

Handbook of Zoology

Echinodermata

Echinoidea

Volume 2: Irregularia

Handbook of Zoology

Founded by Willy Küenthal
Editor-in-chief Andreas Schmidt-Rhaesa

Echinodermata

Edited by Andreas Schmidt-Rhaesa

DE GRUYTER

Echinoidea

Volume 2:

Echinoidea with bilateral symmetry. Irregularia

Heinke Schultz

DE GRUYTER

Author

Heinke Schultz
Dorfstr. 32
25485 Hemdingen, Germany

Scientific Editor

Andreas Schmidt-Rhaesa
Centrum für Natukunde (CeNak)
Universität Hamburg
Zoologisches Museum
Martin-Luther-King-Platz 3
20146 Hamburg, Germany

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Foreword

The present volume follows and complements volume 1, published in 2015. Whereas volume 1 presented a brief introduction and the “regular” sea urchins, this volume treats the “irregular” sea urchins. Irregular sea urchins fascinate by their bilateral symmetry and their endobenthic mode of life. After a brief introduction and an overview on the classification, species are described and illustrated in systematic order. For a brief introduction to echinoids (sea urchins) and a glossary, the reader is referred to volume 1.

The two Echinoidea volumes in the Handbook of Zoology series were generated from a three-volume

book publication, *Sea Urchins: A Guide to Worldwide Shallow Water Species* (published in 2005 by Heinke & Peter Schultz Partner Scientific Publications), followed by the supplement volumes, *Sea Urchins II: Worldwide Irregular Deep Water Species* (2009) and *Sea Urchins III: Worldwide Regular Deep Water Species* (2011). All three volumes had a limited distribution and are out of print.

Andreas Schmidt-Rhaesa
Chief and Volume Editor

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Abbreviations

In the text, the names of the museums or collections are abbreviated. The following abbreviations were used:

AWI Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung, Bremerhaven, Germany

HF Heidi Friedhoff, Norderstedt, Germany

MfN Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitäts-Forschung, Berlin, Germany

NHM The Natural History Museum, London, UK

NIWA National Institute for Water and Atmospheric Research Ltd., Wellington, New Zealand

VT Hans-Volker Thiel, Düsseldorf, Germany

ZMUC Zoological Museum, Natural History Museum of Denmark, Copenhagen, Denmark

ZMH Zoologisches Museum, Centrum für Naturkunde, Hamburg, Germany

ZSM Zoologische Staatssammlung, Munich, Germany

1 Introduction

Early diademataceans are the ancestors of the Irregularia. They evolved in the Lower Jurassic occupying a new habitat: they burrow more or less deeply into the sediment, where they live and feed. In adaptation to a life in this “new” environment, the morphology of these sea urchins changed radically. The test developed a bilateral symmetry, which also established the anterior-posterior axis and, simultaneously, unidirectional movement: the irregulars moved forward, with the anterior side (ambulacrum A III) ahead.

The new morphology followed a general trend. The test became flatter and the spines much shorter and more densely distributed, forming a uniform canopy, which implied less resistance to the surrounding substrate. When the animal ploughs through the sand, a mucus shield, created by the miliary spines, prevents particles from falling onto the epithelium of the animal. The tube feet of the upper side of the test were modified into flat, flap-like structures with an enlarged surface area and thin walls.

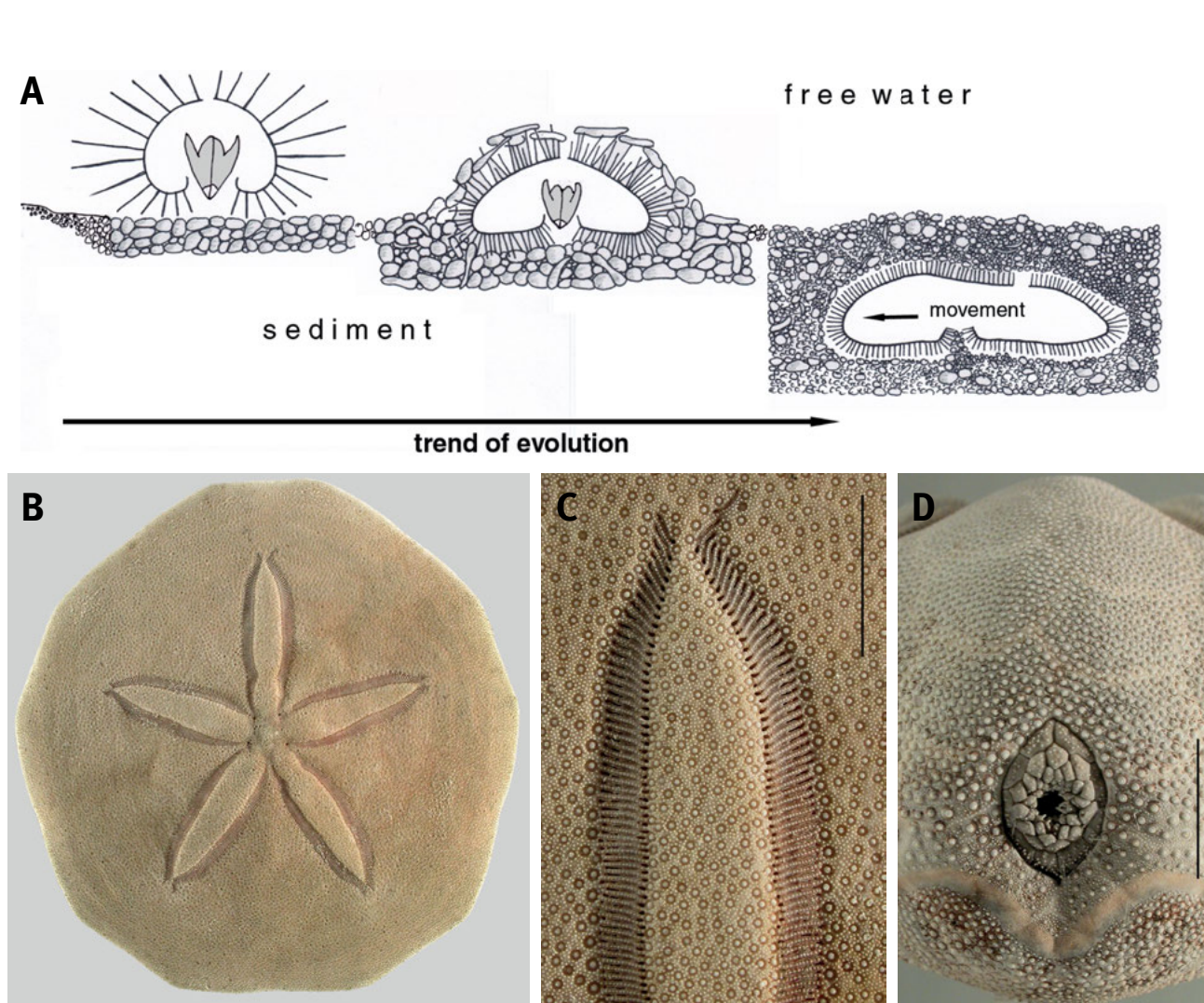


Fig. 1.1: (A–D) Irregular sea urchins. (A) General trend of evolution in early irregular echinoids: the trend leads from a globose regular sea urchin with long spines living on the sediment to a flatter test with shorter spines and teeth still present to a flat, short-spined specimen without teeth, the periproct separated from the central apical system in an anal groove, and living infaunally (anterior to the left). Modified after A.B. Smith (1984). (B, C) Petals of irregulars: (B) On the upper side, the pore pairs in the ambulacra are concentrated in leaf-shaped densely packed bands. (C) The inner pore is subcircular, the outer one more or less elongated. The associated podia are long lobes with an extremely thin surface specialized for gaseous exchange (*Peronella japonica*). Scale bar is 5 mm. (D) The periproct is at the posterior end of the test (*Brissus unicolor*). Scale bar is 10 mm.

This specialization increased the efficiency of respiration, because oxygen in the sediment is not as available as in the free water. The pore pairs in the ambulacra of the upper side are arranged in four or five leaf-shaped patterns (the petals). The periproct shifted to the posterior or even to the oral side. The feces were not released on the top of the test, in the apical shield, but posteriorly, clearing the rear of fecal material when burrowing.

This fundamental morphological change since the Early Jurassic (approximately 190 million years ago) generated a multiplicity of forms of echinoids (Fig. 1.1); many of which would later become extinct. Two groups succeed to date, the Clypeasteroidea and the Spatangoida (Smith 1984).

2 Classification

The taxa included in this volume belong, together with all regular sea urchins except for the subclass Cidaroidea, to the subclass Euechinoidea Bronn, 1860 (see volume 1: Schultz 2015).

Order Echinoneoidea H.L. Clark, 1925

- Family Echinoneidae L. Agassiz & Desor, 1847
 - Genus *Echinoneus* Leske, 1778
 - Genus *Koehleraster* Lambert & Thiéry, 1921
 - Genus *Micropetalon* A. Agassiz & H.L. Clark, 1907

Superorder Neognathostomata Smith, 1984

- Family Apatopygidae Kier, 1962
 - Genus *Apatopygus* Hawkins, 1920
 - Genus *Porterpygus* Baker, 1983

Order Cassiduloidea L. Agassiz & Desor, 1847

- Family Cassidulidae L. Agassiz & Desor, 1847
 - Genus *Cassidulus* Lamarck, 1801
 - Genus *Eurhodia* Haime in d'Archiac & Haime, 1853
 - Genus *Oligopodia* Duncan, 1869
 - Genus *Rhyncholampas* A. Agassiz, 1869
- Family Echinolampadidae Gray, 1851
 - Genus *Conolampas* A. Agassiz, 1883
 - Genus *Echinolampas* Gray, 1825
- Family Neolampadidae Lambert, 1918
 - Genus *Anochanus* Grube, 1868
 - Genus *Aphanopora* de Meijere, 1902, 1903
 - Genus *Nannolampas* Mortensen, 1948
 - Genus *Neolampas* A. Agassiz, 1869
 - Genus *Studeria* Duncan, 1891
 - Genus *Tropholampas* H.L. Clark, 1923

Order Clypeasteroidea L. Agassiz, 1835

Suborder Clypeasterina L. Agassiz, 1835

- Family Arachnoididae
 - Genus *Ammotrophus* H.L. Clark, 1928
 - Genus *Arachnoides* Leske, 1778
 - Genus *Fellaster* Durham, 1955
- Family Clypeasteridae L. Agassiz, 1835
 - Genus *Clypeaster* Lamarck, 1801

Suborder Scutellina Haeckel, 1896

Infraorder Laganiformes Desor, 1847

- Family Echinocyamidae Lambert & Thiéry, 1914
 - Genus *Echinocyamus* van Phelsum, 1774
 - Genus *Mortonia* Gray, 1851

