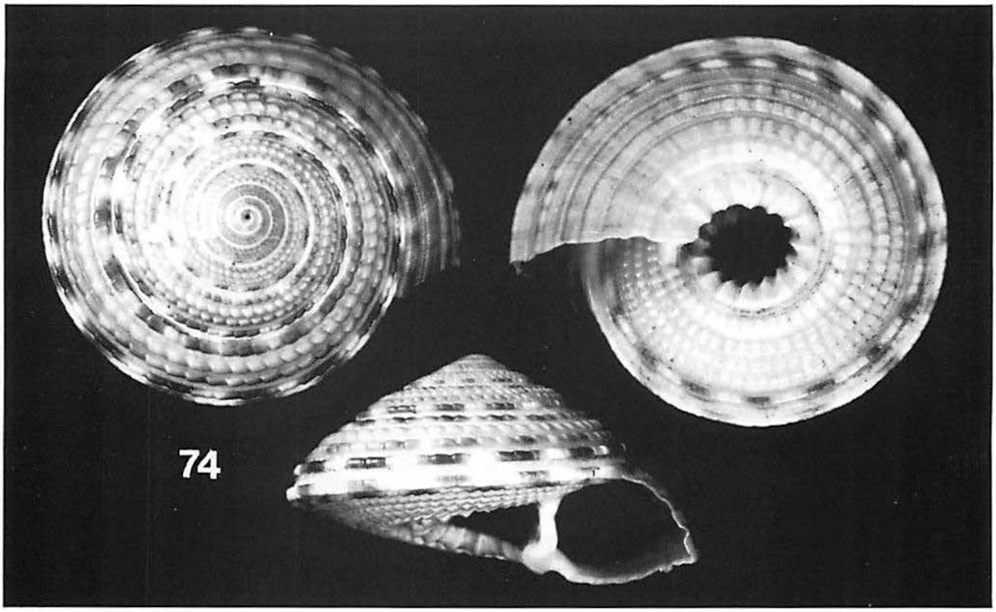


Fig. 74. *Architectonica consobrina* n.sp.; holotype; Philippines; LACM 2279; SD = 28.9.

Geographical distribution (Fig.73): Only known from the central Philippines.

Habitat: Upper bathyal; available depth records (fresh, empty shells) from between 249–370 m, on sand and coral substrates.

Discussion:

The only other Recent *Architectonica* species with a multi-ribbed base is *A. nobilis*. The sculpture of *A. consobrina* is much more regular, with midribs and proxumbical rib being wider and the shell nodules smoother and not scaly as in *A. nobilis*. *Architectonica consobrina* lacks the irregular brown markings displayed by *A. nobilis* on midribs and basal field.

Architectonica regia (HANLEY, 1862) [INCERTAE SEDIS]
Fig.75

*1862 *Solarium regium* HANLEY, Proc. zool. Soc. Lond., *1862*: 205.
1864 *Solarium regium*, – REEVE, Conch. icon., *15*: no.16, pl.3 fig.16.
1887 *Solarium (Solarium) regium*, – MARSHALL, Man. conch., *9*: 11, pl.2 fig.30 [after REEVE].
1940 *Solarium regium*, – BAYER, Zool. Meded., *22*: 252.
1984 *Architectonica regia* [incertae sedis], – BIELER, 1984d, Verh. natw. Ver. Hamburg, (NF)*27*: 483, pl.4 fig.XV.
1989 *Architectonica regia* [incertae sedis], – BIELER, Amer. Conch., *17*(1): 22, fig.6.

Type measurements (holotype): SD = 30.1, H = 14.0, PD = 1.32, Tw = 5 7/8, UD = 8.0.

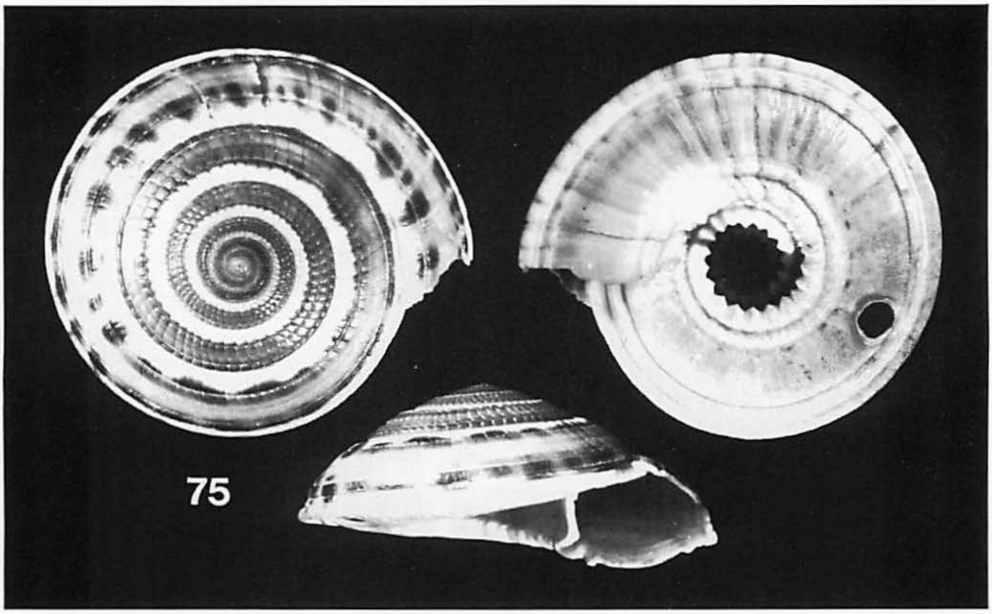


Fig. 75. Unidentifiable aberrant specimen of the *Architectonica maxima*-group; holotype of *Solarium regium* HANLEY, 1862; BMNH 1981159; SD = 30.1.

Type locality: "Hab. ---" [unknown].

Etymology: *regius-a-um* [adjective]; Latin: royal.

Material studied: Holotype (BMNH 1981159).

Discussion:

The single known specimen of this form shows many signs of an aberrant shell, such as unusual inflation of the shell base and poor definition of spiral sculpture and color pattern. Although certainly a member of the *Architectonica maxima*-group, it cannot be positively assigned to any of the recognized species.

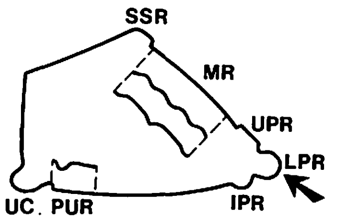
Genus *Adelphotectonica* BIELER, 1987

Adelphotectonica BIELER, 1987: 208; introduced as subgenus of *Architectonica*. Type species by original designation: *Solarium reevei* HANLEY, 1862; Recent, Indo-Pacific.

Description (Fig.76):

Teleoconch: shell medium-sized to large (usually 11–32 mm), low to tall cone-shaped; umbilicus always open, moderately wide to wide (ca. 20–32% of shell diameter); upper point of whorl attachment at peripheral keel of the preceding whorl, resulting in absence of a distinct suture; upper (apical) side with weak to strong growth lines; subsutural and upper peripheral rib usually weak; mid-rib area undivided, or 1–4fold

Fig.76. Schematic representation of placement of major spiral ribs in *Adelphotectonica*, apertural aspect. Arrow shows point of attachment of next whorl, intrageneric variation indicated by dotted lines.



weakly subdivided [intraspecific variability]; base smooth except for nodose rib surrounding umbilicus (UC) and, in some cases, proxumbical rib; umbilical wall without spiral ribs; indistinctly colored in shades of tan, regular fleck pattern usually restricted to peripheral ribs. *Protoconch:* medium-sized to very large (ca. 1.04–1.56), distinctly heterostrophic, frequently with distinct anal keel. *Radula:* ptenoglossate-like; rachidian with 3 cusps, flanked by 7 marginals on either side; marginals with 2 long processes each. *Operculum:* horny, ear-shaped with broad last whorl, flat with peg-like projection on body side.

For a more extensive description and discussion of this genus see Bieler (1987: 208).

Adelphotectonica reevei (Hanley, 1862)

Fig.77–80; Tab.1

*1862 *Solarium reevei* Hanley, Proc. zool. Soc. Lond., *1862*(2): 204.
1863 *Solarium (Architectonica) Reevei*, - Hanley, Thes. conch., *3*: 234, pl.250 figs.9–10.
1864 *Solarium Reevei*, - Reeve, Conch. icon., *15*: no.20, pl.3 fig.20.
1867 *Solarium reevei*, - Angas, Proc. zool. Soc. Lond., *35*: 201.
1886 *Solarium (Architectonica) reevei*, - Watson, Rep. sci. Res. Voy. Challenger, Zool., *15*(42)(2): 136.
1887 *Solarium Reevei*, - Marshall, Man. conch., *9*: 12, pl.4 figs.45–46.
1887–1888 *Solarium Reevei*, - Paetel, Cat. Conch.-Slg., (4)*1*: 287.
1901 *Solarium Reevei*, - Tate & May, Proc. linn. Soc. N. S. Wales, *1901*(3): 380.
1903 *Solarium maximum*, - Hedley, Mem. Austr. Mus., *4*(6): 349, fig.73 [non *S. maximum* Philippi, 1849].
1913–1915 *Architectonica (Architectonica) Reevei*, - Suter, Man. N. Zeal. Moll.: 316, pl. 44 fig.16.
1918 *Solarium reevei*, - Hedley, J. r. Soc. N. S. Wales, *51* (1917) (Suppl.): 102.
1921 *Architectonica reevei*, - May, Check-list moll. Tasmania: 102.
1923 *Architectonica reevei*, - May, Illus. index Tasman. shells: 97, pl.46 fig.2.
1924 *Architectonica reevi* [sic], - Bucknill, Sea shells N. Zeal.: 57, pl.7 fig.19.
1926 *Architectonica reevei*, - Finlay, Trans. Proc. N. Zeal. Inst., *57*: 401.
1931 *Architectonica reevei*, - Iredale, Rec. Austr. Mus., *18*(4): 228.
*1931 *Architectonica offlexa* Iredale, Rec. Austr. Mus., *18*(4): 229, pl.25 figs.15–16.
*1936 *Architectonica relata* Iredale, Rec. Austr. Mus., *19*(5): 326, pl.23 fig.19.
1936 *Architectonica offlexa*, - Iredale, Rec. Austr. Mus., *19*(5): 326.
1937 *Architectonica reevei*, - Powell, 1937a, Shellfish N. Zeal.: 75, pl.9 fig.34.
1940 *Architectonica reevei*, - Powell, Trans. r. Soc. N. Zeal., *70*(3): 213.
1940 *Solarium reevei*, - Bayer, Zool. Meded., *22*: 251.
1960 *Architectonica venusta* Kuroda (MS), - Azuma, Cat. shell-bear. Moll. Okinoshima: 13, pl.4 fig.2 [*nomen nudum*].
1961 *Architectonica offlexa*, - Garrard, J. malac. Soc. Austr., *1*(5): 23.
1962 *Architectonica offlexa*, - Iredale & McMichael, Mem. Austr. Mus., *11*: 68.
1962 *Architectonica relata*, - Iredale & McMichael, Mem. Austr. Mus., *11*: 68.

1971 *Architectonica reevei*, - WILSON & GILLETT, Austr. shells: 34, pl.13 figs.10-10a.
*1971 *Architectonica reevei venusta* KURODA & HABE *in* KURODA, et al., Sea shells Sagami Bay: 261, 419, pl.61 figs.15-16.
1973 *Architectonica reevei venusta*, - AZUMA, Venus, *32*(2): 36, 38.
1973 *Architectonica reevei venusta*, - HIGO, Cat. moll. fauna Jap. Ids.: 228.
1975 *Architectonica reevei*, - CLIMO, J. r. Soc. N. Zeal., *5*(3): 281, figs.4G-H, 5B.
1977 *Architectonica (Architectonica) reevei*, - GARRARD, Rec. Austr. Mus., *31*(13): 509, fig.4 [operculum]; 515, pl.3 figs.1-9 [figs.4-6 = holotype of *A. offlexa*; figs.7-9 = holotype of *A. relata*].
1979 *Architectonica venusta*, - KOSUGE, Bull. Inst. Malac. Tokyo, *1*(2): 33.
1979 *Architectonica reevei*, - POWELL, N. Zeal. Moll.: 247, pl.48 fig.1.
1979 *Architectonica reevei venusta* KURODA & HABE var., - MATSUMOTO, Moll. shells Mie Pref.: 21.
1983 *Architectonica reevei venusta*, - OKUTANI, KAWAMURA coll.: 11, pl.41 fig.10.
1984 *Architectonica reevei*, - BOSS & MERRILL, 1984b, Occas. Pap. Moll., *4*(66): 357, pl.49 figs.7-10 [after CLIMO] [radula].
1985 *Architectonica reevei*, - BIELER, 1985a, Arch. Moll., *115*(4/6): 233.
1987 *Architectonica (Adelphotectonica) reevei*, - BIELER, Arch. Moll., *117*(4/6): 208, pl.2 fig.2 [holotype].

Type measurements: Holotype of *S. reevei*: SD = 23.1, H = 16.9, PD = 1.38, Tw = 5 9/10, UD = 5.1. Holotype of *A. offlexa*: SD = 23.4, H = 17.5, PD = 1.50, Tw = 6 1/8, UD = 5.7. Holotype of *A. relata*: SD = 24.0, H = 13.3, PD = ca. 1.40, Tw = 5 3/8, UD = 7.2. Holotype of *A. reevei venusta*: SD = 18.5, H = 10.0 [after KURODA & HABE], Tw = 5 1/8 [from photograph of type specimen].

Type localities: *S. reevei*: "Hab. ---?" [HANLEY (1863): "Sydney"]; *A. offlexa*: Sydney Harbour, N.S.W., ex 'TRITON' dredge; *A. relata*: "from 75-85 fathoms, off Bateman's Bay ... Continental Shelf of New South Wales"; ssp. *venusta*: "Jogashima W 5.5km (100-110m), W 5km (110-150m); Sagami Bay (alive)" [Japan].

Etymology: *reevei* [genitive singular case-ending]. Named after LOVELL AUGUSTUS REEVE (1814-1865), British conchologist.

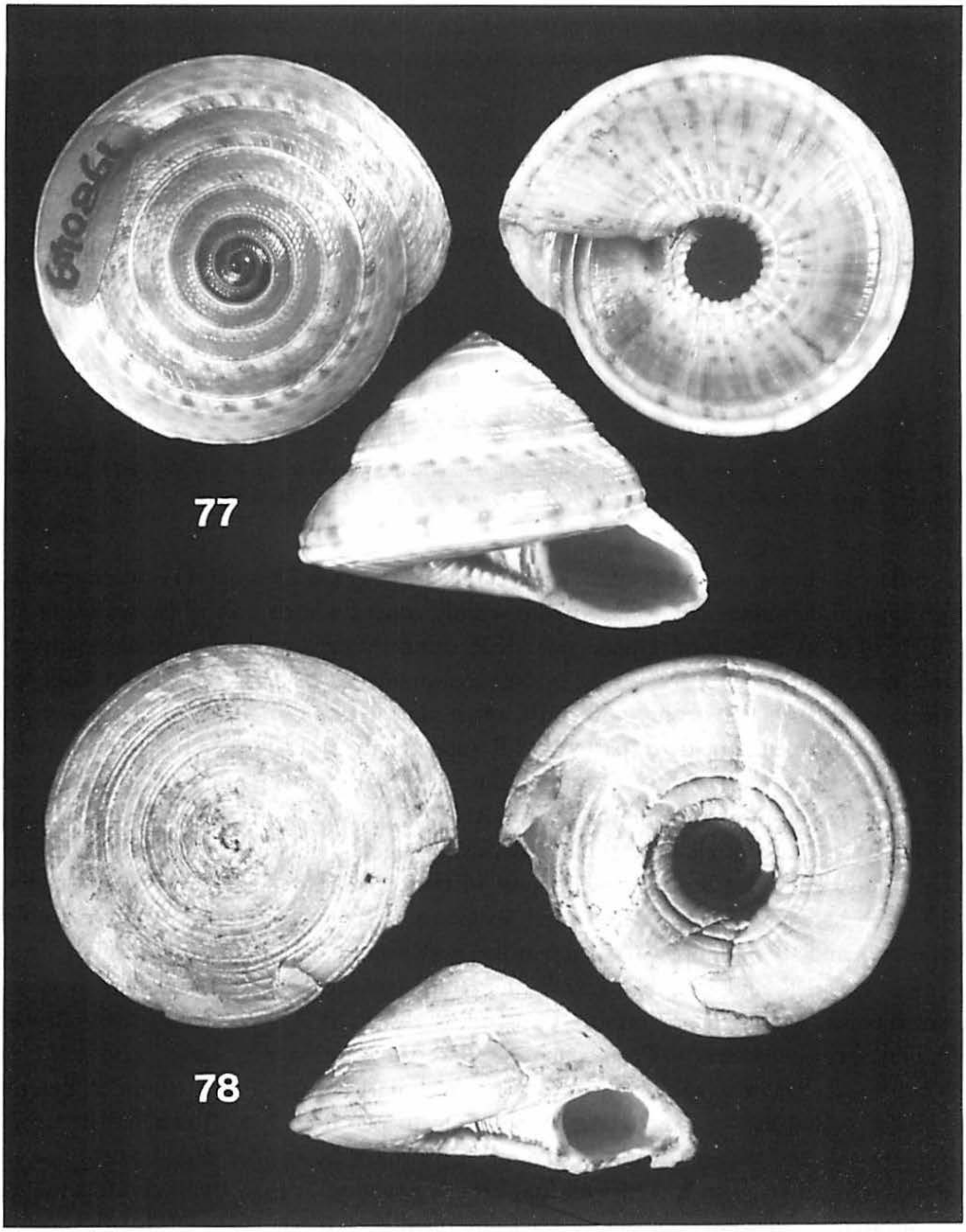
Material studied: 242 specimens (AMNH, AMS, ANSP, BMNH, BPBM, CAS, DMNH, FMNH, HUJ, IRSNB, LACM, MCZ, MNHNP, NMNZ, NMW, RNHL, SMF, SMNS, USNM, ZMA, ZSM), including holotype of *S. reevei* (BMNH 198049), holotype of *A. offlexa* (AMS C.57774), holotype of *A. relata* (AMS C.60680), and photograph of holotype of nominal ssp. *venusta* (BLIHT).

Diagnosis

Medium-sized to large, depressed to high-spired cone-shaped shell with moderately wide umbilicus; whorls inflated, on upper side gemmate (with axial sculpture dominant); subsutural rib distinctly separated, midrib-area undivided or divided by 1-3 faint spiral grooves; upper point of whorl attachment on lower part of lower peripheral rib; proxumbical rib absent to distinctly separated. Color pattern of distinct brown blotches on subsutural rib, upper peripheral rib and proxumbical-rib area (also on umbilical crenae in some specimens). Protoconch diameter 1.36-1.56 mm; dark brown.

Description:

Teleoconch: Medium-sized to large, diameter of specimens in collections usually 17-24 at 5 1/8 to 6 1/8 whorls. Shape: specimens from sublittoral high-spired cone-shaped



Figs. 77, 78. *Adelphotectonica reevei* (Hanley, 1862). Fig. 77: holotype of *Solarium reevei*; BMNH 198049; SD = 23.1. Fig. 78: holotype of *Architectonica relata* Iredale, 1936; New South Wales, Australia; AMS C.60680; SD = 24.0.

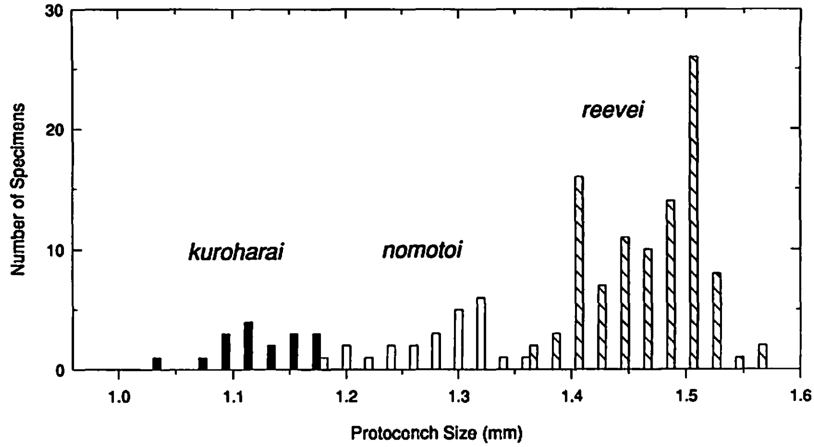


Fig. 79. Histogram of measured protoconch size. *Adelphotectonica kuroharai* (n = 17, x̄ = 1.13, sd = 0.04), *A. nomotoi* (n = 24, x̄ = 1.28, sd = 0.05), and *A. reevei* (n = 100, x̄ = 1.46, sd = 0.05).

with inflated whorls and moderately wide umbilicus (UD ca. 23% of SD), specimens from upper bathyal depressed cone-shaped with weakly convex whorls and wider umbilicus (UD ca. 29% of SD). Sculpture: Upper side: SSR distinctly separated; dominant sculpture in midrib-area by oblique axial grooves; midrib-area undivided or divided by 1–3 ± faint spiral grooves; Periphery: PR strong, with UPR often almost as prominent as LPR; upper point of whorl attachment on lower part of LPR (upper part of LPR thereby forming part of upper-side sculpture); no distinct suture; Base: IPR strong; BF often with 1–2 ± wide, weakly separated spiral ribs in front of PUR; PUR almost absent to distinctly separated; UC clearly separated, relatively small and usually regular; columellar wall forming almost straight inner lip with plications for support of the columellar muscle, with deepest groove in UC overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration: midrib-area and BF light brown, often marbled with slightly darker shades of brown; ground color of SSR, PR and UC distinctly lighter; SSR and UPR well-marked with pattern of brown blotches (about 16–22 on 4th Tw of UPR); LPR, IPR, PUR-area (rarely also UC) with faint brown pattern. – Protoconch (see Fig.79): large to very large (1.36–1.56, x̄ = 1.46); distinctly heterostrophic, with weak anal keel; dark brown. – Operculum: as described for genus. – Radula: "ptenoglossate," with 15 teeth per row (7-1-7). Rachidian stronger than marginals and tricuspid with the central cusp flanked by smaller lateral cusps. Marginal teeth strongly curved and forked with long tapering subequal cusps; the outermost marginal teeth shorter. – Anatomy: alimentary tract described by Climo, 1975: 281 ff., figs. 4H, 5B [but see corrections in Haszprunar, 1985b].

Geographical distribution (Fig.80): Subtropical to temperate western Pacific and Australian coastline including Tasmania. Record from Ceylon (Sri Lanka) in need of verification.

Habitat: Sublittoral to upper bathyal (most depth records between 30 and 400 m), live records from 100–150 m, sandy substrates.

Discussion:

Adelphotectonica reevei is often confused with *Architectonica perdix,* which is similar in shell shape and coloration. Distinguishing characters for *A. perdix* are the much more prominent axial sculpture, an upper point of whorl attachment that is at the *upper* edge of the lower peripheral rib, and a much smaller (≤ 0.96), yellowish to light-brown protoconch. *Adelphotectonica kuroharai*, *A. nomotoi* and the Atlantic species *A. uruguaya* CARCELLES, 1953, are similar to this species (see discusssion under *A. nomotoi*; below).

HANLEY (1862: 204) described *Solarium reevei* as an "elevated abnormal form," based on a single specimen (see Fig.77), and subsequently gave a locality for it (1863: figure caption for pl.250: "Sydney"). IREDALE (1931: 228) doubted its Australian origin and described the nominal species *Architectonica offlexa* based on Australian material, and later (1936: 326), *A. relata*, as a "deepwater representative of *A. offlexa*" (see Fig.78).

KURODA & HABE (*in* KURODA et al., 1971: 261, 419) introduced the nominal subspecies *Architectonica reevei venusta*, which had been mistakenly cited and figured much earlier by AZUMA (1960: 13) as "*Architectonica venusta* KURODA," a *nomen nudum*. The type specimen has a wider umbilicus than most Australian specimens, but otherwise agrees with the nominate form. Narrowly umbilicated specimens from Japan are known (e.g., ANSP 330192). Subspecific status for this form is here considered unjustified.

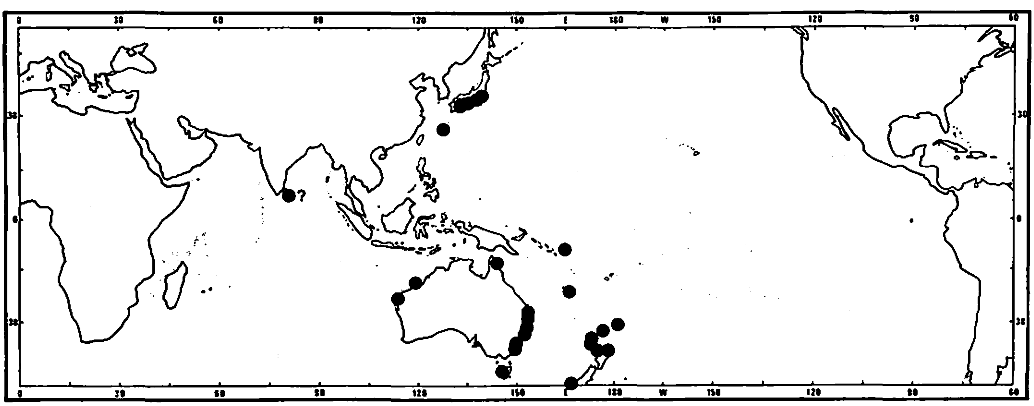


Fig. 80. Geographical distribution of *Adelphotectonica reevei.*

Adelphotectonica kuroharai (KURODA & HABE *in* HABE, 1961)

Figs.79, 81–83; Tab.1

1909 *Solarium* sp., - SCHEPMAN [in part], Monogr. Res. SIBOGA Exped., *49*(1b): 219.

*1961 *Architectonica kuroharai* KURODA & HABE *in* HABE, Col. illus. shells Japan (*II*): 30, Append.: 9, pl.13 fig.20.

1961 *Architectonica kuroharai* KURODA & HABE, - AZUMA, Cat. shell-bear. Moll. Okinoshima, Suppl: 1.

1964 *Architectonica kuroharai* HABE [sic], - HABE, Shells w. Pac. col., 2: 45, pl.13 fig.20.

1973 *Architectonica kuroharai*, - HIGO, Cat. moll. Jap. Ids.: 228.

1973 *Architectonica quinquisulcosa* KURODA, - HIGO, Cat. moll. Jap. Ids.: 228 [*nomen nudum*].
*1973 *Architectonica pentacyclota* AZUMA, Venus, *32*(2): 36, 38, figs.4-5.
1979 *Architectonica kuroharai* HABE [sic], - KOSUGE, Bull. Inst. Malac. Tokyo, *1*(2): 33.
1979 *Architectonica kuroharai*, - MATSUMOTO, Moll. shells Mie Pref.: 21.
1983 *Architectonica kuroharai*, - OKUTANI, KAWAMURA coll.: 11, pl.41 fig.11.
1985 *Architectonica kuroharai*, - BIELER, 1985a, Arch. Moll., *115*(4/6): 241.
1987 *Architectonica (Adelphotectonica) kuroharai*, - BIELER, Arch. Moll., *117*(4/6): 209, pl.2 fig.3 [holotype].

Type measurements: Holotype of *A. kuroharai*: SD = 25.3, H = 10.6, PD = 1.12, Tw = 4 5/8, UD = 6.5. Holotype of *A. pentacylota*: SD = 32.9, H = 15.4, PD = 1.10, Tw = 6 5/8, UD = 9.9.

Type localities: *A. kuroharai*: off Cape Ashizuri, Kochi Pref., Shikoku, at 100–150 m [Japan; from type label]; *A. pentacyclota*: "Tosa Bay (Okezoko Deep), 150 fathoms deep" [Shikoku, Japan].

Etymology: *kuroharai* [genitive singular case-ending]. Named after Mr. KUROHARA, who collected the type specimen.

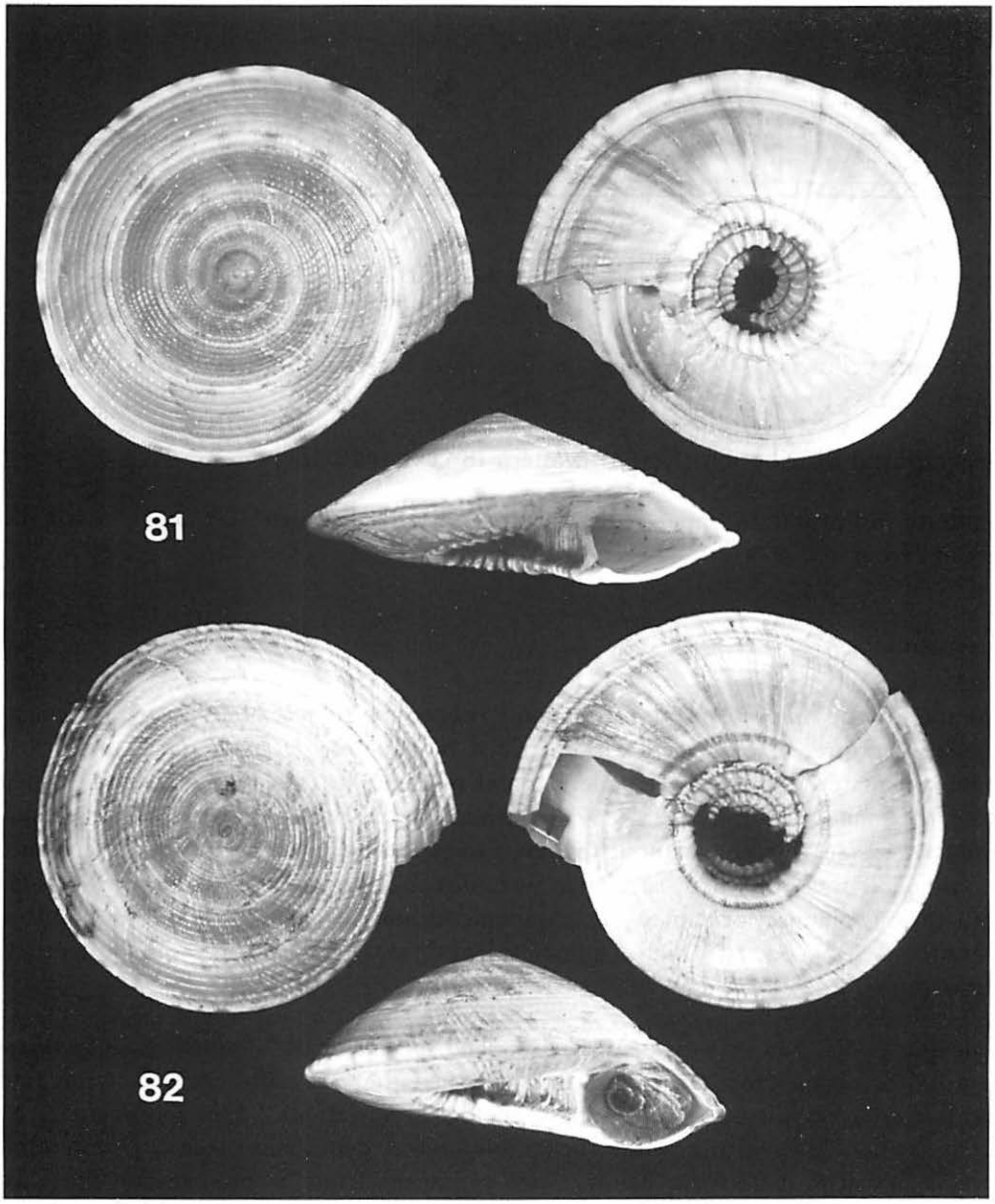
Material studied: 19 specimens (AMNH, ANSP, BPBM, FLMNH, LACM, MNHNP, NSMT, USNM, ZMA, Coll. AZUMA); including holotypes of *A. kuroharai* (NSMT Mo 53232) and *A. pentacyclota* (AZUMA private collection).

Diagnosis

Medium-sized to large, depressed cone-shaped shell with widely open umbilicus; whorls somewhat inflated, with axial sculpture dominant; subsutural rib distinctly separated, midrib-area divided by 1-3 ± deep spiral grooves; upper point of whorl attachment on central to lower part of lower peripheral rib; proxumbical rib absent. Color pattern of distinct brown blotches on lower peripheral rib. Protoconch diameter 1.04–1.18 mm; yellowish.

Description:

Teleoconch: Medium-sized to large, diameter of specimens in collections usually 15–32 at 4 5/8 to 6 5/8 whorls. Shape: depressed cone-shaped, with somewhat inflated whorls; large specimens similar in shape to *Discotectonica* spp. (but lack a distinct concave area before the peripheral keel); umbilicus wide (UD ca. 29% of SD); Sculpture: Upper side: SSR distinctly separated; MR-area divided by 1–2 ± deep spiral grooves, crossed by oblique axial grooves; spiral sculpture dominant (at least on later whorls), with SSR and MR very similar in appearance; often with shallow depression at base of MR-area; Periphery: UPR weak, similar to SSR and MR; LPR narrow, but strong and prominent; upper point of whorl attachment on central to lower part of LPR (upper part of LPR thereby forming part of upper-side sculpture; no distinct suture); Base: IPR strong, often with an additional spiral rib between LPR and IPR; BF without spiral ribs; PUR absent; UC distinctly separated; columellar wall forming almost straight inner lip with plications for support of the columellar muscle, with deepest groove in UC overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration: SSR, MR and UPR marbled with shades of light-brown; LPR and entire base lighter colored; LPR well-marked with pattern of brown blotches (about 16–21 on 4th Tw; in some specimens also UPR with faint pattern). - Protoconch (see Fig.79): medium-sized (1.04–1.18, $\bar{x}$ = 1.13); distinctly heterostrophic; anal keel week



Figs. 81, 82. *Adelphotectonica kuroharai* (KURODA & HABE *in* HABE, 1961). Fig. 81: holotype of *Architectonica kuroharai*; Japan; NSMT Mo 53232; SD = 25.3. Fig. 82: holotype of *Architectonica pentacyclota* AZUMA, 1973; Japan; Coll. AZUMA; SD = 32.9.

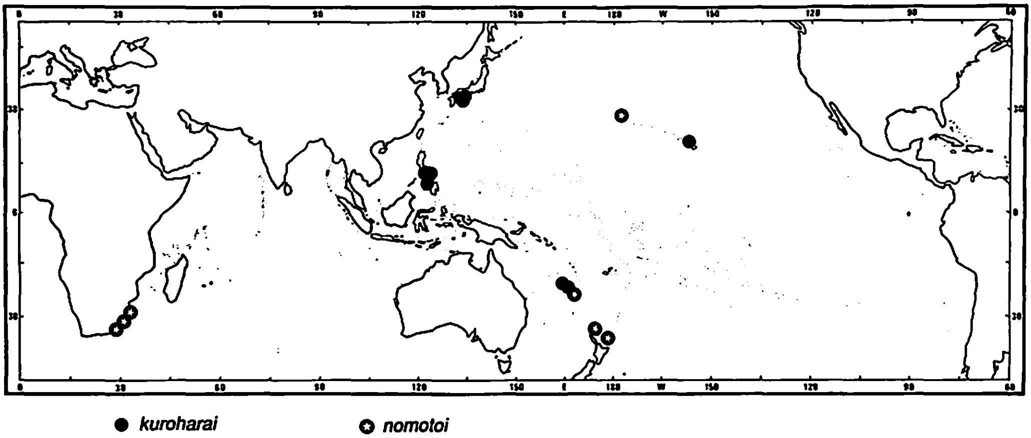


Fig. 83. Geographical distribution of *Adelphotectonica kuroharai* and *A. nomotoi.*

or absent; yellowish. - Operculum: as described for genus. - Radula and Anatomy: not known.

Geographical distribution (Fig.83): western to central Pacific.

Habitat: Sublittoral to upper bathyal (depth records between 100 and 494 m), live records from 100–274 m.

Discussion:

The identity of *Adelphotectonica kuroharai* has been the subject of confusing statements in the literature. The species was described by KURODA & HABE *in* HABE (1961), based on material from the Japanese island of Shikoku (see Fig.81). For specimens from the same island, AZUMA (1973) introduced the nominal species *Architectonica pentacyclota* (see Fig.82), without reference to *A. kuroharai*. Before the description of *A. kuroharai* was published, specimens were distributed to several collections, labelled with various manuscript names [e.g., "quinquesulcata KURODA (MS)," "quinquesulcosa KURODA (MS)"], one of which ("quinquisulcosa") was published, as a nude name, by HIGO (1973: 228).

GARRARD (1977: 518, pl.1 figs.10–12) described specimens of "*Architectonica kuroharai* KURODA & HABE" from Australia, and suggested that the differences between them and the original diagnosis were "only ecological variations." His specimens (AMS C.68518, C.77065; vidi), however, belong to another genus and species, *Discotectonica petasus* (TOMLIN, 1928) (see below). Two specimens from 'SIBOGA' station 95 (ZMA unnumbered, vidi), listed by SCHEPMAN (1909: 219) as "*Solarium* sp.," belong here.

Adelphotectonica reevei, *A. nomotoi* and the Atlantic species *A. uruguaya* are similar to this species (see discussion under *A. nomotoi*, below; Tab. 1).

Table 1: Comparison between Recent *Adelphotectonica* species

		INDO-PACIFIC				ATLANTIC
		reevei		*kuroharai*	*nomotoi*	*uruguaya*
	shape	sublitoral form: turbiniform	bathyal form: trochiform	depressed trochiform	trochiform	trochiform
Teleoconch	relative umbilical diameter (UD in % of SD)	22.0–24.9 $\bar{x}$=23.4	26.2–31.0 $\bar{x}$=28.6	25.4–33.4 $\bar{x}$=28.6	21.4–34.1 $\bar{x}$=26.7	18.7–27.3 $\bar{x}$=24.4
Teleoconch	division of midrib area	undivided or divided by 1-3 faint spiral grooves; axial growth lines dominant		± distinctly divided by 1-2 spiral grooves; spiral sculpture dominant on later whorls	distinctly divided by 1-3 spiral grooves; spiral sculpture dominant	early whorls ± strongly spirally divided; later smooth
Teleoconch	proxumbical rib (PUR)	absent to distinctly developed		absent	absent	absent
Teleoconch	blotch pattern	brown, demarcated		brown, demarcated	brown, demarcated	light brown flames
Teleoconch	position of blotches	SSR, UPR (LPR, IPR, PUR-area with faint pattern)		LPR	UPR, LPR, often area next to UC (SSR usually weakly colored)	SSR, UPR, LPR
Teleoconch	no. of PR blotches at 4 whorls	16–22		16–21	18–24	16–18
Protoconch	protoconch diameter	1.36–1.56, $\bar{x}$=1.46		1.04–1.18, $\bar{x}$= 1.13	1.18–1.36, $\bar{x}$=1.28	1.24–1.36
Protoconch	anal keel	weak		absent to weak	distinct	weak to distinct
Protoconch	coloration	dark brown		yellowish	yellowish to brown	light brown to brown

Adelphotectonica nomotoi (Kosuge, 1979)

Figs.79, 83, 84; Tab.1

1928 *Architectonica reevei*, – Tomlin, Ann. S. Afr. Mus., *25*(2): 333 [non *Solarium reevei* Hanley, 1862].
1931 *Architectonica reevei*, – Tomlin, Ann. Natal Mus., *6*(3): 432.
1963 *Solarium reevei*, – Barnard, 1963b, Ann. S. Afr. Mus., *47*(1): 157.
1974 *Solarium reevei*, – Barnard, Ann. S. Afr. Mus., *47*(5): 711.
*1979 *Architectonica nomotoi* Kosuge, Bull. Inst. Malac. Tokyo, *1*(2): 33, pl.5 figs.11-12.
1987 *Architectonica (Adelphotectonica) nomotoi*, – Bieler, Arch. Moll., *117*(4/6): 209.

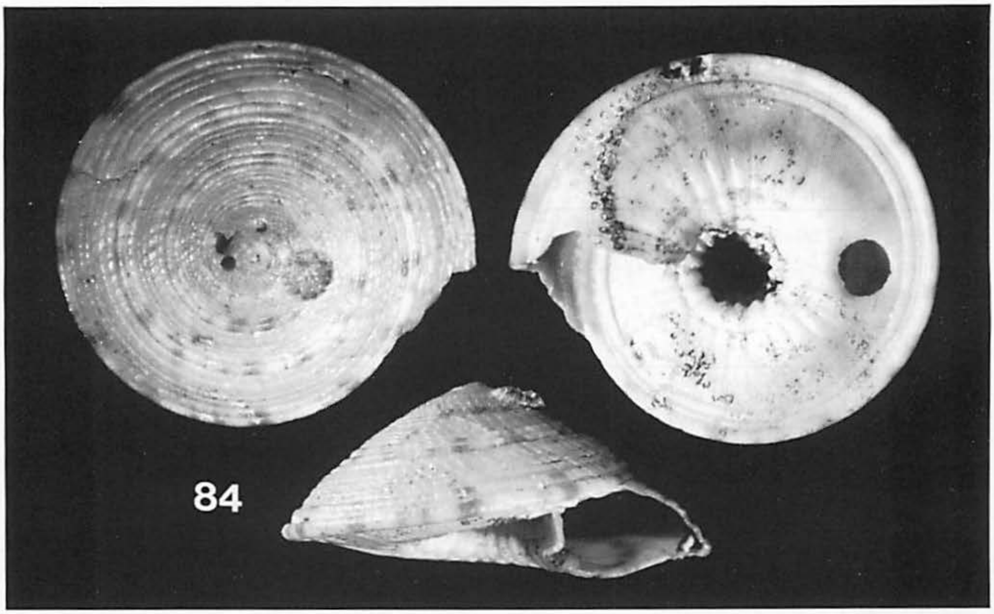


Fig. 84. *Adelphotectonica nomotoi* (Kosuge, 1979); holotype of *Architectonica nomotoi*; Midway Island; IMT-79-21; SD = 16.4.

Type measurements (holotype): SD = 16.4, H = 7.7, PD = 1.2, Tw = 4 9/10, UD = 3.6.

Type locality: "Off Midway Island (29°50.0' Lat.(N), 179°01.6' Long. (E)) at the depth of 270m."

Etymology: *nomotoi* [genitive singular case-ending]. Named after Mr. Kojo Nomoto, who assisted the original author in obtaining the material.

Material studied: 27 specimens (IMT, MNHNP, NMNZ, NMP, SAM); including holotype (IMT-79-21).

Diagnosis

Medium-sized, depressed cone-shaped shell with widely open umbilicus; whorls somewhat inflated, with spiral sculpture dominant; subsutural rib ± distinctly separated, midrib-area divided by 1-3 spiral grooves; upper point of whorl attachment on central to lower part of lower peripheral rib; proxumbical rib absent. Color pattern of distinct brown blotches on upper and lower peripheral ribs (in darker-colored specimens also in area next to umbilical crenae). Protoconch diameter 1.18-1.36 mm; yellowish to brown.

Description:

Teleoconch: medium-sized, diameter of specimens in collections usually 11-16 (rarely up to 20) at 3 3/4 to 4 3/4 (5) whorls. Shape: depressed cone-shaped, with whorls somewhat inflated; umbilicus wide (UD ca. 27% of SD); Sculpture: Upper side: spiral sculpture dominant; SSR ± distinctly separated; MR-area distinctly divided by 1–3 spiral grooves, crossed by ± faint oblique axial grooves; Periphery: UPR not as strong and prominent as LPR; upper point of whorl attachment on central to lower part of LPR (upper part of LPR thereby forming part of upper-side sculpture); no distinct suture; Base: IPR ± strongly developed, often with an additional spiral rib between LPR and IPR; BF without spiral ribs; PUR absent; UC distinctly separated; columellar wall forming almost straight inner lip with plications for support of the columellar muscle, with deepest groove in UC overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration: MR-area light-brown; SSR, PR and base lighter in color; SSR with faint, PR with distinct pattern of brown blotches (about 18–24 on 4th Tw; in darker-colored specimens also brown blotches on IPR and in area in front of UC). – Protoconch (see Fig.79): medium-sized to large (1.18–1.36, $\bar{x}$ = 1.28); distinctly heterostrophic; anal keel well-developed; yellowish to brown. – Operculum: as described for genus. – Radula and Anatomy: not known.

Geographical distribution (see Fig.83): Known from disjunct localities in southern Africa, New Caledonia, New Zealand and the Midway Islands.

Habitat: Sublittoral to upper bathyal (depth records between 74 and 430 m), live records from 100–115 m.

Discussion:

Kosuge (1979: 33) described this species, as *Architectonica nomotoi*, based on a single specimen from the Midway Islands. Comparison with the South African specimen (SAM A3580) referred to as "*reevei*" by Tomlin (1928, 1931) and Barnard (1963, 1974), and with further material from that region (NMP, SAM), revealed their specific identity. *Adelphotectonica reevei* has not been found in South Africa to date.

The three Indo-Pacific forms of this subgenus, *Adelphotectonica nomotoi*, *A. reevei*, and *A. kuroharai*, are very similiar to each other, but all specimens studied to date could be assigned to one of the three. They cannot be interpreted as ecological or geographical forms, because all of them were present in a single sample (New Caledonia; MNHNP unnumbered). The sublittoral morph of *A. reevei* reaches the greatest shell height; *A. kuroharai* attains the greatest shell diameter. A comparison of teleoconch diameter versus number of whorls (SD at 4 Tw) revealed no significant statistical difference; all forms showed almost the same range of variation (ca. 10.0–13.5 mm). Differences are found mainly in upper-side teleoconch sculpture, coloration and protoconch size (see Tab.1). The three forms are here provisionally accepted as species; further material, and a study of anatomy and radulae, are necessary. An Atlantic "sibling" is *Adelphotectonica uruguaya* (Carcelles, 1953) (see Bieler, 1987: 209, and Tab.1), of which the recently described nominal species *Architectonica sindermanni* Merrill & Boss, 1984 (1984: 339, pl.45 figs.1–3, pl.46 figs.1, 2; based on a single specimen from Brazil; holotype MCZ 294313, vidi), and *Architectonica sunderlandi* Petuch, 1987 (1987: 21, pl.10 figs.1–4; based on two specimens from the Florida Keys; holotype USNM 859906, paratype Kevan Sunderland Coll.; vidi) are junior synonyms.

Genus *Philippia* J.E. Gray, 1847

Philippia J.E. Gray, 1847: 166; introduced as subgenus of *Trochus*. Type species by monotypy: *Solarium luteum* Lamarck, 1822; Recent, Indo-Pacific.

Description (Fig.85):

Teleoconch: shell medium-sized (approximately 10 mm), roundly cone-shaped with narrow umbilicus (ca. 14 % of shell diameter); whorls bulging; upper (apical) side usually completely smooth, rarely with weak spiral striae; early postlarval shell sometimes with ± weak nodular sculpture; in Recent species upper peripheral rib completely reduced, therefore shell periphery formed by two ribs (LPR and less prominent IPR); upper point of whorl attachment at or below LPR; base smooth except for nodose rib surrounding umbilicus (UC); umbilical wall without spiral ribs; uniformly yellowish to dark brown, with regular fleck pattern on peripheral ribs, surrounding umbilicus (UC) always light. *Protoconch:* small to medium-sized (ca. 0.7–1.0), distinctly heterostrophic, callous with distinct, short anal keel. *Radula:* five-toothed taenioglossate; rachidian with narrow central cusp flanked on either side by an equally strong, filiform cusp (*P. lutea*). *Operculum:* horny, circular with broad last whorl, flat with mushroom-shaped, peg-like projection on body side; peg with grooves arranged in clockwise fashion.

For a more extensive description and discussion of this genus see Bieler (1985a: 236–238).

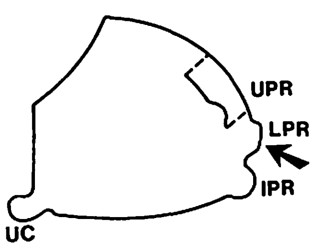


Fig. 85. Schematic representation of placement of major spiral ribs in *Philippia*, apertural aspect. Arrow shows point of attachment of next whorl, intrageneric variation indicated by dotted lines.

Philippia lutea (Lamarck, 1822)
Fig.86–89

*1822 *Solarium luteum* Lamarck, Hist. nat., *7*: 5.
1830 *Solarium luteum*, – Deshayes, 1830a, Encycl. méth, *2*(1): 159.
1838–1839 *Solarium luteum*, – Kiener [in part], Spéc. gén. icon. coqu., *10*: 9, pl.4 fig.9 [fig.9a = *Philippia hybrida* (Linné, 1758)].
1841 *Solarium luteum*, – Delessert, Rec. coqu. Lamarck: pl.24 figs.2a-c.
1843 *Solarium luteum*, – Deshayes, Hist. nat. (2nd ed.), *9*: 100.
1853 *Solarium luteum*, – Philippi, 1853b [in part], Syst. Conch.-Cab. II, *7*: 9, 31, pl.1 figs.10–11 [not pl.4 fig.11 = *Ph. hybrida*].
*1853 *Solarium luteum* var. *Novae Hollandiae?* Philippi, Syst. Conch.-Cab. II, *7*: 41, pl.1 figs.10–11.
1858 *Philippia lutea*, – Adams & Adams, Gen. Rec. Moll., *1*: 243; *3*: pl.25 figs.8, 8a-b [operculum].
1859 *Solarium (Philippia) luteum*, – Chenu, Man. conch. Paléont., *1*: 233, fig.1355.

1863 *Solarium (Philippia) luteum*, - HANLEY, Thes. conch., *3*: 237, pl.253 figs.53–54 [not fig.52 = *Ph. hybrida*].
1864 *Solarium luteum*, - REEVE [in part], Conch. icon., *15*: no.14, pl.3 fig.14.
1867 *Philippia lutea*, - ANGAS, Proc. zool. Soc. Lond., *35*: 201.
1875 *Solarium luteum*, - MARTENS, Jb. dtsch. malak. Ges., *2*: 103ff.
1883–1884 *Solarium luteum*, - TRYON, Struct. syst. conch., *2*: 217, *3*: pl.66 fig.36.
1887 *Solarium (Philippia) luteum*, - MARSHALL, Man. conch., *9*: 16, pl.5 figs.71–72 [after HANLEY].
1913–1915 *Architectonica (Philippia) lutea*, - SUTER, Man. N. Zeal. Moll.: 316, pl.46 fig.4.
1915 *Heliacus luteus*, - BARTSCH, Bull. U.S. natl. Mus., *91*: 124 [cited locality "Cape of Good Hope" unlikely].
1921 *Architectonica lutea*, - MAY, Check-list Moll. Tasmania: 102.
1923 *Architectonica lutea*, - MAY, Illus. index Tasman. shells: 97, pl.46 fig.1.
1924 *Architectonica lutea*, - BUCKNILL, Sea shells N. Zeal.: 56, pl.7 fig.20.
1926 *Philippia lutea*, - FINLAY, Trans. Proc. N. Zeal. Inst., *57*: 401.
1929 *Philippia lutea*, - THIELE, Handb. syst. Weichtierkd., *1*(1): 184, fig.170.
1933 *Philippia lutea*, - COTTON & GODFREY, S. Austr. Natur., *14*(3): 72, pl.1 fig.1.
1937 *Philippia lutea*, - POWELL, 1937a, Shellfish N. Zeal.: 75, pl.9 fig.35.
1939 *Philippia lutea*, - WENZ, Handbuch Paläozool., *6*(3): 670, fig.1911 [after PHILIPPI, 1853b].
1940 *Torinia luteum*, - M. SMITH, World-wide sea shells: 29, fig.403.
1942 *Philippia lutea*, - BAYER, Zool. Meded., *24*(1–2): 12, figs.1c-d [synonymy].
1946 *Philippia lutea*, - COTTON, S. Austr. shells: 5, pl.5 fig.82.
1962 *Philippia lutea*, - MACPHERSON & GABRIEL, Mar. moll. Victoria: 100, fig.126.
1973 *Philippia (Philippia) lutea*, - ROBERTSON, 1973b, Proc. Acad. nat. Sci. Philad., *125*(2): 37.
1977 *Philippia (Philippia) lutea*, - GARRARD, Rec. Austr. Mus., *31*(13): 509, fig.14 [operculum], p.525, pl.5 figs.13–18.
1978 *Philippia hybrida*, - HINTON, Guide Austr. shells: pl.10 fig.10 [not *Trochus hybridus* LINNÉ, 1758].
1979 *Philippia lutea*, - POWELL, N. Zeal. Moll.: 248, pl.48 fig.2.
1984 *Philippia (Philippia) lutea*, - BOSS & MERRILL, 1984b, Occas. Pap. Moll., *4*(66): 359, pl.57 fig.1 [radula, jaws; cited locality "Cape of Good Hope" unlikely].
1985 *Philippia (Philippia) lutea*, - BIELER, 1985a, Arch. Moll., *115*(4/6): 236ff, pl.2 fig.8 [lectotype designation].
1985 *Philippia lutea*, - HASZPRUNAR, 1985c, Zool. Scr., *14*(3): 211 [anatomy].

Type measurements: Lectotype of *S. luteum*: SD = ca. 10.5, H = ca. 7.5, UD = ca. 1.5 [from type photograph]. Original specimen of var. *novaehollandiae*: SD = 12.0, H = 7.6 [after PHILIPPI, 1853b].

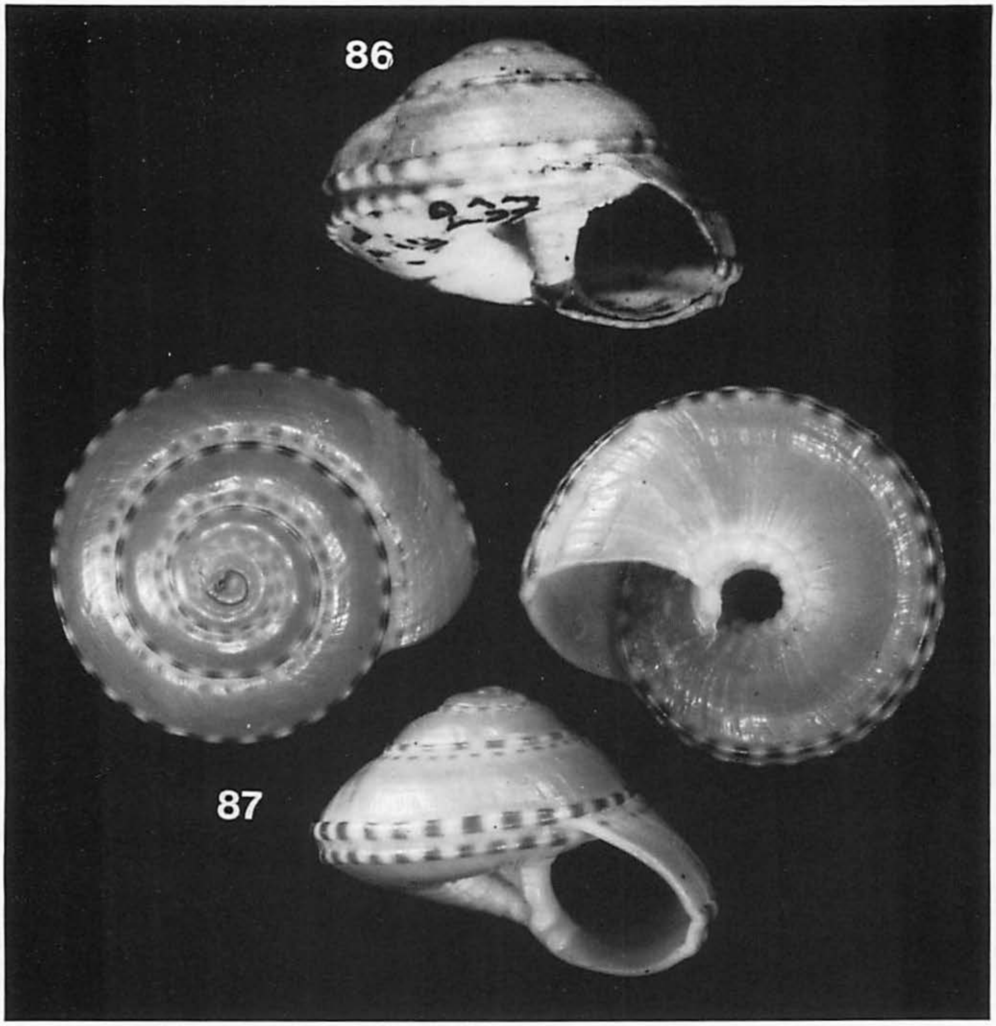
Type localities: *S. luteum*: "Habite les mers de la Nouvelle-Hollande" [Australia]; var. *novaehollandiae*: "Neuholland ?" [Australia].

Etymology: *luteus-a-um* [adjective]; Latin: of mud or clay, yellow.

Material studied: 238 specimens (AMNH, ANSP, BMNH, BPBM, CAS, DMNH, FLMNH, FMNH, HUJ, IRSNB, LACM, MHNG, MNHNP, NMNZ, NMP, NMW, OUM, RNHL, SMF, SMNS, UMZC, USNM, ZIMH, ZMA, ZSM); and lectotype and 5 paralectotypes of *S. luteum* (MHNG 1095/41). Original material of *S. luteum* var. *novaehollandiae* not located.

Diagnosis

Small to medium-sized, ovoid to high-spired cone-shaped shell with narrow umbilicus; whorls inflated, smooth and glossy (in fresh specimens); spiral sculpture restricted to two peripheral ribs (upper one stronger), and one rib (umbilical crenae) surrounding



Figs. 86, 87. *Philippia lutea* (LAMARCK, 1822). Fig. 86: lectotype of *Solarium luteum*; Australia; MHNG 1095/41 (photograph: G. DAJOZ, MHNG); SD = ca. 10.5. Fig. 87 (three aspects): specimen from New South Wales, Australia; FMNH 223425; SD = 9.4.

umbilicus. Overall yellowish to dark reddish-brown, with regular pattern of dark-brown spots on whitish background on peripheral ribs; umbilical crenae white. Protoconch with anal keel overlayed by callus; diameter 0.86–1.02 mm.

Description:

Teleoconch: small to medium-sized, glossy (in fresh specimens); diameter of specimens in collections usually 9–13 at 3 5/8 to 4 1/2 whorls. Shape: ovoid to high-spired cone-shaped with inflated whorls and narrow umbilicus (UD ca. 13% of SD).

Sculpture: Upper side: ± smooth, SSR and MR not developed (± weak nodulose spiral and/or axial sculpture on early whorls of some specimens, partly with indistinct spiral threads on later whorls); Periphery: UPR completely reduced, UPR-area therefore indistinguishable from likewise smooth MR-area; double-keel formed by distinctly separated LPR and less prominent IPR; upper point of whorl attachment at, or immediately below, LPR; Base: BF smooth except for axial plications, stronger towards the umbilicus (and weak spiral threads near the IPR in some specimens); PUR not developed; UC separated by a narrow, ± shallow groove, with crenae relatively small; columellar wall forming inner lip with plications for support of columellar muscle, with two grooves of about equal depth (one in UC overhanging umbilicus, one next to base of penultimate whorl); no distinct ribs on convex umbilical side of wall. Coloration: overall yellowish to dark reddish-brown, with regular pattern of rectangular, ± well-defined brown spots on whitish background on LPR and IPR (thereby about 24–34 blotches on 4th whorl); most shells with (often ill-defined) pattern in SSR-area; UC white, always lightest-colored area of shell. – Protoconch (see Fig.88): small to medium-sized (0.86–1.02, $\bar{x}$ = 0.94), distinctly heterostrophic, callus overlaying short anal keel; light- to dark-brown (depending on teleoconch-coloration), usually darkest along anal keel, varix and suture. – Periostracum and Operculum: as described for genus. – Radula: five-toothed taenioglossate (2–1–2); rachidian with narrow central cusp flanked on either side by a long filiform cusp; inner marginal tooth with three, outer marginal tooth with two cusps (Boss & Merrill, 1984b: 359, pl.57 figs.1b-f). – Jaws: consisting of rounded, pointed rod-shaped elements (Boss & Merrill, 1984b: 359, pl.57 fig.1a). – Anatomy: sexes separate; males with sperm-filled receptaculum apparatus (Haszprunar, 1985c: 211, and in litt.).

Geographical distribution (Fig.89): Australian region (records from the Philippines and Howland Island in need of verification).

Habitat: Intertidal to sublittoral (depth records between 0 and 82 m), live records from shallow water.

Discussion:

Philippia lutea, type species of the genus, has often been confused with the very similar Mediterranean/Atlantic species *Ph. hybrida* (Linné, 1758) (e.g., Philippi, 1836: 174, pl.10 fig.27; see synonymies and discussions by Martens, 1875: 103 ff., Bayer, 1942: 12, and Bieler, 1985a: 237). The most reliable distinguishing character is the color pattern of the peripheral ribs: *Ph. lutea* shells have 23–52, usually sharply delineated, color spots on the body whorl, while *Ph. hybrida* shells have only 19–26, usually not sharply delineated blotches.

Garrard (1977: 526) remarked on the great variation in shape and color between Australian populations: east coast specimens are invariably elevated conic and colored yellow-ochre or light buff to grey; in Victoria, light to dark grey specimens predominate; in South Australia, specimens are more depressed (height/width ratio decreasing from 70–80% to 60–70%) and have a reddish tinge; and in West

Australia, most shells are light to deep blackish-red in color and very depressed (ratio decreasing to 45–55%).

Philippia japonica (PILSBRY & STEARNS *in* PILSBRY, 1895) is very similar and probably only a locally restricted form of *Ph. lutea* (see below).

One of the six syntypes of *Solarium luteum* in Geneva (MHNG 1095/41) was selected as lectotype (BIELER, 1985a: 237, pl.2 fig.8; and Fig.86); a "Holotype" (GARRARD, 1977: 525) does not exist.

Philippia japonica (PILSBRY & STEARNS *in* PILSBRY, 1895)

Fig.88–90

*1895 *Solarium conulum* var. *japonicum* PILSBRY & STEARNS *in* PILSBRY, Cat. mar. moll. Japan: 65.
1967 *Philippia japonica* PILSBRY [sic], - HABE & KOSUGE, Stand. illus. book Jap. shells: 106, fig.24.
1973 *Philippia (Philippia) japonica*, - ROBERTSON, 1973b, Proc. Acad. nat. Sci. Philad., *125*(2): 37.
1979 *Philippia japonica* PILSBRY & STANDEN [sic], - MATSUMOTO, Moll. shells Mie Pref.: 22, pl.3 fig.5.

Type measurements (lectotype, here designated): SD = 10.7, H = 8.3, PD = 0.78, Tw = 4 5/8, UD = 2.

Type locality: "Hazaburo, Boshiu coast" [Japan].

Etymology: *japonicus-a-um* [adjective]; Japanese.

Material studied: 5 specimens (ANSP, FMNH, USNM); including lectotype (ANSP 71020).

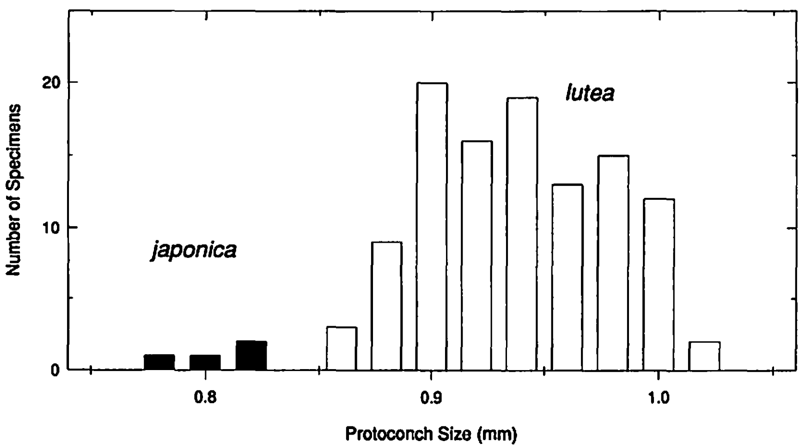


Fig. 88. Histogram of measured protoconch size. *Philippia japonica* (n = 4, $\bar{x}$ = 0.81), and *Ph. lutea* (n = 109, $\bar{x}$ = 0.94, sd = 0.04).

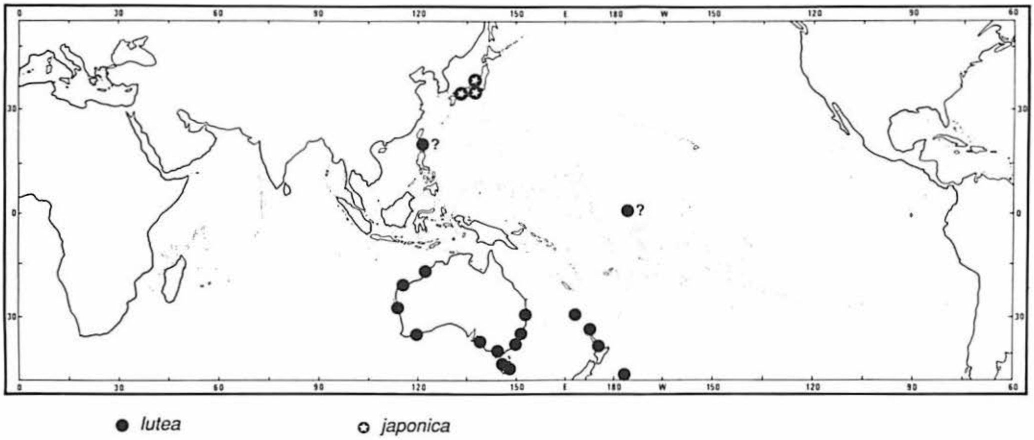


Fig. 89. Geographical distribution of *Philippia lutea* and *Ph. japonica*.

Diagnosis:

Small to medium-sized, ovoid to high-spired cone-shaped shell with narrow umbilicus; whorls inflated, smooth and glossy (in fresh specimens); spiral sculpture restricted to two peripheral ribs (upper one stronger), and one rib (umbilical crenae) surrounding umbilicus. Overall reddish-brown, with regular pattern of dark-brown blotches or

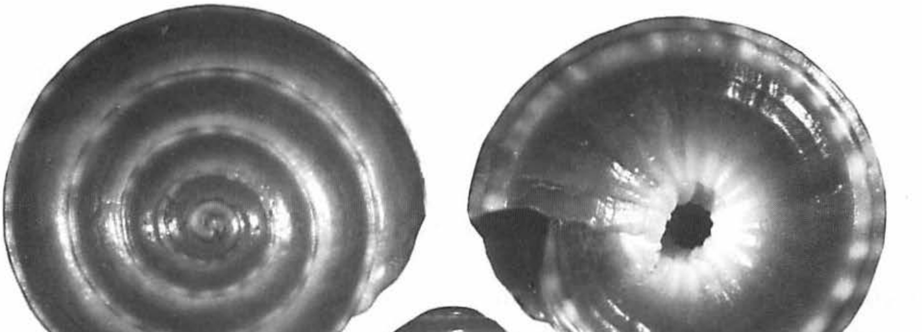


Fig. 90. *Philippia japonica* (PILSBRY & STEARNS *in* PILSBRY, 1895); lectotype of *Solarium conulum japonicum*; ANSP 71020; Japan; SD = 10.7.

flames on lighter-colored background on peripheral ribs; umbilical crenae white. Protoconch with anal keel overlayed by callus; diameter 0.78–0.82 mm.

Description:

Teleoconch: size, shape and sculpture as in *Philippia lutea*. Coloration: overall reddish-brown, with regular pattern of brown blotches or flames on lighter background on LPR and IPR (22–35 blotches on 4th whorl); UC white. – Protoconch (see Fig.88): small (0.78–0.82, $\bar{x}$ = 0.81), distinctly heterostrophic, with callus overlaying short anal keel; brown. – Periostracum, Operculum, Radula and Anatomy: not known.

Geographical distribution (Fig.89): Known only from Japan.

Habitat: not known.

Discussion:

Pilsbry & Stearns described this form as a variety of the Mediterranean *Solarium conulum* Weinkauff, 1868 [= *Ph. hybrida* Linné, 1758]. It is probably only a local form of *Ph. lutea* (see above). The type specimen (Fig.90) has fewer color markings on the peripheral ribs than other specimens known from Japan (see, e.g., Matsumoto, 1979: pl.3 fig.5). The only constant character separating it from *Ph. lutea* is the smaller protoconch size (see Fig.88). Since the geographical range of these forms is to date poorly understood, *Ph. japonica* is here provisionally retained at the species level.

The original description by Pilsbry & Stearns *in* Pilsbry (1895: 65) does not mention the number of specimens studied. The remark "sometimes larger" in reference to dimensions, however, indicates the existence of more than one specimen. Measurements of the syntype in Philadelphia (ANSP 71020; Fig.90) are close to those of the original diagnosis ("Alt. 8 1/2, diam. 10 mm"), and this specimen is here selected as lectotype.

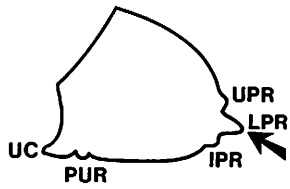
Genus *Psilaxis* Woodring, 1928

Psilaxis Woodring, 1928: 355; introduced as "section" of *Architectonica*. Type species by original designation: *Architectonica (Philippia) krebsii* Mörch, 1875; Recent, Atlantic Ocean.

Description (Fig.91):

Teleoconch: shell medium-sized to large (usually 10–25 mm), from roundly to depressed cone-shaped; umbilicus always open, moderately wide to wide (19–30% of shell diameter); whorls somewhat bulging; upper (apical) side usually completely smooth, rarely with weak spiral striae; early postlarval shell sometimes with ± weak nodular sculpture; sharp peripheral keel formed by LPR (here upper point of whorl attachment), flanked on either side one weak rib (UPR and IPR); base in Recent species smooth except for two nodose rib surrounding umbilicus (PUR and UC); umbilical wall without spiral ribs; coloration of spiral bands or ± distinctly demarcated

Fig. 91. Schematic representation of placement of major spiral ribs in *Psilaxis*, apertural aspect. Arrow shows point of attachment of next whorl.

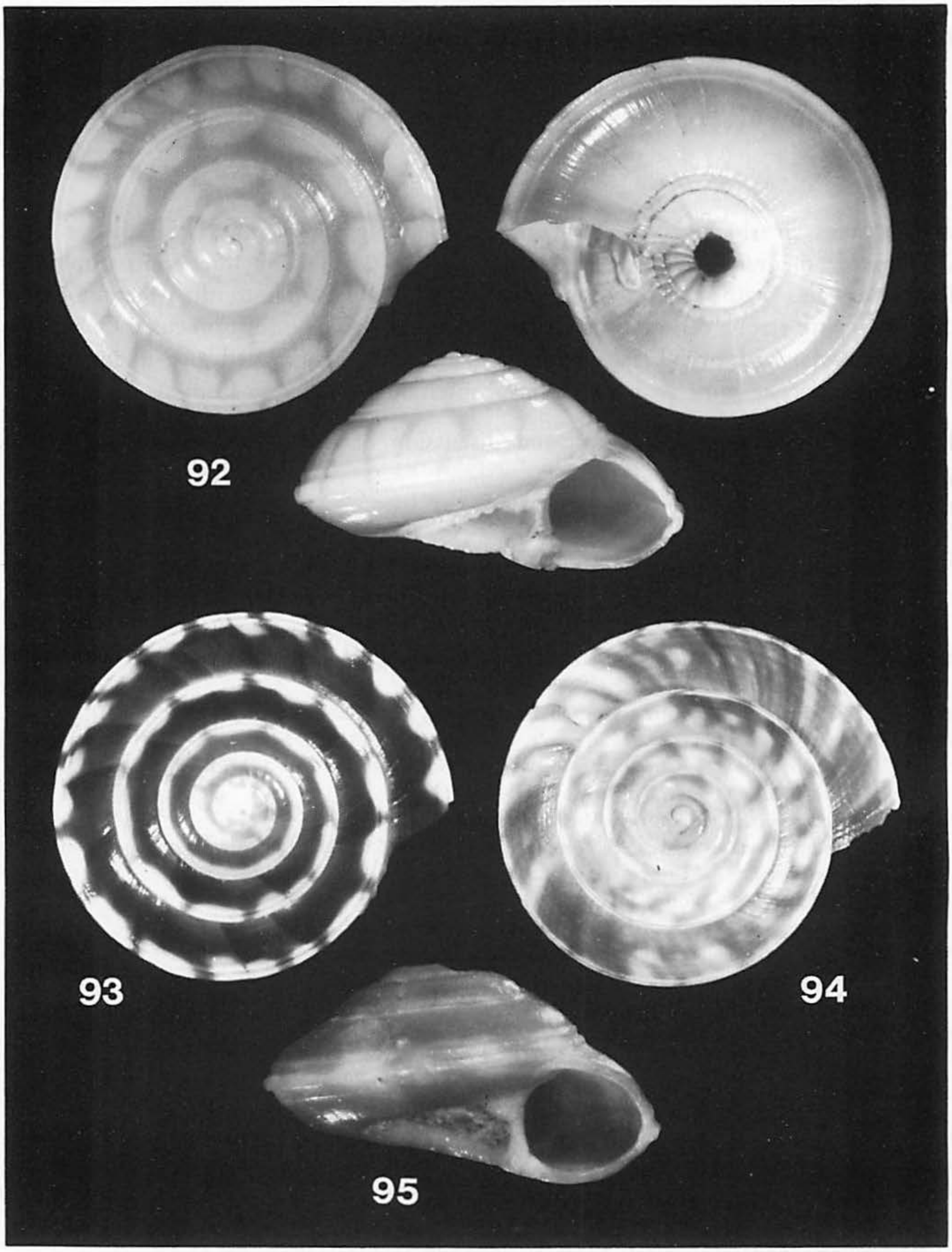


axial flames in shades of brown, rib surrounding umbilicus (UC) always light. *Protoconch:* medium-sized to very large (ca. 1.1–1.8), distinctly heterostrophic, in Recent species with distinct, long anal keel. *Radula:* five-toothed-taenioglossate; rachidian with strong central cusp flanked on either side by a filiform cusp. *Operculum:* horny, circular with broad last whorl, flat with mushroom-shaped, peg-like projection on body side; peg with grooves arranged in counter-clockwise fashion.

For a more extensive description and discussion of this genus see BIELER (1985a: 238–239).

Psilaxis radiatus (RÖDING, 1798)
Figs.20, 92–100

?1781 "Trochus testa crenulato-umbilicata, ...", - GRONOVIUS, Zoophylac. Gronov.: 323, no.1486 [not binominal].
?1781 "Perspectiviunculus", - MEUSCHEN, [Index vermium] Zoophylac. Gronov. [not binominal].
1781 "Trochus hybridus Linnaei", - CHEMNITZ, Conch.-Cab., *5*: 13, pl.173 figs.1702–1705 [not binominal].
1781 "Trochus hybridus", - CHEMNITZ, Conch.-Cab., *5*: 132, pl.173 figs. 1702–1705 [not binominal].
1790 -, GEVE, Belustigung: pl.25 figs.274a-b.
*1798 *Architectonica Radiata* RÖDING, Mus. Boltenianum: 79.
1816 *Solarium hybridum*, - LAMARCK, Tabl. encycl. méth., *21*: pl.446 figs.2a-b [non *Trochus hybridus* LINNÉ, 1758].
1822 *Solarium hybridum*, - LAMARCK, Hist. nat., *7*: 4.
1825 *Trochus hybridus*, - WOOD, Index testac.: 137, pl.29, fig.61.
1830 *Solarium hybridum*, - DESHAYES, 1830a, Encycl. méth., *2*(1): 158.
*1838–1839 *Solarium cingulum* KIENER, Spéc. gén. icon. coq., *10*: 6, pl.3 figs.6–6a.
1838–1839 *Solarium hybridum*, - KIENER, Spéc. gén. icon. coq., *10*: 7, pl.3 figs.5–5a.
1853 *Solarium hybridum*, - PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 14, pl.2 figs.14–17.
*1855 *Philippia Layardi* A. ADAMS, Proc. zool. Soc. Lond., *22*(1854): 317.
1856 *Solarium hybridum*, - HANLEY, [WOOD's] Index testac.: 143, pl.29 fig.61.
1859 *Solarium cingulum*, - CHENU, Man. conch. paléont., *1*: 232, fig.1351.
1859 *Solarium (Philippia) hybridum*, - CHENU, Man. conch. paléont., *1*: 233, fig.1356.
1863 *Solarium (Philippia) hybridum*, - HANLEY, Thes. conch., *3*: 236, pl.253 figs.39–41.
*1863 *Solarium (Philippia) hybridum* var. *undata* HANLEY, Thes. conch., *3*: 236, pl.253 figs.42–43.
*?1863 *Solarium (Philippia) hybridum* var. *australis* HANLEY, Thes. conch., *3*: 236 [non *S. australe* PHILIPPI, 1849 = *Architectonica perspectiva* (LINNÉ, 1758)].
1863 *Solarium (Philippia) cingulum*, - HANLEY, Thes. conch., *3*: 237, pl.253 figs.55–56.
1864 *Solarium cingulum*, - REEVE, Conch. icon., *15*: no.19, pl.3 fig.19.
1864 *Solarium hybridum*, - REEVE, Conch. icon., *15*: no.21, pl.3 fig.21.
1875 *Solarium hybridum*, - MARTENS, Jb. dtsch. malak. Ges., *2*: 116.
1875 *Solarium cingulum*, - MARTENS, Jb. dtsch. malak. Ges., *2*: 116.
1876–1878 *Solarium (Solarium) cingulum*, - KOBELT, Illus. Conchylienb., *1*: 87, pl.32 fig.6.
*1880 *Solarium (Philippia) cingulum* var. *subconcolor* MARTENS, Beitr. Meeresfauna Mauritius: 290.
1887 *Solarium (Philippia) hybridum*, - MARSHALL, Man. conch., *9*: 14, pl.5 figs.59–60 [after HANLEY, 1863].



Figs. 92–95. *Psilaxis radiatus* (RÖDING, 1798). Fig. 92 (three aspects): holotype of *Philippia stipator* IREDALE, 1931; New South Wales; AMS 93224; SD = 17.2. Fig. 93: specimen from Mozambique; NMP H4905; SD = 20.6. Fig. 94: specimen from Mozambique; NMP H4897; SD = 19.6. Fig. 95: syntype of *Solarium kowiensis* TURTON, 1932; UMZC; SD = 9.4.

1887 *Solarium (Philippia) hybridum* var. *undatum*, - MARSHALL, Man. conch., *9*: 14, pl.5 figs.61-62 [after HANLEY, 1863].
1887 *Solarium (Philippia) cingulum*, - MARSHALL, Man. conch., *9*: 15, pl.5 fig.63 [after HANLEY, 1863], fig.64 [after REEVE, 1864].
1892 *Solarium cingulum*, - SOWERBY (III), Mar. shells S. Afr.: 28.
1897 *Solarium (Philippia) hybridum*, - SOWERBY (III), Append. mar. shells S. Afr.: 15.
1909 *Solarium (Philippia) hybridum*, - SCHEPMAN, Monogr. Res. SIBOGA Exped., *49*(1b): 219.
1909 *Solarium (Philippia) cingulum*, - SCHEPMAN, Monogr. Res. SIBOGA Exped., *49*(1b): 219.
1909 *Solarium (Philippia) cingulum* var. *subconcolor*, - SCHEPMAN, Monogr. Res. SIBOGA Exped., *49*(1b): 220.
1915 *Solarium cingulatum* [sic], - DALL, Smiths. Inst. Publ., *2360*: 52.
*1931 *Philippia stipator* IREDALE, Rec. Austr. Mus., *18*(4): 229, pl.25 figs.17-18.
*1932 *Solarium kowiensis* TURTON, Mar. shells Port Alfred: 134, pl. 29 fig. 971.
1940 *Architectonica cingula*, - M. SMITH, World-wide sea shells: 29, fig.400.
1940 *Torinia hybrida*, - M. SMITH, World-wide sea shells: 29, fig.402.
1942 *Philippia layardi*, - BAYER, Zool. Meded., *24*(1-2): 8 [synonymy].
1942 *Philippia layardi* var. *kowiensis*, - BAYER, Zool. Meded., *24*(1-2): 10 [synonymy].
1942 *Philippia layardi* var. *undata*, - BAYER, Zool. Meded., *24*(1-2): 11 [synonymy].
1942 *Philippia radiata*, - BAYER, Zool. Meded., *24*(1-2): 15 [synonymy].
1942 *Philippia radiata* var. *subconcolor*, - BAYER, Zool. Meded., *24*(1-2): 16 [synonymy].
1952 *Philippia hybridum*, - TINKER, Pac. sea shells: 176, pl. p. 178, second row.
1953 *Phillipia* [sic] *cingulum*, - DIETRICH & MORRIS, Nautilus, *67*(1): 16, pl.4 fig.7.
1954 *Philippia hybrida*, - HIRASE (& TAKI), Illus. handbook shells: pl.128 fig.8.
1954 *Philippia radiata*, - KIRA, Col. illus. shells Jap.: 24, pl.12 fig.5.
1961 *Philippia radiata*, - RIPPINGALE & MCMICHAEL, Queensld. Gr. Barr. Reef shells: 63, pl.6 fig.22.
1962 *Philippia radiata*, - KIRA, Shells w. Pac. col., *I*: 24, pl.13 fig.5.
1962 *Philippia stipator*, - IREDALE & MCMICHAEL, Mem. Austr. Mus., *11*: 68.
1966 *Philippia hybrida*, - HABE & KOSUGE, Shells world col., *II*: 101, pl.40 fig.3.
1966 *Philippia radiata*, - HABE & KOSUGE, Shells world col., *II*: 101, pl.40 fig.4.
1970 *Philippia (Psilaxis) radiata*, - ROBERTSON et al., Pac. Sci., *24*(1): 55 ff., figs.1-3.
1970 *Philippia (Psilaxis) radiata*, - ROBERTSON, Pac. Sci., *24*(1): 66 ff., figs.1, 3, 5-7, 9-10, 12-17.
1971 *Philippia layardi*, - KURODA et al., Sea shells Sagami Bay: 263, pl.61 figs.21-25.
1971 *Philippia layardi undata*, - KURODA et al., Sea shells Sagami Bay: 263, pl.61 fig.20.
1971 *Philippia radiata*, - WILSON & GILLETT, Austr. shells: 34, pl.13 figs.13-13a.
1972 *Philippia radiata*, - CERNOHORSKY, Mar. shells Pac., *II*: 195, pl.56 figs.1-1a.
1972 *Philippia radiata*, - HINTON, Shells New Guinea: 4, pl.2 fig.29.
1973 *Philippia (Psilaxis) radiata*, - ROBERTSON, 1973b, Proc. Acad. nat. Sci. Philad., *125*(2): 37 ff.
1975 *Philippia radiata*, - SALVAT & RIVES, Coqu. Polynesie: 265, fig.47.
1977 *Philippia (Psilaxis) radiata*, - GARRARD, Rec. Austr. Mus., *31*(13): 509, fig.15 [operculum], p.527, pl.3 figs.10-18 [figs.16-18 = holotype of *Ph. stipator*].
1978 *Philippia hybrida*, - KIRTISINGHE, Sea shells Sri Lanka: 55, pl.29 fig.5.
1978 *Philippia radiata*, - HINTON, Guide Austr. shells: pl.10 fig.11.
1979 *Philippia (Psilaxis) radiata*, - ROBERTSON, Veliger, *22*(2): 191 ff., figs.1-4.
1979 *Philippia radiata*, - HINTON, Guide shells Papua: pl.1 figs.9-9a.
1979 *Philippia radiata*, - MATSUMOTO, Moll. shells Mie Pref.: 22, pl.3 fig.2.
1979 *Philippia radiata*, - KAY, Hawaii. mar. shells: 101, fig.34 [after ROBERTSON et al., 1970], figs.36C-E.
1979 *Philippia (Psilaxis) radiata*, - POWELL, N. Zeal. Moll.: 248, pl.48 fig.3.
1982 *Philippia radiata*, - KILBURN & RIPPEY, Sea shells s. Afr.: 77, pl.11 fig.11.
1983 *Philippia radiata*, - EMERSON, Nautilus, *97*(4): 123.
1983 *Philippia radiata*, - SCHELTEMA & WILLIAMS, Bull. mar. Sci, *33*(3): 549, figs. 1D-F, 2B-D [larvae].
1984 *Philippia radiata*, - EMERSON, Hawaii. Shell News, *32*(1): 5, fig.
1984 *Philippia (Psilaxis) radiata*, - BOSS & MERRILL, 1984b, Occas. Pap. Moll., *4*(66): 355, pl.49 figs.4-6 [after ROBERTSON, 1970] [radula].
1985 *Philippia radiata*, - DRIVAS & JAY, La Conchiglia, *17*(190-191): 8, figs.3, 5-6 [fig.4 = ? *Ph. oxytropis* ADAMS, 1855].

1986 *Philippia (Psilaxis) radiata*, - SPRINGSTEEN & LEOBRERA, Shells Philippines: 26, pl.2 fig.15.
1988 *Philippia (Psilaxis) radiata*, - BIELER, Malac. Rev., Suppl. *4*: 236 [radula].

Type measurements: Syntype (larger of 2 in MHNG) of *S. cingulum*: SD = 24.1, H = 13.2, PD = 1.5, Tw = 4 7/8, UD = 4.1. Holotype of *Ph. stipator*: SD = 17.2, H = 9.9, PD = 1.4, Tw = 4 1/4+, UD = 2.4. Syntype (larger of 2 in UMZC) of *kowiensis*: SD = 9.4, H = ca. 5.7 [apex damaged], UD = 2.5.

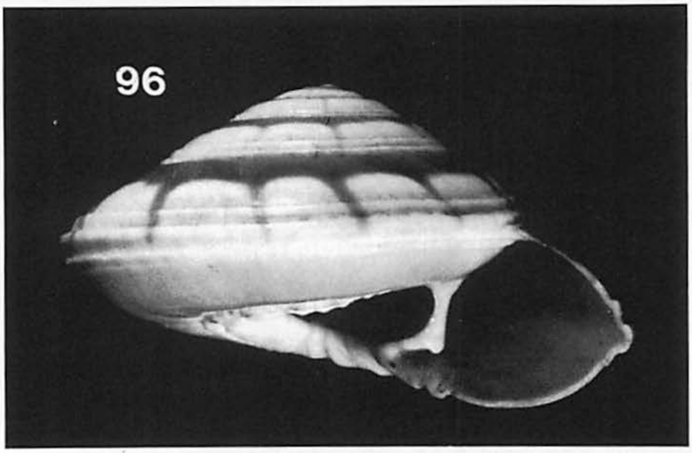


Fig. 96. *Psilaxis radiatus* (RÖDING, 1798); larger of two syntypes of *Solarium cingulum* KIENER, 1838-1839; MHNG 1151/80; SD = 24.1 (photograph G. DAJOZ, MHNG).

Type localities: *A. radiata*: not given; *S. cingulum*: "Habite la mer des Indes"; *Ph. layardi*: "Ceylon"; var. *undata*: not given; var. *subconcolor*: "Mauritius"; var. *australis*: not given; *Ph. stipator*: Sydney Harbour, N.S.W., Australia; ex 'TRITON' dredge; *S. kowiensis*: Port Alfred, South Africa.

Etymology: *radiatus-a-um* [adjective]; Latin: having rays, radiant.

Material studied: 1800+ specimens (AMS, ANSP, BMNH, BPBM, CAS, DMNH, ELM, FLMNH, FMNH, LACM, LMA, MNHNP, NMNZ, NMP, NMW, SAM, SMF, SMNS, UCMP, UMZC, USNM, ZIMH, ZMA, ZSM, Coll. ALF, Coll. MARAIS); including holotype of *Ph. stipator* (AMS 93224), 2 syntypes of *S. kowiensis* (UMZC unnumbered), 2 syntypes of *Ph. kowiensis* (USNM 406472), 3 possible syntypes of *Ph. kowiensis* (BMNH 1935.2.8.138-140), and photographs of 2 syntypes of *S. cingulum* (MHNG 1151/80). Original material of *Ph. layardi*, *S. hybridum* vars. *undata* and *australis* (BMNH) and of *S. cingulum* var. *subconcolor* (MHNU) not located. *Architectonica radiata* was based in part on figures by GEVE and CHEMNITZ; original material not located.

Diagnosis:

Small to large cone-shaped shell with rounded to prominently angulated peripheral keel and moderately wide umbilicus; whorls inflated, smooth and glossy; spiral sculpture restricted to three peripheral ribs (central one stronger and more prominent), and two ribs surrounding umbilicus (narrow proxumbical rib and wider umbilical crenae). Striped, flamed or mottled in shades of brown, usually lighter color pattern on periphery; umbilical crenae whitish. Protoconch diameter 1.16–1.52 mm; with long, sharply crested anal keel (< 0.34 mm); whitish without distinct pattern in center of last whorl.

Description:

Teleoconch: small to large, diameter of specimens in collections usually 7–22 at 2 1/2 to 5 1/4+ whorls. Shape: cone-shaped with rounded to prominently angulated peripheral keel, inflated whorls and moderately wide umbilicus (UD ca. 19% of SD). Sculpture: Upper side: ± smooth, SSR and MR not developed (weak nodulose sculpture on early whorls of some specimens, sometimes with indistinct spiral threads on later whorls); Periphery: ± prominent keel formed by strong LPR, with weaker UPR and IPR on either side; upper point of whorl attachment on LPR; Base: BF smooth (in small specimens with axial plications, stronger towards umbilicus); IPR and UC distinctly separated, UC much wider and bearing large nodules; columellar wall forming almost straight inner lip with plications for support of columellar muscle, with deepest groove in UC overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration: highly variable, always in shades of brown; usually whitish with a wide brown subsutural band with ± regular axial flames extending over the upper side (see Figs.92–93); these flames often fading into an irregularly mottled pattern (see Fig.94); other specimens overall brown with a lighter-colored pattern at the periphery (see Fig.95); UC always whitish. - Protoconch (Fig.97): medium-sized to very large (1.16–1.52, $\bar{x}$ = 1.36), distinctly heterostrophic, with long, sharply crested anal keel (0.18–0.34, $\bar{x}$ = 0.27; see Fig.99); usually white, with anal keel and outer corner in front of varix brown. - Periostracum and Operculum: as described

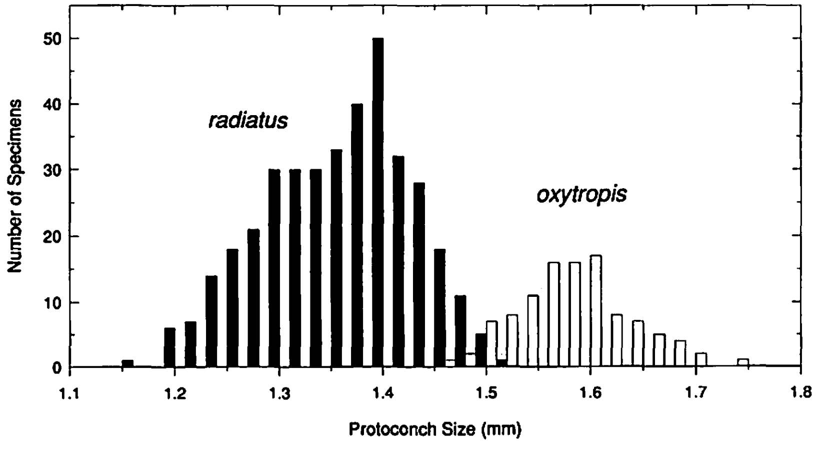


Fig. 97. Histogram of measured protoconch size. *Psilaxis radiatus* (n = 375, $\bar{x}$ = 1.36, sd = 0.07) and *Ps. oxytropis* (n = 105, $\bar{x}$ = 1.58, sd = 0.05).

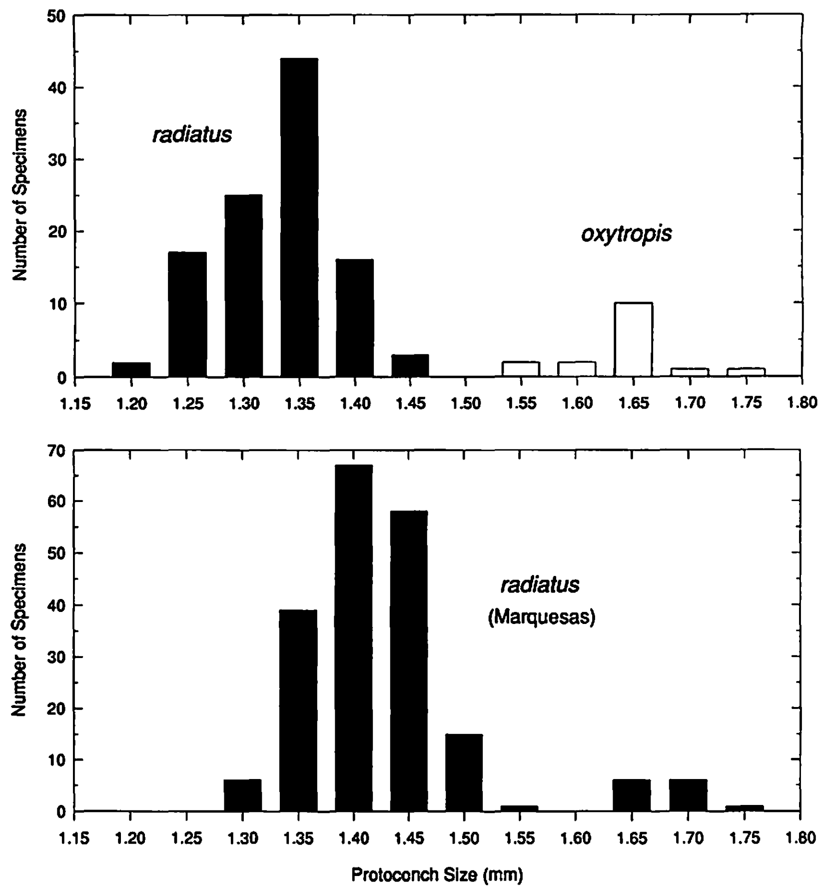


Fig. 98. Histograms of measured protoconch size (after ROBERTSON, 1970: 80). Above (all Indo-Pacific localities except Marquesas): *Psilaxis radiatus* (n = 107, x̄ = 1.33, sd = 0.05) and *Ps. oxytropis* (16, x̄ = 1.64, sd = 0.05). Below (Marquesas only): *Psilaxis radiatus* (n = 199, x̄ = 1.43, sd = 0.08).

for genus (operculum figured by ROBERTSON, 1970: 74, figs.10a-c). – Radula: five-toothed taenioglossate (2–1–2); rachidian with strong central cusp flanked on either side by a filiform cusp; inner and outer marginal teeth each with 5–6 long, filiform cusps (BIELER, 1988: 236; some teeth figured by ROBERTSON, 1970: 73, fig.9). – Jaws: consisting of elongated elements (ROBERTSON, 1970: 73, fig.7). – Anatomy: not studied. – Soft-body coloration of living animal: translucent white with solid-white granules embedded in head-foot except for sole of foot (pers. observ., South Africa).

Reproduction and larval development: ROBERTSON (1970: 78–79, figs.16–17) reported on an egg mass of *Psilaxis radiatus* found in the outer part of the umbilicus of an adult specimen from Rarotonga, Cook Islands. The gelatinous egg mass contained 361 encapsulated, mostly uncleaved eggs (61–67 µm, x̄ = 63 µm; after alcohol preservation). The ovoid capsules, interconnected by chalazae and each containing a single egg, ranged in size from 79–90 µm (x̄ = 84 µm) and contained various-sized

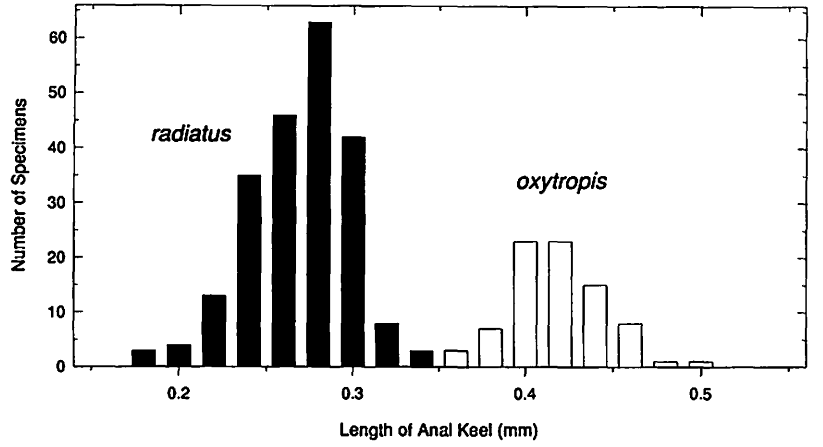


Fig. 99. Histogram of measured anal keel length. *Psilaxis radiatus* (n = 217, x̄ = 0.27, sd = 0.03), and *Ps. oxytropis* (n = 81, x̄ = 0.42, sd = 0.03).

granules around the eggs. SCHELTEMA & WILLIAMS (1983: 549, figs.1E-F, 2B-D) found larvae measuring 1.20–1.66, average 1.50, in samples from the Pacific Ocean (near the equator, between Samoa and the Christmas Atoll). HADFIELD (1976: 135) reported data obtained by BONAR in Hawaii, stating that metamorphosis of *Psilaxis radiatus* larvae occured more readily in the presence of the host, living *Porites* (a hermatypic coral). Growth of the teleoconch was strictly dependent on the presence of coral, and growth after metamorphosis was depending on teleoconch size at settlement: only larvae with teleoconch sizes above 1.70 mm demonstrated teleoconch growth in the presence of living coral. One animal, reared in the laboratory, began laying eggs at a shell diameter of 7.2 mm, less than three months after it had metamorphosed.

Geographical distribution (Fig.100): Subtropical and tropical Indian Ocean and western to central Pacific. Occasionally reported from eastern Pacific [Isla Gorgona, Colombia (ROBERTSON, 1979), Golfo de Veraguas, Panama (EMERSON, 1983, 1984) and Cabra

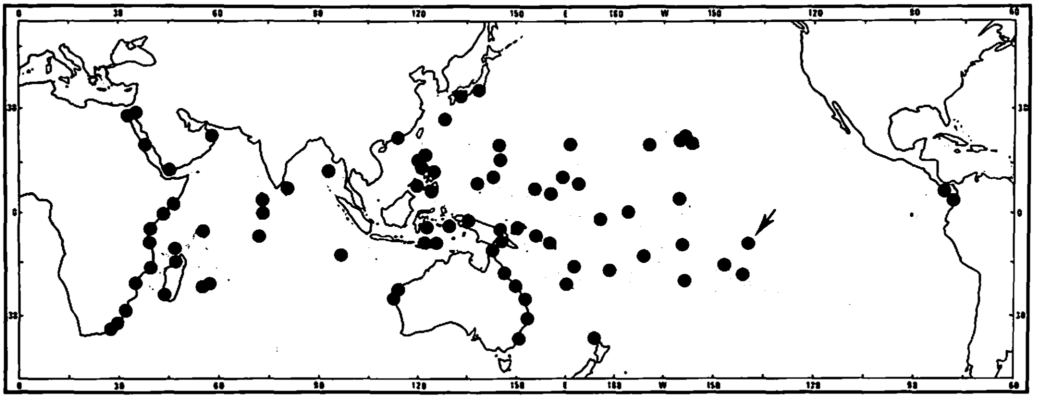


Fig. 100. Geographical distribution of *Psilaxis radiatus*. Arrow indicating Marquesas records.

Island, Panama (specimen in NMW)], but probably no brooding populations are established in that area (ROBERTSON, 1979: 192).

Habitat: Sublittoral (most depth records between 10 and 200 m), live records from shallow water and between 60 and 70 m, sandy substrates.

Habits/feeding behavior: ROBERTSON et al. (1970: 58–59) reported on specimens from the Hawaiian Islands: "The postlarvae, rarely collected alive, are known from shallow water to about 150 feet. During daylight, the animals are usually buried 1 to 4 inches in silty sand or loose, algal-covered rubble ... . In every case known to us, the living animals were near massive or incrusting colonies of *Porites lobata*." One specimen was maintained in an aquarium and observed under infrared light, and "was seen with its proboscis fully everted adjacent to the *Porites* colony as it fed delicately on the still partly expanded polyps ... . The drawing ... probably does not show the full length of the extended proboscis" (here reproduced in Fig.20).

Discussion:

The identity of *Psilaxis radiatus* has been a matter of dispute in the literature, especially because many authors have confused it with *Philippia hybrida* (LINNÉ, 1758); *Ph. hybrida* is the Mediterranean/Atlantic "sibling" of *Ph. lutea* (see above). BAYER (1942) discussed the Recent *Philippia* (and *Psilaxis*) species extensively, and distinguished many different species and "varieties" in the complex now considered as the genus *Psilaxis*. ROBERTSON (1970: 66ff.) critically revised that group and, in agreement with the present study, found it to consist of only three Recent species, *Ps. radiatus* and *Ps. oxytropis* ADAMS, 1855, in the Indo-Pacific, and *Ps. krebsii* (MÖRCH, 1875) in the Atlantic Ocean. The two Indo-Pacific species are very similar to each other, with *Psilaxis radiatus* usually having shells with a narrower umbilicus. While white shells with brown subsutural bands and radial flames can be readily recognized as *Ps. radiatus*, it is necessary to study the protoconchs of specimens with other color patterns.

ROBERTSON found that the protoconch of *Psilaxis oxytropis* is larger, has a different coloration with a fairly sharply differentiated, centrally placed white mark surrounded by brown (ROBERTSON, 1970: 67, figs.1–2), and a longer, more rounded anal keel that is not lined by a darker band. All specimens studied by ROBERTSON can be placed in either *Ps. radiatus* or *Ps. oxytropis* by use of the protoconch-size character alone, with the exception of material from the Marquesas Islands (ROBERTSON, 1970: 80, fig.17; here modified in Fig. 98). Some Marquesas specimens, otherwise displaying characters typical for *Ps. radiatus*, have protoconch diameters in the *Ps. oxytropis* size range. Typical *Ps. oxytropis* is not known from the Marquesas. Since character displacement was out of the question (ROBERTSON did not find any protoconch size increase in *Ps. radiatus* at the many places besides the Marquesas where *Ps. oxytropis* is also absent), ROBERTSON (1970: 81) tentatively attributed the phenomenon (without chromosomal evidence) to polyploidy.

A study of additional material (Indo-West-Pacific, excluding Marquesas and other specimens already studied by ROBERTSON) supports the separation of the two species:

they can be distinguished by a significant difference in protoconch size (see Fig.97). An even better character is the length of the anal keel, which is not correlated with protoconch diameter [e.g., a relatively small protoconch of *Ps. oxytropis* can have a relatively long anal keel (1.50 : 0.46) or vice versa (1.64 : 0.36); specimens in MNHNP without no.] (see Fig.99).

The "variety" *australis* HANLEY, 1863, is a junior synonym of either *Psilaxis radiatus* or *Ps. oxytropis* (see also BAYER, 1942: 10; ROBERTSON, 1970: 78). With the type material unfigured and not located, it is here listed among the synonyms of the species more commonly represented in collections, *Ps. radiatus*.

The non-binominal "Solarium perspectiviunculum" of MEUSCHEN (1781) referred most likely to what is now understood as *Psilaxis radiatus* (see also BAYER, 1942: 8). The likewise non-binominal "Solarium perspectiviunculum" of CHEMNITZ (1781) is recognized as a member of *Heliacus* (see discussion under *H. variegatus*). PAETEL & SCHAUFUSS (1869: 43, 1888: 287) used the erroneous spelling "perspectiviusculum" for a specimen from New Zealand. Although they referred to CHEMNITZ, not MEUSCHEN, as author of this name, the placement of the species in *Solarium* s.s. and the synonymy given by PAETEL (1887–1888: 287) indicate that a larger form, perhaps *Psilaxis radiatus,* was meant.

Psilaxis oxytropis (A. ADAMS, 1855)
Pl.3 Figs.B-F; Figs.97–99, 101–103

*1855 *Philippia oxytropis* A. ADAMS, Proc. zool. Soc. Lond., *22*(1854): 317.
1863 *Solarium (Philippia) oxytropis*, - HANLEY, Thes. conch., *3*: 236, pl.253 figs.46–47.
1864 *Solarium oxytropis*, - REEVE, Conch. icon., *15*: no.15, pl.3 fig.15.
1887 *Solarium (Philippia) oxytropis*, - MARSHALL, Man. conch., *9*: 15, pl.5 figs.65-66 [after HANLEY, 1863].
1887–1888 *Solarium (Philippia) oxytrope*, - PAETEL, Cat. Conch.-Slg., (4)*1*: 286.
*1931 *Philippia manifesta* IREDALE, Rec. Austr. Mus., *18*(4): 229, 235, pl.25 fig.9.
1942 *Philippia manifesta*, - BAYER, Zool. Meded., *24*(1–2): 14.
1942 *Philippia oxytropis*, - BAYER, Zool. Meded., *24*(1–2): 14 [synonymy].
1962 *Philippia manifesta*, - IREDALE & McMICHAEL, Mem. Austr. Mus., *11*: 68.
1962 *Philippia radiata*, - KIRA, Shells w. Pac. col., *1*: 24, pl.13 fig.5.
1967 *Philippia radiata*, - HABE & KOSUGE, Stand. illus. book Jap. shells: 106, fig.23.
1971 *Philippia manifesta*, - KURODA et al., Sea shells Sagami Bay: 263, pl.61 figs.18–19.
1970 *Philippia (Psilaxis) oxytropis*, - ROBERTSON, Pac. Sci., *24*(1): 66 ff., figs.2, 4, 5, 17.
1973 *Philippia (Psilaxis) oxytropis*, - ROBERTSON, 1973b, Proc. Acad. nat. Sci. Philad., *125*(2): 37 ff.
1975 *Philippia (Psilaxis) oxytropis*, - CLIMO, J. r. Soc. N. Zeal., *5*(3): 282, figs.4A [radula], 5C, 5F, 5G [anatomy].
1977 *Philippia (Psilaxis) oxytropis*, - GARRARD, Rec. Austr. Mus., *31*(13): 526, pl.5 figs.19–24 [figs.22–24 = holotype of *Ph. manifesta*].
1979 *Philippia oxytropis*, - KAY, Hawaii. mar. shells: 100, figs.36A-B.
1979 *Philippia (Psilaxis) oxytropis*, - POWELL, N. Zeal. Moll.: 248.
1982 *Philippia (Psilaxis) oxytropis*, - HEALY, Zoomorph., *101*(3): 197 ff., fig. [spermiogenesis].
1983 *Philippia oxytropis*, - SCHELTEMA & WILLIAMS, Bull. mar. Sci., *33*(3): 547, figs. 1A-C, 2A [larvae].
1984 *Philippia (Psilaxis) oxytropis*, - BOSS & MERRILL, 1984b, Occas. Pap. Moll., *4*(66): 357, pl.49 figs.11–14 [after CLIMO, 1975] [radula].
1986 *Philippia (Psilaxis) oxytropis*, - SPRINGSTEEN & LEOBRERA, Shells Philippines: 26, pl.2 fig.14.
1988 *Philippia (Psilaxis) oxytropis*, - BIELER, Malac. Rev., Suppl. *4*: 236 [radula].

Type measurements: Presumed type specimen of *Ph. oxytropis*: SD = 10.3, H = 5.1, PD = 1.56, Tw = 3 1/8, UD = 3.1. Holotype of *Ph. manifesta*: SD = 18.3, H = 12.4, PD = 1.64, Tw = 4 7/8, UD = 4.2.

Type localities: *Ph. oxytropis*: "New Caledonia"; *Ph. manifesta*: Sydney Harbour, N.S.W., Australia, ex 'TRITON' dredge.

Etymology: *oxytropis-e* [adjective]; compound word from Greek adjective ὀξύς (sharp, pointed) and noun τρόπις (keel): possessing a sharp keel.

Material studied: 397 specimens (AMS, AMNH, ANSP, BMNH, FLMNH, FMNH, IRSNB, LACM, LMA, MNHNP, NMNZ, NMP, NMW, USNM); including presumed type specimen of *Ph. oxytropis* (BMNH 1980127) and holotype of *Ph. manifesta* (AMS 57775).

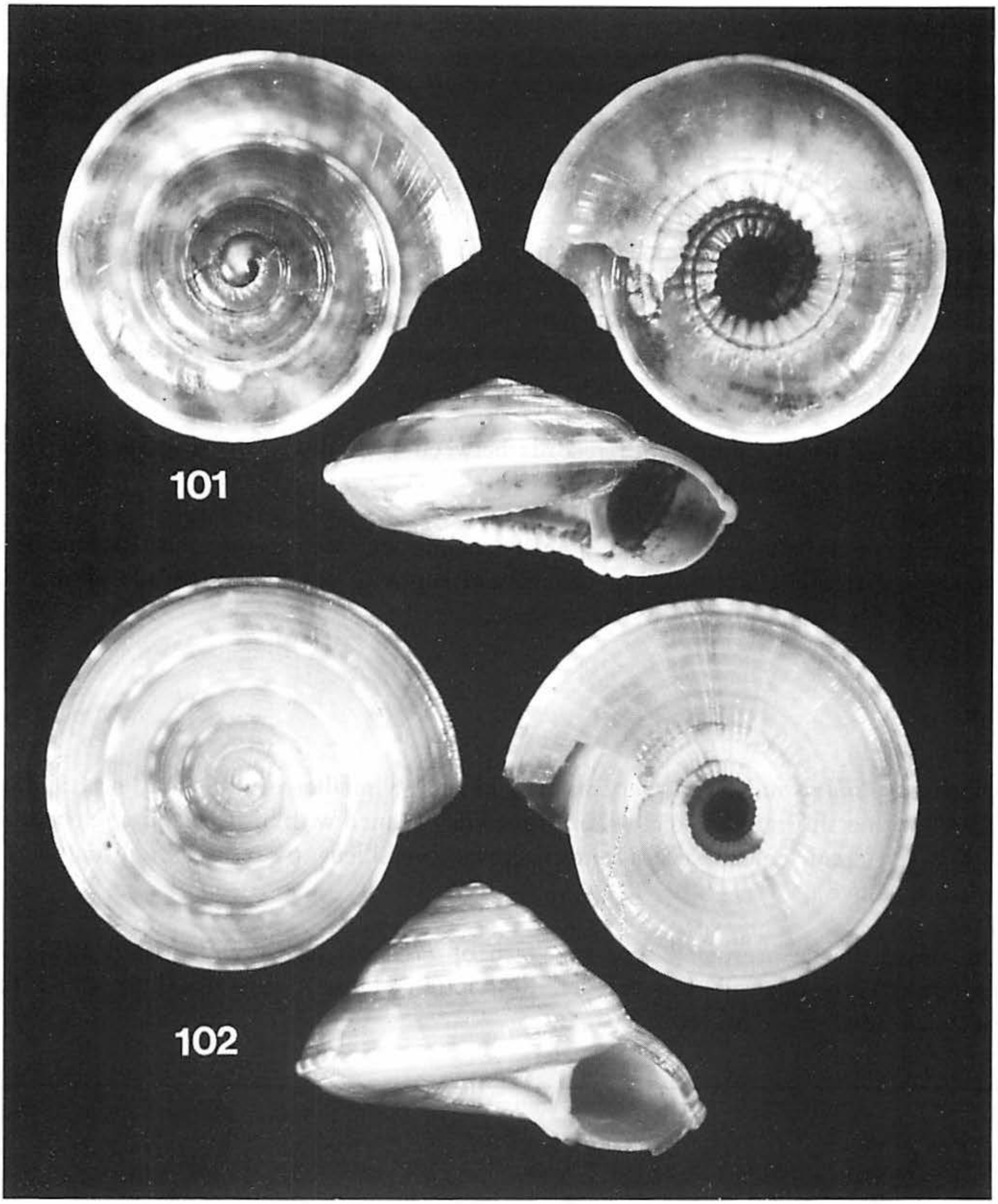
Diagnosis:

Small to medium-sized, moderately depressed to fairly high-spired cone-shaped shell with prominently angulated peripheral keel and wide umbilicus; whorls inflated, smooth and glossy; spiral sculpture restricted to three peripheral ribs (central one stronger and more prominent), and two ribs surrounding umbilicus (narrow proxumbical rib and wider umbilical crenae). Axially flamed or mottled in shades of brown, usually lighter colored on periphery; umbilical crenae always lighter colored. Protoconch diameter 1.46–1.74 mm; with very long (> 0.36), rounded anal keel; usually brown with white spot in center of last whorl.

Description:

Teleoconch: small to medium-sized, diameter of specimens in collections usually 7–19 at 2 1/2 to 4 1/2 whorls. Shape: moderately depressed to fairly high-spired cone-shaped with prominently angulated peripheral keel, inflated whorls and wide umbilicus (UD ca. 30% of SD). Sculpture: as in *Psilaxis radiatus*, but with UC narrower and less nodose. Coloration: overall yellowish-brown, sometimes with lighter areas towards periphery, usually with weak darker spiral lines on MR- and BF-areas, reddish-brown band on SSR-area, and irregular darker flames on upper side (Fig.101); UC always lighter colored. – Protoconch (see Fig.97 and Pl.3): large to very large (1.46–1.74, $\bar{x}$ = 1.58), distinctly heterostrophic; with very long, rounded anal keel (0.36–0.50, $\bar{x}$ = 0.42; see Fig.99); usually brown with white spot in center, often with a darkened spot at each end and indenting the white mark; without brown line along anal keel (see ROBERTSON, 1970: 67, fig.2). – Periostracum and Operculum: as described for genus. – Radula: five-toothed taenioglossate (2-1-2); rachidian with strong central cusp flanked on each side by a filiform cusp; inner marginal tooth with three, shorter outer marginal tooth with 4–5 long, filiform cusps (CLIMO, 1975: 282, fig.4A). – Anatomy: gross anatomy, especially buccal apparatus, described by CLIMO (1975: 282 ff.) [but see corrections by HASZPRUNAR, 1985b: 29].

Reproduction and larval development (see Pl.3 Figs.B-F): TAYLOR (1975: 62) described Hawaiian *Ps. oxytropis* veligers: four-lobed velum, edged with brillant red-orange



Figs. 101, 102. *Psilaxis oxytropis* (A. ADAMS, 1855). Fig. 101: possible type specimen of *Philippia oxytropis*; BMNH 1980127; SD = 10.3. Fig. 102: holotype of *Philippia manifesta* IREDALE, 1931; New South Wales, Australia; AMS 57775; SD = 18.3.

suffusion; velar lobes elongate; ingested during metamorphosis, later appearing red-orange in digestive gland. – Cephalic area: white; cephalic tentacles long, tapered, white. – Foot: white; propodium deeply cleft; mesopodial region expanded laterally; metapodial margin broadly rounded. – Viscera: digestive gland white, granular with vitreous beads; an opaque contractile white area posterior to a large black area. –

Months found in plankton: greatest abundance in March through September; sporadically occurring throughout remaining months. SCHELTEMA & WILLIAMS (1983: 547, figs.1B-C, 2A, 4) found larvae, measuring 1.50–1.78 ($\bar{x}$ = 1.70), in samples from the central Pacific Ocean.

Geographical distribution (see Fig.103): Subtropical. Known from western Indian Ocean and western to central Pacific. SCHELTEMA & WILLIAMS (1983: 549, fig.4) did not find larvae of this species between 20°N and 20°S latitude in the central Pacific. ROBERTSON (1970: 69, fig.5) knew *Ps. oxytropis* only from the western to central Pacific, with the exception of a "disjunct population" at the northern end of the Red Sea. Additional populations are now known from the southwestern Indian Ocean and Australia.

Habitat: Sublittoral (most depth records between 15 and 220 m), live records from 20–85 m, sandy substrates.

Habits/feeding behavior: Probably feeds mainly on hermatypic coral polyps (see ROBERTSON et al., 1970: 60), but juveniles in captivity are known to accept the sea anemone *Aiptasia* as food (TAYLOR, 1975).

Discussion:

Sympatric *Psilaxis radiatus* is very similar, but has a smaller protoconch (< 1.54; see Fig.97) with a shorter anal keel (<0.36; see Fig.99) lined with brown, and a teleoconch with a different color pattern and narrower umbilicus (see discussion under *Ps. radiatus*, above).

The status of the presumed type specimen of *Philippia oxytropis* (BMNH 1980127; see Fig.101) is unclear; the original description states a type locality, while the specimen label says "no loc."

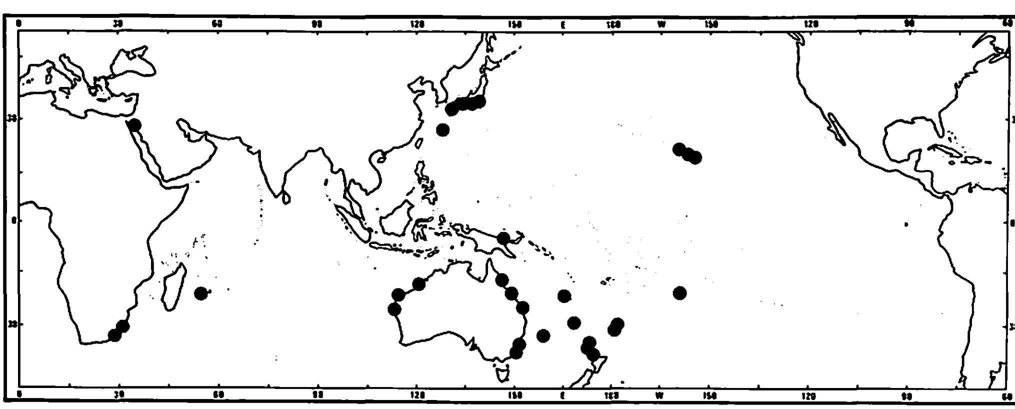


Fig. 103. Geographical distribution of *Psilaxis oxytropis*.

Genus *Discotectonica* MARWICK, 1931

Discotectonica MARWICK, 1931: 101; introduced as subgenus of *Architectonica*. Type species by original designation: *Architectonica balcombensis* FINLAY, 1927 (*nomen novum* for *Solarium acutum* TENISON-WOODS, 1879, not *Solarium acutum* CONRAD in WAILES, 1854); Middle-Miocene, Australia.

Synonyms:

Acutitectonica HABE, 1961: Appendix p.10. Type species by monotypy: *Solarium acutissimum* SOWERBY, 1914; Recent, Indo-Pacific.

Russetia GARRARD, 1961: 23. Type species by monotypy: *Russetia dilaniatus* GARRARD, 1961 [= *Discotectonica acutissima*].

Description (Fig.104):

Teleoconch: shell small to very large (usually 6–45 mm), depressed cone-shaped; umbilicus always open, wide to extremely wide (26–47% of shell diameter); whorls somewhat bulging, on either side of the peripheral keel distinctly concave; both sides usually with numerous spiral ribs or threads; juvenile whorls usually with distinct subsutural rib, 5–7 spiral ribs and distinct upper peripheral rib above the peripheral keel; later whorls with 6–10 spiral ribs between subsutural rib and upper peripheral rib (SSR and UPR then hardly stronger than other spiral ribs); 0–4 narrow spiral threads between UPR and keel-forming lower peripheral rib; spiral ribs nodose or almost smooth; upper point of whorl attachment at or below center of keel-forming rib; base: concave area near peripheral keel with 4–6 fine spiral ribs; convex basal area with about 10 spiral ribs, increasing in width towards umbilicus; 2–4 broad spiral ribs surrounding umbilicus, innermost of which (UC) broadest and flattened; umbilical wall with growth lines, without spiral ribs; coloration a diffuse yellowish-tan, with indistinct axial flames, occasionally also with regular white-brown fleck pattern on peripheral keel; base in most cases lighter, innermost basal rib (UC) always light. *Protoconch:* small to medium-sized (ca. 0.6–1.0), weakly heterostrophic, without anal keel. *Radula:* cuticularized, large rod-like structure with five rows of cusped tooth-like appendages instead of true radula. *Operculum:* horny, roundly and later (due to asymmetrically broad last whorl) ovate ear-shaped, flat with (often callously reinforced) peg-like projection on body side.

Discussion:

ROBERTSON (*in* MARCHE-MARCHAD, 1969: 486) first synonymized *Acutitectonica* with *Discotectonica*. MERRILL & BOSS (1984) separated the two nominal genera again, and reinstated the name *Acutitectonica* for the species here under consideration. Their evaluation of the type species of *Discotectonica* (*Solarium acutum* TENISON-WOODS, 1879; a preoccupied name subsequently replaced by *Architectonica balcombensis* FINLAY, 1927) was based on a poor original line drawing (TENISON-WOODS, 1879b: pl.21 fig.11).

For the lost type specimen of *Solarium acutum*, GARRARD (1977: 520, pl.10 figs.7–9) designated a neotype (see also BIELER, 1985a: pl.3 fig.12). The neotype designation is

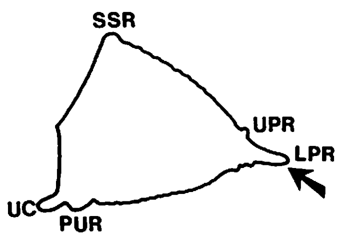


Fig. 104. Schematic representation of placement of major spiral ribs in *Discotectonica*, apertural aspect. Arrow shows point of attachment of next whorl. Sketch approximates condition in type species, for intrageneric variation see text.

in agreement with the usage of the species name by other authors (e.g., HARRIS, 1897: 244, pl.7 figs.6a-c). MERRILL & BOSS (1984: 337, text-fig.1c) compared the original figure of *S. acutum* with a small specimen of what they called "*Acutitectonica lepida* (BAYER 1941)," to illustrate the "structure of the aperture of a typical *Acutitectonica*" [The species originally described as *Philippia lepida* BAYER, 1942, is a member of another genus, subsequently introduced as *Basisulcata* by MELONE & TAVIANI, 1985]. The differences found by MERRILL & BOSS prompted the authors to reject GARRARD's neotype designation and to a renewed separation between *Acutitectonica* and *Discotectonica*. It was overlooked, however, that while juvenile *Basisulcata* (as well as *Architectonica* and *Psilaxis*) specimens do show a more or less convex shell base and are thus different from the *acutum* original, juvenile *Discotectonica* shells display concave outer base areas. The difference in shell shape stressed by MERRILL & BOSS (1984) between the juvenile *acutum* of TENISON-WOODS' (greatly depressed) and GARRARD's adult *acutum/balcombensis* neotype (depressed cone-shaped) is explained by the ontogenetic change in shell shape typical for this genus.

The neotype designation by GARRARD (1977) was made in agreement with ICZN Article 75; according to ICZN (1985) Article 75(e) it has priority over all later designations. *Discotectonica* MARWICK, 1931, is here maintained as senior subjective synonym of *Acutitectonica* HABE, 1961, and *Russetia* GARRARD, 1961. For additional description and discussion of this genus see BIELER (1985a: 241–242).

Discotectonica acutissima (SOWERBY, 1914)
Figs.105–107

*1914 *Solarium acutissimum* SOWERBY (III), Ann. Mag. nat. Hist., (8)*14*: 36, pl.2 fig.9.
1929 *Architectonica acutissima*, - KURODA, Venus, *1*(4): 126.
1940 *Solarium acutissimum* (incertae sedis), - BAYER, Zool. Meded., *22*: 254.
1952 *Discotectonica acutissima*, - KURODA & HABE, Check list bibl. Rec. mar. Moll. Jap.: 53.
1952 *Discotectonica acutissima*, - HABE, Illus. cat. Jap. shells, *1*(18): 132, fig. 9 [rodlike structure].
1960 *Architectonica acutissima*, - AZUMA, Cat. shell-bear. Moll. Okinoshima: 13.
1961 *Acutitectonica acutissima*, - HABE, Col. illus. shells Japan, (*II*): 30, Appendix p.10, pl.13 fig.21.
*1961 *Russetia dilaniatus* GARRARD, J. malac. Soc. Austr., *1*(5): 23, pl.1 figs.11a-b.
1963 *Architectonica (Acutitectonica) acutissima*, - SHIKAMA & HORIKOSHI, Select. shells world: 30, pl.22 fig.2.
1964 *Acutitectonica acutissima*, - HABE, Shells w. Pac. col., *2*: 46, pl.13 fig.21.
1967 *Acutitectonica acutissima*, - HABE & KOSUGE, Stand. illus. book Jap. shells: 106, pl.41 fig.22.
1971 *Acutitectonica acutissima*, - KURODA et al., Sea shells Sagami Bay: 262, pl.61 fig.1.

1973 *Acutitectonica acutissima*, - HIGO, Cat. moll. fauna Jap. Ids.: 228.
1975 *Acutitectonica acutissima*, - MELONE, Conchiglie, *11*(7-8): 165, pl.1 figs.1-6 [shell, operculum, rodlike structure], pl.2 figs.1-5 [rodlike structure].
1977 *Architectonica (Acutitectonica) acutissima*, - LAN, Bull. malac. Soc. China, *4*: 41, fig.41.
1977 *Architectonica (Discotectonica) acutissima*, - GARRARD, Rec. Austr. Mus., *31*(13): 509, fig.6 [operculum], p.517, pl.1 figs.16-18, pl.2 figs.19-21.
1979 *Acutitectonica acutissima*, - MATSUMOTO, Moll. shells Mie Pref.: 22.
1980 *Acutitectonica acutissima*, - LAN, Rare shells Taiwan: 97, figs.98, 98a-b.
1983 *Acutitectonica acutissima*, - OKUTANI, KAWAMURA coll.: 11, pl.41 figs.8-9.
1984 *Acutitectonica acutissima*, - MERRILL & BOSS, Occas. Pap. Moll., *4*(65): 335, pl.44 figs.1-3.
1984 *Acutitectonica acutissima*, - BOSS & MERRILL, 1984b, Occas. Pap. Moll., *4*(66): 360 ff., pl.54 figs.1-3 [after MELONE, 1975], pl.58 fig.2 [after HABE, 1952] [rodlike structure].
1985 *Discotectonica acutissima*, - BIELER, 1985a, Arch. Moll., *115*(4/6): 241 ff., pl.3 fig.13 [holotype], fig.14 [holotype of *R. dilaniatus*].
1986 *Discotectonica acutissima*, - SPRINGSTEEN & LEOBRERA, Shells Philippines: 26, pl.2 fig.11.
1986 *Acutitectonica acutissima*, - LAI, Mar. gastr. Taiwan, *1*: 38, fig.1.

Type measurements: Holotype of *S. acutissimum*: SD = 46.6, H = 14.0, PD = 0.80, Tw = 6 3/4+, UD = 15.3. Holotype of *R. dilaniatus*: SD = 43.0 [damaged], H = 17.7, PD = 0.80, Tw = 7 1/8, UD = 12.7.

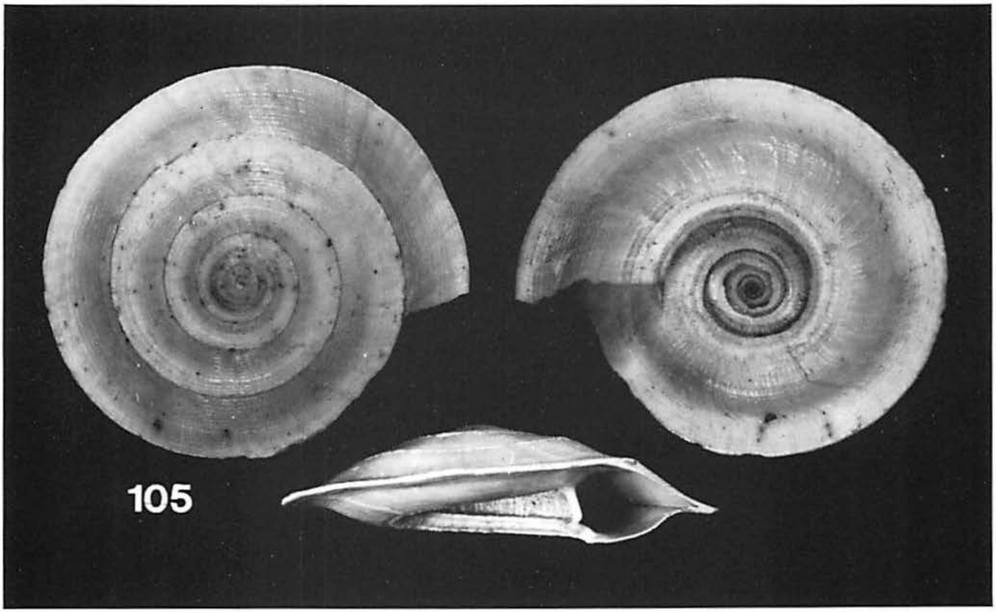


Fig. 105. *Discotectonica acutissima* (SOWERBY, 1914); holotype of *Solarium acutissimum*; Japan; BMNH 1915.1.6.100; SD = 46.6.

Type localities: *S. acutissimum*: "Kii, Japan." *R. dilaniatus*: "Trawled in 160 fathoms east of Newcastle" [Australia].

Etymology: *acutissimus-a-um* [adjective]; Latin: superlative of *acutus-a-um*; sharp, pointed.

Material studied: 103 specimens (AMNH, AMS, ANSP, BMNH, DMNH, FLMNH, FMNH, IRSNB, LACM, MCZ, MNHNP, NMP, NMW, RNHL, SMF, USNM, Coll. ALF), including holoype of *S. acutissimum* (BMNH 1915.1.6.100) and holotype of *R. dilaniatus* (AMS C.63345).

Diagnosis:

Medium-sized to very large, discoid, "sand-dollar-like" shell with inflated whorls, concave zones on both sides of very prominent peripheral keel, widely open umbilicus and fine sculpture of numerous flattened, almost smooth spiral ribs; ribs surrounding umbilicus widest and almost plate-like. Overall yellowish or off-white, with irregular reddish-brown axial flames on upper side (fresh specimens with one elongated dark-brown blotch in upper part of aperture). Protoconch diameter 0.76–0.88 mm; weakly heterostrophic, without anal keel.

Description:

Teleoconch: medium-sized to very large, diameter of specimens in collections usually 25–45 at 5 3/4 to 7 3/8 whorls. Shape: very flat, discoid, with somewhat inflated whorls; concave zones on both sides of very prominent peripheral keel; umbilicus

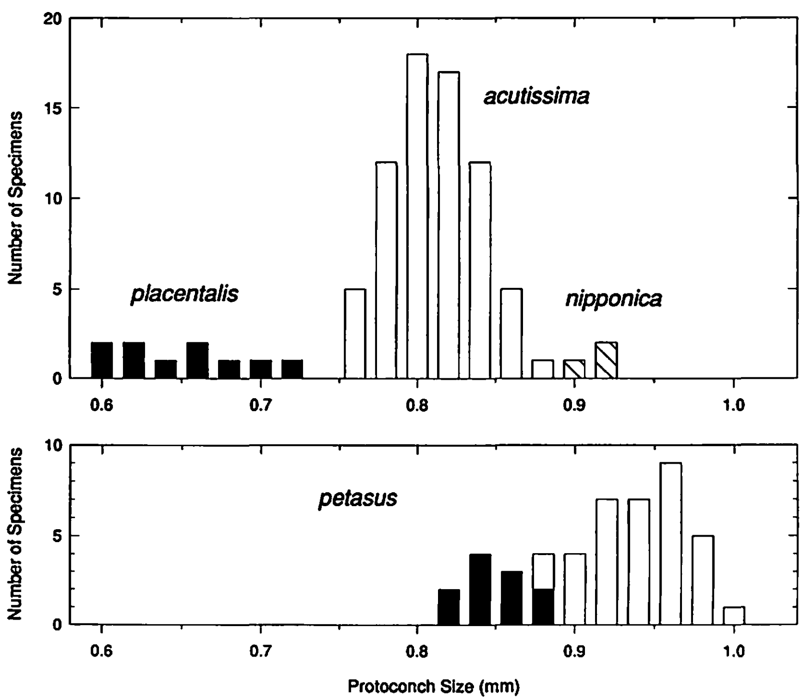


Fig. 106. Histograms of measured protoconch size. *Discotectonica placentalis* (n = 10, x̄ = 0.65, sd = 0.04), *D. acutissima* (n = 70, x̄ = 0.81, sd = 0.03), *D. nipponica* (n = 3, x̄ = 0.92), and *D. petasus* (Australia [black]: n = 11, x̄ = 0.85, sd = 0.02; western Indian Ocean [white]: n = 35, x̄ = 0.94, sd = 0.30; total: n = 46, x̄ = 0.92, sd = 0.05).

widely open (UD ca. 27–34% of SD). Sculpture: Upper side: on early whorls SSR ± distinctly separated and MR-area with 5–7 spiral ribs; on later whorls 8–10 spiral ribs in MR-area, SSR hardly stronger than MR; Periphery: UPR initially ± strong, on later whorls hardly stronger than MR; almost smooth LPR forms prominent keel, also serving as upper point of whorl attachment; 3–4 additional fine spiral threads between UPR and LPR; no distinct IPR; Base: concave area next to peripheral keel with ca. 4 fine spiral threads; BF with ca. 10 spiral ribs (increasing in width towards umbilicus), followed by 2–4 wider spiral ribs bearing flattened nodules; innermost rib (UC) very wide with almost flattened crenae; columellar wall forming almost straight inner lip; with one deep groove in UC overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration: overall yellowish or off-white, with very irregular reddish-brown axial flames on upper side including PR; base usually much lighter colored, with 1–2 spiral ribs surrounding umbilicus brownish; fresh specimens with 1 elongated dark-brown blotch in upper part of aperture. – Protoconch (see Fig.106): small (0.76–0.88, $\bar{x}$ = 0.81), weakly heterostrophic, without anal keel; yellowish. – Operculum: as described for genus. – Radula: replaced by rod-like structure (see below). – Anatomy: buccal apparatus (as described for genus) with long (about 1/3 of SD) rod-like structure bearing five rows of cusped tooth-like appendages (see figs. in HABE, 1952: 132, fig.9; MELONE, 1975: 165 ff., pl.1 figs.5–6, pl.2 figs.1–5; BOSS & MERRILL, 1984b: 360, pl.54 figs.1–3 [after MELONE, 1975], pl.58 fig.2 [after HABE, 1952]).

Geographical distribution (Fig.107): Subtropical and tropical western Pacific. North Australian record in need of verification.

Habitat: Sublittoral (most depth records between 50 and 200 m), live records from 80–190 m, sandy substrates.

Discussion:

Discotectonica acutissima can hardly be confused with any other species; the spiral sculpture of each of its closest congeners, *D. nipponica*, *D. petasus* (see below), and *D. discus* (PHILIPPI, 1844) of the Atlantic Ocean, is much coarser.

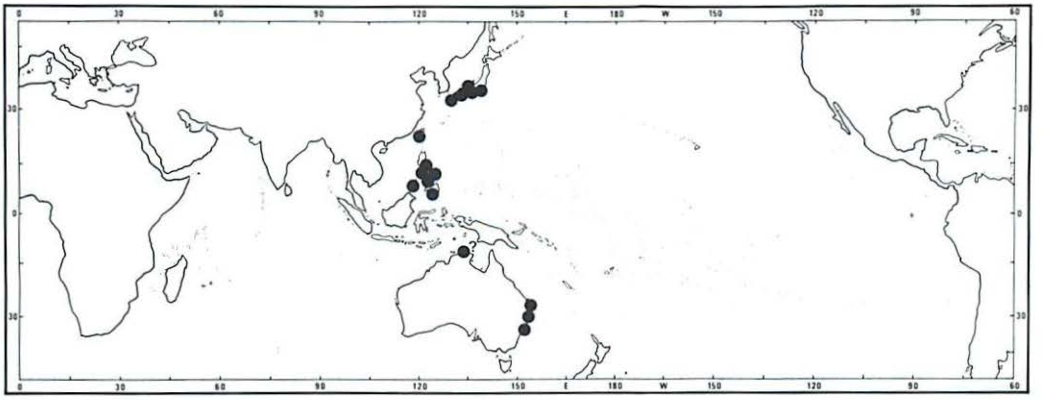


Fig. 107. Geographical distribution of *Discotectonica acutissima*.

Russetia dilaniatus was described as type species of a new monotypic genus by GARRARD (1961: 23). It was based on a single, worn specimen of *D. acutissima* (see GARRARD, 1977: 517; BIELER, 1985a: pl.3 fig.14).

Discotectonica petasus (TOMLIN, 1928)

Figs.106, 108–110

*1928 *Heliacus petasus* TOMLIN, Ann. S. Afr. Mus., *25*(2): 334, pl.26 fig.4.
1931 *Heliacus petasus*, – TOMLIN, Ann. Natal Mus., *6*(3): 433.
1948 *Torinia petasus*, – BAYER, Zool. Verh., *4*: 30.
1963 *Heliacus petasus*, – BARNARD, 1963b, Ann. S. Afr. Mus., *47*(1): 162.
1973 *Heliacus petasus*, – KENSLEY, Sea-shells s. Afr.: 76, fig.255.
1974 *Heliacus petasus*, – BARNARD, Ann. S. Afr. Mus., *47*(5): 711.
1977 *Architectonica (Discotectonica) kuroharai*, – GARRARD, Rec. Austr. Mus., *31*(13): 509, fig.7 [operculum], p.518, pl.1 figs.10–12 [non *A. kuroharai* KURODA & HABE in HABE, 1961).
1978 *Architectonica acutissima*, – HINTON, Guide Austr. shells: pl.10, fig.6 [non *Solarium acutissimum* SOWERBY, 1914].
1983 *Heliacus petasus*, – GILES & GOSLINER, Ann. S. Afr. Mus., *92*(1): 15.
1984 *Acutitectonica kuroharai*, – MERRILL & BOSS, Occas. Pap. Moll., *4*(65): 335.
1985 *Discotectonica petasus*, – BIELER, 1985a, Arch. Moll., *115*(4/6): 241.

Type measurements (holotype): SD = 16.1, H = 6.0, PD = 0.96, Tw = 5 3/4, UD = 6.9.

Type locality: "Scottburgh, dredged in 92 fathoms" [168 m; Republic of South Africa].

Etymology: *petasus* [noun in apposition]; Latin: a broad brimmed, large, round traveller's hat.

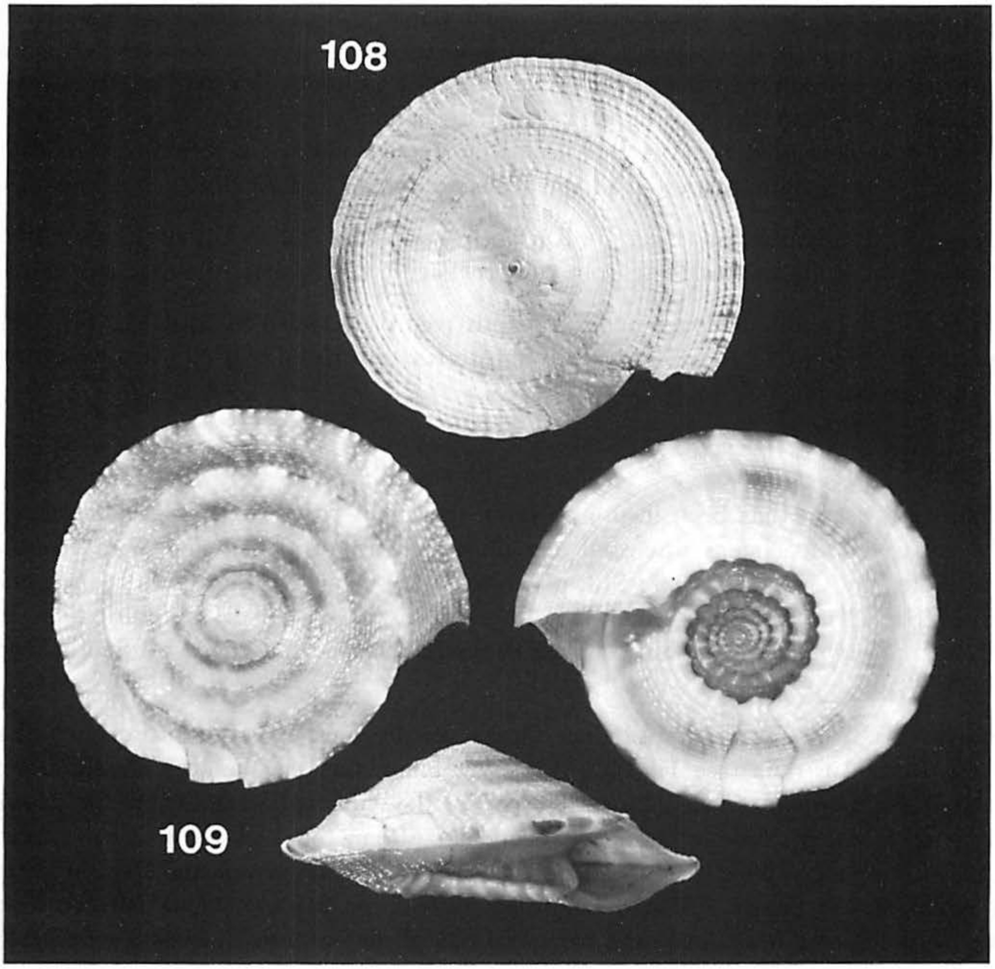
Material studied: 45 specimens (AMNH, AMS, FMNH, MNHNP, NMP, SAM, SMF); including holotype (SAM A3579).

Diagnosis:

Medium-sized to large, depressed cone-shaped shell with somewhat inflated whorls, concave zones on both sides of very prominent peripheral keel, very wide to extremely wide umbilicus and sculpture of finely granulated spiral ribs; upper side with weak subsutural rib and 3–5 ribs in midrib-area; upper peripheral rib slightly stronger than midribs and less granose than keel-forming lower peripheral rib; peripheral keel often somewhat undulating; base with 10–15 spiral ribs, the innermost of which (umbilical crenae) with fairly strong nodules. Overall light-tan or off-white color; fresh specimens with weakly defined brown axial flames on upper side which form distinct blotches, 2–3 nodules wide, on periphery. Protoconch diameter 0.82–1.00 mm, weakly heterostrophic, without anal keel.

Description:

Teleoconch: medium-sized to large, diameter of specimens in collections usually 15–27 at 5 to 7 1/4 whorls. Shape: depressed cone-shaped, with somewhat inflated whorls and concave zones on both sides of very prominent peripheral keel; umbilicus very



Figs. 108, 109. *Discotectonica petasus* (Tomlin, 1928). Fig. 108: holotype of *Heliacus petasus*; South Africa; SAM A3579; SD = 16.1. Fig. 109 (three aspects): specimen from Queensland, Australia; AMNH 182020; SD = 22.0.

wide to extremely wide (UD ca. 35–47% of SD). Sculpture: Upper side: on early whorls SSR usually distinctly separated and MR-area with about three spiral ribs; on later whorls 4–5 spiral ribs in MR-area, SSR hardly stronger than MR; Periphery: UPR usually weak, somewhat stronger than MR; strong, irregularly nodulose LPR forms prominent keel, also serving as upper point of whorl attachment; peripheral keel often somewhat undulating (resulting in a wavy crest on upper side); 1–3 additional narrow spiral ribs between UPR and LPR; weak IPR only distinct on early whorls; Base: with 10–15 spiral ribs, increasing in width towards umbilicus; innermost (UC) wide with fairly strong crenae; columellar wall forming almost straight inner lip, with one deep groove in UC overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration: overall light tan or off-white; upper side of fresh specimens with weakly defined brown axial flames which are darker towards the periphery and form distinct blotches, 2-3 nodules wide, on LPR; area between these blotches lighter colored than surrounding area; base without color pattern, UC lightest colored. - Protoconch (see Fig.106): small to medium-sized (0.82–1.00, $\bar{x}$ = 0.92), weakly heterostrophic, without anal keel; whitish with outer corner next to varix often brown. - Operculum: as described for genus. - Radula and Anatomy: not known.

Geographical distribution (Fig.110): Known from western Indian Ocean (South Africa, Réunion, Isles Glorieuses) and from western Pacific (Australia).

Habitat: Sublittoral to upper bathyal (depth records between 80 and 625 m), fresh specimens between 80 and 150 m, sandy substrates; upper side of shell often overgrown by bryozoans.

Discussion:

The name *petasus* has been in use only for specimens from South Africa. However, the Australian specimens discussed and illustrated as "*Architectonica (Discotectonica) kuroharai*" by GARRARD (1977: 518, pl.1 figs.10–12) belong to this species (specimens in AMS, vidi). Australian shells (Fig.109) usually have coarser sculpture than the African holotype (Fig.108), but comparable material has been dredged off South Africa (NMP, vidi).

Individuals from the western Indian Ocean usually have a larger protoconch than those from Australia (see Fig.106). A similar bimodality can be seen in the closely related *Discotectonica discus* (PHILIPPI, 1844) of the Atlantic Ocean. There the eastern Atlantic specimens have a larger protoconch size than those of the western Atlantic (BIELER, unpubl.). *Discotectonica discus* (of which *Solarium peracutum* DALL, 1889, is a synonym; see BIELER, 1985a: 242) differs in teleoconch sculpture: usually only one midrib is strongly developed, and the spiral ribs of the basal field are at least partially fused.

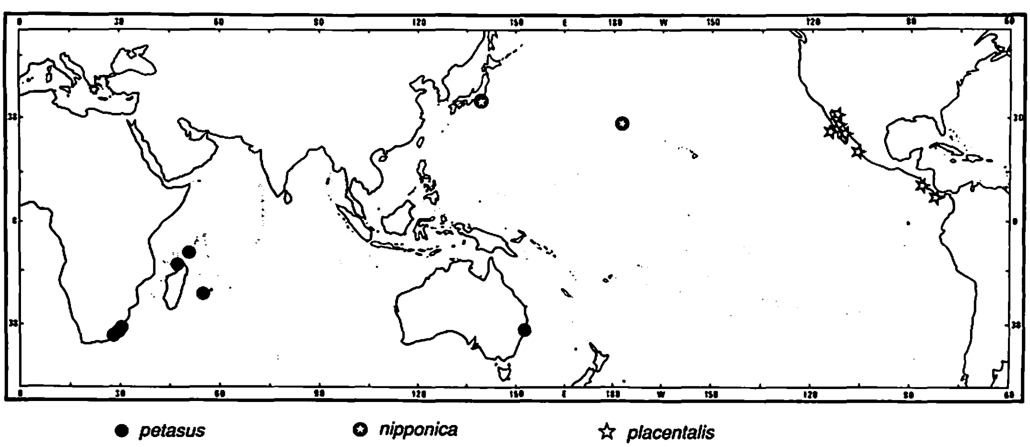


Fig. 110. Geographical distribution of *Discotectonica petasus*, *D. nipponica* and *D. placentalis*.

Discotectonica nipponica (KURODA & HABE *in* KURODA, HABE & OYAMA, 1971)
Figs.106, 110–112

*1971 *Solariaxis nipponicus* KURODA & HABE *in* KURODA et al., Sea shells Sagami Bay: 262, pl.61 fig.12.
*1979 *Solariaxis granulata* KOSUGE, Bull. Inst. Malac. Tokyo, *1*(2): 34, pl.5 figs.13–14.
*?1979 *Solariaxis nasui* KOSUGE, Bull. Inst. Malac. Tokyo, *1*(2): 33, pl.5 figs.15–16.
1979 *Solariaxis nipponica*, - KOSUGE, Bull. Inst. Malac. Tokyo, *1*(2): 34.

Type measurements: Holotype of *S. nipponicus*: SD = 9.0, H = 4.2 [after KURODA & HABE]. Paratype of *S. nipponicus*: SD = 6.1, H = 3.5 [after KURODA & HABE], PD = 0.92, Tw = 3 1/8 [from photograph, courtesy Prof. HABE]. Holotype of *S. granulata*: SD = 16.0, H = 6.4, PD = 0.90, Tw = 5 1/4, UD = 4.6. Holotype of *S. nasui*: SD = 16.1, H = 6.6, PD = 0.92, Tw = 5 3/8–, UD = 5.7.

Type localities: *S. nipponicus*: "Sagami Bay (alive)" [Honshu, Japan], *S. granulata*: "Off Midway Islands (29°48.8' Lat.(N), 179°00.5' Long.(E)) at the depth of 265m"; *S. nasui*: "Off Midway Island (32°01.8' Lat.(N), 173°06.0' Long.(E)) at the depth of 365m."

Etymology: *nipponicus-a-um* [adjective]; Japanese.

Material studied: Holotype of *S. granulata* (IMT-79-23), holotype of *S. nasui* (IMT-79-22), and photograph of paratype of *S. nipponicus* (courtesy Prof. Habe; type material not available on loan, BLIHT). According to KOSUGE (1979: 34), a paratype of *S. granulata* (SD = 14.3, H = 5.0) was deposited in USNM; it has not been registered as received at that collection.

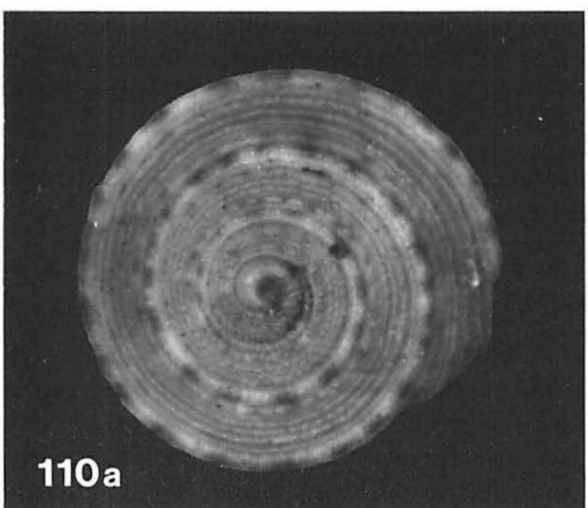


Fig. 110a. *Discotectonica nipponica* (KURODA & HABE *in* KURODA, HABE & OYAMA, 1971). Paratype of *Solariaxis nipponicus*; BLIHT, photograph courtesy Prof. T. HABE).

Diagnosis:

Small to medium-sized, depressed cone-shaped shell with inflated whorls, prominent peripheral keel, widely open umbilicus and sculpture of granose spiral ribs; upper side with distinctly separated subsutural rib and three midribs; upper peripheral rib wider than midribs, less nodose than keel-forming lower peripheral rib; base with two spiral ribs between lower peripheral rib and infraperipheral rib, and up to nine between infraperipheral rib and umbilicus; innermost rib (umbilical crenae) surrounding umbilicus very wide and strongly nodose. Upper side overall orange-yellow to light tan, lower peripheral rib with weak, upper peripheral rib with distinct pattern of orange-brown blotches; base off-white. Protoconch diameter 0.90–0.92 mm, weakly heterostrophic, without anal keel.

Description:

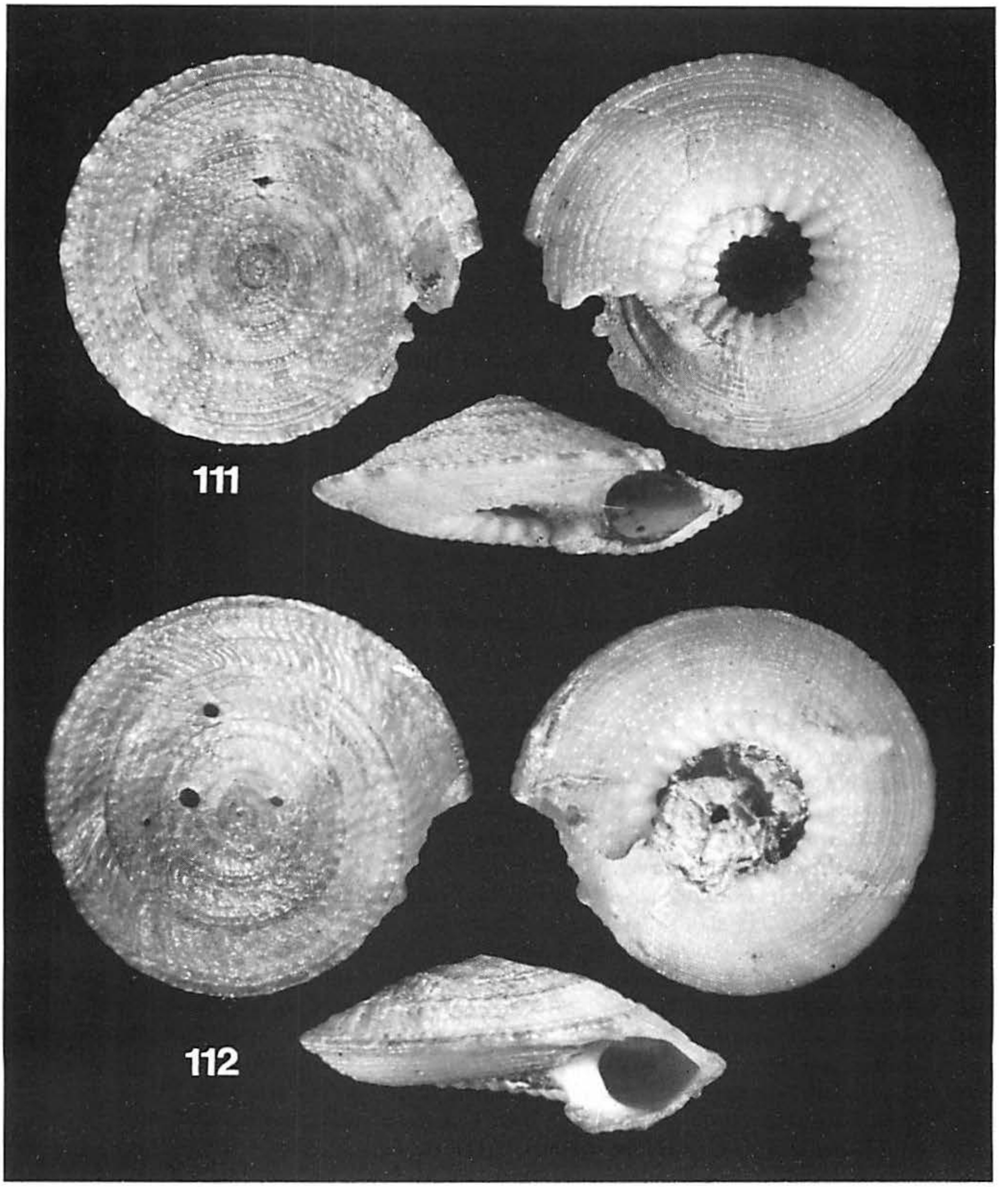
Teleoconch: small to medium-sized, diameter 6.1–16.1 at 3 1/8 to 5 3/8– whorls. Shape: depressed cone-shaped with inflated whorls and prominent peripheral keel; umbilicus widely open (UD ca. 29% of SD). Sculpture: Upper side: SSR after first whorl distinctly separated, hardly stronger than MR; MR-area on first whorl almost smooth, thereafter divided into three MR; Periphery: UPR somewhat prominent, wider than MR; ± strongly nodose LPR forms prominent keel, also serving as upper point of whorl attachment; Base: two additional spiral ribs between slightly stronger IPR and keel-forming LPR; up to nine spiral ribs between IPR and umbilicus, increasing in width towards umbilicus; innermost rib (UC) very wide, with strong nodules; columellar wall forming almost straight inner lip, with one deep groove in UC overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration: upper side orange-yellow to light tan; LPR with weak, UPR with distinct pattern pattern of orange-brown blotches (about 2 nodules wide); base off-white. – Protoconch (Fig.106): medium-sized (0.90–0.92), weakly heterostrophic, without anal keel; light-brown with darker outer corner next to varix. – Periostracum, Operculum, Radula and Anatomy: not known.

Geographical distribution (see Fig.110): Known from western and central Pacific (Midway Islands and Honshu, Japan).

Habitat: Sublittoral to upper bathyal (depth records between 50 and 365 m).

Discussion:

Discotectonica nipponica is characterized by its distinctive, regular, sparsely ribbed spiral sculpture of the upper side. The similar *D. placentalis* of the eastern Pacific (see below) has a much smaller protoconch size (Fig.106), wider midribs and fused areas on the shell base. It also differs by lacking the additional spiral rib between the upper and lower peripheral ribs on the early whorls, which is present in *D. nipponica*. Small *D. petasus* specimens, superficially similar, can be distinguished by the larger number of basal ribs of that species. See also *Solatisonax? orba* n.sp. (below).



Figs. 111, 112. *Discotectonica nipponica* (KURODA & HABE *in* KURODA, HABE & OYAMA, 1971). Fig. 111: holotype of *Solariaxis granulata* KOSUGE, 1979; Midway Islands; IMT-79-23; SD = 16.0. Fig. 112: aberrant specimen; holotype of *Solariaxis nasui* KOSUGE, 1979; Midway Islands; IMT-79-22; SD = 16.1.

With their original description of *S. nipponicus*, KURODA & HABE (1971: 262, pl.61 fig.12) published a small color photograph of the upper side of the holotype that is not suitable for identification purposes. For this monograph, photographs representing the holotype were received (courtesy Prof. HABE; one here reproduced in Fig.110a). However, according to the scale shown with the shell on some of the photographs, the greatest diameter is only 6.1 mm, which is the measurement originally given for the single paratype specimen.

KOSUGE (1979: 34) described *Solariaxis granulata*, based on two specimens from the Midway Islands (see Fig.111). He stated that it differed "from *S. nipponica* KURODA & HABE in its color pattern and basal sculpture, and also in its brim-like periphery of the shell." Judged from the known range of variability in related species, e.g., in *D. petasus*, these seem to be individual rather than specific differences. The two nominal species are here synonymized.

In the same publication, KOSUGE (1979: 33) described *S. nasui*. The single known specimen (see Fig.112) shows signs of aberrant shell growth, which in architectonicids often occurs after a major shell break: the teleoconch underwent several repairs during the first three whorls; the whorls, especially on the upper side, are unusually convex; coloration is diffuse, and the spiral ribs on the upper side are partly fused. The holotype of this nominal species (IMT-79-22) is most likely an aberrant specimen of *D. nipponica*.

Discotectonica placentalis (HINDS, 1844)
Figs.106, 110, 113

*1844 *Solarium placentale* HINDS, 1844b, Proc. zool. Soc. Lond., *1844*: 22.
1844–45 *Solarium placentale*, - HINDS, 1844c–1945, Zool. voy. SULPHUR, *3*: 50; *2*: pl.14 figs.5–6.
1844 *Solarium placentale*, - HINDS, 1844d, Ann. Mag. nat. Hist., *14*: 437.
1853 *Solarium placentale*, - PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 18, pl.3 fig.6 [after HINDS, 1844c].
1863 *Solarium (Architectonica) placentula* [sic], - HANLEY, Thes. conch., *3*: 235, pl.252 figs.23–24.
1864 *Solarium placentula* [sic], - REEVE, Conch. icon., *15*: no.13, pl.3 fig.13.
1887 *Solarium (Solarium) placentula* [sic], - MARSHALL, Man. conch., *9*: 13, pl.4 figs.51–52 [after HINDS, 1844c].
1887 *Solarium placentulum* [sic], - PAETEL, Cat. Conch.-Slg., *1*: 287.
1940 *Solarium placentale*, - BAYER [in part], Zool. Meded., *22*: 248.
1964 *Architectonica placentalis*, - PARKER, Mem. mar. Geol. Gulf Calif. Symp., *3*: 349, 372, pl.5 fig.4.
1966 *Architectonica placentalis*, - KEEN, 1966a, Veliger, *8*(4): 269, pl.46 fig.5 [syntypes].
1971 *Architectonica (Discotectonica) placentalis*, - KEEN, Sea shells trop. w. Amer. (2nd ed.): 389, fig.426 ["top left, top right, below" = syntypes; "left, right" after HINDS, 1844c].
1974 *Architectonica (Discotectonica) placentalis*, - ABBOTT, Amer. seashells (2nd ed.): 97.
1976 *Discotectonica placentalis*, - ROBERTSON, 1976a, Bull. Amer. malac. Union, *1975*: 51.
1977 *Architectonica placentalis*, - HERTZ, Festivus, *9*(11): 80, fig.
1984 *Acutitectonica disca*, - BOSS & MERRILL, 1984b, [in part], Occas. Pap. Moll., *4*(66): pl.55 figs.1–4 [rodlike structure] [non *Solarium discus* PHILIPPI, 1844].

Type measurements (lectotype, here designated): SD = 15.8, H = 5.1, PD = 0.62, Tw = 4 7/8, UD = 5.3.

Type locality: "Bay of Magdalena, California; in seven fathoms, sand."

Etymology: *placentalis-e*; Latin [adjective]: shaped like a flat, round cake.

Material studied: 36 specimens (ANSP, BMNH, CAS, LACM, MCZ, MNHNP); including lectotype (BMNH 1874.12.11.200, ex Coll. TAYLOR) and 1 paralectotype (BMNH 1844.6.7.33, ex Coll. BELCHER).

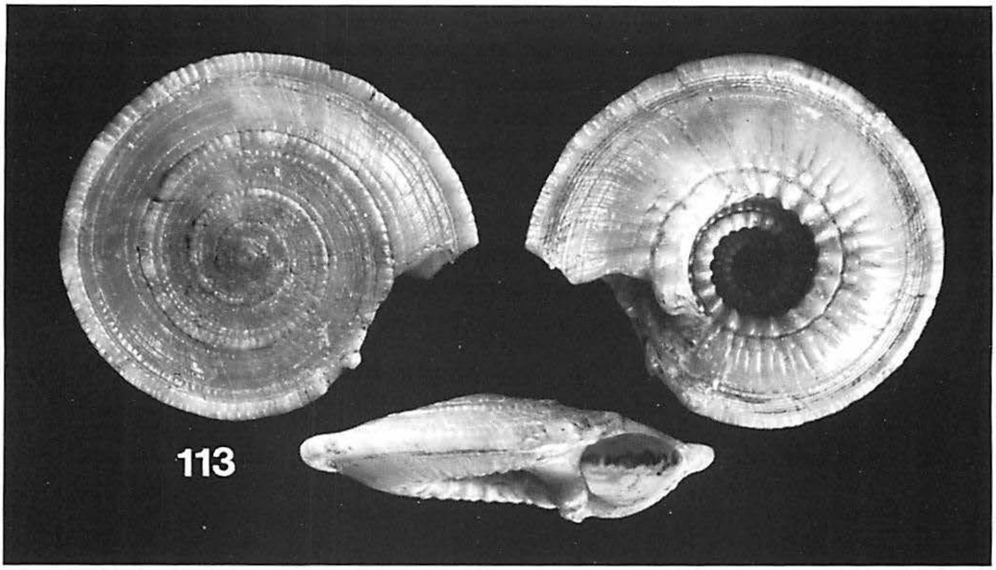


Fig. 113. *Discotectonica placentalis* (HINDS, 1844); lectotype of *Solarium placentale*; California; BMNH 1874.12.11.200; SD = 15.8.

Diagnosis:

Small to medium-sized, discoid shell with somewhat inflated whorls, concave zones on both sides of very prominent peripheral keel and widely open umbilicus; upper side with sculpture of distinctly separated subsutural rib and three flattened (often spirally subdivided) midribs; upper peripheral rib and much stronger, keel-forming lower peripheral rib granose; base with narrow spiral threads in infraperipheral rib area and two spiral ribs around umbilicus, the inner one (umbilical crenae) wider and with strong nodules; remainder of base smooth except for axial plications towards umbilicus. Fresh specimens brown, umbilical crenae lighter colored; peripheral ribs with dark brown blotches, 3–4 nodules wide. Protoconch diameter 0.60–0.72 mm; weakly heterostrophic, without anal keel.

Description:

Teleoconch: small to medium-sized, diameter of specimens in collections 9–15.8 at 4 to 5+ whorls. Shape: very flat, discoid, with somewhat inflated whorls; concave zones on both sides of very prominent peripheral keel; umbilicus widely open (UD ca. 26–34% of SD). Sculpture: Upper side: SSR distinctly separated; three flattened, ± smooth MR (sometimes, as in lectotype, one or several MR subdivided by spiral grooves); Periphery: UPR narrower but more prominent than MR; LPR set with ± regular nodules, forms strong, prominent keel, also serving as upper point of whorl attachment; one additional fine narrow spiral rib between UPR and LPR; Base: on both sides of weak IPR a few additional spiral threads; BF ± smooth, with axial folds (stronger towards umbilicus); 1–2 spiral ribs surrounding umbilicus, the inner one (UC) wider and with stronger nodules; columellar wall forming almost straight inner lip, with one deep groove in UC overhanging umbilicus; no spiral sculpture on umbilical side of wall. Coloration: fresh specimens brown on upper side; PR, especially LPR, with dark-brown blotches, ca. 3–4 nodules wide; blotches separated by distinctly lighter-colored zones on LPR, these zones partly extending onto base; base otherwise brown, with UC lighter colored. - Protoconch (see Fig.106): small (0.60–0.72, $\bar{x}$ = 0.65), weakly heterostrophic, without anal keel; light-brown. - Periostracum and Operculum: as described for genus. Radula: replaced by rod-like structure (see below). - Anatomy: buccal apparatus (as described for genus) with long (about 1/3 of SD) rod-like structure bearing rows of cusped, tooth-like appendages (see figs. in Boss & MERRILL, 1984b: pl.55 figs.1–4; as "*Acutitectonica disca*").

Geographical distribution (Fig.110): Only known from the eastern Pacific, from Mexico (Sonora and Baja California) to Panama.

Habitat: Sublittoral (depth records between 12 and 200 m), sandy substrates.

Discussion:

The Atlantic species *Discotectonica discus* (PHILIPPI, 1844) [synonym: *Solarium peracutum* DALL, 1889] is very similar, and several authors (e.g., E.A. SMITH, 1890: 281; BAYER, 1940: 248; MARCHE-MARCHAD, 1969: 481; MERRILL & BOSS, 1984: 335) have synonymized the two. However, the two forms can be distinguished by the following characters: in *D. discus* the midrib area is subequally divided into two ribs, the shell coloration is much lighter (yellowish), and the protoconch size is usually larger. The two are therefore here maintained as separate species; further study of this complex is necessary. *Solatisonax? orba* n.sp. (below) is the only other species known from the eastern Pacific with a similar shell shape and sculpture.

The larger of the two syntypes of *Solarium placentale* in the British Museum, which was figured by the original author (HINDS, 1844c: pl.14 figs.5–6; see KEEN, 1966a: 269), is here selected as lectotype (BMNH 1874.12.11.200, ex LOMBE TAYLOR Collection; see Fig.113).

Genus *Granosolarium* SACCO, 1892

Granosolarium SACCO, 1892: 59; introduced as subgenus of *Solarium* [= *Architectonica*]. Type species by original designation: *Solarium millegranum* LAMARCK, 1822; Tertiary, Italy.

Synonyms:

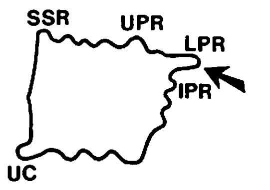
Solariaxis DALL, 1892: 323. Type species by original designation: *Solarium elaboratum* CONRAD, 1833; Middle-Eocene; Alabama, U.S.A.

Claraxis IREDALE, 1936: 327. Type species by monotypy: *Claraxis illustris* IREDALE, 1936 [= *Granosolarium asperum* HINDS, 1844]; Recent, Indo-Pacific.

Description (Fig.114):

Teleoconch: shell very small to large (usually 8–30 mm), depressed cone-shaped with sharp peripheral keel and very wide umbilicus (ca. 40% of shell diameter); whorls in

Fig. 114. Schematic representation of placement of major spiral ribs in *Granosolarium*, apertural aspect. Arrow shows point of attachment of next whorl. Sketch approximates condition in type species, for intrageneric variation see text.



larger specimens bulging, concave on either side of the peripheral keel; distinct axial growth marks on entire shell surface; upper (apical) side with four distinct, nodose spiral ribs and often finer threads between them, followed by a peripheral region of two stronger spiral ribs (UPR and LPR) with several interspersed threads; this peripheral area variously formed, in Recent species as part of the apical sculpture under formation of a concave area, with the LPR forming the peripheral keel; upper point of whorl attachment at peripheral keel; nodules of keel often produced into numerous narrow spines or few flattened teeth; base bulging, with numerous fine spiral ribs, increasing in width towards the umbilicus (larger specimens with finer threads between them); innermost basal rib (UC) deeply sunken into umbilicus, often appearing as sculpture of umbilical wall; area between UC and usually stronger proxumbical rib in Recent species at oblique angle to base; umbilical wall with growth lines, occasionally with very fine spiral sculpture; coloration: off-white or irregularly blotched yellowish tan. *Protoconch:* small to medium-sized (ca. 0.7–1.2), distinctly heterostrophic, without anal keel. *Radula:* cuticularized, large rod-like structure instead of true radula (*asperum*, others unknown). *Operculum:* horny, round, cone-shaped, with peg-like projection on body side.

For a more extensive description and discussion of this genus, see BIELER (1985a: 245–247).

Granosolarium asperum (HINDS, 1844)
Figs.7, 115–121

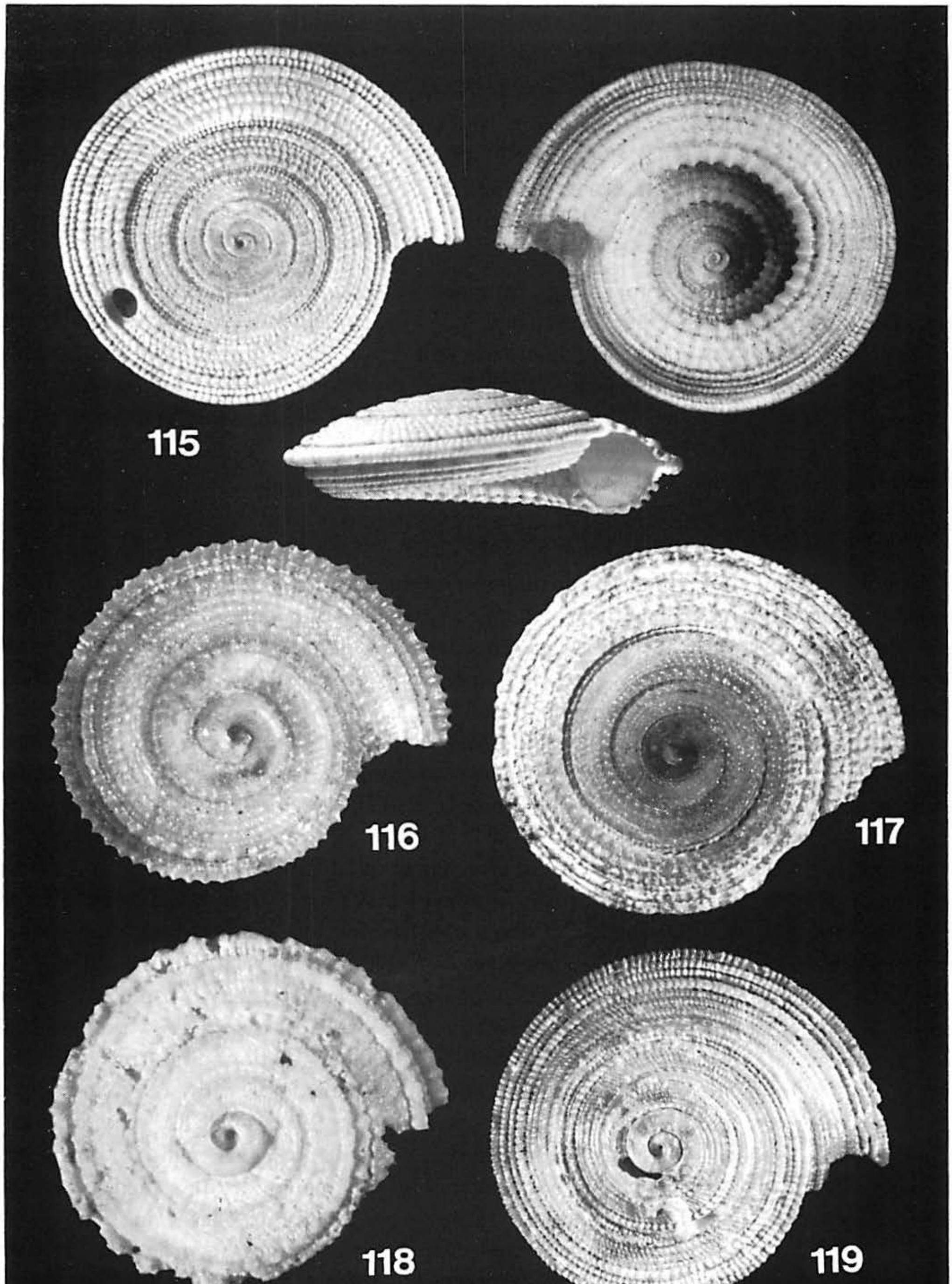
*1844 *Solarium asperum* HINDS, 1844b, Proc. zool. Soc. Lond., *1844*: 23.
1844–1845 *Solarium asperum*, – HINDS, 1844c–1845, Zool. voy. SULPHUR, *3*: 50 (1845); *2*: pl.14 (1844c) figs.9–10.
1844 *Solarium asperum*, – HINDS, 1844d, Ann. Mag. nat. Hist., *14*: 438.
1845 *Solarium asperum*, – CATLOW & REEVE, Conch. nomencl.: 213.
1853 *Solarium asperum*, – PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 22, pl.3 fig.12 [after HINDS, 1844c].
1853 *Architectonica aspera*, – ADAMS & ADAMS, Gen. Rec. Moll., *1*: 242.
*1863 *Solarium dilectum* DESHAYES, Cat. moll. Ile Réunion: 68, pl.9 figs.3–6.
1863 *Solarium (Torinia) asperum*, – HANLEY, Thes. conch., *3*: 241, pl.254 figs.77–78.
1863 *Solarium (Torinia) dilectum*, – HANLEY, Thes. conch., *3*: 241, pl.253 figs.50–51 [after DESHAYES, 1863].
1887 *Torinia (Torinia) dilecta*, – MARSHALL, Man. conch., *9*: 19, pl.6 figs.91–92 [after DESHAYES, 1863].
1887 *Torinia (Torinia) aspera*, – MARSHALL, Man. conch., *9*: 21, pl.6 figs.7–8 [after HINDS, 1844c].
1887 *Solarium asperum*, – PAETEL, Cat. Conch.-Slg., (4)*1*: 285.
1887–1888 *Solarium (Solarium) dilectum*, – PAETEL, Cat. Conch.-Slg., (4)*1*: 286.
*1903–1888 *Solarium (Torinia) admirandum* MELVILL & STANDEN, Ann. Mag. nat. Hist., (7)*12*: 322.
1904 *Solarium (Torinia) admirandum*, – MELVILL, J. Malac., *11*(4): 84, pl.8 figs.6–6A.

1925 *Torinia aspera*, - THIELE, 1925a, Wiss. Ergeb. dtsch. Tiefsee-Exped. VALDIVIA, *17*(2): 302[268], pl.21[9] figs.6-7.
1928 *Heliacus asper*, - TOMLIN, Ann. S. Afr. Mus., *25*(2): 333.
1931 *Heliacus asper*, - TOMLIN, Ann. Natal. Mus., *6*(3): 432.
1934 *Heliacus dilectus*, - NOMURA & ZINBO, Sci. Rep. Tohoku Imp. Univ., (2)*16*(2): 144, pl.5 figs.35a-b.
*1936 *Claraxis illustris* IREDALE, Rec. Austr. Mus., *19*(5): 327, pl.24 fig.16.
1937 *Heliacus dilectus*, - VIADER, Bull. Mauritius Inst., *1*(2): 46.
1939 *Mangonuia (Claraxis) illustris*, WENZ, Handb. Paläozool., *6*(3): 668, fig.1905 [after IREDALE, 1936].
1948 *Torinia admiranda*, - BAYER, Zool. Verh., *4*: 4.
1948 *Torinia aspera*, - BAYER, Zool. Verh., *4*: 6.
1948 *Torinia dilecta*, - BAYER, Zool. Verh., *4*: 15.
1960 *Architectonica (Solariaxis) dilecta*, - MacNEIL, U.S. geol. Surv. prof. Pap., *339*: 39, pl.1 figs.13-15.
1963 *Heliacus asper*, - BARNARD, 1963b, Ann. S. Afr. Mus., *47*(1): 159, fig.31d.
1971 *Claraxis* cf. *illustris*, POWELL, Rec. Auckland Inst. Mus., *8*: 212, figs.2-4.
1971 *Claraxis asperus*, - KURODA et al., Sea shells Sagami Bay: 264, pl.61 figs.13-14.
1973 *Claraxis asperus*, - HIGO, Cat. moll. fauna Jap. Ids.: 230.
1973 *Heliacus asper*, - KENSLEY, Sea-shells s. Afr.: 76, fig.251.
1974 *Heliacus dilectus*, - MICHEL, Bull. Mauritius Inst., *7*(2): 218.
1974 *Heliacus asper*, - BARNARD, Ann. S. Afr. Mus., *47*(5): 711.
1977 *Heliacus (Claraxis) asperus*, - GARRARD, Rec. Austr. Mus., *31*(13): 509, fig.16 [operculum], p.554, pl.6 figs.1-3, 12-14, pl.7 figs.1-6.
1979 *Claraxis illustris*, - POWELL, N. Zeal. Moll.: 247, pl.48 figs.7-8.
1979 *Climacopoma elegantissimus*, - MATSUMOTO, Moll. shells Mie Pref.: 22, pl.3 fig.4 [non *Heliacus elegantissimus* KURODA & HABE *in* HABE, 1961].
1982 *Claraxis asperus*, - OKUTANI & MATSUKUMA, Mem. natl. Sci. Mus. Tokyo, *15*: 171, pl.9 fig.9.
*1982 *Mangonuia kerensis* LADD, U.S. Geol. Surv. prof. Pap., *1171*: 30, pl.31 figs.6-8.
1985 *Granosolarium asperum*, - BIELER, 1985a, Arch. Moll., *115*(4/6): 254ff., pl.5 fig.23 [holotype of *C. illustris*].
1985 *Granosolarium asperum*, - DRIVAS & JAY, La Conchiglia, *17*(190-191): 8, fig.12.
1985 *Granosolarium asper*, - HASZPRUNAR, 1985c, Zool. Scr., *14*(3): 210-211 [anatomy].
1987 *Solarium (Torinia) admirandum*, - TREW, MELVILL's new moll. names: 20.

Type measurements: Holotype of *S. asperum*: SD = 10.0, H = 3.3, PD = 0.86, Tw = 4 3/8+, UD = 4.4. Lectotype of *S. dilectum* [here designated]: SD = 9.2, H = 4.0, PD = 0.84, Tw = 4-, UD = 3.3. Lectotype of *S. admirandum* [here designated]: SD = 4.0, H = 1.3, PD = 0.96, Tw = 2+, UD = 2.4. Holotype of *C. illustris*: SD = 8.3, H = 3.2, PD = 0.92, Tw = 3 3/4, UD = 3.1. Holotype of *M. kerensis*: SD = 4.4, H = 1.3, PD = 0.94, Tw = 2 5/8.

Type localities: *S. asperum*: "Straits of Macassar; in eleven fathoms, coarse sand" (Indonesia); *S. dilectum*: "Ile de la Réunion (Bourbon)"; *S. admirandum*: "Gulf of Oman, lat. 24°58'N., long. 56°54'E., 156 fathoms"; *C. illustris*: "Continental shelf of New South Wales. Type from 45 fathoms off Crowdy Head, near Manning River" [Australia]; *M. kerensis*: "USGS [U.S. Geological Survey] locality 25715, Kere River, Santo, New Hebrides; age, Pleistocene."

Figs. 115-119. *Granosolarium asperum* (HINDS, 1844). Fig. 115 (three aspects): holotype of *Solarium asperum*; Straits of Macassar, Indonesia; BMNH 1879.2.26.159; SD = 10.0. Fig. 116: lectotype of *Solarium (Torinia) admirandum* MELVILL & STANDEN, 1903; Gulf of Oman; BMNH 1905.6.12.5; SD = 4.0. Fig. 117: lectotype of *Solarium dilectum* DESHAYES, 1863; Réunion; MNHNP unnumbered; SD = 9.2. Fig. 118: holotype of *Mangonuia kerensis* LADD, 1982; New Hebrides (Pleistocene); USNM 250151; SD = 4.4. Fig. 119: holotype of *Claraxis illustris* IREDALE, 1936; Australia; AMS C.60694; SD = 8.3.


115
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Etymology: *asper-a-um* [adjective]; Latin: rough, uneven.

Material studied: 210 specimens (AMS, ANSP, BGU, BMNH, BPBM, DMNH, MCZ, MNHNP, NMNZ, NMP, NMW, SAM, USNM, ZMA); including holotype of *S. asperum* (BMNH 1879.2.26.159), lectotype of *S. dilectum* (MNHNP without no.), lectotype of *S. admirandum* (BMNH 1905.6.12.5), holotype of *C. illustris* (AMS 60694), and holotype of *M. kerensis* (USNM 250151).

Diagnosis:

Small to medium-sized, trapezoid to rounded lens-shaped shell with beaded spiral sculpture, prominent peripheral keel and very wide umbilicus in which the strong innermost basal rib is sunken; one, later two, spiral ribs between upper and (undivided) lower peripheral rib; outer base area with three almost identical, well-separated ribs; followed by a relatively prominent basal keel. Overall off-white, sometimes with weak, regular pattern of brown flames. Protoconch diameter 0.78–1.06 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: small to medium-sized, diameter of specimens in collections usually 5–17, mostly under 5 whorls. Shape: early stages depressed trapezoid (similar to specimens of *Pseudomalaxis*), later depressed to rounded lens-shaped with somewhat inflated whorls, prominent peripheral keel, and very wide umbilicus (UD ca. 36% of SD). Sculpture: consisting of beaded spiral ribs; Upper side: SSR distinctly separated, often somewhat stronger than following three MR (outermost usually weaker; all of them weak on first whorl); Periphery: UPR almost as strong as keel-forming LPR; one (later two) additional spiral ribs between UPR and LPR; LPR roundish in cross-section, with ± strong, often pointed nodules (ca. 40 at 3 Tw, ca. 55 at 4 Tw; with additional fine ones interspersed); upper point of whorl attachment at LPR; Base: IPR plus two, almost identical, prominent narrow spiral ribs in convex outer area; four wider spiral ribs in concave area towards umbilicus, the outer one forming a ± distinct basal keel (more prominent on early whorls), and a coarsely sculptured inner one (UC) depressed slightly (about 2/5 of whorl height) into umbilicus; larger specimens often with one additional spiral thread before UC; remaining umbilical wall almost straight, without spiral sculpture; inner margin of aperture often with grooves lining major spiral ribs (especially keel-forming LPR and UC). Coloration: off-white, sometimes with weak, ± regular pattern of brown flames. – Protoconch (see Figs.7, 120): small to medium-sized (0.78–1.06, $\bar{x} = 0.91$), distinctly heterostrophic, without anal keel; whitish with outer corner in front of varix brown. – Periostracum and Operculum: as described for genus. Radula: replaced by rod-like structure (see below). – Anatomy: buccal apparatus with rod-like structure as described for genus *Discotectonica*; sexes separate, males with sperm-filled receptaculum apparatus (HASZPRUNAR, 1985c: 211, and in litt.).

Geographical distribution (Fig.121): Subtropical and tropical Indian Ocean to central Pacific.

Habitat: Sublittoral and upper bathyal (most depth records between 35 and 380 m); live records from 50–100 m; muddy, sandy, and rubble substrates.

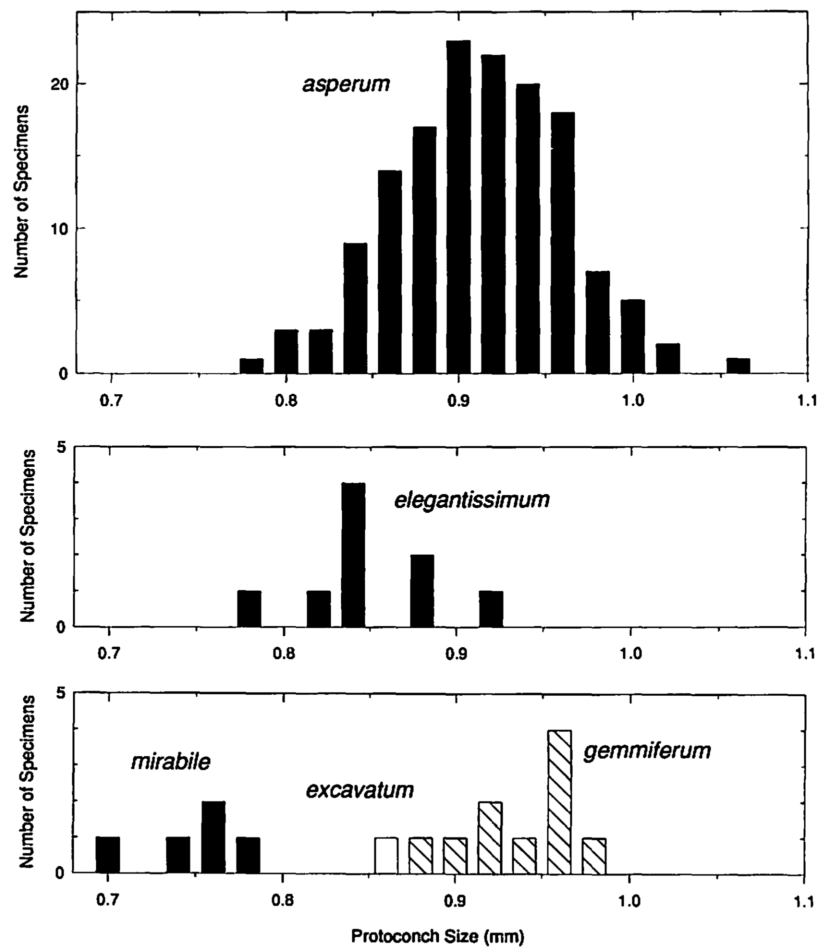


Fig. 120. Histograms of measured protoconch size. *Granosolarium asperum* (n = 145, $\bar{x}$ = 0.91, sd = 0.05), *G. elegantissimum* (n = 9, $\bar{x}$ = 0.85, sd = 0.04), *G. mirabile* (n = 5, $\bar{x}$ = 0.75), *G. excavatum* (n = 1), and *G. gemmiferum* (n = 9, $\bar{x}$ = 0.94, sd = 0.03).

Discussion:

Granosolarium asperum (see Figs.115–119) is readily recognized by the three narrow but strong spiral ribs on its outer shell base, and by the strong umbilical crenae that are somewhat depressed into the umbilicus. *Granosolarium elegantissimum* (Fig.122) has a different, much finer peripheral sculpture (with the lower peripheral rib spirally subdivided) and a shell base with the finer umbilical crenae more deeply depressed into the umbilicus. *Granosolarium gemmiferum* n.sp. is also similar (see below). *Granosolarium asperum* occurs sympatrically with both species (e.g., with *G. elegantissimum* in Sagami Bay, Japan; with *G. gemmiferum* n.sp. in Réunion).

Originally described from Indonesia, *Granosolarium asperum* has a wide range of distribution in the Indo-Pacific. Three nominal species based on Recent material fall in its synonymy:

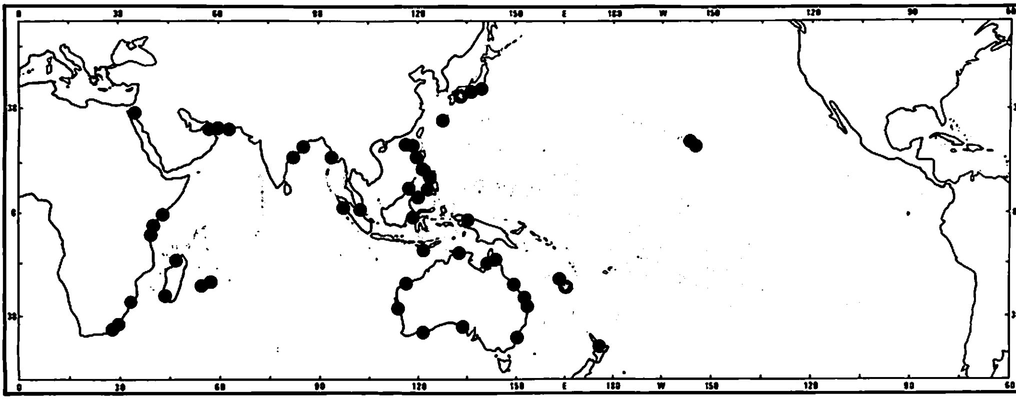


Fig. 121. Geographical distribution of *Granosolarium asperum* and *G. elegantissimum*.

Solarium dilectum DESHAYES, 1863: The specimen figured by DESHAYES (1863: 68, pl.9 figs.3–6) in the original description is here selected as a lectotype (MNHNP unnumbered; see Fig.117; the dimensions are somewhat smaller than those stated by the original author). Two additional specimens formerly considered syntypes (MNHNP) are not conspecific, but belong to a species of *Heliacus (Teretropoma)*.

Solarium admirandum MELVILL & STANDEN, 1903: MELVILL & STANDEN (1903: 322) mentioned three syntypes for their new species, one of which was subsequently figured by MELVILL (1904: pl.8 figs.6–6A). This specimen is here selected as a lectotype (BMNH 1905.6.12.5; see Fig.116).

Claraxis illustris IREDALE, 1936: IREDALE (1936: 327) described this species as the type of a new genus, *Claraxis*. The holotype (AMS C.60694; see Fig.119) is a specimen of *G. asperum*; the nominal genus was synonymized under *Granosolarium* by BIELER (1985a: 247).

Granosolarium asperum is known from the fossil record. GARRARD (1977: 555) reported it from the Middle Miocene of Australia, and MacNEIL (1960: 39) from the Miocene of Okinawa. LADD (1982: 30) described the nominal species *Mangonuia kerensis* from the Pleistocene of the New Hebrides. Its characters fall into the range of variability of Recent *G. asperum* shells, and *M. kerensis* is here synonymized. The originally published figures of the holotype (LADD, 1982: pl.31 figs.5–7) show the specimen in much better condition than it is found today (USNM 250150; see Fig.118, photograph taken in 1984). *Architectonica (Pseudotorinia) euprepes* WOODRING, 1928, from the Neogene of Jamaica is very similar. The relationships between *G. asperum*, *A. euprepes*, and other Mediterranean and North American Neogene fossils need further study.

Granosolarium elegantissimum (KURODA & HABE *in* HABE, 1961) Figs.120–122

1960 *Heliacus elegantissimus* KURODA (MS), - AZUMA, Cat. shell-bear. Moll. Okinoshima: 13 [*nomen nudum*].

*1961 *Heliacus elegantissimus* KURODA & HABE *in* HABE, Coll. illus. shells Japan, (*II*): 31, Appendix p.10 [as *elegantissima*], pl.14 fig.2.

1964 *Heliacus elegantissimus*, - HABE, Shells w. Pac. col., *2*: 47, pl.14 fig.2.

1973 *Climacopoma elegantissimus*, - HIGO, Cat. moll. fauna Jap. Ids.: 229.

Type measurements: SD = 19.8, H = 8.8, PD = 0.84, Tw = 6 7/8–, UD = 9.6.

Type locality: "Off Cape Ashizuri, Kochi Pref., Shikoku, 100–150m" [type label]; "Tosa Bay, Shikoku at a depth of 100–150 m" [HABE, 1964: 47].

Etymology: *elegantissimus-a-um* [adjective]; Latin: superlative of *elegans-antis*; fine, elegant.

Material studied: 10 specimens (AMNH, ANSP, MNHNP, NSMT); including holotype (NSMT Mo49890).

Diagnosis:

Medium-sized, thin-walled, depressed cone-shaped shell with finely beaded spiral sculpture, prominent peripheral keel, and very wide umbilicus in which the fine innermost rib is sunken; keel-forming lower peripheral rib spirally subdivided and consisting of inner part similar to upper peripheral rib, and outer part that is triangular in cross-section and bears many fine, pointed nodules; outer base area with many fine spiral threads. Translucent whitish. Protoconch diameter 0.78–0.92 mm, heterostrophic, without anal keel.

Description:

Teleoconch: medium-sized, thin-walled, diameter of specimens in collections usually 13–19 at 5 to 6 1/2 whorls. Shape: depressed cone-shaped with somewhat inflated whorls, prominent peripheral keel, and very wide umbilicus (UD ca. 42% of SD). Sculpture: consisting of beaded spiral ribs (large specimens with many additional ± fine spiral threads): Upper side: SSR distinctly separated on first whorl only; MR-area with axial growth lines; up to second whorl SSR still stronger than single rib in MR-area, on later whorls up to four ribs in MR-area; Periphery: UPR more prominent than SSR and MR; LPR distinctly divided into inner part similar to UPR and outer part that is triangular in cross-section (beak-shaped, bent towards the base in larger specimens), spirally subdivided, and bearing many fine, pointed nodules (ca. 90 at 3 Tw, ca. 115–120 at 4 Tw); upper point of whorl attachment at the outer part of LPR; "false suture" between UPR and inner part of LPR, bearing one (initially weak, later strong) additional spiral rib; Base: IPR distinctly stronger than following numerous fine spiral threads in area close to peripheral keel, followed by 5–6 distinct spiral ribs (increasing in width towards umbilicus), of which the coarser sculptured innermost surrounds umbilicus and has a groove on the umbilical side, and a further, much more finely sculptured spiral rib on umbilical wall, at about half of visible whorl-

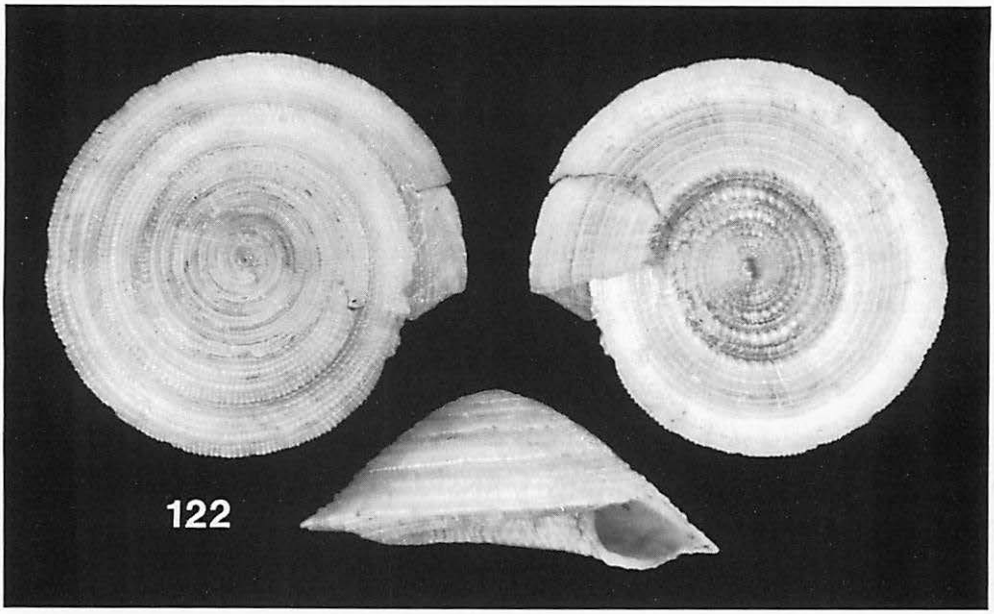


Fig. 122. *Gransolarium elegantissimum* (KURODA & HABE *in* HABE, 1961); specimen from Tosa, Shikoku, Japan; AMNH 180988; SD = 18.9.

height, lined by microscopic spiral threads on each side. Coloration: translucent whitish. - Protoconch (see Fig.120): small to medium-sized (0.78-0.92, $\bar{x}$ = 0.85), heterostrophic, without anal keel; translucent milky white. - Periostracum and Operculum: as described for genus [for operculum see HABE, 1964: 47]. - Radula and Anatomy: not known.

Geographical distribution (Fig.121): Subtropical western Pacific (Japan, New Caledonia).

Habitat: Sublittoral to upper bathyal (depth records between 100 and 545 m), live records from 100-150 m, sandy substrates.

Discussion:

This species, formerly known only from Japan, is similar to *G. asperum*, but has much finer sculpture (see discussion above).

Granosolarium excavatum n.sp.

Figs.120, 123, 124

Type measurements (holotype): SD = 11.4, H = 5.2, PD = 0.86, Tw = 5, UD = 4.8.

Type locality: off the southern coast of Molokai (Hawaiian Islands), NW of Lae-O Ka Laau Light, 309-333 m, fine brown sand and mud, bottom temperature 12.8°C ['ALBATROSS' Sta. 3835; 03 April 1902].

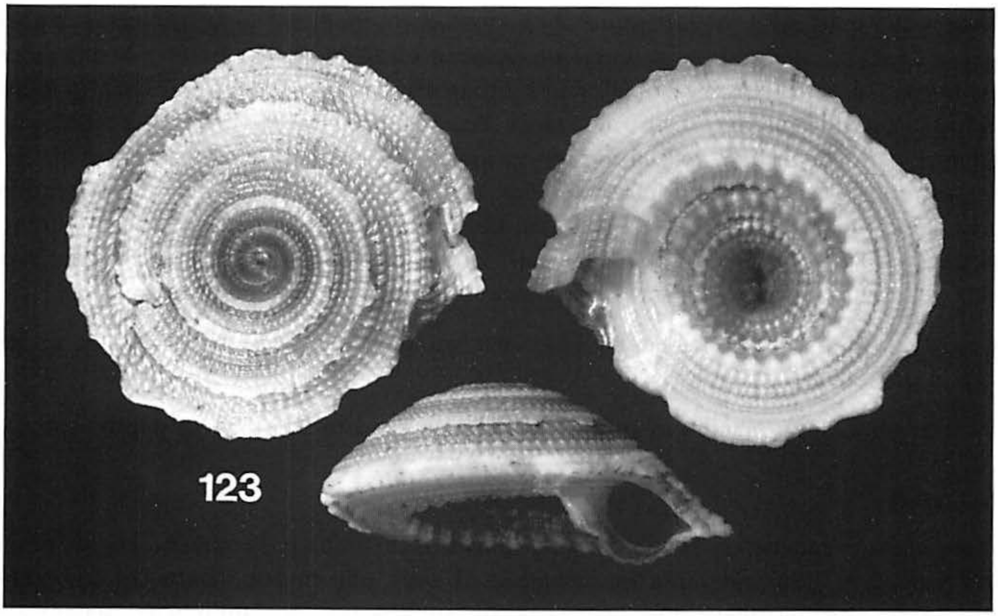


Fig. 123. *Granosolarium excavatum* n.sp.; holotype; Hawaiian Islands; USNM 173050; SD = 11.4.

Etymology: *excavatus-a-um* [adjective]; Latin: hollowed out. The name, referring to the deeply excavated umbilicus, was originally proposed for this specimen by WILLIAM H. DALL, in an unpublished manuscript on the marine gastropod fauna of Hawaii (WILLIAM HEALY DALL Sectional Library, Division of Mollusks, USNM).

Material studied: holotype (USNM 173050).

Diagnosis:

Medium-sized, depressed bell-shaped shell with beaded spiral sculpture, very prominent peripheral keel, and very wide, funnel-shaped umbilicus, in which one fine spiral rib is sunken; keel-forming lower peripheral rib spirally subdivided and consisting of inner part similar to upper peripheral rib, and outer part that bears coarse, flattened triangular nodules (which overlap onto following whorl); midrib-area with only one rib. Yellowish-brown with peripheral keel lighter-colored. Protoconch diameter 0.86 mm, weakly heterostrophic, without anal keel.

Description:

Teleoconch: medium-sized (11.4 at 5 Tw). Shape: depressed bell-shaped, with very wide, funnel-shaped umbilicus (UD ca. 42% SD). Sculpture: consisting of beaded spiral ribs; Upper side: SSR about as strong as UPR, one rib in MR-area; Periphery: UPR about as strong as upper part of LPR; LPR distinctly divided into inner part similar to UPR and keel-forming outer part that is spirally subdivided and bears pointed, flattened triangular nodules (ca. 23 at 4 Tw); upper point of whorl attachment somewhat below outer part of LPR, therefore LPR-nodules overlapping onto following whorl; after 2 1/4 Tw, one additional spiral rib between UPR and LPR; Base: 1-2 fine spiral ribs in area close to periphery, followed by four distinct spiral ribs (increasing in width towards umbilicus), of which the more coarsely sculptured innermost surrounds umbilicus (with ± distinct central groove on umbilical side); an additional spiral rib (the weakest on the base) sunken into umbilicus, to about 2/5 of whorl height. Coloration: early whorls mauve-brown, later yellowish-brown; LPR with peripheral nodules lighter colored. - Protoconch (see Fig.120): small (0.86), weakly heterostrophic, without anal keel; yellowish. - Periostracum, Operculum, Radula and Anatomy: not known.

Geographical distribution (see Fig.124): Known only from the type locality in the Hawaiian Islands.

Habitat: One empty shell was dredged from fine sand in 309-333 m depth.

Discussion:

Granosolarium excavatum is to date only known from a single specimen. The different shell sculpture, especially the combination of only one midrib, flattened-triangular nodules on the periphery and one weak rib sunken into the umbilicus, separate it clearly from its known congeners. The closest form is *G. mirabile* (see below).

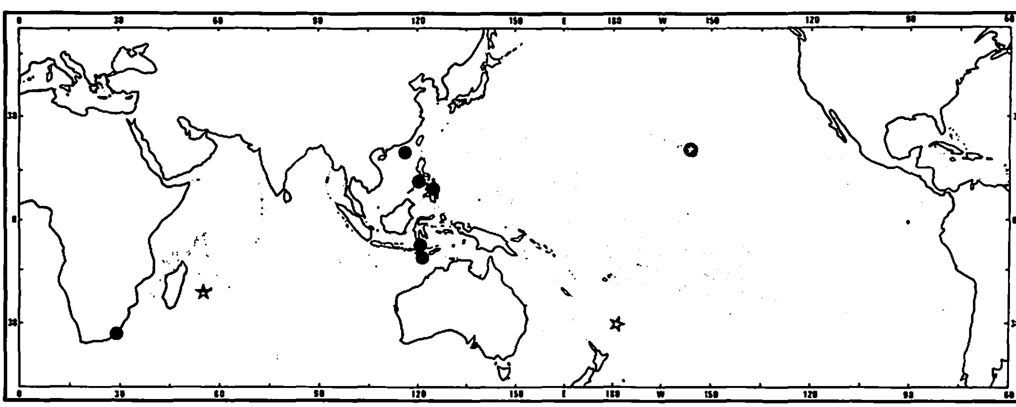


Fig. 124. Geographical distribution of *Gransolarium mirabile, G. excavatum* n.sp. and *G. gemmiferum* n.sp.

Granosolarium mirabile (SCHEPMAN, 1909)
Figs.120, 124, 125

*1909 *Torinia mirabilis* SCHEPMAN, Monogr. Res. SIBOGA Exped., *49*(1b): 222, pl.14 figs.6a-c.
1948 *Torinia mirabilis*, - BAYER, Zool. Verh., *4*: 29.
*1960 *Climacopoma serratomarginata* MacNEIL, U.S. geol. Surv. prof. Pap., *339*: 37, pl.7 figs.17, 23, 27 [Neogene fossil].
1960 *Climacopoma mirabilis*, - MacNEIL, U.S. geol. Surv. prof. Pap., *339*: 37.
1985 *Granosolarium mirabile*, - BIELER, 1985a, Arch. Moll., *115*(4/6): 246.

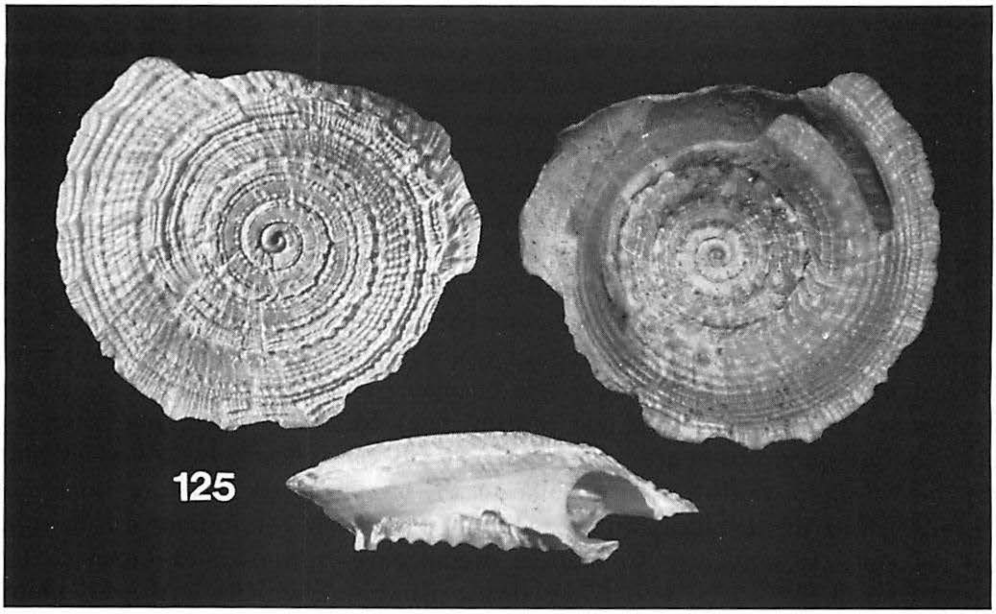


Fig. 125. *Granosolarium mirabile* (SCHEPMAN, 1909); holotype of *Torinia mirabilis*; Indonesia; ZMA 3.09.068; SD = 8.9.

Type measurements: Holotype of *T. mirabilis* (damaged): SD = 8.9, H = 2.9, PD = 0.76, Tw = 3 7/8 (originally 4 1/5), UD = 4.6. Holotype of *C. serratomarginata*: SD = 11.8, H = 4.5, PD = 0.76, Tw = 5 1/2, UD = 6.5.

Type localities: *T. mirabilis*: "[SIBOGA] Stat.212. 5°54'.5S., 120°19.2' E. Banda Sea. 462m. Fine grey and green mud" [Indonesia]; *C. serratomarginata*: "Shinzato tuff member, 17454" (N of Asato, South Okinawa; Upper Miocene or Pliocene).

Etymology: *mirabilis-e* [adjective]; Latin: wonderful, amazing.

Material studied: 7 specimens (MNHNP, USNM, ZMA); including holotypes of *T. mirabilis* (ZMA 3.09.068) and *C. serratomarginata* (USNM 562801).

Diagnosis:

Very small to medium-sized, depressed-trapezoid, later depressed lens-shaped shell with finely beaded spiral sculpture, very prominent peripheral keel, and extremely wide, funnel-shaped umbilicus, in which 2–4 fine spiral ribs are sunken; keel-forming lower peripheral rib spirally subdivided and consisting of inner part similar to upper peripheral rib, and outer part that bears coarse, flattened triangular nodules (which overlap onto the following whorl); midrib-area with 2–3 relatively fine ribs. Overall olive-brownish. Protoconch diameter 0.70–0.78 mm; almost planispiral, without anal keel.

Description:

Teleoconch: very small to medium-sized, diameter of specimens in collections 4.2–12.4; mostly ca. 4 whorls. Shape: early stages depressed trapezoid, later depressed lens-shaped with very prominent peripheral keel and extremely wide, funnel-shaped umbilicus (UD ca. 54%, measured at basal keel). Sculpture consisting of beaded spiral ribs (larger specimens with many fine additional threads): Upper side: SSR distinctly separated, usually stronger than 2–3 MR (MR lacking on first whorl); Periphery: UPR strong, more prominent than SSR and MR; LPR distinctly divided into inner part similar to UPR and keel-forming outer part that is often spirally subdivided and bears coarse, flattened-triangular nodules (ca. 20 at 3 Tw, ca. 25 at 4 Tw); upper point of whorl attachment on lower side of outer part of LPR; weak "false suture" between UPR and LPR, here one (usually fine) additional spiral rib; Base: 3–4 relatively fine spiral ribs in area close to peripheral keel, followed by 3–4 wider spiral ribs (increasing in width towards umbilicus), the more coarsely sculptured innermost rib surrounding the umbilicus with a ± distinct basal keel; 2–4 additional, fine spiral ribs lowered into umbilicus. Coloration: overall olive-brownish. – Protoconch (see Fig.120): small (0.70–0.78, $\bar{x}$ = 0.75), almost planispiral, without anal keel; whitish to yellowish-brown. – Periostracum and Operculum: as described for genus. – Radula and Anatomy: not known.

Geographical distribution (Fig.124): Eastern Indian Ocean (South Africa) and western Pacific (Indonesia, South China Sea, Philippines), and as Neogene fossil in Japan. Frequently listed (but never illustrated) in faunal lists of Recent Japanese mollusks; no Recent Japanese material studied.

Habitat: Sublittoral to upper bathyal (depth records between 15 and 494 m), live specimen from 462 m, sandy and muddy substrates.

Discussion:

Granosolarium excavatum n.sp. (see above) is similar, but has a much coarser shell sculpture, only one midrib, only one spiral rib on the umbilical wall and a distinctly larger (0.86) protoconch. *Granosolarium asperum* and *G. elegantissimum* lack the coarse, flattened triangular peripheral nodules, and have only one rib sunken into the umbilicus.

Granosolarium mirabile was described by SCHEPMAN (1909: 222), based on a single live-collected but badly damaged specimen (see Fig.125). The nominal species *Climacopoma serratomarginata* MACNEIL, 1960, decribed from the Upper Miocene or Pliocene of Okinawa, is here synonymized. The differences in sculpture to *G. mirabile*, as stated by MACNEIL (1960: 37), fall within the range of variation of the known Recent material. The genus *Climacopoma* FISCHER, 1885 (of which *Patulaxis* DALL, 1892, is a synonym), is not known from Recent material (see discussion and figures in BIELER, 1985a: 244–245, pl.4 figs.16–18).

Granosolarium gemmiferum n.sp.
Figs.120, 124, 126

Type measurements:

	SD	H	PD	Tw	UD	Collection
Holotype	5.0	2.0	0.90	2 3/4-	1.5	MNHNP unnumbered
Paratype 1	5.9	2.3	0.96	3 1/8	2.0	MNHNP unnumbered
Paratype 2	5.0	2.0	0.96	2 7/8-	1.6	MNHNP unnumbered
Paratype 3	4.6	1.9	0.96	2 1/2	1.3	MNHNP unnumbered
Paratype 4	4.2	1.7	0.92	2 1/2	1.3	MNHNP unnumbered
Paratype 5	3.7	1.5	0.92	2 1/8	1.2	MNHNP unnumbered
Paratype 6	4.7	2.1	0.94	2 3/4+	1.4	WAM 484-91
Paratype 7	4.9	2.1	0.88	2 9/10	1.4	FMNH 223419
Paratype 8	4.2	1.7	0.96	2 3/8	1.2	NMP S3418/T370
Paratype 9	5.8	2.3	0.98	2 7/8	2.0	NMNZ MF.25546

Type locality: Réunion (21°05'S, 55°12'E), 170–225m [Cruise "MD32 Réunion" of R/V 'Marion-Dufresne' (1982), Sta. DC56]. Paratypes 1–8 from holotype lot. Paratype 9 from E of Chanter Islets, Raoul Island, Kermadec Islands (29°15.5'S, 177°50'W), 366–402 m [R/V 'Acheron' BS 441, 28 October 1975].

Etymology: *gemmifer-a-um* [adjective]; Latin: bearing precious stones or pearls; referring to the granular shell surface.

Material studied: Holotype and 9 paratypes, as listed above.