- Family Fibulariidae Gray, 1855
 - Genus *Fibularia* Lamarck, 1816
 - Genus *Fibulariella* Mortensen, 1948
- Family Laganidae A. Agassiz, 1873
 - Genus *Laganum* Link, 1807
 - Genus *Peronella* Gray, 1855
- Family Rotulidae Gray, 1855
 - Genus *Heliophora* L. Agassiz, 1840
 - Genus *Rotula* Schumacher, 1817

Infraorder Scutelliformes Haeckel, 1896

- Family Astrictypeidae Stefanini, 1912
 - Genus *Astrictypeus* Verrill, 1867
 - Genus *Echinodiscus* Leske, 1778
- Family Dendrasteridae Lambert, 1900
 - Genus *Dendraster* L. Agassiz, 1847
- Family Echinarachniidae Lambert in Lambert & Thiéry, 1914
 - Genus *Echinarachnius* Gray, 1825
- Family Mellitidae Stefanini, 1912
 - Genus *Encope* L. Agassiz, 1840
 - Genus *Leodia* Gray, 1852
 - Genus *Mellita* L. Agassiz, 1841
 - Genus *Mellitella* Duncan, 1889
- Family Scutellidae Gray, 1825
 - Genus *Scaphechinus* A. Agassiz, 1864
- Family Taiwanasteridae Wang, 1984
 - Genus *Sinaechinocyamus* Liao, 1979
- Incertae sedis: *Marginoproctus* Budin, 1980

Superorder Atelostomata von Zittel, 1879

Order Holasteroidea Durham & Melville, 1957

- Family Calymnidae Mortensen, 1907
 - Genus *Calymne* Thomson, 1877
 - Genus *Sternopatagus* de Meijere, 1903
- Family Carnarechinidae Mironov, 1993
 - Genus *Carnarechinus* Mironov, 1978
- Family Corystusidae Foster & Philip, 1978
 - Genus *Corystus* Pomel, 1883
- Family Plexechinidae Mooi & David, 1996
 - Genus *Plexechinus* A. Agassiz, 1898
- Family Pourtalesiidae A. Agassiz, 1881
 - Genus *Ceratophysa* Pomel, 1883
 - Genus *Cystocrepis* Mortensen, 1907
 - Genus *Echinocrepis* A. Agassiz, 1879
 - Genus *Echinograna* Mortensen, 1907

Genus *Helgocystis* Mortensen, 1907
 Genus *Pourtalesia* A. Agassiz, 1869
 Genus *Rictocystis* Mironov, 1996
 Genus *Solenocystis* Mironov, 2008
 Genus *Spatagocystis* A. Agassiz, 1879

Family Urechinidae Duncan, 1889

Genus *Antrechinus* Mooi & David, 1996
 Genus *Cystechinus* A. Agassiz, 1879
 Genus *Pilematechinus* A. Agassiz, 1904
 Genus *Urechinus* A. Agassiz, 1879

Order Spatangoida L. Agassiz, 1840

Family Hemiasteridae H.L. Clark, 1917

Genus *Holanthus* A. Agassiz, 1848
 Genus *Kupeia* McKnight, 1974

Family Palaeostomatidae Lovén, 1868

Genus *Palaeostoma* Lovén, in A. Agassiz, 1872
 Genus *Sarsiaster* Mortensen, 1950

Suborder Brissidina Stockley et al., 2005

Family Brissidae Gray, 1855

Genus *Anabrissus* Mortensen, 1950
 Genus *Anametalia* Mortensen, 1950
 Genus *Brissalius* Coppard, 2008
 Genus *Brissopsis* L. Agassiz in L. Agassiz & Desor, 1847
 Genus *Brissus* Gray, 1825
 Genus *Cionobrissus* A. Agassiz, 1879
 Genus *Idiobrissus* H.L. Clark, 1939
 Genus *Meoma* Gray, 1851
 Genus *Metalia* Gray, 1855
 Genus *Neopneustes* Duncan, 1889
 Genus *Plagiobrissus* Pomel, 1883
 Genus *Rhynobrissus* A. Agassiz, 1872
 Genus *Taimanawa* Henderson & Fell, 1969

Family Palaeotropidae Lambert, 1896

Genus *Kermabrissoides* Baker, 1998
 Genus *Palaeobrissus* A. Agassiz, 1883
 Genus *Palaeotropus* Lovén, 1874
 Genus *Paleotrema* Koehler, 1914
 Genus *Scrippsechinus* Allison, Durham & Mintz, 1967

Superfamily Spatangoidea Gray, 1825

Family Eupatagidae Lambert, 1905

Genus *Eupatagus* L. Agassiz in L. Agassiz & Desor, 1847

Family Eurypatagidae Kroh, 2007

Genus *Elipneustes* Koehler, 1914
 Genus *Eurypatagus* Mortensen, 1948
 Genus *Linopneustes* A. Agassiz, 1881
 Genus *Paramaretia* Mortensen, 1950
 Genus *Platybrissus* Grube, 1866

Family Loveniidae Lambert, 1905

Genus *Araeolampas* Serafy, 1974
 Genus *Breynia* Desor in L. Agassiz & Desor, 1847
 Genus *Echinocardium* Gray, 1925
 Genus *Lovenia* Desor, in L. Agassiz & Desor, 1847
 Genus *Pseudolovenia* A. Agassiz & H.L. Clark, 1907

Family Maretidae Lambert, 1905

Genus *Granobrissoides* Lambert, 1920
 Genus *Gymnopatagus* Döderlein, 1901
 Genus *Hemimaretia* Mortensen, 1950
 Genus *Homolampas* A. Agassiz, 1874
 Genus *Maretia* Gray, 1855
 Genus *Nacospatangus* A. Agassiz, 1873
 Genus *Pycnolampas* A. Agassiz & H.L. Clark, 1907
 Genus *Spatagobrissus* H.L. Clark, 1923

Family Spatangidae Gray, 1825

Genus *Plethotaenia* H.L. Clark, 1917
 Genus *Spatangus* Gray, 1825

Family Macropneustidae Lambert, 1895

Genus *Argopatagus* A. Agassiz, 1879

Suborder Micrasterina Fischer, 1966

Family Aeropsidae Lambert, 1896

Genus *Aeropsis* Mortensen, 1907

Family Micrasteridae Lambert, 1920

Genus *Cyclaster* Cotteau, 1856
 Genus *Isopatagus* Desor, 1858

Suborder Paleopneustina Markov & Solovjev, 2001

Family Paleopneustidae A. Agassiz, 1904

Genus *Paleopneustes* A. Agassiz, 1873
 Genus *Peripatagus* Koehler, 1895
 Genus *Plesiozonon* de Meijere, 1903

Family Pericosmidae Lambert, 1905

Genus *Faorina* Gray, 1851
 Genus *Pericosmus* L. Agassiz in L. Agassiz & Desor, 1847

Family Prenasteridae Lambert, 1905

Genus *Agassizia* Valenciennes, 1846
 Genus *Prenaster* Desor, 1853
 Genus *Tripylus* Philippi, 1845

Family Schizasteridae Lambert, 1905

Genus *Abatus* Troschel, 1851
 Genus *Aceste* Thomson, 1877
 Genus *Brisaster* Gray, 1855
 Genus *Diploporaster* Mortensen, 1950
 Genus *Hypselaster* H.L. Clark, 1917
 Genus *Moira* A. Agassiz, 1872
 Genus *Moiropsis* A. Agassiz, 1881
 Genus *Ova* Gray, 1825

Genus *Protenaster* Pomel, 1883

Genus *Schizaster* L. Agassiz, 1835

Genus *Tripylaster* Mortensen, 1907

Paleopneustina incertae sedis A

Genus *Schizocosmus* Markov, 1990

Paleopneustina incertae sedis B

Genus *Amphipneustes* Koehler, 1900

Genus *Brachysternaster* Larrain, 1985

Genus *Genicopatagus* A. Agassiz, 1879

Genus *Heterobrissus* Manzoni & Mazzetti, 1878

Genus *Parapneustes* Koehler, 1912

3 Taxonomy: systematic description

Infraclass Acroechinoidea Smith, 1981

3.1 Irregularia Latreille, 1825

Today, the taxon Irregularia includes three well differentiated groups:

- Order Echinoneoidea
- Superorder Neognathostomata: one family and two orders: Cassiduloidea, Clypeasteroidea
- Superorder Atelostomata: two orders: Holasteroidea, Spatangoidea

3.1.1 Order Echinoneoidea H.L. Clark, 1925

The members of this order are the most primitive irregular echinoids, widely distributed, and partly very common

in the Tertiary. Only three nearly related genera survive today (Fig. 3.1). The extant members of this family have nonpetaloid ambulacra, this means that their pore zones are narrow and undifferentiated. They are a sister group to the Neognathostomata and Atelostomata, which are more advanced clades that have well-developed petals with specialized pore pairs and tube feet.

3.1.1.1 Family Echinoneidae L. Agassiz & Desor, 1847

There are three genera:

Echinoneus Leske, 1778. Monospecific; imperforated primary tubercles.

Koehleraster Lambert & Thiéry, 1921. Monospecific; perforated primary tubercles.