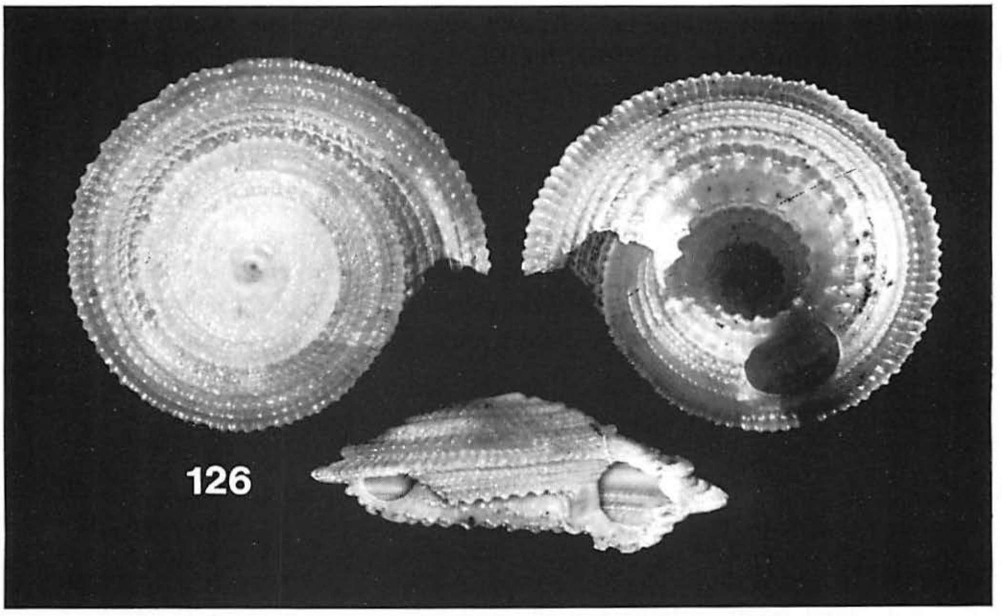


Fig. 126. *Granosolarium gemmiferum* n.sp.; holotype; Réunion; MNHNP unnumbered; SD = 5.0.

Diagnosis:

Very small to small, depressed lens-shaped shell with beaded spiral sculpture, prominent peripheral keel, widely open umbilicus, and a prominent ridge on the upper side, formed by the upper peripheral rib; one, later two, spiral ribs between upper and (undivided) keel-forming lower peripheral rib; outer base area with two almost identical, well-separated ribs; no distinct basal keel formed; umbilical crenae only slightly sunken into umbilicus. Translucent milky white with brown blotches. Protoconch diameter 0.88–0.98 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: very small to small, diameter 3.5–5.9 at 2 1/8 to 3 1/8 whorls. Shape: depressed lens-shaped with widely open umbilicus (UD ca. 31% of SD). Sculpture: consisting of beaded spiral ribs; Upper side: SSR distinctly separated, up to ca. 2 Tw stronger than following two (in some specimens later three) MR; Periphery: UPR very prominent; keel-forming LPR undivided, with relatively fine sculpture (ca. 65 nodules at 3 Tw); false suture between UPR and LPR, here 1–2 additional spiral ribs; upper point of whorl attachment at LPR; 2 ± fine spiral threads between LPR and IPR; Base: well-defined, narrow IPR and 1 almost identical spiral rib in convex outer area (often with additional finer threads interspersed), followed by 4 wider spiral ribs, of which coarser innermost (UC) ± slightly sunken into umbilicus; no basal keel formed. Coloration: translucent milky white with pattern of well-defined light-brown blotches on SSR and UPR (ca. 9–13 per whorl), rarely also on UPR and as flames on MR-area. – Protoconch (see Fig.120): small to medium-sized (0.88–0.98, $\bar{x}$ = 0.94), distinctly heterostrophic, without anal keel; milky white with outer corner in front of varix brown. – Operculum: as described for genus. – Periostracum, Radula and Anatomy: not known.

Geographical distribution (Fig.124): Known only from the type locality, Réunion, in the western Indian Ocean, and from the Kermadec Islands in the western Pacific.

Habitat: Lower sublittoral to upper bathyal (depth records between 170 and 402 m), live record from 366–402 m.

Discussion:

Granosolarium gemmiferum n.sp. differs from the other species of its genus mainly by its prominent, ridge-forming upper peripheral rib. *Granosolarium asperum* (see above) is similar, but its shell has coarser sculpture, umbilical crenae that are more deeply sunken into the umbilicus, and three, instead of two, distinct spiral ribs in the convex outer basal area.

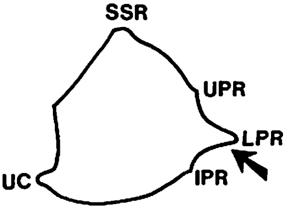
Genus *Solatisonax* Iredale, 1931

Solatisonax Iredale, 1931: 229. Type species by original designation: *Solatisonax injussa* Iredale, 1931; Recent, Indo-Pacific.

Description (Fig.127):

Teleoconch: shell small to large (usually under 15 mm, rarely to 30 mm), in most cases thin-shelled, lens-shaped to roundly cone-shaped; umbilicus always open, mod-

Fig. 127. Schematic representation of placement of major spiral ribs in *Solatisonax*, apertural aspect. Arrow shows point of attachment of next whorl. Sculpture highly variable, see text.



erately wide to wide (ca. 15–35 % of shell diameter); whorls inflated, large specimens frequently on either side of the peripheral keel distinctly concave; distinct axial growth marks on entire shell surface; upper (apical) side: juvenile shell whorls with strong, wavy axial ribs crossing a strong nodose spiral rib (UPR) at a distance from the periphery of 1/3 to 1/2 of the whorl width; nodose rib weaker on subsequent whorls, above it (convex area of apical side) usually several weak and ± smooth spiral ribs, below it (concave area of apical side in larger specimens) 1–5 ± distinct, often finely nodose spiral ribs; prominent peripheral keel formed by lower peripheral rib, with upper point of whorl attachment at or somewhat below this rib; keel simple or traversed by several weak spiral sutures; base either (a) with distinct fine infraperipheral rib and few weaker spiral ribs on either side of it, otherwise ± smooth except for axial folds forming coarse, non-demarcated umbilical crenae which occasionally are sunken into the umbilicus, or (b) infraperipheral rib very weak and entire base with ca. 15–20 fine spiral ribs increasing in width towards umbilicus, innermost of which is wider with ± regular nodes; umbilical wall with growth lines, with or without fine spiral ribs; apical side colored off-white or diffusely blotched with tan, concave area and base lighter. *Protoconch:* small to large (ca. 0.7–1.3), weakly to distinctly heterostrophic, without anal keel. *Radula:* five-toothed taenioglossate (*injussa*). *Operculum:* horny, round, flat to concave, with peg-like projection on body side.

For a more extensive description and discussion of this genus see BIELER (1985a: 242–244). *Solatisonax* s.l. is currently the least understood of the extant architectonicid groups, its monophyly is questionable. Most species are only known from few shells collected in deep water.

Solatisonax injussa (IREDALE, 1931)
Figs.128–130

*1931 *Solatisonax injussa* IREDALE, Rec. Austr. Mus., *18*(4): 229, pl.25 figs.7–8.
1939 *Architectonica (Solatisonax) injussa*, – WENZ, Handb. Paläozool., *6*(3): 671, fig.1914 [fig. caption: "*atkinsoni* E.A. SMITH"].
1942 *Philippia injussa*, – BAYER, Zool. Meded., *24*(1–2): 7.
1962 *Solatisonax injussa*, – IREDALE & MCMICHAEL, Mem. Austr. Mus., *11*: 68.
1977 *Architectonica (Solatisonax) injussa*, – GARRARD, Rec. Austr. Mus., *31*(13): 509, fig.8 [operculum], p.523, pl.4 figs.13–15.
1978 *Architectonica injussa*, – HINTON, Guide Austr. shells: pl.10 fig.7.
1985 *Solatisonax injussa*, – BIELER, 1985a, Arch. Moll., *115*(4/6): 242ff., pl.4 fig.19 [holotype].
1988 *Solatisonax injussa*, – BIELER, Malac. Rev., Suppl. *4*: 237 [radula].

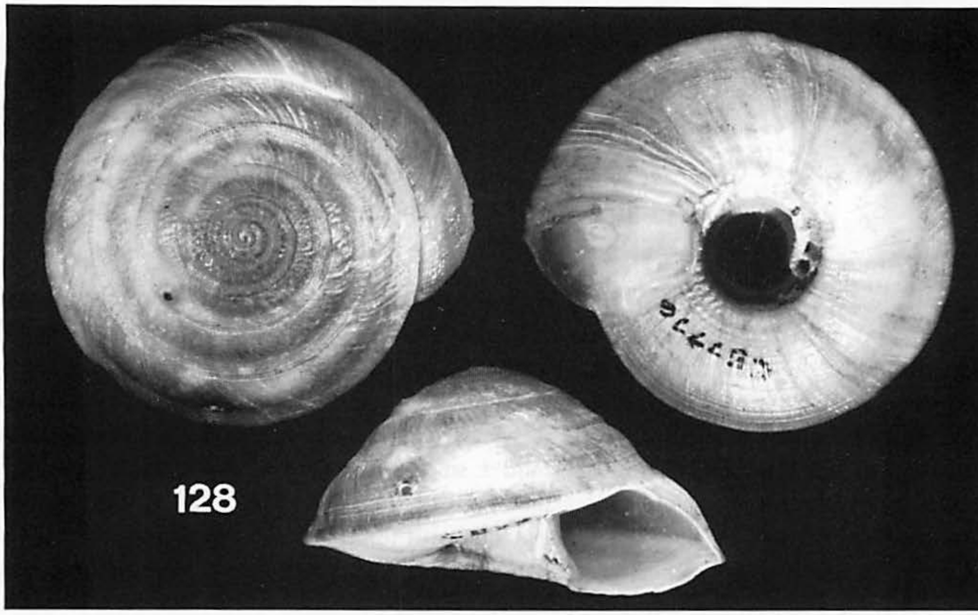


Fig. 128. *Solatisonax injussa* IREDALE, 1931; holotype; Australia; AMS C.57776; SD = 26.0.

Type measurements (holotype): SD = 26.0, H = 15.4, PD = ca. 1.1 [damaged], Tw = ca. 5 7/8, UD = 8.3.

Type locality: "from about 100 fathoms between Gabo and Flinders Island, Bass Strait" [Furneaux Group, Tasmania, Australia].

Etymology: *injussus-a-um* [adjective]; Latin: unasked, voluntary.

Material studied: 9 specimens (AMS, NMNZ); including holotype (AMS C.57776).

Diagnosis:

Large, roundish lens-shaped to depressed cone-shaped shell with inflated whorls (except for upper side of early whorls), distinctly developed concave zones on both sides of prominent peripheral keel, widely open umbilicus, sculpture of numerous fine spiral ribs, and strong axial folds on early whorls; subsutural rib not distinctly separated; strong, nodose upper peripheral rib about 1/3 - 1/2 of whorl-width from periphery (fading after ca. 4 whorls); umbilical crenae not sunken into umbilicus. Diffusely marbled with shades of tan, with concave area of upper side and entire base lighter colored. Protoconch diameter 1.06–1.14 mm, distinctly heterostrophic, without anal keel. Operculum flat to concave.

Description:

Teleoconch: large, relatively thin-walled, diameter of specimens in collections usually 26–31 at 5 5/8 to 6 1/4 whorls. Shape: juveniles roundish lens-shaped with upper side not inflated, later usually ± depressed cone-shaped, with inflated whorls; larger specimens with ± distinctly developed concave zones on both sides of prominent peripheral keel; umbilicus widely open (UD ca. 33% of SD). Sculpture: distinct axial growth lines on entire surface; Upper side: SSR not distinctly separated; early whorls (up to ca. 1 1/2 Tw) with strong axial sculpture, crossing strong, nodose UPR (about 1/3 - 1/2 of whorl-width from periphery); MR-area with numerous (> 5) ill-defined spiral threads; convex area between suture and UPR with 7–12 weak, ill-defined, ± smooth spiral ribs; Periphery: UPR strong and nodose up to about 4 Tw, then fading; concave area between UPR and keel-forming, often spirally grooved LPR with ca. 3-5 fine, ± distinct, sometimes finely granulated spiral ribs; upper point of whorl attachment on, or somewhat below, UPR; IPR weak or lacking; Base: with ca. 15–20 fine, ill-defined spiral ribs or threads, somewhat increasing in strength towards umbilicus; innermost (UC) wider and with ± regular nodules; umbilical side of columellar wall with numerous microscopic spiral threads, without distinct spiral ribs; inner lip with weak groove in UC. Coloration: diffusely marbled with shades of tan, with concave area of upper side and entire base lighter colored. - Protoconch (see Fig.129): medium-sized (1.06–1.14, $\bar{x}$ = 1.11), distinctly heterostrophic (shaped as in *S. radialis*; see Fig.135), without anal keel; yellowish. - Periostracum: thin, brown; forming axial scales on umbilical side of columellar wall. - Operculum: consisting of horny, multispiral lamellae; round, flat to concave; with plug-shaped projection on body side. - Radula: five-toothed taenioglossate (2–1–2); rachidian with triangular central cusp flanked on each side by about 8 shorter cusps which decrease in size distally; inner and outer marginal tooth with 5–6 cusps. - Anatomy: without 'rod-like structure' (Haszprunar, in litt.).

Geographical distribution (Fig.130): Southwestern Pacific (Australia, Kermadec Islands).

Habitat: Lower sublittoral to upper bathyal (depth records between 137 and 567 m), live specimen from 366 m.

Discussion:

Solatisonax injussa, type species of the genus, was introduced by Iredale (1931: 229), as a "deep-water relative of *Architectonica*." It differs from its congeners by the large shell and the very fine upper-side spiral sculpture of the teleoconch. Large and flat individuals (e.g., AMS C.100603) are similar to members of the genus *Discotectonica*, which lack the undulating axial sculpture on the early whorls (and have a flat operculum and a "rod-like structure" instead of a normal five-toothed taenioglossate radula).

Mediterranean *Solatisonax bannocki* (Melone & Taviani, 1980) and *S. kilburni* n.sp. (see below) are similar.

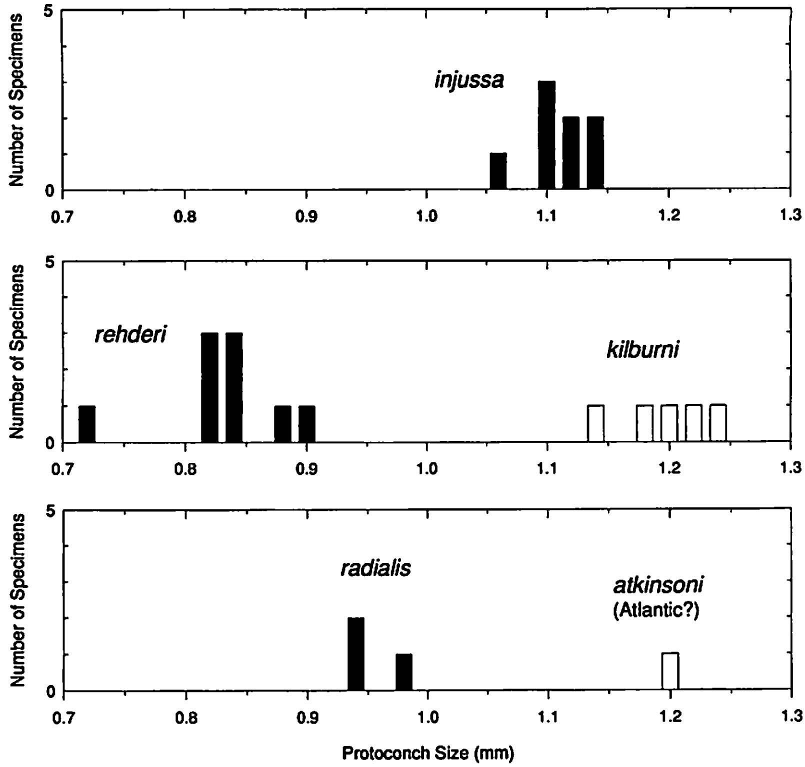


Fig. 129. Histograms of measured protoconch size. *Solatisonax injussa* (n = 8, x̄ = 1.11, sd = 0.03), *S. rehderi* n.sp. (n = 9, x̄ = 0.83, sd = 0.05), *S. kilburni* n.sp. (n = 5, x̄ = 1.20), *S. radialis* (n = 3, x̄ = 0.95), and *S. atkinsoni*.

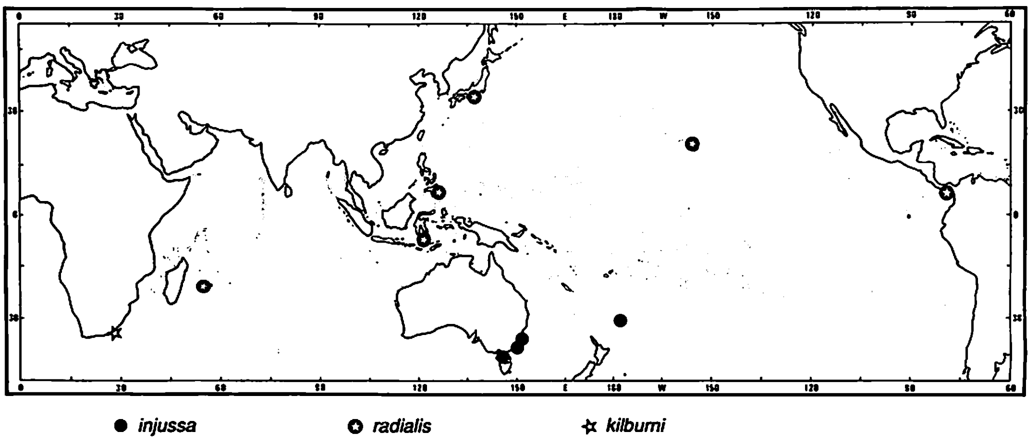


Fig. 130. Geographical distribution of *Solatisonax injussa, S. radialis* and *S. kilburni* n.sp.

Solatisonax kilburni n.sp.

Figs.129–131

Type measurements:

	SD	H	PD	Tw	UD	Collection
Holotype	20.6	11.7	1.24	5–	6.0	NMP C6615/T373
Paratype 1	12.8	6.4	1.14	4 1/8	3.6	NMP S3419/T374
Paratype 2	22.1	13.3	1.22	5 3/8	6.5	NMP S3419/T374 [damaged]
Paratype 3	17.3	10.1	1.18	4 5/8–	5.0	FMNH 223420
Paratype 4	4.6	2.2	ca.1.2	2–	1.8	NMP C8690/T826

Type locality: off Shixini Point, Transkei, South Africa (32°31.6'S, 28°53.0'E), 500 m; muddy sand and coral rubble [R/V 'Meiring Naudé' Sta. T17, dredge; 13 July 1984]. Paratypes 1–2 from holotype lot. Paratypes 3–4 from off Nthlonyane River, Transkei, South Africa (32°18.2'S, 29°06.2'E), 550 m; sand, stones, broken *Dendrophyllia* [R/V 'Meiring Naudé' Sta. P13, dredge; 5 July 1985].

Etymology: *kilburni* [genitive singular case-ending]; named for Dr. Richard N. Kilburn of the Natal Museum, who dredged the type material, and whose constant support throughout the study is gratefully acknowledged.

Material studied: 5 type specimens (as listed above).

Diagnosis:

Small to large, depressed cone-shaped shell with inflated whorls, a distinct concave area on upper side next to prominent peripheral keel, widely open umbilicus, sculpture of numerous, narrow, finely beaded spiral ribs (and weak axial plications on early whorls); convex midrib area of early whorls with only 3–5 spiral ribs, flanked by a relatively weak upper peripheral rib; umbilical crenae not sunken into umbilicus. Off-white to yellowish. Protoconch diameter 1.14–1.24 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: small to large, diameter of known specimens 4.6–22.1 at 2– to 5 3/8 whorls. Shape: depressed cone-shaped with inflated whorls and distinct concave area on upper side next to prominent peripheral keel; early whorls with ± strongly convex MR-area, followed by a strongly concave area between upper and lower peripheral rib; umbilicus widely open (UD ca. 29% of SD, larger in juveniles [paratype 4: 39%]). Sculpture: slight depression in SSR-area (SSR not distinctly separated); 3–5 weakly defined, narrow, almost smooth MR; up to 4 Tw, upper side crossed by ± weak, regular axial folds, then fading into growth lines; Periphery: UPR up to ca. 3 Tw slightly more prominent and nodose than MR; 2–4 spiral threads (later ribs) between UPR and spirally grooved LPR; on body whorl all ribs of upper side and periphery of almost equal strength; IPR not distinctly developed; Base: with 13–30 spiral threads; innermost (UC) wider, not or only weakly separated; umbilical side of columellar wall

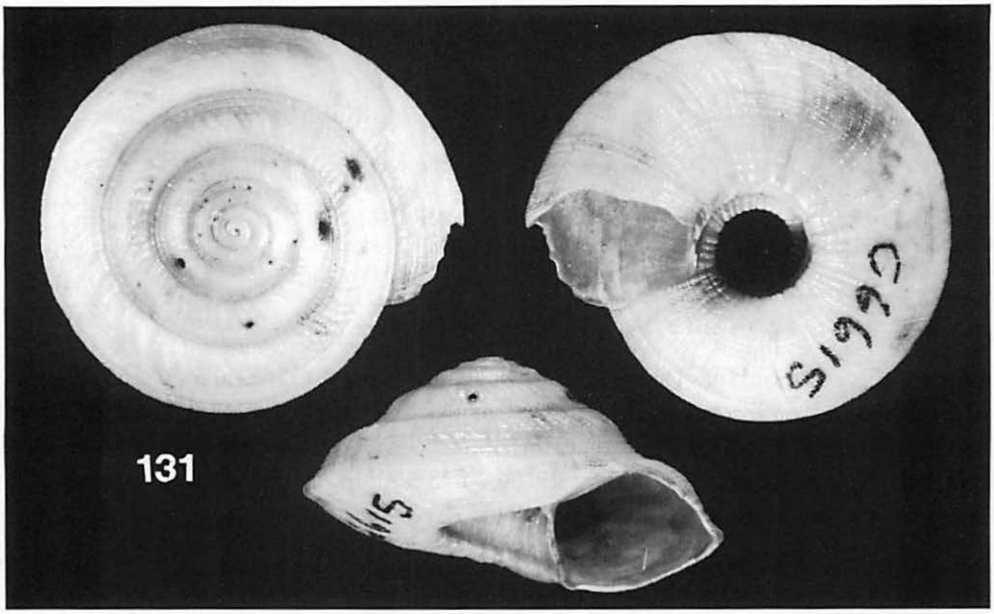


Fig. 131. *Solatisonax kilburni* n.sp.; holotype; Transkei, South Africa; NMP C6615/T373; SD = 20.6.

almost straight (somewhat convex on body whorl) with axial growth lines and microscopic spiral threads, without spiral ribs or with 1–2 spiral threads located closer to base of foregoing whorl; inner lip with weak groove in UC. Coloration: off-white to yellowish [probably faded]. – Protoconch (Fig.129): medium-sized to large (1.14–1.24, $\bar{x}$ = 1.20), distinctly heterostrophic (shaped as in *S. radialis*; see Fig.135), without anal keel; off-white to yellowish. – Periostracum, Operculum, Radula and Anatomy: not known.

Geographical distribution (Fig.130): Known only from two localities in Transkei, South Africa.

Habitat: Upper bathyal (500m), from muddy sand and coral rubble (empty shells).

Discussion:

Specimens of *Solatisonax injussa* (see above) are similar, but have a much finer spiral sculpture (more than five spiral ribs in the midrib area), a smaller protoconch, and, on the early whorls of their teleoconchs, the upper peripheral rib forms a prominent, coarsely nodulated ridge, while the subsutural and midrib areas are concave (convex in *S. kilburni*).

Mediterranean *Solatisonax bannocki* (Melone & Taviani, 1980) is very similar (see, e.g., Melone & Taviani, 1980: figs.1, 2), but has one coarsely nodulated spiral rib on the umbilical side of the columellar wall at about one-half whorl-height (specimens MNHNP unnumbered, vidi).

Solatisonax atkinsoni (E.A. SMITH, 1891)
Figs.129, 132

*1891 *Solarium atkinsoni* E.A. SMITH, 1891b, Proc. zool. Soc. Lond., *1891*: 441, pl.35 figs. 19, 19a-b.
1918 *Architectonica atkinsoni*, - HEDLEY, J. r. Soc. N. S. Wales, *51*(Suppl.): 101.
1942 *Philippia atkinsoni*, - BAYER, Zool. Meded., *24*(1-2): 1.
1985 *Solatisonax atkinsoni*, - BIELER, 1985a, Arch. Moll., *115*(4/6): 243.

Type measurements (holotype): SD = 7.5, H = 4.0, PD = 1.2, Tw = 2 3/4+, UD = 2.2.

Type locality: "... dredged off Sydney in 410 fathoms [750 m]. At this [R/V 'CHALLENGER'] station (164B), in addition to the new species here described were ... undoubtedly Atlantic forms".

Etymology: *atkinsoni* [genitive singular case-ending]; named after a Mr. ATKINSON.

Material studied: holotype (BMNH 1889.10.12.41).

Diagnosis [based on holotype]:

Small, roundish lens-shaped shell with inflated whorls, prominent peripheral keel, widely open umbilicus, and strong axial sculpture on early whorls; subsutural rib not separated; nodose upper peripheral rib about 1/3 - 1/4 of whorl-width from periphery (fading after 1 201/2 whorls); base without spiral sculpture except for umbilical crenae (separated only on early whorls), which are not lowered into umbilicus. Greyish-white. Protoconch diameter 1.20 mm, distinctly heterostrophic, without anal keel.

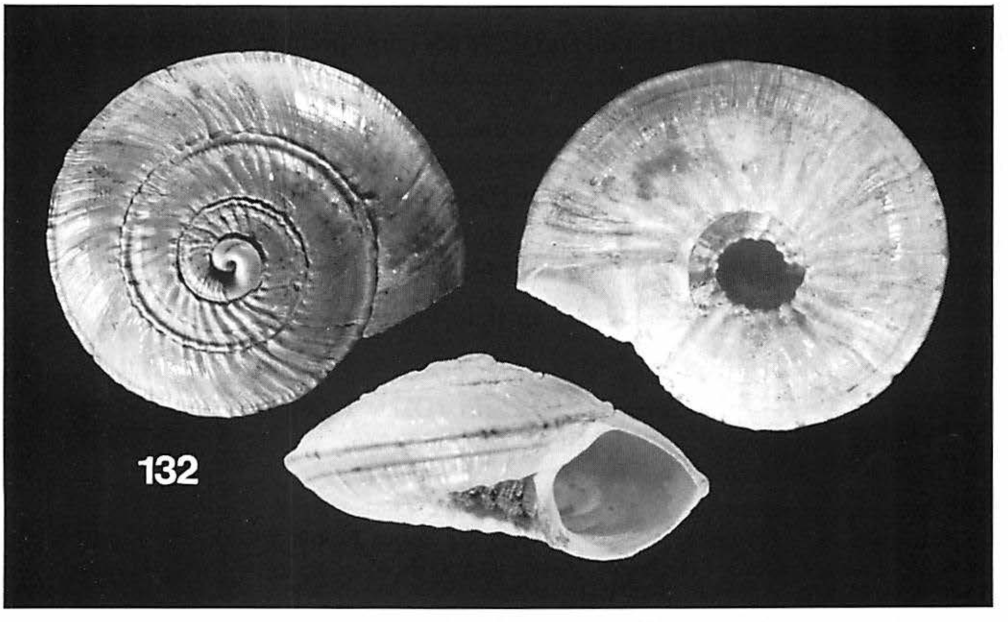


Fig. 132. *Solatisonax atkinsoni* (E.A. SMITH, 1891); holotype of *Solarium atkinsoni*; "off Sydney" [Atlantic Ocean?]; BMNH 1889.10.12.41; SD = 7.5.

Description [based on holotype]:

Teleoconch: small, thin-walled. Shape: roundish lens-shaped with inflated whorls and prominent peripheral keel; areas above and below the keel slightly concave; umbilicus widely open (UD ca. 29% of SD). Sculpture: Upper side: SSR-area weakly elevated, nodose, not separated; up to ca. 2 Tw, with coarse distinct axial folds, crossing nodose UPR (about 1/3 - 1/4 of whorl-width from periphery); after about 2 Tw, ± smooth except for growth lines; Periphery: UPR initially prominent and nodose, fading after 1 1/2 Tw; keel-forming LPR strong with upper point of whorl attachment at base of keel; IPR distinctly separated; Base: BF with undulating axial folds (stronger towards umbilicus), without spiral sculpture; one rib (UC) surrounding umbilicus distinctly separated only on early whorls; umbilical side of columellar wall with axial growth lines, without spiral ribs. Coloration: greyish-white. - Protoconch (see Fig.129): 1.20, distinctly heterostrophic, without anal keel; white. - Periostracum, Operculum, Radula and Anatomy: not known.

Geographical distribution: Uncertain (see discussion).

Habitat: Probably upper bathyal.

Discussion:

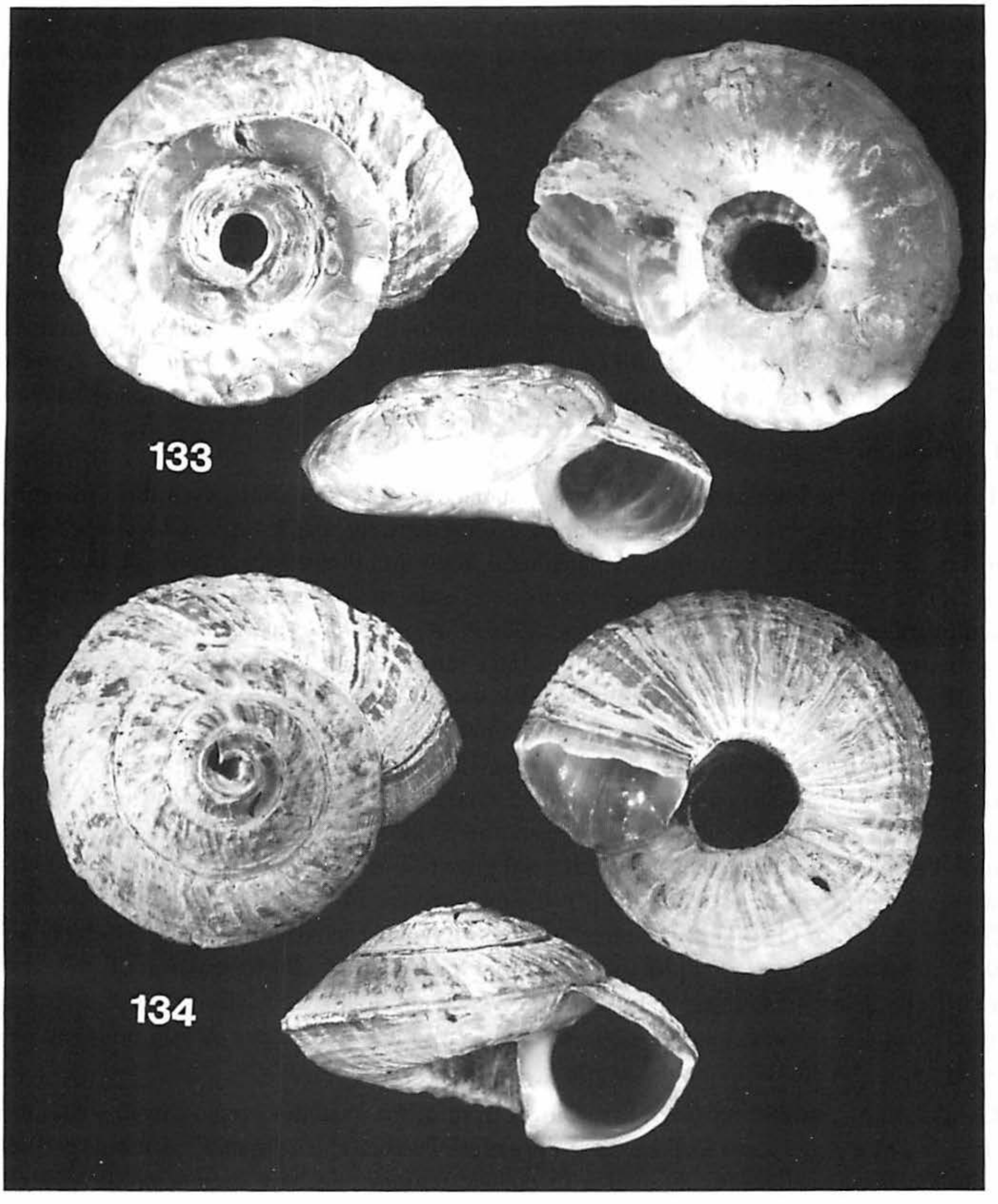
E.A. SMITH (1891b: 441) described *S. atkinsoni* based on a specimen from 'CHALLENGER' Station 164B (Fig.132). Material from that supposed Australian station is known to contain Atlantic species (see "Type locality"; HEDLEY, 1918: 3; IREDALE & MCMICHAEL, 1962; MERRILL, 1970a: 155). Additional specimens assignable to this species are not known from the Indo-Pacific to date; material referred to as "*Architectonica atkinsoni*" by HEDLEY (1907a: 285) and GARRARD (1977: 524) are specimens with distinctive spiral sculpture and probably belong to *S. supraradiata* (see below).

Solatisonax radialis (see below) is very similar, but the upper peripheral rib has a different form and position on the early teleoconch whorls, and the protoconch size is smaller (0.94–0.98). *Solatisonax certesi* (DAUTZENBERG & FISCHER, 1896) (1896: 452, pl.19 figs.3–5, one syntype in IRSNB, vidi) of the Atlantic Ocean differs only by its more rounded shell base and might be conspecific.

Solatisonax atkinsoni is probably not an Indo-Pacific species.

Solatisonax radialis (DALL, 1908)
Figs.129, 130, 133–135

*1908 *Architectonica radialis* DALL, Bull. Mus. comp. Zool., *43*(6): 327.
1909 *Solarium* sp., - SCHEPMAN [in part], Monogr. Res. SIBOGA Exped., *49*(1b): 219.
1944 *Architectonica radialis*, - M. SMITH, Panam. mar. shells: 15.
1948 *Torinia radialis*, - BAYER, Zool. Verh., *4*: 30.
1962 *Architectonica radialis*, - CLARKE, Bull. natl. Mus. Canada, *181*: 16.
1971 *?Heliacus radialis*, - KEEN, Sea shells trop. w. Amer. (2nd ed.): 391, fig.432 [holotype].
1976 *?Heliacus radialis*, - ROBERTSON, 1976a, Bull. Amer. Malac. Union, *1975*: 51.



Figs. 133, 134. *Solatisonax radialis* (DALL, 1908). Fig. 133: holotype of *Architectonica radialis*; Gulf of Panama; USNM 123037; SD = 9.6. Fig. 134: specimen from Oahu, Hawaiian Islands; USNM 335340; SD = 15.7.

Type measurements (holotype): SD = 9.6, H = >5, Tw = ca. 3 [badly corroded].

Type locality: "U.S.S. 'ALBATROSS,' station 3392, in 1270 fathoms [2324m], hard bottom, temperature 36.4°F. [2.4°C], in the Gulf of Panama" [07°05'30"N, 079°40'00"W; trawled 10 March 1891].

Etymology: *radialis-e* [adjective]; Late Latin: arranged like the radii of a circle.

Material studied: 7 specimens (MNHNP, USNM, ZMA); including holotype (USNM 123037).

Diagnosis:

Medium-sized, roundish lens-shaped shell with inflated whorls, prominent peripheral keel, widely open umbilicus, and usually corroded surface; subsutural rib not separated; upper peripheral rib on early whorls usually distinctly separated and situated immediately above keel-forming lower peripheral rib; base with weak sculpture of numerous spiral threads and coarse undulating axial folds; umbilical crenae (separated only on early whorls) not sunken into umbilicus. Off-white. Protoconch diameter 0.94–0.98 mm; distinctly heterostrophic, without anal keel. Operculum cone-shaped.

Description:

Teleoconch: medium-sized, diameter of specimens in collections (excluding juveniles) 9.6–15.7. Shape: roundish lens-shaped to moderately depressed cone-shaped with inflated whorls and ± prominent peripheral keel; umbilicus widely open (UD ca. 29% of SD). Sculpture (usually heavily corroded; even in live-collected specimens surface sculpture only partially present): Upper side: SSR not distinctly separated; early whorls with strong, undulating axial sculpture, later fading into growth lines; MF with weak, ill-defined spiral sculpture; Periphery: UPR usually distinctly separated on early whorls and placed immediately above the prominent, keel-forming LPR; IPR ± weak or lacking; additional spiral threads between LPR and IPR-area; Base: BF with weak sculpture of numerous spiral threads and ± coarse, undulating axial folds that terminate as UC surrounding umbilicus; UC separated as spiral rib only on early whorls; umbilical side of columellar wall with axial growth lines and microscopic spiral threads, without spiral ribs; inner lip with ± distinct groove in UC. Coloration: off-white. – Protoconch (based on 3 specimens; see Figs.129, 135): medium-sized (0.94–0.98, $\bar{x}$ = 0.95), distinctly heterostrophic, without anal keel; white. – Periostracum: olive-brown, relatively thick; obscuring shell coloration. – Operculum: consisting of horny, multispiral lamellae; round, weakly cone-shaped; with plug-shaped projection on body side. – Radula and Anatomy: not known.

Geographical distribution (Fig.130): Known from a few localities ranging from Réunion in the western Indian Ocean to Panama in the eastern Pacific. This "disjunct" pattern is probably only a reflection of the small number of bathyal stations that have been sampled to date.

Habitat: Bathyal (depth records between 556 and 2324 m); live records from throughout that range, mud, sand and hard substrates.

Discussion:

This species, previously known only from the holotype (Fig.133), was assigned to *Heliacus* (or its synonym *Torinia*) by Bayer (1948), Keen (1971) and Robertson (1976a), based on its cone-shaped operculum. Although live-collected, the holotype's shell surface is almost entirely corroded and the apex is missing. More material has now been located in other collections, partly in much better condition (e.g., Fig.134,

Figs. 135–138. SEM photomicrographs of protoconch and early teleoconch whorls. Fig. 135: *Solatisonax radialis* (Réunion; MNHNP unnumbered; SD = 6.6). Fig. 136: *S. supraradiata* (Réunion; MNHNP unnumbered; SD = 3.5). Fig. 137: *S. acutecarinata* (Cebu, Philippines; USNM 839049; SD = 2.8). Fig. 138: *S. rehderi* n.sp. (paratype 4, China Sea; USNM 839052; SD = 3.1). Scale bar = 200 µm, for all figures.

and the specimen described as "*Solarium* sp." by SCHEPMAN, 1909: 219, 'SIBOGA' Sta. 45, Flores Sea; ZMA unnumbered, vidi).

The few known specimens display high variability in shell sculpture. Number and strength of spiral ribs are not constant; the upper peripheral rib can be distinctly developed ('SIBOGA' specimen) or absent (USNM 205587). Larger specimens are usually smoother and more rounded.

Specimens of *Solatisonax supraradiata* (see below) have a similar shape, but lack the fine basal sculpture. The protoconch size in that species is larger (compare Figs.135 and 136) and the operculum is flat (although only known from juveniles).

Solatisonax certesi (DAUTZENBERG & FISCHER, 1896) from the Atlantic Ocean is similar (see discussion under *S. atkinsoni*, above), but has a convex umbilical wall, evident even in small specimens. The type specimen of *S. atkinsoni* differs by the position and strength of the upper peripheral rib.

Solatisonax supraradiata (MARTENS, 1904)
Figs.136, 139–142

*1904 *Solarium supraradiatum* MARTENS, Wiss. Ergeb. dtsch. Tiefsee-Exped. VALDIVIA, *7*: 118, pl.4 fig.16.
?1907 *Architectonica atkinsoni*, - HEDLEY, 1907a, Rec. Austr. Mus., *6*(4): 285 [non *Solarium atkinsoni* E.A. SMITH, 1891].
1940 *Solarium supraradiatum* (incertae sedis), - BAYER, Zool. Meded., *22*: 255.
?1977 *Architectonica (Solatisonax) atkinsoni*, - GARRARD, Rec. Austr. Mus., *31*(13): 524, pl.4 figs.7–9.

Measurements: Holotype: SD = 6.5, H = 3.5, PD = 1.14, Tw = 2 1/2, UD = 1.14. Largest specimen examined: SD = 10.8, H = 6.0, Tw = 3 1/2, UD = 1.7 [USNM 279093, see Fig.140].

Type locality: Indian Ocean, near the Nicobares (7°48'N, 93°7'E), in 805 m depth, on coarse sand ['VALDIVIA' Sta. 211].

Etymology: *supraradiatus-a-um* [adjective]; compound word from Latin adverb *supra* (on top, above) and adjective *radiatus-a-um* (having rays, radiant).

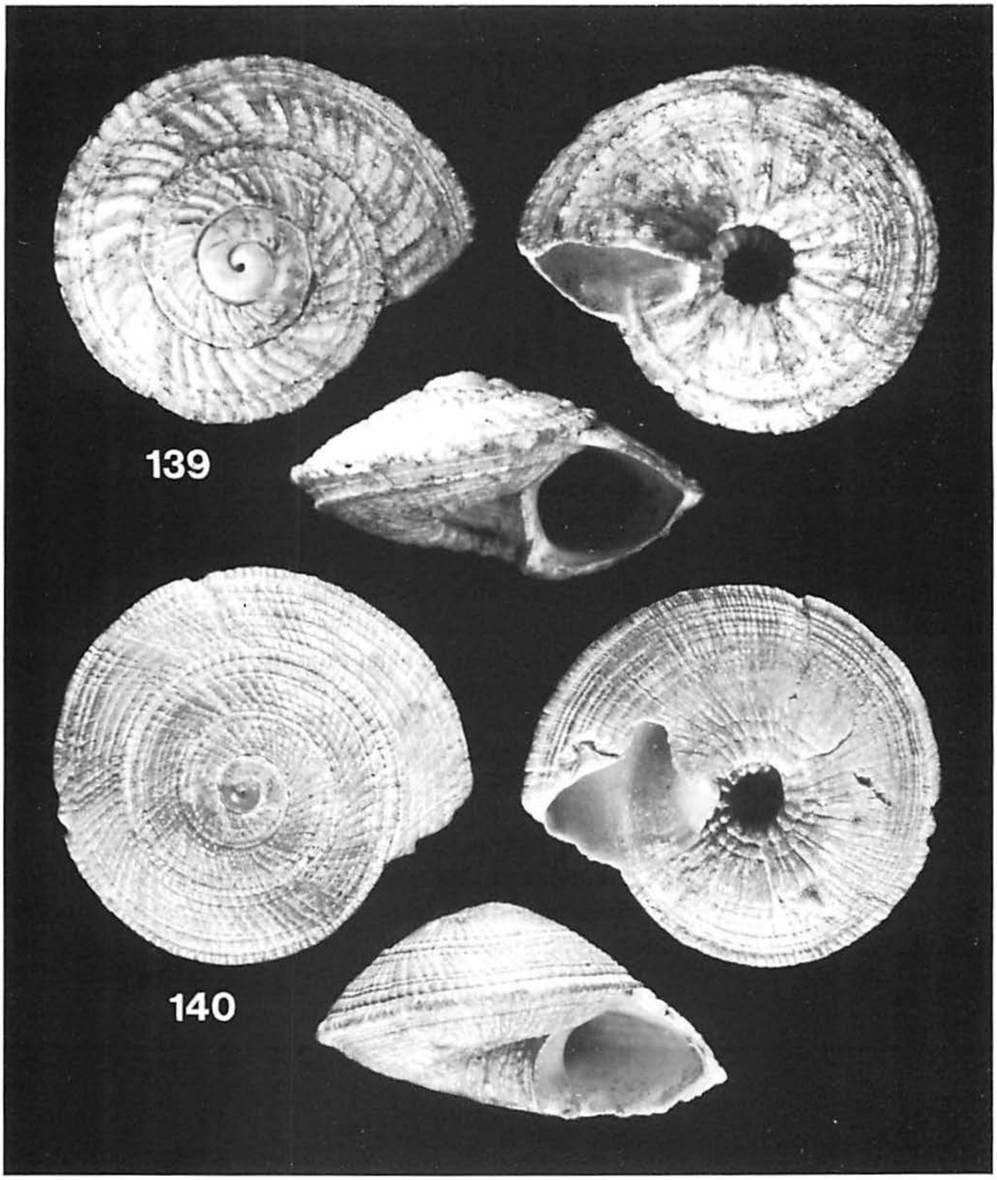
Material studied: 44 specimens (MNHNP, MNHU, NMP, USNM); including holotype (MNHU 59986).

Diagnosis:

Very small to small, lens-shaped shell with inflated whorls, prominent peripheral keel, moderately wide umbilicus and distinct axial and/or spiral sculpture; subsutural rib distinctly separated, early whorls often with strong, undulating axial ribs; usually 3–4 midribs of about equal strength (often with finer threads interspersed); distinctly separated upper peripheral rib more prominent but not wider than midribs; base usually with numerous spiral ribs; umbilical crenae not sunken into umbilicus. Off-white or light tan with peripheral keel lighter colored. Protoconch diameter 1.04–1.22 mm; distinctly heterostrophic with area next to varix lowered into teleoconch; without anal keel. Operculum flat.

Description:

Teleoconch: very small to small, diameter of specimens in collections 4–10, with often less than two, rarely more than three whorls. Shape: lens-shaped with ± inflated whorls and prominent peripheral keel; umbilicus moderately wide (UD ca. 18% of SD). Sculpture: Upper side: SSR distinctly separated, often prominent; early whorls with strong undulating axial ribs, later fading into growth lines; usually 3–4 MR of about equal strength, often with additional finer spiral threads interspersed; Periphery: UPR distinctly separated, more prominent but not wider than MR; between UPR and ± finely granulose, keel-forming LPR usually one additional fine spiral rib; upper point of whorl attachment on LPR; IPR distinctly separated; between LPR and IPR at least one additional spiral rib; Base: BF with numerous spiral ribs, usually increasing in width towards umbilicus (in some specimens BF partly or entirely smooth except for coarse axial folds that terminate in UC); one rib (UC) surrounding umbilicus usually separated, not sunken into umbilicus; ± convex umbilical side of columellar



Figs. 139, 140. *Solatisonax supraradiata* (MARTENS, 1904). Fig. 139: holotype of *Solarium supraradiatum*; Nicobares; MNHU 59986; SD = 6.5. Fig. 140: specimen from Borneo, Indonesia; USNM 279093; SD = 10.8.

wall with axial growth lines, without spiral ribs; inner lip with groove in UC; in some specimens entire shell crossed by ± deeply incised oblique axial grooves, resulting in beaded sculpture. Coloration: off-white or light tan with peripheral keel lighter colored. Protoconch (see Fig. 141): medium-sized to large (1.04–1.22, $\bar{x}$ = 1.13), distinctly heterostrophic, with area next to varix flattened and sunken into teleoconch;

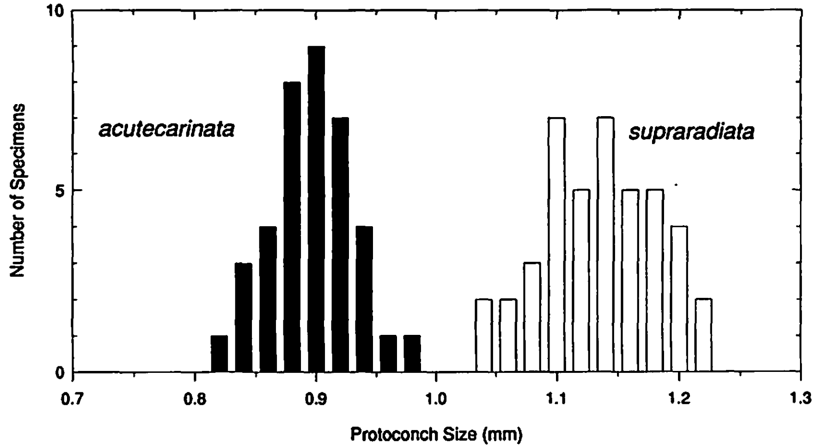


Fig. 141. Histograms of measured protoconch size. *Solatisonax acutecarinata* (n = 38, x̄ = 0.90, sd = 0.04), and *S. supraradiata* (n = 42, x̄ = 1.13, sd = 0.05).

without anal keel; whitish to yellowish, often with corners next to varix darker. - Periostracum: greyish-brown, obscuring shell coloration. - Operculum (only known from juveniles): consisting of horny, multispiral lamellae, round, flat; with plug-shaped projection on body side. - Radula and Anatomy: not known.

Geographical distribution (Fig.142): Tropical and subtropical Indian Ocean and western Pacific (possibly also in eastern Pacific; see discussion).

Habitat: Sublittoral to upper bathyal (depth records between 105 and 805 m), live records from 193–510 m, fine sand and mud. Appears to feed on zoanthids (a specimen was dredged with polyps of *Epizoanthus* sp. from 510 m depth in the northern Mozambique channel; MNHNP, unnumbered).

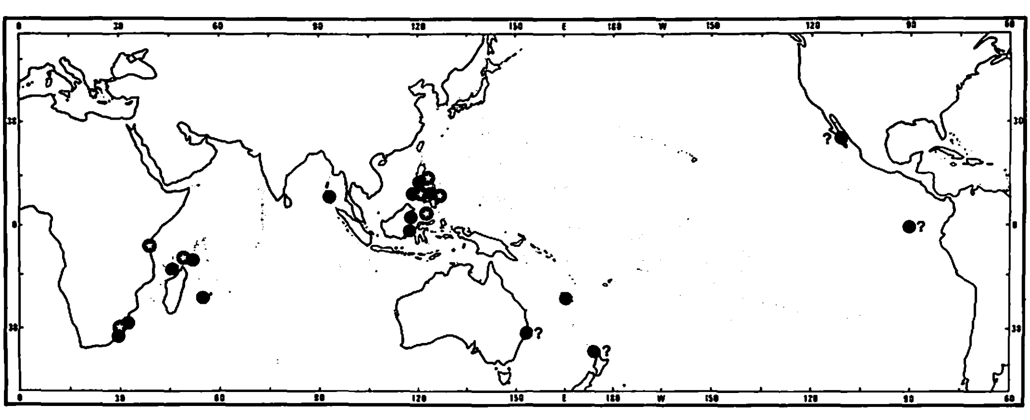


Fig. 142. Geographical distribution of *Solatisonax supraradiata* and *S. acutecarinata*.

Discussion:

Solatisonax supraradiata has been known in the literature only from the holotype. Further material available in various collections shows the high variability of shell characters in this species: specimens from the African east coast (NMP, MNHNP) are similar to the holotype (Fig.139; Nicobares) in having more or less strong axial plications on the upper side, while the strongly spiral-sculptured shells from the Philippines and Borneo (e.g., USNM 279093; see Fig.140) are lacking same. One specimen from Borneo (USNM 278688) shows an intermediate condition.

Solatisonax radialis has comparable shell shape, but a smaller protoconch size (compare Figs.135 and 136) and it lacks the distinct, more or less regular, spiral sculpture of *S. supraradiata*.

Two additional unnamed forms, known from only a few, mostly juvenile specimens, might belong to this species (data not included in description above):

In New Zealand, there is a form with 2–3 smooth and flattened midribs, with a wider umbilicus (ca. 22% of SD), and lacking a distinct infraperipheral rib below the very prominent (*Discotectonica*-like) peripheral keel [e.g., NMNZ M.87378, M.87403]. Specimens from Australia, reported as "*Architectonica atkinsoni*" by HEDLEY (1907a: 285) and GARRARD (1977: 524, pl.4 figs.7–9) belong to this form.

In the Galapagos Islands (LACM 38–192.1) and Baja California (LACM 65–63), a form occurs with well-defined spiral sculpture (two midribs, infraperipheral rib strong and almost forming a second peripheral keel), and umbilical crenae that are somewhat sunken into the umbilicus.

Atlantic *Solatisonax borealis* (VERRILL & SMITH *in* VERRILL, 1881) (1881: 376; VERRILL, 1882: pl.57 figs.29–30; figured syntype, USNM 45298, vidi) is very similar to *S. supraradiata*; the relationship between the two needs further study.

Solatisonax acutecarinata (THIELE, 1925)
Figs.137, 141–144

*1925 *Solarium*(?) *acutecarinatum* THIELE, 1925a, Wiss. Ergeb. dtsch. Tiefsee-Exped. "VALDIVIA," *17*(2): 114 [80], pl.21 [9] figs.1–1a.
1940 *Solarium acutecarinatum* (incertae sedis), - BAYER, Zool.Meded., *22*: 254.

Measurements: Holotype [juvenile]: SD = 3.55, H = 1.6, PD = 0.98, Tw = 1 1/2. UD = 0.95. Largest specimen examined: SD = 12.4, H = 7.2, Tw = 4 3/8, UD = 3.3 [LACM 72787; Philippines].

Type locality: off Dar es Salaam, Tanzania (6°39.1'S, 39°30.8'E), 400m ['VALDIVIA' Sta. 243].

Etymology: *acutecarinatus-a-um* [adjective]; compound word from Latin adverb *acute* (acutely, sharply) and adjective *carinatus-a-um* (keel-bearing).

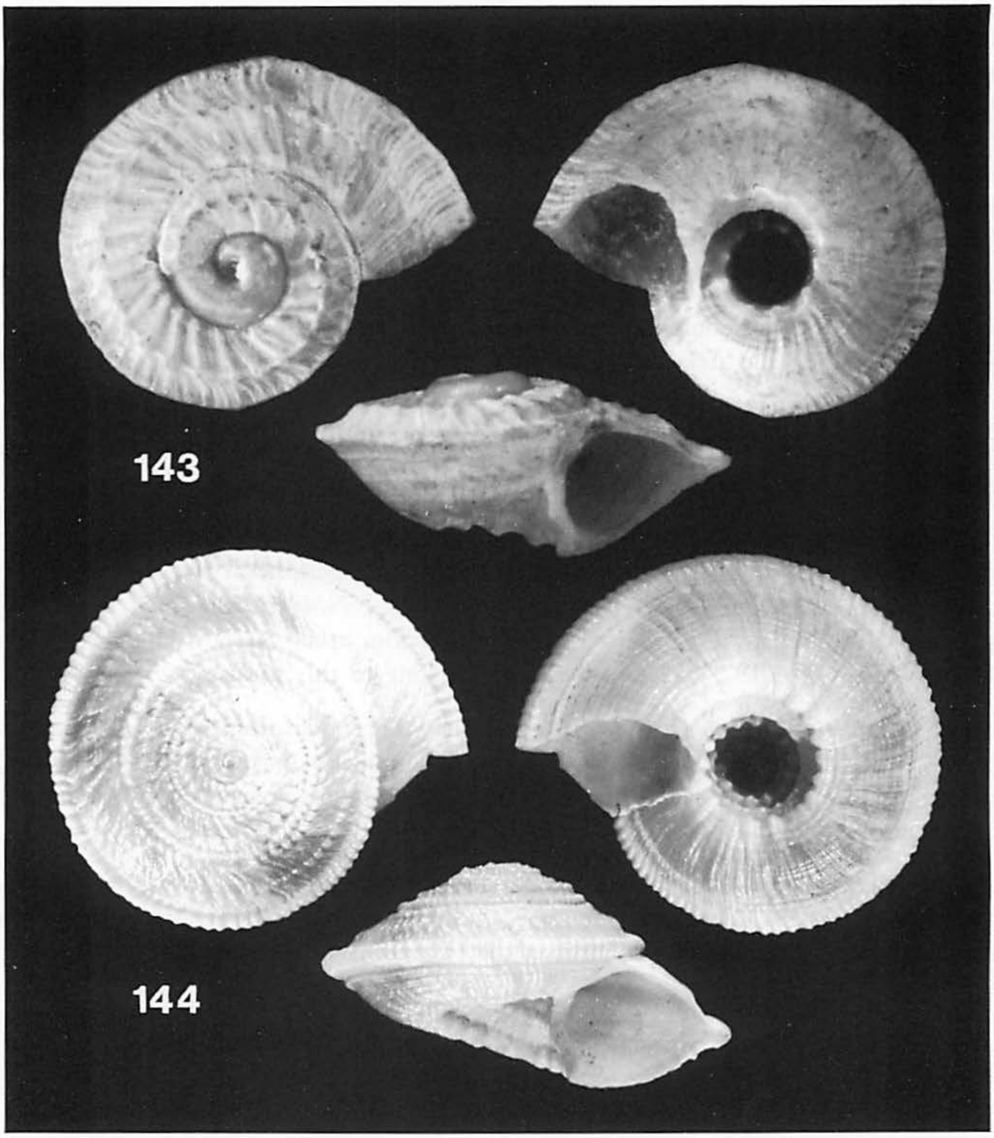


Fig. 143, 144. *Solatisonax acutecarinata* (THIELE, 1925). Fig. 143: holotype of *Solarium*(?) *acutecarinatum*; Tanzania; MNHU unnumbered; SD = 3.55. Fig. 144: specimen from Philippines, USNM 274804; SD = 9.8.

Material studied: 41 specimens (LACM, MNHNP, MNHU, NMP, SMF, USNM); including holotype (MNHU unnumbered).

Diagnosis:

Small to medium-sized, depressed cone-shaped shell with weakly convex whorls, concave zones on both sides of prominent peripheral keel, widely open umbilicus, and sculpture of numerous, partly microscopic spiral threads and coarser, undulating axial folds; subsutural rib nodose, but usually not separated; upper peripheral rib prominent even on body whorl, but weaker than keel-forming lower peripheral rib; one narrow, nodose spiral rib in center of umbilical wall. White to yellowish-tan with peripheral keel and umbilical area lighter colored. Protoconch diameter 0.82–0.98 mm; almost planispiral, without anal keel. Operculum concave.

Description:

Teleoconch: small to medium-sized, diameter of specimens in collections usually 5–12 at 2 1/2 to 4 whorls. Shape: ± depressed cone-shaped with weakly convex whorls (base of juveniles strongly convex), with concave zones on both sides of prominent peripheral keel; umbilicus widely open (UD ca. 28% of SD). Sculpture: Upper side: SSR usually nodose on early whorls, but not distinctly separated (resembles UPR); MR-area with numerous microscopic spiral threads, crossed by undulating axial folds (coarser on early whorls) that form nodules with SSR and UPR; Periphery: UPR prominent, but much weaker than keel-forming LPR; LPR with ± fine, very regular nodules; upper point of whorl attachment below LPR (peripheral keel therefore somewhat overlapping onto following whorl); IPR narrow, distinctly separated; Base: BF with axial folds and numerous fine spiral threads, increasing in width towards umbilicus; umbilicus surrounded by relatively coarse nodules, hardly separated as a spiral rib; one narrow, nodose spiral rib on umbilical side of columellar wall at about 1/2 of whorl-height; inner lip with groove in UC. Coloration: white to yellowish-tan, with peripheral keel and umbilical area lighter colored. – Protoconch (see Fig.141): small to medium-sized (0.82–0.98, $\bar{x}$ = 0.90), almost planispiral, without anal keel; whitish or yellowish, often with brown corners next to weak varix. – Periostracum: thin, olive- to light-brown. – Operculum: consisting of horny, multispiral lamellae; round, concave; with plug-shaped projection on body side. – Radula and Anatomy: not known.

Geographical distribution (Fig.142): Known from the western Indian Ocean and western Pacific.

Habitat: Sublittoral to upper bathyal (depth records between 161 and 704 m); live records from 296–454 m; mud, sand and coral substrates.

Discussion:

This species, known in the literature only from the juvenile holotype specimen, can readily be distinguished from its congeners by the weakly heterostrophic protoconch (see Fig.137), the presence of a strongly nodose and axially plicated upper peripheral rib on the body whorl of adult specimens, and by the presence of a distinct spiral rib on the umbilical side of the columellar wall.

Solatisonax rehderi n.sp.

Figs.129, 138, 145, 146

Type measurements:

	SD	H	PD	Tw	UD	Locality	Collection
Holotype	7.2	3.4	0.90	3 1/2-	2.1	Hawaiian Ids.	USNM 173045
Paratype 1	7.3	3.5	0.88	3 1/2-	2.3	Hawaiian Ids.	FMNH 223409
Paratype 2	7.4	3.6	ca.0.84	3 1/2+	2.0	Philippines	USNM 839069
Paratype 3	5.2	2.4	0.82	2 3/4	1.2	China Sea	USNM 277323
Paratype 4	3.1	1.3	0.82	1 5/8+	0.5	China Sea	USNM 839052

Type locality: Oahu, Kauai Channel, vicinity of Kauai Island, SW of Hanamaulu Warehouse, Hawaiian Islands, 75–302 m, fine grey sand and rocks, 6.5°C bottom temperature [USBF Sta. 4133, 'ALBATROSS' Expedition, trawled 1 August 1902]. Paratype 1 from type locality. Paratype 2 from Observatory Island, Linacapan Strait, Philippines (11°37'15–45"N, 119°46–48'E), 84 m, sand and mud [USBF Stas. 5335/5336, 'ALBATROSS' Expedition, 18 December 1908]. Paratypes 3–4 from off Pratas Island [Tung-sha Tao], China Sea (20°37'N, 115°43'E), 381 m, grey mud and sand [USBF Sta. 5301, 'ALBATROSS' Expedition, 8 August 1908].

Etymology: *rehderi* [genitive singular case-ending]; named for Dr. HARALD A. REHDER, Curator Emeritus of the National Museum of Natural History, Washington, D.C.

Material studied: 5 type specimens (as listed above), and 3 additional specimens (MNHNP, USNM).

Diagnosis:

Very small to small, depressed cone-shaped shell with whorls concave on upper side, convex on base; prominent peripheral keel, widely open umbilicus, and sculpture of coarse nodules; subsutural rib not distinctly separated; midrib area without distinct spiral ribs; upper peripheral rib distinctly developed, narrower than subsutural rib; lower peripheral rib forming peripheral keel (with spiral groove on peripheral side usually visible); umbilicus surrounded by two rows of coarse nodules, the inner one of which is sunken into umbilicus. Off-white to yellowish-tan, with peripheral keel lighter colored. Protoconch diameter 0.72–0.90 mm; heterostrophic, without anal keel. Operculum cone-shaped.

Description:

Teleoconch: very small to small, diameter of specimens in collections 3.9–7.4 at 1 5/8+ to 3 1/2 whorls. Shape: depressed cone-shaped with whorls concave on upper side, convex on base; prominent peripheral keel; umbilicus widely open (UD ca. 27% of SD). Sculpture: Upper side: SSR not distinctly separated, with ± coarse nodules; MR-area without spiral sculpture or with very fine, flattened spiral threads; UPR narrower than SSR (weakly developed or lacking on first whorl) of increasing strength; Periphery: often one ± fine spiral thread between UPR and LPR; UPR forms

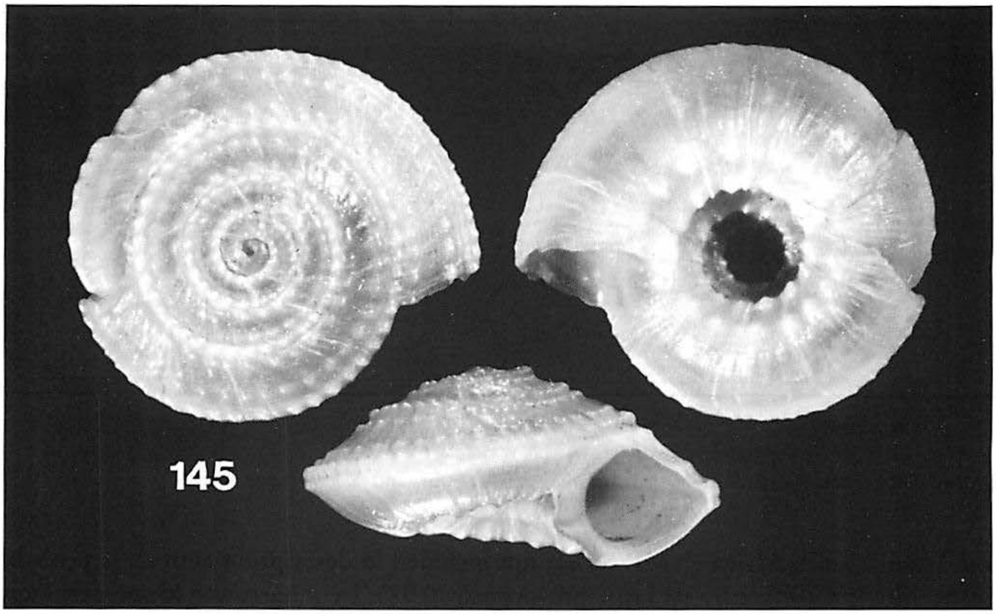


Fig. 145. *Solatisonax rehderi* n.sp.; holotype; Hawaiian Islands; USNM 173045; SD = 7.2.

prominent, ± finely granulose peripheral keel (usually with spiral groove on upper or peripheral side); here also upper point of whorl attachment; IPR-area with very weak, fine spiral threads (IPR not always distinctly separated); Base: BF with very weak, fine spiral threads; umbilicus surrounded by two almost identical rows of coarse crenae (not separated as spiral ribs), of which the inner one is sunken into the umbilicus; inner lip with groove in UC. Coloration: Off-white to yellowish-tan, with peripheral keel lighter colored. - Protoconch (see Figs.129, 138): small (0.72–0.90, $\bar{x}$ = 0.83), heterostrophic, without anal keel; off-white. - Periostracum: olive- or greyish-brown, covering shell coloration. - Operculum: consisting of horny, multispiral lamellae; round, cone-shaped; with plug-shaped projection on body side. - Radula and Anatomy: not known.

Geographical distribution (Fig.146): Known from western Indian Ocean and western to central Pacific.

Habitat: Sublittoral to upper bathyal (depth records between 75 and 624 m), live records from throughout that range, sand and mud.

Discussion:

Solatisonax rehderi n.sp. differs from other Indo-Pacific *Solatisonax* species by its very coarse umbilical crenae which are sunken into the umbilicus. Small specimens (e.g., paratype 4) are similar in shape and sculpture to members of the *Pseudotorinia numulus*-group (see below), but lack the distinct coin-shape and the more regular spiral sculpture of midrib area and outer base of that group. An additional specimen

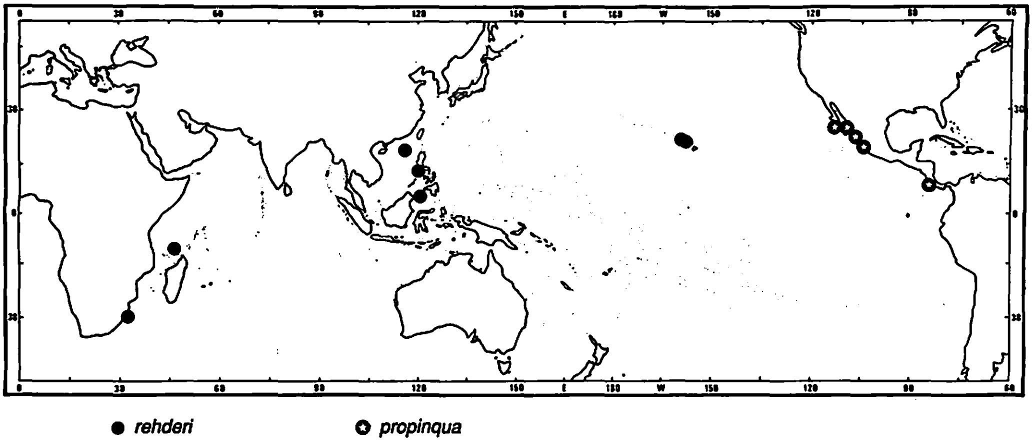


Fig. 146. Geographical distribution of *Solatisonax rehderi* n.sp. and *S. propinqua* n.sp.

from Natal, South Africa (NMP D761, not included in description above), is probably conspecific, but differs by its large protoconch (0.98), by a narrower lower peripheral rib, and by having a sculpture of numerous, more or less regular spiral threads in midrib area and outer base.

Very similar is an Atlantic species, described as *Solarium sigsbeei* DALL, 1889 (1889a: 275, pl.23 figs.3-3a; holotype in USNM 508722, vidi). *Solatisonax sigsbeei* differs from *S. rehderi* especially in the upper side teleoconch sculpture: in *S. sigsbeei* the upper peripheral rib is not fused with the keel-forming lower peripheral rib, but forms an almost identical, separated rib; in addition, 2-3 distinct spiral ribs are found in the midrib-area, between upper peripheral rib and the often distinctly-marked subsutural rib.

Solatisonax propinqua n.sp.
Figs.146–148

1976 *Heliacus* n.sp. aff. *alleryi*, - ROBERTSON, 1976a, Bull. Amer. malac. Union, *1975*: 51.

Type measurements:

	SD	H	PD	Tw	UD	Locality	Collection
Holotype	8.2	4.1	0.82	3 1/4-	2.0	Baja California	ANSP 328074
Paratype 1	8.1	4.4	0.90	3 1/4+	2.0	Baja California	ANSP 387031
Paratype 2	6.2	2.8	0.88	2 5/8	1.3	Baja California	ANSP 387031
Paratype 3	5.5	2.7	0.86	2 5/8	1.2	Jalisco, Mexico	LACM 2473
Paratype 4	6.5	3.5	0.88	3-	1.7	Jalisco, Mexico	FMNH 223413
Paratype 5	ca.10.6	5.7	0.86	3 7/8-	2.9	Costa Rica	LACM 2474 [damaged]

Type locality: Los Frailes, between Cape San Lucas and La Paz, close to Cabo Pulmo, Baja California Sur, W. Mexico (23°21'N, 109°25'W); 46–60 m [leg. JIM BAILEY, March 1972]. Paratypes 1–2 from holotype lot. Paratypes 3–4 from Bahía Banderas, Jalisco, W. Mexico (20°40'N, 105°25'W); 37–73 m [leg. GEORGE WILLETT, 14 February

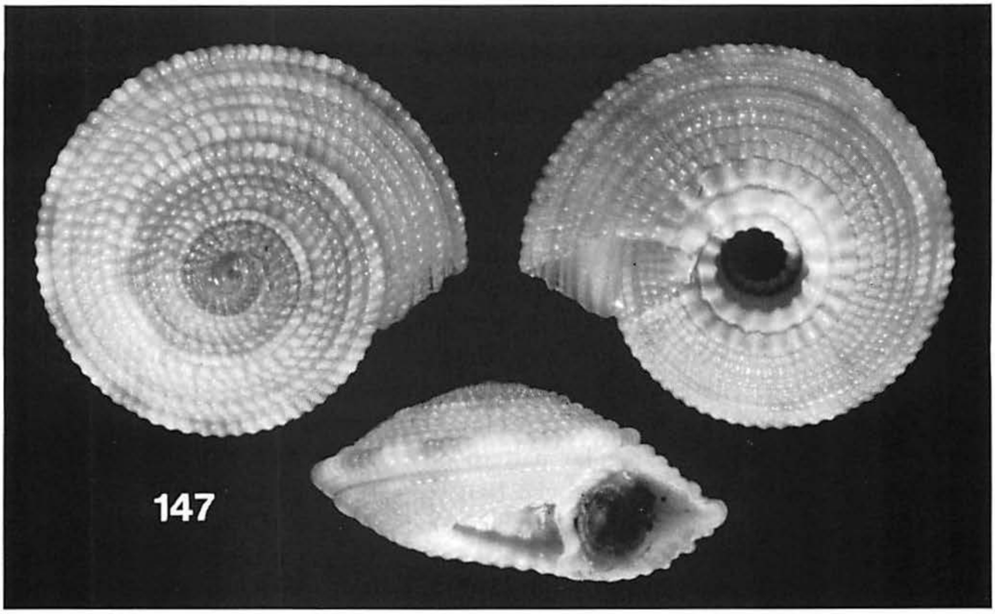


Fig. 147. *Solatisonax propinqua* n.sp.; holotype; Baja California Sur, Mexico; ANSP 328074; SD = 8.2.

1938]. Paratype 5 from off Isla del Caño, Puntarenas, Costa Rica (8°45'N, 83°54'W), 55 m ['SEARCHER' Stas. 479, 484, 485; leg. JAMES F. MCLEAN, 16–17 March 1972].

Material studied: 6 type specimens (as listed above), and 4 additional Mexican specimens from Baja California, Nayarit and Jalisco (AMNH, LACM).

Etymology: *propinquus-a-um* [adjective]; Latin: related; referring to the great similarity (and possibly close relationship) to its Atlantic 'sibling,' *Solatisonax alleryi* (SEGUENZA, 1876).

Diagnosis:

Small, lens-shaped shell with weakly convex whorls, prominent peripheral keel, moderately wide umbilicus, and regular sculpture of beaded, well-separated spiral ribs (subsutural rib, two midribs, upper peripheral rib, keel-forming lower peripheral rib, infraperipheral rib and six ribs on base; larger specimens with additional finer spiral threads, especially flanking infraperipheral rib); umbilical crenae not sunken into umbilicus. Overall yellowish-tan, with umbilical crenae lighter colored and peripheral ribs with regular pattern of orange-brown blotches. Protoconch diameter 0.82–0.92 mm; distinctly heterostrophic, without anal keel. Operculum concave.

Description:

Teleoconch: small, diameter of specimens in collections 6.2–10.0 at 2 5/8 to 3 5/8 whorls. Shape: lens-shaped with weakly convex whorls, prominent peripheral keel;

umbilicus moderately wide (UD ca. 24% of SD). Sculpture: very regular; consisting of beaded spiral ribs; Upper side: SSR and (slightly weaker) two MR distinctly separated and with regular, ± fine granules (in one specimen with only one MR developed); larger specimens with additional fine spiral threads between ribs, especially between LMR and UPR. Periphery: UPR stronger than MR, similar to SSR; keel-forming LPR strong, with regular granules; one additional spiral rib between UPR and LPR; upper point of whorl attachment on lower part of LPR, thereby forming a narrow suture; narrow IPR distinctly separated, flanked on both sides by additional spiral threads; Base: 6 ± strong, beaded spiral ribs (increasing in width towards umbilicus), the innermost (UC) surrounding umbilicus with moderately strong nodules; umbilical side of columellar wall convex, without distinct spiral ribs, but area next to base of preceeding whorl often with prominent, ± wide ridge bearing spiral threads; inner lip with groove in UC. Coloration: overall yellowish-tan; UC lighter colored; LPR and IPR with regular pattern of orange-brown blotches, each blotch about three nodules wide. - Protoconch (see Fig.148): small to medium-sized (0.82–0.92, $\bar{x}$ = 0.88), distinctly heterostrophic (shaped as in *Solatisonax radialis*; see Fig.135), without anal keel; yellowish to tan. - Periostracum: thin, brownish. - Operculum: consisting of horny, multispiral lamellae; round, concave; with plug-shaped projection on body side. - Radula and Anatomy: not known.

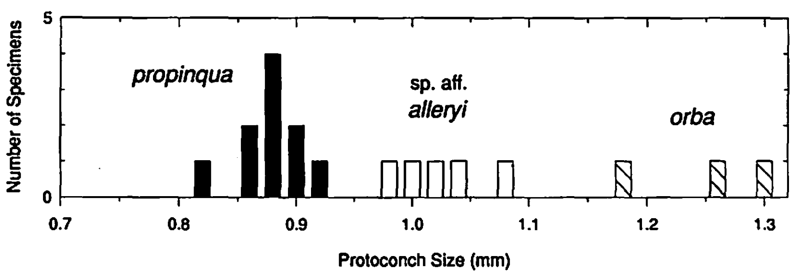


Fig. 148. Histograms of measured protoconch size. *Solatisonax propinqua* n.sp. (n = 10, $\bar{x}$ = 0.88, sd = 0.03), *S.* sp. aff. *alleryi* (n = 5, $\bar{x}$ = 1.02), and *S.? orba* n.sp. (n = 3, $\bar{x}$ = 1.25).

Geographical distribution (see Fig.146): Eastern Pacific (known from Baja California, Nayarit and Jalisco in western Mexico, and Puntarenas in Costa Rica).

Habitat: Sublittoral (depth records between 18 and 88 m), live specimens from 37– 73 m.

Discussion:

The regular shell sculpture of beaded ribs of *Solatisonax propinqua* n.sp. is reminiscent of *Heliacus*. In the latter genus, however, the infraperipheral rib forms a second peripheral keel almost as prominent as the upper peripheral rib, and the operculum is high-spired (or secondarily depressed) cone-shaped.

Sympatric *Solatisonax? orba* n.sp. (see below) and the Atlantic species *Solatisonax alleryi* (G. SEGUENZA, 1876) (see discussion under *S.* sp. aff. *alleryi*; below) are very similar.

Solatisonax sp. aff. *alleryi* (G. SEGUENZA, 1876)

Figs.148–150

Measurements (figured specimen): SD = 5.3, H = 2.8, PD = 1.02, Tw = 2 5/8+, UD = 1.2 [NMP C1810, South Africa].

Material studied: 5 specimens (NMNZ, NMP).

Diagnosis:

Small, lens-shaped to depressed cone-shaped shell with weakly convex whorls, prominent peripheral keel, widely open umbilicus, and sculpture of beaded spiral ribs of various width; subsutural and upper peripheral ribs stronger than 2–3 (usually flattened) midribs; basal ribs next to umbilical crenae often weakly developed or even fused; umbilical crenae separated, not lowered into umbilicus. Overall off-white to yellowish; keel-forming lower peripheral rib with regular pattern of orange-brown blotches. Protoconch diameter 0.98–1.08 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: small, diameter of specimens in collections 3.9–6.1 at 1 7/8 to 3 1/4-whorls. Shape: lens-shaped to depressed cone-shaped with weakly convex whorls, prominent peripheral keel; umbilicus widely open (UD ca. 26% of SD). Sculpture: consisting of beaded spiral ribs of various width; Upper side: SSR and 2–3 finer MR distinctly separated and with ± regular, fine granules; larger specimens with additional fine spiral thread between LMR and UPR. Periphery: UPR stronger than MR (in some specimens strongly nodose on early whorls), similar to SSR; keel-forming LPR strong, with fine, ± regular granules; one additional spiral rib between UPR and LPR; upper point of whorl attachment at base of LPR, peripheral keel therefore overlapping onto SSR of following whorl; narrow IPR distinctly separated, but hardly stronger than basal ribs; one additional spiral thread between LPR and IPR; Base: with up to 6 ± well-defined spiral ribs (increasing in width towards umbilicus), the innermost (UC) surrounding umbilicus with moderately strong nodules; basal ribs next to UC often fused, forming a ± smooth plane; umbilical side of columellar wall straight or somewhat convex, with microscopic spiral threads, without spiral ribs. Coloration: off-white to yellowish; LPR (sometimes also SSR and UPR) with regular pattern of orange-brown blotches, each about 2–3 nodules wide. – Protoconch (see Fig.148): medium-sized (0.98–1.08, $\bar{x}$ = 1.02), distinctly heterostrophic (shaped as in *Solatisonax radialis*; see Fig.135), without anal keel; whitish with outer corner next to varix darker. – Periostracum, Operculum, Radula and Anatomy: not known.

Geographical distribution (see Fig.150): Known from western Indian Ocean (Transkei in South Africa) and western Pacific (Kermadec Islands).

Habitat: Lower sublittoral (depth records between 178 and 430 m), mud and sand and stone substrates, no live records.

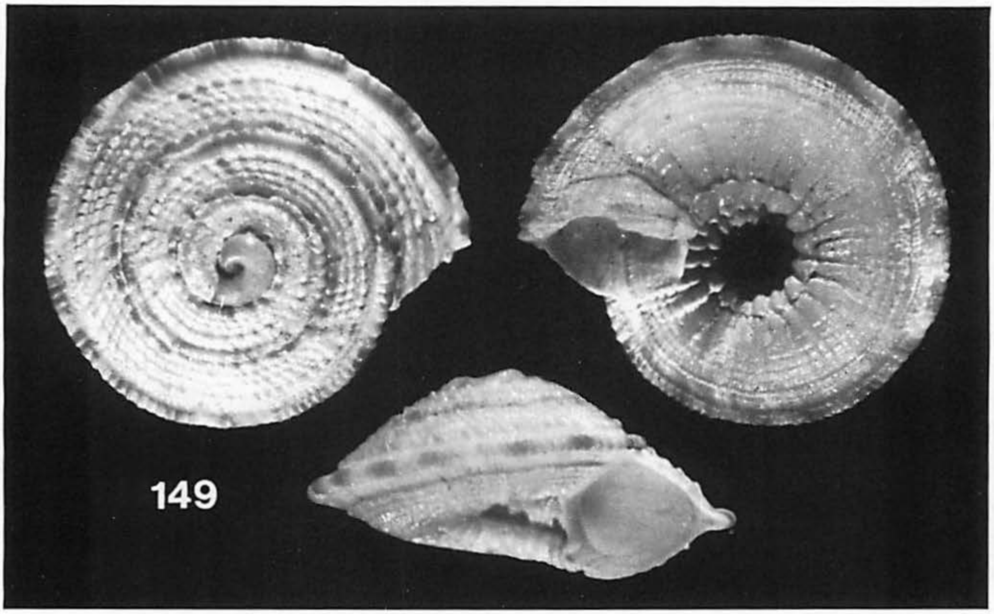


Fig. 149. *Solatisonax* sp. aff. *alleryi* (G. SEGUENZA, 1876); specimen from Transkei, South Africa; NMP C.1810; SD = 5.3.

Discussion:

The known Indo-Pacific specimens of this form seem to fall within the range of variation displayed by *Solatisonax alleryi* (SEGUENZA, 1876) in the Atlantic Ocean. The latter species is often erroneously assigned to MONTEROSATO, who (1878: 97) justifiably emendated SEGUENZA's (1876: 10) original spelling "allerii" to "*alleryi*" [named after MARCHESE T. ALLERY DI MONTEROSATO].

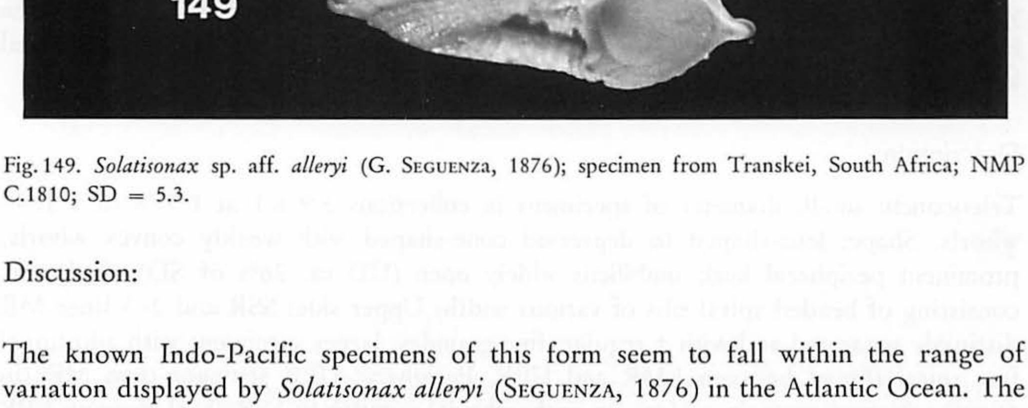


Fig. 150. Geographical distribution of *Solatisonax* sp. aff. *alleryi* and *S.? orba* n.sp.

Number and arrangement of spiral ribs are similar to those of *Solatisonax propinqua* n.sp. (see above). That species, however, has much more regular sculpture (with the two midribs, upper peripheral rib and the basal ribs better defined), and a smaller protoconch (0.82–0.92 mm).

Solatisonax? orba n.sp.
Figs.148, 150, 151

Type measurements:

	SD	H	PD	Tw	UD	Locality	Collection
Holotype	23.5	10.1	1.26	5 1/10	7.9	Gorda Bank	LACM 2471
Paratype 1	13.6	6.9	1.18	4 3/8	3.7	Bahía Concepcíon	LACM 2472
Paratype 2	12.1	5.9	1.30	3 7/8	3.6	San Jaime Bank	FMNH 223412 [damaged]

Type locality: Inner Gorda Bank, Baja California Sur, W. Mexico (23°02'27"N, 109°30'42"W); 108–143 m, on coarse grey sand; 17 February 1940. Paratype 1 from Bahía Concepción, Baja California Sur, W. Mexico (26°44'40"N, 110°54'W); intertidal on west beach; 14 March 1936. Paratype 2 from San Jaime Bank, off Cabo San Lucas, Baja California Sur, W. Mexico (22°50'30"N, 110°15'W); 137 m, on rocks; 3 March 1937.

Material studied: 3 type specimens (as listed above); and one very worn specimen from north of Isla San Pedro Nolasco, Gulf of California, Baja California, Mexico (28°00'20"N, 111°24'40"W); 183 m, on sand bottom; 12 March 1936 (LACM 36-89.2).

Etymology: *orbus-a-um* [adjective]; Latin: orphaned; here referring to its currently uncertain generic position.

Diagnosis:

Medium-sized to large, depressed cone-shaped shell with inflated whorls, prominent peripheral keel, widely open umbilicus, and regular sculpture of finely beaded, well-separated spiral ribs; subsutural rib, 3–5 narrow midribs, upper peripheral rib, keel-forming lower peripheral rib, infraperipheral rib and numerous, well-defined threads or ribs on base; no additional spiral threads between upper and lower peripheral or lower and infraperipheral ribs; umbilical crenae not sunken into umbilicus. Overall yellowish-tan on upper side, subsutural rib with solid brown band, upper and lower peripheral ribs with regular pattern of brown blotches; base fawn with ribs surrounding umbilicus darkest. Protoconch diameter 1.18–1.30 mm; distinctly heterostrophic, without anal keel.

Description:

Teleoconch: medium-sized to large, diameter of known specimens 12.1–23.5 at 3 7/8 to 5 1/4 whorls. Shape: depressed cone-shaped with ± inflated whorls and prominent peripheral keel; umbilicus widely open (UD ca. 29% of SD). Sculpture: very regular;

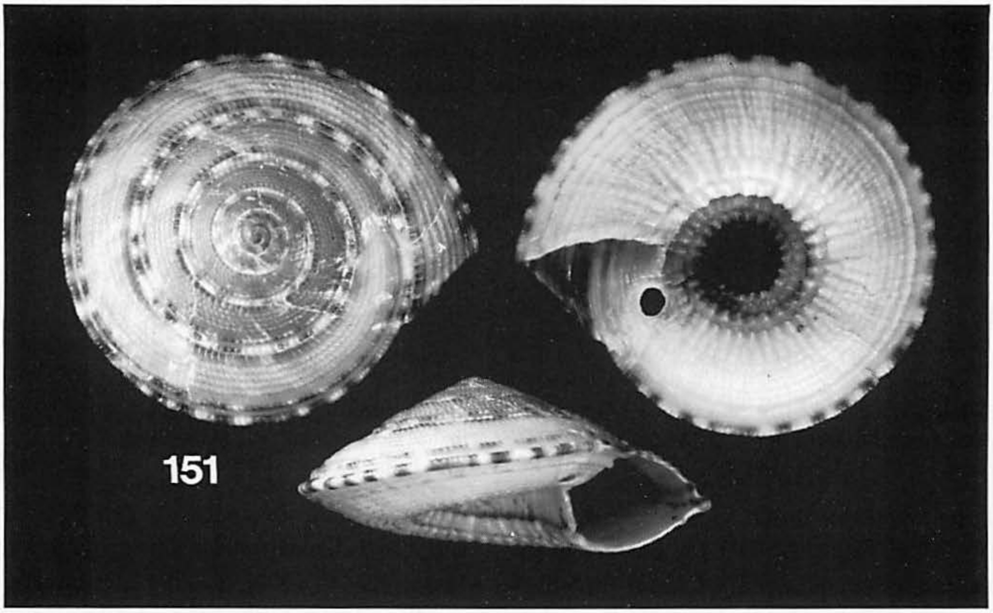


Fig. 151. *Solatisonax? orba* n.sp.; holotype; Baja California Sur, Mexico; LACM 2471; SD = 23.5. Fig. 152 not used.

consisting of finely beaded spiral ribs; Upper side: SSR and narrower 3–5 MR distinctly separated and with regular, ± fine granules (specimens with 3–4 MR have ± wide groove before UPR); Periphery: UPR more prominent than MR, not as strong as SSR; keel-forming LPR with fine, ± regular granules; without additional spiral ribs between UPR and LPR and LPR and IPR; upper point of whorl attachment at center of LPR (LPR thereby forming part of the upper side sculpture); narrow IPR distinctly separated; Base: ca. 7 ± ill-defined spiral threads or ribs (increasing in width towards umbilicus), and two stronger, ± well-defined ribs (PUR and UC) surrounding umbilicus with fine, regular nodules; umbilical side of columellar wall straight, with microscopic spiral threads, without spiral ribs; inner lip with groove in UC and shallow depression close to base of preceding whorl. Coloration: upper side yellowish-tan; SSR with ± solid brown band, UPR and LPR (sometimes also IPR) with regular pattern of brown blotches; base fawn with ribs surrounding umbilicus darker. – Protoconch (Fig. 148): medium-sized to large (1.18–1.30, $\bar{x}$ = 1.25), distinctly heterostrophic (shaped as in *S. supraradiata*; see Fig. 136), without anal keel; yellowish to tan. – Periostracum: thin, light-brown; scaly on umbilical wall. – Operculum, Radula and Anatomy: not known.

Geographical distribution (Fig. 150): Known only from Gulf of California and from off southern tip of Baja California, Mexico.

Habitat: Sublittoral (depth records from 108–183 m, one empty shell from intertidal), sand and hard substrates, no live records, but holotype very fresh.

Discussion:

The generic position of *Solatisonax? orba* n.sp. is problematic. While it has the inflated shell and an upper-side spiral sculpture as in some species of *Solatisonax* (e.g., *S. propinqua* n.sp., see above), the sculpture of the base is reminiscent of *Discotectonica* spp., while the color pattern and overall shell shape (especially of the higher-spired paratypes) are similar to species of *Adelphotectonica*. All three genera in question differ greatly in features of the buccal apparatus and radula, but since only empty shells are available to date, a positive assignment cannot be made at this point.

Two superficially similar species are sympatric: *Solatisonax propinqua* n.sp. (above), with a much smaller shell that differs in having only two midribs, well-defined outer basal ribs and a different color pattern, and *Discotectonica placentalis*, which has three flattened, more or less smooth midribs on the teleoconch and a much smaller (0.62–0.72) protoconch.

Genus *Heliacus* Orbigny *in* Sagra, 1842

Heliacus Orbigny *in* Sagra, 1842: 68; introduced as "Division" of *Solarium* [= *Architectonica*]. Type species by monotypy, using the incorrect secondary spelling "heberti": *Solarium herberti* Deshayes, 1830 [= *Heliacus cylindricus* (Gmelin, 1791)]; Recent, Atlantic Ocean.

Synonyms:

Torinia Gray [1840: 147, *nomen nudum*], 1842: 60 [no nominal species included]. Type species by secondary monotypy: *Trochus cylindraceus* Dillwyn, 1817 [= *Trochus cylindricus* Gmelin, 1791].

Incorrect subsequent spellings:

"Helicarius" Biggs, 1972; "Thorinia" Deshayes, 1863; "Tornia" Habe & Kosuge, 1966; "Trinia" Carus, 1875 [non *Trinia* Polataeva, 1956 (Trilobita)].

Description:

Teleoconch: very small to large (usually 5–12 mm, rarely over 30 mm), almost disk-shaped to tall roundly cone-shaped, with very narrow *(Gyriscus)* to extremely wide umbilicus *(Torinista, Teretropoma)*; whorls weakly to distinctly bulging; sculpture: distinct axial (growth) sculpture crossing spiral ribs on entire surface; apical side: subsutural rib, 1–3 midribs and upper peripheral rib usually ± equally developed; midribs, occasionally also upper peripheral ribs fused (*Torinista* spp.); periphery formed by 2 in most cases ± equally strong ribs (LPR and IPR), between them often additional weaker spiral ribs; upper point of whorl attachment at lower peripheral rib, infraperipheral rib, or between them; base with 5–6 main spiral ribs, increasing in width towards umbilicus; innermost basal rib (UC) surrounding umbilicus with ± coarse nodules; in some species (*Teretropoma*, *Gyriscus*) fine additional ribs between main ribs on entire surface; umbilical wall usually with 1–2 narrow spiral ribs; coloration usually of distinct flecks and flames in brown or black on lighter, often white background. *Protoconch:* very small to large (0.55–1.4), distinctly heterostrophic, rarely with anal keel. *Radula:* five-toothed-taenioglossate; rachidian with strong central cusp flanked by numerous (6–22) smaller cusps on either side; inner and outer marginals with 4–13 cusps each. *Operculum:* horny, round, almost flat to tall cone-shaped, with pointed, peg-like projection on body side; peg not reinforced by external callus.

For a more extensive description and discussion of this genus and its subgenera see Bieler (1985b: 95–105; 1987: 206–208).

Subgenus *Heliacus (Heliacus)* Orbigny *in* Sagra, 1842

Description (Fig. 153):

Teleoconch: small to medium-sized (usually 6–13 mm, rarely over 20 mm), depressed to tall roundly cone-shaped, with narrow to very wide umbilicus (ca. 8–40% of shell diameter); whorls weakly to distinctly bulging; sculpture: spiral ribs with relatively large nodules on entire surface; number of ribs constant, only between lower peripheral and infraperipheral ribs occasionally with 1 ± strong additional rib; apical side: subsutural rib, single midrib (or two narrow ones) and upper peripheral rib usually equally developed, rarely upper peripheral rib somewhat stronger; periphery

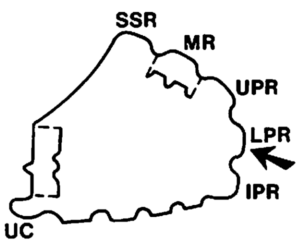


Fig. 153. Schematic representation of placement of major spiral ribs in *Heliacus (Heliacus)*, apertural aspect. Arrow shows point of attachment of next whorl, intrageneric variation indicated by dotted lines.

formed by lower peripheral rib and only slightly weaker infraperipheral rib (occasionally with additional rib between them); upper point of whorl attachment at or below lower peripheral rib; base usually with 5 spiral ribs, increasing in width towards umbilicus; umbilical wall usually with 1–2 strong, narrow spiral ribs; coloration of (in most cases distinctly demarcated) brown to black flecks and flames on ± white background, with peripheral ribs as a rule with very regular pattern; subsutural rib, infraperipheral rib and rib surrounding umbilicus (UC) often lighter colored. *Protoconch:* very small to medium-sized (0.55–1.05), distinctly heterostrophic, without anal keel. *Radula:* five-toothed-taenioglossate; rachidian with strong central cusp flanked by numerous (12–20) smaller cusps on either side; inner and outer marginals with 5–13 cusps each. *Operculum:* horny, round, cone-shaped, with peg-like projection on body side.

Heliacus (Heliacus) variegatus (GMELIN, 1791)
Pl.2 Fig.C, Pl.3 Fig.A, Figs.6, 154–158

1781 "Trochus perspectiviunculus", - CHEMNITZ, Conch.-Cab., *5*: 13 [not binominal].
1781 "Trochus perspectiviunculus variegatus ...", - CHEMNITZ, Conch.-Cab., *5*: 134, pl.173 figs.1708–1709 [not binominal].
1783 "Das bunte Perspectivchen", - SCHRÖTER, Einl. Conchylienkenntniß, *1*: 718.
1790 -------, GEVE, Belustigung, pl.25 figs.275a-c, 276a-b.
*1791 *Trochus variegatus* GMELIN, Syst. nat. (13.ed.), *1*(6): 3575.
1793 *Trochus variegatus*, - SCHREIBERS, Vers. vollst. Conchylienkenntniß, *1*: 247.
1801 *Trochus variegatus*, - BOSC, Hist. nat. coqu, *4*: 163 [referring to CHEMNITZ 1781: fig. 1709 only].
1816 *Solarium variegatum*, - LAMARCK, Tabl. encycl. méth.: pl.446 figs.6a-b.
*1817 *Trochus perspectiviunculus* DILLWYN, Descr. cat. Rec. shells, *2*: 783.
1822 *Solarium variegatum*, - LAMARCK, Hist. nat., *7*: 4.
1825 *Trochus variegatus*, - WOOD, Index testac.: 137, pl.29 fig.59.
1825 *Solarium variegatum*, - BLAINVILLE, Man. Malac. Conchyl.: 424.
1830 *Trochus variegatus*, - BOSC, Hist. nat. coqu., *4*: 154.
1830 *Solarium variegatum*, - DESHAYES, 1830a, Encycl. méth., *2*(1): 159 [excluding var.B].
1838–1839 *Solarium variegatum*, - KIENER, Spéc. gén. icon. coqu., *10*: 10, pl.4 fig.7a.
1843 *Solarium variegatum*, - DESHAYES, Hist. nat., *9*: 99.
1853 *Solarium perspectiviunculum*, - PHILIPPI, 1853b [in part], Syst. Conch.-Cab. II, *7*: 12, pl.2 figs.10–11 [after CHEMNITZ, 1781].
*1853 *Solarium perspectiviunculum* varietas *depressa* PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 30, pl.4 fig.10 [non *Solarium depressum* GRATELOUP, 1832, nec *Solarium depressum* ALTH, 1850, nec *Solarium depressum* PIETTE *in* TERQUEM & PIETTE, 1865].
1853 "Solarium articulatum" PHILIPPI, 1853b, Syst.Conch.-Cab. II, *7*: 30 [not available; published as junior synonym].
1856 *variegatus (Solarium)*, - HANLEY, [WOOD's] Index testac.: 143, pl.29 fig.59.
*1863 *Solarium (Torinia) perspectiviunculus* Var.? *planulata* HANLEY, Thes. conch., *3*: 238, pl.254 fig.63.
1865 *Torinia variegata*, - CARPENTER, 1865a, Proc. zool. Soc. Lond., *1865*: 516.
1865 "Torinia corrugata PEASE" CARPENTER, 1865a, Proc. zool. Soc. Lond., *1865*: 516 [not available; published as junior synonym].
1869 *Torinia planulata*, - PEASE, 1869b, Amer. J. Conch., *5*(2): 80.
1876–1878 *Solarium (Torinia) variegatum*, - KOBELT, Illus. Conchylienb., *1*: 87, pl.32 fig.10.
1887 *Torinia (Torinia) variegata* var. *depressa*, - MARSHALL, Man. conch., *9*: 17, pl.5 figs.78–79 [after PHILIPPI, 1853b].
1887 *Torinia (Torinia) variegata* var. *planulata*, - MARSHALL, Man. conch., *9*: 17, pl.5 fig.77 [after HANLEY, 1863].
1889 *Solarium (Torinia) variegatum*, - SOWERBY (III) [in part], - J. Conch., *6*: 9.
1892 *Solarium variegatum*, - SOWERBY (III) [in part], Mar. shells S. Afr.: 28.
1909 *Torinia planulata*, - SCHEPMAN, Monogr. Res. SIBOGA Exped., 49(1b): 221.
1933 *Torinia variegata depressa*, - EDMONDSON, Bernice P. Bishop Mus. Spec. Publ., *22*: 136, fig.60b.
*1948 *Torinia gyrus* subsp. *depressiuscula* nom. nov. BAYER, Zool. Verh., *4*: 22.
1948 *Torinia gyrus* subsp. *variegata*, - BAYER [in part], Zool. Verh., *4*: 23.
1952 *Torinia variegata*, - TINKER [in part], Pac. sea shells: 177, pl. p.179 (third row, left) [right = *Heliacus areola* GMELIN].
1954 *Heliacus dorsuosus*, - HIRASE (& TAKI), Illus. handbook shells: pl.128 fig.9.
1963 *Heliacus variegatus*, - BARNARD, 1963b [in part], Ann. S. Afr. Mus., *47*(1): 162.
1966 *Heliacus depressiusculus*, - HABE & KOSUGE, Shells world col., *II*: 102, pl.40 fig.8.
1967 *Heliacus variegatus*, - ROBERTSON, Science, *156*(3772):246.
1974 *Torinia variegata*, - DANCE, Coll. encycl. shells: 63, fig.
1974 *Torinia variegata*, - MORRIS, Field guide Pac. coast shells: 223, pl.8 fig.4, pl.67 fig.9.
1975 *Heliacus variegatus*, - SALVAT & RIVES, Coqu. Polynesie: 265, fig.48.

1975 *Torinia variegata*, - COLEMAN, What shell is that?: 46, fig.104.
1977 *Heliacus (Heliacus) variegatus*, - GARRARD [in part], Rec. Austr. Mus., *31*(13): 539, pl.7 figs.16-18 [non figs.13-15 = *H. areola*].
1978 *Heliacus variegatus*, - KIRTISINGHE, Sea shells Sri Lanka: pl.29 fig.4.
1978 *Heliacus dorsuosus*, - CERNOHORSKY, Trop. Pac. mar. shells: 165, pl.58 fig.9.
1979 *Heliacus variegatus*, - KAY, Hawaii. mar. shells: 99, fig.35 M-N.
1982 *Heliacus variegatus*, - KILBURN & RIPPEY, Sea shells s. Afr.: 77, pl.11 fig.10, pl.3 fig.4 [*in situ*].
1982 *Heliacus variegatus*, - BOSCH & BOSCH, Seashells Oman: 43, fig.
1984 *Heliacus variegatus*, - BIELER, 1984b, Arch. Moll., *115*(1/3): pl.1 fig.3 [operculum].
1984 *Heliacus variegatus*, - SHARABATI, Red Sea shells: pl.5 figs.4-4a.
1985 *Heliacus (Heliacus) variegatus*, - BIELER, 1985b, Arch. Moll., *116*(1/3): 98.
1985 *Heliacus variegatus*, - DRIVAS & JAY [in part], La Conchiglia, *17*(190-191): 8, fig.8 [not fig.7 = *H. areola*].
1985 *Heliacus variegatus*, - HAZPRUNAR, 1985b, Zool. Scr., *14*(1): 25ff., figs.1, 3, 4, 16, 17, 21, 23, 24 [anatomy], 6, 8 [shell], 13-15 [larvae].
1986 *Heliacus (Torinista) dorsuosus*, - SPRINGSTEEN & LEOBRERA, Shells Philippines: 26, pl.2 fig.13.
1988 *Heliacus variegatus*, - BIELER, Malac. Rev., Suppl. *4*: 212, 237, fig.2 [operculum], p. 215, fig.12 [radula].
1988 *Heliacus variegatus*, - HEALY, Malac. Rev., Suppl. *4*: 263, figs.41, 49, 50.
1989 *Heliacus variegatus*, - BOSCH & BOSCH, Seashells s. Arabia: 35, text-fig.

Type localities: *T. variegatus*: "Habitat: ---" [unknown]; *T. perspectiviunculus*: none given; *S. perspectiviunculum* var. *depressa*: none given; *S. perspectiviunculus* var. *planulata*: none given.

Etymology: *variegatus-a-um* [adjective]; Latin: with diverse colors, streaked.

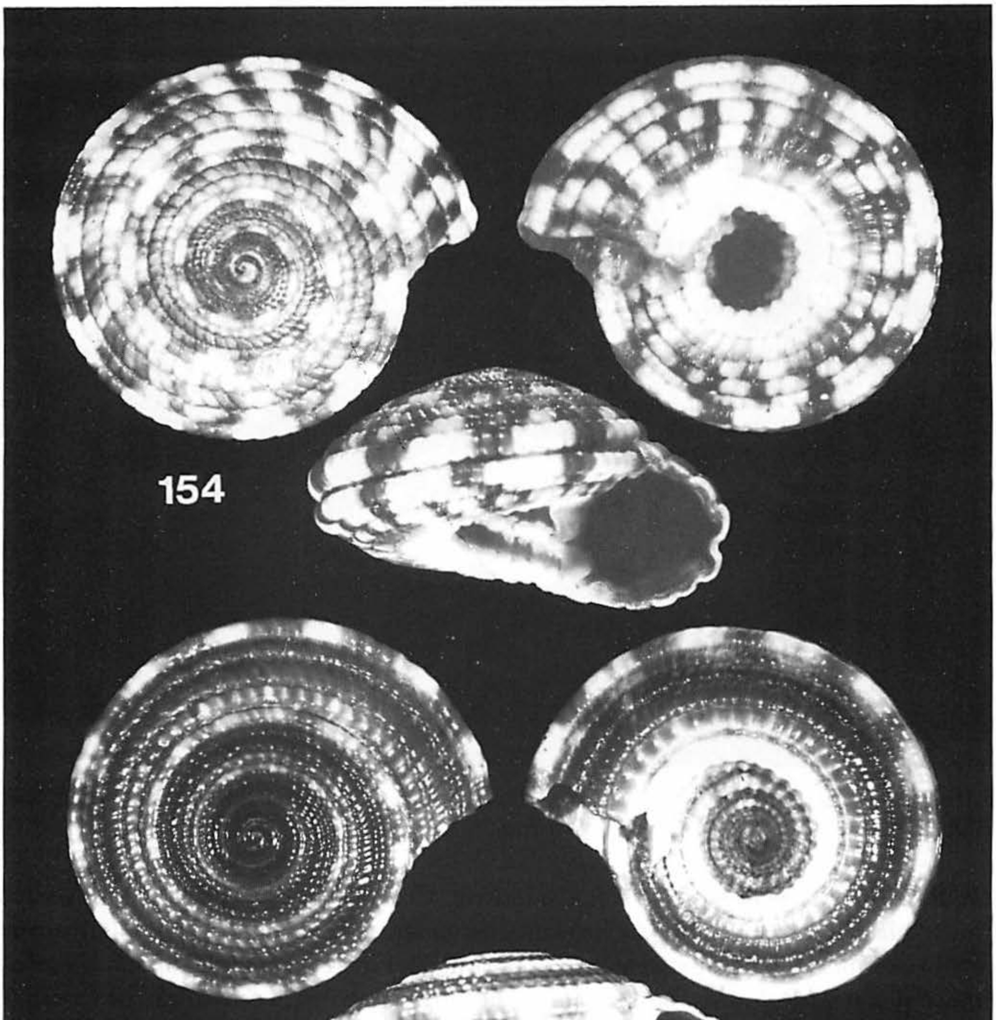
Material studied: 2000+ specimens (AMNH, AMS, ANSP, BMNH, BPBM, CAS, DMNH, FLMNH, FMNH, HUJ, IRSNB, LACM, LMA, MCZ, MNHNP, MNHU, NMP, NMW, OUM, RNHL, SMF, SMNS, UCMP, UMZC, USNM, ZMA, ZSM, Coll. MARAIS, Coll. TRONDLE), including original material ex SPENGLER Coll. (ZMK), and holotype of var. *planulata* (BMNH 1907.10.28.64). Original material of var. *depressa* PHILIPPI not located.

Diagnosis:

Small to medium-sized, depressed to rounded cone-shaped shell with very narrow to wide umbilicus; upper-side sculpture of 3 almost-identical ribs with more or less flattened nodules; rounded double keel formed by 2 almost-identical ribs; basal sculpture of 5 very regular spiral ribs; umbilical side of columellar wall with 1 strong spiral rib. Bluish white with pattern of brown to near-black flames, increasing in size with number of whorls; parietal region usually brownish. Protoconch diameter 0.76-0.88 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: small to medium-sized, diameter of specimens in collections usually 7-13 at 3 1/3 to 4 2/3 whorls (rarely more than 15 at 5 1/2 whorls). Shape: from depressed cone-shaped with wide umbilicus to rounded cone-shaped with very narrow umbilicus (UD 8-31% of SD, $\bar{x}$ = 17.5). Sculpture: Upper side: SSR, single MR and UPR almost identical, with ± flattened nodules; Periphery: rounded double keel formed by



Figs. 154, 155. *Heliacus (Heliacus) variegatus* (GMELIN, 1791). Fig. 154: specimen from SPENGLER coll.; ZMK unnumbered. Fig. 155: holotype of *Solarium perspectiviunculus planulata* HANLEY, 1863; BMNH 1907.10.28.64.

almost identical LPR and IPR, rarely (in large specimens) with 1 additional, much finer rib between them; upper point of whorl attachment between LPR and IPR, suture shallow; Base: 5 very regular spiral ribs, somewhat increasing in width towards umbilicus, innermost forming UC; UC with 9–24 nodules on body whorl; umbilical

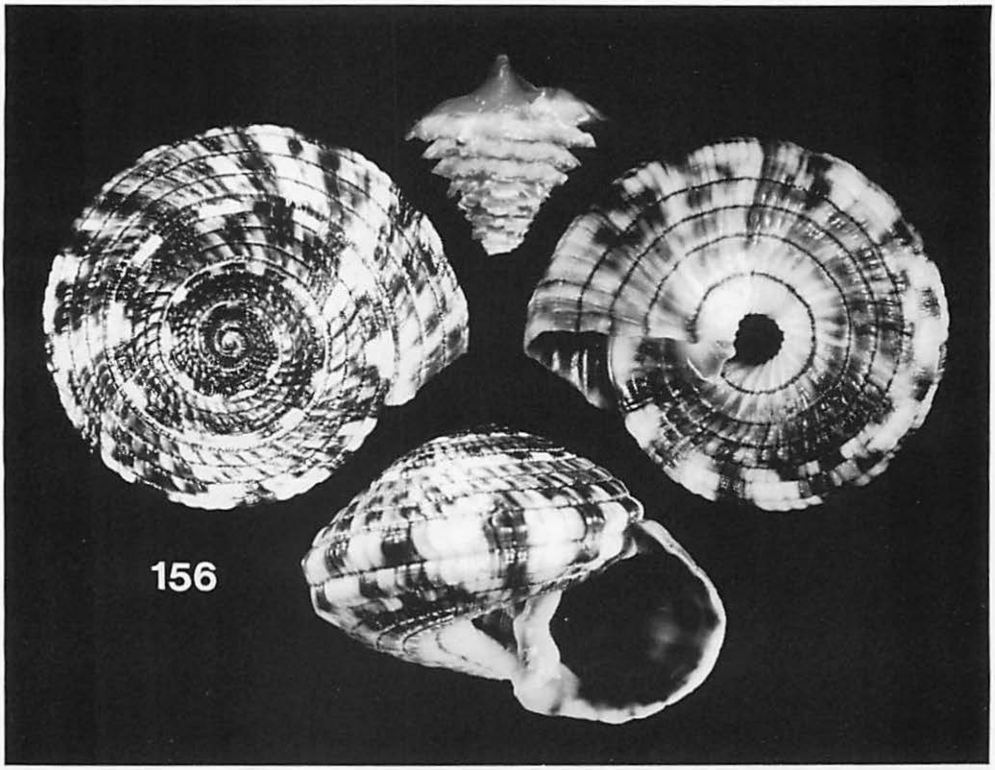


Fig. 156. *Heliacus (Heliacus) variegatus* (Gmelin, 1791); specimen from Port St. Johns, Transkei, South Africa; FMNH 223430; SD = 14.7. With operculum.

side of columellar wall with 1 strong spiral rib. Coloration: bluish white with pattern of near-black flames (fading to brown after death); especially peripheral ribs with lively brown-black/white pattern; size of dark flames increasing with whorls, therefore number per whorl almost constant in specimen; grooves between spiral ribs orange-brown; UC usually white, parietal region usually brownish. – Protoconch (Figs.6, 157): small (0.76–0.88, $\bar{x}$ = 0.83), multispiral, distinctly heterostrophic, without anal keel; bicolored, with area before peritreme dark brown to black and remainder glassy white; if dark area does not cover highest point of apex, with 1 brown fleck. – Operculum (Fig.156): as described for subgenus. – Radula: five-toothed taenioglossate (2–1–2); rachidian tooth stronger than marginal teeth, with prominent, pointed median cusp flanked by more than 20 smaller, blunt cusps; marginal teeth longer, curved and forked, inner marginals with 9–10, outer with 10–13 tapering cusps (Bieler, 1988: 215, 237, fig.12). – Anatomy: described by Haszprunar (1985b). – Soft-body coloration of living animal: body color milky to orange-white, tentacles and upper side of foot ± strongly speckled with black pigment (in larger animals tentacle tips and anterior margin of foot without black pigment); embedded white granules loosely distributed, including anterior foot margin; sole of foot with thin layer of black chromatophores, resulting in light-grey coloration (pers. obs., South Africa; see also Haszprunar, 1985b: figs.13–15).

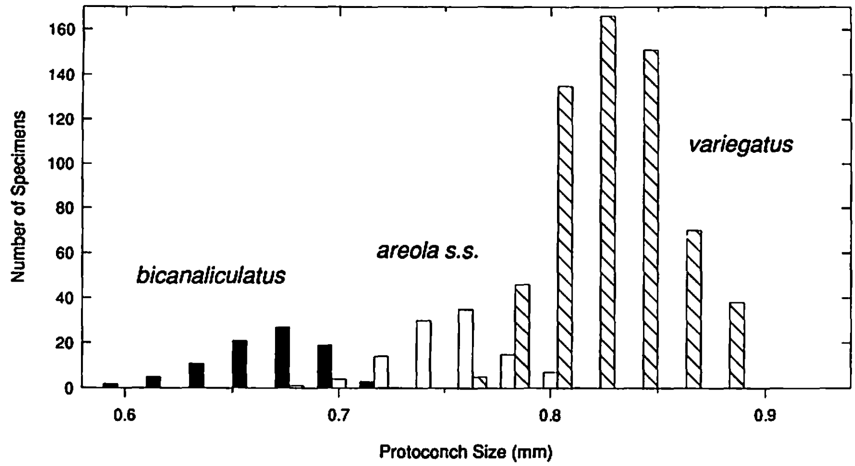


Fig. 157. Histograms of measured protoconch size. *Heliacus variegatus* (n = 611, $\bar{x}$ = 0.83, sd = 0.03), *H. areola* s.s. (n = 106, $\bar{x}$ = 0.75, sd = 0.03), and *H. areola bicanaliculatus* (n = 88, $\bar{x}$ = 0.67, sd = 0.03).

Reproduction and larval development: sausage-shaped, mucous egg masses of variable length (16–42 mm, $\bar{x}$ = 31, n =40) and a diameter of 2.8–3.1 mm, containing about 300 weakly oval eggs (0.1 x 0.13 mm) per mm. Eggs interconnected by chalazae and covered by an additional membrane within the mucous mass (see Pl.3 Fig.A) as described in the general part. Development time from single-cell stage to hatching 18 days at 20°C. Veliger at hatching with small velum, large larval organ and transparent, thin shell (pers. obs., South Africa). Sperm ultrastructure and spermiogenesis studied by HEALY (1988: 263, figs.41, 49, 50) and HEALY & JAMIESON (1991).

Geographical distribution (Fig.158): Continuous range from the African east coast to central Pacific.

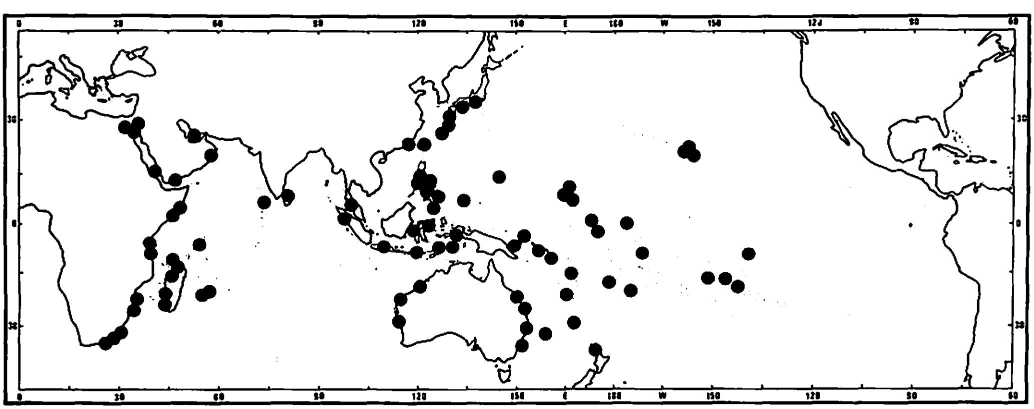


Fig. 158. Geographical distribution of *Heliacus variegatus*.

Habitat: Lives near or between polyps of intertidal and upper subtidal zoanthinarian colonies (see Pl.2 Fig.C).

Habits/feeding behavior: Feeds on zoanthinarian polyps (various species of zoanthid genera *Palythoa* and *Zoanthus*; see also ROBERTSON, 1967: 246). In exposed environments at the South African Natal and Transkei coasts, it prefers *Palythoa nelliae* PAX, 1935. This preference appears to be based on physical constraints (relation of shell size/polyp size; pers. obs.).

Discussion:

Heliacus variegatus is the most common intertidal species of this family in the Indo-Pacific. It shows a high intraspecific variability, similar to the range of variation displayed by *H. implexus* (MIGHELS, 1845) (see below). Within one population specimens can be found with very narrow or very wide umbilici, with very depressed or relatively high-spired shells (see Figs.154–156). As a result, several forms have been described and named as "variations," "forms," subspecies or even nominal species. The discussion usually focussed upon the interpretation of the figures in CHEMNITZ's 'Conchylien-Cabinet' (1781: pl.173 figs.1708–1709 and 1710–1711) which GMELIN (1791: 3575) cited in his description of the two nominal species *Trochus variegatus* and *Trochus areola*, respectively. According to GARRARD (1977: 540), these are members of the same polymorphic species and display within one population "every possible intergrade in colour pattern." This is not the case. Studies by the present author on South African populations of these forms, as well as comparative analyses of collection material from many localities throughout the Indo-Pacific, revealed two sympatric morphs that were always distinguishable by several characters. These two morphs are here interpreted as two species, *Heliacus variegatus* (GMELIN, 1791) and *Heliacus areola* (GMELIN, 1791). They differ in protoconch size (Fig.157) and in the coloration of the subsutural, infraperipheral and parietal ribs (usually white in *H. areola*). Other characters to distinguish the two are the number, shape and size of the color flecks on the peripheral ribs (counted on body whorl of specimens with more than 3 1/4 teleoconch whorls): in *H. variegatus* the number of the flecks on the peripheral ribs of the body whorl ranges from 6 to 16 ($\bar{x} = 10$, $n = 476$; flecks extending as flames), in *H. areola* this ranges from 10 to 23 ($\bar{x} = 15$, $n = 68$; flecks small and well-defined). In *H. areola* the subsutural rib is the lightest colored part of the teleoconch upper-side and periphery, in *H. variegatus* it is the lower peripheral rib. In *H. variegatus* the shell-shape varies from depressed to rounded cone-shaped, in *H. areola* it is always rounded cone-shaped.

Heliacus variegatus is often confused with *H. (Torinista) implexus* (MIGHELS, 1845) [= *dorsuosus* auct.; see below] and with *H. (T.) sterkii* PILSBRY & VANATTA, 1908. Members of those species, however, have two midribs, resulting in a total of five, not four, ribs visible on the upper side of the shell.

At least three names have been introduced for the depressed form of *Heliacus variegatus*. Two were named as "varieties" of *Solarium perspectiviunculum*: *depressa* PHILIPPI, 1853, and *planulata* HANLEY, 1863. BAYER (1948) recognized *Solarium* *depressum* and *S. planulatum* as preoccupied by GRATELOUP (1832) and introduced the new name *depressiuscula* for both of them. The names *perspectiviunculum* and *gyrus* originate from the non-binominal work of MEUSCHEN (1781), and were first validly introduced by DILLWYN (1817) and BAYER (1948), respectively (see also discussion under *Heliacus areola)*.

Trochus variegatus GMELIN and *T. perspectiviunculus* DILLWYN were both based on the mentioned description and illustrations of "Trochus perspectiviunculus variegatus" by CHEMNITZ (1781: 134, pl.173 figs.1708, 1709). These in turn were founded on material in the SPENGLER collection (now ZMK, Copenhagen). One of the SPENGLER originals is here shown in Fig.154. It should be noted that "Trochus perspectiviunculus" of CHEMNITZ (1781) is not identical with the likewise non-binominal "Perspectiviunculus" of MEUSCHEN (1781). The latter most likely belongs to *Psilaxis radiatus* RÖDING, 1798 (see also BAYER, 1942: 8).

PHILIPPI (1853: 30), in the description of his "varietas *depressa*," mentioned that he had earlier intended to name this form as an independent species, "Solarium articulatum." This name was published as a junior synonym and, since the name has not been used by subsequent authors, it is not available [ICZN, 1985: Art. 11(e)]. Another name that is unavailable for the same reason is "Torinia corrugata." Based on a manuscript name by PEASE, it was cited by CARPENTER (1865a: 516) as a synonym of "*Torinia variegata* LAMARCK" [= *H. variegatus* (GMELIN)].

SCHELTEMA & WILLIAMS (1983: 551, figs.1G, 3C, G) reported on the larvae of an architectonicid identified as "cf. *Heliacus variegatus*." The great range in larval shell size found by the authors (0.82–1.02, as opposed to 0.76–0.88 measured protoconch size in this study), indicates that they were working with members of more than one species.

Heliacus (Heliacus) areola (GMELIN, 1791) s.s.

Figs.157, 159–161

1742 "Cochlea marina Depressa, ...", - GUALTIERI, Index test. conch.: pl.65 fig.L [not binominal].
1781 "Trochus testa subcrenulato-umbilicata...", - GRONOVIUS, Zoophylac. Gronov.: 323, no. 1487 [not binominal].
1781 "Gyrus", - MEUSCHEN, Index vermium, Zoophylac. Gronov. [not binominal].
1781 "Areola", - CHEMNITZ, Conch.-Cab., *5*: 13 [not binominal].
1781 "Areolo. Trochus exiguus ...", - CHEMNITZ, Conch.-Cab., *5*: 134, pl.173 figs.1710–1711 [not binominal].
1783 "Das Gartenbeetchen" - SCHRÖTER, Einl. Conchylienkenntniß, *1*: 718.
*1791 *Trochus areola* GMELIN, Syst. nat. (13th ed.), *1*(6): 3575.
1793 *Trochus Areola*, - SCHREIBERS, Vers. vollst. Conchylienkenntniß, *1*: 248.
1801 *Trochus areola*, - BOSC, Hist. nat. coqu., *4*: 163.
1817 *Trochus areola*, - DILLWYN, Descr. cat. Rec. shells, *2*: 782.
1825 *Trochus areola*, - WOOD, Index testac. (2nd ed.): 137, pl.29 fig.56.
1824 *Trochus areola*, - BOSC, Hist. nat. coqu. (2nd ed.), *4*: 154.
*1830 *Solarium tessellatum* DESHAYES, 1830a, Encycl. méth., *2*(1): 160.

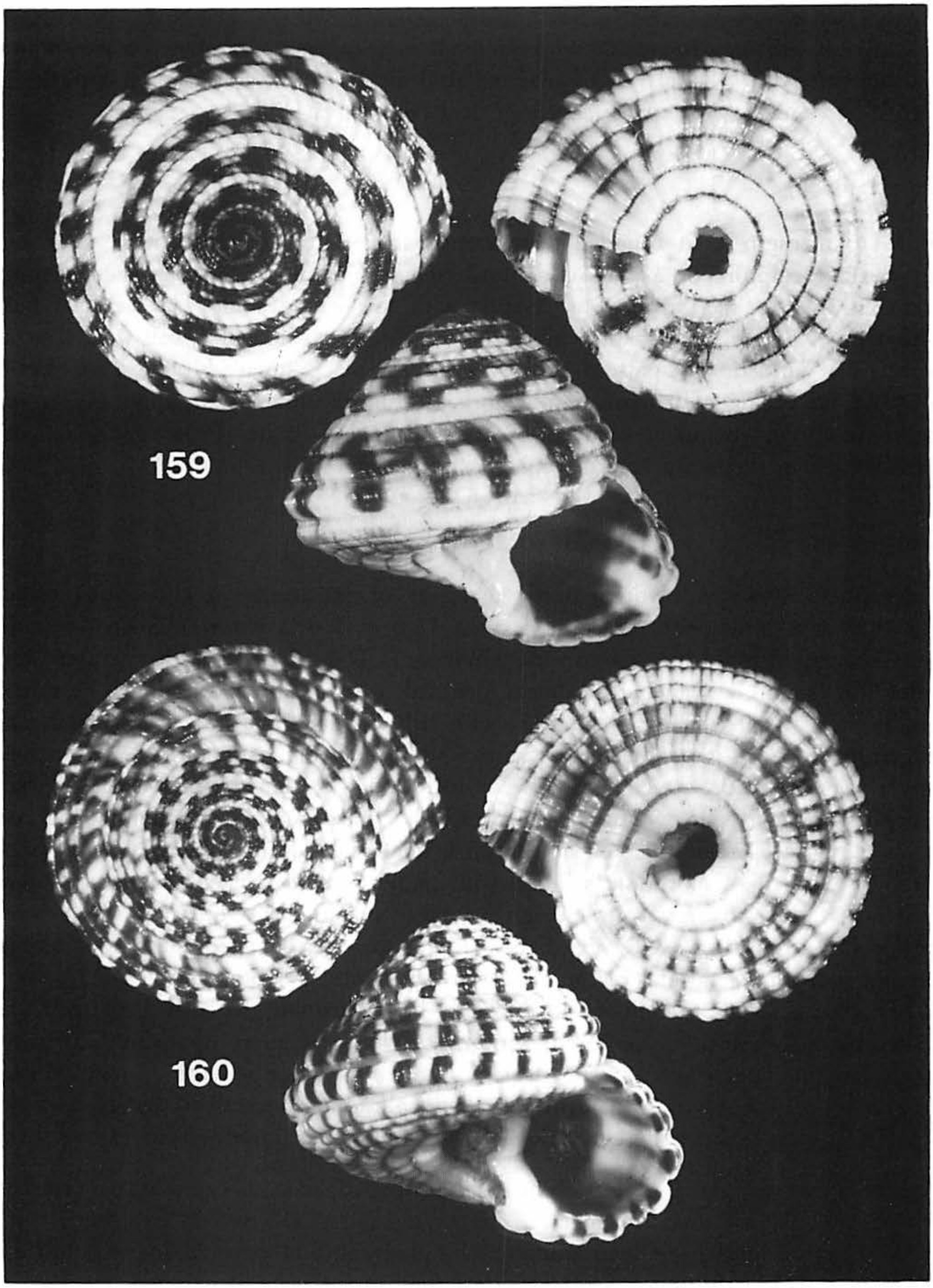
1834 *Solarium variegatum*, - QUOY & GAIMARD, Voy. l'ASTROLABE, *3*: 283, pl.62 figs.24-25 [base of living animal, operculum].
1838-1839 *Solarium variegatum*, - KIENER, Spéc. gén. icon. coqu., *10*: 10, pl.4 fig.7 [not 7a = *Heliacus variegatus*].
1842-1850 *Solarium variegatum*, - M.E. & J.E. GRAY, Fig. moll. anim, *1*: 19, pl.41 figs.3-4 [after QUOY & GAIMARD; base of living animal, operculum].
1843 *Solarium areola*, - DESHAYES, Hist. nat., (2)*9*: 100.
1853 *Solarium areola*, - PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 13, pl.2 figs.12-13 [after CHEMNITZ, 1781], pl.4 fig.15.
1853 *Solarium tessellatum*, - PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 30, pl.4 fig.12.
*1853 *Solarium perspectiviunculum* var. *pallida* PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 41, pl.4 fig.13.
1856 *Solarium areola*, - HANLEY, [WOOD's] Index testac.: 143, pl.29 fig.56.
1859 *Solarium (Torinia) variegatum*, - CHENU, Man. conch. paléont., *1*: 233, fig.1354.
1863 *Solarium (Torinia) perspectiviunculum*, HANLEY [in part], Thes. conch., *3*: 237, pl.254 fig.64.
1863 *Solarium (Torinia) perspectiviunculus* var. *tessellata*, - HANLEY, Thes. conch., *3*: 238.
1883-84 *Solarium (Torinia) variegatum*, - TRYON, Struct. syst. conch., *2*: 217, *3*: pl.66 fig.35.
*1948 *Torinia gyrus* BAYER, Zool. Verh., *4*: 20.
1948 *Torinia gyrus* forma typica, - BAYER, Zool. Verh., *4*: 21.
1948 *Torinia gyrus* forma *areola*, - BAYER, Zool. Verh., *4*: 21.
1948 *Torinia gyrus* subsp. *variegata*, - BAYER [in part], Zool. Verh., *4*: 22.
1951 *Torinia variegata*, - BARNARD, Beginner's guide S. Afr. shells: 102, pl.13 figs.18-19.
1952 *Torinia variegata*, - TINKER [in part], Pac. sea shells: 177, pl. p.179 (third row, right).
1954 *Heliacus variegatus*, - KIRA, Col. illus. shells Jap.: 24, pl.12 fig.4.
1961 *Torinista variegata*, - RIPPINGALE & MCMICHAEL, Queensld. Gr. Barr. Reef shells: 63, pl.6 fig.27.
1962 *Heliacus variegatus*, - KIRA, Shells w. Pac. col., *I*: 24, pl.13 fig.4.
1963 *Heliacus variegatus*, - BARNARD, 1963b [in part], Ann. S. Afr. Mus., *47*(1): 162.
1966 *Heliacus variegata*, - HABE & KOSUGE, Shell world col., *II*: 102, pl.40 fig.7.
1967 *Heliacus variegatus*, - HABE & KOSUGE, Stand. illus. book Jap. shells col.: 106, fig.25.
1971 *Torinia variegata*, - WILSON & GILLETT, Austr. shells: 34, pl.13 figs.15, 15a-b.
1972 *Heliacus variegatus*, - CERNOHORSKY, Mar. shells Pac., *II*: 195, pl.56 fig.2.
1972 *Torinia variegata*, - HINTON, Shells New Guinea: 4, pl.2 fig.28.
1973 *Heliacus variegatus*, - KENSLEY, Sea-shells s. Afr.: 76, pl. p.77 fig.257.
1977 *Heliacus (Heliacus) variegatus*, - GARRARD [in part], Rec. Austr. Mus., *31*(13): 539, pl.7 figs.13-15.
1978 *Torinia variegata*, - HINTON, Guide Austr. shells: pl.10, fig.12.
1979 *Torinia variegata*, - HINTON, Guide shells Papua: pl.1 figs.10-10a.
1980 *Heliacus variegatus*, - SHIRAI, Ecol. encycl. Ryukyu Ids.: 277, fig.
1982 *Torinia variegata*, - ROBERTS et al., Shall. wat. mar. moll. NW Java: 28, pl. 6 fig.4.
1984 *Heliacus areola*, - SHARABATI, Red Sea shells: pl.5 fig.4-4a.
1985 *Heliacus areola*, - HASZPRUNAR, 1985a, Phil. Trans. r. Soc. Lond., *B307*: 498 ff., figs.1, 8 [anatomy].
1985 *Heliacus variegatus*, - DRIVAS & JAY [in part], La Conchiglia, *17*(190-191): 8, fig.7.
1986 *Heliacus (Heliacus) variegatus*, - SPRINGSTEEN & LEOBRERA, Shells Philippines: 26, pl.2 fig.12.

Type measurements: *Solarium tessellatum*: SD = 14 mm [DESHAYES, 1830].

Type localities: *T. areola*: "Habitat ---" [unknown]; *S. tessellatum*: none given; *S. perspectiviunculum* var. *pallida*: none given; *T. gyrus* BAYER: "Habitat in Mari Americano" [error, based on MEUSCHEN, 1781].

Etymology: *areola* [noun in apposition]; late Latin usage: pigmented area around the human nipple.

Material studied: 1500+ specimens (AMNH, AMS, ANSP, BMNH, BPBM, CAS, DMNH, FLMNH, FMNH, IRSNB, LACM, LMA, MCZ, MNHNP, MNHU,



Figs. 159, 160. *Heliacus (Heliacus) areola* (GMELIN, 1791). Fig. 159: specimen from Port St. Johns, Transkei, South Africa; FMNH 223431; SD = 11.8. Fig. 160: specimen from Santa Cruz, Galapagos Islands, phenotypically intermediate between nominate form and subspecies *bicanaliculatus*; USNM 678873; SD = 16.3.

NMP, NMW, OUM, RNHL, SMF, SMNS, UCMP, UMZC, USNM, ZMA, ZSM, Coll. ALF, Coll. MARAIS); including original material of BAYER's *T. gyrus* "forma typica" and forma *areola* (RNHL). Original material ex SPENGLER collection not positively identified (ZMK); type of *S. tessellatum* lost (BOUCHET, in litt.).

Diagnosis:

Small to medium-sized rounded cone-shaped shell with narrow to wide umbilicus; upper-side sculpture of 3 almost identical ribs with more or less flattened nodules; rounded double keel formed by 2 ribs, with lower one somewhat weaker; basal sculpture of 5 very regular spiral ribs; umbilical side of columellar wall with 1 strong spiral rib. Whitish with pattern of brown to near-black square blotches, number of blotches increasing with number of whorls; subsutural and infraperipheral ribs very lightly colored, umbilical crenae and parietal region white. Protoconch diameter 0.68–0.80 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: small to medium-sized, diameter of specimens in collections usually 9.5–14.0 at 4–5 whorls (rarely more than 18.0 at 5 2/3 whorls). Shape: rounded cone-shaped with very narrow to wide umbilicus (UD 8–32% of SD). Sculpture: Upper side: SSR, single MR and UPR almost identical, with ± flattened nodules; Periphery: double keel formed by LPR and IPR, with IPR usually somewhat weaker and more angular; rarely (in large specimens) with 1 additional, much finer rib between them; upper point of whorl attachment between LPR and IPR, suture shallow; Base: 5 very regular spiral ribs, somewhat increasing in width towards umbilicus, innermost forming UC; UC with 9–22 nodules on body whorl; umbilical side of columellar wall with 1 strong spiral rib. Coloration: whitish with pattern of near-black, ± regular square blotches (fading to brown after death); number of blotches increasing with whorls; SSR, IPR, often also PUR very light-colored; grooves between spiral ribs orange-brown; UC white, parietal region almost always white. – Protoconch (Fig.157): small (0.68–0.80, $\bar{x} = 0.75$), multispiral, distinctly heterostrophic, without anal keel; solid dark brown to black, or bicolored, with glassy-white periphery opposite peritreme. – Operculum: as described for subgenus. – Radula: as described for *H. variegatus*. – Anatomy: mantle cavity organs, especially osphradium, described by HASZPRUNAR (1985a: 498 ff.). – Softbody coloration of living animal: as described for *H. variegatus*.

Reproduction and larval development: sausage-shaped, mucous egg masses of variable length and 2.8–3.1 mm in diameter, containing about 300 weakly oval eggs (0.1 x 0.13 mm) per mm. Eggs interconnected by chalazae and covered by an additional membrane within the mucous mass as described in the general part.

Geographical distribution (Fig.161): Continuous range from African east coast to central Pacific. Record of *H. areola* s.s from Galapagos Islands in need of verification.

Habitat and Habits/feeding behavior: as described for *H. variegatus*.

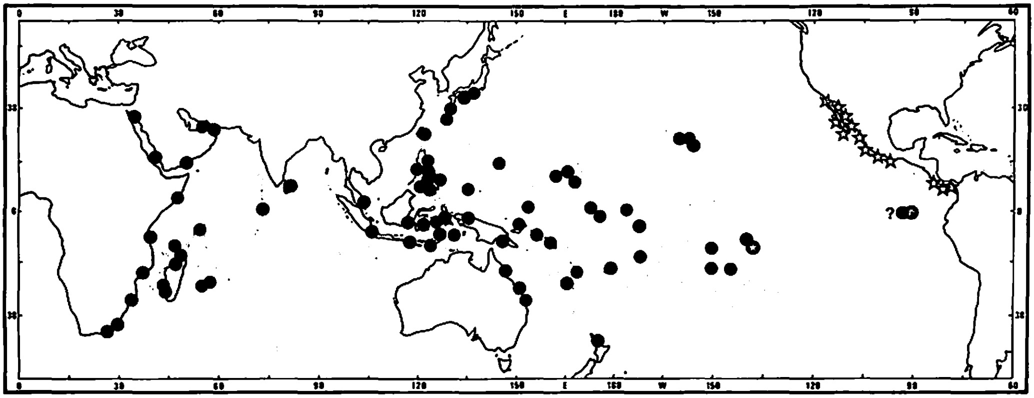


Fig. 161. Geographical distribution of *Heliacus areola* s.s., *H. areola bicanaliculatus*, and intermediate form.

Discussion:

Heliacus areola is very similar to the sympatric *H. variegatus* (see discussion above), and most collections have mixed lots of the two common species. As is the case for *H. variegatus*, *H. areola* has been the subject of considerable confusion in the literature. Originally named in non-binominal works, as "*gyrus*" by MEUSCHEN (1781) and "*areola*" by CHEMNITZ (1781), the species was first validly described ten years later, as *Trochus areola* GMELIN, 1791. The following 150 years saw extensive discussions on the identity of this form and its possible synonymy with *H. variegatus* (e.g., PEASE, 1869b: 82; MENKE, 1850: 170; PHILIPPI, 1853b: 12, 30; HANLEY, 1863: 238; PAETEL, 1887–1888; MARSHALL, 1887: 16), culminating in BAYER's (1848) treatment of this group. A study of the material on which BAYER's (1948: 20 ff.) work was based (RNHL), revealed that he correctly distinguished between two forms: *H. variegatus* (as *Torinia gyrus* ssp. *depressiuscula*) and *H. areola* (as *T. gyrus*; BAYER validated the previously unavailable name). However, *variegatus* sensu BAYER (1948: 23) was a mixture of three forms, *variegatus*, *areola* s.s. and *bicanaliculatus*. BAYER (1948) considered all of these forms as belonging to a single species, and subsequent authors replaced his name *gyrus* with the earlier name *variegatus*. The name *areola* was thus forgotten.

Trochus areola GMELIN was founded on description and illustrations of "Areolo" by CHEMNITZ (1781: 134, pl. 173 figs. 1710, 1711). These in turn were based on material in the SPENGLER collection. No positively matching material was located in that collection (ZMK).

Heliacus bicanaliculatus (VALENCIENNES, 1832) was previously considered a distinct species, but is here interpreted as a geographic subspecies of *Heliacus areola* (see discussion below).

Heliacus (Heliacus) areola bicanaliculatus (VALENCIENNES, 1832)
Figs.157, 161-163

*1832 *Solarium bicanaliculatum* VALENCIENNES, Rec. Observ. Zool. Anat. comp., *2*: 270.
*1850 *Euomphalus radiatus* MENKE, Z. Malakozool., *7*: 170.
1857 *Torinia ?variegata*, - CARPENTER, 1857a [in part], Cat. coll. Mazatlan: 407.
1857 *Euomphalus radiatus*, - CARPENTER, Cat. coll. Mazatlan: 541.
1863 *Solarium (Torinia) bicanaliculatum*, - HANLEY, Thes. conch., *3*: 237.
*1868 *Torinia variegata* var. *sinistrorsa* LAGODA, J. Conch., *16*: 264, pl.9 fig.7.
*1932 *Heliacus chiquita* PILSBRY & LOWE, Proc. Acad. nat. Sci. Philadelphia, *84*: 83, pl.8 figs.12-14.
1943 *Heliacus radiatus*, - SORENSEN, Nautilus, *57*(1): 5.
1948 *Torinia bicanaliculata*, - BAYER, Zool. Verh., *4*: 7.
1948 *Torinia chiquita*, - BAYER, Zool. Verh., *4*: 10.
1948 *Torinia gyrus* subsp. *variegata*, - BAYER [in part], Zool. Verh., *4*: 23.
1963 *Heliacus bicanaliculatus*, - ROBERTSON & MERRILL, Veliger, *6*(2): 76ff., pl.13 figs.1-4, pl.14 figs.1-4.
1964 *Heliacus bicanaliculatus*, - KEEN, Proc. Calif. Acad. Sci., (4)*30*(9): 198.
1967 *Heliacus bicanaliculatus*, - ROBERTSON, Science, *156*(3772): 246.
1968 *Heliacus bicanaliculatus*, - DUSHANE & SPHON, Veliger, *10*(3): 241.
1971 *Heliacus bicanaliculatus*, - KEEN, Sea shells trop. w. Amer. (2nd ed.): 389, fig.428.
1974 *Heliacus bicanaliculatus*, - ABBOTT, Amer. seashells (2nd ed.): 98.
1976 *Heliacus bicanaliculatus*, - ROBERTSON, 1976a, Bull. Amer. malac. Union, *1975*: 51.
1976 *Heliacus bicanaliculatus*, - ROBERTSON, 1976b, Veliger, *19*(1): 17.

Type measurements: Lectotype of *S. bicanaliculatum* [here designated]: SD = 14.2, H = 10.5, PD = 0.64, Tw = 5 1/7, UD = 3.1. *E. radiatus*: SD = 12.0, H = 5.2 [teste MENKE, 1850]. *T. variegata* var. *sinistrorsa*: "La longeur totale .... 13 millimètres, son plus grand diamètre de 7 7/10" [teste LAGODA, 1868]. *H. chiquita*: SD = 4.4, H = 2.0, PD = 0.7, Tw = 2 3/4, UD = 1.6.

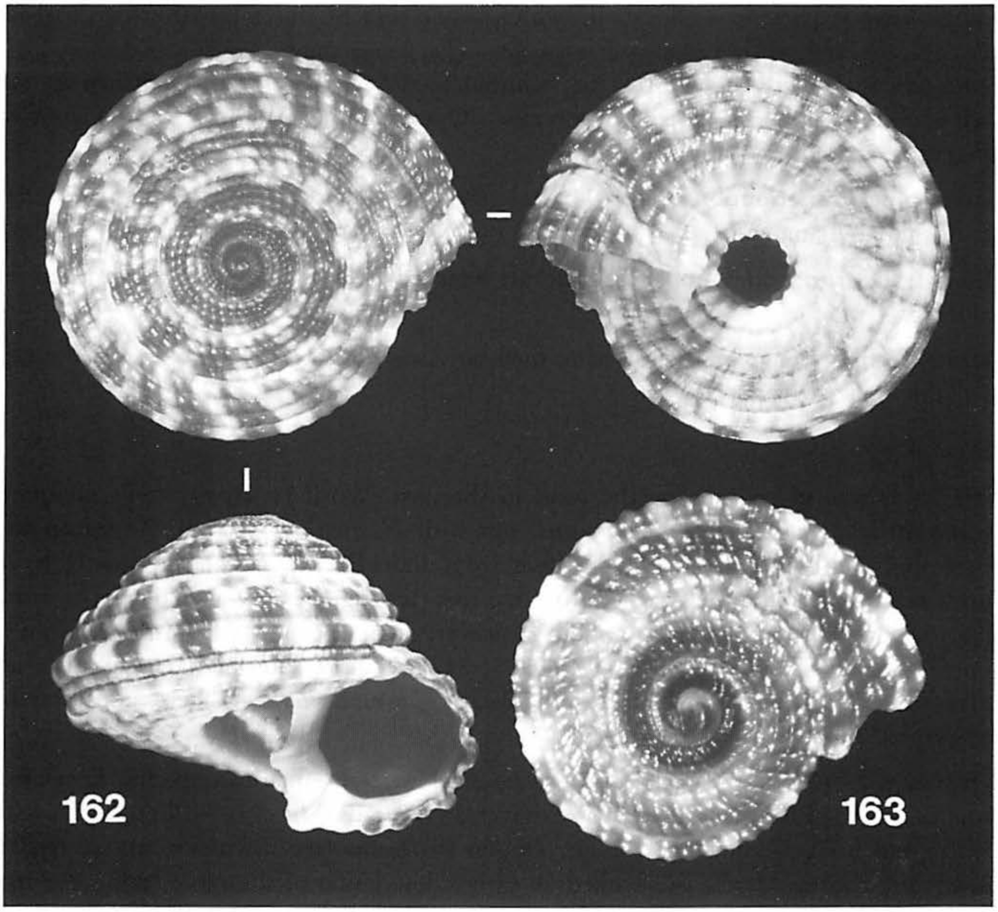
Type localities: *S. bicanaliculatum*: "Habitat ad Acapulco Mexicanorum" [Acapulco, Guerrero State, Pacific coast]; *E. radiatus*: Mazatlan, Mexico (Pacific coast); var. *sinistrorsa*: "Californie"; *H. chiquita*: "Acapulco, Mexico."

Etymology: *bicanaliculatus-a-um* [adjective]; Latin: with two grooves or channels.

Material studied: 700+ specimens (AMNH, ANSP, BMNH, CAS, DMNH, FLMNH, FMNH, IRSNB, LACM, LMA, MCZ, MNHNP, MNHU, NMP, NMW, RNHL, SMF, UCMP, USNM, ZMA, ZSM, Coll. ALF); including lectotype of *S. bicanaliculatum* (MNHNP unnumbered), and holotype of *H. chiquita* (ANSP 155440).

Diagnosis:

Small to medium-sized rounded cone-shaped shell with narrow to wide umbilicus; upper-side sculpture of 3 almost-identical ribs with more or less flattened nodules; double keel formed by 2 strong ribs and always 1 weaker rib between them; basal sculpture of 5 very regular spiral ribs; umbilical side of columellar wall with 1 strong spiral rib. Light tan with pattern of brown, more or less regular streaks and blotches, often fusing into irregular radial flames; subsutural and (in smaller specimens) peripheral ribs more lightly colored; early whorls much darker. Protoconch diameter 0.60-0.72 mm, distinctly heterostrophic, without anal keel.



Figs. 162, 163. *Heliacus (Heliacus) areola bicanaliculatus* (Valenciennes, 1832). Fig. 162 (three aspects): lectotype of *Solarium bicanaliculatum*; Acapulco, Mexico; MNHNP unnumbered; SD = 14.2. Fig. 163: holotype of *Heliacus chiquita* Pilsbry & Lowe, 1932; Acapulco, Mexico; ANSP 155440; SD = 4.4.

Description:

Teleoconch: small to medium-sized, diameter of specimens in collections usually 9–20 at 4 to 6 1/8 whorls. Shape: rounded cone-shaped with narrow to wide umbilicus (UD 12–36% of SD). Sculpture: Upper side: SSR, single MR and UPR almost identical, with ± flattened nodules; Periphery: double keel formed by LPR and IPR (with IPR usually somewhat weaker); with 1 narrow additional rib between them; upper point of whorl attachment above this additional rib; suture shallow; Base: 5 very regular spiral ribs, somewhat increasing in width towards umbilicus, innermost forming UC; umbilical side of columellar wall with 1 strong spiral rib. Coloration: ± regular brown streaks and blotches (often fusing into irregular radial flames) on whitish to reddish or yellowish-tan background; initial teleoconch whorls much darker; SSR, PR (especially in subadults) often somewhat lighter; grooves between spiral ribs orange-brown; parietal wall usually white, inner side of outer lip often with brown streaks reflecting spiral ribs. – Protoconch (Fig.157): small (0.60–0.72, $\bar{x}$ = 0.67), multispiral, distinctly heterostrophic, without anal keel; bicolored, dark brown with glassy-white periphery opposite peritreme. – Operculum and Radula: as described for subgenus. – Anatomy: not studied.

Geographical distribution (Fig.161): East Pacific, American west coast from Baja California to Panama.

Habitat: Intertidal and upper sublittoral; near or between polyps of zoanthinarian colonies.

Habits/feeding behavior: Reported to feed on *Zoanthus danai* (LE CONTE) in the Gulf of California (ROBERTSON, 1967).

Discussion:

This form was given full specific rank in the past. Workers usually have compared *bicanaliculatus* with *Heliacus variegatus*, not with *H. areola*. A typical American west coast specimen of *bicanaliculatus* differs from Indo-Pacific *H. areola* mainly by its additional rib between the two keel-forming ribs (see Fig.162), by a smaller protoconch (Fig.157) and, often, by a larger shell. However, some specimens from the Marquesas and Galapagos Islands (e.g., ANSP 80208, 317860) have intermediate sculpture and coloration (Fig.160) and thus eastern Pacific *bicanaliculatus* is here considered a geographic subspecies of *H. areola*.

When MENKE (1850: 170) described his nominal western American species *Euomphalus radiatus*, he cited the same figures of CHEMNITZ (1781: 173, figs.1708–1709) that GMELIN (1791) had used as reference for his *Trochus variegatus* (see discussion under *Heliacus variegatus*, above). Menke overlooked an earlier description of the same form, also from Mexico: *Solarium bicanaliculatum* VALENCIENNES, 1832. Subsequent authors (e.g., PEASE, 1869) discussed the eastern Pacific *variegatus* "sibling," and with HANLEY (1863: 237) the name *bicanaliculatus* came into use for it. Two additional names were introduced, *Torinia variegata* var. *sinistrorsa* LAGODA, 1868 (for an abnormal shell; see ROBERTSON & MERRILL, 1963) and *Heliacus chiquita* PILSBRY & LOWE, 1932 (based on a subadult shell, see Fig.163).

VALENCIENNES (1832: 270) did not illustrate his new species or indicate the number of specimens on which he based the original description. The MNHNP syntype here figured (Fig.162) is selected as lectotype of *Solarium bicanaliculatum*. Its dimensions are close to the ones mentioned by VALENCIENNES for this species (6 x 4 lignes, corresponding to 13.5 x 9.0 mm).

Heliacus (Heliacus) trochoides (DESHAYES, 1830)
Pl.2 Fig.E, Figs.164, 165

*1830 *Solarium trochoides* DESHAYES, 1830a, Encycl. méth., *2*(1): 160.
*1844 *Solarium dealbatum* HINDS, 1844b, Proc. zool. Soc. Lond., *1844*: 24.
1844 *Solarium dealbatum*, – HINDS, 1844d, Ann. Mag. nat. Hist., *14*: 439.
1844–1845 *Solarium dealbatum*, – HINDS, 1844c–1845, Zool. Voy. SULPHUR, *3*: 51, *2*:pl.14 figs.13–14.

1853 *Solarium dealbatum*, - PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 19, pl.3 fig.7 [after HINDS, 1844d].
1859 *Solarium trochoides*, - CROSSE, J. Conch., *7*: 378, pl.14 fig.2.
1863 *Solarium (Torinia) trochoides*, - HANLEY, Thes. conch., *3*: 243, pl.254 figs.89-90.
*1865 *Torinia conica* PEASE, Proc. zool. Soc. Lond., *1865*: 514.
1869 *Torinia trochoides*, - PEASE, 1869c, Amer. J. Conch., *5*(2): 86.
1887 *Torinia (Torinia) trochoidea* [sic], - MARSHALL, Man. conch., *9*: 18, pl.5 figs.87-88 [after HANLEY, 1863].
1903 *Solarium trochoides*, - E.A. SMITH, 1903a, Proc. malac. Soc. Lond., *5*(6): 383.
1909 *Torinia trochoides*, - SCHEPMAN, Monogr. Res. SIBOGA Exped., *49*(1b): 222.
1925 *Torinia trochoidea*, - THIELE, 1925a, Wiss. Ergeb. dtsch. Tiefsee-Exped. VALDIVIA, *17*(2): 113 [79], pl.46 [34] figs.16-17 [radula, jaw].
1933 *Torinia trochoidea*, - EDMONDSON, Bernice P. Bishop Mus. Spec. Publ., *22*: 136.
1948 *Torinia trochoides*, - BAYER, Zool. Verh., *4*: 36 [synonymy].
1952 *Torinia trochoidea*, - TINKER, Pac. sea shells: 178, pl. p.179 (fifth row).
1963 *Heliacus trochoides*, - BARNARD, 1963b, Ann. S. Afr. Mus., *47*(1): 162.
1967 *Heliacus trochoides*, - ROBERTSON, Science, *156*(3772): 246, fig.1.
1973 *Heliacus trochoides*, - KENSLEY, Sea-shells s. Afr.: 76, pl. p.77 fig.256.
1975 *Heliacus trochoides*, - SALVAT & RIVES, Coqu. Polynésie: 265, fig.49.
1976 *Heliacus trochoides*, - ROBERTSON, 1976a, Bull. Amer. malac. Union, *1975*: 51.
1976 *Heliacus trochoides*, - ROBERTSON, 1976b, Veliger, *19*(1): 13ff., figs.1-3.
1977 *Heliacus (Heliacus) trochoides*, - GARRARD, Rec. Austr. Mus., *31*(13): 538.
1978 *Heliacus trochoides*, - CERNOHORSKY, Trop. Pac. mar. shells: 165, pl.58 fig.8.
1979 *Heliacus trochoides*, - KAY, Hawaii. mar. shells: 99, fig.35K.
1982 *Heliacus trochoides*, - KILBURN & RIPPEY, Sea shells s. Afr.: 77.
1984 *Heliacus trochoidea*, - BOSS & MERRILL, 1984b, Occas. Pap. Moll., *4*(66): 352, pl.48 figs.3 [after THIELE, 1925a], 6 [radula, jaws].
1985 *Heliacus trochoides*, - DRIVAS & JAY, La Conchiglia, *17*(190-191): 8, fig.9.

Type measurements: *S. trochoides*: SD = 9.5, H = 11 [teste DESHAYES, 1830]. *T. conica*: SD = 10, H = 10 [teste PEASE, 1865]. *S. dealbatum*: SD = 12.7, H = 14.8 [teste HINDS, 1844b].

Type localities: *S. trochoides*: given as unknown; *S. dealbatum*: "Manila" [Philippines]; *T. conica*: "From the islands of the Central Pacific."

Etymology: *trochoides-es-es* [adjective]; Latinized form of a Greek adjective formation (τϱοχοείδης), meaning "like *Trochus*."

Material studied: 320 specimens (AMNH, ANSP, BMNH, CAS, DMNH, FLMNH, FMNH, IRSNB, LACM, LMA, MCZ, MNHNP, MNHU, NMP, NMW, RNHL, UMZC, USNM, ZMA, Coll. TRONDLE); type material of *S. dealbatum* und *T. conica* not located (for the latter see also KAY, 1965: 86), type of *S. trochoides* considered lost (BOUCHET, in litt.).

Diagnosis:

Small to medium-sized, high-spired cone-shaped shell with narrow to wide umbilicus, distinctly angular at base; upper-side sculpture of 3 almost identical ribs with more or less flattened nodules; double keel formed by 2 ribs, with the lower one weaker; basal sculpture of 5 very regular spiral ribs; umbilical side of columellar wall with 1 strong spiral rib. White. Protoconch diameter 0.88-1.02 mm, distinctly heterostrophic, without anal keel.

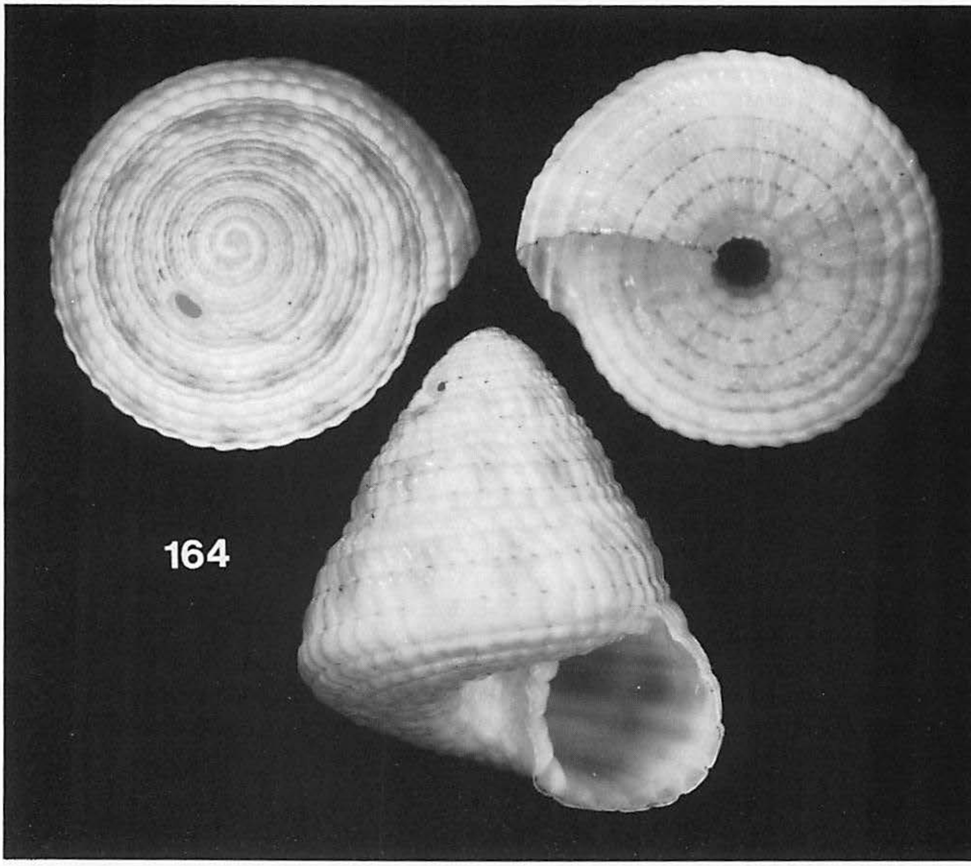


Fig. 164. *Heliacus (Heliacus) trochoides* (Deshayes, 1830); specimen from Shakas Rock, Natal, South Africa; FMNH 223428; SD = 10.7.

Description:

Teleoconch: small to medium-sized, diameter of specimens in collections usually 8–13 at 4 1/2–5 5/8 whorls (rarely over 15.0 with more than 6 1/2 whorls). Shape: high-spired cone-shaped with narrow to wide umbilicus (UD ca. 13–32% of SD, $\bar{x}$ = 19%); distinctly angular at base. Sculpture: Upper side: SSR, single MR and UPR almost identical, with ± flattened nodules; Periphery: double keel formed by LPR and IPR, with IPR weaker; upper point of whorl attachment between LPR and IPR, suture shallow; Base: 5 very regular spiral ribs, somewhat increasing in width towards umbilicus, innermost forming UC; UC with 9–19 nodules on body whorl; umbilical side of columellar wall with 1 strong spiral rib. Coloration: greyish-white to pure white; sometimes with light-tan, somewhat translucent square blotches on upper side (numbering 7–23 on body whorl, $\bar{x}$ = 13), and orange lines in grooves between spiral ribs. – Protoconch: small to medium-sized (0.88–1.02, $\bar{x}$ = 0.94), multispiral, distinctly heterostrophic, without anal keel; white with brown outer corners of peritreme and

1 small brown fleck close to highest point of apex. – Periostracum: greyish-white, thin; usually only retained in grooves between spiral ribs and on umbilical wall. – Operculum: as described for subgenus. – Radula: five-toothed taenioglossate (2–1–2); rachidian tooth stronger than marginal teeth, with prominent, pointed median cusp flanked by about 12 smaller, blunt cusps; marginal teeth longer, curved and forked with 6–10 tapering cusps (see THIELE, 1925a: 113, pl.46 fig.16). – Anatomy: not studied. – Soft-body coloration of living animal: milky white to salmon-colored (not correlated with presence/absence of shell pattern); anterior foot and upper side of tentacles weakly speckled with small black chromatophores, few embedded white granules (pers. obs., South Africa).

Reproduction and larval development: sausage-shaped, mucous egg masses of variable length (5–95 mm, $\bar{x} = 40$, $n = 12$) and relatively narrow diameter (ca. 2.1 mm), containing about 250 weakly oval eggs per mm. Eggs interconnected by chalazae and covered by an additional membrane within the mucous mass as described in the general part (see Pl.2 Fig.E).

Geographical distribution (Fig.165): From the African southeast coast to the central Pacific. Also reported from mainland Ecuador, east Pacific (ROBERTSON, 1967).

Habitat & Habits/feeding behavior: As described for *H. variegatus* (see Pl.2 Fig.E). ROBERTSON (1967) reported it to feed on *Palythoa tuberculosa* (ESPER) in the Maldive Islands, and *Palythoa vestitus* (VERRILL) in the Hawaiian Islands.

Discussion:

Heliacus trochoides is readily distinguished from other species in this group by its overall white, conical shell. Other white forms with which it could be confused, are *H. (Teretropoma) mighelsi* PHILIPPI (with a rounded peripheral area formed by two almost identical ribs that are flanked by weaker threads), and *H. (Gyriscus) asteleformis* POWELL (with a much finer sculpture including at least five spiral ribs on the upper side of the shell).

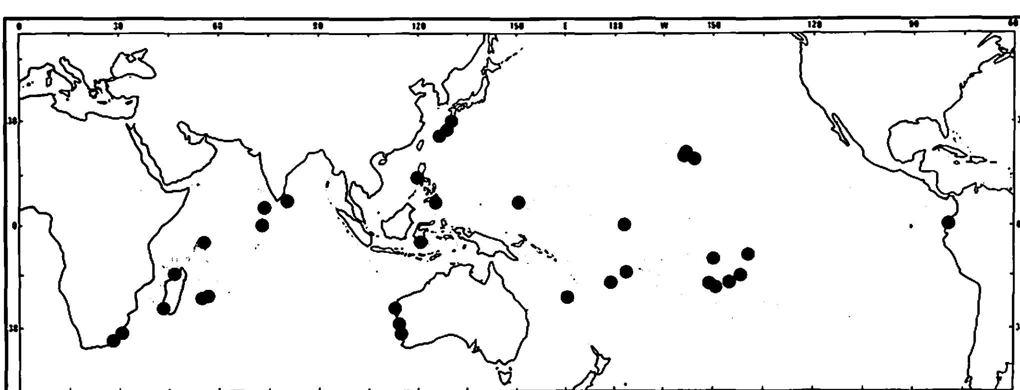


Fig. 165. Geographical distribution of *Heliacus trochoides*.

Although the type specimens of the nominal species *Solarium dealbatum* HINDS, 1844, and *Torinia conica* PEASE, 1865, have not been located, their original descriptions and illustrations allow positive identification and they are synonymized with *Heliacus trochoides*.

This is not the species identified as "cf. *Heliacus trochoides*" by SCHELTEMA & WILLIAMS (1983: 551, figs.1H, 3A, B). The larval shells illustrated by these authors possess anal keels, a feature lacking in *H. trochoides*. "*Heliacus* cf. *trochoides*," a name used by COSEL (1982a: 17, 1982b: 49) for a high-spired form of *Heliacus* from the Atlantic Cape Verde Islands, was subsequently described as *Heliacus verdensis* BIELER, 1984 (1984c).

Subgenus *Heliacus (Pyrgoheliacus)* BIELER, 1987

Pyrgoheliacus BIELER, 1987a: 206; introduced as subgenus of *Heliacus*. Type species by original designation: *Heliacus (Pyrgoheliacus) turritus* BIELER, 1987; Recent, Indo-Pacific.

Description (Fig.166):

Teleoconch: very small to small (usually 2.6 to 8 mm), tall cone-shaped (in large specimens, height ± equals diameter), with narrow to moderately wide umbilicus (ca. 10–20% of shell diameter); whorls distinctly bulging, periphery rounded; sculpture: spiral ribs with ± rounded nodules on entire surface; apical side: subsutural rib, and 1–2 midribs of about equal strength, upper peripheral rib more prominent and sometimes (*turritus*) already part of the periphery; periphery otherwise formed by ± equally strong lower peripheral rib (most prominent part of periphery), strong infraperipheral rib, and an almost equally strong additional rib between them (here upper point of whorl attachment); suture distinct; base with 6 spiral ribs, increasing

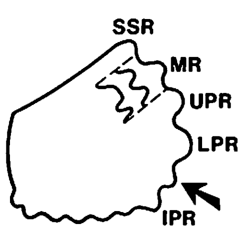


Fig. 166. Schematic representation of placement of major spiral ribs in *Heliacus (Pyrgoheliacus)*, apertural aspect. Arrow shows point of attachment of next whorl, intrageneric variation indicated by dotted lines.

in width towards umbilicus, innermost somewhat sunken into umbilicus; umbilical wall bulging, with or without weak spiral threads; coloration off-white to yellowish-tan; peripheral ribs with pattern of brown flecks (pattern corresponding between various ribs); inner lip off-white to dark brown. *Protoconch:* small to medium-sized (0.82–0.98), distinctly heterostrophic, with or without anal keel. *Radula:* five-toothed taenioglossate; rachidian with strong central cusp flanked by smaller cusps on either side; inner and outer marginals with several cusps each (Atlantic *H. verdensis*). *Operculum:* horny, round, cone-shaped, with peg-like projection on body side.

Heliacus (Pyrgoheliacus) turritus Bieler, 1987
Fig.167

*1987 *Heliacus (Pyrgoheliacus) turritus* Bieler, Arch. Moll., *117*(4/6): 204, text-fig.1, pl.1 fig.1.

Type measurements (holotype): SD = 4.8, H = 4.6, PD = 0.90, Tw = 4, UD = 0.9.

Type locality: "W. Banc du Geyser (12°22'S, 46°23'7|E), 5–20 m" [Benthedi–1977 Sta.14, S.W. Indian Ocean]. Paratypes from 500 m E.S.E. Zampa-misaki (Bolo Point), Okinawa, Japan (26°26.1'N, 127°42.5'E), 46 m, sand and coral rubble.

Etymology: *turritus-a-um* [adjective]; Latin: tower-like.

Material studied: 26 specimens (LACM, MNHNP, SMF, USNM); including holotype (MNHNP unnumbered) and paratypes (3 paratypes: LACM 2116; 1 paratype SMF 305965; 1 paratype: USNM 859079).

Diagnosis:

Very small high-spired, turreted cone-shaped shell with narrow to moderately wide umbilicus; upper-side sculpture with 2 ribs of similar width and 1 distinctly narrower rib; with more or less flattened nodules; periphery formed by 4 ribs, of which the second from below is the weakest and less prominent; basal sculpture of 6 spiral ribs with the 2 innermost (surrounding umbilicus) widest; umbilical side of columellar wall without distinct spiral sculpture. Whitish to light tan with pattern of brown and white blotches on peripheral ribs. Protoconch diameter 0.88–0.98 mm, distinctly heterostrophic, with strong anal keel.

Description:

Teleoconch: very small, diameter of specimens in collections 2.6–4.8 at 2–4 whorls. Shape: high-spired, turreted cone-shaped with narrow to moderately wide umbilicus (UD 13–20% of SD); distinctly angular at base. Sculpture: Upper side: SSR and UMR almost identical, LMR distinctly narrower; with ± flattened nodules; Periphery: periphery formed by 4 ribs: strong UPR, LPR and IPR, and weaker, less prominent additional rib between LPR and IPR (this rib serving as upper point of whorl attachment); Base: 6 spiral ribs, the two outermost narrow, the two inner ones widest; innermost rib (UC) somewhat lowered into umbilicus; umbilical side of columellar wall convex, without distinct spiral sculpture. Coloration: off-white to light tan; peripheral ribs with pattern of brown and white blotches (about 11–12 brown blotches per whorl); blotches corresponding between ribs; porcellaneous inner lip and umbilical wall whitish. – Protoconch (SEM photograph in Bieler, 1987: 205, fig.1): medium-sized (0.88–0.98), multispiral, distinctly heterostrophic, with strong anal keel (0.26–0.32); whitish with 2 distinct brown blotches, outer corner of varix and adjacent area brown. – Periostracum: thin, yellowish when dry. – Operculum: as described for subgenus. – Radula and Anatomy: unknown.

Geographical distribution: Known from two separated regions: type locality Banc du Geyser in the SW Indian Ocean (between northern Madagascar and the Comores) and from Okinawa in the western Pacific.

Habitat: Sublittoral (depth records between 0.3–58 m; on sand and coral rubble).

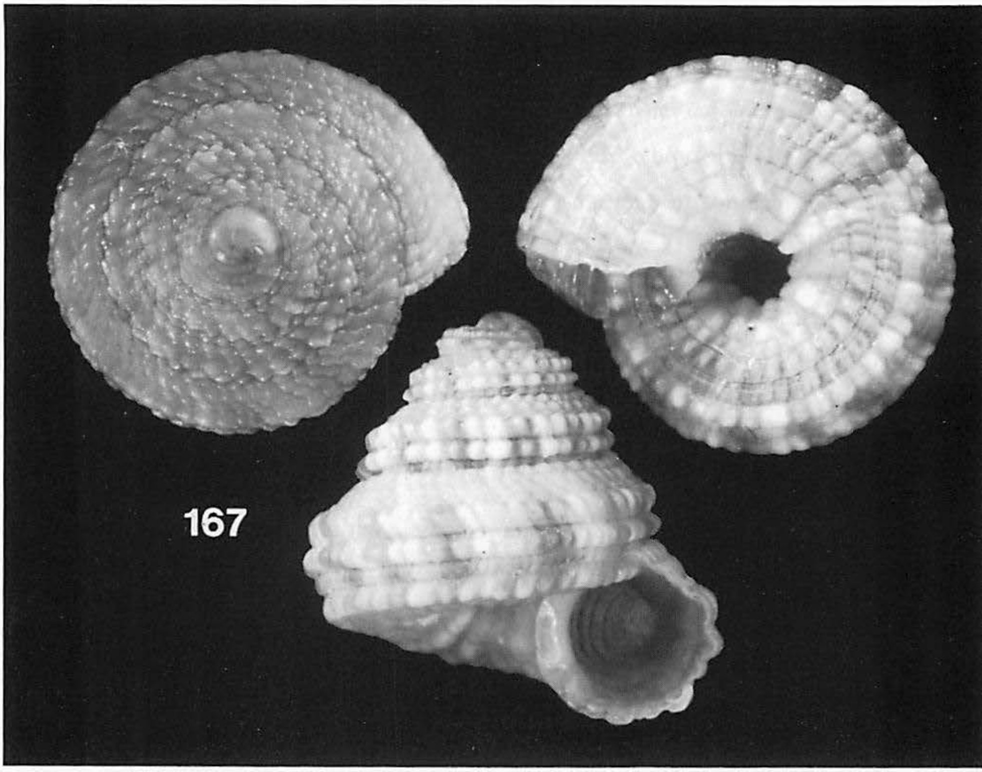


Fig. 167. *Heliacus (Pyrgoheliacus) turritus* Bieler, 1987; holotype; Banc du Geyser, S.W. Indian Ocean; MNHNP unnumbered; SD = 4.8.

Discussion:

The turriculate shell shape in connection with its light-tan coloration distinguish *Heliacus (Pyrgoheliacus) turritus* from all other Indo-Pacific architectonicids. Two other Indo-Pacific species possess protoconch anal keels; both are low-spired forms: *Heliacus (Torinista) corallinus* and *H. (T.) mazatlanicus*. Two Atlantic species, *Heliacus (Pyrgoheliacus) worsfoldi* Quinn, 1981, and *H. (P.) verdensis* Bieler, 1984, are similar (see discussion in Bieler, 1987: 206).

Subgenus *Heliacus (Torinista)* Iredale, 1936

Torinista Iredale, 1936: 327. Type species by original designation: *Torinista popula* Iredale, 1936 [= *Solarium implexum* Mighels, 1845]; Recent, Indo-Pacific.

Synonym:
Astronacus Woodring, 1959: 168; introduced as subgenus of *Heliacus*. Type species by original designation: *Heliacus planispira* Pilsbry & Lowe, 1932; Recent, East Pacific.

Incorrect subsequent spelling:
"Tornista" Azuma, 1960; Habe, 1961.

Description (Fig.168):

Teleoconch: very small to medium-sized (usually 3–12 mm), in most cases disk-shaped with weakly bulging whorls, occasionally depressed cone-shaped; umbilicus very narrow to extremely wide (ca. 9–55% of shell diameter); sculpture: spiral ribs with ± fine nodules, often flattened on the midribs; distinct axial sculpture in forms with fused spiral ribs; apical side: subsutural rib usually somewhat wider than following (often fused) midrib; periphery formed by somewhat stronger lower peripheral rib and infraperipheral rib, between them often 1–2 ± strong additional ribs; upper point of whorl attachment at lower peripheral rib, infraperipheral rib, or between them; base usually with 6 spiral ribs, increasing in width towards umbilicus; umbilical wall smooth except for axial growth lines, or with 1–2 ± demarcated spiral ribs; coloration of usually irregular flames in various shades of brown on apical and basal sides, only peripheral ribs often with regular pattern of light and dark brown flecks; innermost rib on base (UC) in most cases light in color. *Protoconch:* small to large (0.65–1.40), distinctly heterostrophic, in most cases with several folds in false umbilicus, rarely with anal keel. *Radula:* five-toothed taenioglossate; rachidian with strong central cusp flanked by numerous (6–20) smaller cusps on either side; inner and outer marginals with 6–10 cusps each. *Operculum:* horny, round, cone-shaped (often taller than diameter), with peg-like projection on body side.

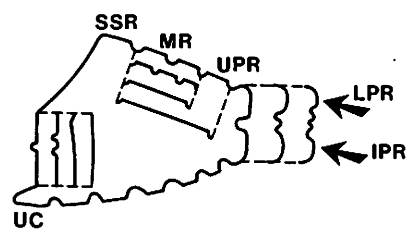
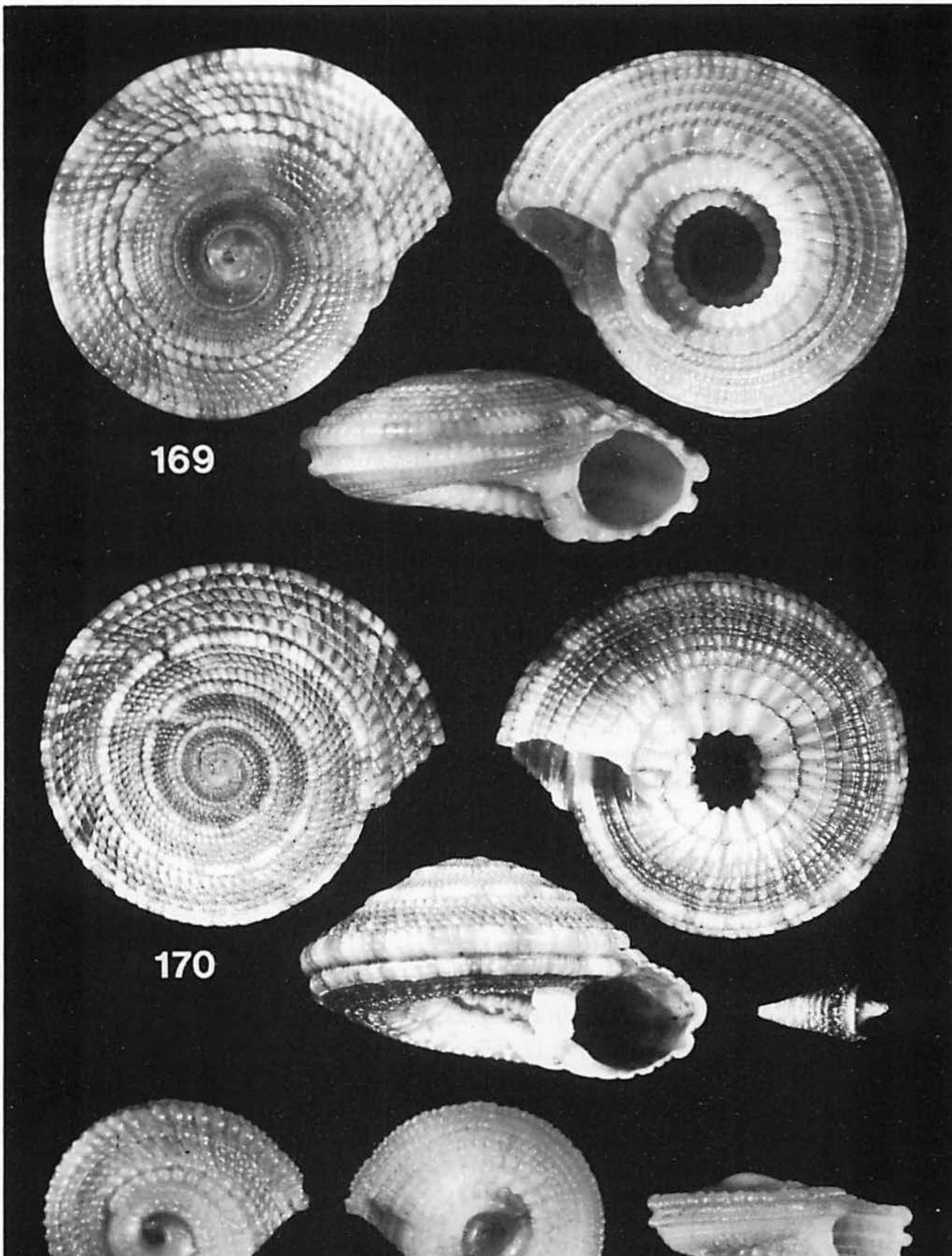


Fig. 168. Schematic representation of placement of major spiral ribs in *Heliacus (Torinista)*, apertural aspect. Arrows indicate the range of points of attachment of next whorl, intrageneric variation indicated by dotted lines.

Heliacus (Torinista) implexus (Mighels, 1845)
Pl.2 Fig.D, Figs.5, 169–179

*1845 *Solarium implexum* Mighels, Proc. Boston Soc. nat. Hist., *1*: 22.
1853 *Solarium implexum*, – Philippi, 1853b, Syst. Conch.-Cab. II, *7*: 37.
1863 *Solarium (Torinia) dorsuosum*, – Hanley, Thes. conch., *3*: 238, pl.254 figs.73–74 [non *Solarium dorsuosum* Hinds, 1844 = *nomen dubium*].
1863 ?*Solarium implexum*, – Hanley, Thes. conch., *3*: 244.
1879 *Torinia perspectiviunculus*, var., – E.A. Smith, Proc. zool. Soc. Lond., *1878*: 816, pl.50 figs.17a-b.
1893 *Solarium (Torinia) homalaxis* (Melvill MSS.) Melvill & Abercrombie, Mem. Proc. Manch. Lit. Phil. Soc., (4)*7*: 35 [*nomen nudum*].
*1893 *Solarium (Torinia) homalaxis* Melvill, Mem. Proc. Manch. Lit. Phil. Soc., (4)*7*: 58.
1896 *Solarium (Torinia) homalaxis*, – Melvill, Proc. malac. Soc. Lond., *2*(3): 110, pl.8 fig.12.
1897 *Solarium (Torinia) dorsuosum*, – Sowerby (III), Append. mar. shells S. Afr.: 15.
1900 *Solarium caelatum*, – Sowerby (III), Proc. malac. Soc. Lond., *4*: 4 [non *S. caelatum* Hinds, 1844].
1903 *Solarium caelatum*, – E.A. Smith, 1903a, Proc. malac. Soc. Lond., *5*(6): 382.
1909 *Torinia dorsuosa*, – Schepman, Monogr. Res. Siboga Exped., 49(1b): 221.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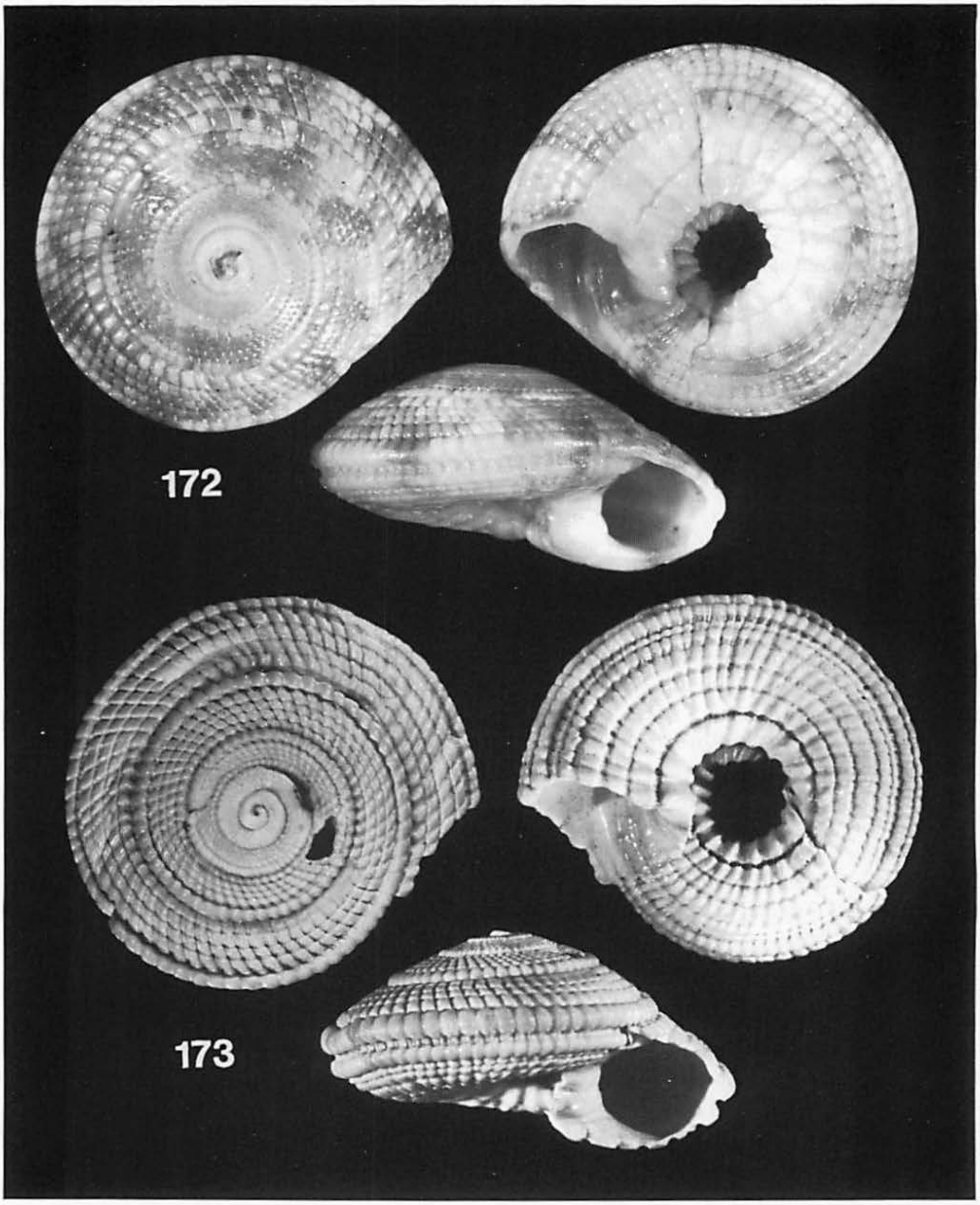
170
171

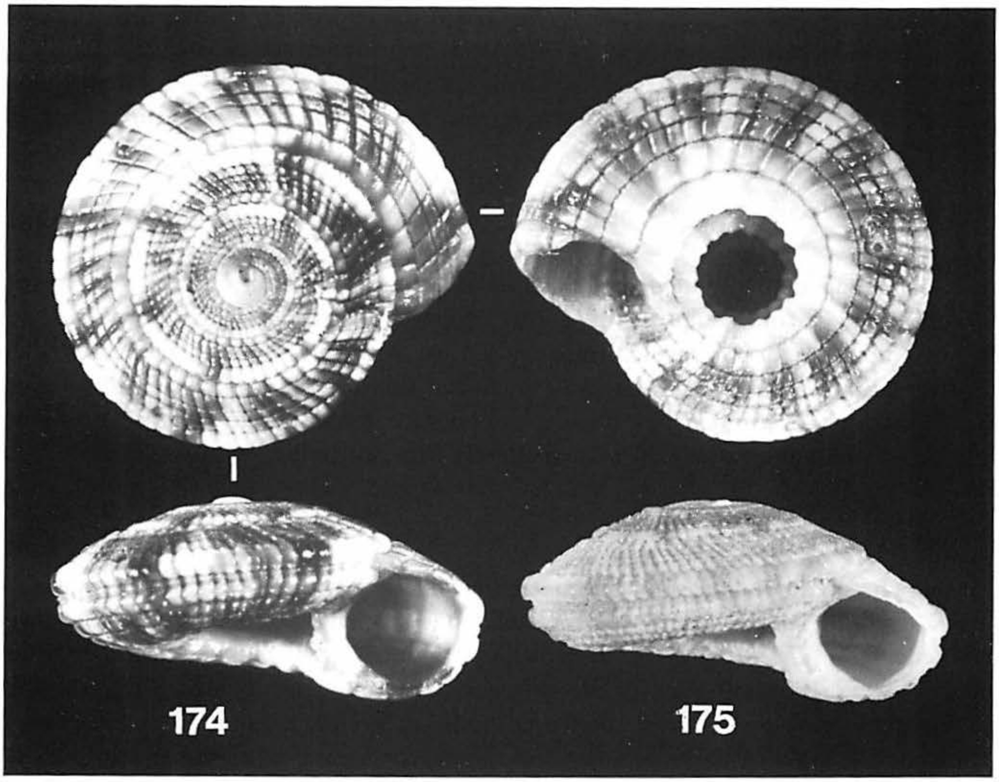
*1911 *Solarium (Torinia) omalaxis* IREDALE, 1911a, Proc. malac. Soc. Lond., *9*(4): 255 [unjustified emendation].
1913-1915 *Heliacus variegatus*, - SUTER, Man. N. Zeal. Moll.: 317, pl.15 fig.20 [non *Trochus variegatus* GMELIN, 1791].
*1915 *Heliacus africanus* BARTSCH, Bull. U.S. natl. Mus., *91*: 123, pl.24 figs.1, 3, 5.
1928 *Heliacus africanus*, - TOMLIN, Ann. S. Afr. Mus., *25*(2): 333.
*1932 *Solarium alfredensis* TURTON, Mar. shells Port Alfred: 134, pl.29 fig.967.
*1934 *Heliacus maorianus* POWELL, Rec. Auckland Inst. Mus., *1*(5): 268, pl.58 figs.5-7.
*1936 *Torinista popula* IREDALE, Rec. Austr. Mus., *19*(5): 327, pl.24 fig.15.
1939 *Mangonuia (Torinista) popula*, - WENZ, Handb. Paläozool., *6*(3): 668, fig.1904 [after IREDALE, 1936].
1943 *Heliacus dorsuosus*, - HABE, Venus, *13*(1-4): 75, pl.4 fig.5.
1948 *Torinia dorsuosa*, - BAYER, Zool. Verh., *4*: 16 [synonymy].
1948 *Torinia dorsuosa* var. *africana*, - BAYER, Zool. Verh., *4*: 17 [synonymy].
1948 *Torinia dorsuosa* var. *alfredensis*, - BAYER, Zool. Verh., *4*: 18.
1948 *Torinia homalaxis*, - BAYER, Zool. Verh., *4*: 28.
1948 *Torinia implexa* (species incertae sedis & species dubiae), - BAYER, Zool. Verh., *4*: 37 [synonymy].
1952 *Torinia* species, - TINKER, Pac. sea shells: 177, pl. p.179 (fourth row, left and right).
1952 *Torinia dorsuosa*, - SATYAMURTI, Bull. Madras Gov. Mus. (NS) nat. Hist. Sect., *1*(2)(6): 73, pl.5 figs.1a-b.
1961 *Heliacus depressiusculus*, - HABE, Col. illus. shells Japan *(II)*: 31, pl.14 fig.4 [non *Torinia gyrus depressiusculus* BAYER, 1948 = *H. variegatus*].
1963 *Heliacus caelatus*, - BARNARD, 1963b, Ann. S. Afr. Mus., *47*(1): 159.
1963 *Heliacus dorsuosus*, - BARNARD, 1963b, Ann. S. Afr. Mus., *47*(1): 160, fig.31h.
1963 *Heliacus dorsuosus* Form *africanus*, - BARNARD, Ann. S. Afr. Mus., *47*(1): 160, figs.31c, i.
1963 *Heliacus dorsuosus* Form typical *dorsuosus*, - BARNARD, Ann. S. Afr. Mus., *47*(1): 161, fig.31h.
1963 *Heliacus dorsuosus* Form *alfredensis*, - BARNARD, Ann. S. Afr. Mus., *47*(1): 162.
1964 *Heliacus depressiusculus*, - HABE, Shells w. Pac. col., *2*: 47, pl.14 fig.4.
1967 *Heliacus implexus*, - ROBERTSON, Science, *156*(3772): 246.
1973 *Heliacus dorsuosus*, - KENSLEY, Sea-shells s. Afr.: 76, pl. p.77 fig.253.
1974 *Heliacus dorsuosus*, - BARNARD, Ann. S. Afr. Mus., *47*(5): 711.
1975 *Heliacus dorsuosus*, - KILBURN, Ann. Natal Mus., *22*(2): 605.
1976 *Heliacus implexus*, - HADFIELD, Micronesica, *12*(1): 138.
1977 *Heliacus (Torinista) dorsuosue* [sic], - GARRARD, Rec. Austr. Mus., *31*(13): 509, fig.17 [operculum].
1977 *Heliacus (Torinista) dorsuosus*, - GARRARD, Rec. Austr. Mus., *31*(13): 541, pl.2 figs.13-15, pl.9 figs.1-6.
1977 *Heliacus (Torinista)* cf. *implexus*, - GARRARD, Rec. Austr. Mus., *31*(13): 547, pl.9 figs.16-18.
1979 *Heliacus implexus*, - KAY, Hawaii. mar. shells: 98, figs.35G-H.
1979 *Heliacus maorianus*, - POWELL, N. Zeal. Moll.: 249, pl.48 figs.4-6.
*1980 *Heliacus codoceoae* REHDER, Smiths. Contr. Zool., *289*: 32, pl.5 figs.13-15.
1982 *Mangonuia* sp., - LADD [in part], U.S. geol. Surv. prof. Pap., *1171*: 30, pl.32 figs.7-9 [Pleistocene, New Hebrides].
1984 *Heliacus dorsuosus*, - BOSS & MERRILL, 1984b, Occas. Pap. Moll., *4*(66): 354, pl.49 figs.1-3 [after HABE, 1943].
1985 *Heliacus (Torinista) implexus*, - BIELER, 1985b, Arch. Moll., *116*(1/3): 98, pl.2 fig.5 [holotype of *Torinista popula* IREDALE, 1936].
1985 *Heliacus implexus*, - DRIVAS & JAY, La Conchiglia, *17*(190-191): 8, fig.10.
1987 *Solarium homalaxis*, - TREW, MELVILL's new moll. names: 45.
1988 *Heliacus (Torinista) implexus*, - BIELER, Malac. Rev., Suppl. *4*: 237 [radula].

Figs. 169-171. *Heliacus (Torinista) implexus* (MIGHELS, 1845). Fig. 169: paratype of *Solarium alfredensis* TURTON, 1932; Port Alfred, South Africa; NMP B3452/T2468; SD = 9.8. Fig. 170: original specimen of "*Torinia perspectiviunculus* var." E.A. SMITH, 1879; Andaman Islands; BMNH 1878.6.10.62; GD= 12.3; with operculum. Fig. 171: holotype of *Solarium homalaxis* MELVILL, 1893; Bombay; BMNH 1896.10.1.42; SD = 3.0.



Figs. 172, 173. *Heliacus (Torinista) implexus* (MIGHELS, 1845). Fig. 172: holotype of *Heliacus africanus* BARTSCH, 1915; South Africa; USNM 249757; SD = 9.7. Fig. 173: holotype of *Heliacus maorianus* POWELL, 1934; New Zealand (Pleistocene); AIM unnumbered; SD = 11.9.

Type measurements: *S. implexum*: SD = ca. 6.76 [teste MIGHELS]; Holotype of *S. homalaxis*: SD = 3.0, H = 1.1, PD = 1.16, Tw = 1 1/3, UD = 1.2; Holotype of *H. africanus*: SD = 9.7, H = 4.9, PD = 1.06, Tw = 4–, UD = 2.4; Holotype of *S. alfredensis*: SD = 8, H = 2 [teste TURTON]; Holotype of *H. maorianus*: SD = 11.9, H = 6.3, PD = 1.06, Tw = 4 1/4, UD = 2.4; Holotype of *T. popula*: SD



Figs. 174, 175. *Heliacus (Torinista) implexus* (MIGHELS, 1845). Fig. 174 (three aspects): holotype of *Heliacus codoceoae* REHDER, 1980; Easter Islands; ANSP 321078; SD = 7.3. Fig. 175: holotype of *Torinista popula* IREDALE, 1936; Australia; AMS C.60692; SD = 10.1.

= 10.1, H = 5.1, PD = 1.06, Tw = 3 3/4+, UD = 3.0; Holotype of *H. codoceoae*: SD = 7.3, H = 3.5, PD = 1.06, Tw = 3 3/8–, UD = 2.1.

Type localities: *S. implexum*: "Hab. Oahu" [Hawaiian Islands; "Oahu" probably in error for Kauai (see JOHNSON, 1949: 217)]; *S. homalaxis*: "Bombay" [India]; *H. africanus*: "Port Alfred" [South Africa]; *S. alfredensis*: "P.A." [Port Alfred, South Africa]; *H. maorianus*: "Te Piki, Cape Runaway," "Upper Pliocene" [New Zealand, Middle Pleistocene [10]]; *T. popula*: "New South Wales - Type from Sydney Harbour"; *H. codoceoae*: "Easter Island."

Etymology: *implexus-a-um* [adjective]; Latin: woven.

Material studied: 2000+ specimens (AIM, AMNH, AMS, ANSP, BMNH, BPBM, DMNH, ELM, FLMNH, FMNH, HUJ, IRSNB, LACM, LMA, MCZ, MNHNP, MNHU, NMP, NMW, RNHL, UHM, UMZC, USNM, SAM, SMF, SMNS, ZMA, Coll. MARAIS); including holotype of *S. homalaxis* (BMNH 1896.10.1.42), holotype und 1 paratype of *H. africanus* (USNM 249757), paratypes of *S. alfredensis* (1 PT: NMP B3452/T2468; 1 PT: NMW 1955.158.963; 2 PT: UMZC unnumbered; 1 PT:

[10] CERNOHORSKY, in litt.

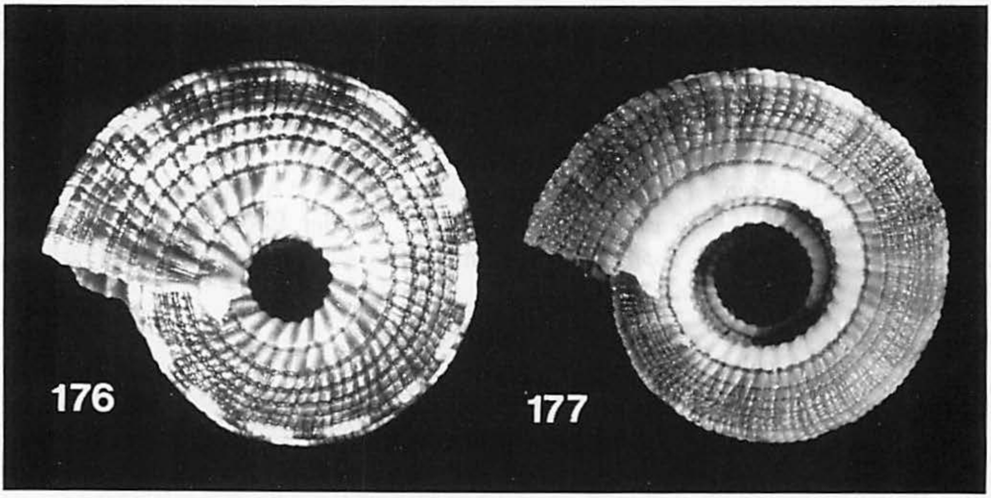
USNM 406489); holotype of *H. maorianus* (AIM unnumbered); holotype of *T. popula* (AMS C.60692), holotype (ANSP 321078) and 2 paratypes (USNM 756010, 756163) of *H. codoceoae* ; original specimen of *Torinia perspectiviunculus*, var. - SMITH (BMNH 1878.6.10.62). Type material of *S. implexum* lost; holotype of *H. alfredensis* not located.

Diagnosis:

Small disk-shaped to rounded depressed cone-shaped shell with narrow to very wide umbilicus; upper-side sculpture of 4 ribs (upper one strongest) with more or less flattened nodules; double-keel formed by 2 ribs, with lower one somewhat weaker; basal sculpture of 6 regular spiral ribs; umbilical side of columellar wall with 1 spiral rib. Yellowish-tan with darker flames, peripheral ribs with tan blotches or flames. Protoconch diameter 0.94–1.40 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: small, diameter of specimens in collections usually 8–10 at 3–4 whorls. Shape: disk-shaped to rounded depressed cone-shaped with narrow to very wide umbilicus (UD 9–37% of SD); early whorls with strongly bulging base. Sculpture: Upper side: SSR usually somewhat stronger then following 2 MR; MR and UPR about equally developed; with ± flattened nodules; Periphery: double-keel formed by LPR and IPR (LPR usually stronger and more prominent); in specimens above 3 Tw often (usually in narrowly umblicate forms) 1 fine additional rib between LPR and IPR; Base: 6 regular ribs, increasing in width towards umbilicus, innermost widest, forming strong UC; UC with 11–34 nodules on body whorl; umbilical side of



Figs. 176, 177. *Heliacus (Torinista) implexus* (MIGHELS, 1845). Umbilical aspects of fresh specimens from South Africa. Fig. 176: "africanus-form"; Coffee Bay, Transkei; FMNH 223429; SD = 9.3. Fig. 177: "alfredensis-form"; Sinkwazi, Natal, FMNH 223432; SD = 8.9.

columellar wall with 1 spiral rib bearing nodules. Coloration: yellowish-tan with darker flames; peripheral ribs light with tan blotches or flames (usually 2–3 nodules wide), interspaced with off-white; PUR and UC light, often white in widely umbilicate specimens. – Protoconch (Figs.5, 178): medium-sized to large (0.94–1.40, $\bar{x}$ = 1.12), multispiral, distinctly heterostrophic, without anal keel; white to light tan, with single darker fleck and brown outer corner of peritreme. – Periostracum: yellowish, thin. – Operculum: as described for subgenus; very high in relation to diameter (Pl.2 Fig.D, Fig.170). – Radula: five-toothed taenioglossate (2–1–2); rachidian tooth stronger than marginal teeth with prominent, pointed median cusp flanked by about 17 smaller, blunt cusps; marginal teeth longer, curved and forked with 8–10 tapering cusps. – Anatomy: not studied. – Soft-body coloration of living animal: body color yellowish, with dense and ± regular speckling of black pigment; white granules embedded in tissue, relatively few in tentacles and anterior margin of foot; sole of foot densely covered with thin layer of black pigment; overall appearance grey with black tentacles [pers. obs., South Africa].

Reproduction and larval development: sausage-shaped, mucous egg masses of variable lengths (often ca. 30 mm) and relatively small diameter (ca. 2.0 mm), containing about 250 weakly oval eggs per mm. Eggs interconnected by chalazae and covered by an additional membrane within the mucous mass as described in the general part (pers. obs., South Africa).

Geographical distribution (Fig.179): Continuous range from the African east coast to Easter Islands (Isla de Pascua).

Habitat: Occasionally encountered intertidally, on colonies of zoanthinarian polyps (mainly *Palythoa nelliae* PAX, 1935; South Africa, pers. obs.), but major habitat apparently sublittoral (most records from below 20 m).

Habits/feeding behavior: Observed while feeding on *Palythoa nelliae* (South Africa; see Pl.2 Fig.D). ROBERTSON (1967) reported it to feed on *Zoanthus confertus* VERRILL (= *Zoanthus pacificus* nom. nov. WALSH & BOWERS, 1971) in Kauai, Hawaiian Islands.

Discussion:

Heliacus implexus is often confused with depressed specimens of *H. variegatus* and *H. sterkii* (PILSBRY & VANATTA, 1908). The teleoconch of *H. variegatus* has only one midrib (two in *H. implexus*); the shell in *H. sterkii* always has an additional spiral rib between the more widely spaced keel-forming ribs (LPR and IPR). See also *H. enoshimensis*, *H. geminus* n.sp. and *H. proteus* n.sp. (below).

Heliacus implexus is the most common sublittoral species of its genus. It is very variable in shell shape and coloration, has a wide distribution throughout the Indo-Pacific and as a result is known under numerous synonyms. In most collections the name "*dorsuosus*" is used for this species. HINDS (1844b: 23) described *Solarium dorsuosum* together with 13 other nominal architectonicid species. For eleven of them, HINDS later (1844d) furnished illustrations of type specimens, but not for *Solarium formosum*,

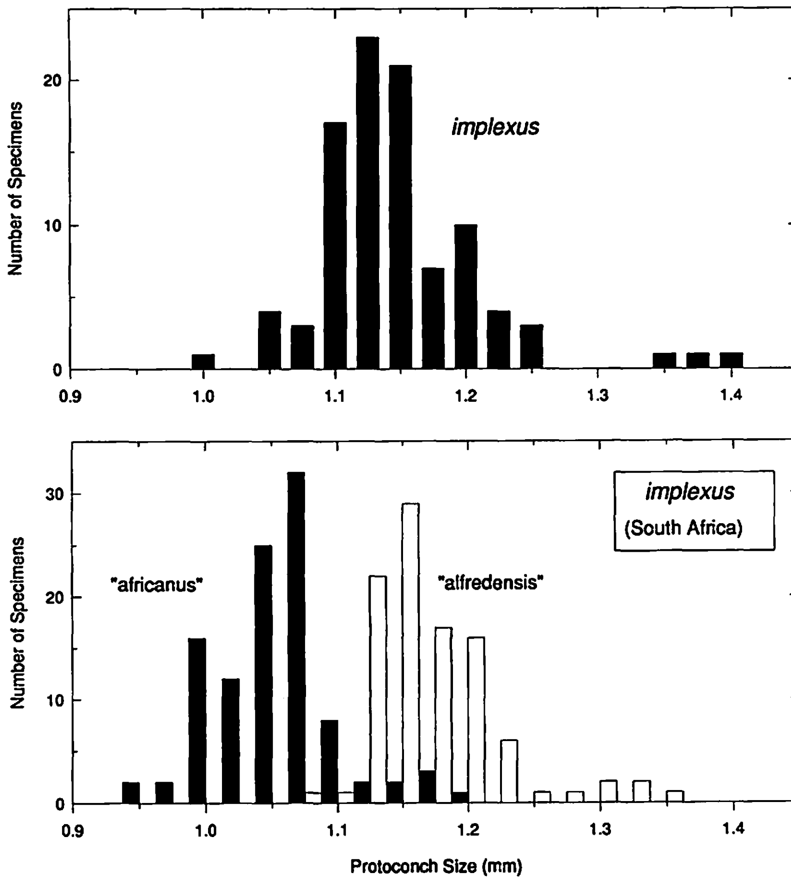


Fig. 178. Histograms of measured protoconch size. *Heliacus (Torinista) implexus*. Above: from Indo-Pacific localities other than South Africa (n = 96, x̄ = 1.15, sd = 0.06). Below: from South African localities ("africanus-form": n = 105, x̄ = 1.06, sd = 0.05; "alfredensis-form": n = 99, x̄ = 1.17, sd = 0.05).

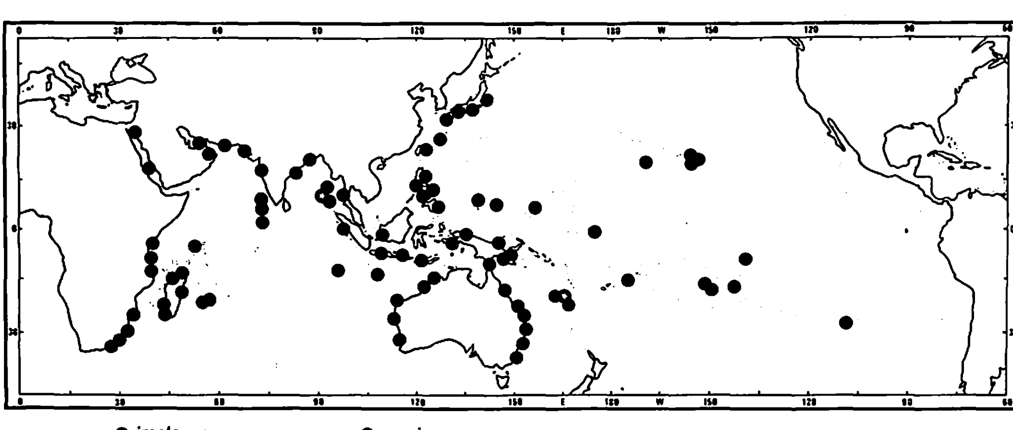


Fig. 179. Geographical distribution of *Heliacus implexus* and *H. geminus* n.sp.

S. trochleare and *S. dorsuosum*. HANLEY (1863: pl.254 figs.73–74) gave the first figure of a "*dorsuosum*," but the illustration does not agree with HINDS' original description:

- HINDS described the shell shape of *Solarium dorsuosum* as "teste conoidea," a term otherwise used only for his *S. perdix* [= *Architectonica perdix*], which is a relatively high-spired species. For species with a shell shape similar to that of *S. dorsuosum* sensu HANLEY (i.e., *caelatus*, *virgatus)* HINDS used the term "discoidea" in the same publication.
- HANLEY's figure shows a distinct color pattern on the shell margin, that was not mentioned by HINDS who only stated "fusca, albo confuse nebulosa."
- The dimensions given [6.5 lines = 13.7 mm] by HINDS are unusually large for a specimen of the species here considered.
- Although HINDS, in the same work, compared pairs of similar species (e.g., *perdix/perspectiva*, *quadriceps/granulatum*, *dealbatum/variegatum)*, he did not compare *dorsuosum* with *caelatum* or *virgatum*, although they are similar to "*dorsuosum*" sensu HANLEY.

Solarium dorsuosum HINDS, 1844, cannot positively be identified by the original description alone, the type specimen is assumed lost ["Mus. Cuming" (BMNH)]. *Solarium dorsuosum* is thus considered a *nomen dubium*.

The type material of *Solarium implexum* MIGHELS, 1845, was never figured and is probably lost (JOHNSON, 1949: 217, 225). The name was therefore treated as a *nomen dubium* by various authors (HANLEY, 1863: 244; PHILIPPI, 1853b: 37; BAYER, 1948: 37). HADFIELD (1976: 138), GARRARD (1977: 547) and KAY (1979: 98) used the name again for the species here considered. The original description given by MIGHELS (1845: 22) for material from Hawaii is very short, but of all the architectonicid species known from that area applies only to this species. *Heliacus implexus* (MIGHELS, 1845) is here employed for *Solarium dorsuosum* auct. non HINDS.

The name *Solarium (Torinia) homalaxis* was first used by MELVILL & ABERCROMBIE (1893: 35), as a *nomen nudum*. MELVILL (1893: 58) then gave a short description, based on a single specimen ("apparently quite a young shell"). He noted: "I have provisionally named it *S. homalaxis*, but await further specimens before attempting a full description." Following ICZN (1985) Article 15, this constitutes a valid description, the juvenile specimen is the holotype of *Solarium homalaxis* MELVILL, 1893. Three years later, MELVILL (1896: 110, pl.8 fig.12) added a more extensive description of the specimen, using the designation "n.sp." at this point. The holotype (see Fig.171) is a juvenile specimen of *Heliacus implexus*; the two nominal species are here synonymized.

The nominal species *Heliacus maorianus* POWELL, 1934, was based on material from the Pleistocene of New Zealand (holotype, see Fig.173), and on a Recent specimen which was earlier listed as "*variegatus*" by SUTER (1913: 317). This material, as well as the holotypes of *Torinista populа* IREDALE, 1936, from Australia (type species of the subgenus, see Fig.175), and *Heliacus codoceoae* REHDER, 1980, from the Easter Islands (see Fig.174) lie in the range of morphological variation of *H. implexus*; the nominal species are here considered synonyms.

Specimens reported as "*caelatus*" from South Africa (SOWERBY, 1900; SMITH, 1903a; BARNARD, 1963) belong to *Heliacus implexus* (see KILBURN, 1975: 605; as "*dorsuosus*").

Throughout the range of *Heliacus implexus*, animals can be found with relatively depressed, widely umbilicated shells, as well as animals with more rounded, relatively narrowly umbilicated shells. The bimodality is especially well developed at the South African east coast where the two morphs usually can also be separated by protoconch size, with the widely umbilicated form having a larger protoconch. For these forms two nominal species were introduced: BARTSCH (1915: 123) described *Heliacus africanus* and selected a narrowly umbilicated specimen as the holotype (see Fig.172). He pointed out the "considerable variation in the width of the umbilicus" in this species. Interpretation of his nominal species was hampered in part by BARTSCH's original figure of the shell base. In an attempt to correct a crack line of the specimen, BARTSCH touched up the photograph and thereby artificially increased the number of umbilical crenae on the body whorl from 16 to 22, a number typical of the widely umbilicate form. TURTON (1932: 134) introduced the name *Solarium alfredensis* for the form with a wide umbilicus (see Fig.169). For South African specimens (see Fig.178), the differences between the two forms are the following [included are only specimens with more than 3 1/4 whorls]:

	"*africanus*" n = 105	"*alfredensis*" n = 99
additional rib between LPR and IPR	present	absent
shape of spire	± convex	flat
relative size of umbilicus	9-33% of GD ($\bar{x}$ = 22)	25-45% ($\bar{x}$ = 36)
no. of umbilical crenae on body whorl	11-21 ($\bar{x}$ = 16)	20-27 ($\bar{x}$ = 27)
color of umbilical crenae	light tan (Fig.176)	white (Fig.177)
protoconch size	0.94-1.20	1.08-1.36

Both forms are here considered belonging to *Heliacus implexus*. The correlations of large protoconch/wide umbilicus and small protoconch/narrow umbilicus suggest that the teleoconch shape in this species is dependent on the protoconch size. It seems that above a certain protoconch size (ca. 1 mm) the postlarval growth will continue in an almost planispiral fashion. Whether ecophenotypic variation plays a role is unclear at present, as the apparently sublittoral habitat of *Heliacus implexus* is little known. A few living specimens of both forms were found by the author in the lower intertidal zone on the South African east coast, occurring sympatrically in zoanthid colonies and, in one case, even feeding on the same zoanthid polyp. The protoconch size correlation is less distinct in other parts of the Indo-pacific, where "africanus"-like specimens often have a larger protoconch (see Fig.178).

Heliacus (Torinista) geminus n.sp.
Figs.179–181

Type measurements:

	SD	H	PD	Tw	UD	Locality	Collection
Holotype	9.0	5.0	0.94	3 7/8–	1.2	New Caledonia	MNHNP unnumbered
Paratype 1	9.7	5.9	0.86	4 1/8	1.2	New Caledonia	AMS 165806
Paratype 2	7.2	3.8	0.90	3 5/8	1.2	New Caledonia	NMNZ MF.58555
Paratype 3	8.0	4.3	0.90	3 5/8	1.2	New Caledonia	FMNH 223427
Paratype 4	6.3	3.3	0.92	3 1/4	1.2	New Caledonia	MNHNP unnumbered
Paratype 5	9.1	5.2	0.90	4	1.3	Andaman Ids.	BMNH 1981105

Type locality: North Lagoon, New Caledonia (19°09'S, 163°35'E), 42 m (B. Richer - ORSTOM coll. station 517, 05.III.1985) (holotype and paratypes 1–4). Paratype 5 from Port Blair, Andaman Islands (Winckworth Coll.).

Etymology: *geminus-a-um* [adjective]; Latin: equal, alike. Here referring to similarity with the common species *Heliacus implexus*.

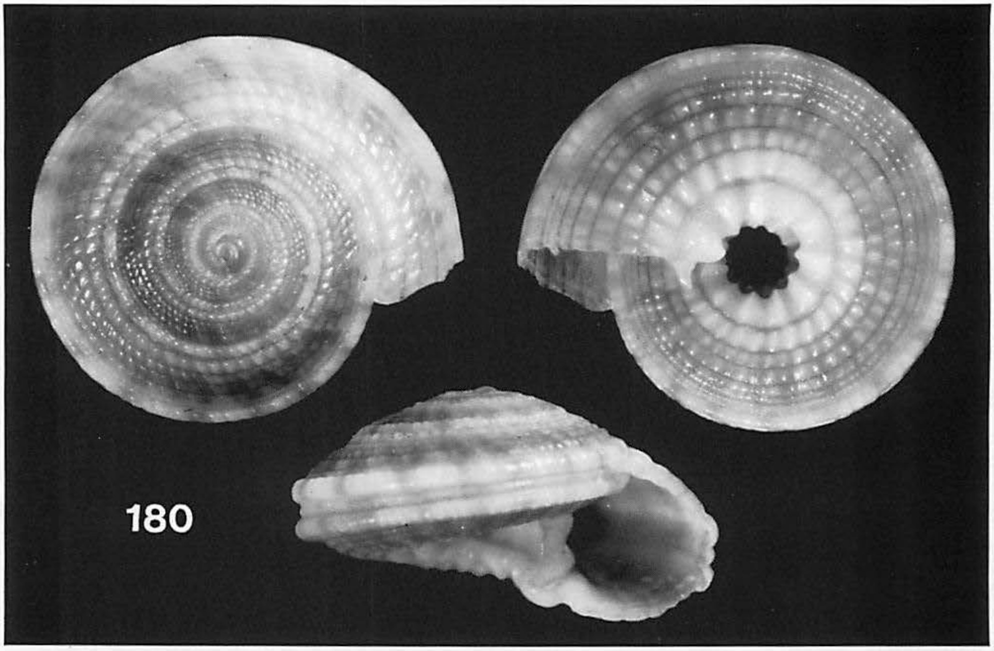
Material studied: 6 type specimens as listed above.