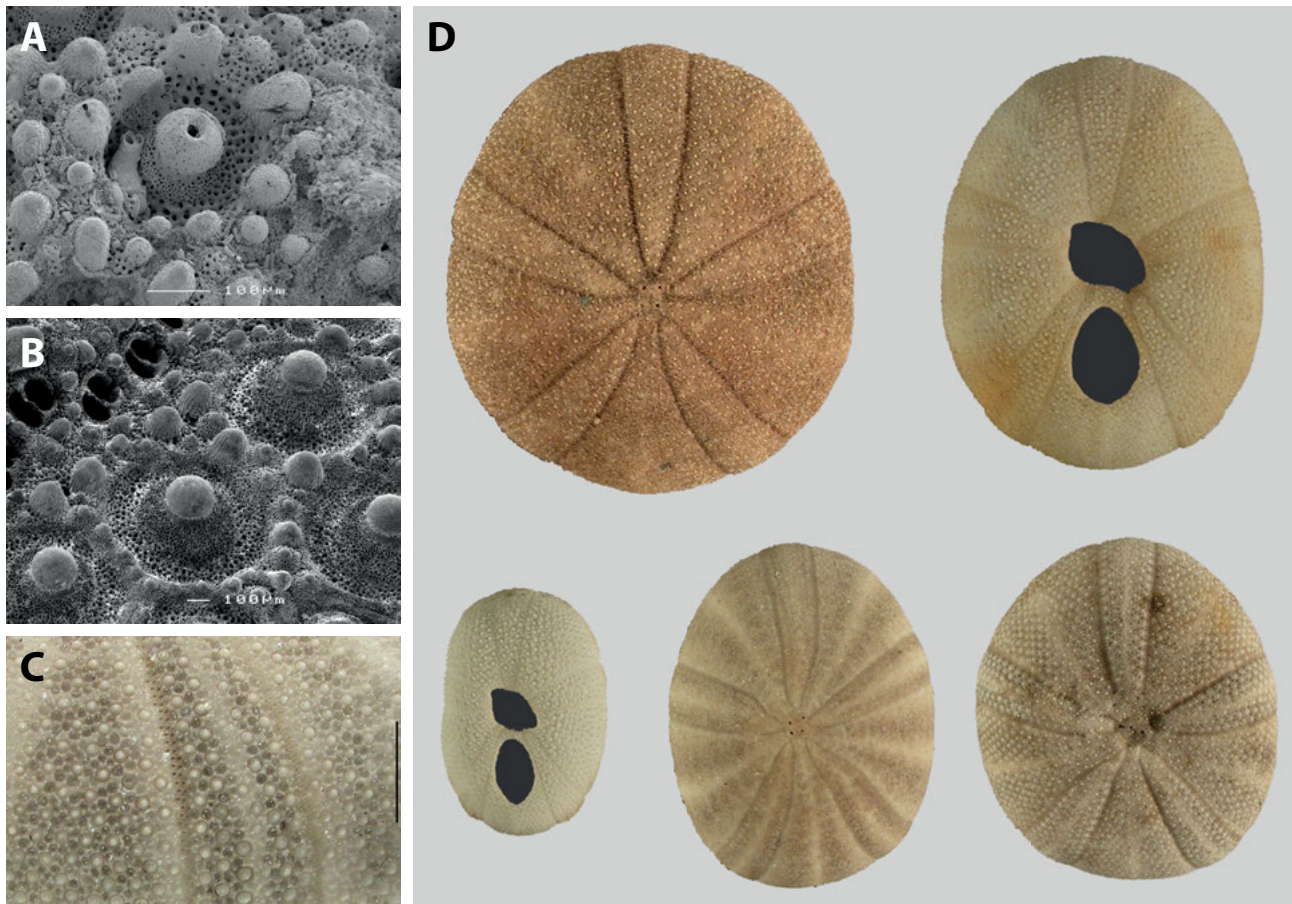


Fig. 3.1: (A–D) Echinoneids. (A) *Koehleraster abnormalis*: the primary tubercles are perforated. (B) *Echinoneus cyclostomus*: the primary tubercles are not perforated. Photos: NHM Wien, courtesy of A. Kroh. (C) *E. cyclostomus*. Ile de la Réunion, France. Close-up of aboral side: the white primary tubercles are surrounded by many glassy knobs that are not set with spines. Scale bar is 2 mm. (D) *E. cyclostomus*. The shape is very variable. The brown specimen retained the skin. All specimens from Réunion. The spines are short and stout, and a little longer on the oral side.

Micropetalon A. Agassiz & H.L. Clark, 1907. Monospecific; oblique periproct.

Literature: Westergren 1911; Hendler et al. 1995; Kroh 2005.

Genus: *Echinoneus* Leske, 1778

The only common Recent genus, *Echinoneus* is reported in the Oligocene and Miocene in the Tethys, the central ocean, to the Caribbean region. After the closure of that ocean during the Miocene, the geographical distribution of *Echinoneus*

changed: in the Mediterranean, a part of the former Tethys, the genus went extinct. It survived in two separate regions in the Tropics, the West Indies in the west and the Indo-Pacific in the east. The genus is monospecific (Fig. 3.2).

Echinoneus cyclostomus Leske, 1778

Test: Rather solid, very variable shape, slightly oval to greatly elongated, highly domed to flattened aborally, oral side more or less concave; margin rounded; maximum length, 50 mm.

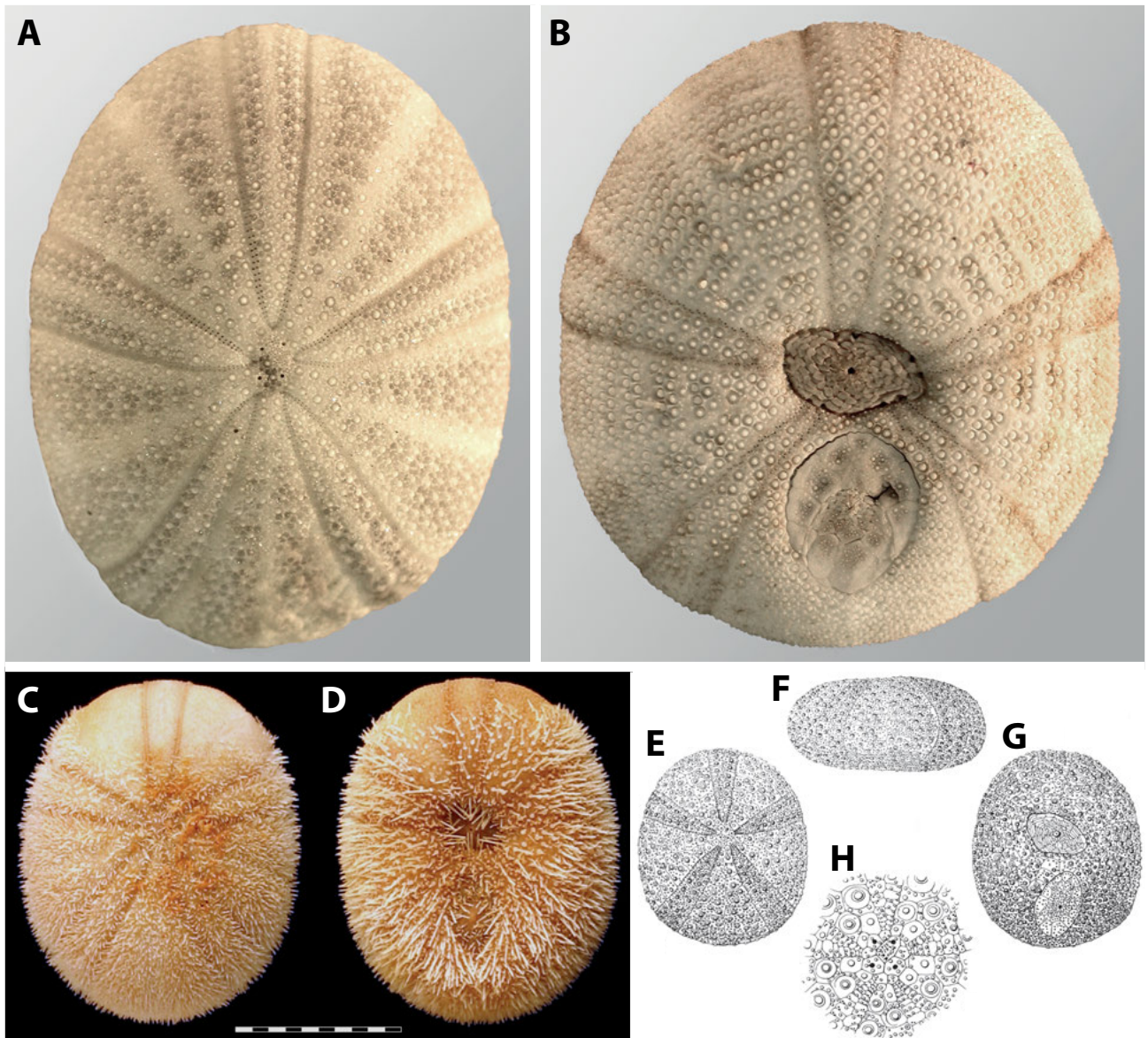


Fig. 3.2: (A–H) Echinoneids: (A, B) *Echinoneus cyclostomus*. (A) Test length 27 mm; Ile de la Réunion, Indian Ocean. The pore zones are narrow bands. The apical system of fused plates is small. (B) Test length 36 mm; Ile de la Réunion; Indian Ocean. Oral side: the irregularly shaped peristome and the large periproct are covered by plates. (C, D) *Koehleraster abnormalis*. Length 21 mm; Aldabra Island, Indian Ocean. Photos: NHM Wien, courtesy of Andreas Kroh. Scale bar is 10 mm. (E–H) *Micropetalon purpureum*. Length 17 mm; Molokai, Hawaii. (E) Aboral side: the ambulacra are nonpetaloid, the simple pores form a straight series. (F) Side view. (G) Oral side: both peristome and periproct are oblique. (H) The apical system is tetrabasal, the genital plates separated. The primary tubercles are not perforated. From Westergren (1911).

Apical system: Small, monobasal with four gonopores; ocular plates very small.

Ambulacra: Pore zones very narrow and slightly depressed, three pore pairs per plate; pore pairs forming a narrow band; tube feet 5 to 6 mm, longer than spines, interporiferous zone might be slightly inflated.

Peristome: In the center of the oral side, more or less depressed, irregularly triangular; membrane densely covered by small, smooth plates.

Periproct: Large, just posterior to the peristome; elongated with sharp or less pointed ends; covered with small, spined plates.

Tuberculation: Densely covered by small imperforated tubercles, each surrounded by a ring of miliary tubercles; numerous glassy knobs at the aboral side, often as large as primary tubercles.

Spines: Short, stout and simple, with longitudinal wedges.

Color: The spines as well as the denuded test may be whitish to light brown. The long tube feet are sometimes a bright red or rich purple, forming 10 conspicuous lines.

Distribution: The species is common in the Tropics around the world, in the Caribbean, and in the Indo-Pacific from East Africa to Hawaii and New Zealand. Bathymetric range: 5 to 570 m, but mostly in shallow water.

Biology: *Echinoneus* has teeth only in early ontogeny. They are resorbed before the mouth opens at a test length of 4 to 5 mm, as are the paired auricles, where the muscles were fixed. These echinoids live in or on coarse sand, feeding selectively on organic material using their oral tube feet and spines, which are not specifically modified.

Genus *Koehleraster* Lambert & Thiery, 1921

The genus is monospecific.

Koehleraster abnormalis (de Loriol, 1883)

Test: Solid, circumference oval, aboral side domed, oral side more or less concave; margin rounded; length may reach more than 50 mm.

Apical system: Slightly anterior, small, monobasal, or tetrabasal with four gonopores; ocular plates very small.

Ambulacra: Pore zones narrow, plating simple throughout with a single pore-pair; pore pairs forming a narrow band.

Peristome: In the center or slightly anterior, more or less depressed, irregularly triangular; membrane densely covered with small, smooth plates.

Periproct: Large, just posterior to peristome; longitudinally elongated; covered with small plates bearing spines.

Tuberculation: In contrast to *Echinoneus*, the small and densely packed primary tubercles are perforated, each surrounded by a ring of miliary tubercles; the glassy knobs are small and inconspicuous.

Spines: Short, stout and simple, with longitudinal wedges.

Color: The spines may be white, or light brown to olive, the denuded test is yellowish to olive.

Distribution: The species is recorded from Mauritius in the Indian Ocean to the China Sea and Hawaii; living from the littoral to a depth of 85 m.

Genus *Micropetalon* A. Agassiz & H.L. Clark, 1907

The genus is monospecific.

Micropetalon purpureum A. Agassiz & H.L. Clark, 1907

Test: Of medium size; oval in outline, low, aboral and oral side flattened, margin broadly rounded.

Apical system: Subcentral, tetrabasal with four gonopores.

Ambulacra: Nonpetaloid, pore zones simple and straight, not widened near the peristome; single pores from the apical system to the peristome.

Peristome: Subcentral, depressed, large and obliquely triangular.

Periproct: Very large, covering most of the area between mouth and posterior margin, obliquely elongated.

Phyllodes and bourrelets: Not developed, no buccal pores.

Primary tubercles: Not perforated, regularly distributed in a mass of small miliary tubercles.

Distribution: The very rare species is recorded from Molokai, Hawaiian Islands, and the Macclesfield Bank in the South China Sea; bathymetric range 45 to 70 m.

Remarks: This species is very similar to *Echinoneus* and *Koehleraster*, but differs in having an oblique periproct. In the two other genera, only the peristome is oblique. The pore zones are not depressed in *Micropetalon* as in *Echinoneus* and *Koehleraster*, but flush with the test.

3.2 Superorder Neognathostomata A.B. Smith, 1981

Typical characteristics: the plating of all five interambulacra on the oral side is principally similar. Their apical disc is either tetrabasal or, more advanced, monobasal. The monobasal madreporite is probably genital plate G2, and the other genital plates have not formed (Mooi, personal communication, 2015). The ocular plates are very small (Fig. 3.3).

This superorder contains three monophyletic groups: Family Apatopygidae as stem group.

Order Cassiduloida with three families.

Order Clypeasteroida with 12 families.

Literature: Mortensen 1948; Mooi 1990a,b; Suter 1994; Kroh & Smith 2010.

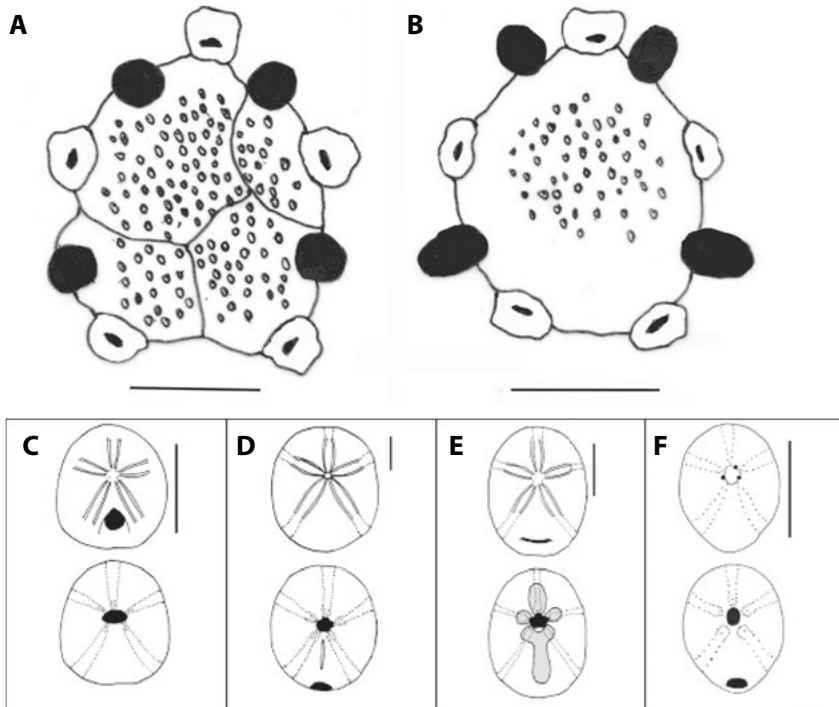


Fig. 3.3: (A–F) Neognathostomata. (A, B) Apical systems: (A) Tetrabasal, young *Apatopygus*, scale bar is 1 mm. (B) Monobasal, *Cassidulus caribaeorum*. Scale bar is 1 mm. After Mooi (1990a). (C–F) Schematic cassiduloid echinoids: upper row aboral side, lower row oral side. (C) *Apatopygus*. (D) *Cassidulus*. (E) *Echinolampas*. (F) *Neolampas*. The naked areas on the oral side are shaded. Scale bars are 10 mm. Modified after Mooi (1990a).

3.2.0.1 Family Apatopygidae Kier, 1962

The family Apatopygidae is a stem group of the superorder Neognathostomata (Fig. 3.4).

Genus *Apatopygus* Hawkins, 1920

Three species are found in Tertiary layers from South Australia and the Chatham Islands, New Zealand. Two further extant species are known from temperate waters of the same geographic region:

Apatopygus occidentalis H.L. Clark, 1938. Southwest Australia.

Apatopygus recens Milne-Edwards, 1926. New Zealand.

Test: Rather thin; in profile upper side convex, oral side flattened to also convex, but sunken toward the periproct; outline trapezoid, the posterior part broader than the anterior one.

Apical system: Tetrabasal in young, monobasal in adults; slightly anterior, with four gonopores.

Petals: Narrow, with narrow pore zones of the same length, distally open; anterior pair shorter than posterior pair.

Oral side: Sunken toward the large, transversely elongated or lozenge-shaped mouth; posterior interambulacrum may be more or less depressed; inconspicuous bourrelets, phyllodes not widened and no specialized spines.

Periproct: In a deep groove between the posterior pair of petals, a shallow furrow leading to the more or less sharp margin.

Spines: On the aboral side short, longer on the oral side.

Literature: Higgins 1974; Baker 1983; Holmes 1999.

The two genera are characterized by having the periproct more or less positioned between the posterior petals

with a shallow groove leading to the posterior margin. The phyllodes are single-pored, forming a simple irregular line in each half column.

Apatopygus occidentalis H.L. Clark, 1938.

Test: May reach a length of 27 mm.

Distribution: This species is endemic to the southwest coast of Australia between Bunbury and Rottnest Island; depth range 18 to 40 m.

Remarks: *A. occidentalis* differs from *A. recens* by its narrower test, its smaller peristome and periproct and by its distinctly separated geographic range. The anterior pair of petals is much shorter than the posterior pair.

Apatopygus recens Milne-Edwards, 1926.

Very similar to *A. occidentalis*. Length may reach more than 40 mm.

Due to the broader test, the anterior pair of petals is only slightly shorter than the posterior one.

Color: The living animals are reddish-brown, turning green after death; the bare test is grayish-white.

Distribution: *A. recens* is confined to New Zealand, from Auckland City to the Auckland Islands in the south at depths of between 2 and 150 m.

Biology: The species lives buried in coarse, shelly bottoms, approximately 30 mm deep. It seems to be an almost continuous deposit feeder. When placed on the sediment, it is able to burrow completely within 20 min. The animal moves forward 1 cm/h (Higgins 1974).

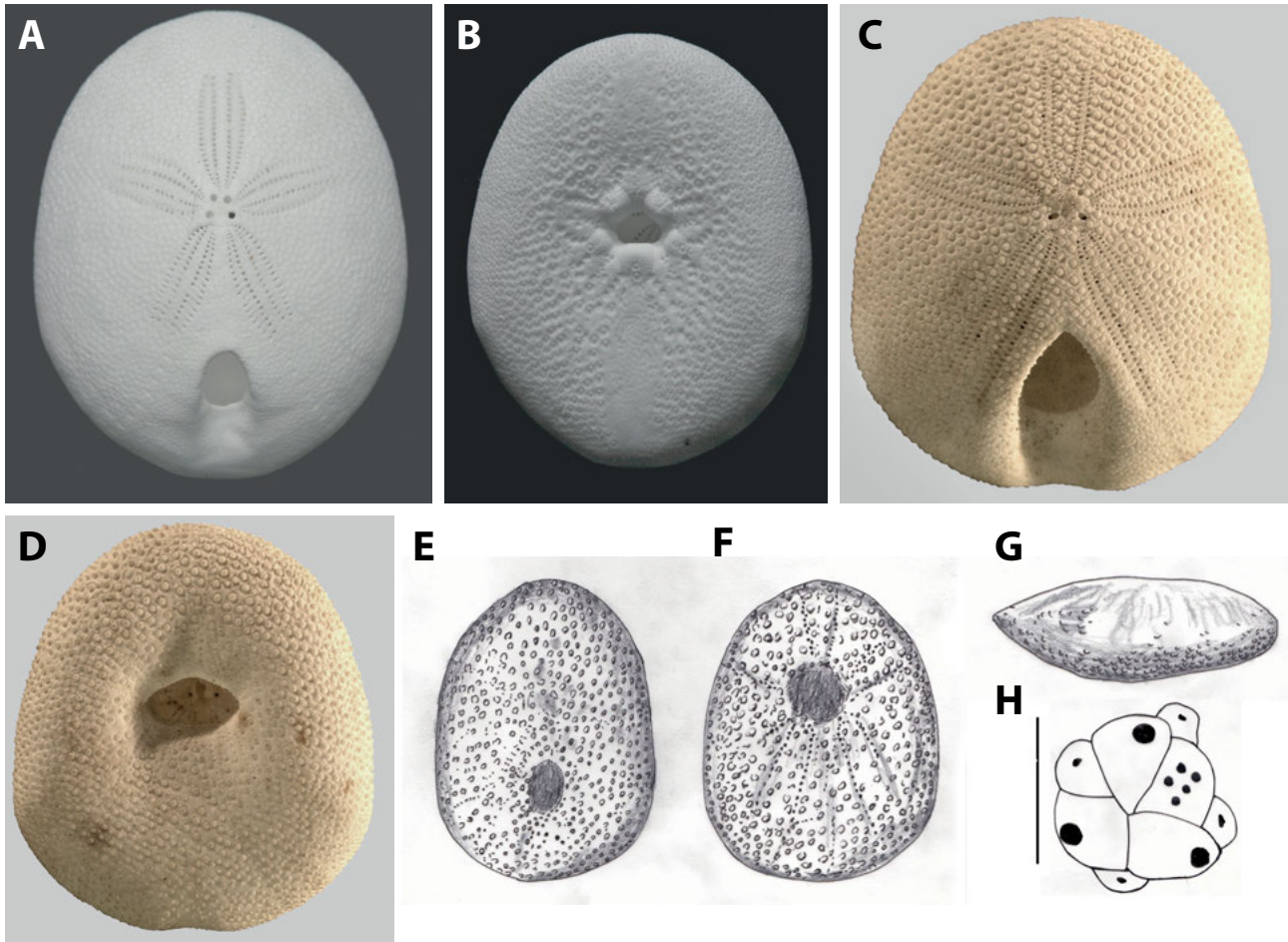


Fig. 3.4: (A–H) Apatopygids. (A, B) *Apatopygus occidentalis*, test length 17 mm, Rottneest Island, Southwest Australia. Photo courtesy of A. Miskelly. (A) Aboral side. (B) Oral side. (C, D) *Apatopygus recens*. Test length 29 mm; New Zealand. (C) Aboral side: the periproct is positioned on the upper side of the test, deeply depressed. A shallow furrow leads to the posterior margin. The petals are open distally, and the pore zones narrow. (D) Oral side: the peristome is large and transversely lozenge-shaped. (E–H) *Porterpygus kieri*. Test length 21.9 mm, Three Kings Islands, North Island of New Zealand. After Baker (1983). (E) Aboral side. (F) Oral side. (G) Side view. (H) Apical system. Scale bar is 1 mm.