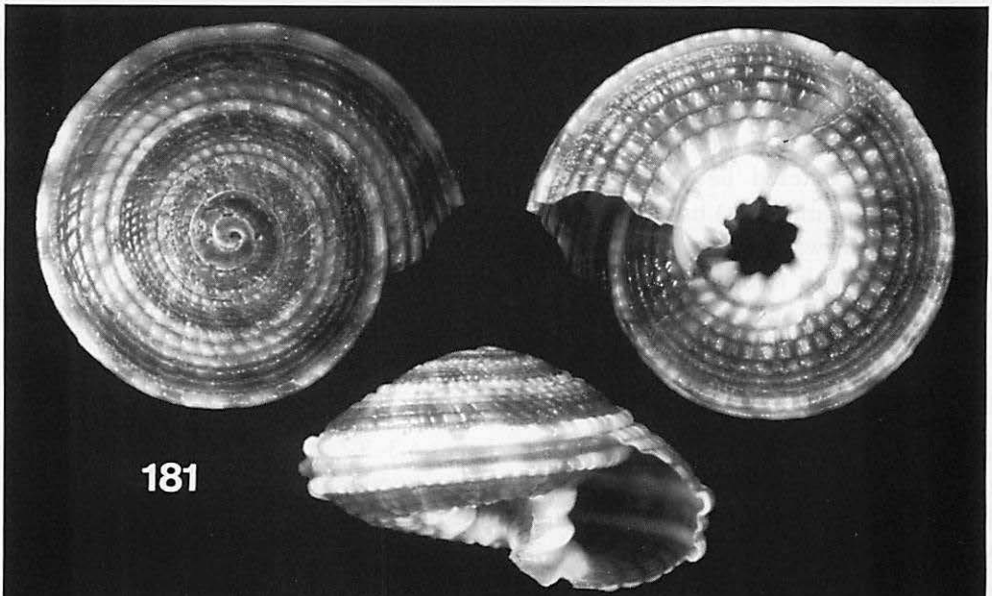
Diagnosis:

Small, depressed cone-shaped shell with angular periphery, shallow suture, moderately wide umbilicus, and sculpture consisting of rounded tubercles; upper-side sculpture with 4 ribs (uppermost coarsest), plus a finer one before the keel-forming ribs; prominent angular double keel formed by 2 almost equally developed ribs, with 1 narrow rib centered between them; basal sculpture of 7–8 spiral ribs, innermost (surrounding umbilicus) broadest and with 8–10 large, regular nodules; umbilical side of columellar wall without spiral sculpture or with weak spiral projection in large shells. Tan, with midrib and basal areas darkest, subsutural rib and periphery white with pattern of orange-tan blotches. Protoconch diameter 0.86–0.94 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: small, diameter of known specimens 6.3–9.7 at 3 1/4–4 1/8 whorls. Shape: depressed cone-shaped with angular periphery; moderately wide umbilicus (UD ca. 15% of SD); suture shallow. Sculpture: consisting of rounded tubercles; Upper side: SSR with coarser granules than following 2 MR; MR and ± equally strong UPR with smooth and flattened nodules; between UPR and keel-forming LPR with 1 narrow additional rib; angular periphery formed by almost equally prominent LPR and IPR, with 1 narrow additional rib centered between them; upper point of whorl attachment at LPR, hence no distinct suture; base with 7–8 spiral ribs, increasing in width towards umbilicus; innermost (UC) broadest and with 8–10 large, regular nodules; umbilical side of columellar wall without distinct spiral sculpture, or, especially in larger specimens, with 1 indistinct ridge not bearing nodules; inner lip strong. Coloration: shades of tan with MR and basal areas darkest; SSR and PR white with pattern of narrow (1–2 nodules wide) orange-tan blotches, the latter often extending as darker





Figs. 180, 181. *Heliacus (Torinista) geminus* n.sp. Fig. 180: holotype; New Caledonia; MNHNP unnumbered; SD = 9.0. Fig. 181: paratype 5; Andaman Islands; BMNH 1981105; SD = 9.1.

flames onto both sides; ribs surrounding umbilicus (UC and PUR) white; grooves between spiral ribs, especially on base, darker. – Protoconch: small to medium-sized (0.86–0.94, $\bar{x}$ = 0.90), multispiral, distinctly heterostrophic, folds visible in false umbilicus; without anal keel; tan, darker towards peritreme . – Operculum as described for subgenus, with height equal to diameter (paratype 5). – Radula and Anatomy: not known.

Geographical distribution (Fig.179): Known only from New Caledonia and the Andaman Islands.

Discussion:

Heliacus geminus n.sp. is similar to the narrowly-umbilicated morph ("africanus-form") of *H. implexus*. However, that form lacks the additional rib between upper peripheral rib (UPR) and keel-forming lower peripheral rib (LPR), possesses a distinctly nodulose spiral rib on the umbilical wall, and has a protoconch larger than 0.94 mm. *Heliacus cerdaleus* (below) has a similarly angular periphery and narrow umbilicus surrounded by coarse nodules. Members of that species have only one midrib and the protoconch is smaller than 0.80 mm. See also *H. enoshimensis* (below).

Heliacus (Torinista) enoshimensis (Melvill, 1893)
Figs.182–184

*1891 *Solarium (Torinia) enoshimense* Melvill, J. Conch., *6*(12): 411, pl.2 fig.12.
*1905 *Torinia densegranosa* Pilsbry, Proc. Acad. nat. Sci. Philadelphia, *57*: 106, pl.3 figs.15–17.
1913 *Heliacus Enoshimensis*, – Melvill, Proc. malac. Soc. Lond., *10*(5): 317.
1948 *Torinia densegranosa*, – Bayer [in part], Zool. Verh., *4*: 15.
1948 *Torinia enoshimensis*, – Bayer, Zool. Verh., *4*: 18.
1961 *Heliacus enoshimensis*, – Habe, Col. illus. shells Japan (*II*): 30, pl.13 fig.18.
1964 *Heliacus enoshimensis*, – Habe, Shells w. Pac. col., 2: 45, pl.13 fig.18.
1971 *Torinista enoshimensis*, – Kuroda et al., Sea shells Sagami Bay: 264, 423, pl.61 figs.10–11.
1977 *Heliacus (Heliacus) enoshimensis*, – Garrard, Rec. Austr. Mus., *31*(13): 533–534, pl.7 figs.22–25.
1987 *Solarium (Torinia) enoshimense*, – Trew, Melvill's new moll. names: 38.

Type measurements: Lectotype of *S. enoshimense* [here designated]: SD = 5.3, H = 2.8, PD = 0.88, Tw = 3, UD = 1.6; Lectotype of *T. densegranosa* [here designated]: SD = 8.6, H = 5.0, PD = 0.88, Tw = 4 1/8, UD = 2.0.

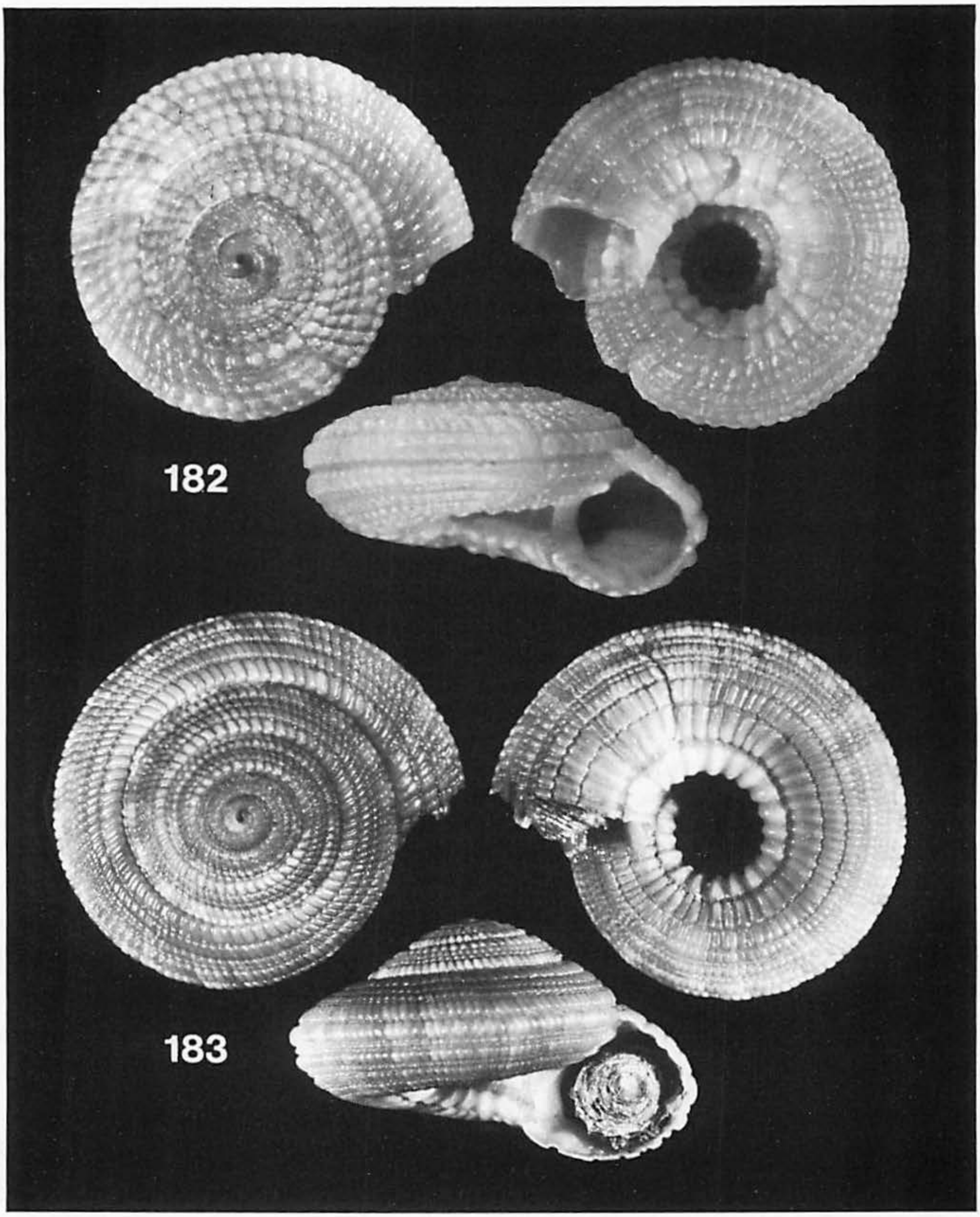
Type localities: *S. enoshimense*: "Enoshima, Japonica"; *T. densegranosa*: "Fukura, Awaji" [Japan].

Etymology: *enoshimensis-e* [adjective]; named after the type locality, Enoshima.

Material studied: 68 specimens (AMS, ANSP, BMNH, CAS, FMNH, IRSNB, MCZ, MNHNP, MNHU, NMW, RNHL, USNM, ZMA); including lectotype and 2 paralectotypes of *S. enoshimense* (BMNH 1884.4.3.10–12), 2 paralectotypes of *S. enoshimense* (NMW 1955.158.202), lectotype and 1 paralectotype of *T. densegranosa* (ANSP 88306).

Diagnosis:

Small, rounded lens-shaped to depressed cone-shaped shell with moderately wide to wide umbilicus and shallow sutures; upper-side sculpture of 4 ribs (2 central ones weaker) with more or less flattened nodules; rounded double keel formed by 2 ribs, with lower one somewhat weaker; fine additional ribs between ribs at periphery; basal sculpture of 5 regular spiral ribs, with innermost (surrounding umbilicus) narrower



Figs. 182, 183. *Heliacus (Torinista) enoshimensis* (MELVILL, 1893). Fig. 182: lectotype of *Solarium enoshimense*; Japan; BMNH 1884.4.3.10; SD = 5.3. Fig. 183: lectotype of *Torinia densegranosa* PILSBRY, 1905; Japan; ANSP 88306; SD = 8.6; with operculum.

then the one before it; outer base area with additional fine spiral threads; umbilical side of columellar wall usually with 1 projection. Fawn with regular darker flames; subsutural rib and umbilical crenae lighter and spire darker. Protoconch diameter 0.82–0.98 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: small, diameter of specimens in collections usually 5-8.9 at 3 to 4 1/8 whorls. Shape: juveniles very rounded, lens-shaped; later depressed cone-shaped with distinctly convex whorls; umbilicus moderately wide to wide (UD 18-30% of SD); suture shallow. Sculpture: Upper side: SSR and UPR usually markedly stronger than the 2 MR between them, UMR usually somewhat wider than LMR; between LMR and UPR on later whorls always 1 additional rib; Periphery: rounded double keel formed by LPR and somewhat weaker IPR, on later whorls always with 1 finer additional rib between the two; upper point of whorl attachment on LPR; Base: usually 5 regular spiral ribs, somewhat increasing in width towards umbilicus; PUR usually distinctly wider than UC; UC with 15-26 nodules on body whorl; outer base area usually with additional fine spiral threads; umbilical side of columellar wall convex, usually with 1 spiral projection. Coloration: fawn, with SSR and UC lighter and spire darker; ± regular darker flames on whole shell (2-3 nodules wide on peripheral ribs). - Protoconch: small to medium-sized (0.82-0.98, $\bar{x}$ = 0.89), multispiral, distinctly heterostrophic, without anal keel; tan. - Operculum (Fig.183): as described for subgenus. - Radula and Anatomy: not known.

Geographical distribution (Fig.184): Known from Japan, eastern Australia and Norfolk Island.

Habitat: Sublittoral; most records from between 35m and 140m.

Discussion:

Heliacus implexus (above) is similar, but has larger shells (8-10 at 3-4 whorls) and 1 distinct spiral rib in the umbilicus. *Heliacus geminus* n.sp. (above) differs by having fewer umbilical crenae, and by much more prominent peripheral ribs, giving the shell an angular appearance.

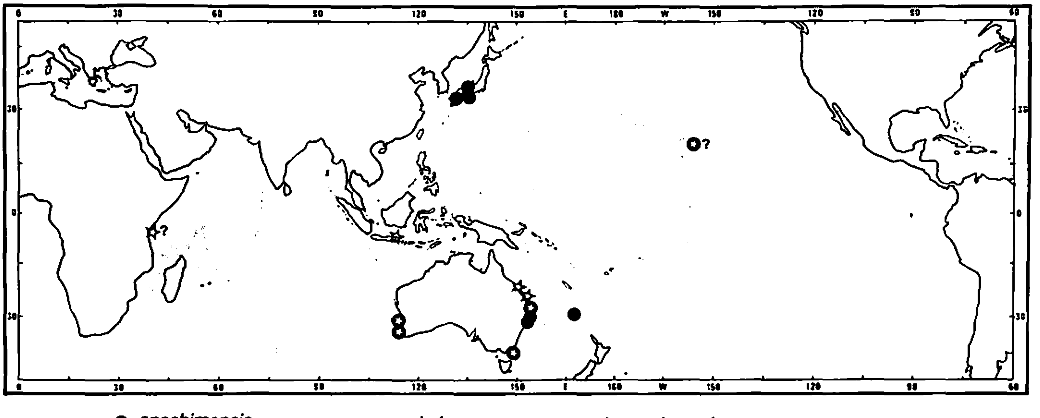


Fig. 184. Geographical distribution of *Heliacus enoshimensis, H. ponderi* and *H. madurensis*.

In the original description of *Solarium enoshimense*, MELVILL (1891: 411) mentioned "two specimens precisely similar" from his collection and "... at the Natural History Museum, South Kensington ... two or three others, unnamed, labelled 'Japan'." For the largest specimen known to him, MELVILL gave the measurements "Long.: 2.50 mill. ..., Lat.: 5 mill." The original sketch (1891: pl.2 fig.12) is not sufficient for interpretation. The largest of three syntypes in the BMNH (1884.4.3.10–12; see Fig.182) is here designated as lectotype. GARRARD's (1977: 534) erroneous reference to a "holotype" does not qualify as lectotype designation by inference, since MELVILL clearly mentioned more than one specimen in the original description (GARRARD himself subsequently referred to "3 syntypes" [1977: 534]). Two additional paralectotypes are in Cardiff (NMW 1955.158.202).

PILSBRY (1905: 106) wrote in the original description of *Torinia densegranosa*: "Types No. 88,306, A.N.S.P., from No. 1,568 of Mr. Hirase's collection." The ANSP collection contains two syntypes under this number, the specimen here figured (see Fig.183) agrees well with the original figure and is selected as lectotype of *Torinia densegranosa*. The collections in Brussels and Washington contain further specimens ex HIRASE's collection number 1,568 (IRSNB unnumbered, USNM 205584, 307816; vidi).

MELVILL (1913: 317) correctly synonymized the two nominal species, *Solarium enoshimense* and *Torinia densegranosa*. BAYER (1948: 15) treated *T. densegranosa* as a valid species, but also listed the name in the synonymy of *S. enoshimense* (1948: 18). For an interpretation of BAYER's description it should be noted that one of the two "*enoshimense*" specimens available to him is a member of *Heliacus implexus* (RNHL, vidi).

Heliacus (Torinista) ponderi GARRARD, 1977
Figs.184–185

1948 *Torinia mighelsi*, - BAYER, Zool. Verh., *4*: 29 [non *Solarium mighelsi* PHILIPPI, 1853].
*1977 *Heliacus (Heliacus) cerdaleus ponderi* GARRARD, Rec. Austr. Mus., *31*(13): 532, pl. 2 figs.10–12 [not pl.9 figs.7–9; see discussion below]; non *Solarium cerdaleum* MELVILL & STANDEN, 1903].

Type measurements (holotype): SD = 9.8, H = 7.3, PD = 1.24, Tw = 3 3/4, UD = 2.0.

Type locality: "Long Reef, Collaroy, near Sydney, New South Wales (33°43'S., 151° 18'E.)."

Etymology: *ponderi* [genitive singular case-ending]; named after Dr. WINSTON F. PONDER, Curator at the Australian Museum, Sydney.

Material studied: 38 specimens (AMS, RNHL); including holotype (AMS C.94479) and 5 paratypes (AMS C.94480).

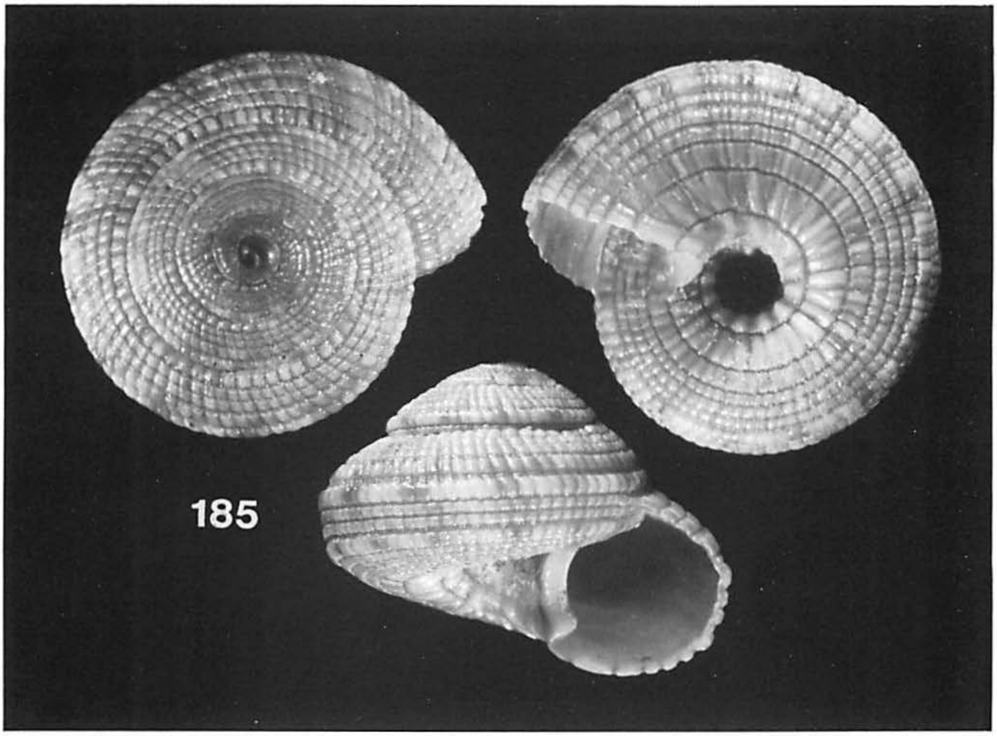


Fig. 185. *Heliacus (Torinista) ponderi* GARRARD, 1977; holotype; New South Wales, Australia; AMS C.94479; SD = 9.8.

Diagnosis:

Small to medium-sized, rounded cone-shaped shell with moderately wide to wide umbilicus; upper-side sculpture of 4 ribs (the 2 central ones often somewhat weaker), frequently flanked by weaker threads; with more or less flattened nodules; rounded periphery formed by 4 ribs (2 central ones weaker); basal sculpture of of 6–7 spiral ribs; convex umbilical side of columellar wall without spiral ribs. Reddish-tan with pattern of regular flames and flecks on peripheral ribs. Protoconch diameter 1.14–1.30 mm, strongly heterostrophic, without anal keel.

Description:

Teleoconch: small to medium-sized, diameter of specimens in collections usually 8–11.5 at 3 1/4–4 1/8 whorls (rarely more than 5 whorls). Shape: rounded cone-shaped with moderately wide umbilicus (UD 15–25% of SD). Sculpture: Upper side: SSR, 2 MR and UPR (MR often weakest), frequently flanked by weaker threads; with ± flattened nodules; Periphery: rounded peripheral area formed by LPR and somewhat weaker IPR, with 2 (rarely 3) relatively strong additional ribs between them; upper point of whorl attachment at the upper additional rib; Base: 6–7 flattened, relatively smooth spiral ribs, increasing in width towards umbilicus, with PUR often considerably wider

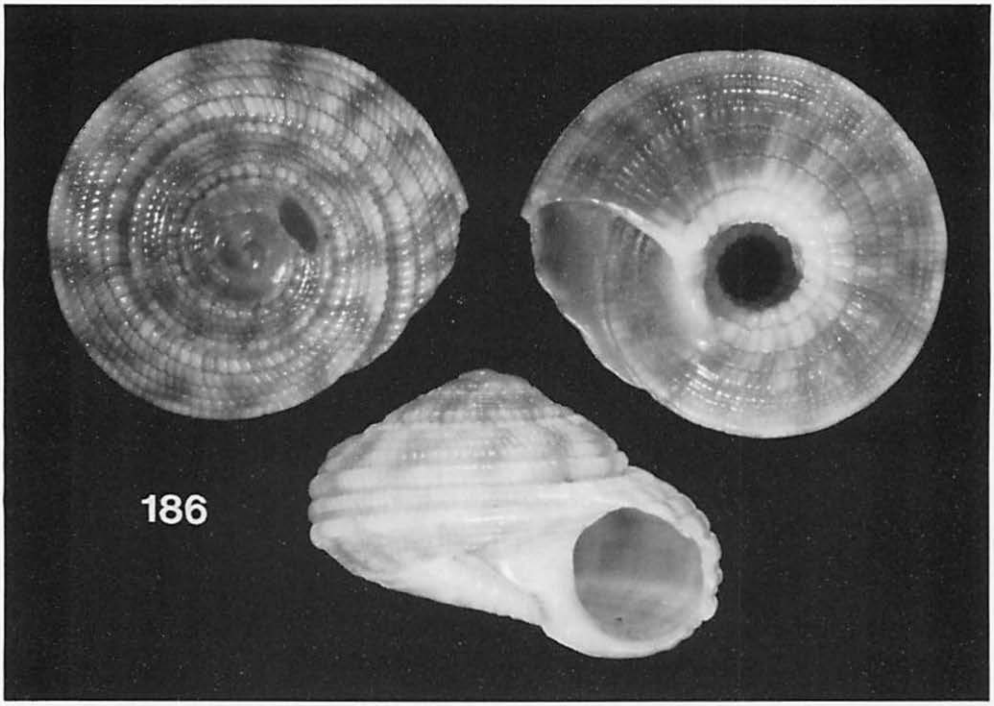


Fig. 186. *Heliacus (Torinista)* sp. aff. *ponderi* GARRARD, 1977; specimen from 3 km S. of Cape Naturaliste, Western Australia; AMS C.90978; SD = 8.3.

than UC; UC with 12–18 nodules on body whorl; umbilical side of columellar wall bulging, without distinct spiral sculpture. Coloration: light reddish-tan with weak pattern of ± regular darker flames; peripheral ribs with regular pattern of brown flecks (each about 2 nodules wide); sutures, especially between SSR and UMR, often darker. – Protoconch: medium-sized to large (1.14–1.30, $\bar{x}$ = 1.22), multispiral, strongly heterostrophic, without anal keel; yellowish-tan with brown patches. – Operculum: low cone-shaped. – Radula and Anatomy: not known.

Geographical distribution (Fig. 184): Known from Australia. Record from Hawaiian Islands doubtful.

Habitat: Sublittoral; records from 15–110 m.

Discussion:

GARRARD (1977: 532) described *ponderi* as a subspecies of *Heliacus cerdaleus* (MELVILL & STANDEN, 1903). Although somewhat similar (see below), that species differs in a number of characters (protoconch size, sculpture of the midrib area, position of whorl attachment, coloration), so that specific identity is highly unlikely. Both forms are now known to occur sympatrically and are even known from a single sample. The former nominal subspecies *ponderi* is here raised to species level.

The specimens referred to in Bayer's (1948: 29) treatment of "*Torinia mighelsi*" belong to *Helicaus ponderi* (material in RNHL, vidi). One of the specimens figured by Garrard in connection with the original description of *ponderi* (1977: pl.9 figs.7–9) is not a member of this species and may represent an undescribed species (see Fig.186). It differs from *H. ponderi* by a finer sculpture (112 nodules on the peripheral ribs of the third teleoconch whorl, compared to about 70 in *H. ponderi*), by having only one additional rib between lower peripheral and infraperipheral ribs (two in *H. ponderi*), by white umbilical crenae (general base color in *H. ponderi*), and by a larger protoconch (1.36 mm). Additional material will be necessary to determine its status. See also *H. madurensis* (below).

Heliacus (Torinista) madurensis (Schepman, 1909)

Figs.184, 187

*1909 *Torinia madurensis* Schepman, - Monogr. Res. Siboga Exped., *49*(1b): 222, pl.14 figs.4a-c.
?1925 *Torinia* sp., - Thiele, 1925a, Wiss. Ergeb. dtsch. Tiefsee-Exped. Valdivia, *17*(2): 115 [81].
1948 *Torinia madurensis*, - Bayer, Zool. Verh., *4*: 29.
1977 *Heliacus (Heliacus) madurensis*, - Garrard, Rec. Austr. Mus., *31*(13): 535, pl.4 figs.10–12.

Type measurements (holotype): SD = 5.6, H = 4.6, PD = 0.82, Tw = 3 5/8–, UD = 1.0.

Type locality: ['Siboga'] "Stat.51. Madura-Bay. 61–91 M. Fine grey sand, coral sand with shells" [N.E. Java, Indonesia].

Etymology: *madurensis-e* [adjective]; named after the type locality, Madura Bay.

Material studied: holotype of *T. madurensis* (ZMA 3.09.067) and original specimen of *Torinia* sp. of Thiele (1925a) (MNHU unnumbered).

Diagnosis:

Small, rounded cone-shaped shell with bulging whorls and moderately wide umbilicus; upper-side sculpture of 4 almost identical ribs, with flattened nodules; rounded peripheral area formed by 2 main ribs, with 2 additional ribs between them; basal sculpture of 6 flattened, partly smooth, spiral ribs; umbilical side of columellar wall without distinct spiral sculpture. Tan. Protoconch diameter (holotype) 0.82 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: small, rounded cone-shaped with bulging whorls and moderately wide umbilicus (UD ca. 18% SD). Sculpture: Upper side: SSR, 2 MR and UPR almost identical, with ± flattened nodules; Periphery: rounded area formed by LPR, 2 additional ribs and IPR, with the lower additional rib somewhat weaker than the others; upper point of whorl attachment between the two additional ribs; Base: 6 flat spiral ribs, increasing in width towards umbilicus; outer ones ± smooth, PUR with ± distinct axial folds; UC narrow, with ca. 13 ribs on body whorl; umbilical side of

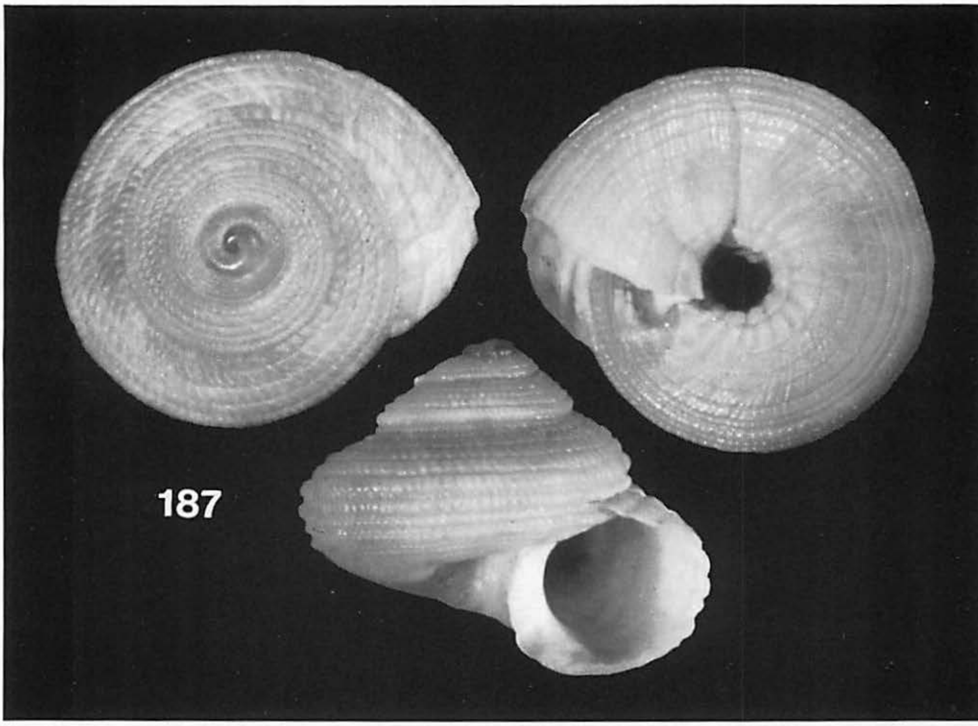


Fig. 187. *Heliacus (Torinista) madurensis* (SCHEPMAN, 1909); holotype of *Torinia madurensis*; Indonesia; ZMA 3.09.067; SD = 5.6.

columellar wall bulging, without distinct spiral scupture. Coloration: tan, with very weak darker pattern on periphery. Protoconch: small (holotype: 0.82), multispiral, distinctly heterostrophic, without anal keel; brown in holotype. - Operculum: apparently relatively flat (visible in aperture of type specimen); described by GARRARD (1977: 535) as with "extremely thin amber chitinous base with microscopic black streaks, central portion of smaller diameter built up to rounded top with many successive layers of thin similar material, apex hollow." - Radula and Anatomy: not known.

Geographical distribution (Fig.184): Known with certainty only from the type locality Java (Indonesia) and Queensland (eastern Australia).

Habitat: Sublittoral; type material live-collected in 61–91 m, other records from as shallow as 4 m.

Discussion:

The shell in this species is relatively tall and rounded, reminiscent of species in the subgenera *Heliacus* s.s. and *Gyriscus* (SCHEPMAN compared his species with *Heliacus trochoides*). Based on sculptural characters, especially the presence of two midribs, *H.*

madurensis is here grouped with *H. (Torinista)*. *Heliacus ponderi* (above) has a very similar shape and sculpture, but is a much larger form.

THIELE's (1925a) "*Torinia* sp." from 'VALDIVIA' station 244 (East Africa; MNHU unnumbered, vidi) appears to be a fragment of a *madurensis* shell, but has a protoconch diameter of only 0.68 mm.

Heliacus (Torinista) corallinus GARRARD, 1977

Figs.9, 188–189

*1977 *Heliacus (Torinista) corallinus* GARRARD, Rec. Austr. Mus., *31*(13): 543–544, pl.6 figs.19–20.
1984 *Heliacus corallinus*, - BIELER, 1984a, Arch. Moll., *114*(4/6): 119.
1985 *Heliacus (Torinista) corallinus*, - 1985b, BIELER, Arch. Moll., *116*(1/3): 97.

Type measurements (holotype): SD = 5.1, H = 3.0, PD = 0.82, Tw = 3 1/5–, UD = 2.5.

Type locality: "Michaelmas Cay, north Queensland (16°36'S., 145°59'E.)" [Australia].

Etymology: *corallinus-a-um* [adjective]; Latin: living in coral; referring to the presumed habitat.

Material studied: 21 specimens (AMS, FMNH, IRSNB, LACM, MNHNP, NMP, USNM); including holotype (AMS C.94340).

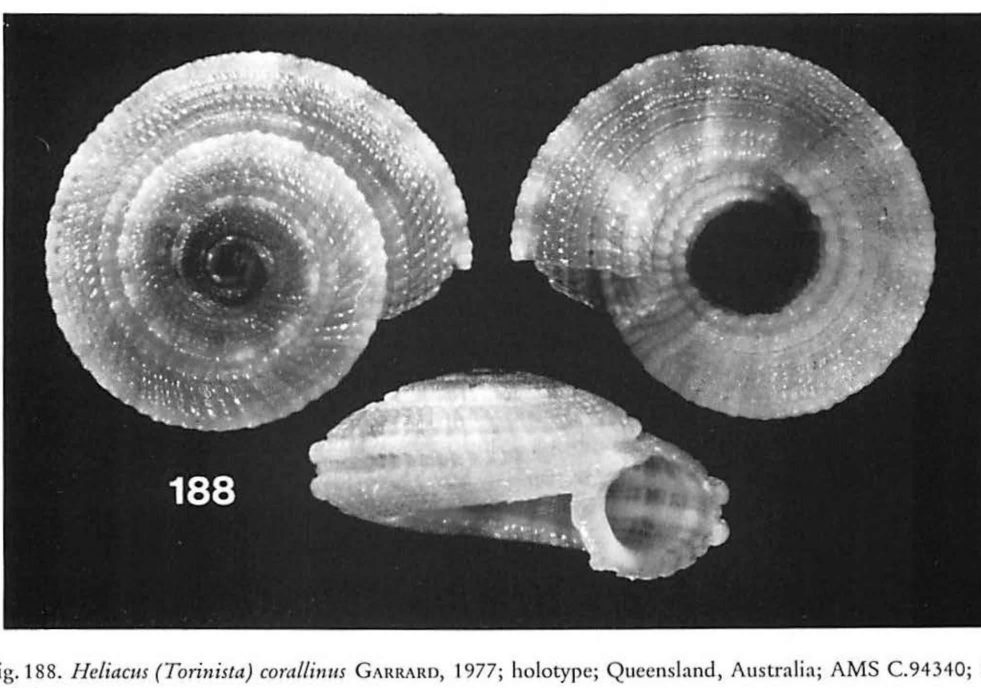


Fig. 188. *Heliacus (Torinista) corallinus* GARRARD, 1977; holotype; Queensland, Australia; AMS C.94340; SD = 5.1.

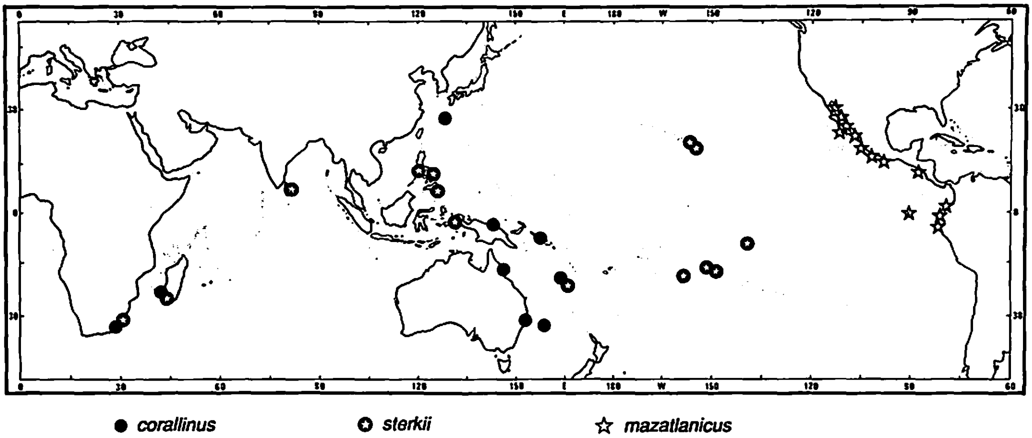


Fig. 189. Geographical distribution of *Heliacus corallinus*, *H. sterkii* and *H. mazatlanicus*.

Diagnosis:

Very small to small disk-shaped to depressed rounded cone-shaped shell with deep suture and very wide umbilicus; upper-side sculpture of 4 ribs with more or less rounded nodules; double-keel formed by 2 almost identical ribs; basal sculpture of 6 regular spiral ribs; umbilical side of columellar wall bulging, with central projection and fine spiral threads. Light to dark brown with pattern of brown blotches on white keel-forming ribs. Protoconch diameter 0.76–0.86 mm, distinctly heterostrophic, with anal keel and *Philippia*-like callus.

Description:

Teleoconch: very small to small, diameter in collections 3.4–6.3 at 2–3 1/4 whorls. Shape: disk-shaped to depressed rounded cone-shaped with very wide umbilicus (UD ca. 45%). Sculpture: Upper side: SSR, 2 MR and UPR almost identical, with ± rounded nodules; UPR very strong in "arrested growth" stage of first whorl; Periphery: double keel formed by almost identical LPR and IPR, usually with 1 additional finer rib between them; upper point of whorl attachment above IPR, suture deep; Base: usually with 6 regular spiral ribs, increasing in size towards umbilicus, innermost (UC) somewhat lowered into umbilicus, with 25–32 nodules on body whorl; umbilical side of columellar wall bulging, often with spiral central projection and 8–10 fine spiral threads. Coloration: light to dark brown (fresh specimens darker), LPR and IPR white with darker blotches, the latter about 2 nodules wide; base, especially UC, often lighter. – Protoconch (Fig.9): small (0.76–0.86, $\bar{x}$ = 0.83), distinctly heterostrophic, with anal keel and strong *Philippia*-like callus; off-white with brown patches, darkest in center. – Operculum, Radula and Anatomy: not known.

Geographical distribution (Fig.189): Known from southwestern Indian Ocean (South Africa and Madagascar) and western Pacific.

Habitat: Sublittoral. "The 5 specimens mentioned ... from 21 metres off Euston Reef, Queensland, were taken from the foot of a sandy slope beneath steep coral walls, indicating almost certainly that when alive the species exists in crevices in the vertical coral" (GARRARD, 1977: 544).

Discussion:

Heliacus corallinus, a species described by GARRARD (1977: 543) as appearing "to be endemic to eastern Australian area," has a wide distribution in the Indo-West Pacific. Specimens are similar in shape and coloration to juveniles of *H. implexus*, but can readily be separated by the unusual, callous anal keel area of the protoconch (see Fig.9).

Heliacus (Torinista) sterkii PILSBRY & VANATTA, 1908
Figs.189–191

*1908 *Torinia discoidea sterkii* PILSBRY & VANATTA, Nautilus, *22*(6): 57, fig.2 [non *T. discoidea* PEASE, 1868].
1932 *Solarium variegatum*, - TURTON [in part], Mar. shells Port Alfred: 134, no.968.
1933 *Torinia discoidea starkii* [sic]. - EDMONDSON, Bernice P. Bishop Mus. Spec. Publ., *22*: 136, fig.60c.
1948 *Torinia discoidea* var. *sterkii*, - BAYER, Zool. Verh., *4*: 16.
1967 *Heliacus discoideus sterkii*, - ROBERTSON, Science, *156*(3772): 246.
1979 *Heliacus sterkii*, - KAY, Hawaii. mar. shells: 99, figs.35 I-J.
1980 *Heliacus sterkii*, - REHDER, Smiths. Contr. Zool., *289*: 32–33.
1984 *Heliacus sterkii*, - BIELER, 1984a, Arch. Moll., *114*(4/6): 119.
1988 *Heliacus (Torinista) sterkii*, - BIELER, Malac. Rev., Suppl. *4*: 238 [radula].

Type measurements (holotype): SD = 4.6, H = 2.2, PD = 0.8, Tw = 2 3/4–, UD = 1.7.

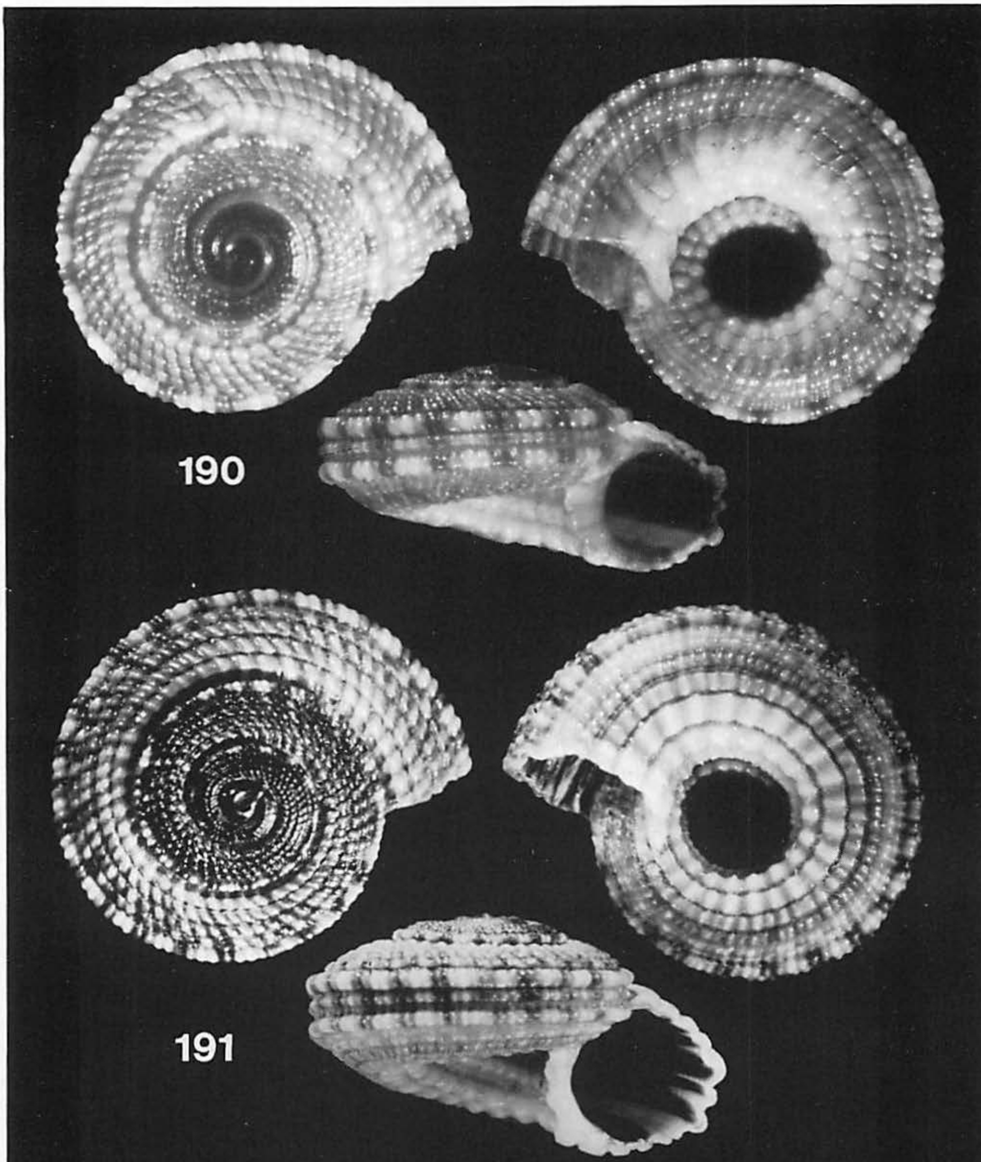
Type locality: "Waikiki Beach, Honolulu" [Oahu, Hawaiian Islands].

Etymology: *sterkii* [genitive singular case-ending]; named after the collector, the physician and malacologist Dr. Victor STERKI (1846–1933).

Material studied: 298 specimens (ANSP, BMNH, BPBM, CAS, DMNH, ELM, IRSNB, FLMNH, FMNH, LACM, MCZ, MNHNP, NMP, NMW, UCMP, UHM, UMZC, USNM, Coll. MARAIS, Coll. TRONDLE); including holotype (ANSP 93833) and 5 paratypes (ANSP 349682).

Diagnosis:

Small rounded lens-shaped shell with angular periphery, deep suture and wide to very wide umbilicus; upper-side sculpture of 4 ribs, with uppermost usually somewhat stronger; with rounded nodules; angular keel formed by 2 almost-identical main ribs, and 1 weaker additional rib between them; basal sculpture of 1 fine and 5 stronger spiral ribs; umbilical side of columellar wall with 2 strong spiral ribs. Dark brown or bluish grey to near-black; periphery with pattern of brown blotches; base much lighter with 1–2 darker ribs in center. Protoconch diameter 0.72–0.88 mm, distinctly heterostrophic, without anal keel.



Figs. 190, 191. *Heliacus (Torinista) sterkii* (PILSBRY & VANATTA, 1908). Fig. 190: holotype of *Torinia discoidea sterkii*; Oahu, Hawaiian Islands; ANSP 93833; SD = 4.6. Fig. 191: specimen from Port St. Johns, Transkei, South Africa; FMNH 223433; SD = 6.6.

Description:

Teleoconch: small, diameter of specimens in collections usually 6–9 at 3–4 whorls. Shape: rounded lens-shaped with angular periphery and wide to very wide umbilicus (UD ca. 28–43% SD). Sculpture: Upper side: SSR usually somewhat stronger than 2

MR and UPR, with rounded nodules; Periphery: angular keel formed by almost-identical LPR and IPR, with 1 additional, weaker but distinctly developed, rib between them; upper point of whorl attachment on this additional rib, suture deep; Base: 1 fine plus 5 strong spiral ribs, increasing in width towards umbilicus, with PUR frequently somewhat wider than UC; UC with 13–29 nodules on body whorl; umbilical side of columellar wall with 2 strong spiral ribs. Coloration: fresh specimens (Fig.191) with the first 1 1/2 whorls near-black, only the tips of the rounded nodules grey to dark brown; after that increasingly lighter, often bluish grey; peripheral ribs lighter with brown blotches (about 2 nodules wide); base overall lighter with PUR and UC usually white; 1–2 ribs in the center of the base darker than others; aperture with dark stripes beneath spiral sculpture; eroded specimens much lighter colored. – Protoconch: small (0.72–0.88, $\bar{x} = 0.82$), multispiral, distinctly heterostrophic, with folds in false umbilicus, without anal keel; black in fresh specimens, brown (false umbilicus darker) when faded. – Periostracum: thick, glassy, enhancing the shell sculpture when wet; yellowish and scaly when dry. – Operculum: as described for subgenus. – Radula: five-toothed taenioglossate (2–1–2); rachidian tooth stronger than marginal teeth with prominent, pointed subtriangular median cusp flanked by 15–17 smaller, blunt cusps; marginal teeth longer, curved and forked with 7–9 tapering cusps. – Anatomy: not studied. – Soft-body coloration of living animal: body color milky white; entire foot with dense pattern of black pigment; head with few tentacles with densely-packed black chromatophores; sole of foot with few black chromatophores along margin; no white granules present; overall appearance grey with black tentacles (pers. obs., South Africa).

Reproduction and larval development: sausage-shaped, mucous egg-masses of variable lengths and relatively small diameter (ca. 2.0 mm), containing about 250 weakly oval eggs per mm. Eggs interconnected by chalazae and covered by an additional membrane within the mucous mass, as described in the general part (pers. obs., South Africa).

Geographical distribution (Fig.189): southwestern Indian Ocean (South Africa, Madagascar) to central Pacific.

Habitat: Lives at the edges of colonies or between polyps of intertidal and upper subtidal zoanthinarian colonies; in shallow water.

Habits/feeding behavior: Feeds on zoanthinarian polyps (various species of zoanthid genera *Palythoa* and *Zoanthus*; pers. observ., South Africa).

Discussion:

Small specimens of this species are often confused with juvenile shells of *Heliacus variegatus*[11]. Separating characters are the two midribs (one in H. variegatus) and the additional rib between the relatively widely-spaced main ribs of the periphery, which is distinctly developed even in young specimens. See also H. mazatlanicus (below).

[11] The collection in Cambridge (UMZC unnumbered), for instance, holds two specimens of *Heliacus sterkii* that were cited by TURTON (1932: 134, no.968) as South African specimens of "*Solarium variegatum*."

Heliacus sterkii was originally described by PILSBRY & VANATTA (1908: 57) as a subspecies of *Torinia discoidea* PEASE, 1868. KAY (1979: 99) was the first to raise the name to species level. *Heliacus discoideus* is a form of the *Heliacus infundibuliformis*-complex (see below). The type specimen of *H. sterkii* (Fig.190) is a faded, subadult shell, and KAY (1979: 99) noted that the "habits of the living animals are unknown, but beach-worn specimens are abundant...". *Heliacus sterkii* was long considered a form restricted to the central Pacific, but has a wide distribution in the Indo-Pacific (see BIELER, 1984a: 119).

Heliacus (Torinista) mazatlanicus PILSBRY & LOWE, 1932
Figs.189, 192

*1932 *Heliacus mazatlanticus* PILSBRY & LOWE, Proc. Acad. nat. Sci. Philadelphia, *84*: 83, pl.8 figs.6–8.
1948 *Torinia mazatlanica*, - BAYER, Zool. Verh., *4*: 29.
1971 *Heliacus mazatlanicus*, - KEEN, Sea shells trop. w. Amer. (2nd ed.): 389, fig.430.
1974 *Heliacus bisulcatus mazatlanicus*, - ABBOTT, Amer. seashells (2nd ed.): 98.
1976 *Heliacus mazatlanicus*, - ROBERTSON, 1976a, Bull. Amer. malac. Union, *1975*: 51.

Type measurements: (holotype): SD = 5.8, H = 3.3, PD = ca.0.8 [eroded], Tw = 3, UD = 1.6.

Type locality: "Mazatlan, Mexico" [Sinaloa State, Pacific coast].

Etymology: *mazatlanicus-a-um* [adjective]; named after the type locality Mazatlán.

Material studied: 280 specimens (AMNH, ANSP, BMNH, CAS, IRSNB, LACM, MNHNP, NMP, NMW, USNM); including holotype and 3 paratypes (ANSP 152121).

Diagnosis:

Very small to small, rounded lens-shaped shell with double keel, shallow suture and wide umbilicus; upper-side sculpture of 4 almost identical ribs with more or less rounded nodules; rounded double keel formed by 2 ribs, upper of which is somewhat stronger; basal sculpture of 5 spiral ribs, with the rib next to the innermost the widest; umbilical side of columellar wall with 1 strong spiral projection. Brown with pattern of blotches on lighter-colored keel-forming ribs, midribs and outer basal ribs lighter. Protoconch diameter 0.70–0.86 mm, distinctly heterostrophic, with anal keel.

Description:

Teleoconch: very small to small, diameter of specimens in collections usually about 5 at ca. 2 1/2 whorls (SD rarely up to 10). Shape: rounded lens-shaped with prominent double keel and wide umbilicus (UD about 28% SD). Sculpture: Upper side: SSR and UPR usually somewhat stronger than 2 MR, with ± rounded nodules; Periphery: rounded double keel formed by LPR and IPR, with LPR somewhat stronger; in large specimens with 1 additional finer rib between them; upper point of whorl attachment on LPR, suture shallow; Base: 5 spiral ribs with PUR often wider than UC, increasing

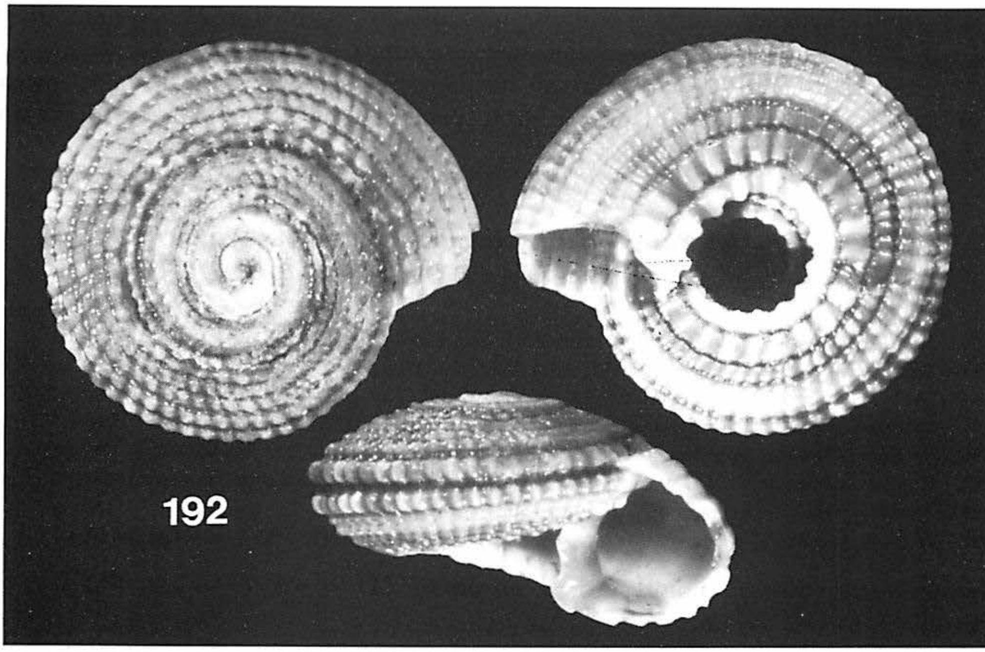


Fig. 192. *Heliacus (Torinista) mazatlanicus* Pilsbry & Lowe, 1932; holotype; Mazatlán, Mexico; ANSP 152121; SD = 5.8.

in width towards umbilicus; larger specimens with one additional rib between IPR and basal ribs; UC with 14–19 nodules on body whorl; umbilical side of columellar wall with 1 strong spiral projection. Coloration: Greyish brown to red-brown, peripheral ribs whitish with brown blotches (about 1–2 nodules wide); UC always light colored; frequently, especially in eroded specimens, MR and outer basal ribs lighter colored. Protoconch: small (0.70–0.86, $\bar{x}$ = 0.79), multispiral, distinctly heterostrophic, with anal keel (about 0.26 in length); off-white with brown patch. – Periostracum: yellowish, scaly when dry. – Operculum: as described for subgenus. – Radula and Anatomy: not known.

Geographical distribution (Fig.189): Eastern Pacific, from northern Gulf of California to Tumbes Province, northern Peru, and the Galapagos Islands.

Habitat: Records from intertidal to 136 m depth.

Discussion:

In this genus, an anal keel on the protoconch is otherwise known only from *Heliacus corallinus* and *H. turritus*. In *H. corallinus*, the protoconch varix bears a callous thickening and the teleoconch has a much wider umbilicus. Members of *H. turritus* have high-spired teleoconchs. *Heliacus sterkii*, which does not have an anal keel on the protoconch, is similar in teleoconch characters, but has a deep suture and a strong additional rib at the periphery.

A very similar sympatric form (not illustrated), usually regarded as *Heliacus mazatlanicus* but probably representing a distinct species, differs in having a larger protoconch (up to 1.06), no well-defined spiral rib on the umbilical wall, and an angle instead of a well-developed anal keel on the protoconch. See also the following discussion under *H. virgatus*.

Heliacus (Torinista) virgatus (HINDS, 1844)
Fig.193

*1844 *Solarium virgatum* HINDS, 1844b, Proc. zool. Soc. Lond., *1844*: 24.
1844 *Solarium virgatum*, - HINDS, 1844d, Ann. Mag. nat. Hist., *14*: 440.
1844–1845 *Solarium virgatum*, - HINDS, 1844c–1845, Zool. Voy. SULPHUR, *3*: 52, *2*: pl.14 figs.18–19.
1853 *Solarium virgatum*, - PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 21, pl.3 fig.10 [after HINDS, 1844d].
1863 *Solarium (Torinia) virgatum*, - HANLEY, Thes. conch., *3*: 240, pl.254, figs.85–86.
1887 *Solarium virgatum*, - MARSHALL, Man. conch., *9*: 20, pl.6 figs.2–3 [after HANLEY, 1863].
1948 *Torinia virgata*, - BAYER, Zool. Verh., *4*: 36.
1977 *Heliacus (Torinista) virgatus*, - GARRARD, Rec. Austr. Mus., *31*(13): 550, pl.8 figs.16–18.

Measurements (possible holotype of *S. virgatum)*: SD = 5.0, H = 2.3, PD = 1.02, Tw = 2 3/8, UD = 1.6.

Type locality: "Hab. New Guinea."

Etymology: *virgatus-a-um* [adjective]; Latin: made of twigs, striped.

Material studied: possible holotype specimen (BMNH 1874.12.11.190).

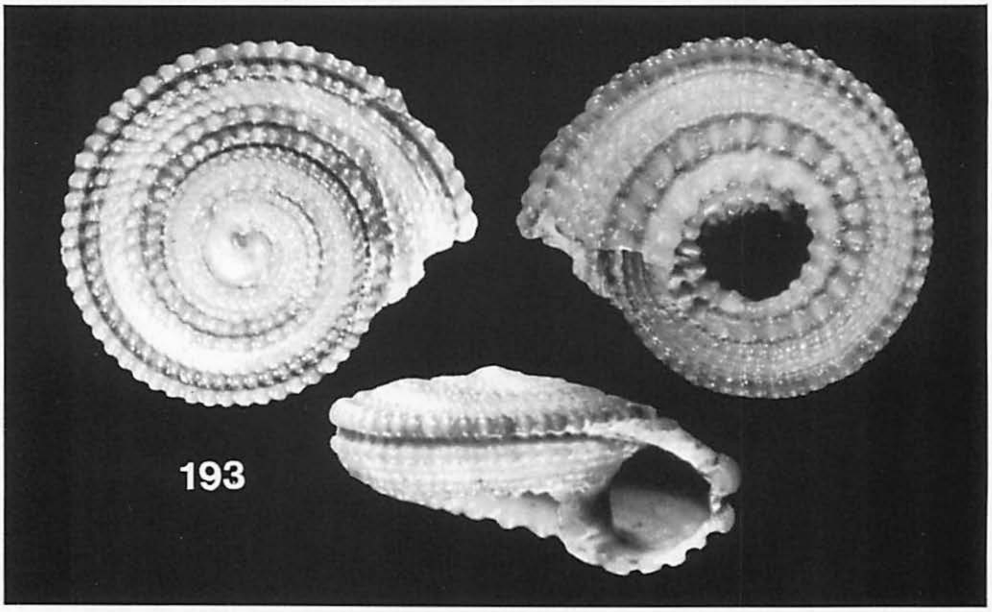


Fig. 193. *Heliacus (Torinista) virgatus* (HINDS, 1844); possible holotype specimen of *Solarium virgatum*; BMNH 1874.12.11.190; SD = 5.0.

Discussion:

All entries in the synonymy above are based on HINDS' (1844b: 24) holotype of *Solarium virgatum* from New Guinea. The figures published by GARRARD (1977: pl.8 figs.16–18) and here (Fig.193) probably show the original specimen.

With the exception of two protoconch characters (larger size and a weak ridge instead of a distinct anal keel) and the absence of a distinct spiral rib on the umbilical wall, the shell agrees with the known specimens of eastern Pacific *Heliacus mazatlanicus* and may be conspecific with the large-protoconch "form" mentioned above. Further material from the western Pacific is not known. Additional study of variability and geographic distribution of the Pacific *mazatlanicus*-like forms is necessary.

Heliacus (Torinista) cerdaleus (MELVILL & STANDEN, 1903)
Fig.194–196

*1903 *Solarium (Torinia) cerdaleum* MELVILL & STANDEN, Ann. Mag. nat. Hist., (7)*12*: 297, pl.20 fig.16.
1948 *Torinia cerdalea*, - BAYER, Zool. Verh., *4*: 10.
*1977 *Heliacus (Heliacus) hedleyi* GARRARD, Rec. Austr. Mus., *31*(13): 534, pl.9 figs.22–24.
1987 *Solarium (Torinia) cerdaleum*, - TREW, MELVILL's new moll. names: 30.

Type measurements: lectotype of *S. cerdaleum*: SD = 8.5, H = 5.6, PD = 0.7, Tw = 3 3/4+, UD = 1.1; holotype of *H. hedleyi*: SD = 8.7, H = 5.9, PD = 0.68, Tw = 4 3/8, UD = 1.5.

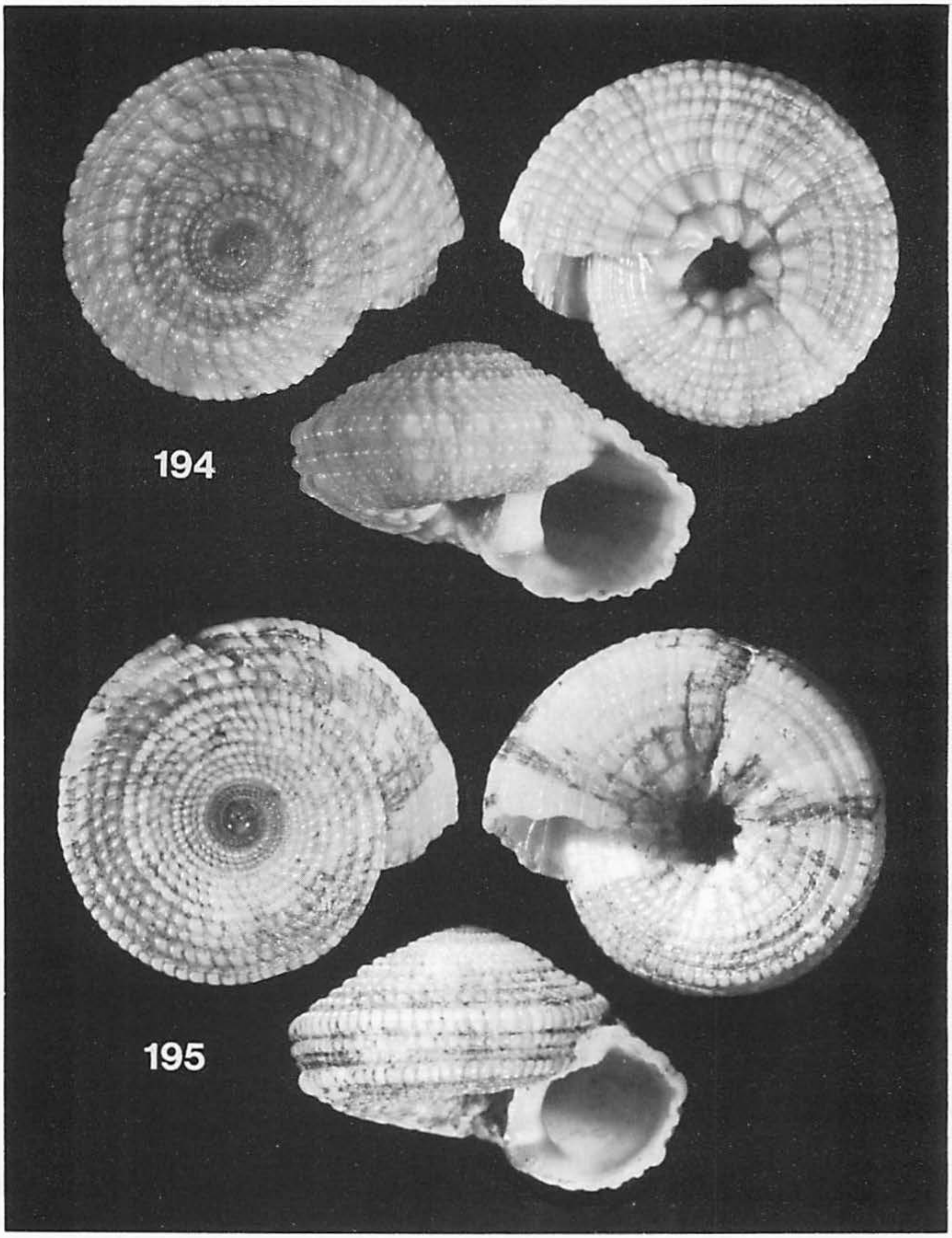
Type localities: *S. cerdaleum*: "Persian Gulf, Fao, on telegraph-cable"; *H. hedleyi*: "Port Curtis, Queensland (23°52'S., 151°21'E.), 13–18 metres."

Etymology: *cerdaleus-a-um* [adjective]; Latinization of Greek adjective κερδαλέος: cunning, advantageous.

Material studied: 12 specimens (AMS, ANSP, BMNH, MNHNP, NMW); including lectotype (BMNH 1903.12.15.107) and 2 paralectotypes (NMW 1955.158.195) of *S. cerdaleum*, holotype of *H. hedleyi* (AMS C.18727).

Diagnosis:

Small depressed cone-shaped shell with angular periphery, shallow suture, moderately wide umbilicus, and sculpture consisting of rounded tubercles becoming coarser with increasing whorls; upper-side sculpture with 3 main ribs (the uppermost somewhat stronger), sometimes with finer threads between them; angular prominent double keel formed by 2 main ribs (lower one somewhat weaker), and between them 1 strong additional rib flanked by finer threads; basal sculpture of 5–6 spiral ribs, innermost 2 with very coarse nodules; umbilical side of columellar wall frequently with 2 indistinct spiral projections. Whitish to light tan, spire darker, periphery lighter, usually with brown blotches; fresh specimens with 1 brown streak in aperture. Protoconch diameter 0.66–0.80 mm, distinctly heterostrophic, without anal keel.



Figs. 194–195. *Heliacus (Torinista) cerdaleus* (MELVILL & STANDEN, 1903). Fig. 194: lectotype of *Solarium (Torinia) cerdaleum*; Persian Gulf; BMNH 1903.12.15.107; SD = 8.5. Fig. 195: holotype of *Heliacus hedleyi* GARRARD, 1977; Queensland, Australia; AMS C.18727; SD = 8.7.

Description:

Teleoconch: small, diameter of specimens in collections usually 5–8.5 at 3 1/8 – 3 7/8 whorls (rarely more than 4 whorls). Shape: depressed cone-shaped with angular periphery; moderately wide umbilicus (UD ca. 20% of SD); shallow suture. Sculpture: consisting of rounded tubercles, becoming coarser with increasing whorls; Upper side: SSR somewhat stronger than following single MR, sometimes with fine threads interspersed; Periphery: UPR almost identical to MR; large specimen usually with fine spiral thread between them; angular prominent double keel formed by LPR and somewhat weaker IPR; between them 1 relatively strong additional spiral rib, with 1 finer thread above (and in larger specimens also below) this rib; upper point of whorl attachment usually on or immediately below LPR; Base: 5–6 spiral ribs, increasing in width towards umbilicus; frequently with additional finer threads interspersed; innermost 2 ribs (PUR and UC) with very coarse nodules, 8–11 on UC of body whorl; umbilical side of columellar wall convex, frequently with 2 indistinct spiral projections. Coloration: whitish to light tan, spire darker; periphery light, usually with ± regular brown blotches (usually only 1 nodule wide); UC lighter than basal area; parietal wall white; fresh specimens with 1 brown streak in the upper part of aperture. – Protoconch: small (0.66–0.80, $\bar{x} = 0.72$), multispiral, distinctly heterostrophic, without anal keel; light tan. – Periostracum: thin, brownish. – Operculum: low cone-shaped, otherwise as described for subgenus. – Radula and Anatomy: not known.

Geographical distribution (Fig.196): Known from several localities in the Indian Ocean (Madagascar, Persian Gulf, India), from Indonesia and Queensland, Australia.

Habitat: Sublittoral; available records from 7–31 m, live-collected type material from unrecorded depth ("on telegraph cable").

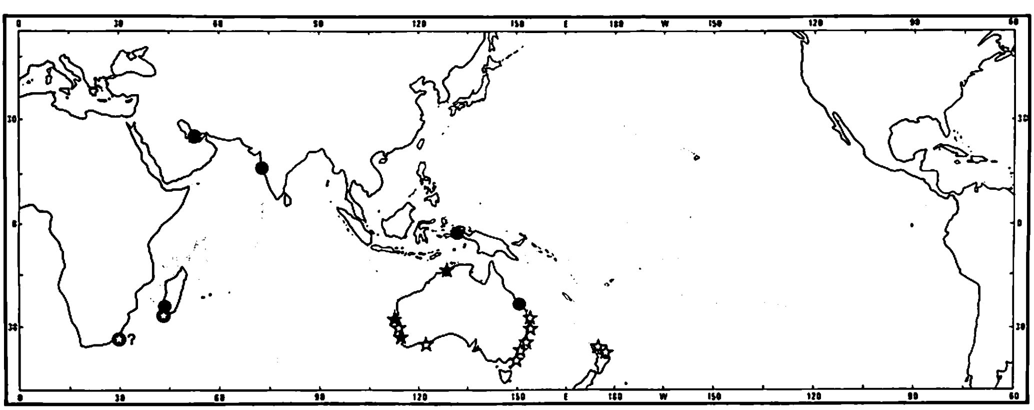


Fig. 196. Geographical distribution of *Heliacus cerdaleus*, *H. oceanitis* n.sp., *H. hyperionis* n.sp. and *H. nereidis* n.sp.

Discussion:

Heliacus cerdaleus differs from most of the other known *Heliacus* species by the coarsely sculptured, angulate shell with narrow umbilicus. *Heliacus geminus* (above) has a similar shell shape, but possesses two midribs and a larger protoconch. See also *H. ponderi* (above), *H. hyperionis* n.sp. and *H. oceanitis* n.sp. (below).

In the original description of *Solarium cerdaleum*, MELVILL & STANDEN (1903: 297) did not indicate the number of specimens available to them but later added the general statement that "types ... will be placed in the British Museum (Natural History)" (1903: 323). The single specimen in London (BMNH 1903.12.15.107) agrees well with the original measurements and figure (see Fig.194). It was referred to by GARRARD (1977: 533) as "holotype," an action here accepted as "designation of lectotype by inference of holotype (ICZN, 1985: Article 74(b)). Two paralectotypes are located in Cardiff (NMW unnumbered, vidi).

GARRARD (1977: 534) described his new nominal species *Heliacus hedleyi* as "apparently endemic to eastern Australia." The holotype (see Fig.195) appears to be a very light-colored shell of *H. cerdaleus*. *H. hedleyi* is here synonymized with *H. cerdaleus*.

Heliacus (Torinista) hyperionis n.sp.
Figs.196–198

1977 *Heliacus (Torinista) delectabilis*, - GARRARD, Rec. Austr. Mus., *31*(13): 545, pl.5 figs.1–3 [non *Solarium delectabile* MELVILL, 1893; see under *Pseudotorinia*].

Type measurements:

	SD	H	PD	Tw	UD	Locality	Collection
Holotype	6.2	3.6	1.16	2 5/8	1.7	New South Wales	AMS C.92021
Paratype 1	7.4	3.7	1.14	2 3/4	2.4	New Zealand	NMNZ M.30764
Paratype 2	5.4	2.9	1.26	2 3/8	1.4	New Zealand	NMNZ M.30764
Paratype 3	6.1	3.7	1.18	2 5/8-	1.5	New South Wales	AMS C.92020
Paratype 4	5.9	3.3	1.22	2 3/8+	1.5	New South Wales	AMS C.92025
Paratype 5	5.3	3.3	1.26	2 1/4+	1.3	Queensland	FMNH 223410
Paratype 6	5.4	3.0	1.16	2 3/8	1.4	New Zealand	NMNZ M.67783
Paratype 7	3.9	2.0	1.24	1 5/8	1.2	New South Wales	FMNH 223416

Type locality: Twofold Bay, New South Wales, Australia (37°06'S, 149°55'E); holotype (C.F. LASERON coll.). Paratypes 1–2 from northeast of Ninepin Rock, Bay of Islands, New Zealand, 75 m (1.XII.1971). Paratype 3 from off Twofold Bay (type locality), 90 m. Paratype 4 from 7 miles off Crowdy Head, Manning River, New South Wales, 82 m. Paratype 5 from southeast of Swain Reefs, Queensland (22°26.27' to 22°20.2'S, 153°17.13' to 153°17.6'E), 187 m (HMAS 'KIMBLA' Sta. 7, 5.VII.1984). Paratype 6 from ca. 24 km north of Motuharo Island (37°37.8'S, 176°59.9'E to

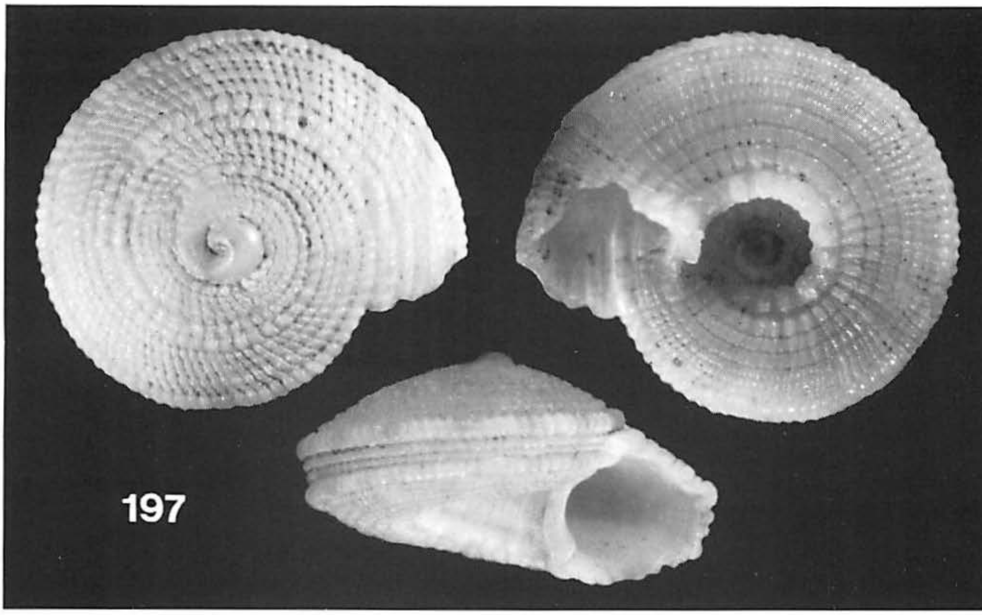


Fig. 197. *Heliacus (Torinista) hyperionis* n.sp.; holotype; New South Wales, Australia; AMS C.92021; SD = 6.2.

37°40.5'S, 177°00.8'E), 129–139 m (R/V 'TANGAROA,' NZOI station R82, 20.I.1979). Paratype 7 from off Cronulla, New South Wales, 100 m.

Etymology: *hyperionis* (genetive singular case-ending); Hyperion: son of Titan and Earth, father of the sun (the generic name *Heliacus* meaning "belonging to the sun").

Material studied: 8 type specimens as listed above, and 35 additional specimens, mostly juveniles and fragments (AMS, NMNZ).

Diagnosis:

Small, depressed cone-shaped shell with very angular periphery, wide suture, moderately wide to wide umbilicus, and gemmate sculpture with distinct axial pattern; upper-side sculpture with 4 ribs, the uppermost of which somewhat coarser, the outermost often flanked by fine threads; periphery formed by 4 ribs, the two central ones of which weakest; basal sculpture of 7 spiral ribs, innermost with fine nodules; umbilical side of columellar wall without strong spiral ribs. Off-white to yellowish-tan, with darker fleck pattern on peripheral ribs. Protoconch diameter 1.14–1.28 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: small, diameter of specimens in collections usually 5–7.4 at 2 1/4 – 2 3/4 whorls. Shape: depressed cone-shaped with very angular periphery; moderately wide to wide umbilicus (UD ca. 27% of SD). Sculpture: gemmate, distinct axial pattern

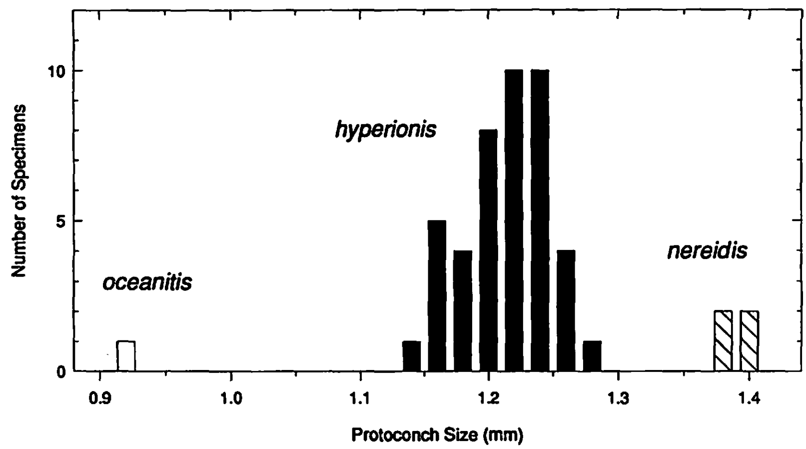


Fig. 198. Histograms of measured protoconch size. *H. oceanitis* n.sp. (n = 1), *Heliacus hyperionis* n.sp. (n = 43, x̄ = 1.21, sd = 0.03), and *H. nereidis* n.sp. (n = 4, x̄ = 1.39).

weaker than spiral ribs; Upper-side sculpture with 4 ribs (somewhat coarser SSR, 2 MR and UPR), the latter in larger specimens often flanked on either side by fine threads; very angular periphery formed by strong LPR, weaker IPR and 2 narrow but well-developed additional ribs between them; upper point of whorl attachment at or immediately below the upper, somewhat stronger developed additional rib; wide suture not very deep; base with 7 ribs increasing in width towards umbilicus, innermost (UC) with relatively fine crenae (13–26 on body whorl), in young specimens somewhat lowered into umbilicus; convex umbilical side of columellar wall with fine spiral threads and axial growth lines, without strong spiral ribs. Coloration: off-white to yellowish-tan, with darker tan fleck pattern on peripheral ribs, interspersed with white; flecks about 2 nodules wide, extending onto either side as weak flames. - Protoconch (Fig.198): small to medium-sized (1.14–1.28, x̄ = 1.21); multispiral, distinctly heterostrophic, without anal keel; glassy yellowish white with brown outer edge at peritreme and with single fleck on highest point; occasionally with brown area extending into false umbilicus. - Periostracum, Operculum, Radula and Anatomy: not known.

Geographical distribution (Fig.196): Only known from Australia and New Zealand, 36–196 m. No live records.

Discussion:

This is the species described and illustrated as "Heliacus (Torinista) delectabilis (Melvill, 1893)" by Garrard (1977: 545). Melvill's (1893) species, however, is a member of *Pseudotorinia* (see below). The following species is similar. See also *H. cerdaleus* (above).

Heliacus (Torinista) nereidis n.sp.
Figs.196, 198, 199

Type measurements:

	SD	H	PD	Tw	UD	Collection
Holotype	6.2	4.3	1.40	2 5/8+	1.5	WAM 486-91
Paratype 1	4.2	2.9	1.38	2	1.1	AMS C.138279
Paratype 2	3.4	2.3	1.40	1 5/8	0.8	FMNH 223411
Paratype 3	3.0	2.2	1.40	1 1/2-	0.8	AMS C.155546

Type locality: Joseph Bonaparte Gulf, Western Australia (14°26.8'S, 128°54.5'E), 35 m, W.M.A.S. 'MORESBY' station 18, 8.X.80). Paratype 1 from off Pelsart Bank, Western Australia (29°28-28.5'S, 114°11-11.2'E), 183 m (M.V. 'SPRIGHTLY' station 21m, 18.II.1976). Paratype 2 from west of Rottnest Island, Western Australia (31°59'S, 115°14'E), 182 m (H.M.A.S. 'DIAMANTINA' station 79, 23.III.1972). Paratype 3 from west of Garden Island, Western Australia (32°15.7'S, 115°06.7'E), 176-182 m (H.M.A.S. 'DIAMANTINA' station 33, 17.III.1972).

Etymology: *nereidis* [genitive singular case-ending]; Nereis: sea nymph, daughter of Greek sea god Nereus.

Material studied: 4 type specimens as listed above.

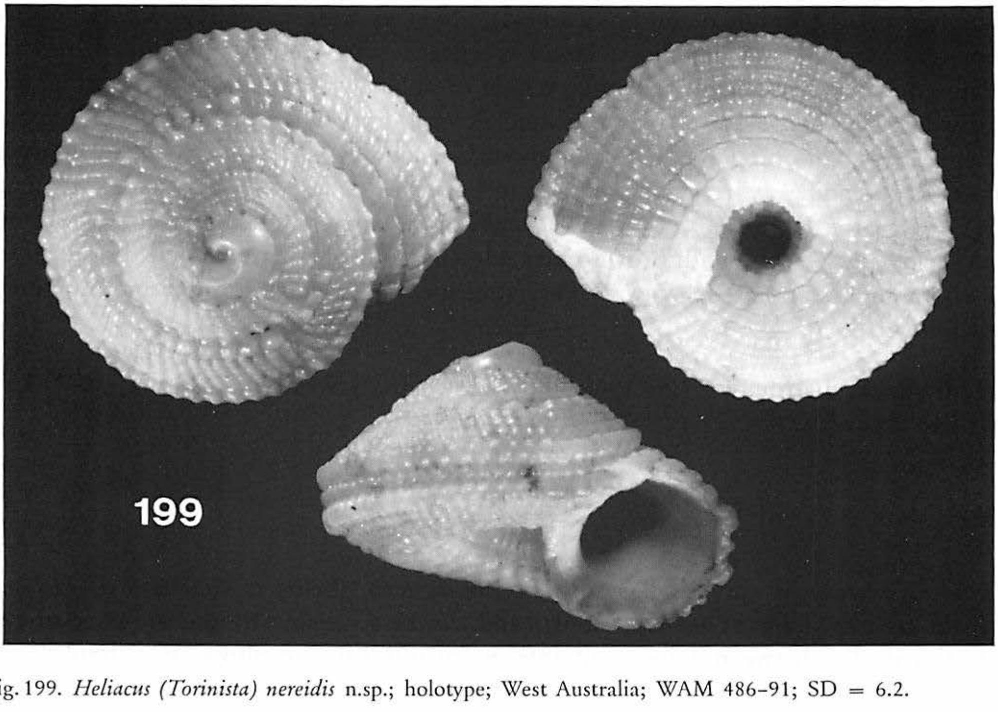


Fig. 199. *Heliacus (Torinista) nereidis* n.sp.; holotype; West Australia; WAM 486-91; SD = 6.2.

Diagnosis:

Very small to small depressed cone-shaped shell with angular periphery, deep suture, moderately wide umbilicus, and sculpture consisting of rounded tubercles; upper-side sculpture with 4 ribs, with uppermost somewhat coarser; periphery formed by 2 main ribs (upper one coarsest) and 1 weaker additional rib between them; basal sculpture of 7 spiral ribs (3 narrow outer ones and 4 increasing in width towards umbilicus), innermost with fine nodules; umbilical side of columellar wall with 2 spiral striae and 1 nodulose spiral rib in center. Yellowish tan with pattern of orange-tan blotches at periphery, extending as flames onto both shell sides. Protoconch diameter 1.38–1.40 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: very small to small, diameter of known specimens 3.0–6.2 at 1 1/2- to 2 5/8+ whorls. Shape: depressed cone-shaped with angular periphery; moderately wide umbilicus (UD ca. 25% of SD). Sculpture: consisting of rounded tubercles; Upper-side sculpture of 4 ribs, with SSR somewhat coarser than 2 MR and UPR; periphery formed by 3 ribs: LPR, IPR and weaker additional rib between them; uppermost (LPR) coarsest; upper point of whorl attachment at or immediately below this additional rib, resulting in deep suture; base with 7 ribs, 3 narrow outer ones and 4 increasing in width towards umbilicus; innermost (UC) with fine crenae (holotype with 15 nodules on body whorl), about as wide as PUR, on early whorls somewhat sunken into umbilicus; larger specimens with 1 additional thread between IPR and 7 basal ribs; convex umbilical side of columellar wall with spiral striae and a distinctly nodulose spiral rib in center. Coloration: yellowish tan with pattern on peripheral ribs of orange-tan blotches (about 1–2 nodules wide) separated by off-white; blotches extending as irregular flames onto both shell sides; UC white. – Protoconch (Fig.198): large (1.38–1.40, $\bar{x} = 1.39$), multispiral, distinctly heterostrophic, without anal keel; glassy white with brown outer edge in front of peritreme and distinct fleck at about highest point on apex. – Periostracum, Operculum, Radula and Anatomy: not known.

Geographical distribution (Fig.196): Only known from Western Australia, 35–183 m. No live records.

Discussion:

Heliacus nereidis is very similar to *H. oceanitis* n.sp. (below). Members of *Heliacus hyperionis* n.sp. (above) are also similar and can be separated by the presence of two additional ribs between lower and infraperipheral ribs, resulting in a four-ribbed periphery. *H. nereidis* has a much larger protoconch than the other two.

Heliacus (Torinista) oceanitis n.sp.
Figs.196, 198, 200

Type measurements (holotype): SD = 4.8, H = 3.5, PD = 0.92, Tw = 2 7/8–, UD = 1.0.

Type locality: Madagascar, Grand Récif de Tuléar, 10 m (THOMASSIN coll., station 843B, 8.VI.1972).

Etymology: *oceanitis* [used as noun in apposition]: sea nymph.

Material studied: holotype (MNHNP unnumbered).

Diagnosis [based on holotype]:

Very small cone-shaped shell with angular periphery, deep suture, moderately wide umbilicus, and sculpture consisting of rounded tubercles; upper-side sculpture with 4 ribs, with the 2 middle ones somewhat weaker; prominent angular double keel formed by 2 almost equally developed main ribs and a distinct additional rib between them; base with 6 spiral ribs, increasing in width towards umbilicus; umbilical side of columellar wall with 1 strong granulose spiral rib, flanked by weaker ones on the body whorl. Yellowish white with orange-tan fleck pattern on peripheral ribs,

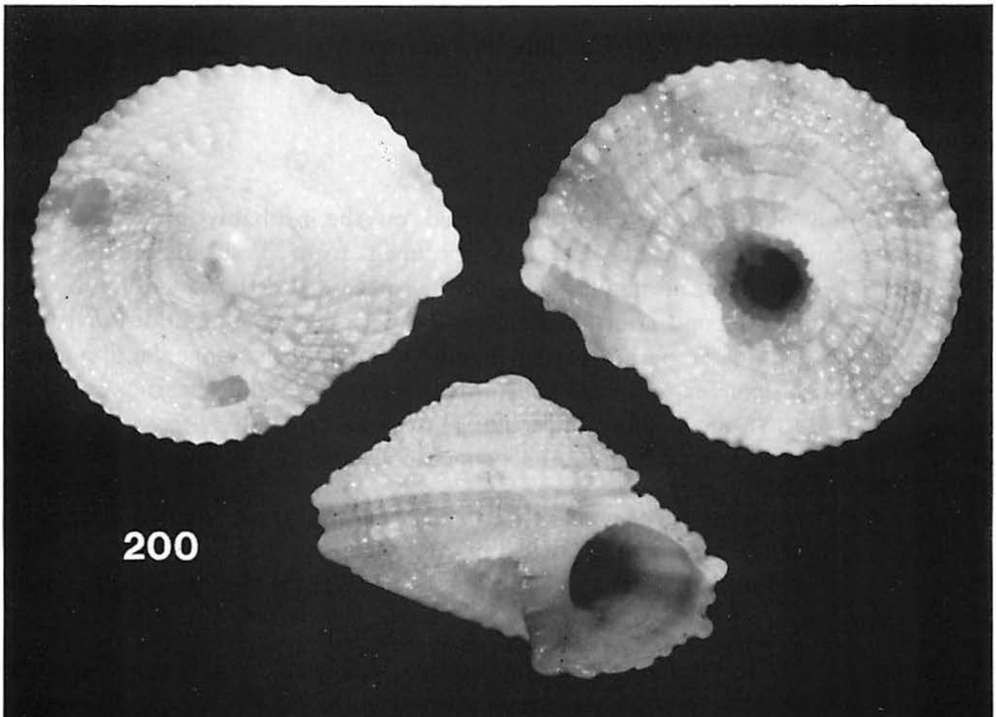


Fig. 200. *Heliacus (Torinista) oceanitis* n.sp.; holotype; Madagascar; MNHNP unnumbered; SD = 4.8.

extending as flames onto both shell sides. Protoconch diameter 0.92 mm, distinctly heterostrophic, without anal keel, with single brown spot on highest point of apex.

Description [based on holotype]:

Teleoconch: very small, diameter of 4.8 at 2 7/8- whorls. Shape: cone-shaped with angular periphery; moderately wide umbilicus (UD ca. 22% of SD); suture deep. Sculpture: consisting of rounded tubercles, becoming coarser with increasing whorls; Upper side of 4 ribs (SSR, 2 MR and UPR), with SSR and similar UPR strongest; angular periphery formed by almost equally strong and prominent LPR and IPR, with 1 distinct additional rib between them; after ca. 2 whorls, 1 fine thread between additional rib and IPR; upper point of whorl attachment below additional rib, resulting in turreted appearance; base with 6 spiral ribs, increasing in width towards umbilicus, innermost (UC) somewhat lowered into umbilicus, with 17 nodules on body whorl; umbilical wall with 1 strong granulose spiral rib in the center, on the body whorl flanked by 3 weaker ones. Coloration: yellowish white with ± regular pattern of orange-tan flecks alternating with off-white areas on peripheral ribs (flecks ca. 1–2 nodules wide), extending as ± distinct flames onto midrib area and base. - Protoconch (Fig.198): medium-sized (0.92), multispiral, distinctly heterostrophic, bulbous, with a few folds visible in false umbilicus; without anal keel; glassy white with brown outer edge in front of peritreme, brown false umbilicus and single spot close to highest point of apex. - Periostracum, Operculum, Radula and Anatomy: not known.

Geographical distribution (Fig.196): Only known from Madagascar, from 10 m depth. No live records.

Discussion:

The description of *Heliacus oceanitis* is based on the probably not fully mature holotype specimen from Madagascar. A specimen from Transkei, South Africa (Fig.200a) is very similar and might belong to this species. It differs from the holotype in having a stronger second additional rib on the periphery, a fine additional thread between upper and lower peripheral ribs, only 11 umbilical crenae, and numerous spiral striae on the convex umbilical wall instead of a few nodule-bearing spiral ribs. Protoconch size (0.98 mm), shape and color pattern agrees with *H. oceanitis*, but the specimen is too eroded to determine teleoconch coloration.

Heliacus oceanitis n.sp. is very similar to *H. nereidis* n.sp. (above), but can be readily distinguished by much smaller size (a shell of 2 1/2 teleoconch whorls measures about 4.2 mm in *H. oceanitis* as compared to 5.6 mm in *H. nereidis*). The protoconch is also much smaller (see Fig.198).

Heliacus turritus is somewhat similar in turreted shape and coloration. The upper peripheral rib in members of that species, however, is much stronger and appears as a part of the peripheral rather than upper-side sculpture, and the protoconch has two color flecks and an anal keel.

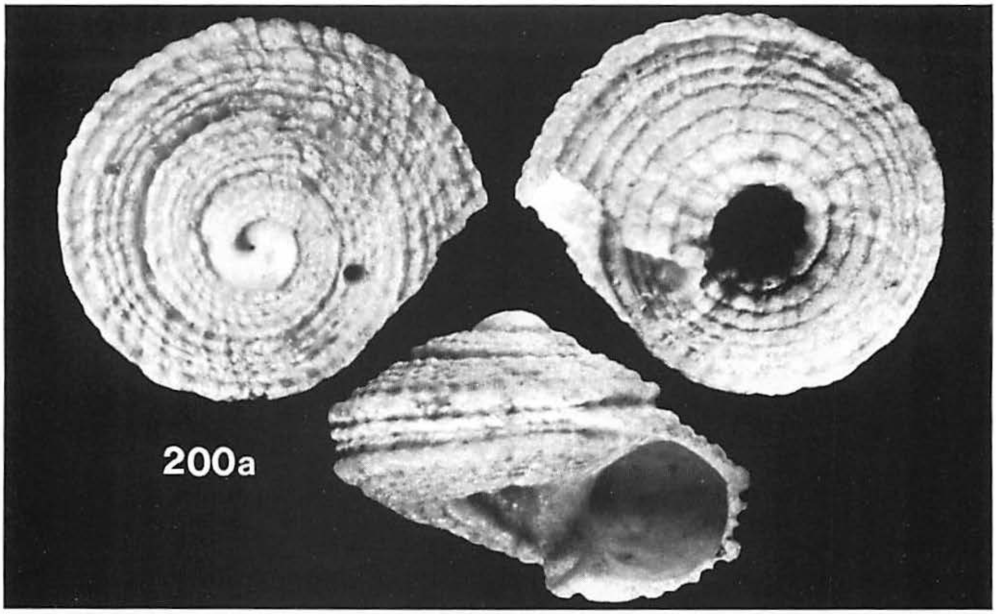


Fig. 200a. *Heliacus (Torinista)* aff. *oceanitis* n.sp.; specimen from Transkei, South Africa; NMP C.1713; SD = 4.5.

Shells of *Heliacus cerdaleus* have similarly angulate peripheries, but only one midrib (often flanked by finer threads), very coarse nodules around the umbilicus and a much smaller protoconch (0.66–0.80 mm). The upper point of whorl attachment in *H. cerdaleus* is positioned higher, at, or immediately below the lower peripheral rib (LPR).

Heliacus (Torinista) caelatus (Hinds, 1844)

Figs.201, 202, 203

*1844 *Solarium caelatum* Hinds, 1844b, Proc. zool. Soc. Lond., *1844*: 25.
1844–1845 *Solarium caelatum*, - Hinds, 1844c–1845, Zool. voy. Sulphur, *3*: 51, *2*: pl.14 figs.11–12.
1844 *Solarium caelatum*, - Hinds, 1844d, Ann. Mag. nat. Hist., *14*: 440.
1853 *Solarium caelatum*, - Philippi, 1853b, Syst. Conch.-Cab. II, *7*: 19, pl.3 fig.8 [after Hinds, 1844d].
1863 *Solarium (Torinia) caelatum*, - Hanley, Thes. conch., *3*: 240, pl.254 figs.75–76.
1887 *Torinia (Torinia) caelata*, - Marshall, Man. conch., *9*: 20, pl.6 figs.4–5 [after Hinds, 1844d].
1948 *Torinia caelata*, - Bayer, Zool. Verh., *4*: 8 [synonymy].
1977 *Heliacus (Torinista) costatus*, - Garrard, Rec. Austr. Mus., *31*(13): 544, pl.5 figs.7–9 [non *Torinia costata* Schepman, 1909].
1985 *Heliacus (Torinista) caelatus*, - Bieler, 1985b, Arch. Moll., *116*(1/3): 99.

Type measurements (holotype): SD = 8.5, H = 4.0, PD = 0.98, Tw = 3 3/4–, UD = 3.9.

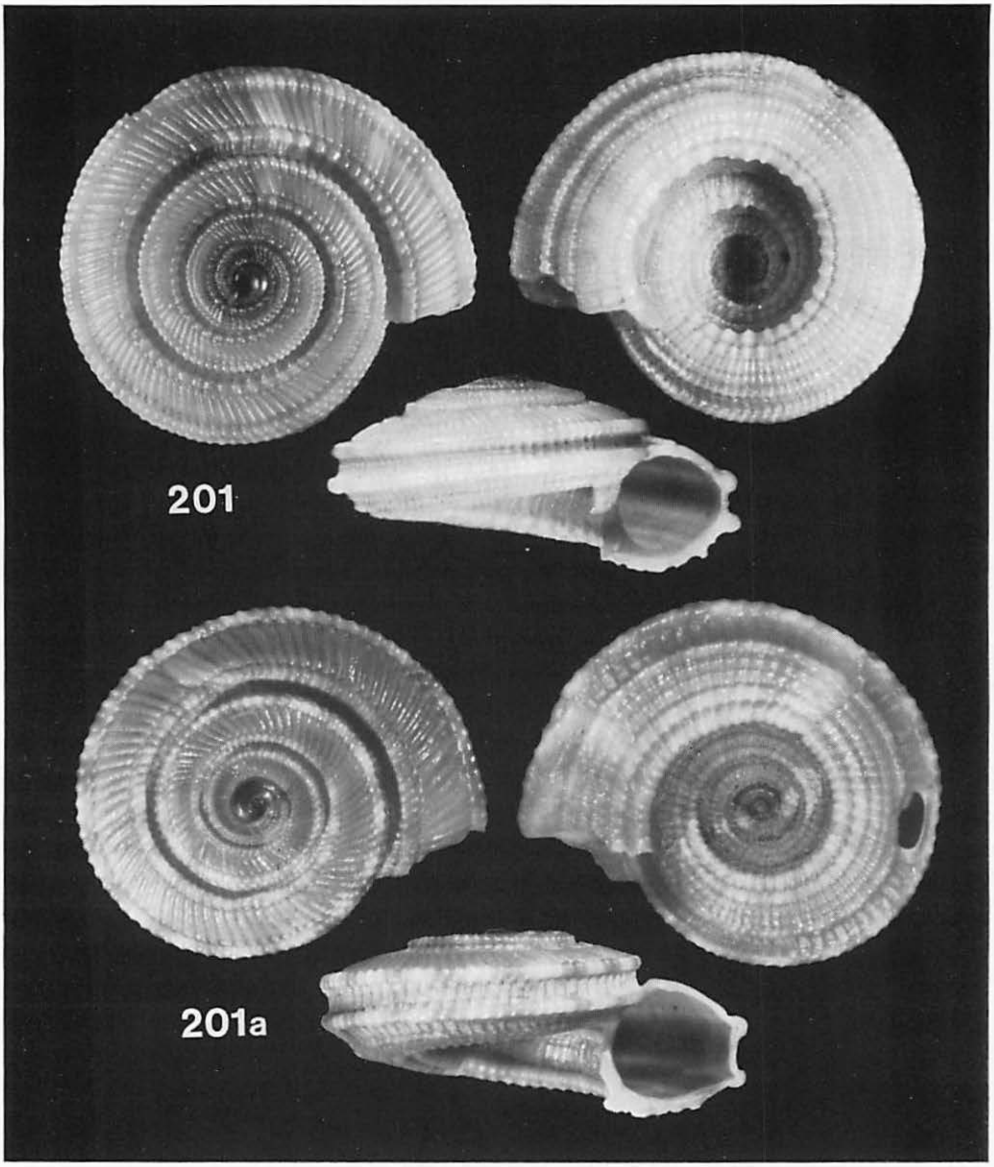


Fig. 201: *Heliacus (Torinista) caelatus* (Hinds, 1844); holotype of *Solarium caelatum*; Indonesia; BMNH 1879.2.26.237; SD = 8.5.
Fig. 201a: *Heliacus (Torinista) costatus* (Schepman, 1909); lectotype of *Torinia costata*; Indonesia; ZMA 3.09.065; SD = 8.7.

Type locality: "Straits of Macassar; in ten fathoms [18 m], among coarse sand."

Etymology: *caelatus-a-um* [adjective]; Latin: engraved.

Material studied: 128 specimens (AMS, ANSP, BMNH, MNHNP, NMW, USNM); including holotype (BMNH 1879.2.26.237).

Diagnosis:

Very small to small disk-shaped to weakly cone-shaped shell with very wide umbilicus and wide and deep sutures; upper-side sculpture with ribs usually fused, forming a plane with strong, regular axial ribs; double keel formed by 2 almost identical ribs; basal sculpture of 5 spiral ribs, rarely partly fused to form a smooth plane; umbilical side of columellar wall usually with 1 more or less prominent spiral rib. Yellowish tan, periphery with regular darker blotches. Protoconch diameter 0.72–0.98 mm, slightly heterostrophic, without anal keel.

Description:

Teleoconch: very small to small, diameter of specimens in collections usually 3–8 at 2 - 3 1/2 whorls (rarely over 10 at 4 1/4). Shape: disk-shaped to weakly cone-shaped with flat-convex whorls and angular periphery; very wide umbilicus (UD ca. 39% of SD); wide and deep suture. Sculpture: Upper side: SSR nodose, usually distinctly separated from MR-area, rarely fused with it; MR and UPR fused, forming a plane with strong, regular axial ribs; Periphery: double keel formed by almost identical LPR and IPR; body whorl with one fine thread between LPR and IPR; upper point of whorl attachment at IPR. Base: 5 spiral ribs (plus finer spiral threads interspersed), usually increasing in width towards umbilicus; rarely partly fused to form ± smooth plane, innermost forming finely nodose UC (15–36 nodules on body whorl); umbilical side of columellar wall with 1 ± prominent spiral rib. Coloration: yellowish tan, periphery lighter with ± regular darker blotches (about 2–3 nodules wide); UC light. - Protoconch (Fig.202): small to medium-sized (0.72–0.98, $\bar{x}$ = 0.84), multispiral, slightly heterostrophic, without anal keel; light tan. - Periostracum, Operculum, Radula, Anatomy: unknown.

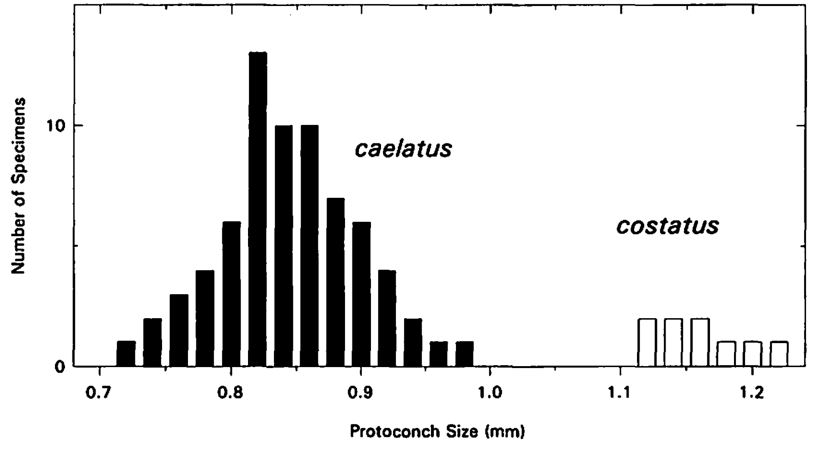


Fig. 202. Histograms of measured protoconch size. *Heliacus (Torinista) caelatus* (n = 70, $\bar{x}$ = 0.84, sd = 0.05), and *Heliacus (Torinista) costatus* (n = 9, $\bar{x}$ = 1.16, sd = 0.04).

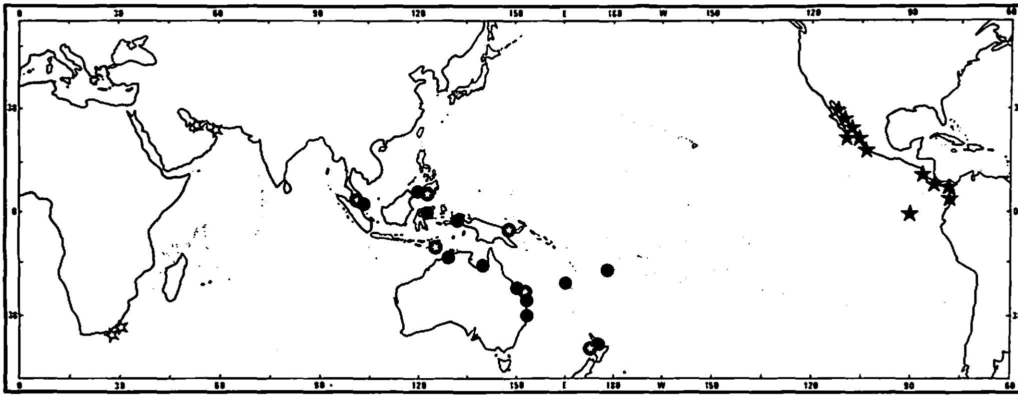


Fig. 203. Geographical distribution of *Heliacus caelatus, H. costatus, H. rotula* and *H. planispira.*

Geographical distribution (Fig.203): Known from various localities, from Singapore to New Zealand.

Habitat: Sublittoral; records from 11–124 m.

Discussion:

Heliacus caelatus is very similar to nominal species *H. costatus*, the two may be conspecific (see discussion below). See also *H. rotula* and *H. planispira* (below).

"*Heliacus costatus*" specimens sensu GARRARD (1977: 544) from Australia belong to *H. caelatus* as defined here (AMS, vidi). The two specimens reported as *Solarium caelatum* from South Africa (SOWERBY (III), 1900: 5; E.A. SMITH, 1903a: 382) are members of *Heliacus implexus* (see KILBURN, 1975: 605; as "*Heliacus dorsuosus*"); *Heliacus caelatus* is not known from South Africa to date.

Heliacus (Torinista) costatus (SCHEPMAN, 1909) [doubtful status]
Figs.201a, 202, 203

*1909 *Torinia costata* SCHEPMAN, Monogr. Res. SIBOGA Exped., *49*(1b): 221, pl.14 figs.5a-c.
1948 *Torinia costata*, - BAYER, Zool. Verh., *4*: 10.

Type measurements (lectotype, here designated): SD = 8.7, H = 3.6, PD = 1.2, Tw = 3 1/8–, UD = 3.6.

Type locality: [R/V 'SIBOGA'] "Stat. 279. Rumah-Kuda-bay, Roma-island. 36 M. Mud and sand" [north-east Timor, Indonesia].

Etymology: *costatus-a-um* [adjective]; Latin: ribbed.

Material studied: 14 specimens (AMS, LACM, USNM, ZMA); including lectotype (ZMA 3.09.065) and 1 paralectotype (ZMA 3.09.066).