Genus *Porterpygus* Baker, 1983

The genus is monospecific.

Porterpygus kieri Baker, 1983

Test: Small, low, in outline rounded trapezoid, widest posterior; oral side concave, strongly sunken toward peristome, flatter and angled upwards to a sharp posterior margin; length hardly 22 mm.

Apical system: Anterior; tetrabasal with three gonopores.

Ambulacra: Petals narrow and short, distally open.

Periproct: Supramarginal, oval, slightly oblique.

Peristome: Anterior, transversely elongated; phyllodes with single pores in a single series per half column; no buccal pores.

Occurrence: Found off the Three Kings Islands, North Island of New Zealand; bathymetric range 90 to 300 m.

3.2.1 Order: Cassiduloidea Claus, 1880

The cassiduloids were abundant during the Jurassic, Cretaceous, and Tertiary, but since the Eocene, they have dramatically decreased in number (Fig. 3.5). A total of 30 species survive today, which is only 5% of all known cassiduloids (Suter 1994).

They are divided into three families:

Cassidulidae L. Agassiz & Désor, 1847

Echinolampadidae Gray, 1851

Neolampadidae Lambert, 1918

Literature: Mortensen 1948; Krau 1954; Kier 1962; Gladfelter 1978; Mooi 1990a,b; Suter 1988, 1994.

3.2.1.1 Family Cassidulidae L. Agassiz & Desor, 1847

The periproct lies on the aboral side just above the ambitus, either on the posterior slope or on the more or less vertical

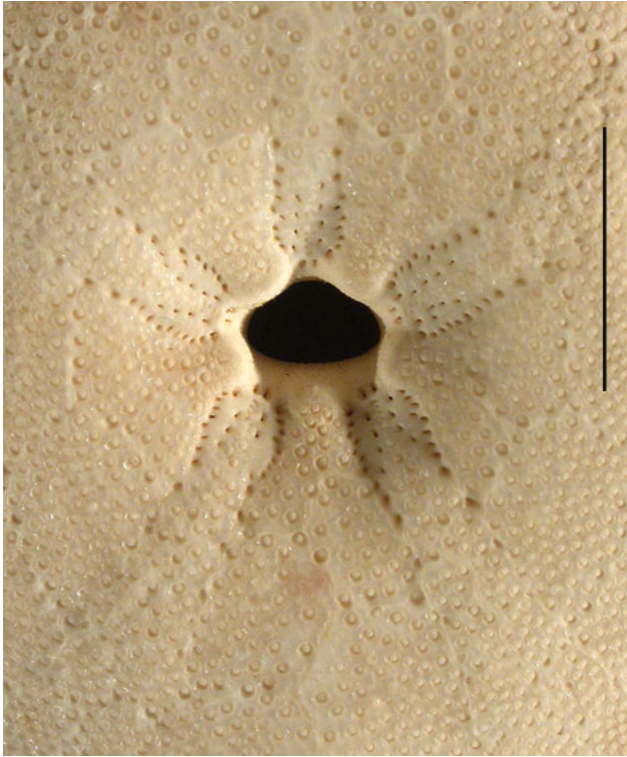


Fig. 3.5: Peristome of a cassiduloid (*Echinolampas ovata*): Close to the peristome, the ambulacral pores are enlarged, forming the leaf-shaped phyllodes. Each pore is associated with a specialized tube foot. Nearest to the peristome, two more or less enlarged pores are developed, which give rise to the two buccal podia. Alternating with the phyllodes, there are the bourrelets, more or less inflated interambulacral plates carrying specialized spines. Scale bar is 5 mm.

posterior end; posterior interambulacrum on oral side with large granuled naked area, extending more or less into the adoral ambulacra; bourrelets distinct.

Three extant genera are included in this family:

Genus *Cassidulus* Lamarck, 1801. Four or five species.

Genus *Eurhodia* Haime in d'Archiac & Haime, 1853. Monospecific.

Genus *Oligopodia* Duncan, 1889. Monospecific.

Genus *Cassidulus* Lamarck, 1801

Test: Small size; rather low; oval, but posteriorly broader; oral side flattened, more or less concave.

Apical system: Anterior, monobasal, four gonopores; few madreporic pores.

Ambulacra: Petals distinct, rather straight; pore zones narrow and mostly of more or less unequal length in one ambulacrum; single pores beyond petals.

Oral side: Distinctly concave along the midline; naked areas in ambulacra and interambulacrum 5 large and finely and irregularly pitted; peristome anterior, transversely pentagonal; bourrelets forming vertical walls, only

slightly inflated; phyllodes mostly with two outer series of single pores, slightly widened toward the peristome; buccal pores present.

Periproct: Supramarginal, transversely oval; short, shallow anal groove down to the posterior margin.

Spines: Aborally short, on the oral side much longer and supported by much larger tubercles.

Four or five species are known:

Cassidulus caribaeorum Lamarck, 1801. Caribbean.

Cassidulus infidus Mortensen, 1948. Bahia, Brazil.

Cassidulus malayanus Mortensen, 1948. Kei Islands, Indonesia.

Cassidulus mitis Krau, 1954. Rio de Janeiro, Brazil.

Krau (1960) described an additional species, *Cassidulus delectus*, from a bay near Rio de Janeiro, a single broken specimen. Thus, there seems to exist three species at the east coast of Brazil, of which only one is fairly common in a very restricted area.

Cassidulus caribaeorum Lamarck, 1801

Test: Depressed; outline ovate; posterior side with projection; length scarcely reaches 25 mm.

Apical system: Slightly anterior, four gonopores.

Ambulacra: Pore series in the petals of unequal length, less than 60 pore pairs in the anterior petal (Fig. 3.6).

Oral side: Flattened and concave along the midline; large, naked median areas with irregular pits; phyllodes slightly widened, fewer than 15 pores in the anterior one.

Periproct: On the aboral side below the posterior projection.

Spines: Aborally short and uniform, much longer on the oral side.

Color: In life, the sea urchin is light brown, the bare test is whitish.

Distribution: The species is known from Belize to the Bahamas and from the Antilles to Barbados. It lives in very shallow water between less than 2 and 10 m.

Biology: *C. caribaeorum* is one of the few brood-protecting species in tropical waters (28°C). After spawning and fertilization of the yolk-rich eggs, the female groups them around the apical pole between the spines. Within 3 to 5 days, the modified larva has formed, after 5 to 7 days, metamorphosis has taken place, and 9 to 11 days after spawning, the little sea urchin is set free. The sex ratio of the populations is greater than five females to one male.

The populations live in isolated patches in habitats with coarse, moderately sorted sand in agitated, shallow water (Gladfelter 1978).

Remarks: *C. caribaeorum* differs from *Rhyncholampas pacificus* by the smaller size and the less numerous pores in its anterior petals and phyllodes.

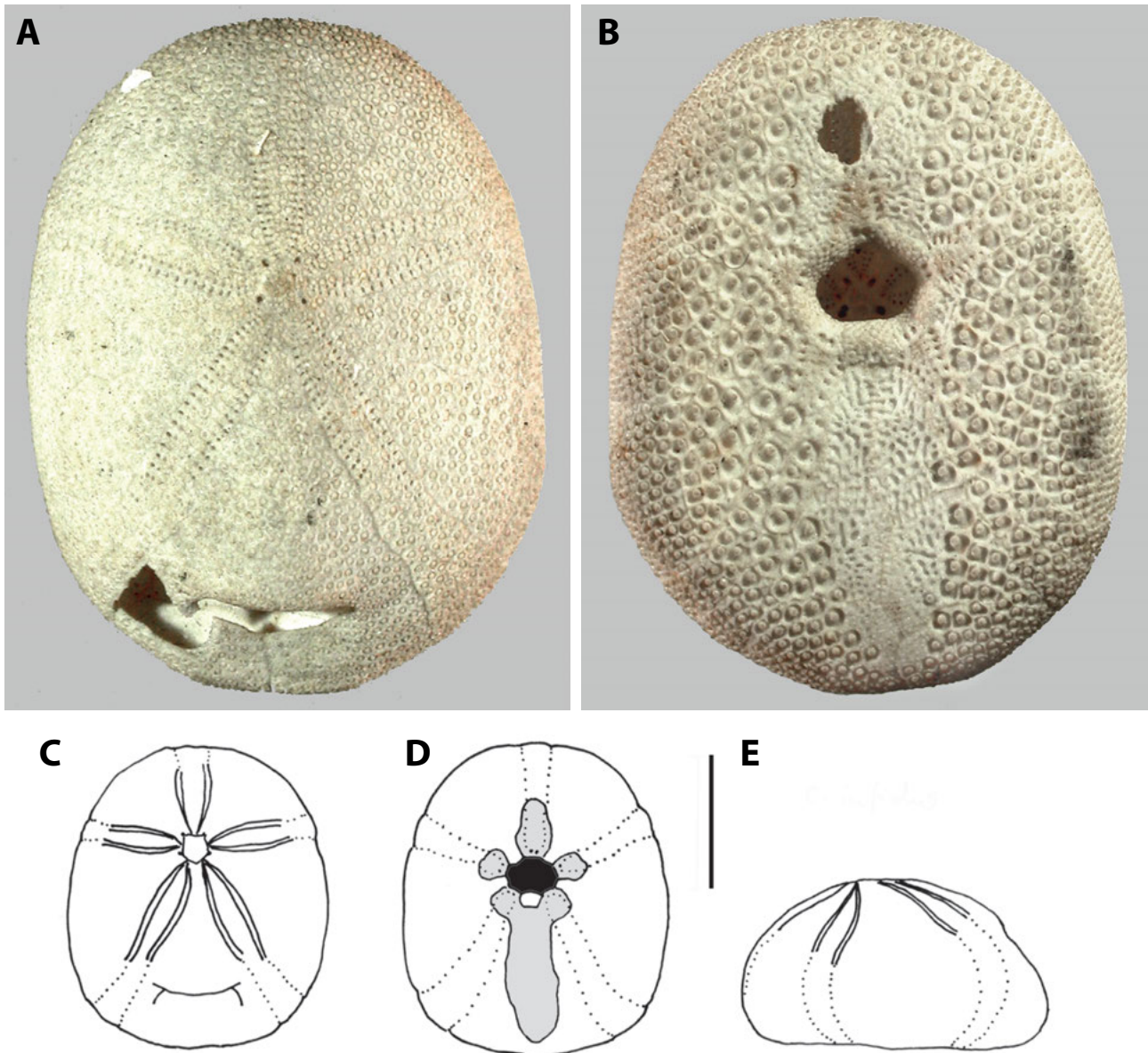


Fig. 3.6: (A–E) Cassiduloids. (A, B) *Cassidulus caribaeorum*. Test length 23 mm, height 11 mm; St. Thomas, Caribbean. ZMUC. (A) Aboral side. The petals are open distally, the pore zones narrow. This brood-protecting species has not developed any brood-pouches (the hole in front of the peristome was created by a predator, a snail). (B) Oral side: the large naked areas are covered in irregular pits. The five pairs of buccal pores are distinct. (C–E) *Cassidulus infidus*. Length 25 mm, Brazil (labeled “Bahia”). (C) Aboral side. (D) Oral side. (E) Side view. Scale bar is 10 mm. Modified after Mooi (1990b).

Cassidulus infidus Mortensen, 1948

This species is known from a single specimen with a length of 10 mm labeled “Bahia, Brazil”. It has not been found again (Fig. 3.7).

Mortensen found it nearly related to *C. caribaeorum*, but he emphasized the following differences: in *C. infidus*, the test is narrower and higher with steeper sides, the margin is rounder, the peristome is more sunken, and the periproct is almost round, not transversely elongate as in *C. caribaeorum*.

Cassidulus malayanus Mortensen, 1948

Test: Delicate and fragile, circumference oval, sides parallel, aboral side lowly arched; length up to 25 mm.

Apical system: Only slightly anterior, small.

Petals: Rather short, of about the same length, posterior pair slightly curved; pore zones of approximately equal length; the single pores beyond the petals very small and inconspicuous.

Peristome: Rounded pentagonal, broader than long; phyllodes distinct, bourrelets well-developed.

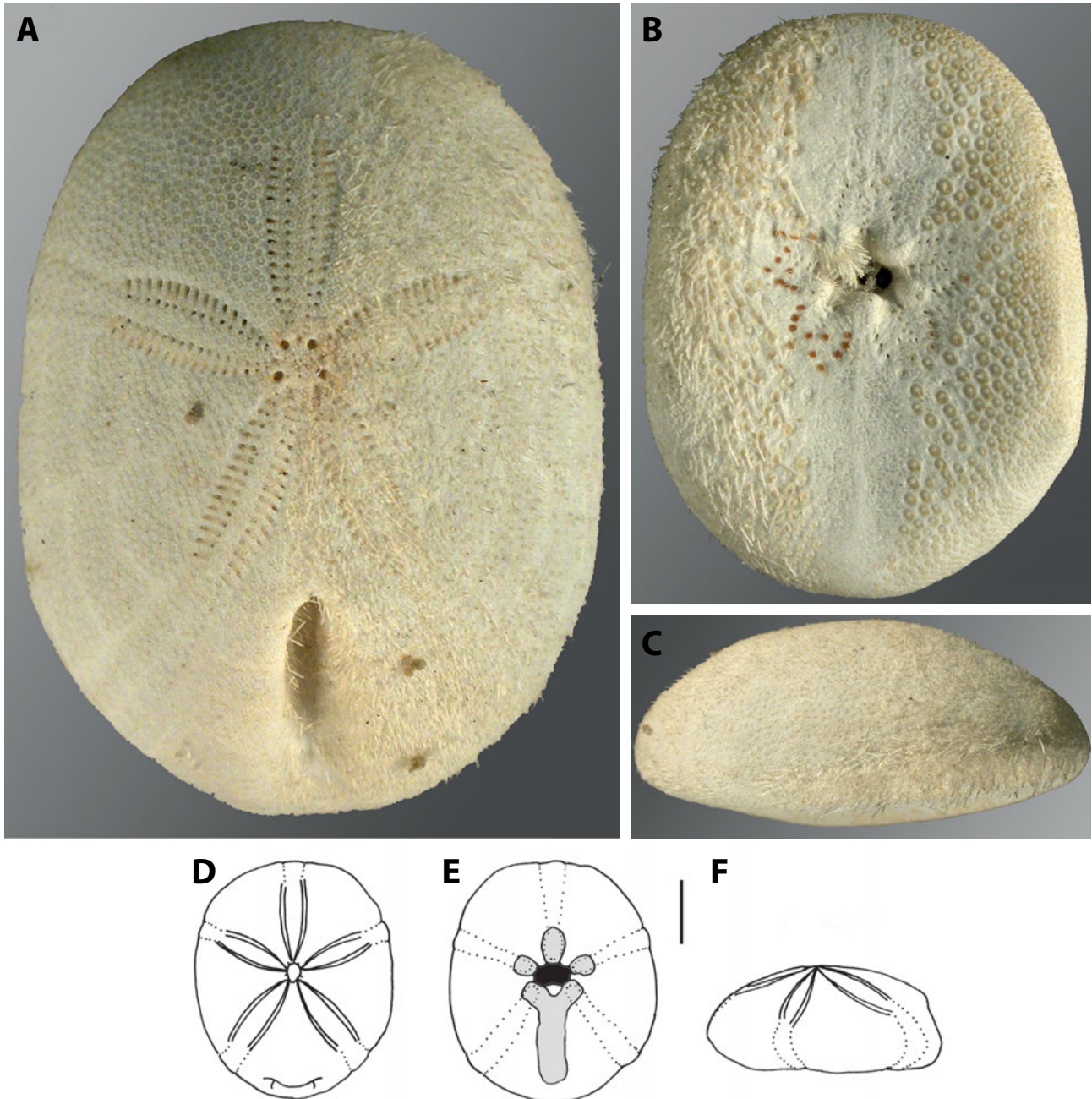


Fig. 3.7: (A–F) Cassiduloids. (A–C) *Cassidulus malayanus*. Test length 25 mm; Kei Islands, Indonesia. ZMUC ECH 236. (A) Aboral side: the periproct is positioned high on the upper side. (B) Oral side. (C) Side view: there is no posterior hook on top of the periproct. (D–F) *Cassidulus mitis*. Length 30 mm, Baia de Sepetiva, Rio de Janeiro, Brazil. (D) Aboral side. (E) Oral side. (F) Side view. Scale bar is 10 mm. Modified after Mooi (1990a).

Periproct: Elongated oval, positioned rather high on the aboral side in a long, narrow, and deep groove, not over-arched by the test.

Tuberculation: Fine and uniform on the aboral side partly much larger on the oral side.

Color: The test and the spines are white.

Distribution: Only two specimens were dredged off the Kei Islands, Indonesia, at a depth of 250 to 290 m.

Cassidulus mitis Krau, 1954

The species is nearly related to *C. caribaeorum*. It differs from that species by its more posterior periproct. The hook is only faintly developed, whereas in *C. caribaeorum*, it is prominent. *C. mitis* differs from *C. infidus* by its lower test, the apical system being positioned more centrally. *C. mitis* lives endemic in some lagoons and along beaches in the vicinity of Rio de Janeiro, Brazil.

Biology: *C. mitis* is brood-protecting, keeping its young among the aboral spines like *C. caribaeorum*. Because of the colder water, the development of the juveniles takes more time. Postmetamorphic individuals of an age of 62 days (diameter 0.5 mm) still retain functional teeth. It seems that they use their lantern to graze on bacterial microfilms covering the sand grains. Later in growth, the echinoids lose their lantern completely, although there is no accurate information on the age or stage of the loss. Afterward, the podia encircling the peristome are used for feeding (Contins & Ventura 2011).

Literature: Freire et al. 1992; MacCord & Ventura 2004; Contins & Ventura 2011.

Genus *Eurhodia* Haime in d'Archiac & Haime, 1853

Approximately 20 species of *Eurhodia* were established from Paleocene and Eocene layers worldwide when two specimens were found in 1968 from the collection of the USNM, dredged by the RV "Pillsbury". Mooi (1990) described them as a new species, a "living fossil". Their nearest relatives were common in the Late Eocene of the southeast USA and the Caribbean, but in later periods, were thought to be extinct.

Eurhodia relictata Mooi, 1990

Test: Small, more or less highly domed, oral side longitudinally concave; length up to 13.2 mm.

Apical system: Slightly anterior, monobasal, madreporite with only five to six hydropores and four gonopores; ocular plates small (Fig. 3.8).

Ambulacra: Petals rather short, posterior pair longest; the two columns per ambulacrum of about equal length; interporiferous zone approximately as wide as pore zones; pore pairs conjugate, outer pore round or only slightly elongated; pores beyond petals simple.

Oral side: Peristome slightly anterior, longitudinally elongated; phyllodes with 7 to 10 pores in outer series, only two or three in inner series; bourrelets distinct, forming slight bulges covered by more than 25 densely arranged tubercles set with curved spines; large naked area in IA 5 and A III, conspicuously pitted.

Periproct: High on the posterior side under a slightly overhanging hood, shallow vertical subanal sulcus down to the margin.

Tubercles: On the oral side distinctly larger than aborally.

Distribution: Only two specimens are known from western Suriname and Venezuela, dredged at 57 and 112 m, respectively.

Biology: *E. relictata* lives shallowly buried in fine to coarser sand.

Genus *Oligopodia* Duncan, 1889

The genus is monospecific.

Oligopodia epigonus v. Martens, 1865

Test: Small and ovoid; aboral side lowly arched, posterior interambulacrum forms a low keel often terminating as a small beak above the periproct; oral side slightly concave and depressed toward the peristome; length up to 17 mm.

Apical system: Slightly anterior, monobasal, four gonopores, distinctly larger in females than in males (Fig. 3.9).

Ambulacra: Petals distinct, flush with the test and distally open; the two columns almost parallel and of about equal length; plates beyond the petals rather high with single, small pores; pore pairs very oblique.

Oral side: Peristome longitudinally elongated, slightly anterior; bourrelets as distinct areas with specialized spines on the almost vertical walls, but not inflated; phyllodal pores arranged in two irregular series, scarcely widened at the peristomial edge; buccal pores distinct; naked areas inconspicuous.

Periproct: On the truncated posterior end, more or less deep subanal groove leading down to the ambitus.