Diagnosis:

Small disk-shaped shell with very wide umbilicus and wide, deep suture; upper-side sculpture with ribs usually fused except for nodose subsutural rib, forming a plane with strong, regular axial ribs; double keel formed by 2 almost identical ribs; basal sculpture of 5 spiral ribs, rarely partly fused to form smooth plane; umbilical side of columellar wall usually with 1 more or less prominent spiral rib. Yellowish tan, periphery with regular darker blotches. Protoconch diameter 1.12–1.22 mm, slightly heterostrophic, without anal keel.

Description:

Teleoconch: small, diameter of specimens in collections less than 9 at about 3 1/8-whorls; Shape: disk-shaped with flat-convex whorls and angular periphery; very wide umbilicus (UD ca. 42% of SD); wide and deep suture. Sculpture: Upper side: SSR nodose, usually distinctly separated from MR-area, rarely fused with it; MR and UPR fused, forming a plane with strong, regular axial ribs; Periphery: double keel formed by almost identical LPR and IPR (without additional rib between them); upper point of whorl attachment IPR. Base: 5 spiral ribs (plus finer spiral threads interspersed), usually increasing in width towards umbilicus; rarely partly fused to form ± smooth plane, innermost forming finely nodose UC; umbilical side of columellar wall with 1 ± prominent spiral rib. Coloration: yellowish tan, periphery lighter with ± regular darker blotches (about 2–3 nodules wide); UC light. - Protoconch (Fig.202): medium-sized to large (1.12–1.22, $\bar{x}$ = 1.16), multispiral, slightly heterostrophic, without anal keel; light tan. - Periostracum: thick and glassy when wet; light in color, relatively thick and scaly when dry. - Operculum: as described for subgenus. - Radula and Anatomy: unknown.

Geographical distribution (Fig.203): Known from various localities, from Singapore to New Zealand.

Habitat: Sublittoral to bathyal; from 36–805 m, live records from upper sublittoral.

Discussion:

GARRARD's statement (1977: 545) about a distinct difference in sculpture between *Heliacus caelatus* and *H. costatus* ("*caelatus* ... having decidedly coarser sculpture") could not by verified when comparing the type specimens and other material. Both forms are variable in sculpture, especially in the degree of "fusion" of spiral ribs; the only reliable character to distinguish the two being protoconch size (see Fig.202). In addition, *H. caelatus* shells have (at same diameter) more teleoconch whorls than the few known *H. costatus* specimens. Whether the two forms represent distinct species is questionable.

The larger of two syntypes of *Torinia costata* in Amsterdam (ZMA 3.09.065) agrees with the original figure and dimensions given by SCHEPMAN (1909: 221, pl.14 fig.5a-c). It is here selected as lectotype (Fig.201a). GARRARD's (1977: 544) erroneous citation of a "holotype" does not qualify as a lectotype designation by inference (ICZN, 1985: Article 74(b)), since SCHEPMAN (1909: 221) clearly mentioned two specimens in the original description.

Heliacus (Torinista) rotula Kilburn, 1975
Figs.8, 203, 204

*1975 *Heliacus (Mangonuia) rotula* Kilburn, Ann. Natal Mus., *22*(2): 605, fig.16.

Type measurements (holotype): SD = 5.3, H = 2.7, PD = 0.70, Tw = 3, UD = 1.8.

Type locality: "Durban Bay, in shallow dredgings" [Natal Province, South Africa].

Etymology: *rotula* [noun in apposition]; Latin: a little wheel (diminutive of *rota*).

Material studied: 13 specimens (FMNH, NMP, NMW, UMZC); including holotype (NMP A1570/T1851) and 2 paratypes (NMP A1569/T1850).

Diagnosis:

Very small to small, disk-shaped to depressed cone-shaped shell with angular periphery, deep and narrow suture and moderately wide to very wide umbilicus; upper-side sculpture of 1 distinct spiral rib and a wide, axially sculptured, fused area; double keel formed by 2 widely spaced, almost identical ribs, with 1–2 fine ribs between them; basal sculpture of 5–6 spiral ribs, partly fused in area before distinctly separate umbilical crenae; umbilical side of columellar wall without spiral ribs. Tan with darker apex, reddish fleck pattern on periphery. Protoconch diameter 0.70–0.82 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: very small to small, diameter of specimens in collections usually 3.9–6.8 at 2 1/4+ to 3 3/8 whorls. Shape: disk-shaped to depressed rounded cone-shaped with moderately bulging whorls, angular periphery, and moderately wide to very wide umbilicus (UD ca. 21–36% of SD). Sculpture: Upper side: SSR nodose, in most cases distinctly separated from MR-area; MR and UPR in most cases completely fused (rarely separated by 1–2 ± distinct spiral grooves), with strong, regular axial sculpture; axial ribs often bifurcating towards periphery; Periphery: double keel formed by widely spaced, almost identical LPR and IPR, with 1 (sometimes 2) additional finer ribs between them; upper point of whorl attachment on or immediately below this additional rib, suture deep and narrow; Base: 5–6 spiral ribs, increasing in width towards umbilicus, of which 2–3 ribs in area next to UC in most cases ± completely fused to form almost smooth, axially grooved area; UC distinctly separated, with 15–21 nodules on body whorl; umbilical side of columellar wall without distinct spiral ribs. Coloration: tan with reddish brown apex, UC lighter; peripheral ribs lighter with pattern of reddish flecks (each ca. 2–3 nodules wide). – Protoconch (Fig.8): small (0.70–0.82, $\bar{x}$ = 0.77), multispiral, distinctly heterostrophic, without anal keel, tan. – Operculum, Radula and Anatomy: not known.

Geographical distribution (Fig.203): Known from southwestern Indian Ocean (South Africa) and Gulf of Oman.

Habitat: Available specimens from beach drift to 285 m depth. No live records.

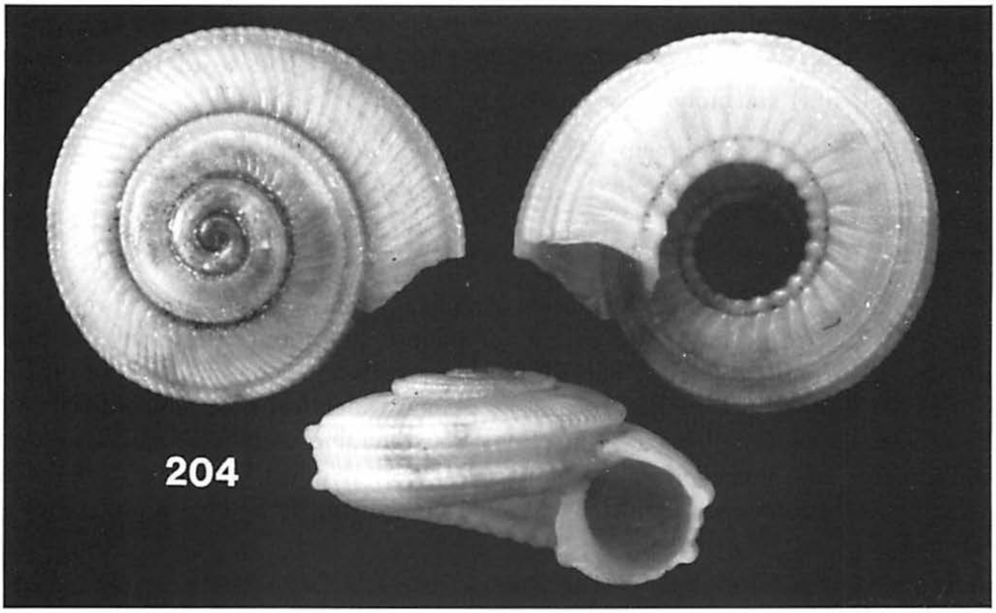


Fig. 204. *Heliacus (Torinista) rotula* Kilburn, 1975; holotype; Natal, South Africa; NMP A1570/T1851; SD = 5.3.

Discussion:

Heliacus rotula resembles *H. caelatus* in having the teleoconch midribs usually fused. However, the *H. rotula* shell is higher-spired and has a narrower umbilicus. Compared to *H. caelatus*, the distance between the keel-forming ribs (lower peripheral and infraperipheral ribs) is great, the additional rib between the two relatively strong, and, because the upper point of whorl attachment in *H. rotula* is at that additional rib, the suture is much shallower. Other separating characters are the usually fused inner basal ribs (forming a more-or-less smooth plane), and the lack of distinct spiral ribs on the umbilical wall.

Heliacus (Torinista) planispira Pilsbry & Lowe, 1932
Figs.203, 205

*1932 *Heliacus planispira* Pilsbry & Lowe, Proc. Acad. nat. Sci. Philadelphia, *84*: 83, pl.8 figs.9–11.
1948 *Torinia planispira*, - Bayer, Zool. Verh., *4*: 30.
1971 *Heliacus caelatus*, - Keen, Sea shells trop. w. Amer. (2nd ed.): 389, fig.429 [non *Solarium caelatum* Hinds, 1844].
1974 *Heliacus planispira*, - Abbott, Amer. seashells (2nd ed.): 98.
1976 *Heliacus caelatus planispira*, - Robertson, 1976a, Bull. Amer. malac. Union, *1975*: 51.
1985 *Heliacus (Torinista) planispira*, - Bieler, 1985b, Arch. Moll., *116*(1/3): 99.

Type measurements (holotype): SD = 4.4, H = 1.8, PD = 0.9, Tw = 2 1/6, UD = 1.4.

Type locality: "Mazatlan, Mexico" [Mazatlán, Sinaloa State, Pacific coast].

Etymology: *planispira* [noun in apposition]; Latin: compound word from adjective *planus* (level, flat) and noun *spira* (something coiled or twisted).

Material studied: 138 specimens (AMNH, ANSP, CAS, IRSNB, LACM, USNM); including holotype (ANSP 155439).

Diagnosis:

Very small disk-shaped shell with wide umbilicus and shallow sutures; upper-side sculpture with ribs usually fused except for nodose subsutural rib, forming a plane with strong, regular axial ribs; one rib on upper surface strong and nodose on first whorl, later lacking; double keel formed by 2 almost identical ribs; base with 5 spiral ribs of various width, rib next to innermost (surrounding umbilicus) usually widest; umbilical side of columellar wall without spiral ribs. Reddish brown, with umbilical crenae lighter. Protoconch diameter 0.86–1.00 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: very small, diameter of specimens in collections usually about 4 at 2+ whorls; Shape: disk-shaped with flat-convex whorls; wide umbilicus (UD ca. 34% of SD); shallow suture. Sculpture: Upper side: SSR nodose, ± distinctly separated from MR-area; MR fused, forming a plane with strong, regular axial ribs; Periphery: on the first teleoconch whorl ("arrested growth stage") UPR strong and nodose, later

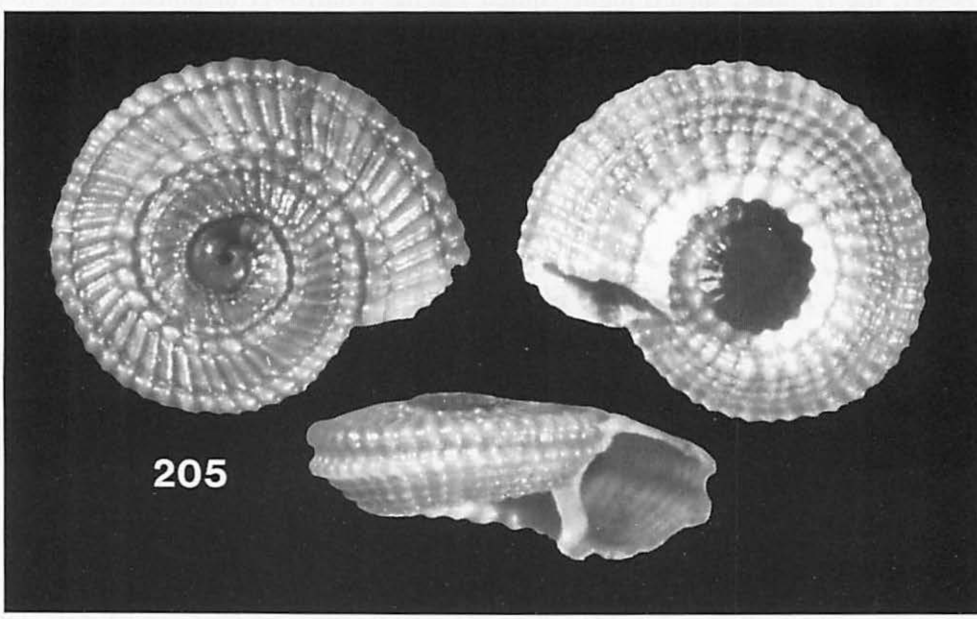


Fig. 205. *Heliacus planispira* Pilsbry & Lowe, 1932; holotype; western Mexico; ANSP 155439; SD = 4.4.

lacking; double keel formed by almost identical LPR and IPR (without additional rib between them); upper point of whorl attachment on or immediately below LPR; Base: 5 spiral ribs of various widths, penultimate (PUR) usually wider than UC; umbilical side of columellar wall with axial growth lines, without spiral sculpture. Coloration: reddish brown, with UC lighter. - Protoconch: small to medium-sized (0.86–1.00, $\bar{x}$ = 0.93), multispiral, distinctly heterostrophic, without anal keel, brown. - Operculum: as described for subgenus. - Radula and Anatomy: not known.

Geographical distribution (Fig.203): Eastern Pacific, from northern Gulf of California to northern Colombia, and Galapagos Islands.

Habitat: Records from intertidal to 75 m depth.

Discussion:

KEEN (1971: 389) synonymized *Heliacus planispira* with *H. caelatus* (HINDS, 1844), while ROBERTSON (1976: 51) regarded it as a subspecies of that species. However, the two species differ by a number of characters: in *H. planispira*, the upper point of whorl attachment is on or shortly below the upper peripheral rib (in *H. caelatus*: on the infraperipheral rib), there is no spiral rib on the umbilical wall (present in *H. caelatus)*, and the upper peripheral rib is always very distinctly developed on juvenile specimens (usually lacking in *H. caelatus)*.

WOODRING (1959: 168) designated *Heliacus planispira* as the type species of a new subgenus, *Heliacus (Astronacus)*, combining Recent and fossil species with axial instead of spiral ribs on the upper side of the teleoconch. Since this character is known from several architectonicid genera (*Architectonica*, *Philippia*, *Nipteraxis*) and can vary within a single species (e.g., *Pseudotorinia gemmulata*), BIELER (1985b: 99) synonymized *Astronacus* under *Torinista*.

Heliacus (Torinista) proteus n.sp.

Figs.206, 208

Type measurements:

	SD	H	PD	Tw	UD	Locality	Collection
Holotype	8.5	4.4	0.90	3 11/12	3.0	Sulu Archipelago	USNM 264061
Paratype 1	6.1	2.9	0.94	3 1/4	2.4	off Tawi-Tawi	USNM 819972
Paratype 2	6.8	3.7	0.88	3 5/8	2.5	Linapacan Strait	USNM 282452
Paratype 3	6.6	3.6	0.88	3 5/8	2.7	Linapacan Strait	USNM 282452
Paratype 4	6.6	3.6	0.90	3 3/8	2.5	Linapacan Strait	USNM 282452
Paratype 5	6.0	3.1	0.90	3 1/8+	2.2	Linapacan Strait	USNM 282452
Paratype 6	6.5	3.4	0.88	3 3/8	2.3	Cebu	FMNH 223417
Paratype 7	5.2	2.5	0.92	2 3/4+	1.9	Cebu	FMNH 223417

Type locality: Off Baluk-Baluk Island, Sulu Archipelago, Philippines (U.S Bureau of Fisheries [R/V 'ALBATROSS'] station 5134. Paratype 1 from off SW Tawi-Tawi, Philippines, 33 m (USBF station 516). Paratypes 2–5 from off Observatory Island,

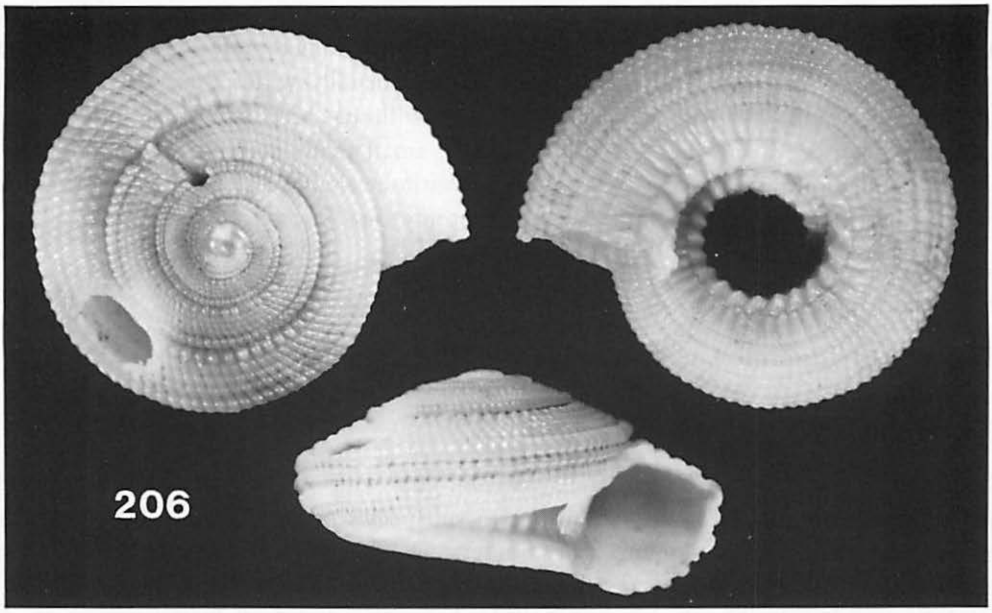


Fig. 206. *Heliacus (Torinista) proteus* n.sp.; holotype; Philippines; USNM 264061; SD = 8.5.

Linapacan Strait, Philippines (USBF stations 5335, 5336). Paratypes 6–7 from Cebu, Philippines, 30–50 m.

Etymology: *proteus* [used as noun in apposition]: God of the Sea with power to assume various forms.

Material studied: 8 type specimens as listed above, and 10 additional specimens (mostly juveniles and fragments, FMNH and USNM).

Diagnosis:

Small, depressed cone-shaped shell with angular periphery, shallow suture, very wide umbilicus, and gemmate sculpture, with nodules of neighboring spiral ribs interconnected by weaker axial ribs; upper-side sculpture with 4 ribs, with uppermost somewhat stronger; prominent double keel formed by 2 main ribs (upper one somewhat stronger) and, occasionally equally strong, additional rib between them; base with 5–6 spiral ribs (increasing in width towards umbilicus), occasionally with finer threads interspersed; rib next to innermost broadest; umbilical side of columellar wall with 1–2 spiral ridges. Overall yellowish tan, some ribs with fleck pattern, sometimes extending as flames onto upper side. Protoconch diameter 0.84–0.94 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: small, diameter of specimens in collections usually 5–8.5 at 2 3/4 – 4 whorls. Shape: rounded depressed cone-shaped with angular periphery; very wide

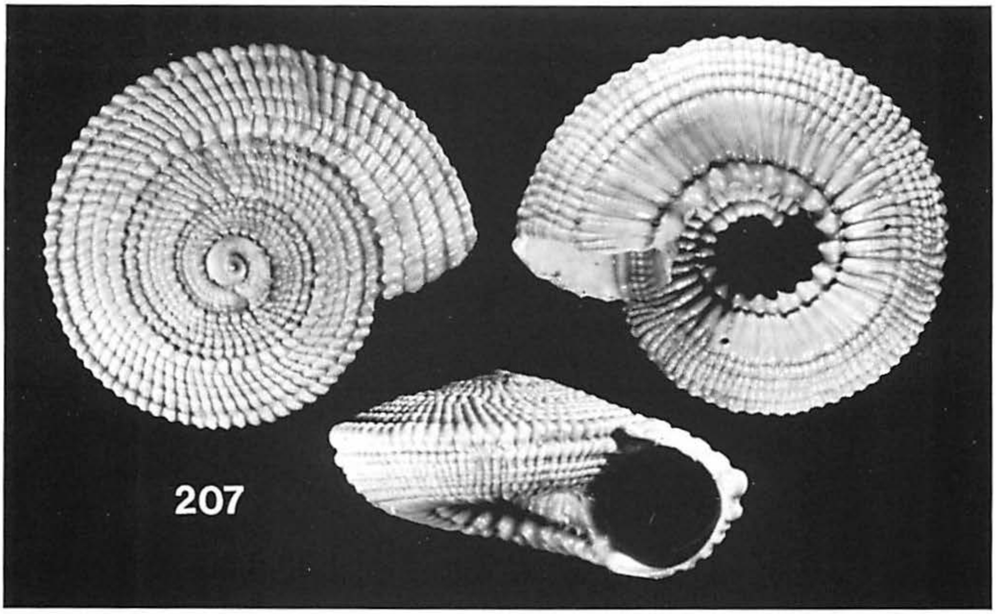


Fig. 207. *Heliacus morningtonenis* GARRARD, 1977; holotype; Fossil Beach, Mornington Peninsula, Victoria, Australia (Balcombian, Middle Miocene); AMS C.94485; SD = 5.9.

umbilicus (UD 35–41% of SD); shallow suture. Sculpture: gemmate, nodules of neighboring spiral ribs interconnected by weaker axial ribs; Upper side: SSR somewhat stronger than 2 MR and UPR; UPR strong on early part of first whorl (arrested growth stage), thereafter similar to MR; angular periphery formed by strong LPR, somewhat weaker IPR and, between them, 1 additional rib occasionally as strong as LPR; large specimens with 1 fine thread below additional rib (here upper point of whorl attachment, resulting in deep suture); 5–6 ribs on base increasing in width towards umbilicus, occasionally with finer threads interspersed; PUR broadest rib on base, often twice as wide as UC; UC narrow, somewhat lowered into umbilicus, with 18–23 nodules on body whorl; convex umbilical wall with 1, later 2, coarse spiral ridges, the one facing the apex with ± distinct nodules. Coloration: overall yellowish tan, SSR, PR and UC with ± distinct pattern of tan and off-white, sometimes extending as flames onto MR-area; UC sometimes white. – Protoconch: small to medium-sized (0.84–0.94, $\bar{x}$ = 0.90), multispiral, distinctly heterostrophic, without anal keel; glassy white with brownish outer edge and suture. – Periostracum, Operculum, Radula and Anatomy: not known.

Geographical distribution (Fig.208): Known only from the Philippines, 30–80 m. No live records.

Discussion:

Heliacus proteus n.sp. is similar to *H. implexus*. Members of the latter species, however, do not have a deep suture (upper point of whorl attachment in *H. implexus* is at the

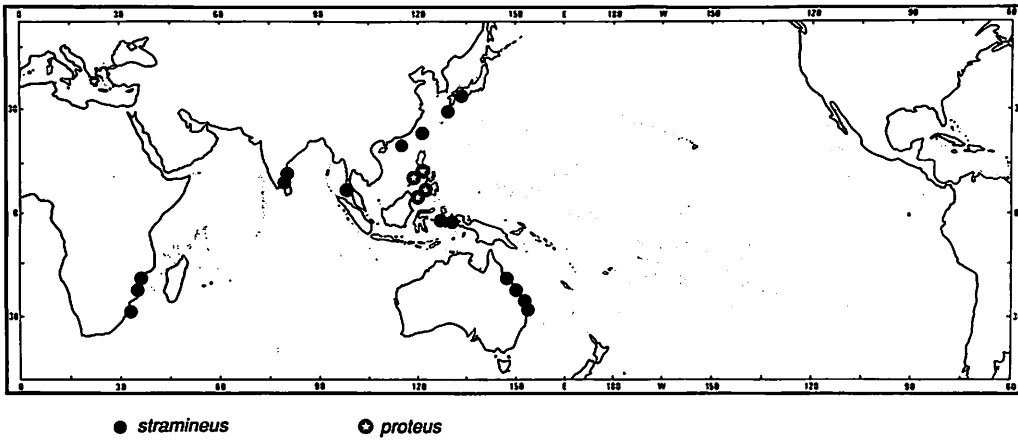


Fig. 208. Geographical distribution of *Heliacus (Grandeliacus) stramineus* and *Heliacus (Torinista) proteus* n.sp.

lower peripheral rib), they have only one distinct spiral rib positioned at the center of the exposed umbilical wall, and the protoconch is larger than 0.94 mm. Another similar form is *Heliacus morningtonensis* GARRARD, 1977 (p.561, pl.9, figs.10–12; see Fig.207), described from the Balcombian (Middle Miocene) of Victoria, Australia. That species lacks the additional rib between LPR and IPR; the upper point of whorl attachment is at the LPR, resulting in the absence of a distinct suture.

Subgenus *Heliacus (Grandeliacus)* IREDALE, 1957

Grandeliacus IREDALE, 1957: 124. Type species by original designation: *Grandeliacus mortensenae* IREDALE, 1957 [= *Trochus stramineus* GMELIN, 1791]; Recent, Indo-Pacific.

Description (Fig.209):

Teleoconch: shell small to large (usually 9–33 mm); small shells with angular periphery and basal area more convex than apical side; larger shells with rounded periphery and bulging whorls; umbilicus moderately wide to wide (ca. 17–36% of shell diameter); sculpture: on early whorls, subsutural rib and 2 midribs ± weakly developed and upper peripheral rib prominent (concave area between upper and lower peripheral rib); on

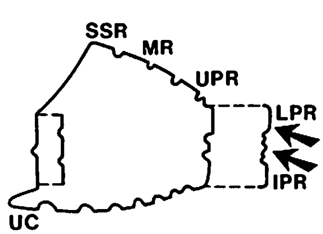


Fig. 209. Schematic representation of placement of major spiral ribs in *Heliacus (Grandeliacus)*, apertural aspect. Arrows indicate alternate points of attachment of next whorl, intrageneric variation indicated by dotted lines.

later whorls, subsutural rib stronger, or subsutural rib, midribs and upper peripheral rib nearly equally strong (often additional rib between upper and lower peripheral rib); periphery: early whorls two-ribbed, with somewhat more prominent lower peripheral rib and infraperipheral rib; later, 1–3 additional spiral ribs between them, one of which often equally prominent; upper point of whorl attachment at lower peripheral or additional rib; base with 6 (later 7) spiral ribs, increasing in width towards umbilicus; large specimens with additional finer ribs interspersed; umbilical wall usually with 1–2 fine spiral ribs; coloration yellowish tan, early whorls often darker; peripheral ribs sometimes with fleck pattern. *Protoconch:* small to medium-sized (0.78–1.20), distinctly heterostrophic, without anal keel. *Radula:* five-toothed-taenioglossate; rachidian with central cusp flanked by numerous (9–22) cusps on either side, with central cusp larger than or equal to flanking cusps; inner and outer marginals with 6–10 cusps each. *Operculum:* horny, round, flat in young individuals, later moderately cone-shaped, with peg-like projection on body side.

Heliacus (Grandeliacus) stramineus (GMELIN, 1791)

Figs.4, 208, 210, 211

1688 "Trochus planior, striatus ...", – LISTER, Hist. conch., *4*: pl.635 fig.23 [not binominal].
1753 "Nerita margine pulvinata ...", – KLEIN, Tent. meth. ostrac.: 7, no.13 [not binominal].
1781 "Trochus perspectivus stramineus", – CHEMNITZ, Conch.-Cab., *5*: 13 [not binominal].
1781 "Trochus perspectivus stromineus [sic]", – CHEMNITZ, Conch.-Cab., *5*: 128, pl.172 fig.1699 [not binominal].
*1791 *Trochus stramineus* GMELIN, Syst. nat. [13th ed.], *1*(6): 3575.
*1798 *Architectonica Gothica* RÖDING, Mus. Boltenianum: 78 [objective synonym of *T. stramineus*].
1801 *Trochus stramineus*, – BOSC, Hist. nat. coqu., *4*: 162.
1817 *Trochus stramineus*, – DILLWYN, Desc. cat. Rec. shells, *2*: 785.
1822 *Solarium stramineum*, – LAMARCK, Hist. nat., *7*: 4.
1830 *Trochus stramineus*, – BOSC, Hist. nat. coqu. (2nd ed.), *4*: 154.
1838–1839 *Solarium stramineum*, – KIENER, Spéc. gén. icon. coqu., *10*: 11, pl.3 fig.4.
1843 *Solarium stramineum*, – DESHAYES, Hist. nat. (2nd ed.), *9*: 99.
?*1844 *Solarium fulvum* HINDS, 1844b, Proc. zool. Soc. Lond., *1844*: 24.
1844–1845 *Solarium fulvum*, – HINDS, 1844c–1845, Zool. Voy. SULPHUR, *3*: 51, *2*: pl.14 figs.17–18.
1844 *Solarium fulvum*, – HINDS, 1844d, Ann. Mag. nat. Hist., *14*: 439.
1853 *Solarium stramineum*, – PHILIPPI, 1853b, [in part], Syst. Conch.-Cab. II, *7*: 32.
1859 *Solarium (Torinia) stramineum*, – CHENU, Man. conch. paléont., *1*: 233, fig.1353.
*1863 *Solarium (Torinia) stramineum*, HANLEY, Thes. conch., *3*: 242, pl.254 figs.95, 97 [not fig.96, = *Heliacus subvariegatus* (ORBIGNY, 1852)].
1863 *Solarium (Torinia) stramineum* Var. *junior* HANLEY, Thes. conch., *3*: 242.
1875 *Solarium stramineum*, – MARTENS, Jb. dtsch. malak. Ges., *2*: 115.
1887 *Torinia (Torinia) straminea*, – MARSHALL [in part], Man. conch., *9*: 19, pl.6 figs.93–94 [after HANLEY, 1863].
1948 *Torinia straminea*, – BAYER, Zool. Verh., *4*: 34 [synonymy].
*1957 *Grandeliacus mortensenae* IREDALE, Proc. r. zool. Soc. N. S. Wales, *1955–56*: 124, fig.1.
1961 *Heliacus stramineus*, HABE, Col. illus. shells Japan *(II)*: 31, pl.14 fig.1.
1961 *Grandeliacus mortensenae*, – RIPPINGALE & MCMICHAEL, Queensld. Gr. Barr. Reef shells: 63, pl.6 fig.26.
1963 *Heliacus stramineus*, SHIKAMA & HORIKOSHI, Select. shells world: 30, pl.22 fig.5.
1964 *Heliacus stramineus*, – HABE, Shells w. Pac. col., *2*: 47, pl.14 fig.1.

1966 *Heliacus straminea*, - HABE & KOSUGE, Shells world col., *II*: 101, pl.40 fig.1.
1971 *Grandeliacus moretensenae* [sic], - WILSON & GILLETT, Austr. shells: 34, pl.13 figs.14-14a.
1977 *Heliacus (Heliacus) stramineus*, - GARRARD, Rec. Austr. Mus., *31*(13): 509, fig.9 [operculum]; p.537, pl.4 figs.1-6.
1978 *Heliacus stramineus*, - HINTON, Guide Austr. shells: pl.10 fig.5.
1982 *Heliacus stramineus*, - ABBOTT & DANCE, Compend. seashells: 62, fig.
1985 *Heliacus (Grandeliacus) stramineus*, - BIELER, 1985b, Arch. Moll., *116*(1/3): 100ff., pl.3 figs.8 [holotype of *Grandeliacus mortensenae*], 9 [synonymy].
1986 *Heliacus stramineus*, - LAI, Mar. gastr. Taiwan (*1*): pl. p.38 fig.5.
1988 *Heliacus (Grandeliacus) stramineus*, - BIELER, Malac. Rev., Suppl. *4*: 238 [radula].
1990 *Heliacus stramineus*, - COLLINS, Cairns Shell News, *45*: 2, fig.4.

Type measurements: holotype of *G. mortensenae*: SD = 38.4, H = 26.8, PD = 0.88, Tw = 5 1/2.

Type localities: *T. stramineus*: "Habitat ad Tranquebariae littora" [Southern India]; *G. mortensenae*: "collected at Hummock Hill Island, Port Curtis area, Queensland" [Australia].

Etymology: *stramineus-a-um* [adjective]; Latin: made of straw.

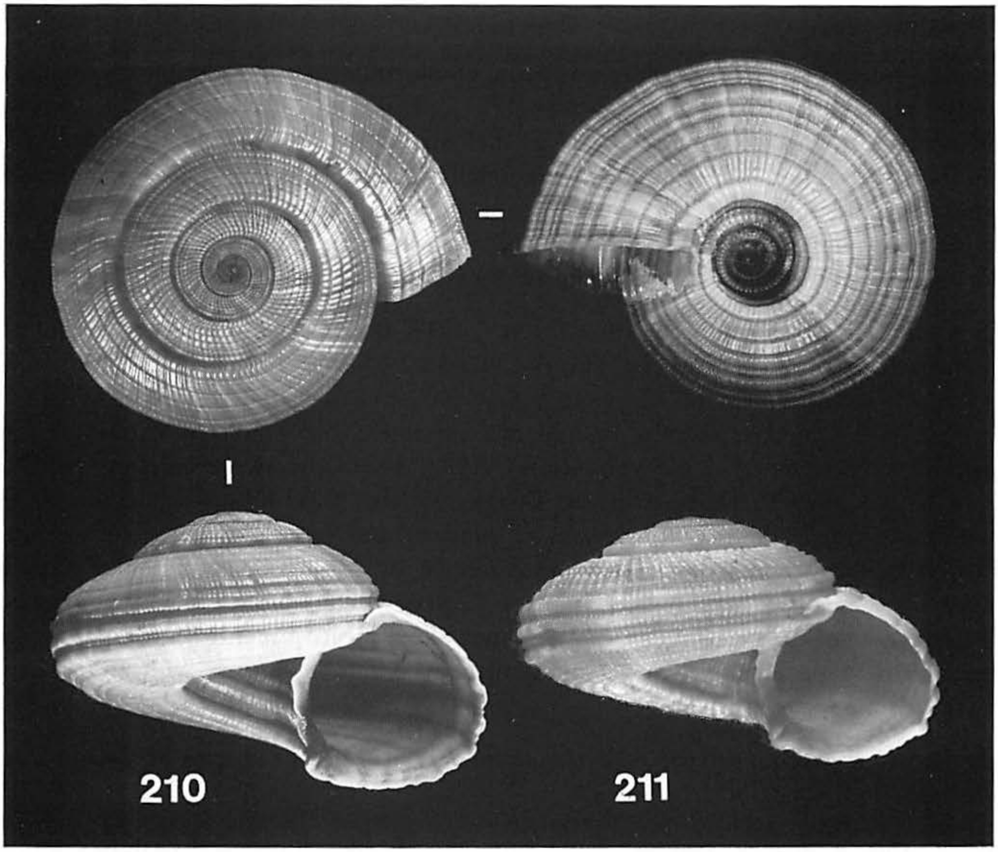
Material studied: 89 specimens (AMNH, ANSP, BMNH, DMNH, FMNH, IRSNB, LMA, MCZ, MNHNP, MNHU, NMP, NMW, SMF, UMZC, USNM, RNHL, LMA, ZMA, Coll. ALF); including holotype of *G. mortensenae* (AMS C.96241).

Diagnosis:

Medium-sized to large rounded cone-shaped shell with strongly bulging whorls, deep suture and moderate to very wide umbilicus; upper-side sculpture of 4 almost equal and 1 narrower ribs, with flattened nodules; rounded peripheral area formed by 3 almost identical ribs, often with finer threads between them; basal sculpture of 6-7 spiral ribs; umbilical side of columellar wall with 2-3 spiral ribs. Yellowish tan with darker apex and pattern of brown blotches on peripheral ribs of early whorls. Protoconch diameter 1.02-1.20 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: medium-sized to large, diameter of specimens in collections usually 18-33 at 3 7/8 to 5 1/4 whorls. Shape: rounded cone-shape with strongly bulging whorls (young specimens with base more convex than upper side) and moderate to very wide umbilicus (UD 17-36% of SD). Sculpture: on early whorls SSR and 2 MR weakly developed, UPR strong, with concave area between UPR and LPR; later SSR stronger or SSR about as strong as MR and UPR; with 1 additional, usually narrower, rib between UPR and LPR; with flattened nodules; Periphery: young specimens initially with double keel formed by LPR and IPR, with LPR somewhat more prominent; later more rounded, with 1 strong additional rib between them, flanked on either side by a finer additional rib; upper point of whorl attachment on or below the stronger, central additional rib; suture deep; Base: 6, later 7, spiral ribs, increasing in width



Figs. 210, 211. *Heliacus (Grandeliacus) stramineus* (GMELIN, 1791). Fig. 210 (three aspects): specimen from Tugela Bank (29°09.5'S, 31°44.4'E), South Africa; NMP B3053; SD = 31.9. Fig. 211: specimen from Philippines; BMNH 1981127; SD = 15.8.

towards umbilicus (larger specimens with additional fine spiral threads); PUR usually wider than UC; UC with ca. 33–55 nodules on body whorl; umbilical side of columellar wall with 2, more seldom 3, ± distinct spiral ribs. Coloration: yellowish tan with darker apex; peripheral ribs at least on early whorls with regular pattern of darker blotches (about 3 nodules wide). – Protoconch (Fig. 4): medium-sized (1.02–1.20, $\bar{x}$ = 1.10), multispiral, distinctly heterostrophic, with strong folds in umbilicus, without anal keel; tan or brown. – Periostracum: thick; glassy yellow when wet; scaly, straw-colored when dry. – Operculum: as described for subgenus. – Radula: five-toothed taenioglossate (2–1–2); rachidian tooth with narrow median cusp flanked by 9 equally strong cusps; marginal teeth longer, curved and flanked with 8–10 tapering cusps (South African specimen, pers. observ.). – Anatomy: not known.

Geographical distribution (Fig. 208): Known from various localities in the Indian and western Pacific Oceans.

Habitat: Sublittoral, to 130 m depth.

Discussion:

Trochus stramineus GMELIN, 1791, was based on illustrations and descriptions by LISTER (1688: pl.635 fig.23) and CHEMNITZ (1781: pl.172 fig.1699) that allow positive identification. Due to its unusually large shell size, *Heliacus stramineus* can hardly be confused with other Indo-Pacific species. Small specimens have a different appearance, which prompted HANLEY (1863: 242) to introduce a "Var. *junior*." They have very convex shell bases, a concave area between the upper peripheral and infraperipheral ribs, fewer "additional ribs," and the suture is often deeper than on later whorls.

The nominal species *Solarium fulvum* HINDS, 1844, from New Guinea, was considered a "variation" of *stramineus* by HANLEY (1863: 242) and BAYER (1948: 35), while SATYAMURTI (1952: 74) and GARRARD (1977: 547, pl.8 figs.10–15) accepted it at the species level. GARRARD thereby figured two specimens for which "it is possible that they represent part of a syntypic series" (1977: 547). The two specimens (BMNH 1844.6.7.34, 1879.2.26.158, vidi; see BIELER, 1985b: 102), however, belong to the similar Mediterranean-Atlantic species *H. subvariegatus* (see below); their dimensions do not fit the original description of *S. fulvum* by HINDS. The original figures by HINDS (1844c: pl.14 figs.17–18), based on "a very young shell now in the collection of Mr. TAYLOR" (HANLEY, 1863: 242), do not allow positive identification with either species; the type locality (New Guinea) groups *Solarium fulvum* with Indo-Pacific *Heliacus stramineus*.

The holotype of *Grandeliacus mortensenae* IREDALE, 1957, type species of *Grandeliacus*, is a large individual of *H. stramineus*.

A very similar species is known from from the Mediterranean and eastern Atlantic, *Heliacus (Grandeliacus) subvariegatus* (ORBIGNY, 1852) [= *Solarium stramineum* var. *mediterranea* PHILIPPI, 1853; ? = *Solarium spencerii* ALLEN, 1856–1858; ? = *Ammonicerina mutabilis* O.G. COSTA, 1861; = *Solarium (Torinia) fallaciosa* TIBERI, 1872; = *Solarium siculum* auct., non CANTRAINE, 1842]. Members of that species have smaller shells (usually 8–15 mm) with less convex, angular margins (lower peripheral and infraperipheral ribs very prominent even in adults), shallow suture (upper point of whorl attachment on or shortly below lower peripheral rib), midribs that are usually narrower than the subsutural and upper peripheral ribs, a shell surface that is non-glossy, a distinctly thickened, white, procellaneous parietal wall, a yellowish shell without pattern of blotches, and a radula with a prominent central cusp on the rachidian. For further discussion of the complex synonymies of *Heliacus stramineus* and *H. subvariegatus*, see BIELER (1985b: 100 20ff.).

A single live-collected specimen from the Persian Gulf Island Shaikh Shu'aib (NMW unnumbered; Fig.212) has many features of a juvenile *Heliacus stramineus*, but is of overall lighter color, lacks the additional rib between upper and lower peripheral ribs (resulting in an upper-side sculpture of only four ribs) and distinct umbilical spiral ribs. This, and the much smaller protoconch size of only 0.78 mm indicate that this specimen may represent an undescribed species; further material will be necessary to determine its status.

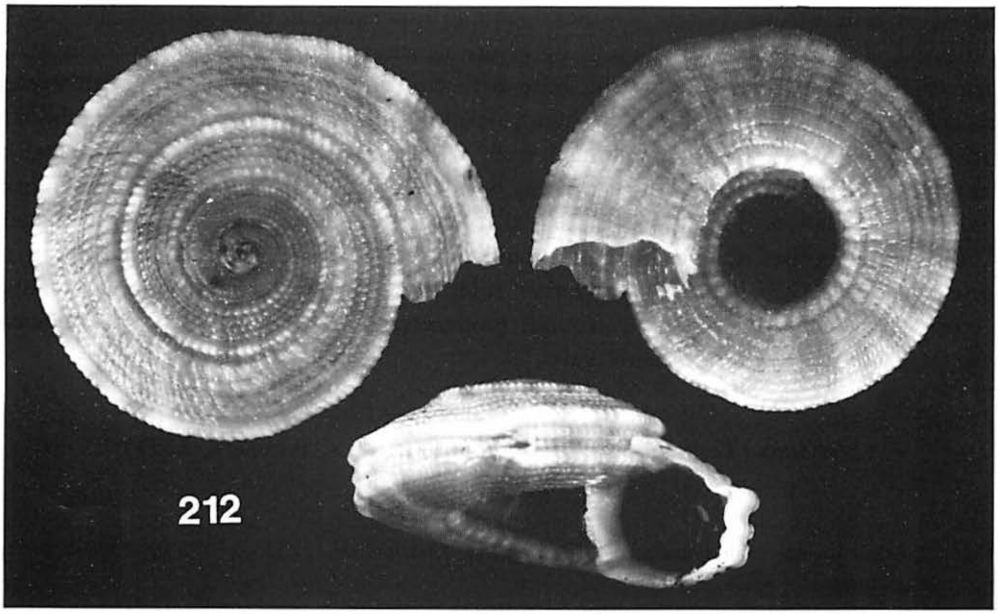


Fig. 212: *Heliacus (Grandeliacus)* sp. aff. *stramineus* (GMELIN, 1791); specimen from Shaikh Shu'aib Island, Persian Gulf (53°15'E, 26°50'N); NMW unnumbered; SD = 7.9.

Subgenus *Heliacus (Teretropoma)* ROCHEBRUNE, 1881

Teretropoma ROCHEBRUNE, 1881: 111; introduced as a genus of land snails. Type species by monotypy: *Teretropoma perrieri* ROCHEBRUNE, 1881; Recent, Atlantic Ocean.

Description (Fig.213):

Teleoconch: small to medium-sized (usually 5.5–13 mm); depressed to turreted cone-shaped, always with distinctly rounded whorls; young or depressed shells with two-ribbed periphery; umbilicus moderately wide to extremely wide (23–65% of shell diameter); sculpture: axial growth sculpture on entire surface; apical side: subsutural rib, single midrib, and upper peripheral rib ± equally strong developed, at least in fully grown specimens interspersed with finer spiral threads; periphery formed by

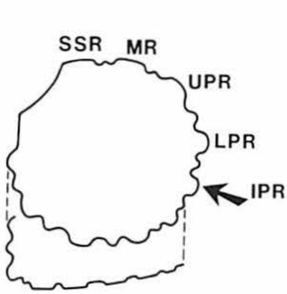


Fig. 213. Schematic representation of placement of major spiral ribs in *Heliacus (Teretropoma)*, apertural aspect. Arrow shows point of attachment of next whorl, intrageneric variation indicated by dotted lines.

almost equally strong lower peripheral and infraperipheral ribs, always flanked by additional weaker ribs; upper point of whorl attachment at infraperipheral rib under formation of a usually deep suture; base with ca. 6 stronger spiral ribs (with usually one weaker additional rib between them); basal area angular or rounded at umbilicus; with spiral sculpture on the umbilical wall; white, solid brown, or with ± irregular flames of tan or reddish to dark brown, with periphery and umbilicus often lighter. *Protoconch*: small to large (0.72–1.24), distinctly heterostrophic, without anal keel. *Radula*: five-toothed-taenioglossate; rachidian with strong central cusp flanked by numerous (9–14) smaller cusps on either side; inner and outer marginals with about 7 cusps each. *Operculum*: horny, round, moderately cone-shaped or flat to concave, with peg-like projection on body side.

Heliacus (Teretropoma) infundibuliformis s.s. (GMELIN, 1791)
Figs.214, 215, 220

1781 "Trochus planior infundibuliformis", - CHEMNITZ, Conch.-Cab., *5*: 133, pl.173 figs.1706–1707 [not binominal].
1783 "Der flache trichterförmige Kräussel", - SCHRÖTER, Einl. Conchylienkenntniß, *1*: 718.
*1791 *Trochus infundibuliformis* GMELIN, Syst. nat. (13th ed.), *1*(6): 3575.
1793 *Trochus infundibuliformis*, - SCHREIBERS, Vers. vollst. Conchylienkenntniß, *1*: 247.
1801 *Trochus infundibuliformis*, - BOSC, Hist. nat. coqu., *4*: 162.
1817 *Trochus infundibuliformis*, - DILLWYN, Descr. cat. Rec. shells, *2*: 783.
1825 *Trochus infundibuliformis*, - WOOD, Index testac.: 137, pl.29 fig.60.
1830 *Trochus infundibuliformis*, - BOSC, Hist. nat. coqu. (2nd ed.), *4*: 154.
*1838–1839 *Solarium Chemnitzii* KIENER, Spéc. gén. icon. coqu., *10*: 12, pl.4 fig.8.
1856 *Solarium infundibuliformis*, - HANLEY, [WOOD'S] Index testac.: 143, pl.29 fig.60.
*1863 *Solarium (Torinia) cylindraceum* Var. *Vermetiformis* HANLEY, Thes. conch., *3*: 242, pl.254 fig.100.
*1863 *Solarium canaliferum* "ADAMS MSS." HANLEY, Thes. conch., *3*: fig. caption to pl.254 figs.98–100.
1863 *Solarium (Torinia) infundibuliforme*, - HANLEY, Thes. conch., *3*: 243, pl.254 figs.91–93.
1863 *Solarium (Torinia) infundibuliforme* Var. *Chemnitzii*, - HANLEY, Thes. conch., *3*: 243.
*1863 *Solarium (Torinia) infundibuliforme* Var.? *strigata* HANLEY, Thes. conch., *3*: 243, pl.254 fig.94.
1880 *Torinia crenella*, - MARTENS, Beitr. Meeresfauna Mauritius Seych.: 290.
1887 *Torinia (Torinia) infundibuliforme*, - MARSHALL, Man. conch., *9*: 19, pl.6 figs.97–98 [after HANLEY, 1863].
1887 *Torinia (Torinia) infundibuliforme* var. *strigata*, - MARSHALL, Man. conch., *9*: 20, pl.6 fig.99 [after HANLEY, 1863].
1897 *Solarium (Torinia) cylindraceum*, - SOWERBY (III), Append. mar. shells S. Afr.: 15.
1910 *Heliacus crenellus*, - E. A. SMITH, Ann. Natal Mus., *2*: 199 [non *Turbo crenellus* LINNÉ, 1767 = *nomen dubium*].
1948 *Torinia crenellus*, - BAYER [in part], Zool. Verh., *4*: 11.
1948 *Torinia crenellus* var. *strigata*, - BAYER, Zool. Verh., *4*: 12.
1953 *Torinia infundibuliformis*, - DIETRICH & MORRIS, Nautilus, *67*(1): 18, pl.4 fig.13.
1961 *Tornista* [sic] *crenellus*, - HABE, Col. illus. shells Japan *(II)*: 31, pl.14 fig.3.
*1962 *Tornista* [sic] *granulata* HABE, Col. illus. shells Japan *(II)*: 31, Append. 43, pl.14 fig.3.
1963 *Heliacus crenellus*, - BARNARD, 1963b, Ann. S. Afr. Mus., *47*(1): 160.
1964 *Tornista* [sic] *granulata*, - HABE, Shells w. Pac. col., *2*: 47, pl.14 fig.3
1966 *Heliacus infundibulum* [sic] *strigata*, - HERTLEIN & ALLISON, Veliger, *9*(2): 140.
1968 *Heliacus infundibuliformis strigatus*, - HERTLEIN & ALLISON, Occas. Pap. Calif. Acad. Sci., *66*: 3.
1971 *Heliacus perrieri*, - KEEN, Sea shells trop. w. Amer. (2nd ed.): 391, fig.431.
1973 *Heliacus crenellus*, - KENSLEY, Sea-shells s. Afr.: 76, pl. p.77 fig.252.
1974 *Heliacus infundibuliformis*, - ABBOTT, Amer. seashells (2nd ed.): 98.

1975 *Heliacus infundibuliformis*, – SALVAT & RIVES, Coqu. Polynésie: 266, fig.50.
1977 *Heliacus (Torinista) infundibuliformis*, – GARRARD, Rec. Austr. Mus., *31*(13): 549, pl.7 figs.19–21.
1978 *Heliacus infundibuliformis*, – CERNOHORSKY, Trop. Pac. mar. shells: 165, pl.58 fig.7.
1979 *Torinista fenestratus*, – MATSUMOTO, Moll. shells Mie Pref.: 22, pl.3 fig.1 [non *Solarium fenestratum* HINDS, 1844].
1982 *Heliacus infundibuliformis*, – KILBURN & RIPPEY, Sea shells s. Afr.: 77.
1982 *Mangonuia* sp., – LADD [in part], U. S. geol. Surv. prof. Pap., *1171*: 30, pl.32 figs.1–6 [Pleistocene, New Hebrides].
1985 *Heliacus (Teretropoma) infundibuliformis*, – BIELER, 1985b, Arch. Moll., *116*(1/3): 104.
1985 *Heliacus dilectus*, – DRIVAS & JAY, La Conchiglia, *17*(190–191): 8, fig.13 [non *Solarium dilectum* DESHAYES, 1863 = *Granosolarium asperum* (HINDS, 1844)].
1985 *Heliacus infundibuliformis*, – DRIVAS & JAY, La Conchiglia, *17*(190–191): 8, fig.11.
1988 *Heliacus (Teretropoma) infundibuliformis*, – BIELER, Malac. Rev., Suppl. *4*: 238 [radula].

Type measurements: syntypes of *Solarium chemnitzii*: SD ranging 12.5–19.6 [MNHG] and 12.4–19.0 [MNHNP]. *S. cylindraceum* var. *vermetiformis*: SD = 16.5, H = 18.2, PD = 0.88, Tw = 5 3/4. *S. infundibuliforme* var.? *strigata*: SD = 10.5, 5.2, PD = 0.94, Tw = 3 2/3, UD = 5.5. *T. granulata*: SD = 7.3, H = 3.3, Tw = 3 1/8, PD = 0.90, UD = 3.9.

Type localities: *T. infundibuliformis*: "Habitat rarissimus ---" [unknown]; *S. chemnitzii*: "Habite la mer des Indes, l'île Bourbon et la mer de la Chine"; var. *vermetiformis*: Philippines [label]; *S. canaliferum*: Philippines; var. *strigata*: Philippines [label]; *T. granulata*: Okinoshima, Kôchi Prefecture, Shikoku, Japan.

Etymology: *infundibuliformis-e* [adjective]; Latin: funnel-shaped.

Material studied: 810 specimens (AMNH, AMS, ANSP, BMNH, CAS, DMNH, FLMNH, FMNH, IRSNB, LACM, LMA, MCZ, MNHNP, MNHU, NMP, NMW, NSMT, OUM, RNHL, SAM, SMF, UMZC, USNM, ZMA, ZSM, Coll. MARAIS); including holotype of var. *vermetiformis* (BMNH 1907.10.28.56; holotype of var. *strigata* (BMNH 1907.10.28.62); holotype of *T. granulata* (NSMT Mo49881); 5 syntypes (MHNG 1151/79) and 2 possible syntypes (MNHNP unnumbered) of *S. chemnitzii*.

Diagnosis:

Small to medium-sized, rounded depressed cone-shaped or disk-shaped shell with bulging whorls, deep suture and extremely wide umbilicus; upper-side sculpture of 3 almost identical ribs, usually with finer threads interspaced; rounded keel area formed by 2 almost identical ribs flanked by weaker threads; convex base with about 6 stronger ribs interspaced by weaker threads; umbilical side of columellar wall with one strong spiral rib plus finer threads. Various shades of brown. Periostracum thick. Operculum moderately cone-shaped. Protoconch diameter 0.78–0.94 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: small to medium-sized, diameter of specimens in collections usually 6–13 at 2 1/2 to 4 whorls (rarely more than 4 1/4 whorls). Shape: rounded depressed cone-shaped to disk-shaped, with bulging whorls and extremely wide umbilicus (UD

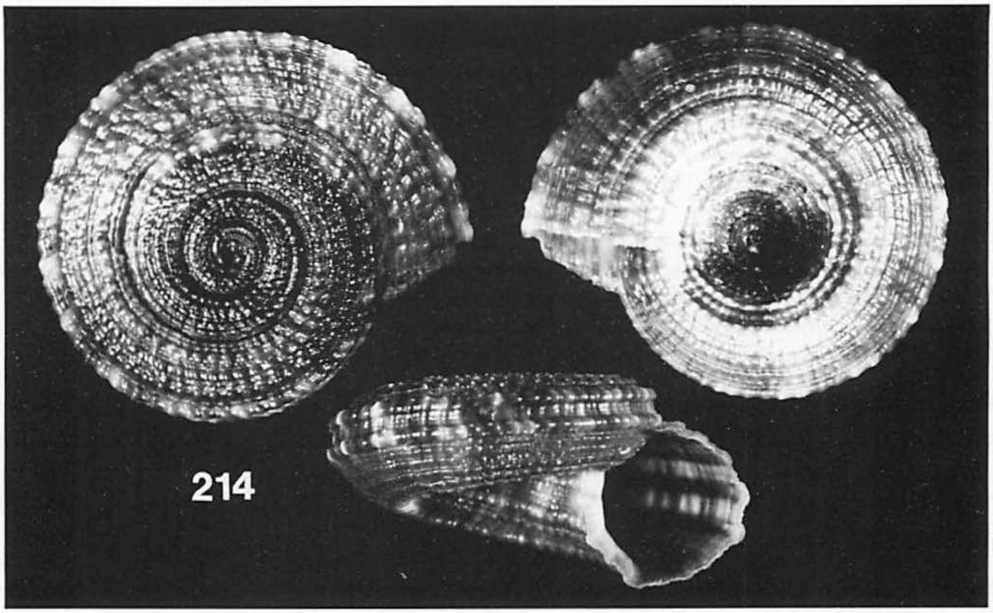


Fig. 214. *Heliacus (Teretropoma) infundibuliformis* (GMELIN, 1791); specimen from Natal, South Africa; SMF 256765; SD = 8.8.

48–65% of SD). Sculpture: Upper side: SSR, single MR and UPR almost identical; between them, at least in larger specimens, finer additional ribs; with ± rounded nodules; Periphery: rounded double keel formed by almost identical LPR and IPR, always flanked by weaker threads; upper point of whorl attachment on IPR, suture ± deep; Base: ca. 6 stronger spiral ribs, usually with weaker additional threads interspaced; UC with 33–51 fine nodules on body whorl; basal area regularly rounded; umbilical side of columellar wall with 1 strong spiral rib and finer threads. Coloration: tan, reddish brown or dark brown, frequently with lighter areas extending over periphery and lighter areas around umbilicus; initial 1 1/2 teleoconch whorls usually darker than protoconch and subsequent teleoconch whorls; inside of aperture with darker spiral lines beneath spiral ribs. – Protoconch: small to medium-sized (0.78–0.94, $\bar{x}$ = 0.87), multispiral, distinctly heterostrophic, without anal keel; solid light brown, or bicolored with light brown and glassy white, with darker fleck in white area opposite peritreme. – Periostracum: very thick, translucent yellowish when wet; scaly, finely reticulated, yellowish tan when dry, giving dry shell an olive-brown appearance. – Operculum: as described for subgenus; moderately cone-shaped. – Radula: five-toothed taenioglossate (2–1–2); rachidian tooth stronger than marginal teeth with prominent, pointed median cusp flanked by 12–14 smaller, blunt cusps; marginal teeth longer, curved and forked with about 7 tapering cusps (pers. obs., South Africa). – Anatomy: described for Atlantic subspecies *perrieri* by HASZPRUNAR (1985b). – Soft-body coloration of living animal: body color milk- to orange-white; tentacles and upper side of foot speckled with black chromatophores, tentacles and anterior margin darker; embedded white granules restricted to tentacles and anterior part of foot; sole of foot with black chromatophores restricted to margins; overall appearance greyish tan with darker tentacles (pers. obs., South Africa).

Reproduction and larval development: sausage-shaped, mucous egg mass of variable length and relatively small diameter (ca. 2.0 mm), containing about 250 weakly oval eggs per mm. Eggs interconnected by chalazae and covered by an additional membrane within the mucous mass, as described in general part (pers. obs., South Africa).

Geographical distribution (Fig.220): Continuous range from western Indian Ocean to Central Pacific. Record from the Marquesas in need of verification.

Habitat: Found at the edges or between polyps of intertidal and upper sublittoral zoanthinarian colonies.

Habits/feeding behavior: Feeds on zoanthinarian polyps (prefers *Isaurus spongiosus* ANDRES over members of *Palythoa* and *Zoanthus*; pers. observ., South Africa).

Discussion:

Typical *Heliacus infundibuliformis*, with its solid or flamed brown color, depressed spire, rounded whorls and extremely wide umbilicus, is readily recognized. *Heliacus mighelsi* (see below) is similar, but differs in its off-white color, higher spire, narrower umbilicus and flat operculum. See also discussion under *H. discoideus* (below).

A very similar form in the Atlantic, tentatively classified as a subspecies, is *H. infundibuliformis perrieri* ROCHEBRUNE, 1881. This form has, statistically, a smaller protoconch and a narrower umbilicus than *infundibuliformis* s.s. (see BIELER, 1985b: 104). Specimens from the coast of western America, with protoconch diameters of less than 0.78, are here interpreted as belonging as belonging to Atlantic *infundibuliformis perrieri* (2 specimens from Islas Secas, Chiriqui Province, Panama, LACM 34-126.6; 2 specimens from Mazatlán, Mexico, ANSP 250799). Additional study of this complex is needed.

A number of authors have used the name *crenellus* for Indo-Pacific *infundibuliformis*. *Turbo crenellus* LINNÉ, 1767, cannot be identified from LINNÉ's description (1767: 1236); LINNÉ did not give a figure reference or locality, and no type material has been located (DANCE, 1967: 21). HANLEY (1855: 337) stated that "by a process of analysis, there being luckily but one shell in the entire collection of LINNAEUS which coincides exactly with the diagnosis, the *Solarium Chemnitzii* of KIENER," the latter being a synonym of *H. infundibuliformis* (GMELIN, 1791). Following this statement, a case could be, and has been, made to accept *crenellus* as the senior synonym of *infundibuliformis*. HANLEY (1855: 337) concluded that "however interesting it may be to ascertain what our author [LINNÉ] intended, the name *crenellus* cannot be preserved, since it was utterly impossible for any one to recognise the species by his publications." BAYER's (1948: 11) concept of *crenellus* was based on a mixture of two species, *H. infundibuliformis* and *H. fenestratus* (specimens in RNHL, vidi). Following HANLEY and DANCE, and in view of the fact that no positive type material of *crenellus* was found, *Turbo crenellus* is here considered a *nomen dubium*.

A study of the type material of the nominal species *Solarium chemnitzii* KIENER, 1838–1839, *Torinista granulata* HABE, 1961, and *Solarium infundibuliforme* var.? *strigata* HANLEY, 1863, suggested synonymy with *Heliacus infundibuliformis* s.s. Another synonym is *Solarium cylindraceum* var. *vermetiformis* HANLEY, 1863, based on an aberrant, giant specimen (BMNH 1907.10.28.56; see Fig.215).

"Solarium canaliferum ADAMS MSS." was first published as a junior synomym (of *Solarium cylindraceum* sensu HANLEY) by HANLEY (1863: figure caption to pl.254 figs.98–100), based on a specimen in the CUMING collection, labelled "Philippines." As Hanley refers to "ADAMS" in other parts of the paper (e.g., as author of *Philippia oxytropis*), it can be safely assumed that he meant the British ARTHUR ADAMS (1820–1878). The cited figures 98 and 99 could refer to either Indo-Pacific *infundibuliformis* or Atlantic *perrieri*; Hanley's figure 100 shows the aberrant *vermetiformis*. Although published as a junior synonym, *Solarium canaliferum* HANLEY, 1863, is available for nomenclatural purposes, since it was used as such by subsequent authors [e.g., PAETEL, 1887–1888: 285, as *canaliferum* ADAMS; ICZN, 1985: Art. 11(e)].

The name *Torinia canalifera* was also used for Atlantic *perrieri*. The first to do so was DALL (1889b: 148), who erroneously credited the name to the American C.B. [CHARLES BAKER] ADAMS (1814–1853). This mistake caused subsequent authors (e.g., BAYER, 1948: 37; CLENCH, 1948: 104; CLENCH & TURNER, 1950: 263) to search in vain for a publication of this species by C.B. ADAMS, and to attribute the species name, as a *nomen nudum*, to DALL. The issue was further confused by W.H. PEASE, who left labels in various collections (e.g., USNM), stating "Torinia variegata canalifera Pse [MS]." His apparently unpublished name referred to specimens of *Heliacus variegatus* and *H. areola*.

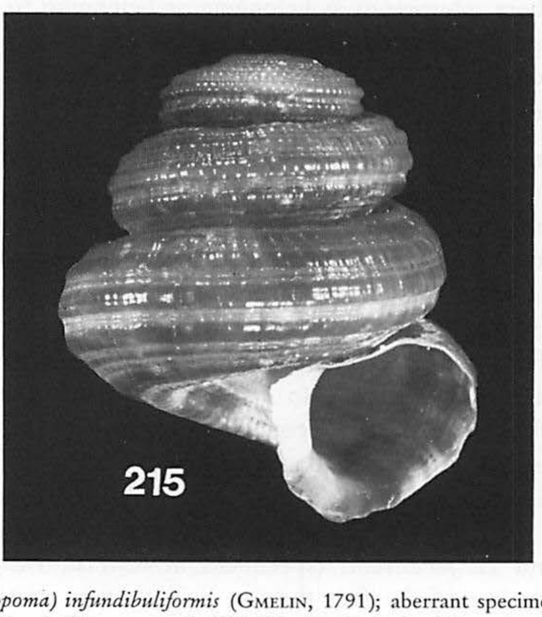


Fig. 215: *Heliacus (Teretropoma) infundibuliformis* (GMELIN, 1791); aberrant specimen, holotype of *Solarium cylindraceum* var. *vermetiformis* HANLEY, 1863; BMNH 1907.10.28.56; SD = 16.5.

Heliacus (Teretropoma) discoideus (PEASE, 1868)

Figs.216–218, 220

*1868 *Torinia discoidea* PEASE, 1868a, Amer. J. Conch., *4*(3): 102, pl. 12 fig.18.
1887 *Torinia discoidea*, - MARSHALL, Man. conch., *9*: 21, pl.6 fig.6 [after PEASE, 1868a].
1948 *Torinia discoidea*, - BAYER, Zool. Verh., *4*: 16.
1979 *Heliacus discoidea*, - KAY, Hawaii. mar. shells: 99.

Type measurements: lectotype (here designated): SD = 5.6, H = 3.0, PD = 0.88, Tw = 3 1/8, UD = 1.9; paralectotype: SD = 6.3, H = 3.0, PD = 0.86, Tw = 3, UD = 2.6 [ANSP 38804].

Type locality: "Paumotus" [= Tuamotu Archipelago, South Pacific].

Etymology: *discoideus-a-um* [adjective]. Clearly PEASE intended this to be a Latin adjective meaning "disc-shaped," although there is no such Latin word. There is a Latin one-ending adjective *discoides*, meaning "shaped like a quoit," from the Greek δισκοείδης. Although grammatically incorrect, the original spelling has to be preserved (ICZN, 1985, Art. 32).

Material studied: 15 specimens (AMS, ANSP, BMNH, USNM, Coll. TRONDLE), including lectotype and paralectotype as above (ANSP 38804).

Diagnosis:

Small to medium-sized, depressed cone-shaped (often somewhat turreted) shell with bulging whorls, ± deep suture and moderately wide to extremely wide umbilicus; upper-side sculpture of 3 almost identical ribs, often with finer threads interspaced; rounded peripheral area formed by 2 almost identical ribs flanked by weaker threads;

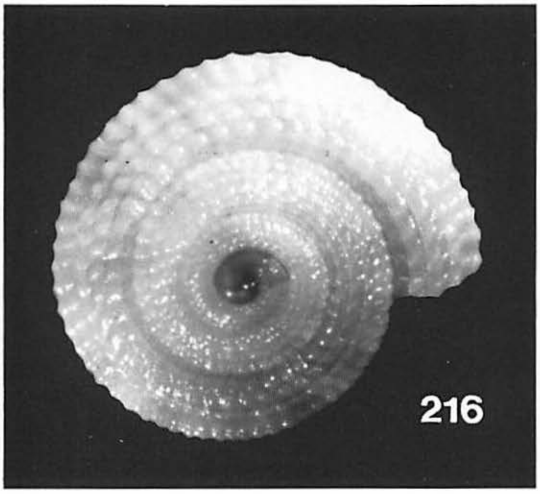


Fig.216–218: *Heliacus (Teretropoma) discoideus* (PEASE, 1868). Fig. 216: lectotype, Tuamotu Archipelago; ANSP 38804; SD = 5.6. Fig.217: specimen from Raroia, Tuamotu Archipelago; USNM 721061; SD =10.0. Fig.218: specimen from Tahiti (BMNH 1886.6.9.243); SD = 13.2.

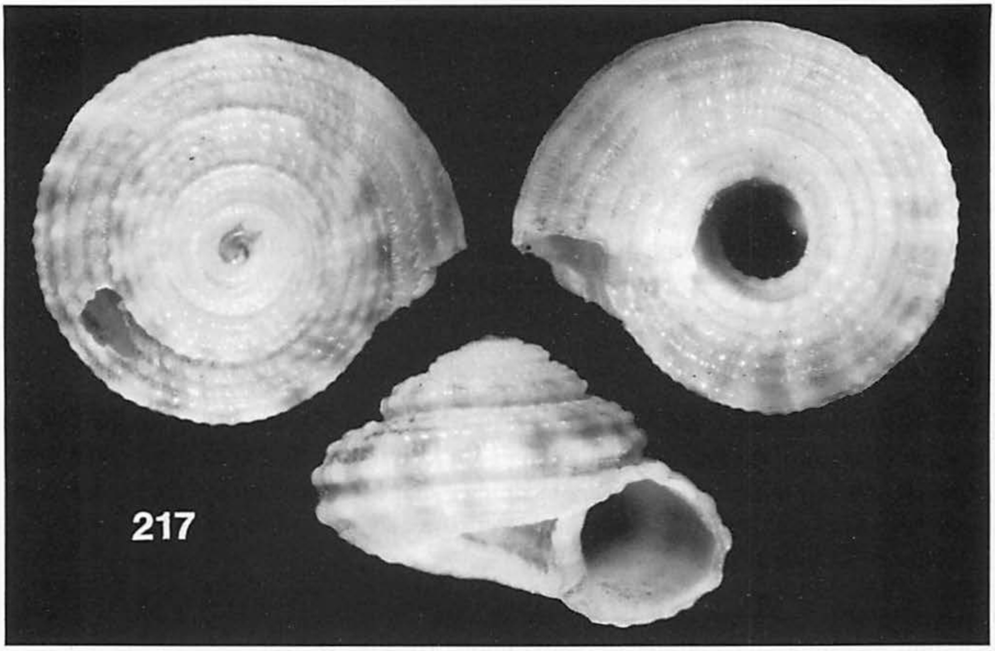


Fig 217

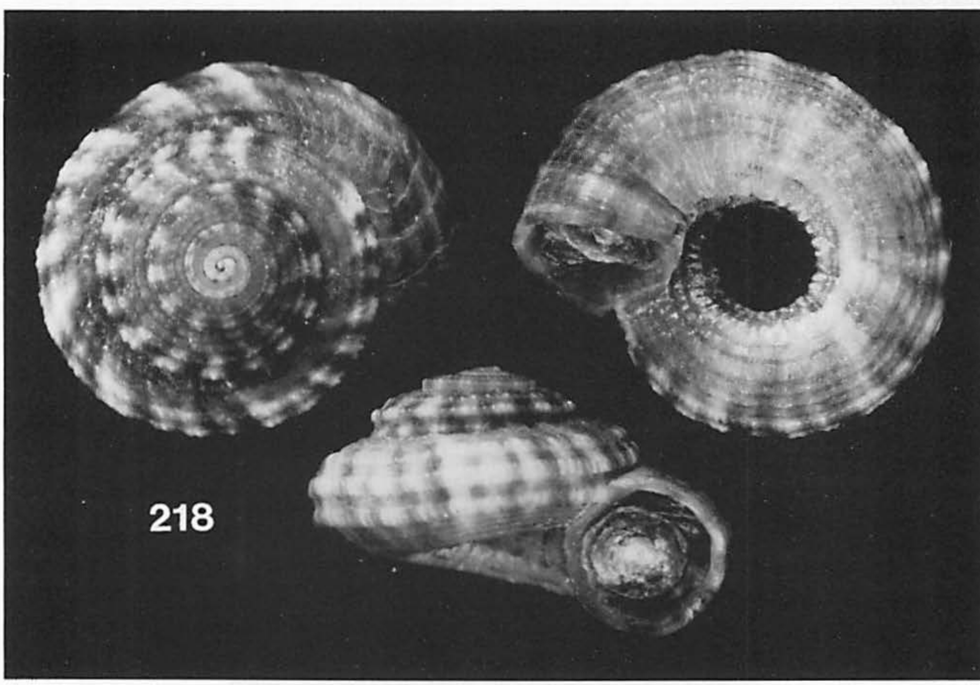


Fig. 218

base with about 6 stronger ribs interspaced by weaker threads; umbilical side of columellar wall with one strong spiral rib plus finer threads. Off-white with darker axial flames. Operculum flat to concave. Protoconch diameter 0.78–0.86 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: small to medium-sized, diameter of specimens in collections usually 6–13 at 3 to 4 5/8 whorls. Shape: depressed cone-shaped with bulging whorls; moderately wide to extremely wide umbilicus (UD 23–47% of SD). Sculpture: Upper side: SSR, single MR and UPR almost identical; between them, at least in larger specimens, finer additional threads; with ± rounded nodules; Periphery: rounded double keel formed by almost identical LPR and IPR, always flanked by weaker threads; upper point of whorl attachment on IPR, suture ± deep; Base: ca. 6 stronger spiral ribs, usually with weaker additional threads interspaced; upper point of whorl attachment on IPR, often resulting in somewhat turreted spire; UC with 2–30, usually ill-defined, nodules on body whorl; umbilical side of columellar wall with 1 strong spiral rib plus finer threads. Coloration: off-white with distinct pattern of darker yellowish- or olive-tan flames. – Protoconch: small (0.78–0.86, $\bar{x}$ = 0.83), multispiral, distinctly heterostrophic, without anal keel; bicolored, light brown and glassy white, with darker fleck in white area, opposite peritreme. – Operculum: flat to concave, as described for subgenus. – Radula and Anatomy: not known.

Geographical distribution (Fig.220): Known from Tuamotu Archipelago and Society Islands.

Discussion:

This form, only known from a relatively restricted area in the Central Pacific, shares several characters with *Heliacus mighelsi* (teleoconch shape of most specimens, white basal color, flat to concave operculum), but in others seems closer to *H. infundibuliformis* (protoconch and teleoconch coloration, extremely wide umbilicus in some specimens). Further study of the three nominal species, especially a better understanding of their geographical distribution in the Pacific, is necessary.

In the original description of this form, Pease (1868a: 102) did not indicate the number of specimens at hand. The given dimensions ("Diam. 6, alt. 3 1/2 mill.") are close to those of the two syntypes in the ANSP collection (ANSP 38804). The original drawing (Pease, 1868a: pl.12 fig.18) is sketchy and does not reflect the relatively fine sculpture of actual specimens (in apertural aspect, the peripheral ribs of the body whorl should have about 30 nodules instead of the illustrated 13). Pease (1868a: 102) described the shell of his new species as "White, radiately striped with yellowish or light chestnut." The smaller of the two ANSP syntypes (Fig.216), with faint radial flames closest to the original illustration, is here selected as lectotype. This specimen also has a light brown protoconch; the larger shell, now paralectotype, is pure white.

Heliacus (Teretropoma) mighelsi (PHILIPPI, 1853)
Fig.219, 220

*1845 *Solarium cyclostomum* MIGHELS, Proc. Boston Soc. nat. Hist., *1*: 22 [non *S. cyclostomum* MENKE, 1830].
*1853 *Torinia Mighelsi* PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 36 [nom nov. pro *Solarium cyclostomum* MIGHELS, 1845].
1863 *Solarium (Torinia) Mighelsii*, - HANLEY, Thes. conch., *3*: 240, pl.254 figs.87-88.
1869 *Torinia Mighelsii*, - PEASE, 1869b, Amer. J. Conch., *5*(2): 81.
1887 *Torinia Mighelsi*, - MARSHALL, Man. conch., *9*: 19, pl.6 figs.89-90 [after HANLEY, 1863].
1933 *Torinia mighelsi*, - EDMONDSON, Bernice P. Bishop Mus. spec. Publ., *22*: 135.
1952 *Torinia mighelsi*, - TINKER, Pac. sea shells: 177, pl. p.179 (fourth row, center).
1967 *Heliacus mighelsi*, - ROBERTSON, Science, *156*(3772): 246.
1977 *Heliacus (Heliacus) mighelsi*, - GARRARD, Rec. Austr. Mus., *31*(13): 536, pl.7 figs.7-9.
1978 *Heliacus mighelsi*, - CERNOHORSKY, Trop. Pac. mar. shells: 166, pl.58 fig.10.
1985 *Heliacus (Teretropoma) mighelsi*, - BIELER, 1985b, Arch. Moll., *116*(1/3): 104.
[----] *Heliacus mighelsi*, - S. JOHNSON, Living seashells: 14, fig. [*in situ*].

Original measurements: SD = ca. 7.6 [teste MIGHELS].

Type locality: "Oahu" [Hawaiian Islands; "Oahu" probably in error for Kauai (see R.I. JOHNSON, 1949: 217)].

Etymology: *mighelsi* [genitive singular case-ending]; named after JESSE WEDGWOOD MIGHELS (1795-1861), American physician and conchologist.

Material studied: 220 specimens (AMS, ANSP, BMNH, BPBM, CAS, DMNH, FLMNH, FMNH, IRSNB, MCZ, MNHNP, MNHU, NMW, RNHL, UMZC, USNM). Original material of *S. cyclostomum* not located.

Diagnosis:

Small, somewhat turreted cone-shaped shell with bulging whorls, deep suture and moderate to wide umbilicus; upper-side sculpture of 3 almost identical ribs, with finer threads interspaced; rounded keel area formed by 2 almost identical ribs flanked by weaker threads; base with about 6 stronger ribs interspaced by weaker threads; umbilical side of columellar wall with one strong spiral rib plus finer threads. Off-white, sometimes with weak darker flames. Periostracum thick, imparting overall dirty-yellowish appearance to shell. Operculum flat to concave. Protoconch diameter 0.74-0.88 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: small, diameter of specimens in collections usually 7-10 at 3 1/2 to 4 1/3 whorls. Shape: cone-shaped with bulging whorls and moderate to wide umbilicus (UD 24-35% of SD); suture deep. Sculpture: Upper side: SSR, single MR and UPR almost identical; with finer additional threads between them; with ± rounded nodules; Periphery: rounded double keel formed by almost identical LPR and IPR, always flanked by additional ribs and weaker threads; upper point of whorl attachment on

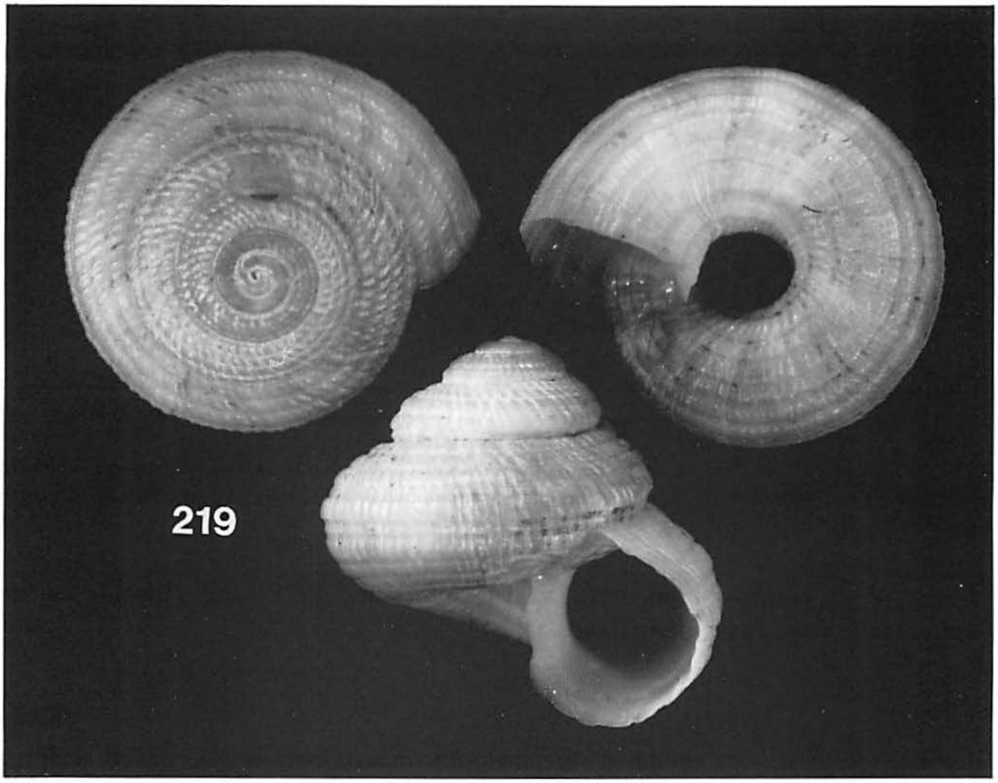


Fig. 219. *Heliacus (Teretropoma) mighelsi* (PHILIPPI, 1853); specimen from Hilo, Hawaii; USNM 339307; SD = 9.1.

IPR, resulting in somewhat turreted spire; Base: ca. 6 stronger spiral ribs, usually with weaker additional threads interspaced; UC with 19–30 ill-defined nodules on body whorl; umbilical side of columellar wall with 1 prominent spiral rib plus weaker threads. Coloration: off-white with pattern of greyish tan flames, the latter more distinct at periphery; large specimens with white porcelaneous parietal region. – Protoconch: small (0.74–0.88, $\bar{x}$ = 0.82), multispiral, distinctly heterostrophic, with folds in false umbilicus, without anal keel; occasionally with brown outer corner of peritreme and single brown fleck, never with solid brown color. – Periostracum: thick, giving dry shell dirty-yellowish appearance. – Operculum: flat to concave, as described for subgenus. – Radula and Anatomy: not known. – Soft-body coloration of living animal: "tentacles ... pale cream" (PEASE, 1869b: 81).

Geographical distribution (Fig.220): Apparently with disjunct pattern: common in the Hawaiian Islands (from Hawaii to Laysan), also reported and illustrated from off eastern Australia (e.g., GARRARD, 1977: 536, pl.7 figs.7–9).

Habitat: Live records from intertidal and upper sublittoral.

Habits/feeding behavior: ROBERTSON (1967) reported it to feed on *Zoanthus confertus*

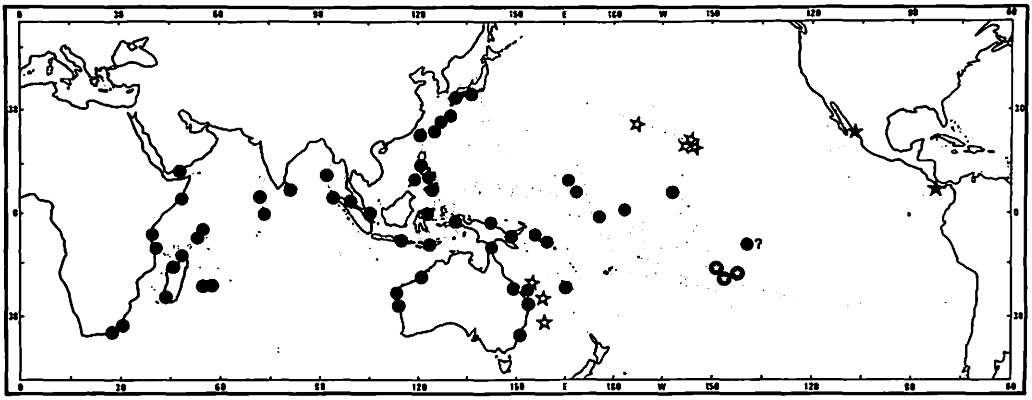


Fig. 220. Geographical distribution of forms in the *Heliacus (Teretropoma) infundibuliformis*-complex: *H. infundibuliformis* s.s., *H. mighelsi*, *H. discoideus* and *H. infundibuliformis perrieri* (Atlantic records of *perrieri* omitted).

VERRILL [= *Z. pacificus* nom. nov. WALSH & BOWERS, 1971] and *Palythoa vestitus* (VERRILL) in Kauai, Hawaiian Islands.

Discussion:

Heliacus mighelsi is very similar to *Heliacus infundibuliformis* in teleoconch sculpture and protoconch characters. The shell is higher-spired (resulting in a relatively narrower umbilicus), much lighter in color, the operculum is flat to concave, never cone-shaped as in *H. infundibuliformis*, and the protoconch is never solid-brown. *Heliacus discoideus* is very similar and may be conspecific (see discussion above).

BAYER's (1948: 29) listing of "*Torinia mighelsi*" was based on material of *Heliacus ponderi* (specimens in RNHL, vidi).

Heliacus (Teretropoma) fenestratus (HINDS, 1844)
Fig.221, 222

*1844 *Solarium fenestratum* HINDS, 1844b, Proc. zool. Soc. Lond., *1844*: 25.
1844–1845 *Solarium fenestratum*, – HINDS, 1844c–1845, Zool. Voy. SULPHUR, *1*: 2, *2*: pl.14 figs.21–22.
1844 *Solarium fenestratum* HINDS, 1844d, Ann. Mag. nat. Hist., *14*: 440.
1853 *Solarium fenestratum*, – PHILIPPI, 1853b, Syst. Conch.-Cab. II, *7*: 23, pl.3 fig.13 [after HINDS, 1844d].
1863 *Solarium (Torinia) fenestratum*, – HANLEY, Thes. conch., *3*: 241, pl.254 figs."77–78" [err. pro 79–80].
1887 *Torinia fenestrata*, – MARSHALL, Man. conch., *9*: 20, pl.6 figs.100 and 1 [after HANLEY, 1863].
1948 *Torinia crenellus*, – BAYER [in part], Zool. Verh., *4*: 11.
1948 *Torinia fenestrata*, – BAYER, Zool. Verh., *4*: 19.
1977 *Heliacus (Torinista) fenestrata*, – GARRARD, Rec. Austr. Mus., *31*(13): 546, pl.4 figs.19–21.
1985 *Heliacus (Teretropoma) fenestratus*, – BIELER, 1985b, Arch. Moll., *116* (1/3: 104

Type measurements: SD = 7.4, H = 3.5 [teste HINDS, 1844b], Tw = 3 [teste HANLEY, 1863].

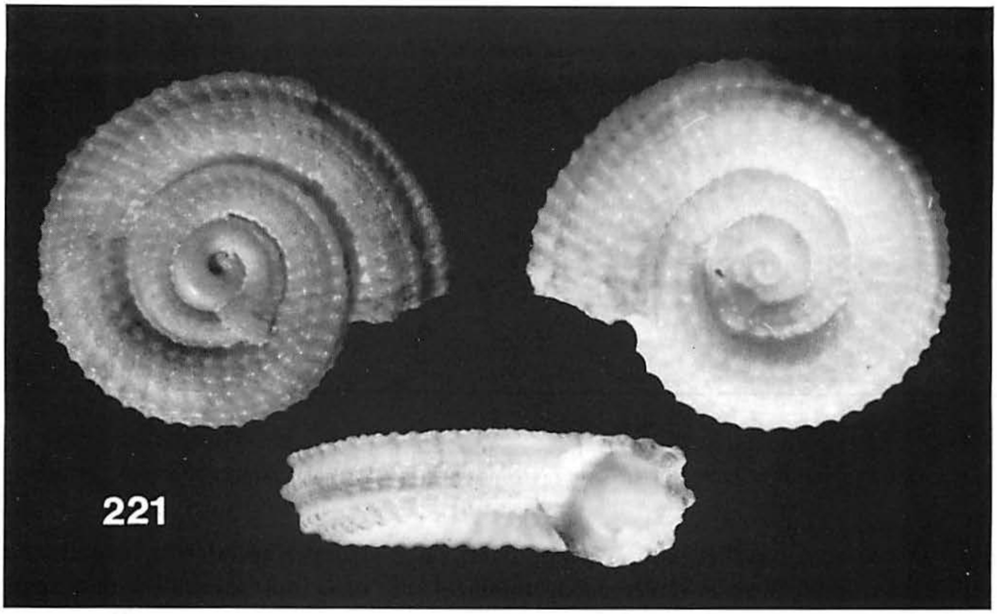


Fig. 221. *Heliacus (Teretropoma) fenestratus* (HINDS, 1844); specimen from South New Caledonia, 250–350 m; MNHNP unnumbered; SD = 5.0.

Type locality: "New Guinea."

Etymology: *fenestratus-a-um* [adjective]; Latin: windowed, with windows.

Material studied: 31 specimens (AMS, BMNH, FMNH, IRSNB, LACM, MCZ, MNHNP, NMW, RNHL, USNM); holotype specimen lost [BMNH; illustrated by HANLEY, 1863].

Diagnosis:

Small flattened, finely sculptured, with deep suture and very wide umbilicus; upper-side sculpture of 3 almost identical ribs, often with finer threads interspaced; rounded peripheral area formed by two almost identical ribs flanked by weaker threads; base with about 6 stronger ribs interspaced by weaker threads; umbilical side of columellar wall with one strong spiral rib. Fawn. Protoconch diameter 1.08–1.24 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: small, diameter of specimens in collections usually 5.5–10.0 at 2 1/4 to 3 3/4 whorls. Shape: flattened, with very wide umbilicus (UD 41–48% of SD). Sculpture: finely cancellate due to closely-spaced axial riblets; Upper side: SSR, single MR and UPR almost identical; between them, at least in larger specimens, finer additional threads; with ± rounded nodules; Periphery: rounded double keel formed by almost identical LPR and IPR, always flanked by weaker threads; upper point of

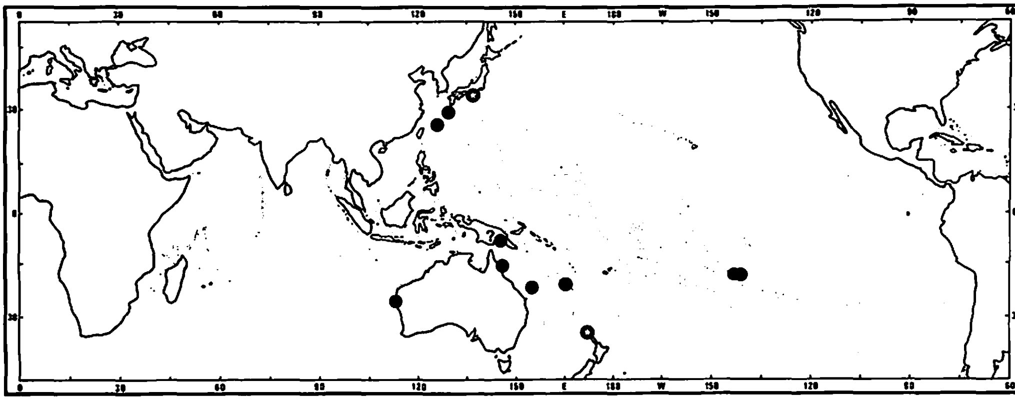


Fig. 222. Geographical distribution of *Heliacus (Teretropoma) fenestratus* and *Heliacus (Gyriscus) asteleformis*.

whorl attachment on IPR, suture deep; Base: ca. 6 stronger spiral ribs, usually with weaker additional threads interspaced; umbilical side of columellar wall with 1 strong spiral rib. Coloration: fawn (faded in most collection specimens). - Protoconch: medium-sized to large (1.08–1.24, $\bar{x}$ = 1.18), multispiral, distinctly heterostrophic, without anal keel; whitish with brown outer corner of peritreme. - Operculum: cone-shaped, as described for subgenus. - Radula and Anatomy: not known.

Geographical distribution (Fig.222): Known from Japan, Austral-Asia, and to Tuamotu Archipelago. Record from New Guinea (type locality!) in need of verification.

Habitat: Records from shallow water to sublittoral.

Discussion:

Shells of *Heliacus fenestratus* differ from the other species of this group by their finely cancellate teleoconchs and large protoconchs.

One of the specimens ("d. Oshima") used by BAYER (1948: 11–12) for the discussion of "*Torinia crenellus*" [= *Heliacus infundibuliformis*] is a member of *H. fenestratus* (RNHL, vidi).

Subgenus *Heliacus (Gyriscus)* TIBERI, 1867

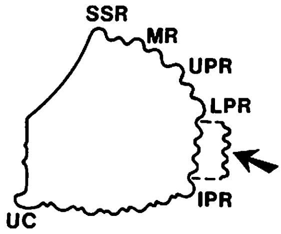
Gyriscus TIBERI, 1867: 303. Type species by monotypy: *Gyriscus jeffreysianus* TIBERI, 1867; Recent, Mediterranean Sea.

Incorrect subsequent spellings:
"Giriscus" F. NORDSIECK, 1982; "Gyrinus" F. NORDSIECK, 1982.

Description (Fig.223):

Teleoconch: small (usually 6–10 mm); tall, roundly cone-shaped with distinctly rounded, bulging whorls; umbilicus very narrow to narrow (ca. 5–10% of shell

Fig. 223. Schematic representation of placement of major spiral ribs in *Heliacus (Gyriscus)*, apertural aspect. Arrow shows point of attachment of next whorl, intrageneric variation indicated by dotted lines.



diameter); entire surface with fine granular sculpture formed by crossing fine axial growth threads and narrow spiral ribs; later whorls with many additional spiral ribs which are almost as strong as the main ribs; apical side: subsutural rib, two midribs, upper peripheral rib, and several additional ribs interspersed; broad, rounded peripheral region demarcated by lower peripheral and infraperipheral rib, with 1–4 ± strong and sometimes numerous weaker, additional ribs between them; upper point of whorl attachment between upper and infraperipheral ribs, at additional ribs of periphery; no distinct suture; base with 6–8 stronger and numerous finer spiral ribs; umbilical wall usually with 1–2 ± irregular spiral ridges, in large specimens often smooth except for growth lines; usually white, occasionally with weak tan flames and brown parietal wall. *Protoconch:* medium-sized (0.90–1.15), distinctly heterostrophic, protruding bubble-like, without anal keel. *Radula:* five-toothed-taenioglossate; rachidian with strong central cusp flanked by numerous (10–12) smaller cusps on either side; inner and outer marginals with 4–8 cusps each [Mediterranean *H. jeffreysianus*]. *Operculum:* horny, round, weakly cone-shaped, with peg-like projection on body side.

Heliacus (Gyriscus) asteleformis (POWELL, 1965)
Figs. 222, 224

*1965 *Gyriscus asteleformis* POWELL, Rec. Auckland Inst. Mus., *6*(2): 161, pl.22 fig.11.
*1970 *Gyriscus hayashii* SHIKAMA, Sci. Rep. Yokohama natl. Univ., (2)*16*: 19, pl.1 fig.3.
1979 *Gyriscus hayashii*, – MATSUMOTO, Moll. shells Mie Pref.: 22, pl.3 fig.3.
1979 *Gyriscus asteleformis*, – POWELL, N. Zeal. Moll.: 247, fig.57-1.
1981 *Heliacus (Gyriscus) asteleformis*, – QUINN, Nautilus, *95*(3): 155.
1984 *Heliacus asteleformis*, – BIELER, 1984c, Arch. Moll., *115*(1/3): 107, pl.1 figs.5 [holotype *asteleformis*], 6 [holotype *hayashii*].
1985 *Heliacus (Gyriscus) asteleformis*, – BIELER, 1985b, Arch. Moll., *116*(1/3): 105.

Type measurements: holotype of *G. asteleformis*: SD = 8.0, H = 8.0, PD = 1.12, Tw = 4, UD = 0.5; holotype of *G. hayashii*: SD = 10.3, H = 10.8, PD = 1.06, Tw = 4 5/8+, UD = 0.5.

Type localities: *G. asteleformis*: "Between the Three Kings Islands and Cape Maria van Diemen [New Zealand], 50 fathoms [91 m], in the cavity of a cup sponge"; *G. hayashii*: "Ensyu-nada" [off Daio-zaki Cape, Honshu, south-western Japan].

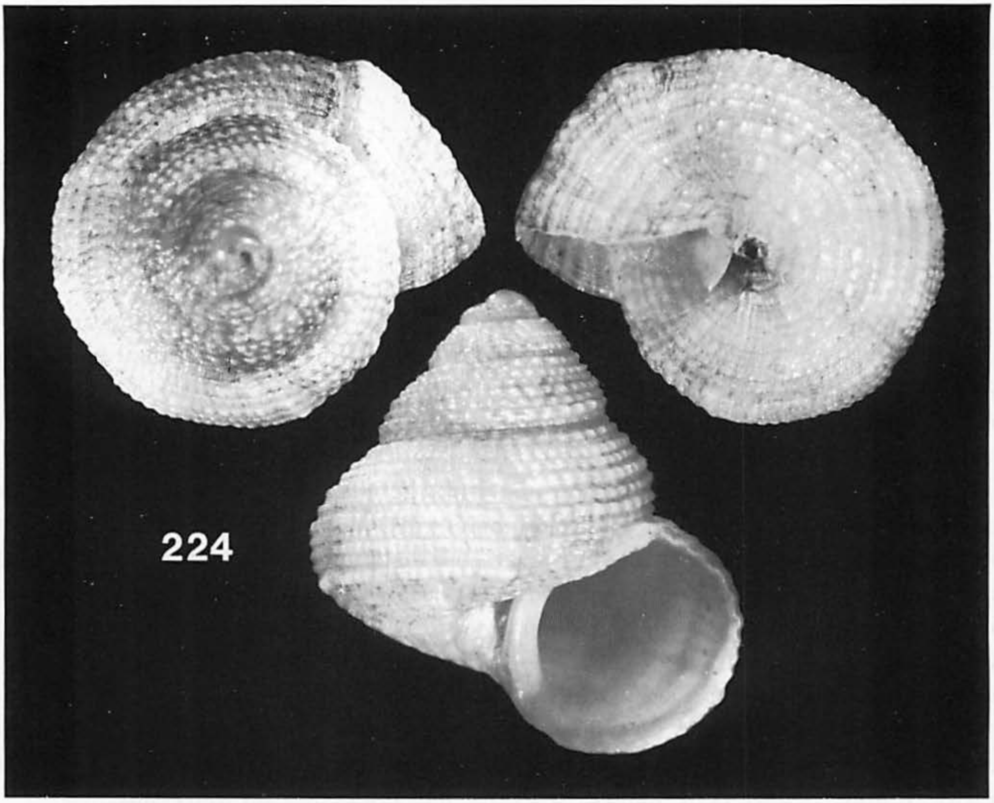


Fig. 224. *Heliacus (Gyriscus) asteleformis* (POWELL, 1965); holotype of *Gyriscus asteleformis*; New Zealand; AIM TM-1241; SD = 8.0.

Etymology: *asteleformis-e* [adjective]; Latin: shaped like *Astele*, a trochid genus.

Material studied: Holotype of *G. asteleformis* (AIM TM-1241) and holotype of *G. hayashii* (currently housed in Kanagawa Pref. Mus., Yokohama).

Diagnosis:

Small to medium-sized, tall, rounded cone-shaped shell with bulging whorls and very narrow umbilicus; sculpture of axial grooves and spiral ribs resulting in granulose appearance; upper side with at least 5 almost identical ribs; rounded peripheral area formed by 2 identical ribs, with at least 3 moderately strong additional ribs between them; basal sculpture of about 10 spiral ribs of various widths; umbilical side of columellar wall without spiral sculpture. Yellowish white. Protoconch diameter 1.06–1.12 mm, distinctly heterostrophic, without anal keel.

Description:

Teleoconch: small to medium-sized, diameter of specimens studied about 10 at 4 – 4 5/8+ whorls. Shape: tall, rounded cone-shaped with distinctly bulging whorls and very narrow umblicus (UD 5–6% of SD). Sculpture with fine granulations resulting from crossing fine axial growth lines with narrow spiral ribs; upper side: SSR, 2 MR, UPR, and 1 additional rib between UPR and LPR, with SSR and UPR somewhat stronger; later whorls with additional ribs between them; Periphery: rounded area formed by UPR and IPR and 3 (in large specimens more) strong additional ribs between them; upper point of whorl attachment on second additional rib; Base: 9–10 spiral ribs of various widths (large specimens more); umbilical side of columellar wall at least in larger specimens (no juveniles studied) without distinct spiral sculpture. Coloration: Yellowish-white. - Protoconch: medium-sized (1.06–1.12), multispiral, distinctly heterostrophic, without pronounced anal keel (type of *asteleformis* with weak edge in anal keel area); glassy white with brown outer corner of peritreme and 1 brown fleck. - Periostracum: yellowish. - Operculum: as described for subgenus. - Radula and Anatomy: not known.

Geographical distribution (Fig.222): Known from Japan and New Zealand.

Habitat: Type material of *H. asteleformis* taken alive in 91 m, in cavity of cup sponge.

Discussion:

A comparison of the holotypes of *Gyriscus asteleformis* Powell, 1965 (see Fig.224) and *G. hayashii* Shikama, 1970, suggested synonymy (Bieler, 1984c: 107, pl.1 figs.5, 6). *Heliacus (Gyriscus) asteleformis* is the only known species of this subgenus in the Indo-Pacific and can be readily distinguished from other *Heliacus* species by the finely granulate sculpture in combination with a narrowly umbilicate, high-spired shell.

Very similar is the Mediterranean species *Heliacus (G.) jeffreysianus* (Tiberi, 1867), type species of *Gyriscus*. Due to additional spiral ribs, the sculpture in that species is even finer; the protoconch diameter is somewhat smaller (about 0.96 mm) [for figures and further discussion see Bieler, 1984c, 1985b].

Genus *Pseudotorinia* Sacco, 1892

Pseudotorinia Sacco, 1892: 66; introduced as subgenus of *Solarium* [= *Architectonica*]. Type species by original designation: *Solarium obtusum* Bronn, 1831; Upper Pliocene, Italy.

Synonyms:

Awarua Mestayer, 1930: 145. Type species by original designation: *Omalaxis amoena* Murdoch & Suter, 1906; Recent, New Zealand.

Calodisculus Rehder, 1935: 129. Type species by original designation: *Discohelix (Discosolis) retifera* Dall, 1892; Pliocene, Florida, U.S.A.

? *Punjabia* Eames, 1952: 38. Type species by original designation: *Punjabia marginostriata* Eames, 1952; Lower Eocene, Punjab [early postlarval stage].

Incorrect subsequent spellings:

"Calodiscus" Wenz, 1939; Eames, 1952; Glibert, 1962.

Description (Fig.224a):

Teleoconch: shell very small to small (usually 2–8 mm), lens-shaped with distinctly rounded base to coin-shaped with strongly angular base; umbilicus moderately to extremely wide (ca. 19–53% of shell diameter); distinct axial growth marks on entire shell surface, but usually only stronger than spiral ribs on early whorls; upper (apical) side: subsutural rib usually stronger and with coarser nodules than following 2–3 midribs; upper peripheral rib prominent and stronger than midribs; peripheral keel formed by very prominent lower peripheral rib (LPR), upper point of whorl attachment here; base: infraperipheral rib hardly stronger than following 2–3 narrow, distinctly demarcated spiral ribs; inner part of base formed by 3–4 wider spiral ribs, the outer one of which representing a ± prominent basal keel, the innermost (UC) surrounding umbilicus with strong nodules; umbilical wall with axial growth lines, in most cases without, rarely with 1–2 ± weak spiral ribs; coloration off-white, yellowish or tan, occasionally with irregular flames; umbilical crenae and peripheral keel often lighter. *Protoconch:* very small to medium-sized (ca. 0.38–0.98), almost planispiral to distinctly heterostrophic, without anal keel. *Radula:* five-toothed-taenioglossate, with strong rachidian tooth and longer, forked cusps (*architae*). *Operculum:* horny, round, cone-shaped, with peg-like projection on body side.

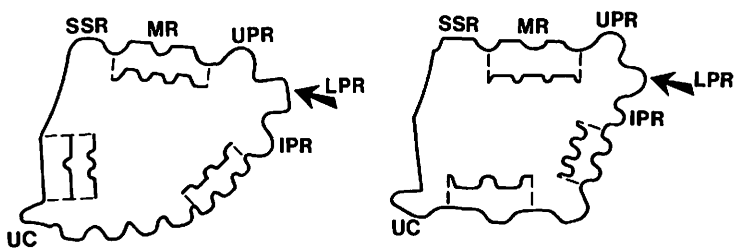


Fig. 224a. Schematic representation of placement of major spiral ribs in the two basic teleoconch shapes of *Pseudotorinia*, apertural aspect. Arrow shows point of attachment of next whorl, intrageneric variation indicated by dotted lines.

The division into groups of species is for convenience in identification and may not always reflect monophyletic units. For a more extensive description and discussion of this genus see Bieler (1985b: 91–94).

Pseudotorinia architae-group

The *Pseudotorinia architae*-group, named after its best-known member, Mediterranean *Pt. architae* (O.G. Costa, 1841), is a complex of very similiar Indo-Pacific and Atlantic forms. Their unifying character is an angular shell base, carrying a prominent keel formed by a spiral rib of the basal field. This keel divides the base into a convex outer and a concave inner part.

Many nominal species have been described for Recent and fossil members of this group (e.g., *Solarium ammonites* Lamarck, 1804; *Solarium architae* O.G. Costa, 1841;

Solarium planulatum GRATELOUP, 1832; *Discohelix retifera* DALL, 1892; *Omalaxis amoena* MURDOCH & SUTER, 1906; *Heliacus panamensis* BARTSCH, 1918; *Torinia elegantula* YOKOYAMA, 1922; *Torinia mitrai* BEETS, 1941, *Heliacus crystallina* NOWELL-USTICKE, 1969). Their synonymy, especially of names based on Atlantic fossil material, is only partly resolved. The present data allow only a preliminary grouping. New names in this group should not be introduced without further study of the fossil record.

Description:

Teleoconch: very small to small, diameter of specimens in collections usually 2–8, rarely over 3 1/2 whorls. Shape: depressed lens-shaped to coin-shaped; always with basal keel dividing base into a peripheral, ± convex part and an inner, ± concave part surrounding the umbilicus; UD ca. 28–40% of SD. Sculpture (consisting of granose spiral ribs): Upper side: SSR and 2–3 MR distinctly developed (larger specimens often with additional spiral threads); Periphery: UPR stronger than SSR and MR; keel-forming LPR strong, upper point of whorl attachment here (thereby forming a ± deep suture); IPR distinctly separated, only somewhat stronger or as strong as following basal ribs; Base: convex area with 1–2 narrow, distinctly separated spiral ribs (very similar to IPR); ± prominent basal keel formed by relatively wide basal rib; umbilicus surrounded by ± strong rib (UC) bearing ± coarse (often pointed) granules; concave area between basal keel and UC with 1–2 spiral threads; umbilical side of columellar wall without spiral sculpture or with 1–2 spiral threads. Coloration: whitish to dark reddish brown, without distinct pattern. - Protoconch: very small to small (0.38–0.74), almost planispiral to weakly heterostrophic, without anal keel.

For comparative purposes, diagnoses of the two Atlantic forms of *Pseudotorinia architae* (O.G. COSTA, 1841) are given:

Pseudotorinia architae (O.G. COSTA, 1841)[12] [Atlantic]

Figs.225, 227, 228

*1841 *Solarium Architae* O.G. COSTA, Fauna Regno Napoli: 5, pl.1 [5], figs.a, A, B, C.
*1862 *Solarium soverbii* HANLEY, Proc. zool. Soc. Lond., *1862*(2): 206.
1873 *Solarium architae*, - MONTEROSATO, 1873a, Notiz. Solarii Medit.: 10, pl.4 figs.21–23.
1887 *Torinia (Torinia) architae*, - MARSHALL, Man. conch., *9*: 21, pl.6 figs.9–11 [after MONTEROSATO, 1873a].
1948 *Torinia architae*, - BAYER, Zool. Verh., *4*: 5 [synonymy].
1948 *Torinia architae* var. *soverbii*, - BAYER, Zool. Verh., *4*: 6 [synonymy].
1974 *Heliacus architae*, - MELONE, Quad. Civ. Staz. Idrobiol. Milano, *5*: 24, pl.1 figs.4–6, pl.3 figs.1–2 [radula].
1974 *Heliacus architae*, - TUROLLA, Conchiglie, *10*(9–10): 193–198, pl.1 [synonymy].
1984 *Heliacus architae*, - Boss & MERRILL, 1984b, Occas. Pap. Moll., *4*(66): 356, pl.51, figs.1–2 [after MELONE]; pl.61 figs.1–2 [radula].
1985 *Heliacus (Torinista) architae*, - MELONE & TAVIANI, Lav. Soc. ital. Malac., *21*(1984): 170, figs.34–38 [shell, operculum, radula].
1985 *Pseudotorinia architae*, - BIELER, 1985b, Arch. Moll., *116*(1/3): 92.
1988 *Pseudotorinia architae*, - BIELER, Malac. Rev., Suppl.*4*: 238 [radula].

[12] In the literature, the date of description is usually given as 1830 or 1839. For a discussion, see BOSS & MERRILL (1987).

Type measurements: *Solarium architae*: SD = ca. 7.3 [after O.G. COSTA]. *Solarium soverbii* (larger of 2 syntypes in BMNH): SD = 6.2, H = 2.3, PD = 0.7, Tw = 3 1/8, UD = 2.1.

Material studied: eastern Atlantic form: 92 specimens (BMNH, FMNH, RNHL, USNM); including 2 syntypes of *S. soverbii* (BMNH 1847.9.10.24-25); western Atlantic form: 147 specimens (DMNH, FMNM, RNHL, USNM, Coll. VON COSEL).

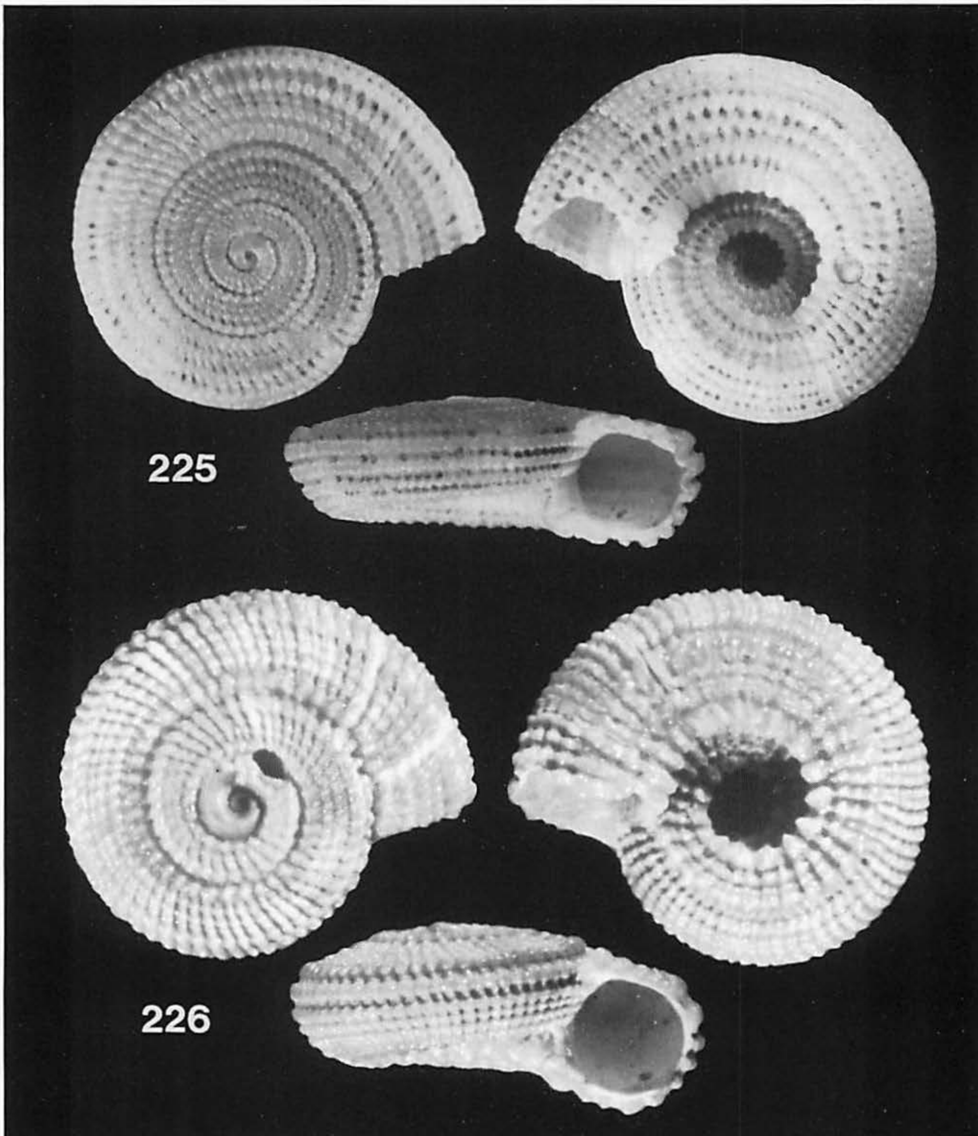


Fig. 225: *Pseudotorinia architae* (O.G. COSTA, 1841); larger of two syntypes of *Solarium soverbii* HANLEY, 1862; BMNH 1847.9.10.24; SD = 6.2. Fig. 226: *Pseudotorinia* sp. aff. *architae* (O.G. COSTA, 1841); specimen from Baja California; USNM 151961; SD = 3.9.

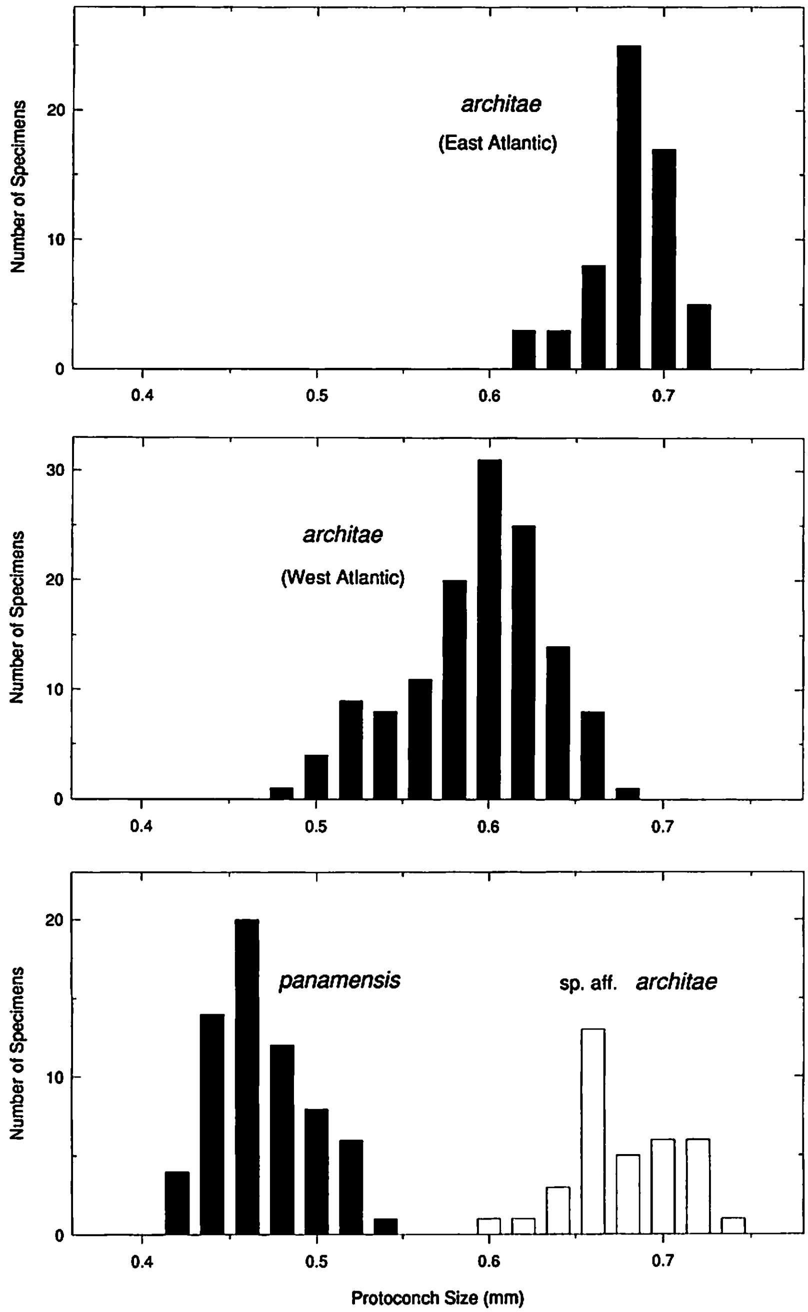


Fig. 227. Histograms of measured protoconch size. *Pseudotorinia architae* from East Atlantic (n = 61, $\bar{x}$ = 0.68, sd = 0.02), *Pt. architae* from West Atlantic (n = 132, $\bar{x}$ = 0.59, sd = 0.04), *Pt. panamensis* (n = 65, $\bar{x}$ = 0.47, sd = 0.03), and *Pt.* sp. aff. *architae* (n = 36, $\bar{x}$ = 0.68, sd = 0.03).

Figs. 228–230. SEM photomicrographs of protoconch and early teleoconch whorls. Fig. 228: *Pseudotorinia architae* (USNM 798065; western Atlantic). Fig. 229: *Pt.* sp. aff. *architae* (USNM 209285; Baja California Sur, Mexico). Fig. 230: *Pt. panamensis* (USNM 211411; Baja California Sur). Scale bar = 200 µm, for all figures.

Type material of *S. architae* destroyed during World War II (Zool. Mus. Univ. Naples; MELONE, in litt.).

Diagnosis – eastern Atlantic form [see also description of '*architae*-group']:

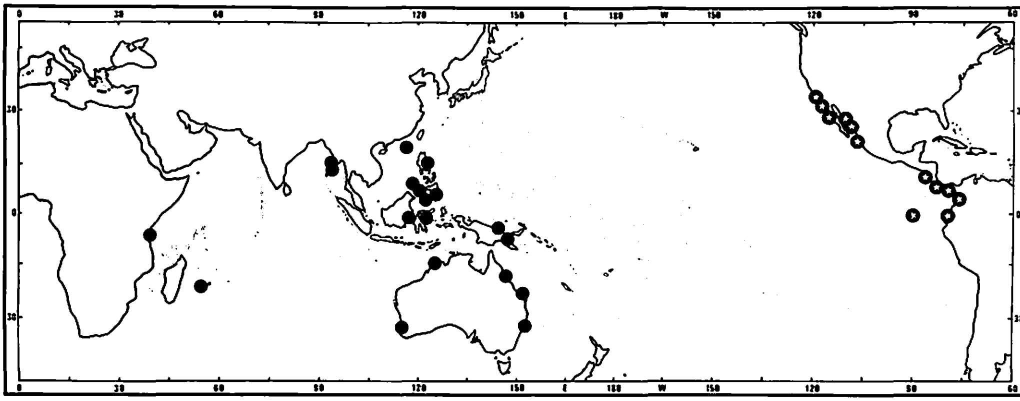
Teleoconch (Fig.225): very small to small (SD usually 4–8 at 2 5/8 to 3 1/2 whorls), ± coin-shaped with strongly angular base, widely open umbilicus (UD ca. 30% of SD), and sculpture of granose spiral ribs; 2 midribs; infraperipheral rib relatively prominent; on early whorls 1, later 2, spiral ribs between basal keel and umbilical crenae; umbilical side of columellar wall without spiral ribs. Coloration: tan, with lighter umbilical crenae. – Protoconch (see Fig: 227): small (0.62–0.72, $\bar{x}$ = 0.68), weakly heterostrophic. – Operculum as described for genus. – Radula: five-toothed taenioglossate (2–1–2); rachidian tooth stronger than marginal teeth with subtriangular median cusp flanked by 13–15 smaller, blunt cusps; marginal teeth longer, curved and forked with ca. 6 tapering cusps [see, e.g., MELONE & TAVIANI, 1985: 170, figs.36–37]. – Anatomy: not known.

Diagnosis – western Atlantic form [see also description of '*architae*-group']:

Teleoconch: very small to small (SD usually 3–6 at 2 1/4 to 3 1/2 whorls), trapezoid in cross-section, with upper side and peripheral base somewhat convex, widely open umbilicus (UD ca. 30% of SD), and sculpture of granose spiral ribs; 2 midribs; infraperipheral rib relatively prominent; on early whorls 1, later 2, spiral ribs between basal keel and umbilical crenae; umbilical side of columellar wall without spiral ribs. Coloration: yellowish, with lighter umbilical crenae. – Protoconch (see Fig: 227): very small to small (0.48–0.68, $\bar{x}$ = 0.59), weakly heterostrophic. – Operculum as described for genus. – Radula and Anatomy: not known.

Discussion:

The typical *Pseudotorinia architae* of Mediterranean and eastern Atlantic waters has a much more angular shell (Fig.225) and a larger protoconch (Fig.227) than the western



● *concava* ○ sp. aff. *architae*

Fig. 231. Geographical distribution of *Pseudotorinia concava* and *Pt.* sp. aff. *architae*.

Atlantic form of this complex. MERRILL (1970a: 94, unpubl.) named the western Atlantic form as a subspecies; this name is not available for nomenclatural purposes. The relationship between the two Atlantic forms is not clear. They probably represent two distinct species; the presence of a pair of similar, sympatric forms in the eastern Pacific (*Pt. panamensis* and *Pt.* aff. *architae*; see below) indicates this.

Pseudotorinia panamensis (BARTSCH, 1918)
Figs.227, 230, 232, 233

*1918 *Heliacus panamensis* BARTSCH, Proc. U.S. natl. Mus., *54*(2250): 573, pl.88 figs.6–8.
1944 *Heliacus panamensis*, – M. SMITH, Panam. mar. shells: 15, fig.163 [after BARTSCH].
1948 *Torinia panamensis*, – BAYER, Zool. Verh., *4*: 30.
1971 *Heliacus architae*, – KEEN, Sea shells trop. w. Amer. (2nd ed.): 389, fig.427 [after BARTSCH; non *Solarium architae* O.G. COSTA, 1841].
1974 *Heliacus architae*, – ABBOTT, Amer. seashells (2nd ed.): 99.
1976 *Heliacus architae panamensis*, – ROBERTSON, 1976a, Bull. Amer. malac. Union, *1975*: 51.

Type measurements (holotype): SD = 3.7, H = 1.6, PD = 0.52, Tw = 2 5/8–, UD = 1.0.

Type locality: "Punta Paitilla, near Panama City, Panama, in siftings from sand and worm burrows."

Material studied: 113 specimens (AMNH, LACM, USNM); including holotype (USNM 216838).

Etymology: *panamensis-e* [adjective]; derived from the geographical name Panama.

Diagnosis [see also description of '*architae*-group']:

Teleoconch: very small (SD usually 2–4 at 1 7/8 to 3 whorls), roundish lens-shaped with upper side and peripheral base convex, widely open umbilicus (UD ca. 34% of SD), and sculpture of granose spiral ribs; subsutural rib relatively wide, coarsely

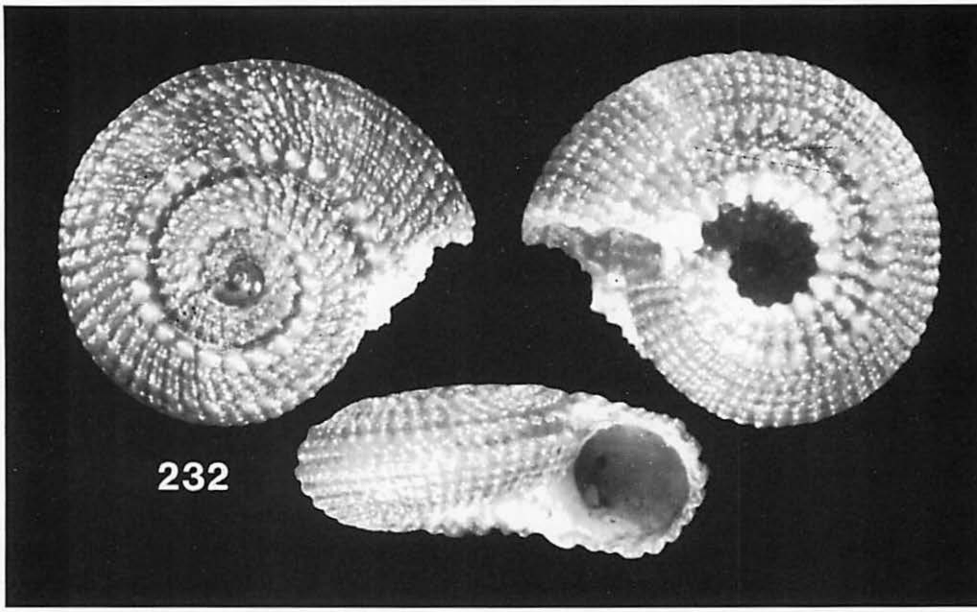


Fig. 232. *Pseudotorinia panamensis* (Bartsch, 1918); holotype of *Heliacus panamensis*; Panama; USNM 216838; SD = 3.7.

sculptured; on early whorls 1, later 2, midribs; infraperipheral rib prominent; on early whorls 1, later 2, spiral ribs between basal keel and umbilical crenae; umbilical side of columellar wall without spiral ribs. Coloration: tan to dark reddish brown. - Protoconch (see Figs. 227, 230): very small (0.42–0.54, $\bar{x}$ = 0.47), almost planispiral. - Operculum as described for genus. - Radula and Anatomy: not known.

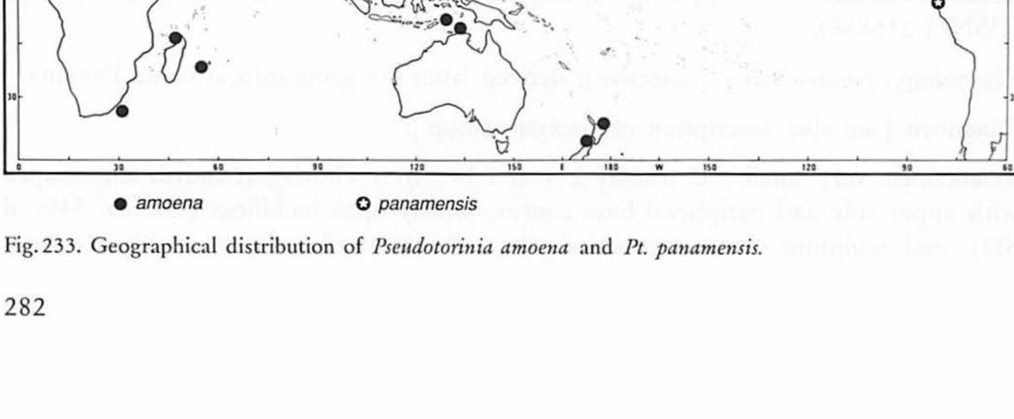


Fig. 233. Geographical distribution of *Pseudotorinia amoena* and *Pt. panamensis.*

Geographical distribution (Fig.233): Eastern Pacific (Baja California and Gulf of California to Ecuador).

Habitat: Upper sublittoral (depth records between 13 and 65 m), live records from 48 m.

Discussion:

Pseudotorinia panamensis is very similar to the Atlantic forms of this complex, especially to the western Atlantic representative, from which it differs only in shell coloration and protoconch size (see Fig.227). MERRILL (1970a: 98) and ROBERTSON (1976a: 51) therefore assigned it the status of a subspecies of *Pt. architae*; KEEN (1971: 389) and ABBOTT (1974: 99) synonymized the two nominal species. However, in the eastern Pacific, an additional, sympatric form (see below) occurs that can always be distinguished from *Pt. panamensis* and that seems to be even closer to the Atlantic forms. Because of this and the uncertain status of the Atlantic "forms," the name *Pt. panamensis* is here retained.

Pseudotorinia sp. aff. _architae_ (O.G. COSTA, 1841)
Fig.226, 227, 229, 231

Measurements (figured specimen): SD = 3.9, H = 1.8, PD = 0.66, Tw = 2 3/8, UD = 1.2 [USNM 151961].

Material studied: 47 specimens (AMNH, LACM, USNM).

Diagnosis [see also description of '*architae*-group']:

Teleoconch: very small to small (SD usually 3-8.8 at 2 1/10 to 3 5/8 whorls), coin-shaped with peripheral base convex, widely open umbilicus (UD ca. 28% of SD), and sculpture of granose spiral ribs; on early whorls 1, later 2, midribs; larger specimens with additional spiral threads; 1-2 spiral ribs between basal keel and umbilical crenae; umbilical side of columellar wall without spiral ribs. Coloration: tan to reddish-brown. - Protoconch (see Figs.227, 229): small (0.60-0.74, $\bar{x}$ = 0.68), heterostrophic. - Operculum: as described for genus. - Radula and Anatomy: not known.

Geographical distribution (Fig.231): Eastern Pacific (Southern California to Ecuador, Galapagos Islands).

Habitat: Sublittoral (depth records between 17 and 201 m), live records from 91-201 m; sand and gravel substrates.

Discussion:

This form has a much larger protoconch (see Figs.227, 229) than the sympatric *Pseudotorinia panamensis* (see above, Fig.230). The teleoconch shape and the protoconch characters agree with those of the eastern Atlantic form of *Pt. architae* (above).

Pseudotorinia amoena (Murdoch & Suter, 1906)

Figs.233, 234, 235, 237

*1906 *Omalaxis amoena* Murdoch & Suter, Trans. Proc. N. Zeal. Inst., *38*(1905): 293, pl.24 figs.30-32.
1911 *Heliacus amoenus*, - Iredale, 1911a, Proc. malac. Soc. Lond., *9*(4): 257.
1913-1915 *Omalaxis amoena*, - Suter, Man. N. Zeal. Moll.: 318, pl.15 [1915] figs.21a-b.
1915 *Heliacus amoenus*, - Iredale, Trans. Proc. N. Zeal. Inst., *47*: 461.
*1922 *Torinia elegantula* Yokoyama, J. Coll. Sci., Tokyo Imp. Univ., *44*(1): 78, pl.4 fig.2 [Pleistocene].
1926 *Heliacus amoenus*, - Finlay, Trans. Proc. N. Zeal. Inst., *57*: 401.

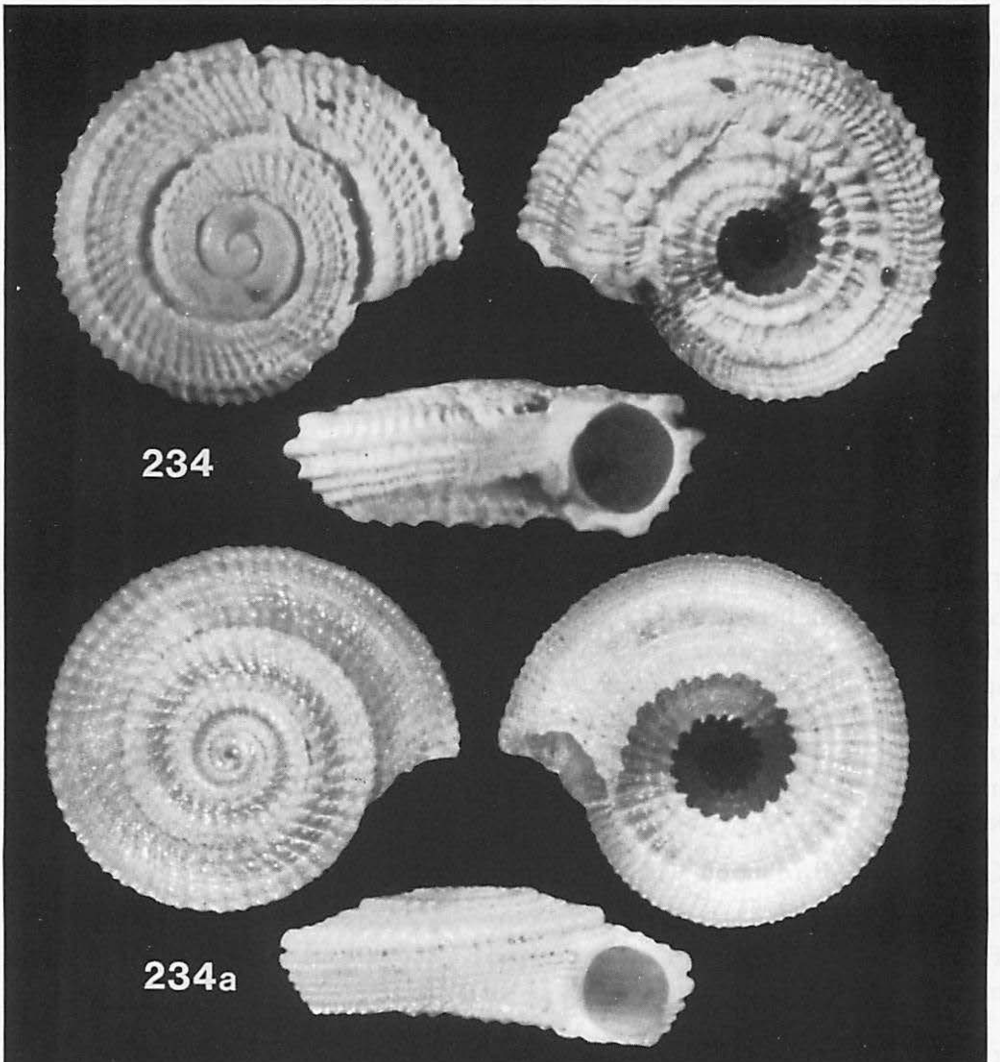


Fig. 234. *Pseudotorinia amoena* (Murdoch & Suter, 1906); holotype of *Omalaxis amoena*; New Zealand; NMNZ M.1680; SD = 3.0. Fig. 234a: *Pseudotorinia concava* (Thiele, 1925); holotype of *Torinia concava*; East Africa; MNHU 101911; SD = 3.7.

1930 *Awarua amoena*, - MESTAYER, Trans. Proc. N. Zeal. Inst., *61*: 145.

1936 *Awarua amoena*, - IREDALE, Rec. Austr. Mus., *19*(5): 326.

1939 *Mangonuia (Awarua) amoena*, - WENZ, Handb. Paläozool., *6*(3): 668, fig.1903 [after MURDOCH & SUTER].

1948 *Torinia amoena*, - BAYER, Zool. Verh., *4*: 5.

1977 *Heliacus (Awarua) amoenus*, - GARRARD, Rec. Austr. Mus., *31*(13): 551, pl.2 figs.16-18.

1979 *Mangonuia amoena*, - POWELL, N. Zeal. Moll.: 248, figs.57(3-4).

1985 *Pseudotorinia amoena*, - BIELER, 1985b, Arch. Moll., *116*(1/3): 93, pl.4 fig.12 [holotype].

Type measurements: Holotype of *Omalaxis amoena*: SD = 3.0, H = 1.3, PD = 0.5, Tw = 2 3/8, UD = 1.1. Holotype of *Torinia elegantula*: SD = 3.8, H = 1.5, PD = 0.6, Tw = 2 3/4+, UD = 1.4.

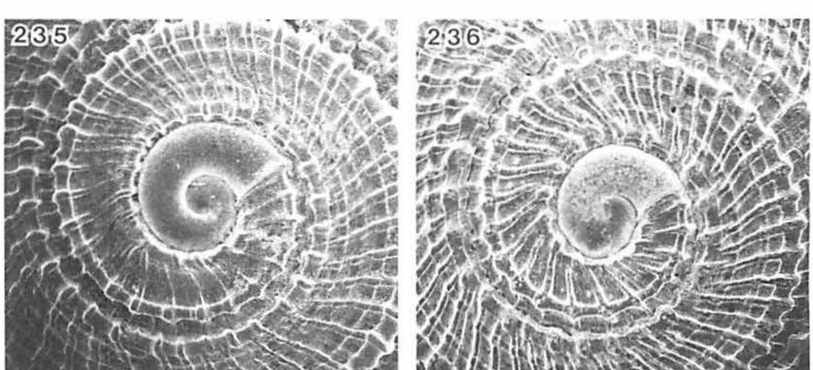
Type localities: *O. amoena*: "dredged by CAPTAIN J. BOLLONS, of the Government Steamer 'HINEMOA', in 37 fathoms [68 m], off Cuvier Island, north by west" [MURDOCH & SUTER, 1906: 303; New Zealand]. *T. elegantula*: "Shito" [Pleistocene; Japan].

Material studied: 106 specimens (AMS, ANSP, BMNH, FMNH, LACM, MCZ, NMP, NMNZ, NMW, UMT, USNM); including holotype of *O. amoena* (NMNZ M.1680) and holotype of *T. elegantula* (UMT CM20972).

Etymology: *amoenus-a-um* [adjective]; Latin: charming, pleasant.

Diagnosis [see also description of '*architae*-group']:

Teleoconch: very small (SD usually 2.5-5 at 2 to 3 1/4 whorls), trapezoid in cross-section, with upper side weakly convex, inner part of base strongly concave, very wide umbilicus (UD ca. 40% of SD), and sculpture of granose spiral ribs; subsutural rib prominent, stronger than midribs; on early whorls 2, later 3, ± fine midribs, crossed by relatively strong axial ribs; concave area of base often coarsely nodose, with 1-2 spiral ribs between basal keel and umbilical crenae; umbilical side



Figs. 235, 236. SEM photomicrographs of protoconch and early teleoconch whorls. Fig. 235: *Pseudotorinia amoena* (USNM 229664; N. of Corregidor Island, Philippines). Fig. 236: *Pt. conacava* (USNM 277633; W. Samar, Philippines). Scale bar = 200 μm, for both figures.

of columellar wall without spiral ribs. Coloration: white to yellowish, sometimes with irregular, somewhat darker flames. - Protoconch (see Figs.235, 237): very small to small (0.50-0.70, $\bar{x}$ = 0.57), weakly heterostrophic. - Operculum: as described for genus. - Radula and Anatomy: not known.

Geographical distribution (Fig.233): Indian Ocean and western Pacific.

Habitat: Sublittoral (depth records between 20 and 285 m), live records from 68-80 m; mud, sand and coral rubble substrates.

Discussion:

Pseudotorinia amoena has a wide geographical distribution in the Indo-Pacific. It is without doubt closely related to the Atlantic/eastern Pacific *architae/panamensis* complex (see above), from which it differs by a less heterostrophic protoconch and a more concave inner basal area with less regular sculpture. In *Pt. concava* (see below) the teleoconch sculpture is finer, the protoconch smaller (see Fig.237), and the umbilical side of the columellar wall usually bears one or two spiral threads or ribs.

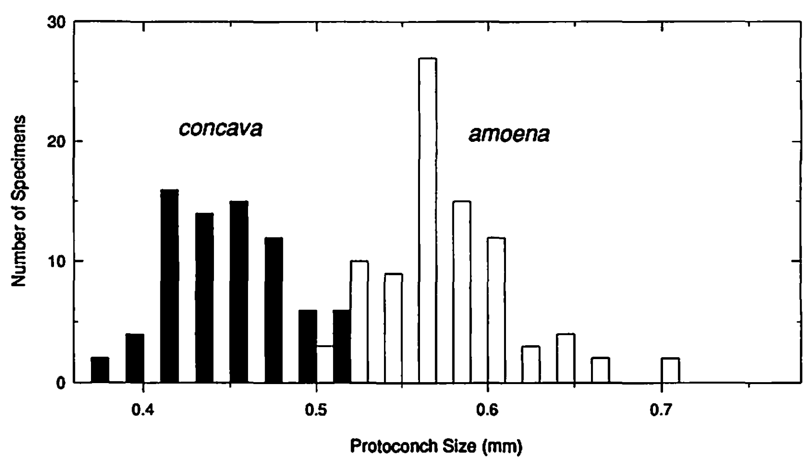


Fig. 237. Histograms of measured protoconch size. *Pseudotorinia concava* (n = 75, $\bar{x}$ = 0.45, sd = 0.03)., and *Pt. amoena* (n = 87, $\bar{x}$ = 0.57, sd = 0.04).

Pseudotorinia concava (Thiele, 1925)
Figs.231, 234a, 236, 237

*1925 *Torinia concava* Thiele, 1925a, Wiss. Ergeb. dtsch. Tiefsee-Exped. Valdivia, *17*(2): 115 [81], 302 [268], pl.21 [9] figs.4-5.
1948 *Torinia concava*, - Bayer, Zool. Verh., *4*: 10.
1963 *Torinia concava*, - Barnard, 1963b, Ann. S. Afr. Mus., *47*(1): 163.
1977 *Heliacus (Torinista) concavus*, - Garrard, Rec. Austr. Mus., *31*(13): 542, pl.4 figs.16-18.

Type measurements (holotype): SD = 3.7, H = 1.5, PD = 0.42, Tw = 3 1/4, UD = 1.5.

Type locality: off Dar es Salaam, Tanzania (5°55.8' S, 39°1.2' E), 50 m ['VALDIVIA' Sta. 244].

Material studied: 101 specimens (AMS, ANSP, BMNH, LACM, MNHNP, MNHU, USNM); including holotype (MNHU 101911).

Etymology: *concavus-a-um* [adjective]; Latin: concave, arched.

Diagnosis [see also description of '*architae*-group']:

Teleoconch: very small (SD usually 2–3.7 at 2 to 3 1/4 whorls), coin-shaped with weakly convex upper side and slightly rounded periphery, widely open umbilicus (UD ca. 32% of SD), and sculpture of often finely granose spiral and axial ribs; subsutural rib prominent, usually 3 midribs, crossed by axial ribs; infraperipheral rib usually somewhat stronger than following 1–3 spiral ribs; 2–3 more or less fine spiral ribs between basal keel and finely granulated umbilical crenae; umbilical side of columellar wall with 1–2 spiral threads or fine, granulated ribs. Coloration: yellowish-white to tan. – Protoconch (see Figs.236, 237): very small (0.38–0.52, $\bar{x}$ = 0.45), paucispiral, almost planispiral. – Operculum as described for genus. – Radula and Anatomy: not known.

Geographical distribution (Fig.231): Indian Ocean and western Pacific.

Habitat: Sublittoral (depth records between 13 and 313 m), live records from 247 m.

Discussion:

Pseudotorinia concava differs from the other members of the *architae*-group by its small, paucispiral protoconch (see Fig.236, 237) and the usually distinctly developed spiral threads or ribs on the umbilical side of the columellar wall. In addition, most *Pt. concava* specimens are sculptured with numerous axial and spiral ribs that are much finer than those seen in other forms.

Pseudotorinia gemmulata-group

The *Pseudotorinia gemmulata*-group, named after its best-known member, *Pt. gemmulata* (THIELE, 1925), is a complex of several Recent and fossil forms of *Pseudotorinia* which share a rounded, convex base, and which differ from each other mainly by protoconch characters. Several nominal species have been described for the Indo-Pacific and Atlantic and their relationships are not clear. At present, the preliminary grouping of the Indo-Pacific forms has to be based entirely on shell characters, as material suitable for anatomical or radular studies has not yet become available.

Description (*Pseudotorinia gemmulata*-group):

Teleoconch: very small to small, diameter of specimens in collections usually 2–6.5, rarely over 4 whorls. Shape: depressed lens-shaped with prominent peripheral keel, moderately wide umbilicus (UD ca. 19–27% of SD). Sculpture (consisting of beaded or granose spiral ribs): Upper side: SSR strong, with sculpture like MR; 2, rarely 3, MR (often weak on first whorl), with granules usually flattened, often plate-like; Periphery: UPR strong, prominent, with sculpture like MR; prominent LPR forming peripheral keel (upper point of whorl attachment here); IPR hardly stronger than following 3 narrow spiral ribs; 3 wider spiral ribs surrounding umbilicus, of which innermost (UC) broadest and with ± coarse granules; umbilical side of columellar wall usually smooth except for axial growth lines, rarely with 1 spiral thread. Coloration: whitish to yellowish, with lighter peripheral keel and umbilical crenae. - Protoconch (see Fig.244): very small to medium-sized (0.42–0.98), almost planispiral to weakly heterostrophic; without anal keel.

Pseudotorinia gemmulata (THIELE, 1925)

Figs.238–240, 244, 245

*1925 *Torinia gemmulata* THIELE, 1925a, Wiss. Ergeb. dtsch. Tiefsee-Exped. VALDIVIA, *17*(2): 114 [80], pl.21 [9] figs.2–3.
*1925 *Torinia aequatorialis* THIELE, 1925a, Wiss. Ergeb. dtsch. Tiefsee-Exped. VALDIVIA, *17*(2): 302 [268], pl.21 [9] figs.8–9.
1948 *Torinia aequatorialis*, - BAYER, Zool. Verh., *4*: 4.
1948 *Torinia gemmulata*, - BAYER, Zool. Verh, *4*: 19.
1985 *Pseudotorinia gemmulata*, - BIELER, 1985b, Arch. Moll., *116*(1/3): 92.

Type measurements: Lectotype of *Torinia gemmulata* [here designated]: SD = 3.6, H = 1.7, PD = 0.56, Tw = 2 3/4+, UD = 0.5. Lectotype of *Torinia aequatorialis* [here designated]: SD = 4.0, H = 1.8, PD = 0.52, Tw = 3–, UD = 0.75.

Type localities: *T. gemmulata*: off Dar es Salaam, Tanzania (5°55.8' S, 39°1.2' E), 50 m ['VALDIVIA' Sta. 244]; *T. aequatorialis*: "von Padang und von Ost-Borneo" [here restricted: lectotype from Padang, Sumatra].

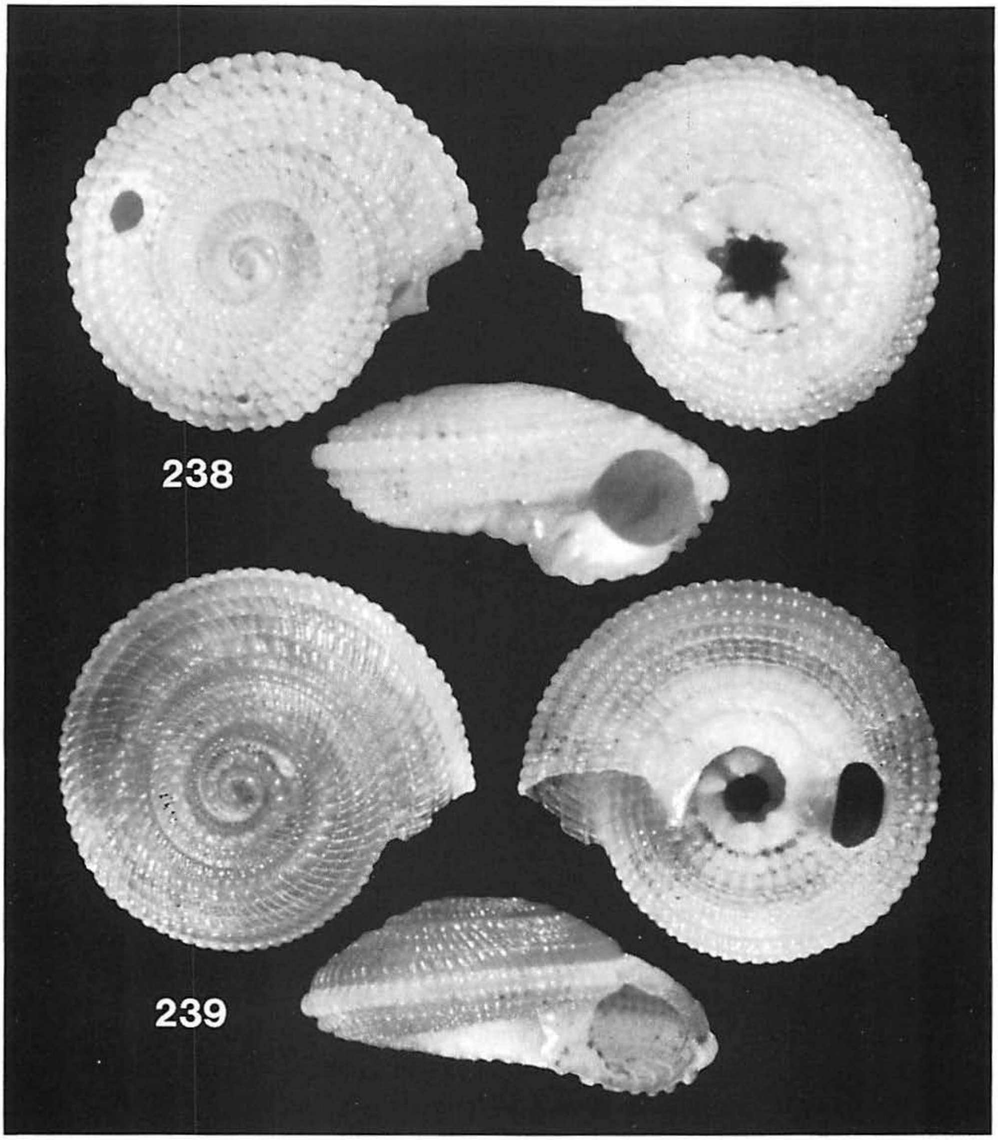
Material studied: 34 specimens (ANSP, BGU, FMNH, MNHNP, MNHU, NMW, USNM); including lectotype of *T. aequatorialis* (MNHU 101908) and lectotype and 5 paralectotypes (3 of which are damaged) of *T. gemmulata* (MNHU unnumbered).

Etymology: *gemmulatus-a-um* [adjective]; Latin: set with small precious stones or pearls.

Diagnosis [see also description of '*gemmulata*-group']:

Teleoconch: very small to small (SD usually 2.8–6.5 at 2 to 4 1/8– whorls), lens-shaped with more or less distinctly convex upper side (juveniles more angular), moderately wide umbilicus (UD ca. 21% of SD), and sculpture of beaded spiral ribs; subsutural rib, 2 midribs (rarely 1 additional spiral thread) and upper peripheral rib usually with flattened, plate-like nodules; infraperipheral rib hardly stronger than following spiral ribs; umbilical side of columellar wall sometimes with 1 relatively weak spiral thread, Coloration: yellowish-white, with lighter peripheral keel and umbilical crenae. - Protoconch (see Fig.240, 244): very small to small (0.52–0.70, $\bar{x}$ = 0.61), paucispiral, almost planispiral.

Geographical distribution (Fig.245): Indo-West Pacific.

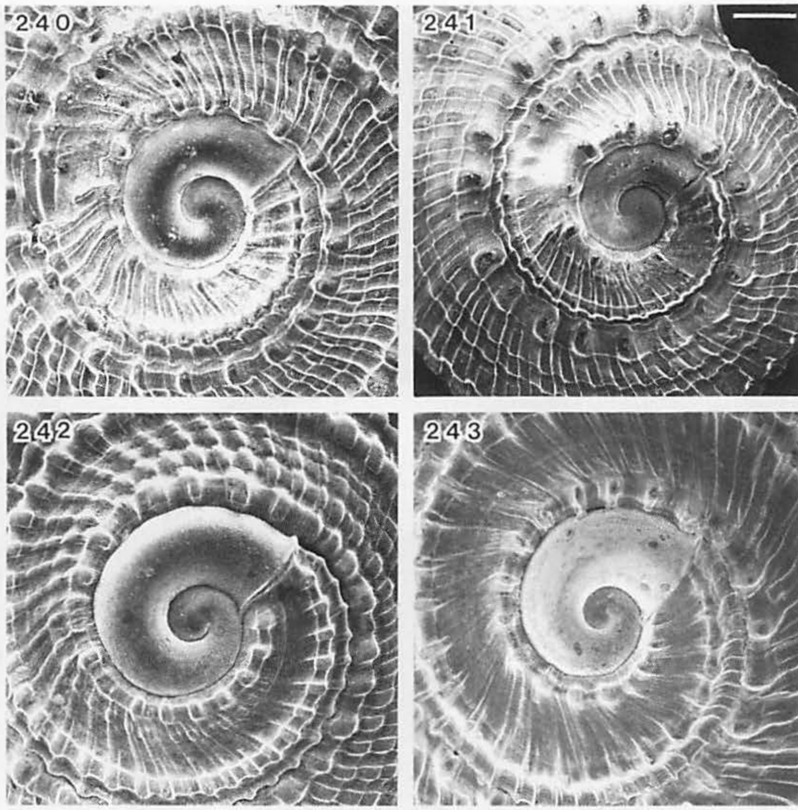


Figs. 238, 239. *Pseudotorinia gemmulata* (THIELE, 1925). Fig. 238: lectotype of *Torinia gemmulata*; East Africa; MNHU unnumbered, SD = 3.6. Fig. 239: lectotype of *Torinia aequatorialis* THIELE, 1925; Sumatra; MNHU 101908; SD = 4.0.

Habitat: Sublittoral to upper bathyal (depth records between 33 and 450 m), live records from throughout that range.

Discussion:

Pseudotorinia gemmulata is the only Indo-Pacific form of this complex in which some specimens show a more or less developed spiral rib on the umbilical side of the columellar wall. *Pseudotorinia* sp.I and sp.II aff. *gemmulata* (see below) are similar,



Figs. 240–243. SEM photomicrographs of protoconch and early teleoconch whorls. Fig. 240: *Pseudotorinia gemmulata* (USNM 280743; W. Samar, Philippines). Fig. 241: *Pt.* sp. I aff. *gemmulata* (ANSP 291434; Phuket Island, Andaman Sea). Fig. 242: *Pt.* sp. II aff. *gemmulata* (USNM 285332; Luzon, Philippines). Fig. 243: *Pt.* sp. III aff. *gemmulata* (USNM 289526; Luzon, Philippines). Scale bar = 200 µm, for all figures.

but differ in protoconch characters (see Figs.240–242, 244) and teleoconch dimensions (at 2 5/8 teleoconch whorls, *Pt. gemmulata* has an average shell diameter of 4.0, *Pt.* sp.I aff. *gemmulata* 2.9, and *Pt.* sp.II aff. *gemmulata* 5.1 mm.

Thiele (1925a: 302) already pointed out the similarity between his two nominal species, *Torinia aequatorialis* and *T. gemmulata*. After comparison of the type material (MNHU), the two are here synonymized. The figured type specimen of *T. aequatorialis* is more inflated (see Fig.239), but falls well within the range of variation of known *Pt. gemmulata* specimens. Garrard (1977: 556) cited a "holotype" for *T. aequatorialis*, but Thiele (1925a: 114, 302) had mentioned "einige Schalen" [a few shells] for both, *T. gemmulata* and *T. aequatorialis*, without designating holotypes. The two specimens originally figured by Thiele (1925a: pl.21 figs.2–3, 8–9; see Figs.238, 239) are here designated as lectotypes. Thiele gave two localities for his *T. gemmulata* material, Padang (Sumatra) and eastern Borneo. Since the lectotype (MNHU 101908) is from Padang, the type locality is here restricted accordingly. It

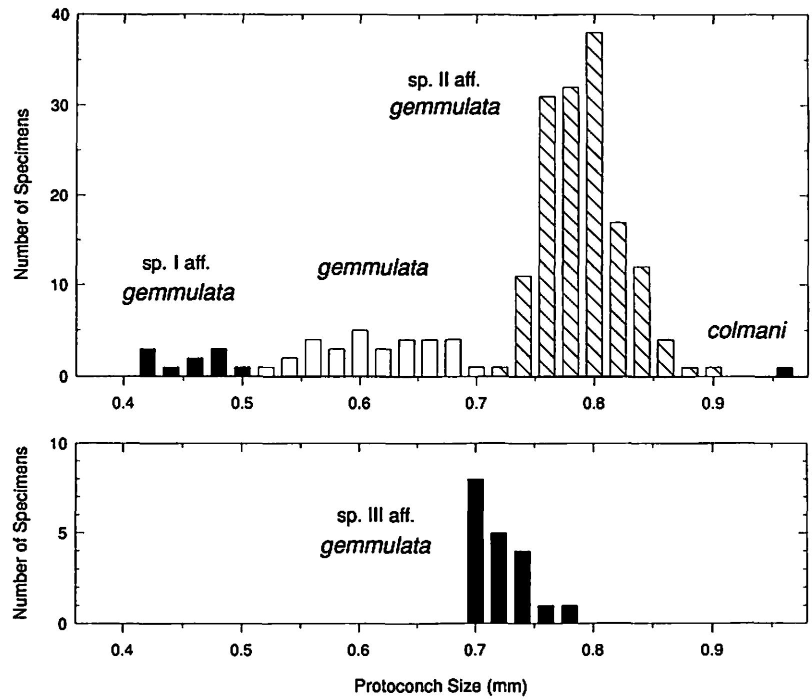


Fig. 244. Histograms of measured protoconch size. *Pseudotorinia gemmulata* (n = 31, x̄ = 0.61, sd = 0.05), *Pt.* sp. I aff. *gemmulata* (n = 10, x̄ = 0.46, sd = 0.03), *Pt.* sp. II aff. *gemmulata* (n = 148, x̄ = 0.79, sd = 0.03), *Pt.* sp. III aff. *gemmulata* (n = 19, x̄ = 0.72, sd = 0.02), and *Pt. colmani* (n = 1).

should be noted that the specimens from Padang were not part of the actual 'VALDIVIA' expedition material (station 188, Padang, did not yield gastropods). The Padang specimens in THIELE's 'VALDIVIA' report (1925a) were sorted from "Schalensand" (shell sand) that he had received from SCHRÖDE (THIELE, 1925a: 3).

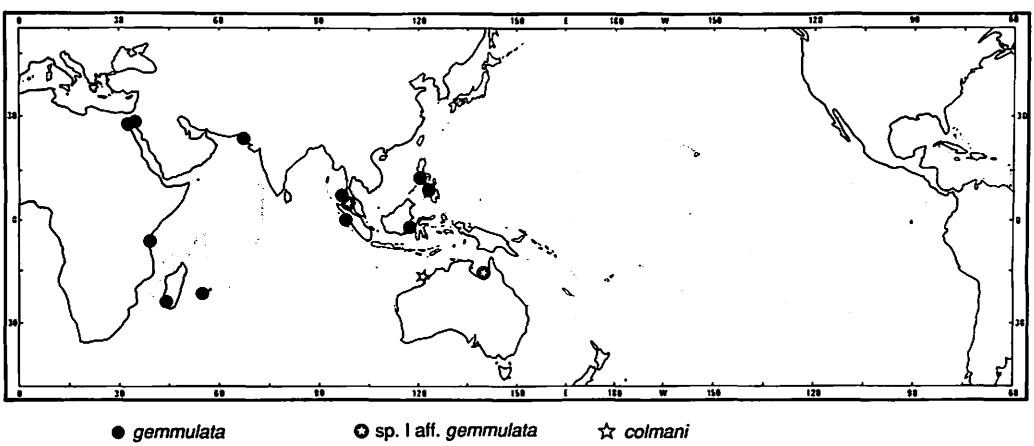


Fig. 245. Geographical distribution of *Pseudotorinia gemmulata*, *Pt.* sp. I aff. *gemmulata* and *Pt. colmani*.

Pseudotorinia sp.I aff. *gemmulata* (THIELE, 1925)
Figs.241, 244–246

1977 *Heliacus (Claraxis) aequatorialis*, - GARRARD, Rec. Austr. Mus., *31*(13): 555, pl.9 figs.13–15 [non *Torinia aequatorialis* THIELE, 1925].

Measurements (figured specimen): SD = 4.0, H = 2.1, PD = 0.42, Tw = 3 3/8, UD = 0.9 [ANSP 291434].

Material studied: 10 specimens (AMS, ANSP).

Diagnosis [see also description of '*gemmulata*-group']:

Teleoconch: very small (SD usually 2–4 at 1 7/8 to 3 3/8 whorls), roundish lens-shaped, moderately wide umbilicus (UD ca. 19% of SD), and sculpture of strong, beaded spiral ribs; 2 midribs; lower peripheral rib not very prominent; infraperipheral rib relatively strong; umbilical side of columellar wall without spiral ribs. Coloration: yellowish white. – Protoconch (see Figs.241, 244): very small (0.42–0.50, $\bar{x}$ = 0.46), paucispiral, almost planispiral.

Geographical destribution (Fig.245): Known from Andaman Sea and Northern Territory, Australia.

Habitat: Upper sublittoral (depths records between 9 and 42 m), no live records.

Discussion:

Pseudotorinia sp.I aff. *gemmulata* is characterized by a very small, paucispiral protoconch (see Figs.241, 244). Shape, size and relative position of peripheral ribs of the teleoconch are reminiscent of the conditions in the fossil genus *Nipteraxis* (see BIELER, 1985b: 94). Based on the few specimens available, it cannot be decided whether this form represents a distinct species within the *gemmulata*-group or just a local form or ecological morph of *Pt. gemmulata*.

"*Heliacus (Claraxis) aequatorialis*" sensu GARRARD (1977: 555) belongs to this form (AMS C.15376; vidi).

Pseudotorinia sp.II aff. *gemmulata* (THIELE, 1925)
Figs.242, 244, 246a

Measurements (figured specimen): SD = 5.0, H = 2.4, PD = 0.8, Tw = 2 7/8, UD = 1.2 [USNM 285332].

Material studied: 142 specimens (USNM).

Diagnosis [see also description of '*gemmulata*-group']:

Teleoconch: very small to small (SD usually 2.8–5.6 at 2 to 3 1/8 whorls), depressed lens-shaped with prominent peripheral keel, moderately wide umbilicus (UD ca. 23% of SD), and sculpture of beaded spiral ribs; 2 midribs, usually with flattened, plate-like

Geographical distribution: Known only from the Philippines.

Habitat: Sublittoral to upper bathyal (depth records between 70 and 525 m), live record from 234 m.

Discussion:

This form differs from the two previously discussed by a considerably larger protoconch with more whorls (see Figs.242, 244). The relationship between this form, *Pt. gemmulata* s.s., and *Pt. colmani* (see below), needs further study.

Pseudotorinia sp.III aff. *gemmulata* (THIELE, 1925)

Figs.243, 244

Measurements (figured specimen): SD = 4.8, H = 2.3, PD = 0.70, Tw = 2 3/4, UD = 1.4 [USNM 839067].

Material studied: 19 specimens (USNM).

Diagnosis [see also description of '*gemmulata*-group']:

Teleoconch: very small (SD usually 3–5 at 2 to 2 3/4 whorls), depressed lens-shaped with prominent peripheral keel, more or less distinctly angular base, widely open umbilicus (UD ca. 27% of SD), and sculpture of beaded spiral ribs; subsutural rib not very prominent; 2, later 3, midribs (upper 2 usually wider); upper peripheral rib strong and prominent; lower peripheral rib strong and forming peripheral keel; infraperipheral keel hardly stronger than following 3 basal ribs; inner (slightly concave) part of base bordered by a wider rib, forming a more or less weak basal keel, and by relatively weak umbilical crenae; larger specimens with one narrow spiral rib between basal keel and umbilical crenae; umbilical crenae weakly separated against umbilical side of columellar wall; the latter without spiral ribs. Coloration: off-white, upper peripheral rib often tan. - Protoconch (see Fig.243, 244): small (0.70–0.78, $\bar{x}$ = 0.72), multispiral, weakly heterostrophic.

Geographical distribution: Known only from the Philippines.

Habitat: Sublittoral to upper bathyal (depth records between 209 and 348 m), live records from 295 m; mud and sand substrates.

Discussion:

This form is especially characterized by the prominent upper peripheral rib of its teleoconch (similar to the conditions seen in *Granosolarium gemmiferum* n.sp., above). Angularity of the shell base is variable; some specimens (USNM 274902) are reminiscent of the shell shape in *Pt. gemmulata* s.s., others are similar to the shape of the western Atlantic form of *Pt. architae* (see above).

It is uncertain whether this form represents a distinct species. The difference in teleoconch shape and sculpture between this and other forms of the group is about as great as that between the two *Pt. architae* forms of the eastern and western Atlantic. The protoconch size range of the specimens is in the upper range of that of *Pt.* sp.II aff. *gemmulata*.

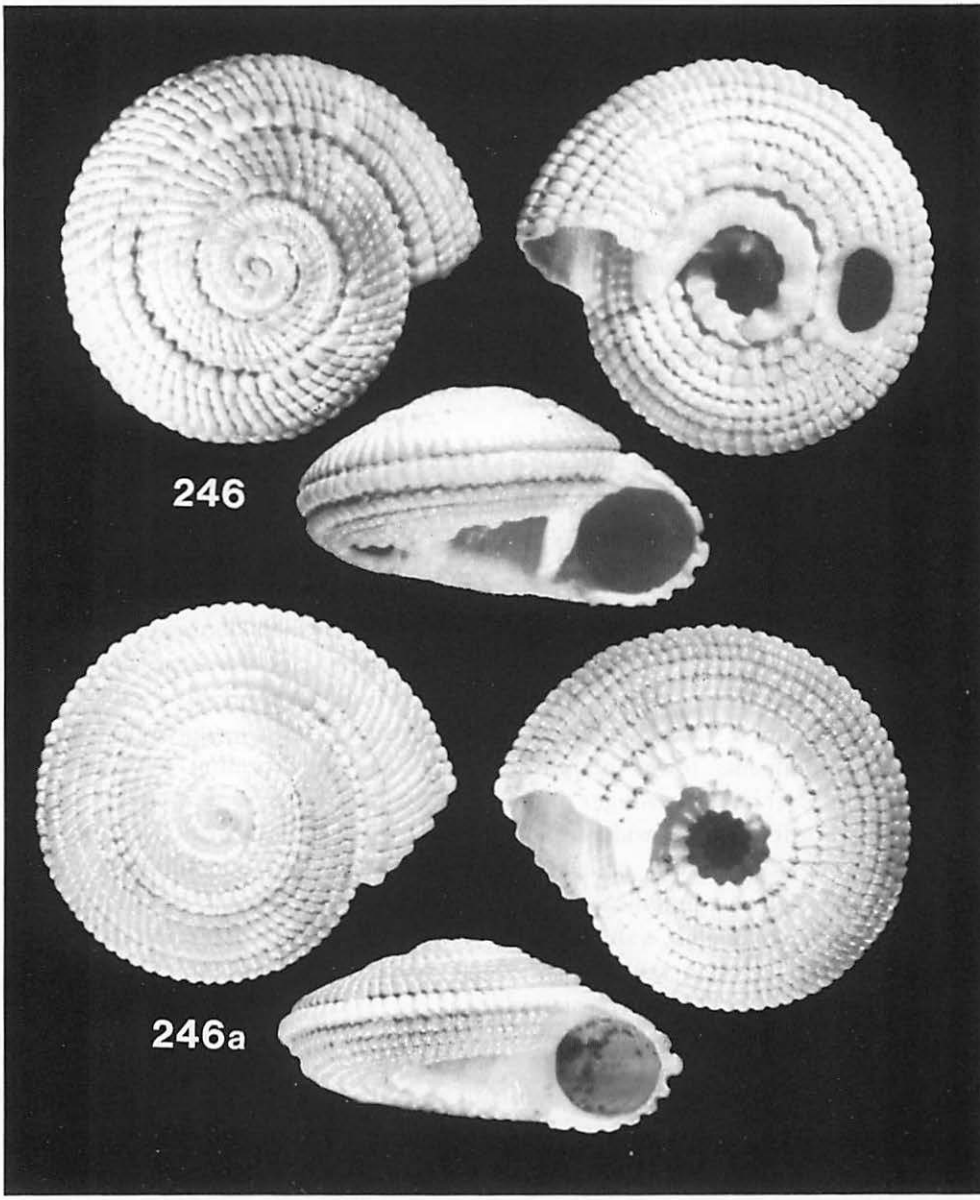


Fig. 246: *Pseudotorinia* sp. I aff. *gemmulata* (THIELE, 1925); specimen from the Andaman Islands; ANSP 291434; SD = 4.0. Fig. 246a: *Pseudotorinia* sp. II aff. *gemmulata* (THIELE, 1925); specimen from the Philippines; USNM 285332; SD = 5.0.

nodules; infraperipheral rib hardly stronger than following spiral ribs; umbilical side of columellar wall without spiral ribs. Coloration: yellowish, with lighter peripheral keel and umbilical crenae. - Protoconch (see Figs.242, 244): small (0.72-0.90, $\bar{x}$ = 0.79), multispiral, weakly heterostrophic.

Pseudotorinia colmani (Garrard, 1977)

Figs.244, 245, 247

*1977 *Heliacus (Claraxis) colmani* Garrard, Rec. Austr. Mus., *31*(13): 556, pl.5 figs.4–6.

Type measurements (holotype): SD = 4.7, H = 1.9, PD = 0.96, Tw = 2 1/2–, UD = 1.2.

Type locality: "370 km W. of Roebuck Bay, western Australia (18°30'S., 118°03'E.), 238 metres."

Material studied: Holotype (AMS C.97687).

Etymology: *colmani* [genitive singular case-ending]; "named for Phillip H. Colman, Dept. of Malacology, Australian Museum, Sydney."

Diagnosis (based on holotype) [see also description of '*gemmulata*-group']:

Teleoconch: very small, depressed lens-shaped with very prominent peripheral keel, widely open umbilicus (UD = 25.5% of SD), and sculpture of granose spiral ribs; 3 midribs (outer one narrow); infraperipheral rib hardly stronger than following basal ribs; umbilical side of columellar wall without spiral ribs. Coloration: white [probably faded]. – Protoconch (see Fig.244): medium-sized (0.98), multispiral, weakly heterostrophic.

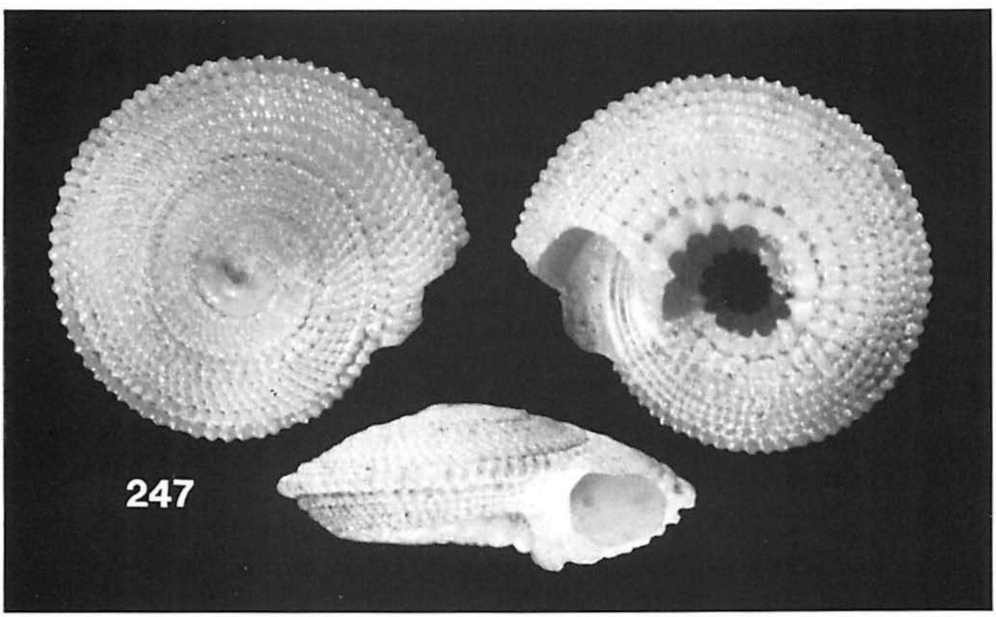


Fig. 247. *Pseudotorinia colmani* (Garrard, 1977); holotype of *Heliacus colmani*; West Australia; AMS C.97687; SD = 4.7.

Geographical distribution (Fig.245): Known only from type locality in Western Australia.

Habitat: Lower sublittoral (238 m) [empty shell].

Discussion:

The holotype specimen of *Pseudotorinia colmani* has an extremely large protoconch for a species of the *gemmulata*-group (see Fig.244). The teleoconch is much more depressed and has a relatively fine sculpture. GARRARD (1977: 557) mentioned six specimens for his new species, but the wide range of protoconch size variation given (".38 - .77") indicates that he was referring to more than one form of this complex.

Pseudotorinia numulus-group

The *Pseudotorinia numulus*-group, named after its best-known member, Indo-Pacific *Pt. numulus* (BARNARD, 1963), is a complex of one Atlantic (*Pt. bullisi* BIELER, MERRILL & BOSS, 1985) and four Indo-Pacific species (three of which are here described as new). The species in this complex share a strongly angular, more or less coin-shaped shell with weak midribs, a very strong lower peripheral rib, a very prominent, coarsely nodulose basal keel, and a wide to extremely wide umbilicus (ca. 32–53%). Some have a general shell shape similar to that of species of *Pseudomalaxis*, but members of that genus differ by having shells with the umbilical crenae directly connected to the basal keel of the foregoing whorl, with only a small part of the columellar wall visible in the umbilicus.

Pseudotorinia numulus (BARNARD, 1963)

Figs.10, 248, 252, 253

*1963 *Heliacus numulus* BARNARD, 1963b, Ann. S. Afr. Mus., *47*(1): 163, fig.31e.
1973 *Heliacus numulus*, - KENSLEY, Sea-shells s. Afr.: 76, fig.254.
1974 *Heliacus numulus*, - BARNARD, Ann. S. Afr. Mus., *47*(5): 711.
1977 *Heliacus numulus*, - KILBURN, Ann. Natal Mus., *23*(1): 186.
1985 *Pseudotorinia numulus*, - BIELER, MERRILL & BOSS, Nautilus, *99*(3): 139, fig.2 [holotype].
1985 *Pseudotorinia numulus*, - BIELER, 1985b, Arch. Moll., *116*(1/3): 92.

Type measurements (holotype): SD = 4.5, H = 1.6, PD = 0.72, Tw = 2 5/8, UD = 1.8. Largest specimen examined: SD = 6.6, H = 2.4, Tw = 3 3/8 [MNHNP without no., Madagascar].

Type locality: "Off Cape Morgan, 77 fathoms" [141 m; east of East London, Cape Province, South Africa; 32°42'S, 28°22'E].

Material studied: 14 specimens (MNHNP, NMP, SAM, USNM); including holotype (SAM A9125).

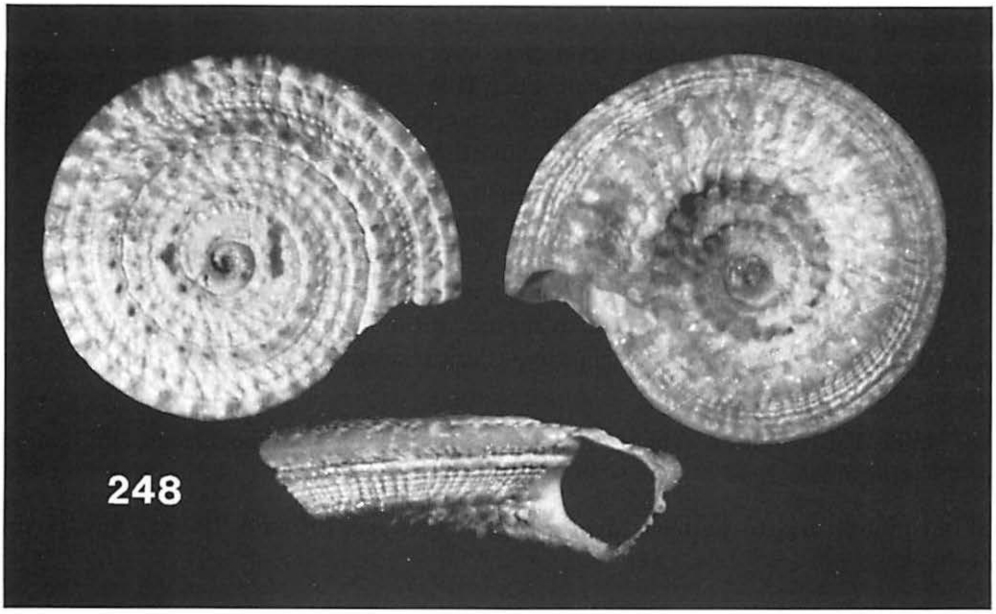


Fig. 248. *Pseudotorinia numulus* (BARNARD, 1963); holotype of *Heliacus numulus*; South Africa; SAM A9125; SD = 4.5.

Etymology: num[m]ulus [noun in apposition]; Latin: small coin. BARNARD's (1963a) spelling is probably a lapsus for *nummulus*. It is here considered an etymological mistake rather then a printer's error and therefore does not justify emendation.

Diagnosis:

Very small to small, coin-shaped shell with upper side of whorls weakly concave, base angular with keel formed by very prominent spiral rib (areas above and below basal keel concave); subsutural rib stronger than upper peripheral rib; midrib-area with weak spiral threads; lower peripheral rib very prominent, forming upper shell keel; infraperipheral rib stronger than following basal ribs; very wide umbilicus with part of oblique columellar wall visible above umbilical crenae, which are sunken into umbilicus; no spiral ribs on umbilical wall. Tan to dark brown. Protoconch diameter 0.70–0.76 mm; weakly heterostrophic, without anal keel.

Description:

Teleoconch: very small to small, diameter of specimens in collections usually 3.0–6.6 at 1 7/8 to 3 3/8 whorls. Shape: coin-shaped with the upper keel stronger (somewhat trapezoid in cross-section); upper side of whorls weakly concave; base angular with keel formed by very prominent spiral rib; area between peripheral and basal keels somewhat concave, inner base concave; umbilicus very wide (UD ca. 45% of SD). Sculpture: Upper side: SSR wide, prominent and coarsely nodulose; MR-area with 1–2 weak spiral threads (if 2, inner one stronger); Periphery: UPR weak on early whorls, later distinct (but always weaker than SSR); very strong LPR forming peripheral (= upper) keel (also serving as upper point of whorl attachment), often with fine subcentral groove on upper side; IPR distinctly developed, stronger than following basal ribs; Base: 2-5 ± distinctly developed spiral ribs below IPR (slightly decreasing in strength towards base), followed by a strong, coarsely nodose rib that forms basal keel; UC sunken into umbilicus, only somewhat overhanging; between basal keel and UC only one ± distinct fine spiral thread in large specimens; umbilical side of columellar wall without spiral ribs. Coloration: tan to dark brown, especially on periphery with ± regular flames. - Protoconch (see Figs.10, 252): small (0.70-0.76, $\bar{x}$ = 0.72), multispiral, weakly heterostrophic, without anal keel; tan to dark brown. - Operculum: as described for genus. - Periostracum, Radula and Anatomy: not known.

Geographical distribution (Fig.253): Known from western Indian Ocean, Philippines and Celebes.

Habitat: Sublittoral to bathyal (depth records between 100 and 990 m), live record from 35-150 m.

Discussion:

For a comparison with the other forms of this group, see discussions under *Pseudotorinia yaroni* and *Pt. sestertius* n.spp. (below).

Pseudotorinia yaroni n.sp.
Figs.249, 252, 253

Type measurements:

	SD	H	PD	Tw	UD	Collection
Holotype	4.5	1.8	0.62	2 7/8	1.7	MZB 10500
Paratype 1	4.5	1.8	0.60	2 7/8	1.5	MZB 10501
Paratype 2	4.2	1.6	0.60	2 3/4	1.6	MZB 10502
Paratype 3	3.7	1.6	0.60	2 3/4-	1.4	MZB 10503
Paratype 4	3.6	1.4	0.60	2 1/2-	1.3	MZB 10504
Paratype 5	4.3	1.8	0.60	2 3/4+	1.6	FMNH 223418
Paratype 6	4.1	1.5	0.60	2 3/4+	1.7	USNM 859458
Paratype 7	3.4	1.3	0.64	2 3/8	1.3	MNHNP unnumbered
Paratype 8	3.5	1.5	0.60	2 5/8	1.2	AMS C.164966
Paratype 9	4.3	1.7	0.64	2 1/4+	1.2	SMF 309210
Paratype 10	4.5	1.9	0.64	3-	1.6	NMP K7449/T700

Type locality: northern central part of the Red Sea (23°50'18" - 23°49'96" N, 36°50'93" - 36°51'59" E), 710-934 m, "pteropod-*Globigerina*-nannooze" (CNR [Italian National Research Council] Cruise MR-79 Sta.40, Cableship 'SALERNUM,' 3-26 March 1979; collector: M. Taviani, Instituto di Geologia Marina, Bologna). Paratypes 1-4 from type locality. Paratypes 5-10 from nearby station MR-79/41 (23°49'32" - 23°49'70" N, 36°49'58" - 36°49'69" E, 722-578 m), other data as above. The heavy dredging equipment for geological sampling used at these stations might in part have recovered

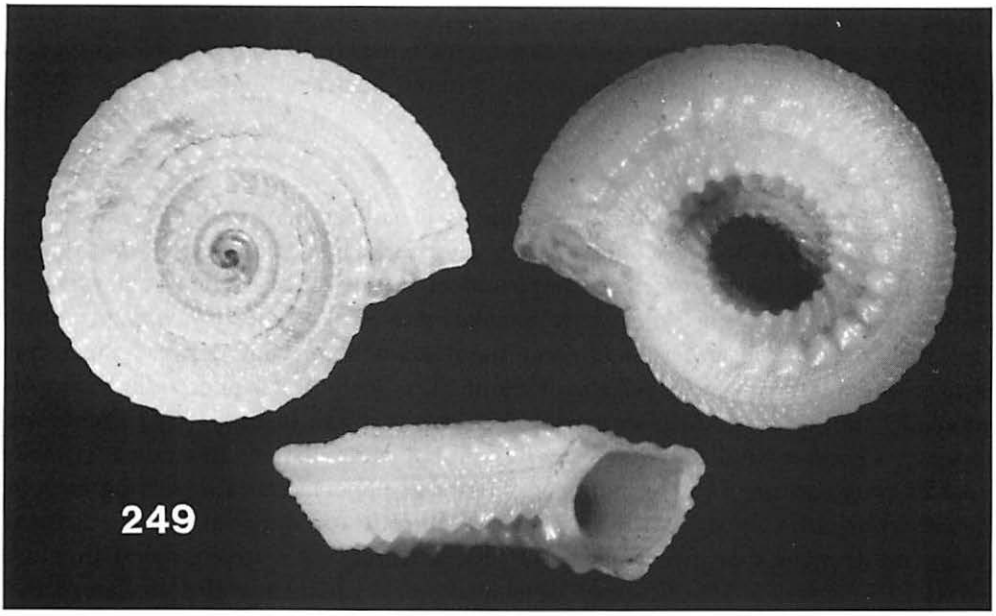


Fig. 249. *Pseudotorinia yaroni* n.sp.; holotype; Red Sea; ZMUB 10500; SD = 4.5.

pre-modern sediments, but not older than ca. 12,000–13,000 years before present (TAVIANI, in litt).

Material studied: 59 specimens and 1 fragment (AMS, FMNH, MNHNP, MZB, USNM), including 11 type specimens as listed above. The majority of the material (50 specimens) was collected during the Italian CNR cruise MR-79 and was made available through the courtesy of Dr. Marco Taviani. The other specimens were collected in the Red Sea during cruises of the German research vessels 'SONNE' (Sta. 02/24, 21°13.20'N, 37°26.00'E, 740 m; and Sta. 02/38, 21°13.80'N, 37°38'E, 836 m) and 'VALDIVIA' (Sta. 29/755, 26°53.76'N, 35°25.14'E, 609 m); voucher material for theses cruises is deposited in SMF.

Etymology: *yaroni* [genitive singular case-ending]. Named in honor of our Israelian colleague Dr. ISAAC ("Jitzchak") YARON (1934–1985), who lost his life in a diving accident before he could complete his dream, a monograph of the molluscan fauna of the Red Sea. Dr. YARON supplied many of the Red Sea data and specimens used in this revision.

Diagnosis:

Very small coin-shaped shell, with apex somewhat elevated, upper side of whorls flat, base angular with keel formed by very prominent spiral rib (area above basal keel somewhat convex, area below concave); subsutural rib stronger than upper peripheral rib; midrib-area with weak spiral threads; lower peripheral rib very prominent, forming upper shell keel; infraperipheral rib stronger than following basal ribs; very wide umbilicus with part of straight columellar wall visible above umbilical crenae, which are sunken into umbilicus; no spiral ribs on umbilical wall. Off-white. Protoconch diameter 0.54–0.66 mm, almost planispiral, without anal keel.

Description:

Teleoconch: very small, diameter of specimens in collections usually 3.1–4.5 (rarely up to 5.1) at 2 1/4 to 2 7/8 (3 1/4+) whorls. Shape: coin-shaped, with upper peripheral keel stronger (somewhat trapezoid in cross-section); apex somewhat elevated, upper side of whorls flat; base angular with keel formed by very prominent spiral rib; area between peripheral and basal keels somewhat convex, inner base concave; umbilicus very wide (UD ca. 40% of SD). Sculpture: Upper side: SSR wide, prominent and nodose; MR-area with 1–2 weak spiral threads (if 2, inner one stronger); Periphery: UPR weak on early whorls, later distinct (but always weaker than SSR); very strong LPR forming peripheral (= upper) keel (also serving as upper point of whorl attachment), with fine subcentral groove on upper side; IPR distinctly developed, stronger than following basal ribs; 1 (rarely 2) ± strong spiral thread at base of LPR; Base: 3–5 ± distinctly developed spiral ribs below IPR, followed by a strong, coarsely nodose rib forming basal keel (often with ± fine groove on umbilical side); UC sunken into umbilicus, somewhat overhanging; 1–2 fine spiral threads between basal keel and UC in large specimens; umbilical side of straight columellar wall with axial growth lines, without spiral ribs. Coloration: translucent off-white, sometimes with weak brown flames and blotches on peripheral ribs. - Protoconch (see Fig.252): very small to small (0.54–0.66, $\bar{x}$ = 0.61), multispiral, almost planispiral, without anal keel; translucent whitish with early whorls brown. - Periostracum, Operculum, Radula and Anatomy: not known.

Geographical distribution (Fig.253): Known only from the Red Sea.

Habitat: Upper bathyal (depth records between 609 and 934 m, soft substrates. No live records.

Discussion:

Pseudotorinia yaroni n.sp. has a considerably smaller protoconch than the other Indo-Pacific species of this complex (see Fig.252). In *Pt. numulus* (see above) the areas between subsutural rib and peripheral keel, and between the basal keel and umbilical crenae are more or less markedly convex, the shell is flat coin-shaped and of dark-brown color, and the protoconch is somewhat more heterostrophic. The shell of *Pt. armillata* n.sp. (see below) has a more elevated apex, the outer basal area is more convex, the coloration is fawn to pinkish brown, and there is a relatively strong spiral rib positioned immediately above the strong rib that forms the basal keel. Atlantic *Pt. bullisi* Bieler, Merrill & Boss, 1985 (1985: 139, fig.1) is similar, but has about eight weak spiral threads between infraperipheral rib and basal keel, and one strong spiral rib between basal keel and umbilical crenae. Juvenile specimens of *Solatisonax rehderi* n.sp. are somewhat similar (see discussion of that species, above).

Pseudotorinia armillata n.sp.

Figs.250, 252, 253

Type measurements:

	SD	H	PD	Tw	UD	Locality	Collection
Holotype	4.8	2.1	0.82	3-	1.6	Réunion	MNHNP unnumbered
Paratype 1	4.6	2.0	0.80	2 7/8-	1.5	Réunion	FMNH 223421
Paratype 2	4.5	1.8	0.78	2 3/4	1.5	Réunion	FMNH 223421
Paratype 3	4.4	1.9	0.80	2 3/4+	1.6	Réunion	WAM 485-91
Paratype 4	2.5	1.1	0.80	1 5/8+	0.8	Réunion	MNHNP unnumbered
Paratype 5	5.0	2.1	0.78	3-	1.5	Réunion	MNHNP unnumbered
Paratype 6	3.9	1.6	0.86	2 1/4	1.2	I. Glorieuses	MNHNP unnumbered
Paratype 7	3.3	1.3	0.84	1 7/8-	ca.1.0	Transkei	NMP C1297/T372

Type locality: Réunion (20°52' S, 55°28' E), 110 m [Cruise "MD32 Réunion" of R/V 'MARION-DUFRESNE' (1982) under the direction of Dr. A. GUILLE; Sta. DC126]. Paratypes 1–4 from type locality. Paratype 5 from Réunion station MD32 Sta. DC128 (20°51' S, 55°36' E), 280–340 m. Paratype 6 from SE Isles Glorieuses, 'BENTHEDI' (1977) Sta. 122 (11°32' S, 47°23'2" E), 615–625 m. Paratype 7 from off Port Grosvenor, Transkei, South Africa (29°57'6" S, 31°26'2" E), 100–115 m; sand, some mud, solitary coral, shells [R/V 'MEIRING-NAUDÉ', August 1981, Sta. D3].

Material studied: 8 type specimens as listed above.

Etymology: *armillatus-a-um* [adjective]; Latin: wearing a bracelet; here referring to the strong spiral thread immediately above the basal keel, a distinguishing character of this species.

Diagnosis:

Very small, angular lens-shaped shell with somewhat elevated apex, upper side of whorls flat, very strong peripheral keel, base angular with keel formed by very prominent spiral rib (area above basal keel convex, below concave); subsutural rib stronger than upper peripheral rib; midrib-area with weak spiral threads; lower peripheral rib very strong, forming upper shell keel; infraperipheral rib about as strong as following basal ribs; one stronger spiral thread immediately above basal keel; widely open umbilicus with large portion of straight columellar wall visible above umbilical crenae, which are sunken into umbilicus; no spiral ribs on umbilical wall. Fawn to pinkish-brown. Protoconch diameter 0.78–0.86 mm, almost planispiral, without anal keel.

Description:

Teleoconch: very small, diameter of specimens in collections 2.5–5.0 at 1 5/8 to 3- whorls. Shape: angular lens-shaped with strong peripheral keel; apex somewhat elevated, upper side of whorls flat, base angular with keel formed by prominent spiral rib; area between peripheral and basal keels convex, inner base concave; umbilicus

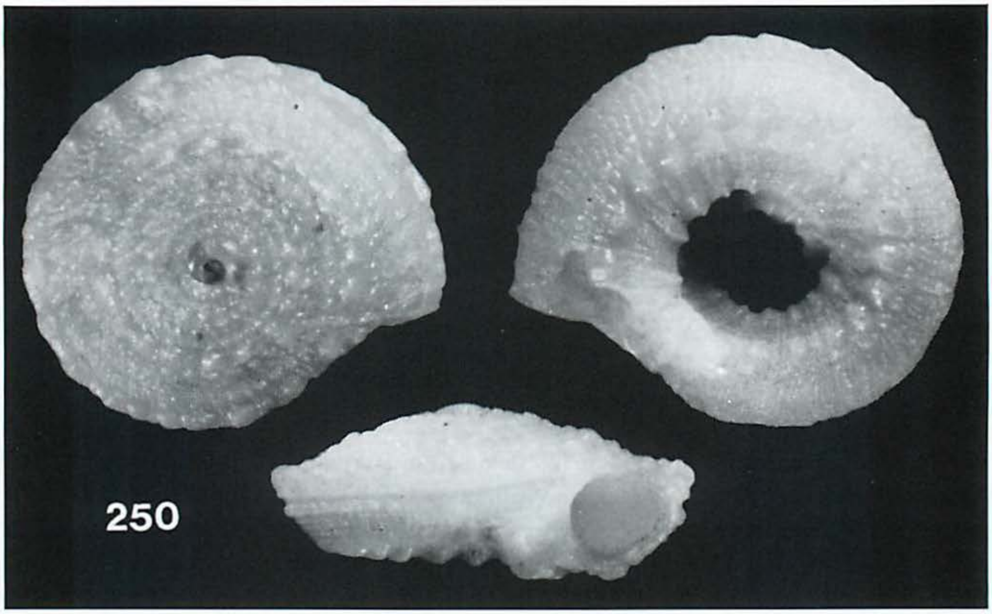


Fig. 250. *Pseudotorinia armillata* n.sp.; holotype; Réunion; MNHNP unnumbered; SD = 4.8.

widely open (UD ca. 32% of SD). Sculpture: Upper side: SSR prominent and nodulose; MR-area with 1–2 weak spiral threads (if 2, inner one stronger); Periphery: UPR weak on early whorls, later distinct (but always somewhat weaker than SSR); sometimes 1 weak spiral thread between UPR and LPR; very strong LPR forming peripheral (= upper) keel (also serving as upper point of whorl attachment); LPR bearing coarse, scaly nodules which sometimes have a fine spiral groove on upper side; 1 (rarely 2) ± strong spiral thread at base of LPR; IPR distinctly developed, stronger than following basal ribs; Base: 2–3 (rarely up to 5) ± distinctly developed spiral ribs of equal strength below IPR, followed by a stronger spiral rib or thread immediately above the coarsely nodose rib that forms basal keel; UC sunken into umbilicus, distinctly overhanging; 1 fine spiral thread between basal keel and UC in large specimens; umbilical side of columellar wall with axial growth lines, without spiral ribs. Coloration: fawn to pinkish-brown, with peripheral nodules lighter. – Protoconch (see Fig.252): small (0.78–0.86, $\bar{x}$ = 0.81), multispiral, almost planispiral, without anal keel; off-white, with early whorls and outer corner next to varix tan. – Periostracum, Operculum, Radula and Anatomy: not known.

Geographical distribution (Fig.253): Known only from the western Indian Ocean (Réunion, Isles Glorieuses and Transkei).

Habitat: Lower sublittoral to upper bathyal (depth records between 100 and 625 m), no live records.

Discussion:

Pseudotorinia armillata n.sp. differs from the other members of the *Pt. numulus*-group mainly by the relatively strong spiral thread immediately above the basal keel and by its larger protoconch (see Fig.252 and discussion under *Pt. yaroni* n.sp., above). *Pseudotorinia armillata* n.sp. and *Pt. numulus* occur sympatrically; specimens of *Pt. numulus* were collected in Réunion in the same sample as was part of the type material of *Pt. armillata* (MNHNP unnumbered).

Pseudotorinia sestertius n.sp.

Fig.251, 253

Type measurements: SD = 3.4, H = 0.9, PD = 0.70, Tw = 2 1/4, UD = ca. 1.8.

Type locality: between Luzon and Mindoro, Philippines (13°32' N, 121°07' E), 130–137 m [R/V 'Coriolis' cruise MUSORSTOM-2, Sta. DR33, 24 November 1980].

Material studied: Holotype (MNHNP unnumbered).

Etymology: *sestertius* [noun in apposition]; Latin: sesterce, small Roman silver coin; here referring to the coin-shaped shell.

Diagnosis [based on holotype]:

Very small coin-shaped shell with upper side of whorls flat, base angular with keel formed by very prominent spiral rib (areas above and below basal keel more or less concave); subsutural rib stronger than upper peripheral rib; midrib-area with numerous ill-defined spiral threads; lower peripheral rib very prominent, forming upper shell keel; infraperipheral rib stronger than following basal ribs; umbilical crenae sunken into extremely wide umbilicus and directly connected to basal keel of previous whorl (no columellar wall visible). Whitish with fawn flames on base. Protoconch diameter 0.70 mm; weakly heterostrophic, without anal keel.

Description [based on holotype]:

Teleoconch: very small, diameter 3.4 at 2 1/4 whorls. Shape: coin-shaped with the upper peripheral keel stronger (somewhat trapezoid in cross-section); upper side of whorl flat; base angular with keel formed by very prominent spiral rib; area between peripheral and basal keels somewhat concave; inner base concave; UC directly connecting to basal keel of previous whorl (therefore no umbilical wall visible); umbilicus extremely wide (UD ca. 53% of SD). Sculpture (appearing very similar on both sides): Upper side: SSR wide, prominent and coarsely nodose; MR-area with numerous ill-defined spiral threads crossed by axial growth lines; Periphery: UPR weak on early whorls, later distinct (but always weaker than SSR); one fine spiral thread between UPR and LPR on body whorl; very strong LPR forming peripheral (= upper) keel, bearing coarse, somewhat scaly nodules; LPR also serving as upper point of whorl attachment; IPR distinctly developed, stronger than following basal ribs; Base: 4–5 ill-defined spiral threads below IPR, followed by a strong, coarsely nodose rib that forms the basal keel; UC sunken into umbilicus and directly connected to basal keel of the previous whorl; ca. 5 ill-defined fine spiral threads between basal

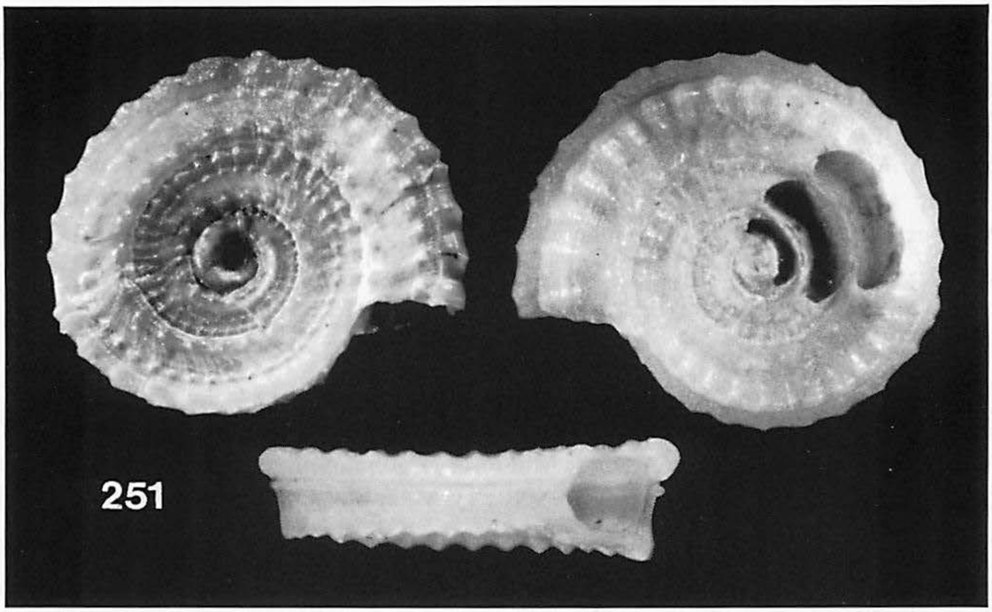


Fig. 251. *Pseudotorinia sestertius* n.sp.; holotype; Philippines; MNHNP unnumbered; SD = 3.4.

keel and UC. Coloration: translucent whitish with fawn flames on base. - Protoconch: small (0.70), multispiral, weakly heterostrophic, without anal keel; white with fawn outer corner next to varix and fawn early whorls. - Periostracum, Operculum, Radula and Anatomy: not known.

Geographical distribution (Fig.253): Known only from type locality in the Philippines.

Habitat: Sublittoral (130-137 m), no live records.

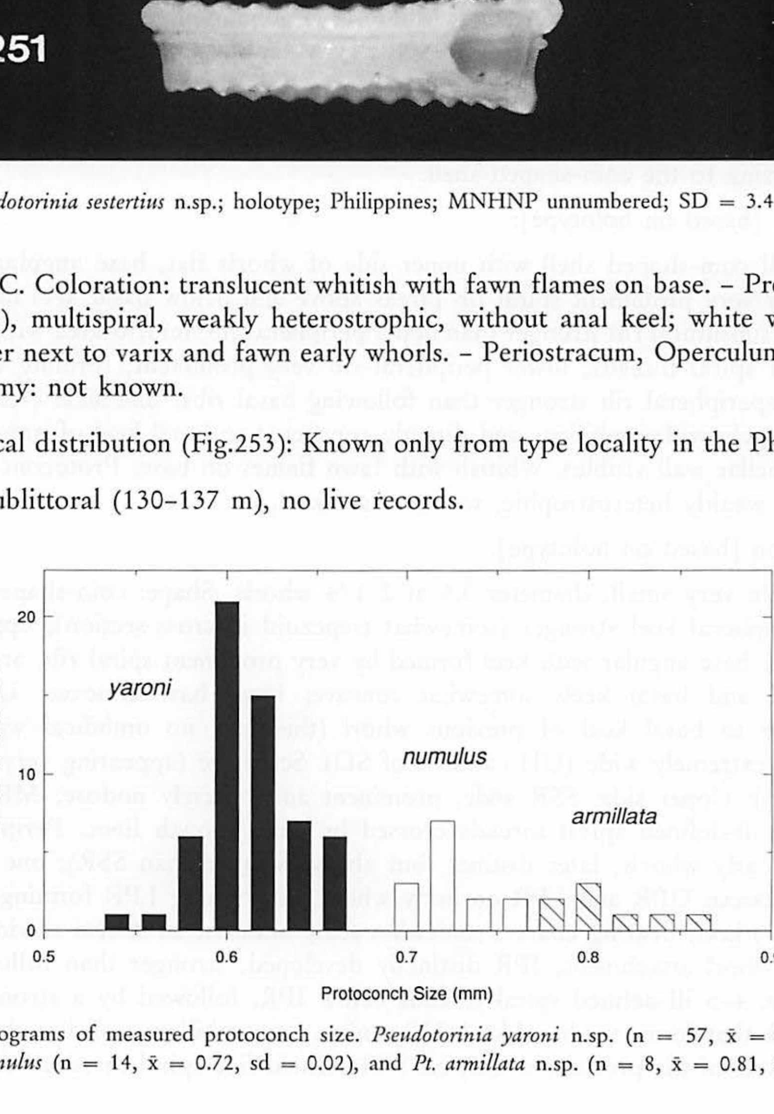


Fig. 252. Histograms of measured protoconch size. *Pseudotorinia yaroni* n.sp. (n = 57, x̄ = 0.61, sd = 0.03), *Pt. numulus* (n = 14, x̄ = 0.72, sd = 0.02), and *Pt. armillata* n.sp. (n = 8, x̄ = 0.81, sd = 0.03).

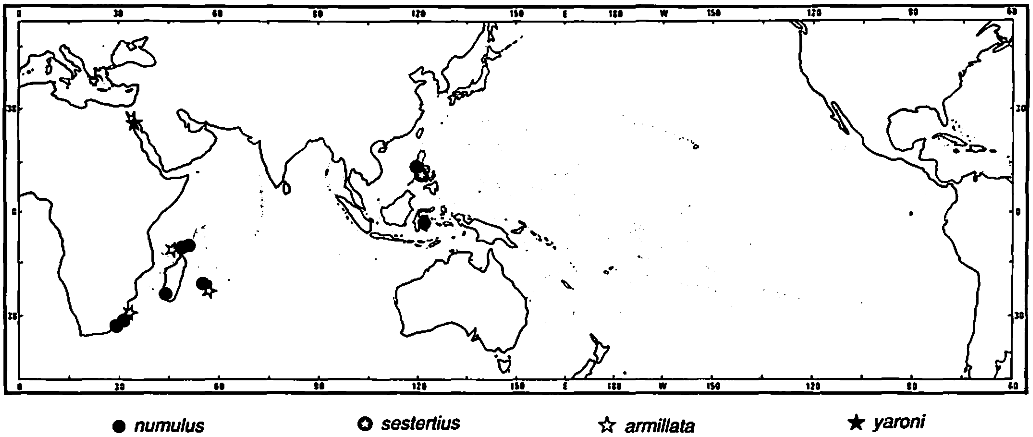


Fig. 253. Geographical distribution of *Pseudotorinia numulus*, *Pt. sestertius* n.sp., *Pt. armillata* n.sp. and *Pt. yaroni* n.sp.

Discussion:

Pseudotorinia sestertius n.sp. is similar to *Pt. numulus* (see above), from which it differs mainly by the shape and sculpture of the shell base: in *Pt. numulus*, a part of the columellar wall is visible between the umbilical crenae and the basal keel of the preceeding whorl, while in this species the umbilical crenae are directly connected to the basal keel of the previous whorl. This character is otherwise only known from the genus *Pseudomalaxis*. Since *Pseudotorinia sestertius* n.sp. shares all other shell characters with the *Pt. numulus*-group, and differs from *Pseudomalaxis* (whose members have, among other differences, much finer sculpture and an upper point of whorl attachment that is below, or at the lower side of, the lower peripheral rib), this species is here grouped with *Pseudotorinia*.

Pseudotorinia kraussi-group

The *Pseudotorinia kraussi*-group, named after its South African member, *Pt. kraussi* (Gray, 1850) (= preoccupied *Solarium cancellatum* Krauss, 1848), is a complex of species with very small, depressed lens-shaped to coin-shaped shells with reticulated sculpture, very wide umbilicus, at least two distinct spiral threads or ribs on the umbilical side of the columellar wall, and a small planispiral protoconch.

Pseudotorinia kraussi J.E. Gray *in* M.E. Gray, 1850 [emend.]
Figs.11, 254–257

*1848 *Solarium cancellatum* Krauss, Südafr. Moll.: 95, pl.5 fig.29 [non *Solarium cancellatum* Conrad, 1833, nec Lea, 1833].

*1850 *Liotia Krausii* J.E. Gray *in* M.E. Gray, Figs. moll. anim., *4*: 88.

1853 *Solarium cancellatum*, - Philippi, 1853b, Syst. Conch.-Cab. II, *7*: 34, pl.4 fig.16 [after Krauss].

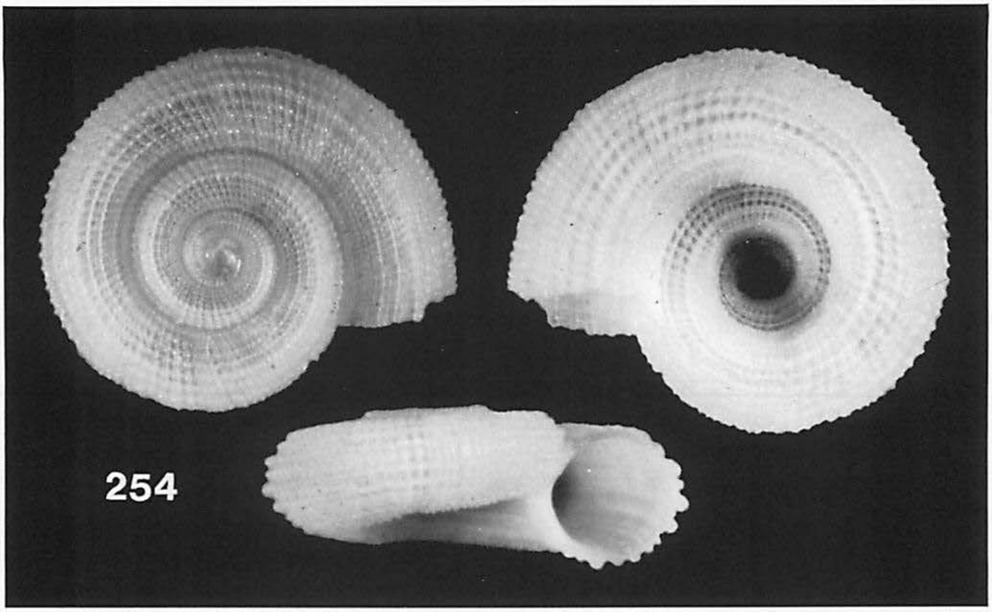


Fig. 254. *Pseudotorinia kraussi* (J.E. Gray *in* M.E. Gray, 1850); specimen from Durban, Natal, South Africa; NMP B2409; SD = 4.1.

1853 *Architectonica cancellata*, - Adams & Adams, Gen. Rec. Moll., *1*: 242.
1863 *cancellatum* Krauss - Not a *Solarium*, - Hanley, Thes. conch., *3*: 246.
1887 *Solarium (Solarium) cancellatum*, - Paetel, Cat. Conch.-Slg., (4)*1*: 285.
1892 *Solarium cancellatum*, - Sowerby (III), Mar. shells S. Afr.: 28.
1904 *Torinia cancellata*, - Martens, Wiss. Ergeb. dtsch. Tiefsee-Exped. Valdivia, *7*: 54.
1911 "*Liotia*" *krausii*, - Iredale, 1911a, Proc. malac. Soc. Lond., *9*(4): 258.
1932 *Solarium cancellatum*, - Turton, Mar. shells Port Alfred: 135.
1963 *Solarium cancellatum* (generic position doubtful), - Barnard, 1963b, Ann. S. Afr. Mus., *47*(1): 155, 164.
1973 *Architectonica cancellata*, - Kensley, Sea-shells s. Afr.: 76, fig.247.
1974 '*Solarium*' *cancellatum*, - Barnard, Ann. S. Afr. Mus., *47*(5): 711.
1977 *Liotella cancellata*, - Kilburn, Ann. Natal Mus., *23*(1): 180.

Original measurements: SD = ca. 2.4, H = ca. 0.9 [after Krauss].

Type locality: "In sinu Algoënsi" [Algoa Bay, eastern Cape Province, South Africa].

Material studied: 74 specimens (FMNH, MCZ, NMP, SAM, USNM, Coll. Marais); original material lost (SMNS; see Janus, 1961).

Etymology: *kraussi* [genitive singular case-ending]. Named after Dr. Christian Ferdinand Friedrich Krauss (1812–1891), author of 'Die südafrikanischen Mollusken' (1848), and former Director of the 'Königliches Naturalienkabinett' in Stuttgart, Germany.

Diagnosis:

Very small, depressed lens-shaped shell with reticulate sculpture, rounded periphery and extremely wide umbilicus; subsutural rib weaker than following two midribs (body whorls with additional spiral threads); upper peripheral rib strong; one fine spiral thread between midrib area and upper peripheral rib, and 1–2 spiral ribs between upper and lower peripheral ribs (at least one of them similar to peripheral ribs in shape and strength); umbilical side of columellar wall with 2–3 major (and often additional finer) spiral threads. Yellowish-white. Protoconch diameter 0.50–0.62 mm; planispiral, without anal keel.

Description:

Teleoconch: very small, diameter of specimens in collections usually 2.5–5, rarely over three whorls. Shape: depressed lens-shaped with rounded periphery and extremely wide umbilicus (UD ca. 46% of SD). Sculpture (see Fig.255): reticulate, consisting of ± fine spiral and axial ribs (in fresh specimens acute granules); Upper side: SSR weaker than following 2 MR; fine spiral threads interspersed; 1 fine spiral thread between MR-area and UPR; Periphery: UPR strong; 2 ± strong spiral threads between UPR

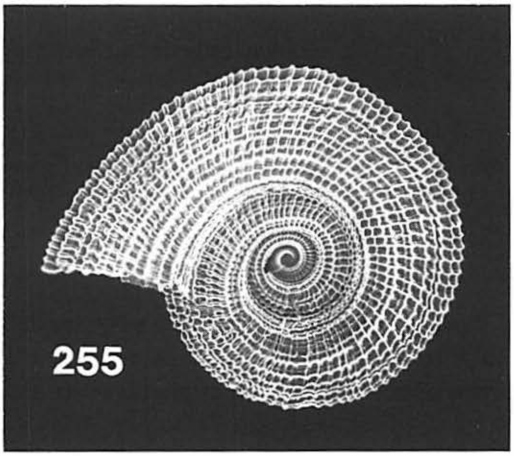


Fig. 255. SEM photomicrograph of the shell base of *Pseudotorinia kraussi* (J.E. GRAY *in* M.E. GRAY, 1850); FMNH 223434; specimen from Scottburgh, Natal, South Africa. SD = 4.8.

and LPR (at least one of them resembling peripheral ribs in shape and strength); LPR somewhat stronger and more prominent than UPR, serving as upper point of whorl attachment; IPR hardly stronger than following basal ribs; Base: 4–5 similar narrow spiral ribs below IPR, of which innermost (in most cases wider than other basal ribs) often somewhat sunken into umbilicus; larger specimens with ± fine spiral threads interspersed; umbilical side of columellar wall with 2–3 ± fine spiral ribs (and often additional threads). Coloration: yellowish-white. – Protoconch (see Figs.11, 256): very small to small (0.50–0.62, $\bar{x}$ = 0.56), planispiral, without anal keel; yellowish white, often with brown suture. – Periostracum: thin, whitish. – Operculum: as described for genus. – Radula and Anatomy: not studied. – Coloration of living animal: white, except for black eye spots.

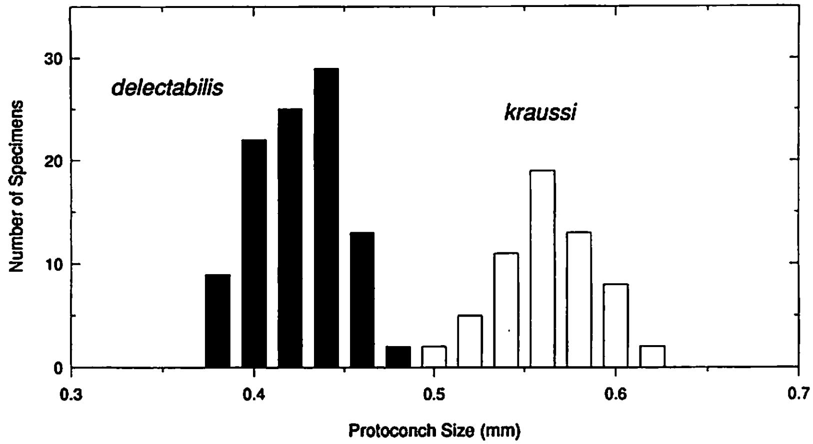


Fig. 256. Histograms of measured protoconch size. *Pseudotorinia delectabilis* (n = 100, x̄ = 0.42, sd = 0.03), and *Pt. kraussi* (n = 60, x̄ = 0.56, sd = 0.03).

Geographical distribution (Fig.257): Known only from South African east coast and Madagascar.

Habitat: Upper sublittoral (shallow dredgings; dead on beach); live specimen found intertidally, crawling on *Palythoa* (Zoanthidae) colonies (Isipingo, Natal Province, South Africa, 30°00'S, 30°56'E; feeding not observed).

Discussion:

The following species, *Pseudotorinia delectabilis*, is very similar, but differs in characters of teleoconch sculpture (upper midrib almost as strong as subsutural rib; only one additional rib between upper and lower peripheral ribs) and protoconch size (see Fig.256).