Primary spines: Very short, approximately 0.5 mm long, smooth and curved.

Color: Test and spines are white.

Distribution: This species is found from East Africa over the Malayan region to the Bonin Islands, Tonga Islands and New Zealand. Bathymetric range: living specimens were found from 35 to 141 m, dead tests from 5 to 390 m.

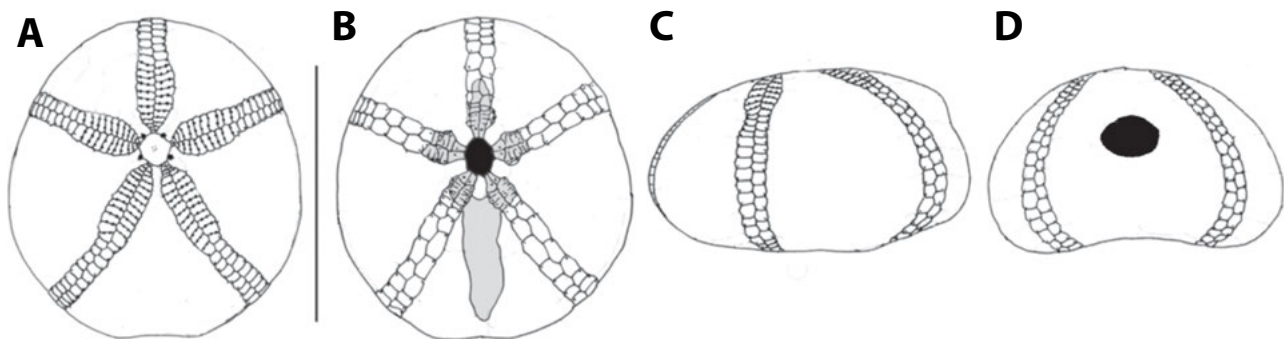


Fig. 3.8: (A–D) Cassiduloids. (A–D) *Eurhodia relictata*. Length 12.5 mm; off Surinam (holotype in USNM). (A) Aboral side. (B) Oral side (naked areas shaded). (C) Side view. (D) Posterior side. Scale bar is 10 mm. Modified after Mooi (1990b).

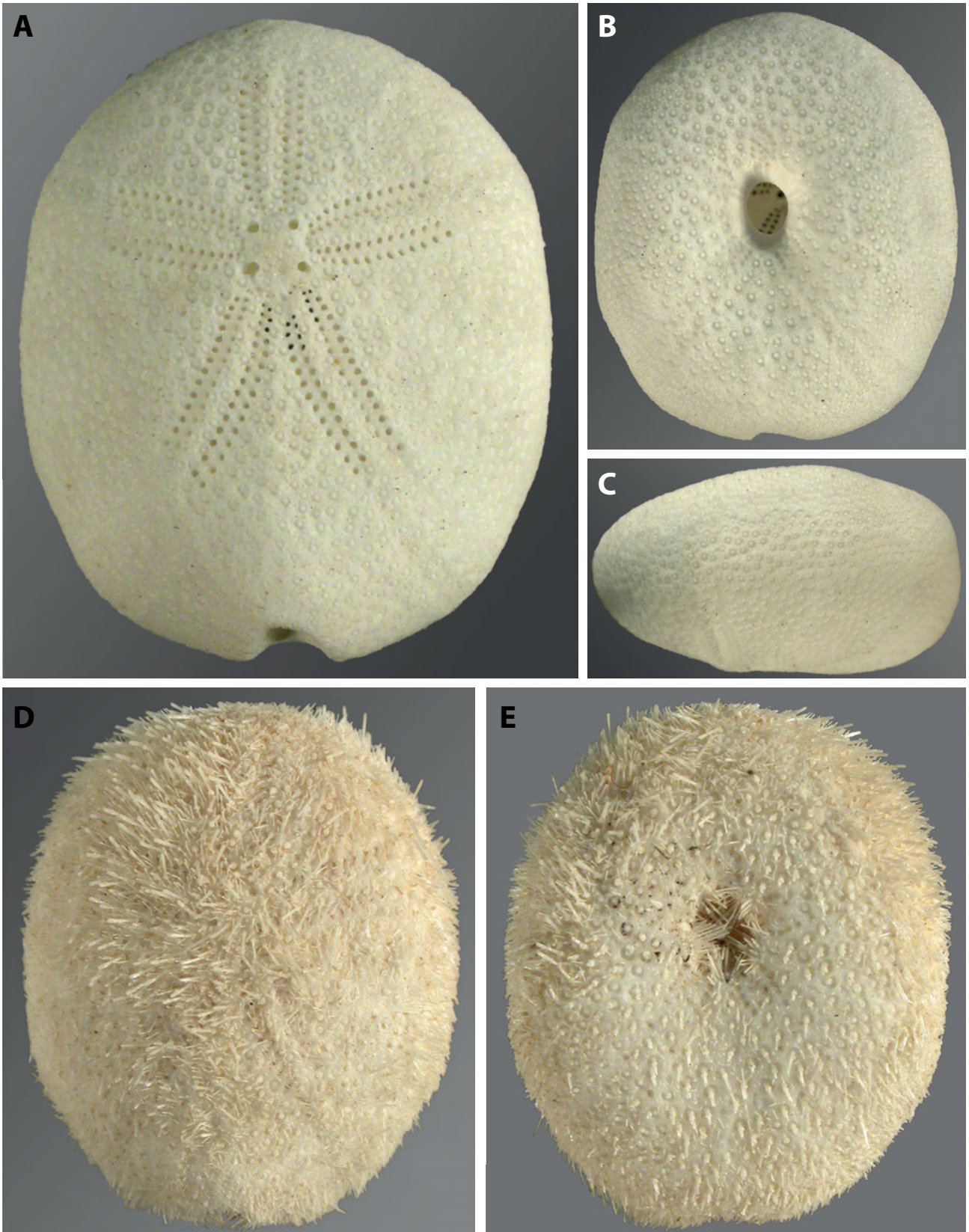


Fig. 3.9: *Oligopodia epigonus*, female. Test length 17 mm; Jolo, Philippines. ZMUC. (A) Aboral side. (B) Oral side: the peristome is deeply sunken with almost vertical walls. (C) Side view. The periproct is positioned on the posterior side opening into a short anal groove. (D, E) Specimen with spines. Test length 16 mm; Jolo, Philippines. ZMUC. (D) Aboral side: the spines are short and uniform. (E) Oral side: the vertical wall of the peristome is set with specialized spines.

Genus *Rhyncholampas* A. Agassiz, 1869

The genus is monospecific.

Rhyncholampas pacificus (A. Agassiz, 1863)

Test: High convex; outline regularly oval or posteriorly slightly wider; maximum length 70 mm.

Apical system: Slightly anterior, four gonopores.

Ambulacra: Petals long and well-developed, pore zones in paired petals of slightly different lengths; more than 70 pore pairs in anterior petals, more than 20 pores in anterior phyllodes; buccal podia large (Fig. 3.10).

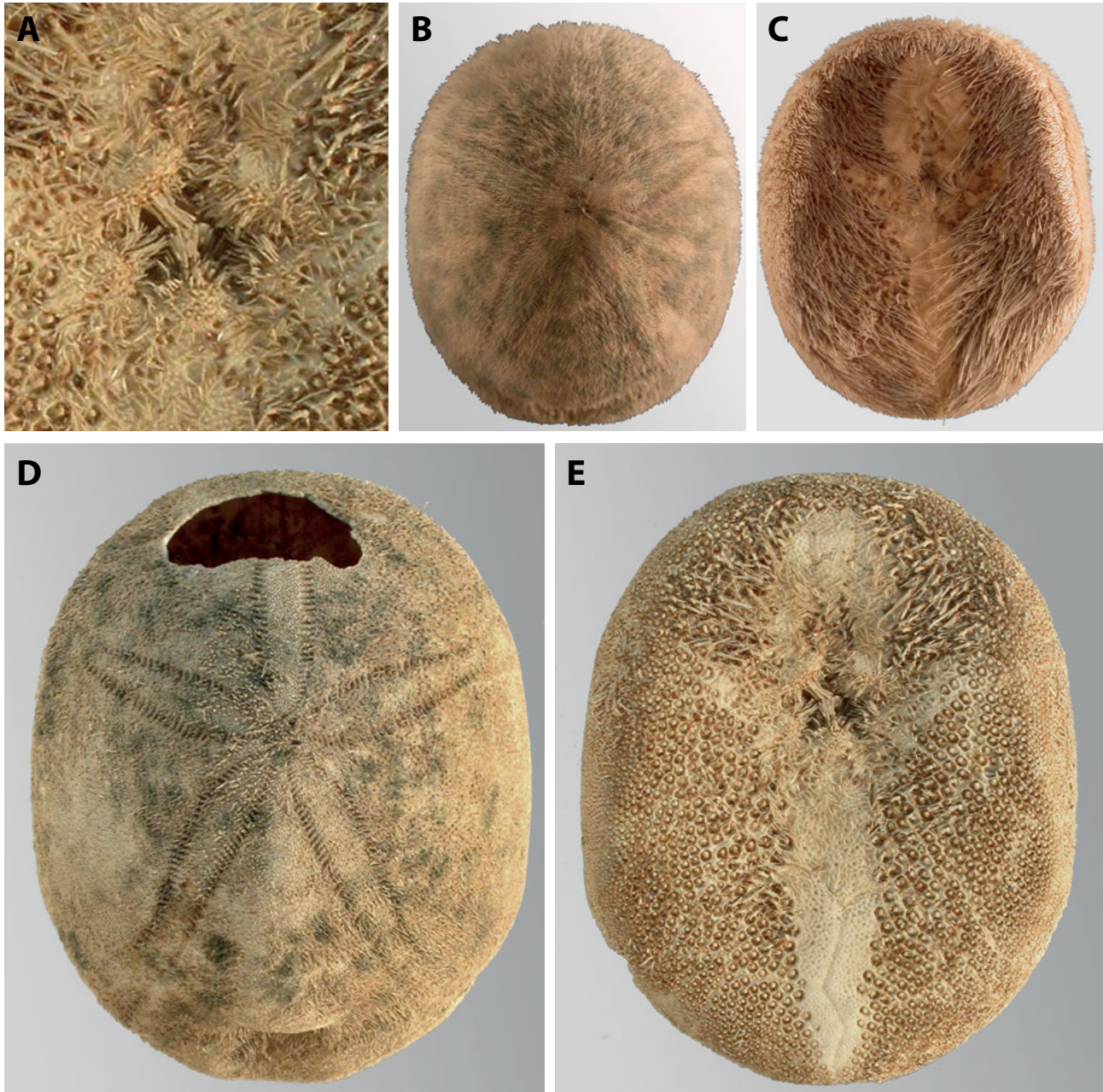


Fig. 3.10: *Rhyncholampas pacificus*. Test length 43 mm; Acapulco, Mexico. MfNB Berlin. (A) Close-up of peristomial region: the inflated bourrelets in the interambulacra are set with tufts of specialized spines. (B, C) Specimen with spines. Length of test 59 mm, height 27 mm; Acapulco, Mexico. ZMH. (B) Aboral side: the spines, short and fur-like, show scattered greenish spots. Near the posterior margin, the periproct opens below a distinct roof-like projection. (C) Oral side: the spines are much longer than on the upper side. Large naked areas are developed in the posterior interambulacrum and around the phyllodes in the ambulacra. The bourrelets are distinct. (D, E) Specimen without spines. Test length 43 mm; Acapulco, Mexico. MfN Berlin. (D) Aboral side: the petals are long and slender. The anterior side of the test is damaged. (E) Oral side: the pits in the large naked area are distinctly smaller than those of *Cassidulus caribaeorum*.