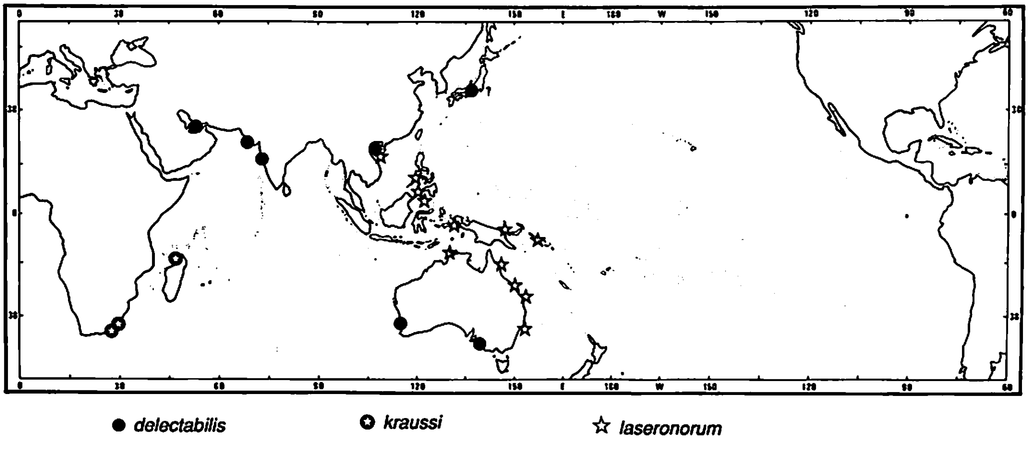


Fig. 257. Geographical distribution of *Pseudotorinia delectabilis*, *Pt. kraussi*, and *Pt. laseronorum*.

The name *Solarium cancellatum* KRAUSS, 1848, is not available, because it is preoccupied twice, by *Solarium cancellatum* CONRAD, 1833, and by *S. cancellatum* LEA, 1833. The fossil type specimens of these nominal species (*S. cancellatum* CONRAD: lectotype in ANSP 15386, vidi; *S. cancellatum* LEA: lectotype in ANSP 5616, vidi) do not belong to the family Architectonicidae.

When J.E. GRAY (*in* M.E. GRAY, 1850: 88) transferred the species to genus *Liotia*, where a nominal species "*cancellata*" already existed, he substituted the name *cancellatum* KRAUSS by the new name "*krausii*." GRAY intended to name the species after its original author, FERDINAND KRAUSS. *Solarium* "*krausii*" is therefore here considered an 'incorrect original spelling' (ICZN, 1985: Art. 32c(ii)), and is emended to *Solarium kraussi* J.E. GRAY *in* M.E. GRAY, 1850 (ICZN, 1985: Art. 32d).

Several authors questioned the position of this species in the Architectonicidae (e.g., HANLEY, 1863: 246; IREDALE, 1911a: 258; BARNARD, 1963b: 155). GRAY (1850: 88) transferred it to the genus *Liotia*, KILBURN (1977: 180) to *Liotella*. This species is positively a member of the Architectonicidae. Contrary to published statements, the interior of the shell is not nacreous, and a living specimen found by the present author at the South African east coast (Isipingo, Natal Province; 1980) had soft-body and opercular morphologies typical of the family.

Pseudotorinia delectabilis (MELVILL, 1893)
Figs.256–259

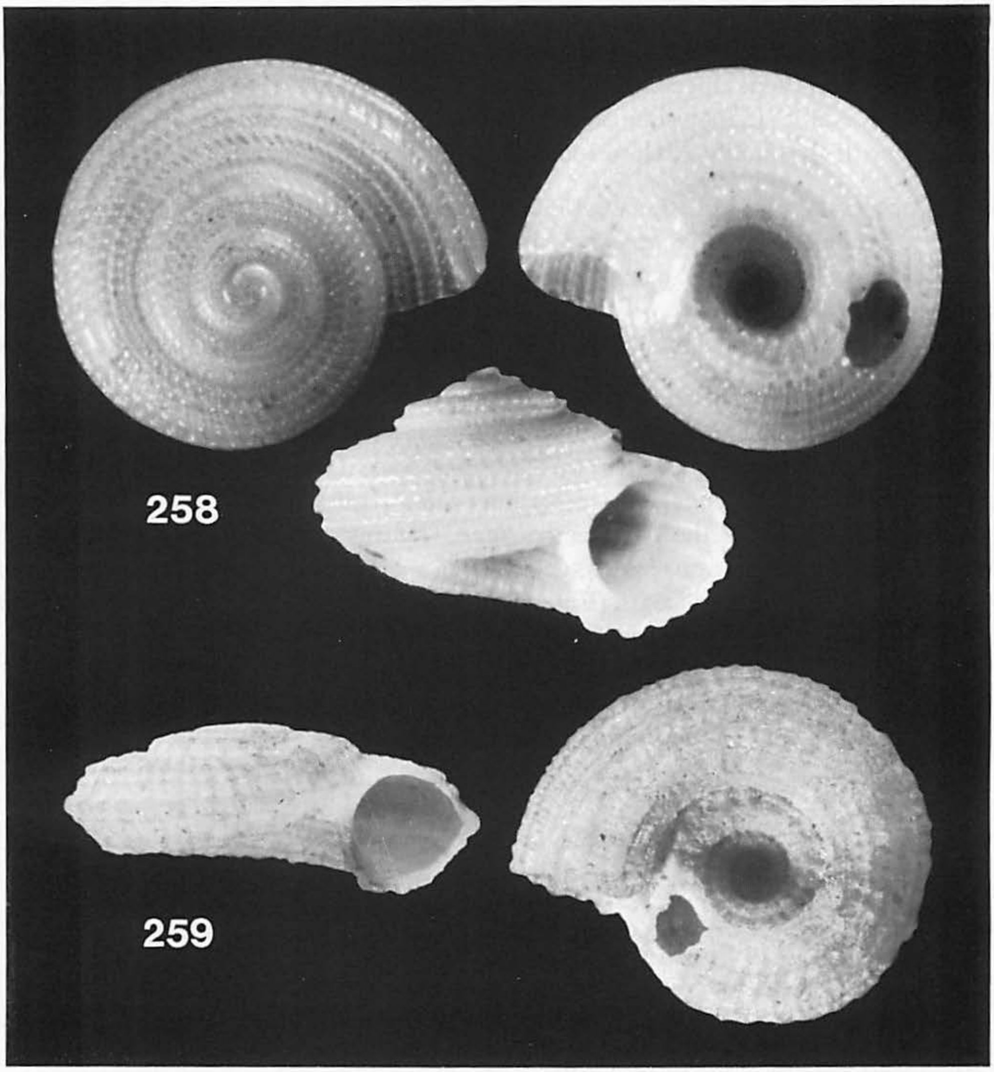
1893 *Solarium (Torinia) delectabile* (MELVILL) n.sp., – MELVILL & ABERCROMBIE, Mem. Proc. Manch. Lit. Phil. Soc., (4)*7*: 35 [*nomen nudum*].
*1893 *Solarium (Torinia) delectabile* MELVILL, Mem. Proc. Manch. Lit. Phil. Soc., (4)*7*: 57, pl.1 fig.11.
*1893 *Torinia foveolata* TATE, Trans. r. Soc. S. Austr., *17*: 191, pl.1 figs.13–13a.
1900 *Heliacus foveolatus*, – HEDLEY, Proc. linn. Soc. N. S. Wales, *25*: 93.
1901 *Solarium (Torinia) delectabile*, – MELVILL & STANDEN, Proc. zool. Soc. Lond., 1901, *2*: 363.
1933 *Heliacus foveolatus*, – COTTON & GODFREY, S. Austr. Natur., *14*(3): 73, pl.1 fig.2.
1948 *Torinia delectabilis*, – BAYER, Zool. Verh., *4*: 14.
1948 *Torinia foveolata*, – BAYER, Zool. Verh., *4*: 19.
1977 *Heliacus (Claraxis)* sp., GARRARD, Rec. Austr. Mus., *31*(13): 559, pl.9 figs.20–21.
1987 *Solarium (Torinia) delectabile*, – TREW, MELVILL's new moll. names: 35.

Type measurements: Lectotype of *Solarium delectabile* [here designated]: SD = 3.1, H = 2.0, PD = 0.46, Tw = 3+, UD = 1.0. Lectotype of *Torinia foveolata* [here designated]: SD = 5.3, H = 2.1, PD = 0.46, Tw = 3 5/8–, UD = 2.6.

Type localities: *S. delectabile*: "Bombay" [India]; *T. foveolata*: "Aldinga Bay and Semaphore" [S. Australia].

Material studied: 136 specimens (AMS, ANSP, BMNH, MCZ, MNHNP, NMNZ, SAusM, UMZC, USNM); including lectotype of *S. delectabile* (BMNH 1893.2.16.38) and lectotype of *T. foveolata* (SAusM D.13431).

Etymology: *delectabilis-e* [adjective]; Latin: delightful, enjoyable.



Figs. 258, 259. *Pseudotorinia delectabilis* (MELVILL, 1893). Fig. 258 (three aspects): lectotype of *Solarium (Torinia) delectabile*; Bombay, India; BMNH 1893.2.16.38; SD = 3.1. Fig. 259 (two aspects): lectotype of *Torinia foveolata* TATE, 1893; South Australia; SAusM D.13431; SD = 5.3.

Diagnosis:

Very small, depressed lens-shaped to roundish cone-shaped shell with reticulate sculpture and moderately to extremely wide umbilicus; one of the 1–2 midribs almost as strong as subsutural rib; upper peripheral rib hardly stronger than midribs; one additional rib between upper and lower peripheral ribs; lower peripheral rib either strong and keel-forming (then infraperipheral rib hardly stronger than basal ribs), or lower peripheral rib part of rounded periphery (then upper peripheral rib, additional rib, lower peripheral rib and infraperipheral rib of about equal strength); umbilical side of columellar wall with two major (and sometimes additional finer) spiral threads. Yellowish white. Protoconch diameter 0.38–0.48 mm; planispiral, without anal keel.

Description:

Teleoconch: very small, diameter of specimens in collections usually 2–3.5, rarely over 3 1/2 whorls. Shape: from depressed lens-shaped with extremely wide umbilicus to roundish cone-shaped with moderately wide umbilicus (UD ca. 24–50% of SD). Sculpture: reticulate, consisting of ± fine spiral and axial ribs, with distance between axial ribs varying widely between individuals; Upper side: SSR and 1–2 MR (inner one almost as strong as SSR); Periphery: UPR hardly stronger than MR; between UPR and LPR always 1 strong additional rib; either (a) LPR very prominent and forming acute peripheral keel, and IPR hardly stronger than following basal ribs, or (b) periphery roundish, consisting of about equally strong UPR, additional rib, LPR and IPR; Base: 2–3 ± fine spiral ribs below IPR, followed by 2 distinctly wider spiral ribs, the innermost (in forms with narrower umbilicus) sunken into umbilicus; umbilical side of columellar wall with 2 spiral ribs, with finer threads interspersed in some specimens. Coloration: yellowish white. – Protoconch (Fig.256): very small (0.38–0.48, $\bar{x}$ = 0.42), planispiral, without anal keel; white. – Operculum: as described for genus. – Periostracum, Radula and Anatomy: not known.

Geographical distribution (Fig.257): Known from various localities in the northwestern Indian Ocean, western Pacific and Australia.

Habitat: Shallow water to upper bathyal (685 m), live records from "under rocks, in shallow water" (BMNH 1981124; Karachi, Pakistan).

Discussion:

Pseudotorinia delectabilis is very similar to *Pt. kraussi* (see above), which differs mainly by having two spiral ribs between the upper and lower peripheral ribs, by less well-developed midribs, and by a much larger protoconch (see Fig.256).

While the type specimens of *Solarium delectabile* and *Torinia foveolata* differ markedly in shell shape ("typical" *delectabile* specimens are more rounded and have a narrower umbilicus), other specimens, e.g. from Karachi (BMNH) and the Gulf of Tonkin (MNHNP), display intermediate conditions. The two nominal species, both introduced in 1893, are here synonymized. The publication date of the description of *Torinia foveolata* Tate is given as June of 1893, while the publication containing the description of *Solarium delectabile* Melvill was received at the British Museum a month earlier (May 6th; K. Way, in litt.). *Torinia foveolata* is therefore here considered a junior subjective synonym of *Solarium delectabile*.

Melvill (1893: 57) mentioned "two or three specimens" in his original description of *Solarium delectabile*. The syntype in London (BMNH 1893.2.16.38) is here selected as lectotype (see Fig.258). Trew (1987: 35) reported two additional syntypes (now paralectotypes) from the Manchester Museum, England.

TATE (1893: 192) referred to "three dead shells" of his new species. The type lot of *Torinia foveolata* in Adelaide (SAusM D.13431) contained three syntypes (not a "holotype" as stated by GARRARD, 1977: 558), the two smallest of which do not belong to the family Architectonicidae. The remaining specimen agrees roughly with the given dimensions and figures of the original description and is here selected as lectotype (see Fig.259).

"*Heliacus (Torinista) delectabilis* (MELVILL, 1893)" sensu GARRARD (1977: 545, pl.5 figs.1-3) is not conspecific, but a specimen of *Heliacus hyperionis* n.sp. (see above). The specimens figured as "*foveolata*" by GARRARD (1977: 557, pl.5 figs.10-12, pl.6 figs.15-17) belong to *Pseudotorinia laseronorum* (see below), while the shell figured as "*Heliacus (Claraxis)* sp." (GARRARD, 1977: pl.9 figs.20-21; AMS C.105175, vidi) is a juvenile specimen of *Pt. delectabilis*.

Pseudotorinia laseronorum (IREDALE, 1936)

Figs.257, 260, 261

*1936 *Torinista laseronorum* IREDALE, Rec. Austr. Mus., *19*(5): 327.

1977 *Heliacus (Claraxis) foveolatus*, - GARRARD, Rec. Austr. Mus., *31*(13): 557, pl.5 figs.10-12, pl.6 figs.15-17 [non *Torinia foveolata* TATE, 1893 = *Pseudotorinia delectabilis* (MELVILL, 1893)].

Type measurements (holotype): SD = 4.6, H = 1.8, PD = 0.46, Tw = 3 1/8, UD = 1.9.

Type locality: "in a couple of fathoms in North Harbour, Port Jackson" [N.S.W., Australia].

Material studied: 22 specimens (AMS, LACM, MNHNP, USNM); including holotype (AMS C.60693).

Etymology: *laseronorum* [genitive plural case-ending]. Named after "Messrs. C.F. and J. LASERON."

Diagnosis:

Very small, depressed lens-shaped shell with reticulate sculpture and very wide umbilicus; subsutural rib stronger than following 2-3 midribs; upper peripheral rib prominent and wider than midribs; no additional ribs between upper and lower peripheral ribs; lower peripheral rib slightly more prominent than upper peripheral rib; umbilical side of columellar wall with two spiral threads (the one next to the umbilical crenae wider). Yellowish white. Protoconch diameter 0.44-0.52 mm; planispiral, without anal keel.

Description:

Teleoconch: very small, diameter of specimens in collections usually 2-3, rarely over 2 1/2 whorls. Shape: depressed lens-shaped (somewhat trapezoid in cross-section) with very wide umbilicus (UD ca. 43% of SD). Sculpture: reticulate, consisting of ± fine spiral and axial ribs; Upper side: SSR prominent; 2-3 fine MR; Periphery: UPR prominent, wider than MR; no additional ribs between UPR and LPR; LPR slightly

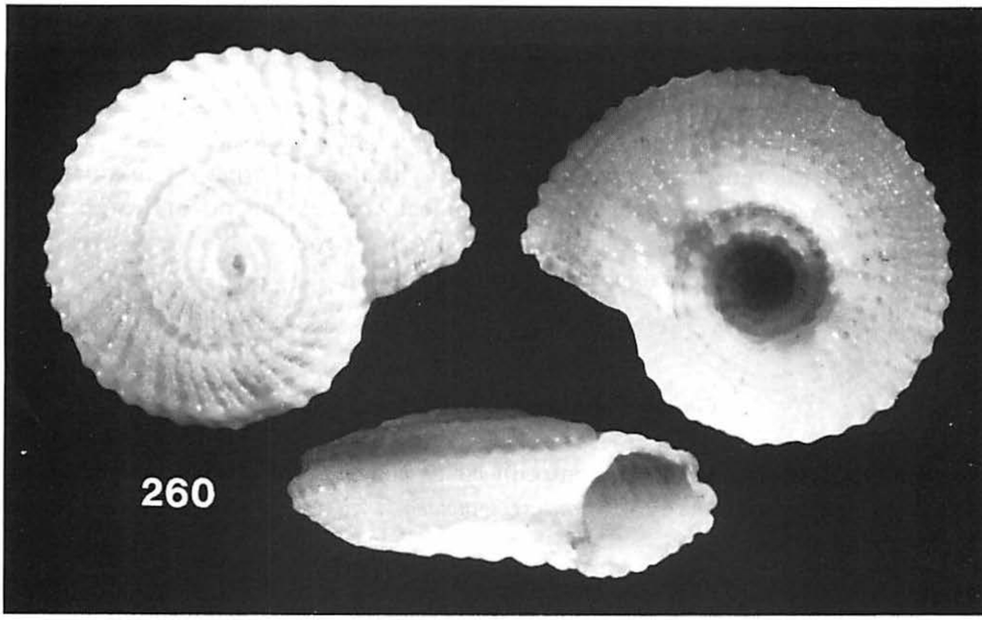


Fig. 260. *Pseudotorinia laseronorum* (IREDALE, 1936); holotype of *Torinista laseronorum*; New South Wales, Australia; AMS C.60693; SD = 4.6.

more prominent than UPR, here upper point of whorl attachment; IPR not or hardly stronger than following basal ribs; Base: 2-3 narrow spiral ribs below IPR, followed by 3 spiral ribs which distinctly increase in width towards umbilicus; innermost rib (UC) surrounding umbilicus with strong nodules; umbilical side of columellar wall with 2 spiral ribs (the one next to UC being wider). Coloration: yellowish white. - Protoconch (see Fig.261): very small (0.44-0.52, $\bar{x}$ = 0.48), planispiral, without anal keel; white. - Operculum: as described for genus. - Periostracum, Radula and Anatomy: not known.

Geographical distribution (Fig.257): Philippines, western Pacific.

Habitat: Upper sublittoral (depth records between 6 and 79 m), live records from 6 to 15 m; sand and coral rubble substrates.

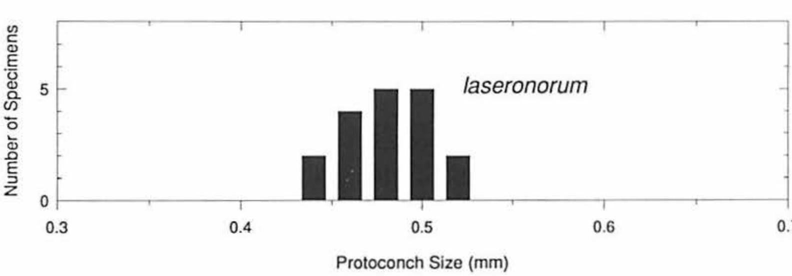


Fig. 261. Histogram of measured protoconch size. *Pseudotorinia laseronorum* (n = 18, $\bar{x}$ = 0.48, sd = 0.02).

Discussion:

Pseudotorinia laseronorum differs from the two previous species, *Pt. kraussi* and *Pt. delectabilis*, mainly by not having additional ribs between the upper and lower peripheral ribs of the teleoconch. Forms of the *Pt. gemmulata*-group are somewhat similar, but lack the reticulate appearance, have a different shell base with a narrower umbilicus with more or less overhanging umbilical crenae, and no or less sculpture on the umbilical side of the collumellar wall. In that group only *Pseudotorinia* sp.I aff. *gemmulata* has a comparably small protoconch size.

Genus *Pseudomalaxis* FISCHER, 1885

Pseudomalaxis FISCHER, 1885: 714; introduced as subgenus of *Torinia* [= *Heliacus*]. Type species by monotypy: *Bifrontia? zanclaea* PHILIPPI, 1844; Pliocene-Recent, Mediterranean Sea.

Synonyms:

Discosolis DALL, 1892: 331; introduced as "section" of *Discohelix* [Euomphalidae]. Type species by original designation: *Omalaxis nobilis* VERRILL, 1885 [= *Pseudomalaxis zanclaeus*]; Recent, Atlantic Ocean.

Mangonuia MESTAYER, 1930: 144. Type species by original designation: *Mangonuia bollonsi* MESTAYER, 1930 [= *Pseudomalaxis zanclaeus meridionalis* (HEDLEY, 1903)]; Recent, Indo-Pacific.

Incorrect subsequent spellings:

"Discosolix" KOROBKOV, 1955; "Pseudomalaxus" Boss, 1982.

Description (Fig.261a):

Teleoconch: shell small (usually 5–10 mm), coin-shaped and largely planispiral; two peripheral keels formed by partly fused spiral ribs of differing strength; upper (apical) surface larger and upper keel stronger, resulting in trapezoidal cross-section of whorl;

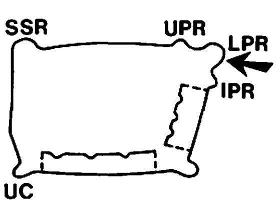


Fig.261a. Schematic representation of placement of major spiral ribs in *Pseudomalaxis*, apertural aspect. Arrow shows point of attachment of next whorl, intrageneric variation indicated by dotted lines.

lower (umbilical) side concave; suture deep because upper point of whorl attachment below upper keel; extremely wide umbilicus; sculpture of usually weakly developed spiral and axial ribs and threads, with upper and lower surfaces similar; rib surrounding umbilicus without distinct crenae; this rib close to peripheral keel of preceding whorl, therefore most of umbilical wall not exposed; peripheral region between keels with few thin spiral threads; coloration indistinctly off-white or yellowish, occasionally with weak irregular flames or blotches. *Protoconch:* small to medium-sized (ca. 0.78–1.12), almost planispiral to distinctly heterostrophic, without anal keel. *Radula:* five-toothed-taenioglossate; rachidian stronger than marginal teeth (*zanclaeus*). *Operculum:* horny, round, flat with peg-like projection on body side.

For a more extensive description and discussion of this genus see BIELER (1984b: 65 ff.).

Pseudomalaxis zanclaeus meridionalis (HEDLEY, 1903)
Figs.262–265

*1903 *Omalaxis meridionalis* HEDLEY, Mem. Austr. Mus., *4*(6): 351, fig.74.
1911 *Discohelix meridionalis*, – IREDALE, 1911a, Proc. malac. Soc. Lond., *9*(4): 257.
*1930 *Mangonuia Bollonsi* MESTAYER, Trans. Proc. N. Zeal. Inst., *61*: 145, pl.26 figs.1–3.
*1938 *Pseudomalaxis solaris* KURODA, Venus, *8*(1): 1, figs.1–3.
1939 *Pseudomalaxis (Mangonuia) solaris*, – KURODA, Venus, *9*(2): 61.
1939 *Mangonuia (Mangonuia) bollonsi*, – WENZ, Handb. Paläozool., *6*(3): 667, fig.1902 [after MESTAYER].
1948 *Torinia bollonsi*, – BAYER, Zool. Verh., *4*: 8.
1954 *Mangonuia solaris*, – KURODA & HABE, Venus, *18*(2): 81, fig.3 [radula].
1963 *Heliacus* sp., – BARNARD, 1963b, Ann. S. Afr. Mus., *47*(1): 164, figs.31 l,m.
1971 *Mangonuia solaris*, – KURODA et al., Sea shells Sagami Bay: 265, pl.61 fig.17.
1975 *Pseudomalaxis? meridionalis*, – BUONAIUTO, Trans. r. Soc. S. Austr., *99*(1): 28.
1977 *Pseudomalaxis (Pseudomalaxis) nobilis meridionalis*, – GARRARD, Rec. Austr. Mus., *31*(13): 509, fig. 10 [operculum], p.563, pl.6 figs.4–5, pl.7 figs.10–12 [holotype].
1979 *Mangonuia bollonsi*, – POWELL, N. Zeal. Moll.: 248, fig.57(2).
1983 *Mangonuia solaris*, – OKUTANI, KAWAMURA coll.: 11, pl.41 fig.12.
1984 *Pseudomalaxis (Pseudomalaxis) zanclaeus meridionalis*, – BIELER, 1984b, Arch. Moll., *115*(1/3): 73, fig.3 [after MESTAYER], pl.2 fig.13 [holotype of *O. meridionalis*], fig.18 [after KURODA, 1938].
1988 *Pseudomalaxis (Pseudomalaxis) zanclaeus meridionalis*, – BIELER, Malac. Rev., Suppl. *4*: 239 [radula].

Type measurements: Holotype of *Omalaxis meridionalis*: SD = 4.3, H = 1.3, Tw = 1 7/8. Holotype of *Mangonuia bollonsi*: SD = 16.5, H = 5.0, Tw = 4 [after MESTAYER]. Holotype of *Pseudomalaxis solaris*: SD = 13.0, H = 4.3, Tw = 4 [after KURODA, 1938].

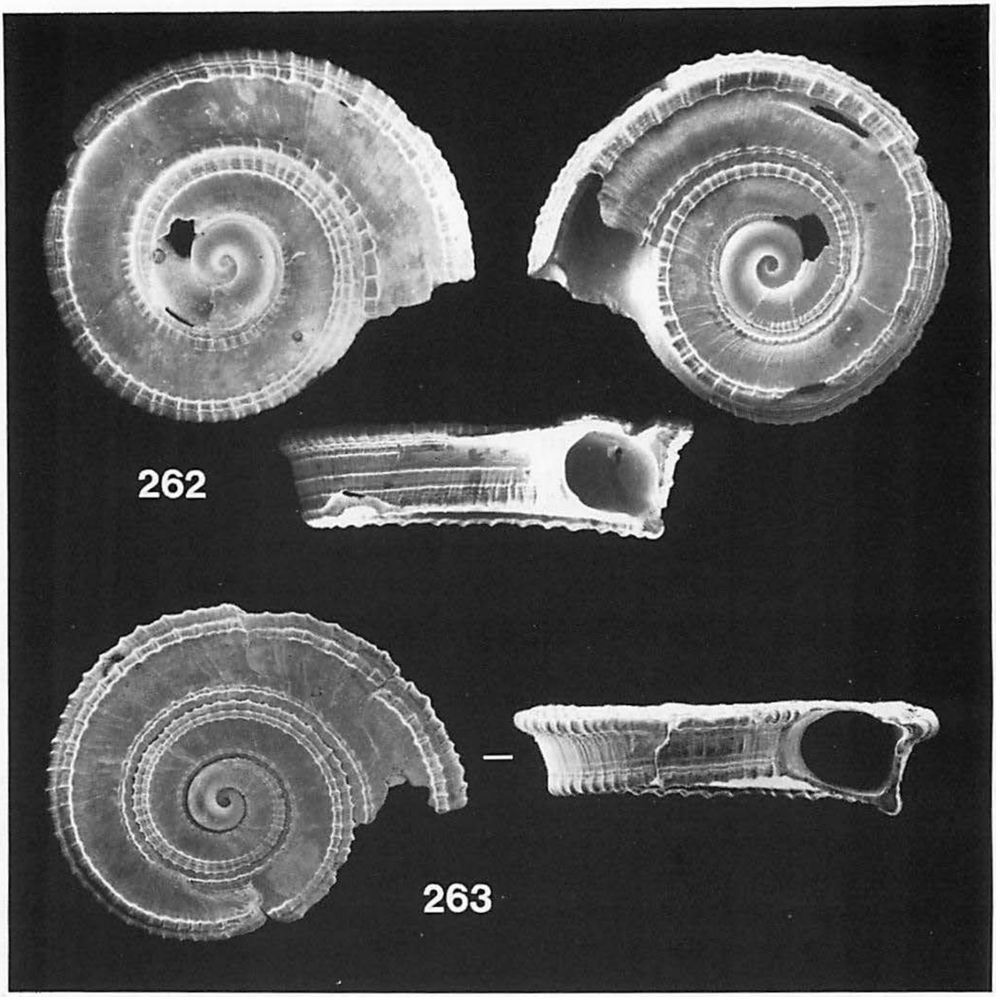
Type localities: *O. meridionalis*: "Port Stephens" [N.S.W., Australia]; *M. bollonsi*: "off North Cape, New Zealand. Depth, about 75 fms. [137 m]"; *Ps. solaris*: "Sagami Bay ... 80 m" [Honshu, Japan].

Material studied: 56 specimens (AMS, BMNH, FMNH, MNHNP, NMNZ, NMP, SAM, USNM), including holotype of *O. meridionalis* (AMS C.16298); and photograph of holotype of *Ps. solaris* (BLIHT, courtesy of Prof. T. HABE; type material not available on loan].

Etymology: *meridionalis-e* [adjective]; Latin: southern.

Diagnosis:

Very small to small coin-shaped shell with upper peripheral keel more prominent, upper side flat and base concave; subsutural rib much weaker than upper peripheral rib situated on upper side immediately next to keel-forming lower peripheral rib; area



Figs. 262, 263. *Pseudomalaxis zanclaeus meridionalis* (HEDLEY, 1903). Fig. 262 (three aspects): holotype of *Omalaxis meridionalis*; New South Wales; AMS C.16298; SD = 4.3. Fig. 263 (two aspects): specimen from off Pratas Id. [Tung-sha Tao], China Sea; USNM 819947; SD = 5.3.

between shell keels straight, with 2–3 fine spiral threads; areas between subsutural rib and upper shell keel and between lower shell keel and weak umbilical crenae smooth or with axial sculpture; umbilical crenae not overhanging, connected by very small oblique area of columellar wall with basal keel of preceding whorl. White, sometimes with fawn blotches. Protoconch diameter 0.88–1.12 mm; weakly heterostrophic, without anal keel.

Description:

Teleoconch: very small to small, diameter of specimens in collections usually 4–9.3 (rarely over 10) at 1 3/4 to 3 1/8 (4) whorls. Shape: coin-shaped (somewhat trapezoid in cross-section, with upper side larger); upper side of whorls flat; base angular with keel formed by prominent spiral rib; area between peripheral and basal keels straight; inner base concave; umbilicus extremely wide (UD ca. 48% of SD). Sculpture (appears very similar on both sides): Upper side: SSR distinctly developed, narrow, with regular sculpture of ± fine nodules; MR smooth or with ± well-developed axial growth lines; Periphery: UPR very close to usually somewhat stronger LPR, forming double keel at upper periphery; upper point of whorl attachment below LPR (therefore suture deep); LPR often with microscopic grooves, especially on peripheral side; IPR developed as weak spiral thread; between IPR and basal keel 1–2 weak spiral threads (one of which close to peripheral keel); basal keel formed by spirally grooved rib, as strong as (but less prominent than) LPR; area between basal keel and UC smooth or with axial sculpture; UC with fine nodules, not overhanging umbilicus; very small, ± oblique area of columellar wall visible in umbilicus, connecting UC with basal keel of preceding whorl. Coloration: translucent to opaque white, fresh specimens with fawn blotches, especially on periphery. - Protoconch (see Fig.265): small to medium-sized (0.88–1.12, $\bar{x}$ = 1.00), multispiral, weakly heterostrophic, without anal keel; white with brown outer corner next to varix. - Periostracum: thin, yellowish. - Operculum: as described for genus. - Radula: five-toothed taenioglossate (2–1–2); rachidian tooth stronger than marginal teeth, with subtriangular median cusp flanked by 15–10 smaller cusps; marginal teeth longer, curved and forked with 4–9 tapering cusps [see KURODA & HABE, 1954: 82, fig.3 (as *Mangonuia solaris*), and BIELER, 1988: 239]. - Anatomy: not known.

Geographical distribution (Fig.264): Known from western Indian Ocean (South Africa) and western Pacific.

Habitat: Sublittoral to upper bathyal (depth records between 18 and 420 m), live record from 113 m; mud, sand, and gravel substrates.

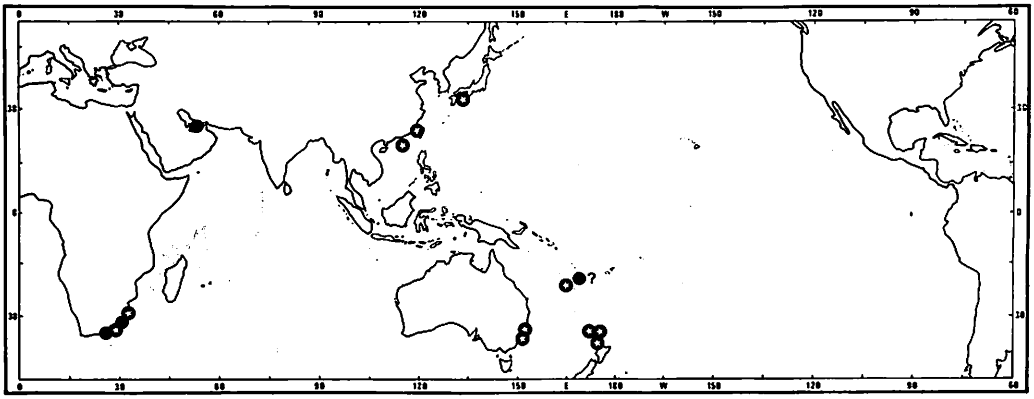


Fig. 264. Geographical distribution of *Pseudomalaxis obolos*, and *Ps. zanclaeus meridionalis*.

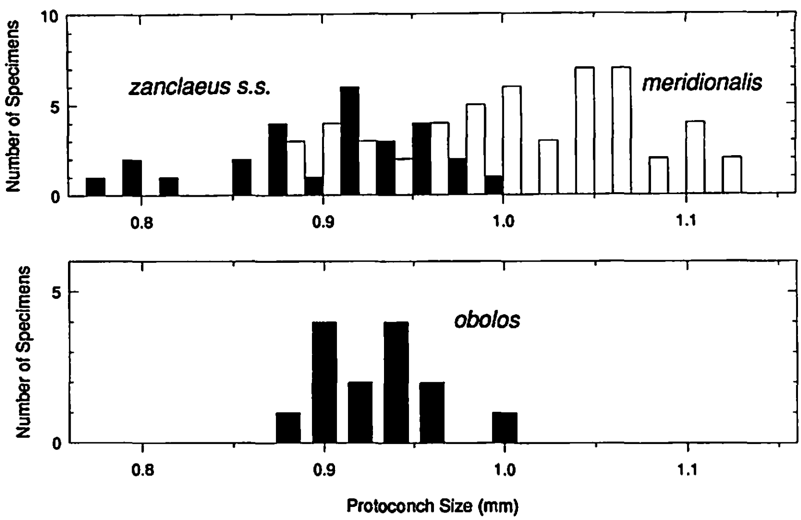


Fig. 265. Histograms of measured protoconch size. *Pseudomalaxis zanclaeus* s.s. (n = 27, x̄ = 0.91, sd = 0.06), *Ps. zanclaeus meridionalis* (n = 52, x̄ = 1.00, sd = 0.07), and *Ps. obolos* (n = 14, x̄ = 0.93, sd = 0.03).

Discussion:

Indo-Pacific *Pseudomalaxis zanclaeus meridionalis* agrees with its nominate form, Mediterranean-Atlantic *Ps. zanclaeus zanclaeus* (Philippi, 1844) [synonyms: *Omalaxis nobilis* Verrill, 1885; *Pseudomalaxis actoni* Monterosato, 1913] in all teleoconch and opercular characters (see Bieler, 1984b: 71 ff.). Earlier light-microscopical studies indicated radular differences between the two: Merrill (1970a: 43, pl.9 fig.1, unpubl.) reported two to five, and Boss & Merrill (1984b: 362, pl.62 fig.1) four cusps on each marginal tooth of *Ps. nobilis* [= *zanclaeus* s.s.], while Kuroda & Habe (1954: 82, fig.3) found six to nine for *Ps. solaris* [= *zanclaeus meridionalis*]. However, recent SEM studies did not show that difference (Melone & Taviani, 1985: 181, figs.56–59, found five to six cusps for *Ps. zanclaeus* s.s.). The only separating character remaining is a statistically smaller protoconch (x̄ = 0.91) for the Mediterranean-Atlantic form (Bieler, 1984b: 73, fig.4).

The differences cited by Merrill (1970a: 52, unpubl.) to recognize *Pseudomalaxis bollonsi* as distinct from *Ps. nobilis* [= *zanclaeus* s.s.], are features of an unusually large individual. A similar form is *Pseudomalaxis obolos* (see discussion below).

Pseudomalaxis obolos (Barnard, 1963)
Figs.264–267

*1963 *Heliacus obolos* Barnard, 1963b, Ann. S. Afr. Mus., *47*(1): 163, figs.3 f,g.
*1977 *Heliacus (Mangonuia) smithae* Kilburn, Ann. Natal Mus., *23*(1): 186, figs.16–18.
1977 *Heliacus obolos*, – Kilburn, Ann. Natal Mus., *23*(1): 186.
*?1982 *Mangonuia navakaensis* Ladd, U.S. geol. Surv. prof. Pap., *1171*: 29, pl.31 figs.3–5 [Pleistocene].
1984 *Pseudomalaxis (Pseudomalaxis) obolos*, – Bieler, 1984b, Arch. Moll., *115*(1/3): 74, pl.2 figs.14 [holotype of *M. navakaensis*], 15 [holotype of *H. obolos*], 16 [holotype of *H. smithae*].

Measurements: Holotype of *Heliacus obolos*: SD = 8.5, H = 2.5, Tw = ca. 3 3/8 [damaged]. Holotype of *Heliacus smithae*: SD = 8.5, H = 2.5, Tw = 3 1/4. Holotype of *Mangonuia navakaensis*: SD = 3.6, H = 1.1, Tw = 1 3/4. Largest specimen studied: SD = 11.0, Tw = 3 2/3 (Coll. QUICKELBERGE via NMP).

Type localities: *H. obolos*: "off Umhloti River (Natal), 40 fathoms [73 m]" [South Africa]; *H. smithae*: "Shelly Beach, just south of Port Shepstone, Natal" [South Africa]; *M. navakaensis*: "station SM43 on the Navaka River. Age of fossils, Pleistocene" [New Hebrides].

Material studied: 17 specimens (NMNZ, NMP, NMW, SAM, USNM, Coll. MARAIS); including holotype of *H. obolos* (SAM A9127), holotype (NMP A4911/T2044) and paratype (Coll. MARAIS) of *H. smithae*, holotype of *M. navakaensis* (USNM 250150).

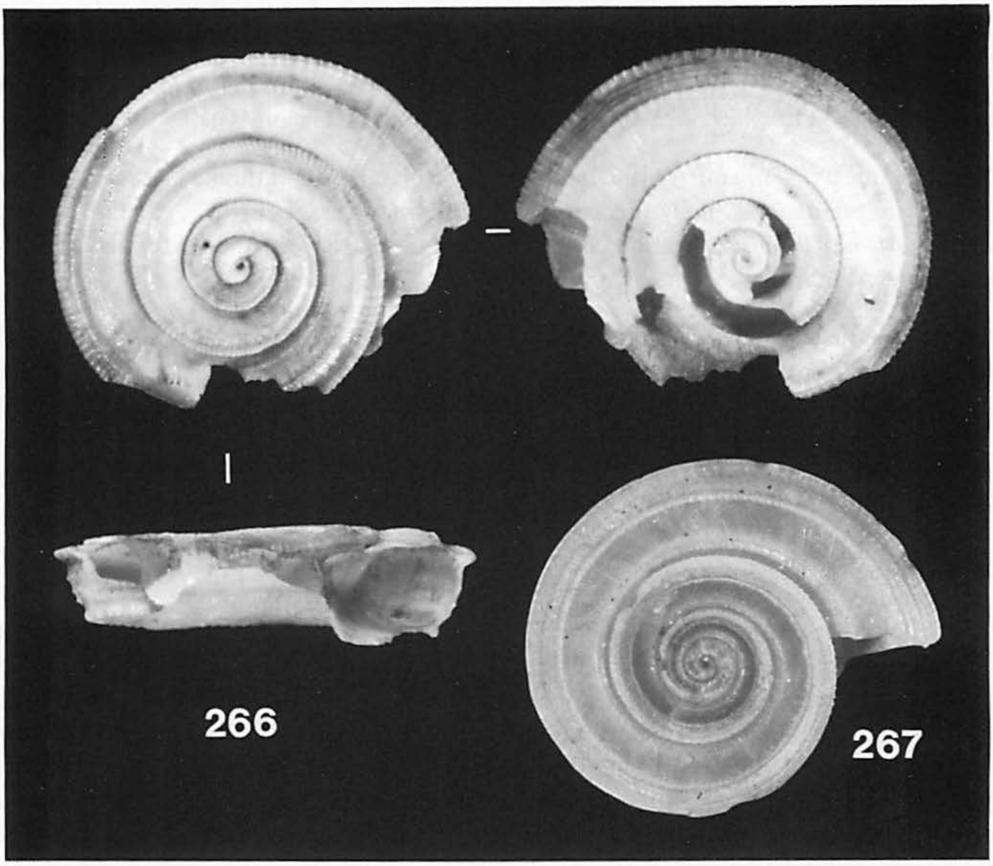
Etymology: *obolos* [noun in apposition]; small coin. BARNARD used the Greek spelling (ὄβολος) rather than the Latin *obolus*.

Diagnosis:

Very small to small coin-shaped shell with upper peripheral keel more prominent, deep suture, extremely wide umbilicus, upper side somewhat convex and base concave; subsutural rib much weaker than upper peripheral rib which forms prominent ridge on upper side, about 1/3 of whorl-width from keel-forming lower peripheral rib; area between subsutural rib and this ridge smooth or with spiral lines and convex, between ridge and upper shell keel distinctly concave; area between shell keels usually somewhat convex, with three more or less identical spiral threads; area between lower shell keel and weak umbilical crenae with spiral threads; umbilical crenae not overhanging, connected by very small area of columellar wall with lower-most spiral thread on area above basal keel of preceding whorl. White, sometimes with brownish flames and blotches. Protoconch diameter 0.88–1.00 mm; weakly heterostrophic, without anal keel.

Description:

Teleoconch: very small to small, diameter of specimens in collections usually 5–8.5 (rarely over 10) at 2 3/8 to 3 3/8 (3 2/3) whorls. Shape: coin-shaped (somewhat trapezoid in cross-section, with upper side larger); whorls usually somewhat convex on all sides; base angular with keel formed by ± weak spiral rib; inner base concave; umbilicus extremely wide (UD ca. 54% of SD). Sculpture: Upper side: SSR narrow, weakly developed; MR-area ± smooth, with microscopic axial and spiral lines; Periphery: UPR distinctly developed, forming narrow spiral ridge ca. 1/3 of whorl-width from keel-forming LPR; area between UPR and LPR distinctly concave; LPR strong, with 2–3 spiral grooves; IPR developed as distinct, fine, spiral thread; 2 similar, often somewhat weaker, threads between IPR and basal keel; upper point of whorl attachment on lower side of LPR (therefore suture deep); area between basal keel and very weak, almost smooth, UC angular and with 1–2 major (and often



Figs. 266–267. *Pseudomalaxis obolos* (Barnard, 1963). Fig. 266: holotype of *Heliacus obolos*; South Africa; SAM A9127; SD = 8.5. Fig. 267: holotype of *Heliacus (Mangonuia) smithae* Kilburn, 1977; South Africa; NMP A4911/T2044; SD = 8.5.

additional finer) spiral threads; very small area of columellar wall visible in umbilicus, connecting UC with lower-most spiral thread on area above basal keel of previous whorl (therefore deep suture on base). Coloration: translucent to opaque white, some specimens with fawn flames, or with brown blotches on periphery and outer base. – Protoconch (see Fig.265): small to medium-sized (0.88–1.00, $\bar{x}$ = 0.93), multispiral, weakly heterostrophic, without anal keel; white with brown early whorls and varix area. – Periostracum: thin, scaly; yellowish. – Operculum: as described for genus. – Radula and Anatomy: not known.

Geographical distribution (Fig.264): Known from Indian Ocean (South Africa, Persian Gulf) and, possibly, western Pacific.

Habitat: Upper to lower sublittoral (depth records between 50 and 300 m), live records from throughout that range; mud and sand substrates.

Discussion:

A similar form is *Pseudomalaxis zanclaeus meridionalis* (see above). That species differs by having the upper peripheral rib immediately adjacent to the keel-forming lower peripheral rib, and not separated by a relatively wide concave area. The area between peripheral and basal keels is straight, not convex as in most *Ps. obolos* specimens, and the area between basal keel and umbilical crenae is either smooth or bearing axial sculpture, not spiral ribs.

Pseudomalaxis praemeridionalis (CHAPMAN, 1912) (1912: 189, pl.12 figs.4–6; see also GARRARD, 1977: 565, pl.10 figs.22–23) from the Australian Tertiary (Balcombian; Victoria) is similar, but has a stronger upper peripheral rib and a broadly V-shaped base of the whorls carrying a stronger basal rib. The protoconch of the fossil species is smaller (0.84 mm; holotype NMV P12360; vidi).

The Pleistocene type specimen of *Mangonuia navakaensis* LADD, 1982 (USNM 250150) from the New Hebrides differs from the Indian Ocean specimens by slightly coarser sculpture, by the straight (not concave) area between the two shell keels, and by the upper peripheral rib being positioned somewhat closer to the periphery (see BIELER, 1984b: 75, pl.2 fig.14). A similar shell (NMNZ M.87397 was recently dredged off New Zealand. The taxonomic status of this form is uncertain.

Genus *Spirolaxis* MONTEROSATO, 1913

Spirolaxis MONTEROSATO, 1913: 363; introduced as subgenus of *Pseudomalaxis*. Type species by monotypy: *Pseudomalaxis centrifuga* MONTEROSATO, 1890; Recent, Atlantic Ocean.

Synonyms:

Paurodiscus REHDER, 1935: 128; introduced as subgenus of *Pseudomalaxis*. Type species by monotypy: *Pseudomalaxis (Paurodiscus) lamellifera* REHDER, 1935; Recent, Atlantic Ocean.

Aguayodiscus JAUME & BORRO, 1946: 16; introduced as subgenus of *Pseudomalaxis*. Type species by monotypy: *Spirolaxis (Aguayodiscus) clenchi* JAUME & BORRO, 1946; Recent, Atlantic Ocean.

Description (Fig.267a):

Teleoconch: very small to small (usually 1.5–2.5); whorls detached ("open coiling") throughout or after about 1.5 whorls; small specimens coin-shaped and largely

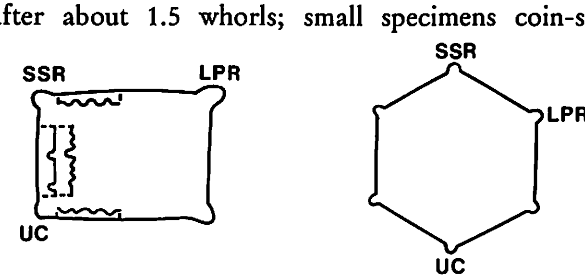


Fig.267a. Schematic representation of placement of major spiral ribs in *Spirolaxis*. Apertural aspects of forms with rectangular and hexagonal cross-sections of shell. Intrageneric variation indicated by dotted lines.

planispiral, larger forms helicoidal; two peripheral keels formed by two usually equally strong ribs (LPR and rib of the basal area), resulting in quadratic (rarely hexagonal) cross-section of whorl; axial sculpture lacking or distinctly developed, with upper and lower surfaces similar; subsutural rib and rib surrounding extremely wide umbilicus often weak, without distinct crenae; peripheral region between keels with few thin spiral threads; coloration indistinctly off-white to tan, occasionally with weak irregular flames or blotches. *Protoconch:* very small to small (ca. 0.48–0.72), almost planispiral to distinctly heterostrophic, without anal keel. *Radula:* five-toothed-taenioglossate; rachidian stronger than marginal teeth (*rotulacatharinea*, *centrifuga*). *Operculum:* horny, round, cone-shaped, with peg-like projection on body side.

For a more extensive description and discussion of this genus see BIELER (1984b: 68 ff.).

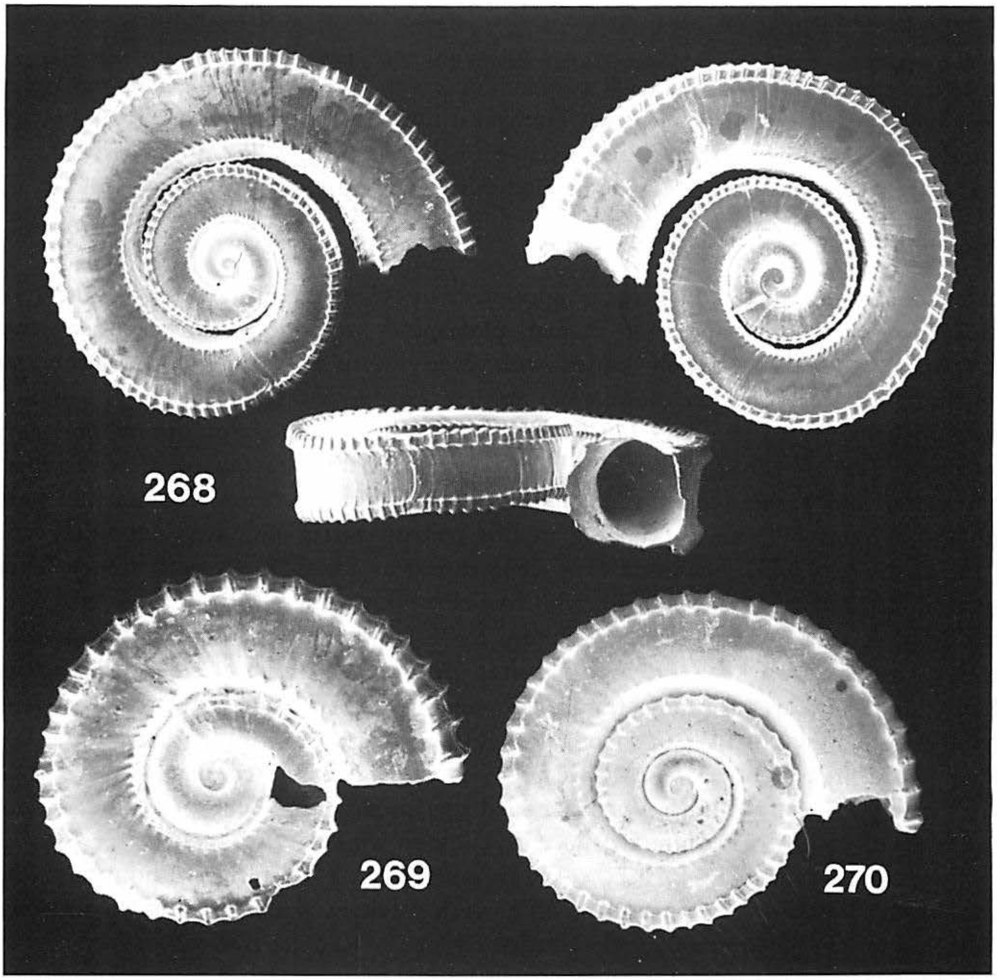
Spirolaxis rotulacatharinea (MELVILL & STANDEN, 1903)
Figs.268–272, 281

*1903 *Homalaxis rotula-catharinea* MELVILL & STANDEN, Ann. Mag. nat. Hist., (7)*12*: 299, pl.21 fig.3.
1911 *Pseudomalaxis rotula-catherina* [sic], - IREDALE, 1911a, Proc. malac. Soc. Lond., *9*(4): 256.
1903 *Omalaxis* sp., - HEDLEY, Mem. Austr. Mus., *4*(6): 351.
1938 *Pseudomalaxis rotula-catherina* [sic], - KURODA, Venus, *8*(1): 3.
*?1944 *Spirolaxis cohaerentia* LAWS, Trans. Proc. r. Soc. N. Zeal., *73*(4): 308, pl.44 fig.22 [Miocene].
*1977 *Pseudomalaxis (Pseudomalaxis) thetidis* GARRARD, Rec. Austr. Mus., *31*(13): 564, figs.1a-b.
1982 *Mangonuia* sp.A, - LADD, U.S. geol. Surv. prof. Pap., *1171*: 30, pl.31 figs.9–11.
*1982 *Pseudomalaxis (Pseudomalaxis?) roddai* LADD, U.S. geol. Surv. prof. Pap., *1171*: 31, pl.32 figs.10–12.
1984 *Pseudomalaxis (Spirolaxis) rotulacatharinea*, - BIELER, 1984b, Arch. Moll., *115*(1/3): 78, pl.4 figs.27 [lectotype designation], 28 [holotype of *Ps. thetidis*], 29 [holotype of *Ps. roddai*], pl.5 fig.30 [original specimen of "*Mangonuia* sp.A" of LADD].
1985 *Pseudomalaxis rotulacatharinea*, - DRIVAS & JAY, La Conchiglia, *17*(190–191): 9, fig.15.
1987 *Homalaxis rotula-catharinea*, - TREW, MELVILL's new moll. names: 62.
1988 *Pseudomalaxis rotula catharinea* [sic], - BANDEL, Mitt. geol.-paläont. Inst. Univ. Hamburg, *67*: 9, pl.2 fig.5.

Type measurements: Lectotype [BIELER, 1984b: 80] of *H. rotulacatharinea*: SD = 3.2, H = 0.9, Tw = 1 207/8. Holotype of *Ps. thetidis*: SD = 1.6, H = 0.5, Tw = 1 1/3. Holotype of *Ps. roddai*: SD = 2.7, H = 0.8, Tw = 2 1/10.

Type localities: *H. rotulacatharinea*: "Gulf of Oman, lat. 24°58'N., long. 56°54'E., 156 fathoms [285 m]"; *Ps. thetidis*: "Off Cape Three Points, New South Wales (33°18'S., 151°30'E.), 89–91 metres"; *Ps. roddai*: "Station C2026, Viti Levu, Fiji; age, Pliocene (Tertiary h)"; *Sp. cohaerentia*: "Pakaurangi Point, Kaipara" [New Zealand, Otaium (Lower Miocene)]; *Mangonuia* sp.A LADD: "station SM43, Navaka River, Santo, New Hebrides; age, Pleistocene."

Material studied: 626 specimens (AMS, ANSP, BMNH, FMNH, IRSNB, LACM, MNHNP, NMNZ, NMP, NMW, SMF, USNM), including: lectotype and 2 paralectotypes of *H. rotulacatharinea* (BMNH 1903.12.15.84–86); paralectotypes of *H. rotulacatharinea* (ANSP 164793: 2 specimens, BMNH 1982178: 12 specimens, NMW 1955.158.216: 35 specimens); holotype of *Ps. thetidis* (AMS C.16297); holotype of *Ps.*



Figs. 268–270. *Spirolaxis rotulacatharinea* (Melvill & Standen, 1903) [SEM]. Fig. 268: lectotype of *Homalaxis rotulacatharinea*; Gulf of Oman; BMNH 1903.12.15.84; SD = 3.2. Fig. 269: holotype of *Pseudomalaxis thetidis* Garrard, 1977; New South Wales; AMS C.16297; SD = 1.6. Fig. 270: holotype of *Pseudomalaxis roddai* Ladd, 1982; Fiji (Pliocene); USNM 250149; SD = 2.7.

roddai (USNM 250149), and original specimen of *Mangonuia* sp.A Ladd (USNM 250160).

Etymology: *rotulacatharinea* [noun in apposition]; Catherine wheel, a symbolic spiked wheel; compound word from Latin *rotula* (small wheel) and *catharinea* (referring to 4th Century St. Catherine of Alexandria, who was martyred by being tied to a wheel).

Diagnosis:

Very small, somewhat loosely coiled, planispiral, coin-shaped shell with identical sculpture on both sides; whorls touching or uncoiling after about one whorl; whorls in cross-section almost rectangular (inner side, facing earlier whorls, somewhat convex); two strong spiral ribs with regular nodules forming outer shell keels; two rows of regular nodules, one each at inner corners of cross-sectional rectangle; convex area facing earlier whorls with two fine spiral threads close to center; areas between spiral ribs smooth or with weak axial growth lines. Translucent yellowish white. Protoconch diameter 0.52–0.72 mm; planispiral, without anal keel.

Description:

Teleoconch: very small, diameter of specimens in collections usually 1.6–4.4 at 1 1/3 to 2 1/2+ whorls. Shape: coin-shaped, planispiral (in some specimens body whorl off-plane), somewhat loosely coiled with deep suture between whorls, either still touching [as in holotypes of nominal species *Ps. thetidis* GARRARD, 1977, and *Ps. roddai* LADD, 1982; see Figs.269, 270], or uncoiling after about one whorl [as in lectotype; see Fig.268]; whorls in cross-section almost rectangular, with upper, peripheral and basal sides ± flat, and side facing earlier whorls ("columellar wall") somewhat convex (whorls touching in this convex part); umbilicus extremely wide (UD ca. 51% of SD). Sculpture (Fig. 281; appearing identical on both sides): Upper side: SSR not distinctly developed, with row of weak nodules; MR-area smooth except for ± weak axial growth lines; Periphery: UPR lacking; LPR with regular nodules, forming upper shell keel, often with spiral groove on peripheral side; IPR lacking; Base: outer basal area forming straight peripheral plane, with axial growth lines; strong basal rib (identical to LPR in shape, strength and sculpture) forming lower shell keel; inner basal area identical to MR-area; UC identical to SSR; columellar wall usually visible only in deep suture, in loosely coiled specimens with 2 fine spiral threads close to center of wall. Coloration: translucent yellowish white. – Protoconch (see Fig.272): very small to small (0.52–0.72, $\bar{x}$ = 0.62), multispiral, planispiral, without anal keel; translucent whitish. – Periostracum: thin, with weak axial lamellae and microscopic spiral threads. – Operculum: as decribed for genus. – Radula: five-toothed taenioglossate (2–1–2). – Anatomy: not known.

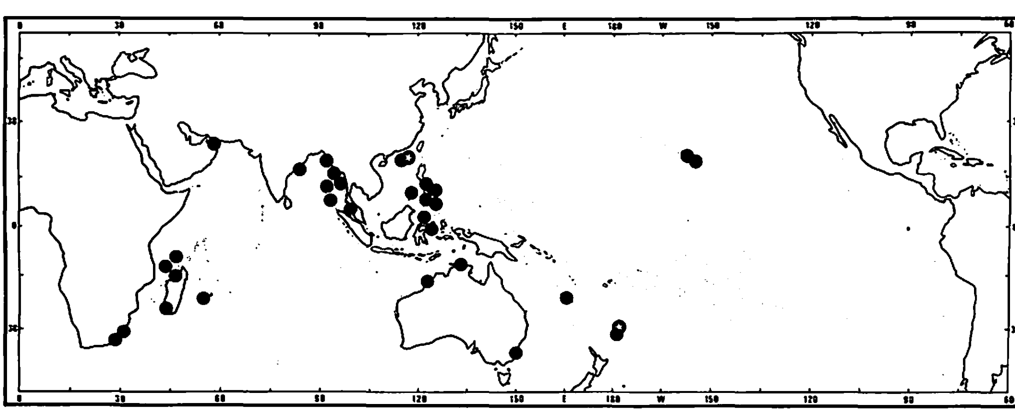


Fig. 271. Geographical distribution of *Spirolaxis rotulacatharinea* and *Sp. argonauta* n.sp.

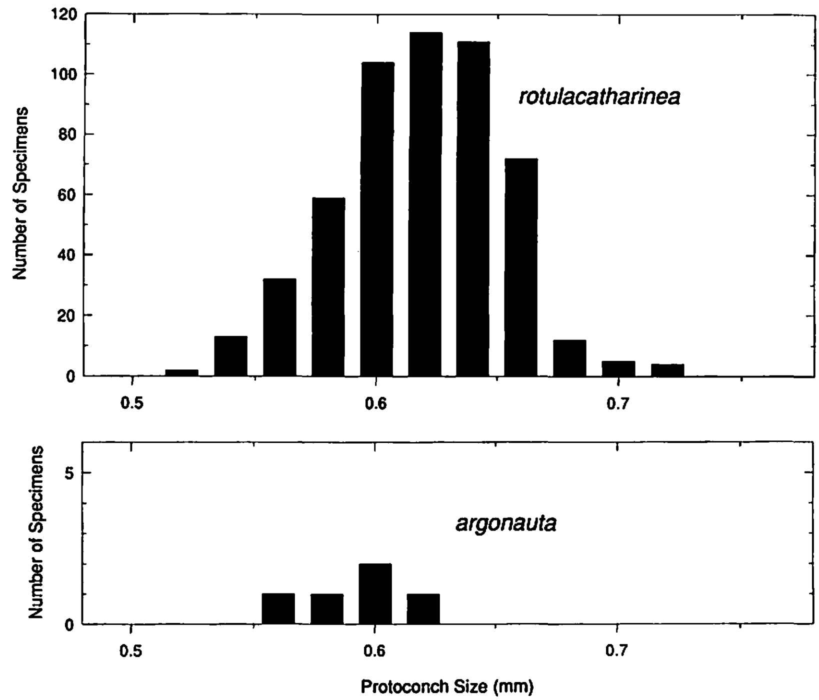


Fig. 272. Histograms of measured protoconch size. *Spirolaxis rotulacatharinea* (n = 528, x̄ = 0.62, sd = 0.03), and *Sp. argonauta* n.sp. (n = 5, x̄ = 0.59).

Geographical distribution (Fig.271): Indian Ocean and western to central Pacific.

Habitat: Sublittoral to upper bathyal (depth records between 27 and 622 m), live records from 146–302 m; mud and sand substrates.

Discussion:

Spirolaxis rotulacatharinea differs from other Indo-Pacific species of this group in having a somewhat loosely coiled shell with the protoconch still tightly surrounded by the first teleoconch whorl (in *Sp. cornuammonis*, *Sp. cornuarietis* n.sp. and *Sp. exornatus* n.sp., the protoconch is completely free; see below). *Spirolaxis argonauta* n.sp. (see below) is similar, but has strong axial ribs on all teleoconch surfaces. In the otherwise very similar Atlantic species *Sp. centrifuga* Monterosato, 1890, at least the early protoconch whorls are free [see, e.g., Bieler, 1984b: pl.3 figs.19–20].

Spirolaxis rotulacatharinea varies in the degree of uncoiling of the later whorls, and a number of names have been given for tightly-coiled forms (*Pseudomalaxis theditis* Garrard, 1977; *Mangonuia* "sp.A" and *Ps. roddai* Ladd, 1982) [Figs.269, 270, and discussion and figures in Bieler, 1984b]. Judged from original text and illustration, the nominal species *Spirolaxis cohaerentia* Laws, 1944, from the New Zealand Miocene, may belong here.

Spirolaxis argonauta n.sp.
Figs.271–273, 282

1984 *Pseudomalaxis (Spirolaxis) rotulacatharinea*, - Bieler [in part], Arch. Moll., 115(1/3): 80 [non *Homalaxis rotulacatharinea* Melvill & Standen, 1903].

Type measurements:

	SD	H	PD	Tw	UD	Collection
Holotype	4.5	1.4	0.62	2 5/8	2.1	USNM 277332
Paratype 1	4.8	1.6	0.60	2 3/4	2.2	FMNH 223408
Paratype 2	4.6	1.5	0.56	2 5/8-	2.1	USNM 859450
Paratype 3	3.3	1.1	?	ca. 2 1/8-	1.4	USNM 859450
Paratype 4	3.0	1.0	0.60	1 9/10	1.3	USNM 859450
Paratype 5	2.6	1.0	0.58	1 3/4+	1.2	USNM 859450
Paratype 6	5.2	1.7	0.60	2 7/8+	2.4	NMNZ MF.25597

Type locality: off Pratas Island [Tung-sha Tao], China Sea (20°37'N, 115°43'E), 380 m, grey mud and sand, 10.3°C bottom temperature ['Albatross' Sta. 5301]. Paratypes 1–5 from holotype lot. Paratype 6 from SE of Chanter Islets, Raoul Island, Kermadec Islands (29°16.5' S, 177°49.5' W), 512–549 m [R/V 'Acheron', BS442, 28 October 1975].

Material studied: 7 type specimens as listed above.

Etymology: *argonauta* [noun in apposition]; referring to the cephalopod genus of the same name, wherein females produce a papery shell-like egg-case somewhat similar in shape and sculpture.

Diagnosis:

Very small, almost planispiral, tightly-coiled, coin-shaped shell with identical sculpture on both sides; whorls in cross-section almost rectangular with all sides more or less flat; entire teleoconch surface sculptured with strong, irregular axial ribs, overlaying numerous microscopic spiral threads; two strong spiral ribs with regular nodules forming outer shell keels; two rows of nodules, one each at inner corners of cross-sectional rectangle. Yellowish white (periostracum darker). Protoconch diameter 0.56–0.62 mm, planispiral, without anal keel.

Description:

Teleoconch: very small, diameter of specimens 2.6–5.2 at 1 3/4+ to 2 7/8+ whorls. Shape: coin-shaped, almost planispiral (with upper side flat or slightly concave and base concave), tightly coiled; whorls in cross-section almost rectangular with all sides ± flat (basal side somewhat convex in larger specimens); umbilicus very wide to extremely wide (UD ca. 45% of SD). Sculpture (Fig.282; appearing identical on both sides): entire surface with strong, irregular axial ribs connecting nodules of spiral ribs, overlaying numerous ± distinctly developed microscopic spiral threads; Upper side: SSR not distinctly developed, with row of weak nodules; MR-area without spiral ribs;

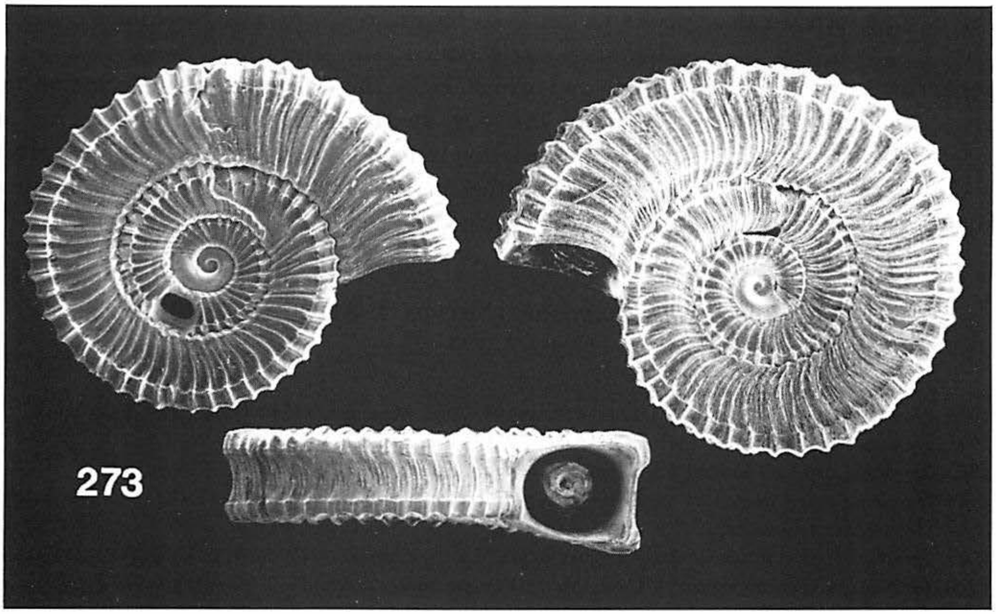


Fig. 273. *Spirolaxis argonauta* n.sp. [SEM]; holotype; China Sea; USNM 277332; SD = 4.5.

Periphery: UPR lacking; LPR very wide and strong, with regular nodules, often with spiral grooves (especially on peripheral side); IPR lacking; Base: without spiral ribs except for strong basal rib (identical to LPR in shape, strength, and sculpture) forming lower shell keel; UC as weak as SSR; no columellar wall visible (SSR and UC directly connecting to shell keels of previous whorl). Coloration: yellowish white. - Protoconch (see Fig.272): very small to small (0.56–0.62, $\bar{x}$ = 0.59), multispiral, planispiral, without anal keel; yellowish white. - Periostracum: thick, forming additional scaly axial ribs; yellowish brown. - Operculum: as decribed for genus. - Radula and Anatomy: not known.

Geographical distribution (Fig.271): Known from China Sea and Kermadec Islands.

Habitat: Upper bathyal (depth records between 380 and 549 m), live records (holotype, paratypes 1,2,5) from 380 m; mud and sand substrates.

Discussion:

Atlantic *Spirolaxis lamellifer* [13] Rehder, 1935, is very similar (1935: 128, pl.7 figs.8–10; holotype USNM 426235, vidi; see Bieler, 1984a: pl.5 figs.1–4). That species differs by having the shell more loosely coiled (resulting in a wide and deep suture), and by more regular axial ribs (only one per nodule on peripheral ribs).

[13] When the generic name *Pseudomalaxis* and *Spirolaxis* were found to be of masculine gender, I incorrectly used the spelling *Ps. lamelliferus* for the species originally described as *Ps. lamellifera* (see Bieler, 1984b: 66, 81). The correct suffix meaning "bearing" is -fer, -fera, -ferum (the Latin adjective ferus-a-um, meaning "wild").

The closest form to this species in the Indo-Pacific is *Spirolaxis rotulacatharinea* (see above), which has the shell more loosely coiled, the subsutural rib and umbilical crenae more strongly developed, and which lacks the coarse axial sculpture of *Sp. argonauta* n.sp. The holotype lot of this new species was previously cited (BIELER, 1984b: 80) as an example for extreme variation in *Sp. rotulacatharinea*; a reinvestigation of the specimens and the discovery of further material revealed additional differences and warranted the description of a new taxon.

Spirolaxis cornuammonis (MELVILL & STANDEN, 1903)

Figs.274–277, 283

*1903 *Homalaxis cornu-Ammonis* MELVILL & STANDEN, Ann. Mag. nat. Hist., (7)*12*: 298, pl.21 fig.4.
1911 *Pseudomalaxis cornu-ammonis*, - IREDALE, 1911a, Proc. malac. Soc. Lond., *9*(4): 256.
1973 *Spirolaxis* [sp.], - SANDVED & ABBOTT, Shells in color: 29, pl.33.
1984 *Pseudomalaxis (Spirolaxis) cornuammonis*, - BIELER, 1984b, Arch. Moll., 115(1/3): 77, pl.3 fig.23 [lectotype designation].
1985 *Pseudomalaxis cornuammonis*, - DRIVAS & JAY, La Conchiglia, *17*(190-191): 8, fig.14.
1987 *Homalaxis cornu-ammonis*, - TREW, MELVILL's new moll. names: 34.

Type measurements (lectotype): SD = 4.9, H = 2.1, Tw = 2 1/8.

Type locality: "Gulf of Oman, Lat. 24°58'N., Long. 56°54'E., 156 fathoms [256 m]."

Material studied: 29 specimens (ANSP, BMNH, IRSNB, MNHNP, NMP, NMNZ, NMW, USNM), including lectotype [BIELER, 1984b: 78] (BMNH 1903.12.15.73) and paralectotypes (NMW 1955.158.197: 3 specimens and 2 fragments; USNM 171385: 2 specimens) of *H. cornuammonis*.

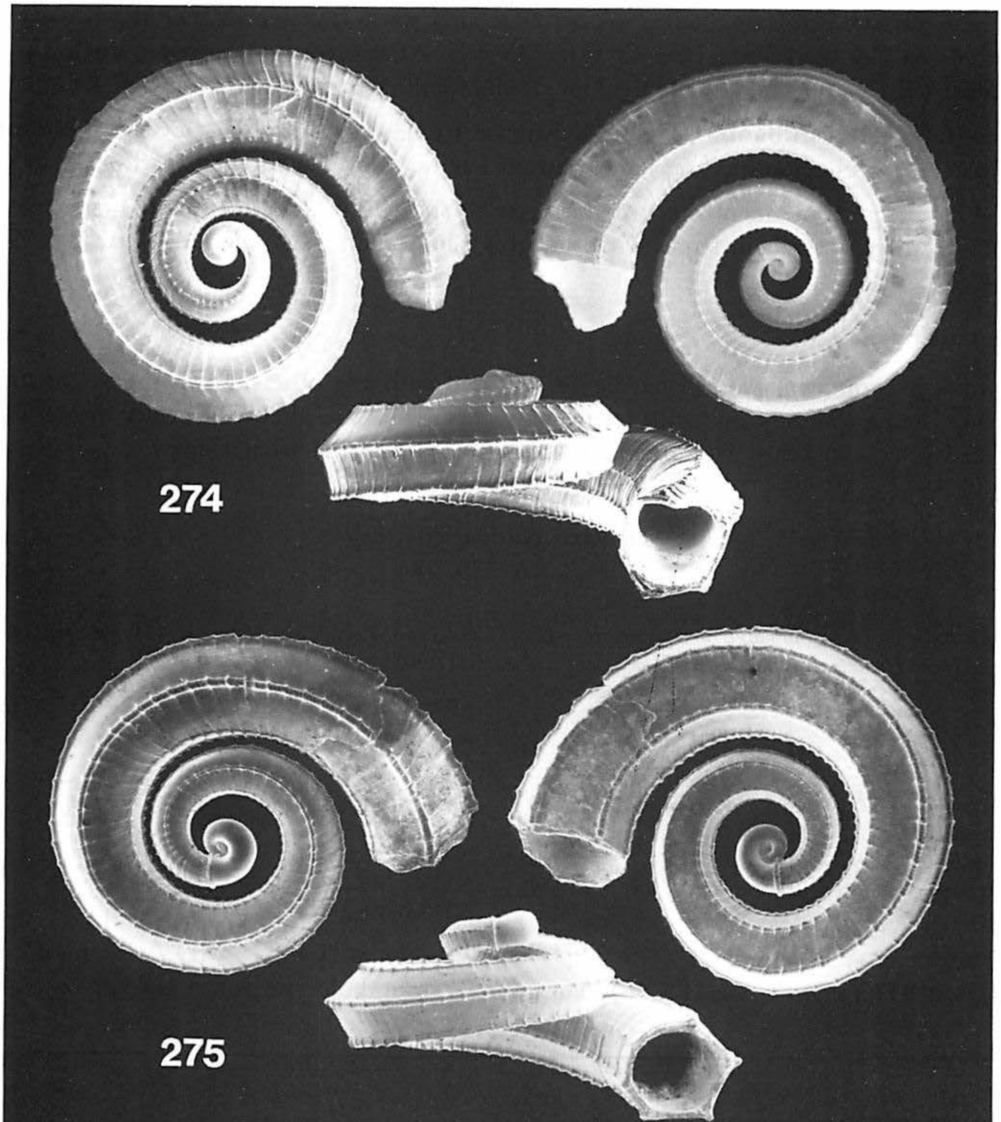
Etymology: *cornuammonis* [noun in apposition]; Ammon's horn, compound word from Latin noun *cornu* (horn) and the Egyptian ram-like deity [H]Ammon (Greek spelling).

Diagnosis:

Very small shell with identical sculpture on both sides, uncoiled in open helicoid spiral; whorls hexagonal in cross-section with areas between corners flat and of almost equal size; the six corners each formed by spiral ribs with weak, widely spaced, regular nodules; upper, two peripheral and basal ribs somewhat stronger than the two slightly closer-spaced ribs facing earlier whorls. Translucent whitish, sometimes with fawn flames. Protoconch diameter 0.56–0.62 mm; planispiral, without anal keel.

Description:

Teleoconch: very small, diameter of specimens in collections usually 1.5–4.9 at 2 1/8 to 3 3/8+ whorls. Shape: open helicoid spiral; whorls in cross-section hexagonal with areas between corners flat and of almost equal size; "umbilicus" extremely wide ("UD" ca. 61% of SD). Sculpture (Fig.283; appearing identical on both sides): entire shell surface with weak axial riblets connecting nodules on spiral ribs; Upper side: well-developed, finely nodulose SSR forming upper shell keel; MR-area without spiral



Figs. 274, 275. *Spirolaxis cornuammonis* (Melvill & Standen, 1903) [SEM]. Fig. 274: lectotype of *Homalaxis cornuammonis*; Gulf of Oman; BMNH 1903.12.15.73; SD = 4.9. Fig. 275: paralectotype from type locality; USNM 171385; SD = 3.4.

sculpture; Periphery: UPR lacking; LPR somewhat stronger than SSR, forming upper peripheral keel; IPR lacking; Base: without spiral sculpture except for strong basal keel (identical to LPR in strength and sculpture); UC identical to SSR; side facing earlier whorls with 2 well-developed nodulose spiral ribs (somewhat finer and more closely-spaced than the other four spiral ribs). Coloration: translucent whitish, some specimens with fawn flames. – Protoconch (see Fig. 277): very small to small (0.56–0.62, x̄ = 0.59), multispiral, planispiral, without anal keel; translucent white, with early whorls and outer corner next to varix darker. - Periostracum: forming thick axial scales; yellowish brown. - Operculum, Radula and Anatomy: not known.

Geographical distribution (Fig.276): Known from western Indian Ocean (Gulf of Oman, Réunion, South Africa) and western Pacific (New Caledonia, Norfolk Island).

Habitat: Sublittoral (depth records between 50 and 340 m), no live records (specimen with fresh periostracum from 80-90 m, grey sandy mud; Natal, South Africa; NMP D4395).

Discussion:

Spirolaxis cornuammonis can hardly be confused with any other known species of this group, being the only one with teleoconch whorls that are almost perfectly hexagonal in cross-section. Only *Sp. cornuarietis* n.sp. (below) is somewhat similar.

Spirolaxis cornuarietis n.sp.
Figs.276-278, 284

1977 *Pseudomalaxis (Spirolaxis) rotulacatherinea* [sic], - GARRARD, Rec. Austr. Mus., *31*(13): 566, figs.2a-b [non *Homalaxis rotulacatharinea* MELVILL & STANDEN, 1903].

Type measurements:

	SD	H	PD	Tw	UD	Collection
Holotype	3.0	0.9	0.66	1 1/2+	2.0	MNHNP unnumbered
Paratype 1	3.0	0.9	0.66	1 3/8	1.8	FMNH 223422
Paratype 2	2.6	0.8	0.68	1 1/4	1.6	NMP K7405/T375
Paratype 3	3.8	1.2	0.66	1 7/8-	2.4	NMNZ MF.25730
Paratype 4	1.8	0.5	0.62	7/8	1.1	NMNZ MF.27189

Type locality: Réunion (21°05'S, 55°12'E), 170-225 m [Cruise "MD32 Réunion" of 'MARION-DUFRESNE'; Sta. DC56]. Paratype 1 from holotype lot. Paratype 2 from

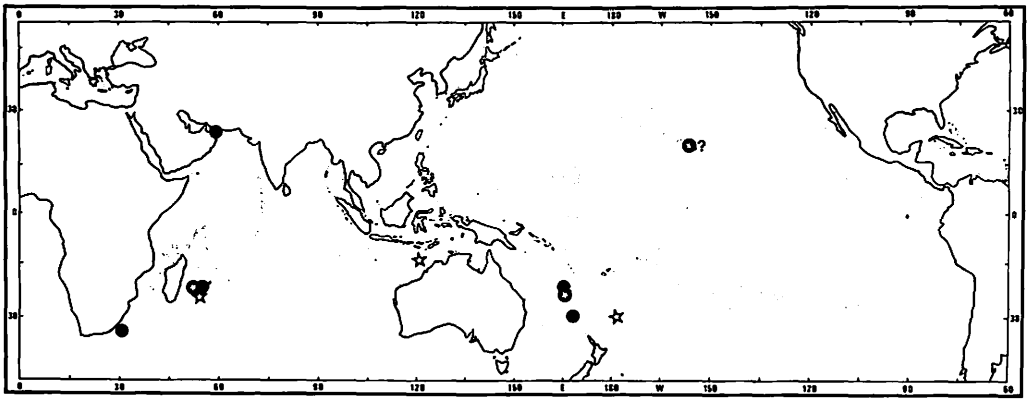


Fig.276. Geographical distribution of *Spirolaxis cornuammonis*, *Sp. exornatus* n.sp., and *Sp. cornuarietis* n.sp.

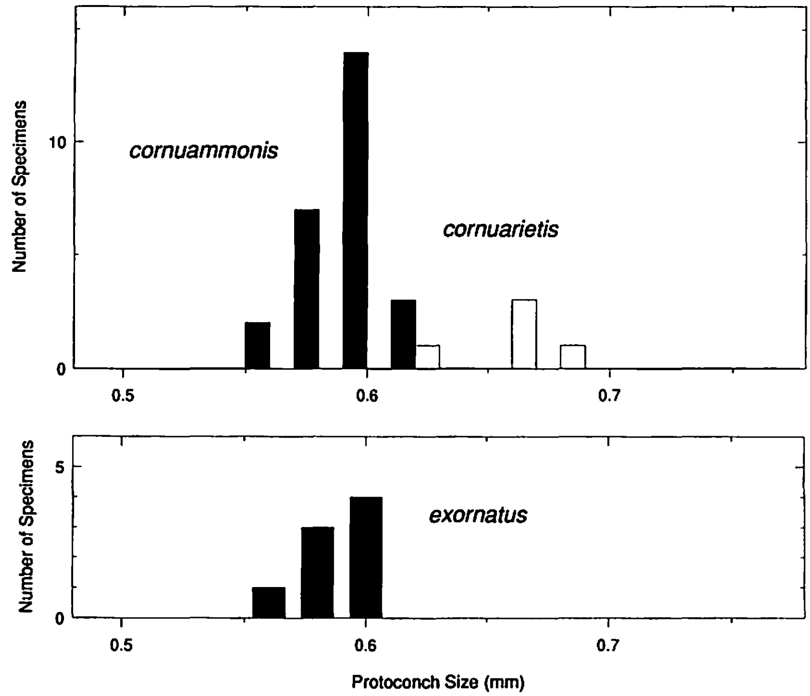


Fig. 277. Histograms of measured protoconch size. *Spirolaxis cornuammonis* (n = 26, x̄ = 0.59, sd = 0.02), *Sp. cornuarietis* n.sp. (n = 5, x̄ = 0.66) and *Sp. exornatus* n.sp. (n = 8, x̄ = 0.59).

nearby Sta. DC128 (20°51'S, 55°36'E), 280–340 m. Paratype 3 from SE of Nugent Island, Raoul Island, Kermadec Islands (29°14.7'S, 177°49.4'W), 146–165 m [R/V 'Acheron' BS438, 28 October 1975]. Paratype 4 from SE of Smith Bluff, Raoul Island, Kermadec Islands (29°18.9'S, 177°56.4'W), 82–100 m [R/V 'Acheron' BS572, 10 September 1976].

Material studied: 5 type specimens as listed above.

Etymology: *cornuarietis* [noun in apposition]; ram's horn, compound word from Latin nouns *cornu* (horn) and *aries* (ram); here referring to the uncoiled shell.

Diagnosis:

Very small, open-coiled, almost planispiral shell with identical sculpture on both sides; whorls in cross-section almost square (inner side, facing earlier whorls, distinctly convex); two strong spiral ribs with regular nodules forming outer shell keels; two similar, but much finer ribs forming inner corners of cross-sectional square; convex area facing earlier whorls initially with two, later up to four, fine nodulose ribs. White, sometimes with fawn spots on periphery. Protoconch diameter 0.62–0.68 mm; planispiral, without anal keel.

Description:

Teleoconch: very small, diameter of specimens 1.8–3.8 at 7/8 to 1 7/8– whorls. Shape: open-coiled, almost planispiral; whorls in cross-section almost square, with upper, peripheral and basal sides ± flat, and side facing previous whorl ("columellar wall") distinctly convex; "umbilicus" extremely wide (UD ca. 62% of SD). Sculpture (Fig.284; appearing identical on both sides): Upper side: SSR distinctly developed, narrow, with fine regular nodules; MR-area smooth; Periphery: UPR lacking; LPR wide and strong, with regular nodules, forming upper shell keel; IPR lacking; Base: outer basal area (between shell keels) smooth; strong basal rib (identical to LPR in shape, strength and sculpture) forming lower shell keel; UC resembles SSR; convex side facing earlier whorls initially with 2 fine nodulose spiral ribs, one in center of whorl, one relatively closely spaced below it (some specimens later with a third rib of about equal strength above the central rib; and even later with a fourth, finer thread). Coloration: translucent to opaque white, some specimens with fawn spots on SSR and periphery, connected by weaker flames on MR-area. – Protoconch (see Fig.277): small (0.62–0.68, $\bar{x}$ = 0.66), multispiral, planispiral, without anal keel; translucent whitish with early whorls and varical area tan. – Periostracum: with fine spiral sculpture; yellowish brown. – Operculum, Radula and Anatomy: not known.

Geographical distribution (Fig.276): Known from Réunion, from off Western Australia, and from the Kermadec Islands.

Habitat: Sublittoral (depth records between 82 and 340 m), no live records.

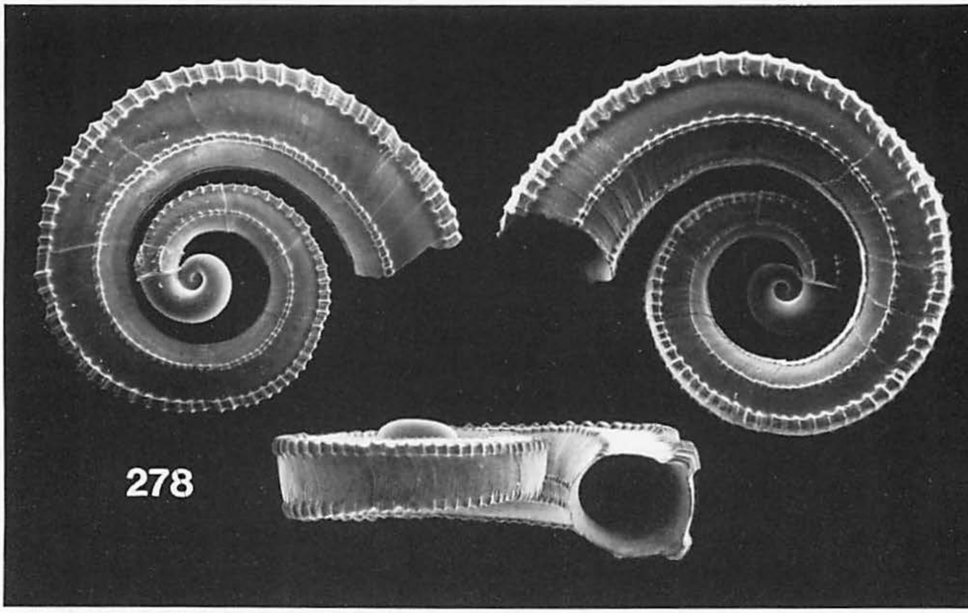


Fig. 278. *Spirolaxis cornuarietis* n.sp. [SEM]; holotype; Réunion; MNHNP unnumbered; SD = 3.0.

Discussion:

Spirolaxis cornuammonis (above) is superficially similar, but shows helicoid coiling, and whorls that are almost perfectly hexagonal in cross-section. Small specimens of *Spirolaxis cornuarietis* n.sp. are similar to the early whorls of *Sp. exornatus* n.sp., before the spiral sculpture of that species is fully developed (see discussion below).

Two Miocene species from Transylvania, *Spirolaxis corniculum* (O. BOETTGER, 1902) and *Sp. quinquangularis* (O. BOETTGER, 1902), share the type of uncoiling and sculptural pattern with this species [see ZILCH, 1934: pl.7 figs.19a-c, 21a-b; BIELER, 1984b: pl.3 figs.21–22]. *Spirolaxis corniculum* differs by lacking spiral sculpture on the straight wall facing the protoconch and by a larger protoconch (0.72 mm; lectotype, SMF 12.2373a, vidi). *Spirolaxis quinquangularis* differs by having finer nodules on the spiral ribs, only one spiral thread on the wall facing the protoconch, and by a larger protoconch (0.72 mm; holotype, SMF 12.2374a, vidi).

Spirolaxis exornatus n.sp.

Figs.276, 277, 279, 280, 285, 286

?1979 *Pseudomalaxis* sp. cf. *cornuammonis*, – KAY, Hawaii. mar. shells: 100 fig.36F [non *Pseudomalaxis cornuammonis* (MELVILL & STANDEN, 1903)].

1984 *Pseudomalaxis (Spirolaxis)* n.sp., – BIELER, Arch. Moll., *115*(1/3): 78, pl.3 fig.25.

Type measurements:

	SD	H	PD	Tw	UD	Locality	Collection
Holotype	3.8	1.0	0.58	1 7/8–	ca. 2.2	Réunion	MNHNP unnumbered
Paratype 1	4.0	1.1	0.60	1 7/8	2.3	Réunion	FMNH 223426
Paratype 2	3.2	0.9	0.56	1 3/4–	1.8	Réunion	NMP K7406/T376
Paratype 3	3.0	0.8	0.58	1 1/8	1.6	Réunion	WAM 484-91
Paratype 4	2.9	0.8	0.58	1 1/2	1.7	Réunion	MNHNP unnumbered
Paratype 5	2.8	0.8	0.60	1 1/2–	1.6	Réunion	MNHNP unnumbered
Paratype 6	2.7	0.8	?	1 5/8	1.5	Réunion	MNHNP unnumbered
Paratype 7	2.6	0.8	0.60	1 3/8	1.5	Réunion	MNHNP unnumbered
Paratype 8	2.8	0.8	0.60	1 5/8	1.6	New Caledonia	MNHNP unnumbered

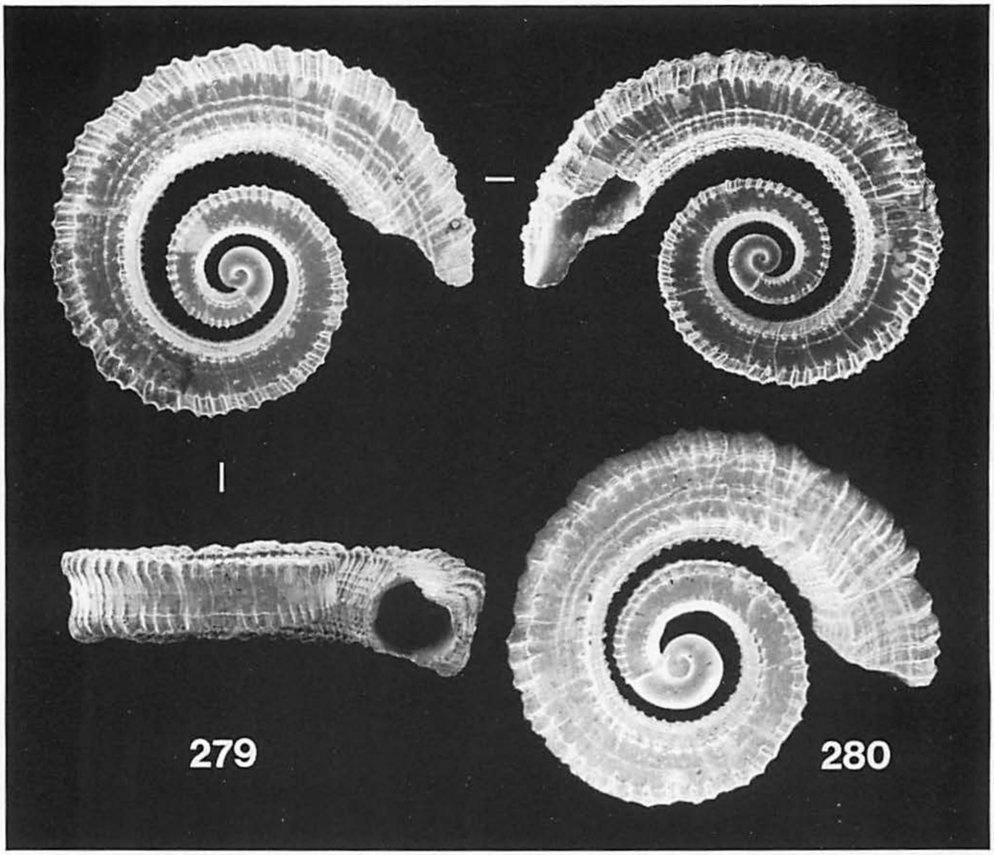
Type locality: Réunion (20°51'S, 55°36'E), 280–340 m [Cruise "MD32 Réunion" of R/V 'MARION-DUFRESNE,' Sta. DC128]. Paratypes 1–7 from holotype lot. Paratype 8 from south of New Caledonia (22°17'S, 167°14'E), 425–430 m ['VAUBAN' 1978–79, Sta.2].

Material studied: 9 type specimens as listed above, and 5 fragments (MNHNP).

Etymology: *exornatus-a-um* [adjective]; Latin: decorated, embellished; here referring to the fine spiral sculpture that separates this species from its congeners.

Diagnosis:

Very small, open-coiled, almost planispiral shell with identical sculpture on both sides; whorls in cross-section almost rectangular (inner side, facing earlier whorls, somewhat convex); 2 very strong nodose spiral ribs forming outer shell keels; 2 much weaker

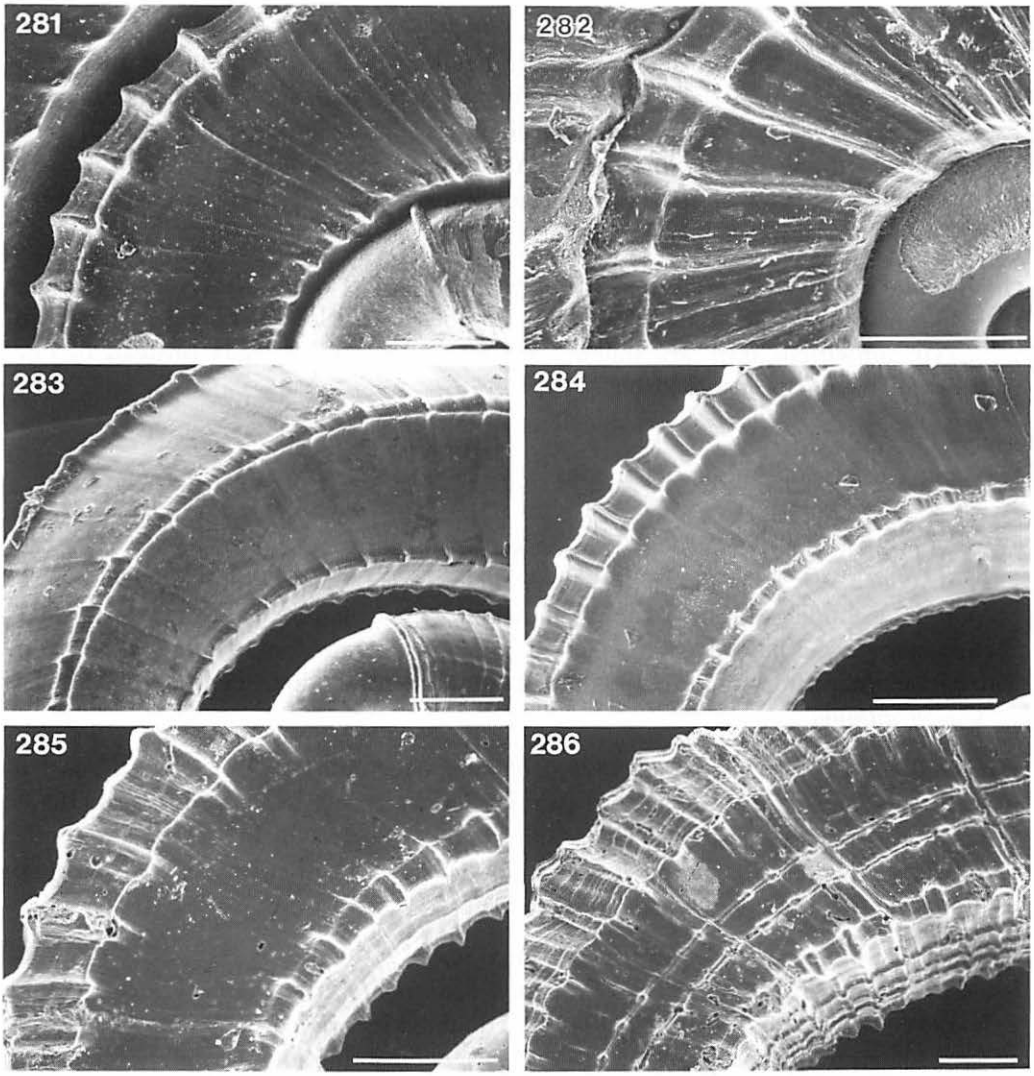


Figs. 279, 280. *Spirolaxis exornatus* n.sp. [SEM]. Fig. 279: holotype; Réunion; MNHNP unnumbered; SD = 3.8. Fig. 280: paratype 8; New Caledonia; MNHNP unnumbered; SD = 2.8.

ribs with more regular nodules forming inner corners of cross-sectional rectangle; upper, peripheral and basal sides initially smooth, later with finely nodulated spiral threads; inner side, facing earlier whorls, initially with 1 central, later with up to 7 spiral threads. White. Protoconch diameter 0.56–0.60 mm; planispiral, without anal keel.

Description:

Teleoconch: very small, diameter of specimens 2.6–4.0 at 1 1/8 to 1 7/8 whorls. Shape: open-coiled, almost planispiral; with whorls in cross-section almost rectangular, with upper, peripheral and basal sides flat, and side facing previous whorl ("columellar wall") somewhat convex; "umbilicus" extremely wide (UD ca. 57% of SD). Sculpture (Figs. 285–286; appearing identical on both sides): Upper side: SSR developed as row of small, ± regular nodules; MR-area originally smooth, later with 1–4 fine, nodulose spiral threads; Periphery: UPR lacking; LPR very wide and strong, with somewhat irregular, spirally grooved nodules, forming upper shell keel; IPR lacking; Base: outer basal area (between peripheral keels) initially smooth or with weak axial growth lines connecting nodules of keel-forming ribs, later with 1-5 fine spiral threads; strong basal rib (identical to LPR in shape, strength and sculpture) forming lower shell keel; sculpture of inner basal area between that keel and weak UC (which resembles SSR) identical to MR-area; area facing earlier whorls initially with 1 central, later flanked on each side by up to 3 narrower, finely nodulated spiral threads. Coloration: white. Protoconch (see Fig.277): very small (0.56-0.60, $\bar{x}$ = 0.59), multispiral, planispiral,



Figs. 281-286. Details of teleoconch sculpture in *Spirolaxis* [SEM] (Figs. 281-285: end of first whorl; Fig. 286: ca. 1 1/2 whorls). Fig. 281: *Sp. rotulacatharinea* (USNM 820307). Fig. 282: *Sp. argonauta* n.sp. (holotype, USNM 277332). Fig. 283: *Sp. cornuammonis* (USNM 171385). Fig. 284: *Sp. cornuarietis* n.sp. (holotype, MNHNP unnumbered). Figs. 285, 286: *Sp. exornatus* n.sp. (holotype, MNHNP unnumbered). Scale bars = 200 µm.

without anal keel; white. – Periostracum: olive-brown. Operculum, Radula and Anatomy: not known.

Geographical distribution (Fig.276): Known from Réunion, New Caledonia and, possibly, Hawaii.

Habitat: Lower sublittoral to upper bathyal (depth records between 280 and 430 m), no live records.

Discussion:

Spirolaxis exornatus n.sp. differs from all other known Recent species of this genus by having distinct spiral sculpture in the upper, peripheral and basal areas between the major spiral ribs of the teleoconch. Similar sculpture is known in several fossil species, e.g., Eocene *Spirolaxis texanus* (ALDRICH, 1911), which has a tightly coiled shell carrying two rows of strong nodules on midrib and inner basal areas (holotype, USNM 639132, vidi; see BIELER, 1984b: 81, pl.5 fig.31).

The juvenile specimen figured by KAY (1979: 100, fig.36F) is most likely an early stage of this species, with the adult spiral sculpture not yet developed. Young specimens of *Spirolaxis cornuarietis* n.sp. are similar, but have two spiral threads (instead of one) on the wall facing the protoconch.

4. Nomina dubia and misplaced species

bairdii HANLEY, 1863, *Solarium* (from unknown locality).
Thes. conch., *3*: 231, pl.254 figs.48, 49. HANLEY (1863: 231) mentioned that the "unique example of our national museum is not mature, but has too salient characters to be passed over." This is possibly a member of *Solatisonax*, but the original description and figures do not allow identification. Type lost (BMNH). *Nomen dubium*.

biangulatum J.E. GRAY *in* KING, 1826, *Solarium* (Australia).
Narr. surv. coasts Australia, 2: 481 [no figure or reference to such]. PHILIPPI (1853b: 34) doubted the generic placement, and HANLEY (1863: 246, index) stated; "Not a *Solarium* ('nacreous')." Type material not located; original description does not allow identification. *Nomen dubium*.

bicarinatum PHILIPPI, 1853, *Solarium* (China Sea).
Syst.-Conch. Cab. II, *7*: 23, pl.3 fig.4 [non *Solarium bicarinatum* GRATELOUP, 1832]. HANLEY (1863: 245) and BAYER (1948: 37) doubted its original taxonomic allocation. Type material lost (BOUCHET, in litt.). *Nomen dubium* and junior primary homonym.

cobijensis "REEVE" PAETEL & SCHAUFUSS, 1869, *Solarium* (Peru).
Moll. Syst. cat.: 43 [no figure or reference to such]. *Nomen nudum*.

egenum GOULD, 1849, *Solarium* (no locality given; New Zealand, teste GOULD, 1852: 196).

Proc. Boston Soc. nat. Hist., *3*: 84. Type species of *Antisolarium* FINLAY, 1926; Trochidae.

impressum G. NEVILL *in* G. NEVILL & H. NEVILL, 1869, *Solarium* (Ceylon).
J. asiat. Soc. Bengal, *38*(2): 162, pl. 17 fig. 11. A species of the trochid genus *Minolia* A. ADAMS, 1860, teste WINCKWORTH *in* BAYER, 1948: 42. Trochidae.

kochii DALL, 1909, *Architectonica* (Chile).
Proc. U.S. natl. Mus., *37*(1704): 232. New name for *Solarium nanum* (KOCH MS.) PHILIPPI, 1853, non *Solarium nanum* GRATELOUP, 1832. Type specimen not located. *Nomen dubium*.

nanum (KOCH MS.) PHILIPPI, 1853, *Solarium* (Chile).
Syst.-Conch. Cab.II, *7*: 27, pl.4 fig.5 [non *Solarium nanum* GRATELOUP, 1832]. PHILIPPI referred to an article by KOCH (1851, Zeitschrift für Malakozoologie) that does not exist. Replaced by *Architectonica kochii* DALL, 1909 *(q.v.)*. Type material not located. *Nomen dubium* and junior primary homonym.

"perspeculatus" MEUSCHEN, 1781, *Trochus* (Indian Ocean).
Index vermium, Zoophylac. Gronov., unpag. [no figure or reference to such]; based on GRONOVIUS (1781: 323, no.1485): "Trochus testa crenato-umbilicata... " and probably referred to a shell of *Architectonica*. Considered an indeterminable "*Solarium*" (HANLEY, 1863: 245, 247) or "*Torinia*" (BAYER, 1948: 39). MEUSCHEN's work (1781) was rejected for nomenclatural purposes (ICZN Opinion 261, 1954). Not binominal.

radiatum G. Fischer, 1807, *Solarium* ("la mer des Indes").
Mus. Demidoff: 214 [non *Solarium radiatum* BORSON, 1821]. Type specimen (ZMUM NL–479; lectotype) identified as *Astraea heliotropium* (MARTYN, 1784) by IVANOV & KANTOR (1991: 25, 39). Turbinidae.

rosulentum WATSON, 1883, *Solarium (Torinia)* (off Port Jackson, Australia).
J. Linn. Soc., *16*: 610; WATSON, 1886, Rep. sci. Res. voy. CHALLENGER, Zool., *15*(42)(2): 136, pl.8 fig.12. Placed in genus *Minolia* A. ADAMS, 1860, by HEDLEY (1903: 332), and in *Minolops* IREDALE, 1929, by IREDALE (1929: 169). Trochidae.

sulcifera PEASE, 1869, *Torinia* (Kauai, Hawaiian Islands).
Amer. J. Conch., *5*(2): 79 [no figure or reference to such]. Type material not located; original description does not allow identification. *Nomen dubium*.

F. Acknowledgments

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Index

Italic type indicates (a) valid names for Recent architectonicid taxa as used here and (b) major text references. Names of accepted architectonicid genus-group taxa are in Capital letters, names of new species in **bold** face. Names in Roman type are extinct species, synonyms, superseded names, or non-architectonicids. Original generic placement in parentheses. Entries marked by an asterisk (*) are not treated critically, such as fossil nominal species entering homonymy.

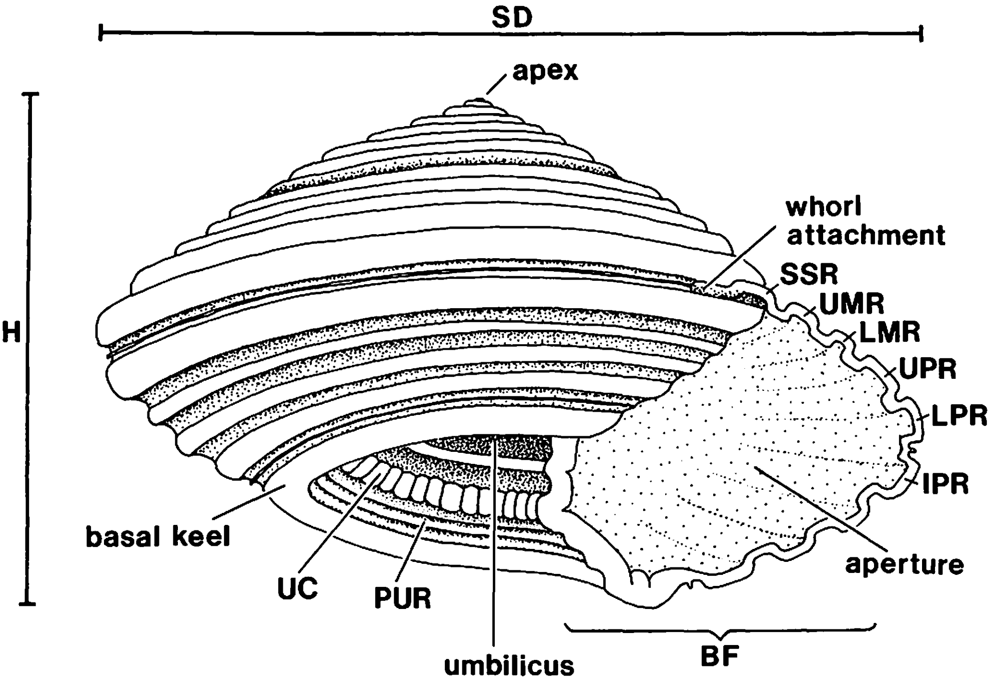

Diagram of idealized architectonicid teleoconch, illustrating major elements of spiral sculpture. - BF basal field, H height, IPR infraperipheral rib, LMR lower midrib, LPR lower peripheral rib, PUR proxumbical rib, SD shell diameter, SSR subsutural rib, UC umbilical crenae, UMR upper midrib, UPR upper peripheral rib.