Oral side: Large naked areas in the posterior interambulacrum and in the ambulacra around the phyllodes; pits small and round; peristome anterior, broadly pentagonal; anterior bourrelets broad.

Periproct: Below a projection on the posterior aboral side.

Spines: Short on the aboral side, a little longer at the projection above the periproct, the oral spines are much longer.

Color: The spines are brownish, and conspicuous green spots are scattered over the aboral side. The bare test is whitish.

Habitat: This species lives gregariously on sandy beaches at a depth of 2 to 130 m.

Distribution: *R. pacificus* is known along the west coast of Central America from Baja California to Panama and the Galapagos Islands.

Remarks: *R. pacificus* differs from *C. caribaeorum* by the larger size and the comparatively more numerous pores in its anterior petals and phyllodes.

Literature: Mooi 1990.

3.2.1.2 Family Echinolampadidae Gray, 1851

This family is characterized by having the periproct just below the ambitus on the oral side. The naked area is small and inconspicuous; the bourrelets are more or less developed.

The family includes two extant genera:

Genus *Conolampas* A. Agassiz, 1883. Four species.

Genus *Echinolampas* Gray, 1825. Ten species.

They differ in the following features:

Echinolampas is more elongated in outline than *Conolampas* and has a slight posterior projection. The tuberculation in *Echinolampas* is denser than in *Conolampas*. The oral side of *Echinolampas* is sunken toward the peristome, in *Conolampas* it is flattened.

Literature: Döderlein 1906; Nisiyama 1968; Thum & Allen 1975; Shigei 1986; Mooi 1990a,b; Rowe & Gates 1995.

Genus *Conolampas* A. Agassiz, 1883

Test: Large and solid, highly vaulted, hemispherically to subconically with sharp margin, oral side flat, very slightly sunken toward peristome; circumference almost circular.

Apical system: Subcentral, monobasal with four gonopores.

Ambulacra: Long, distally open petals, poriferous zones narrow, pore pairs subequal, more or less circular, conjugate; plates beyond petals with single pores (Fig. 3.11).

Oral side: Peristome subcentral and pentagonal, slightly wider than long; phyllodes slightly sunken; single pores,

arranged in three series per half-ambulacrum; buccal pores present; bourrelets distinct.

Periproct: On the flat oral side more or less near the posterior edge, transverse.

Tuberculation: Scarce but evenly distributed, short spines that are a little longer on the oral side.

Color: Yellowish-brown, cleaned test white.

Biology: Mooi (1990b) assumed that the species of *Conolampas* with flat undersides do not live buried on the sediment but feed on fine substrates.

Four species are included in the genus.

Conolampas diomedea Mortensen, 1948. Philippines

Conolampas malayana Mortensen, 1948. Malayan

Conolampas murrayana Mortensen, 1948. Maldives

Conolampas sigsbei A. Agassiz, 1878. Caribbean

The species are very similar.

Conolampas diomedea Mortensen, 1948

Test: Hemispherical with sharp margin, oral side perfectly flat; maximum length 90 mm.

Apical system: Knob-shaped.

Petals: Long, more or less unequal in length.

Oral side: Naked area in posterior interambulacrum inconspicuous; peristome subcentral to slightly posterior; anterior bourrelets more developed than posterior pairs.

Color: In life, the spines are yellowish, the bare test is white.

Distribution: The species is reported only from the Philippines; bathymetric range 80 to 300 m.

Literature: David & de Ridder 1989; Mooi 1990.

Conolampas malayana Mortensen, 1948

Test: Length up to more than 90 mm.

This species differs from the two others, also found in the Malayan/Philippine region, by the length of the petals, which reach only halfway down to the ambitus. In *C. murrayana* and *C. diomedea*, the petals extend almost to the ambitus. *C. malayana* and *C. diomedea* both bear an apical knob (Fig. 3.12).

Distribution: This rare species was found at the Kei Islands, Indonesia, and off Zamboanga, Philippines; at depths of 230 to 400 m.

Conolampas murrayana Mortensen, 1948.

The only two known specimens measure 67 and 68 mm.

The species is distinguished from *C. diomedea* by the broader and more lanceolate petals. Mortensen further mentioned the sparser tuberculation on the proximal oral side, which is denser in *C. diomedea*. *C. murrayana* lacks the apical knob that is present in *C. diomedea* and *C. malayana*. The specimens were found off the Maldives at a depth of 229 m.

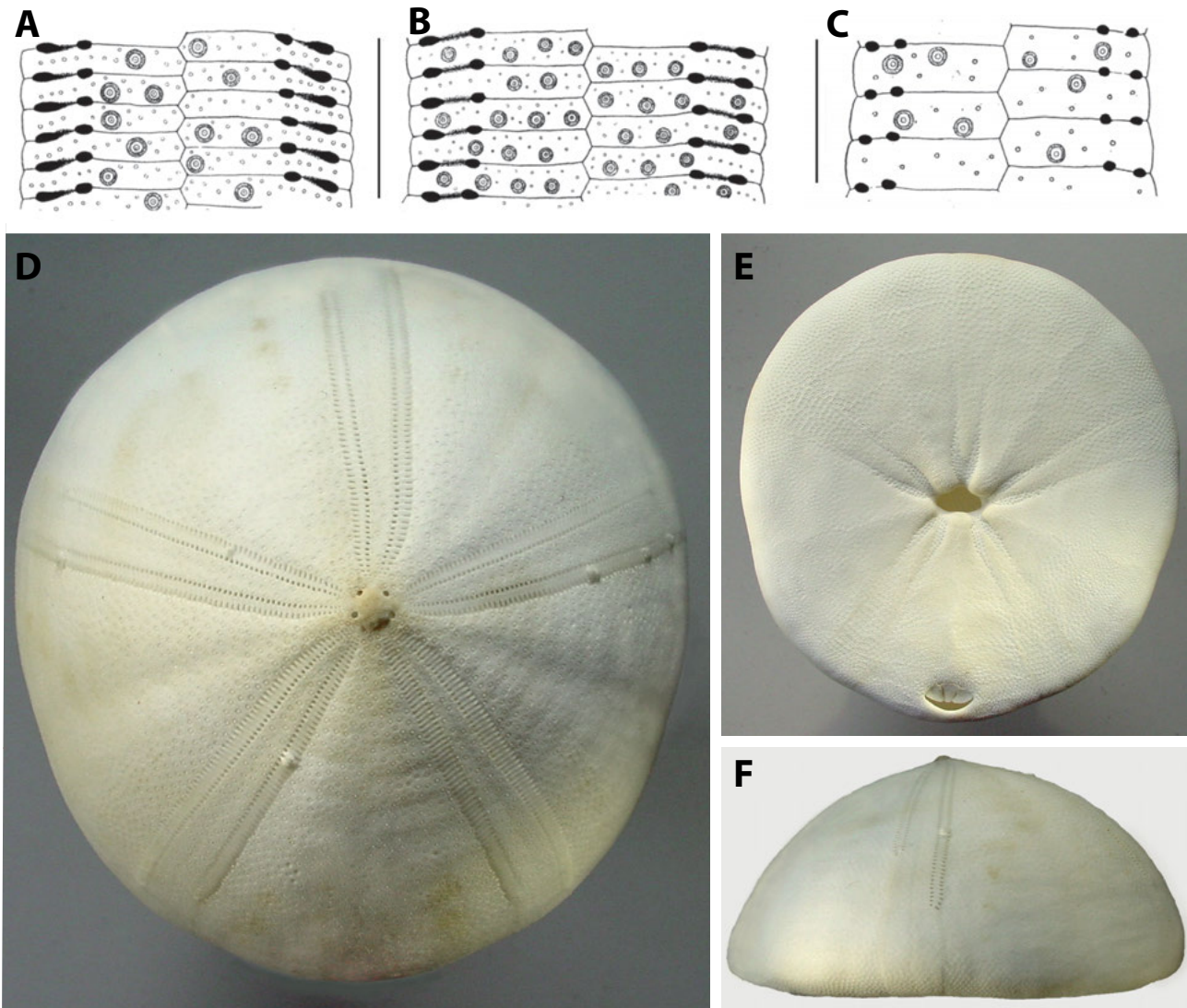


Fig. 3.11: (A–C) *Conolampas*. Ambulacral plates. (A) *Conolampas diomedeeae*. (B) *Conolampas murrayana*: the pore pairs are distinctly conjugate. (C) *Conolampas sigsbei*: the plates are sparsely tuberculated, the pore pairs are distant and nonconjugate. Scale bar in (A) and (B) is 4 mm, in (C) is 3 mm. After Mortensen (1948). (D–F) *C. diomedeeae*. Test length 87 mm, Balicasag Island, Philippines. (D) Aboral side. (E) Oral side. (F) Side view. Photos courtesy of H. van Noordenburg.

Conolampas sigsbei A. Agassiz, 1878.

Test: High with steep sides; length may reach 105 mm.

Ambulacra: In comparison to the Indo-Pacific species, the pore pairs in the petals are more distant.

Oral side: Bourrelets and phyllodes well-developed.

Color: In life, yellowish, cleaned test white (Fig. 3.13).

Distribution: Recorded throughout the West Indies, along the west coast of Florida, and off the northern coast of Yucatan; bathymetric range approximately 120 to 800 m.

Genus *Echinolampas* Gray, 1825

Test: Medium to large size, more or less elongated with a slight projection posteriorly, aborally domed, sunken toward the peristome.

Apical system: Monobasal with four gonopores, positioned anterior to subcentral.

Ambulacra: Five petals well-developed, straight or arched, distally open; pore pairs small, the two columns per petal of more or less unequal length; pores simple beyond petals.

Oral side: Naked area in posterior interambulacrum 5 small and inconspicuous.

Peristome: Subcentral, wider than long and transverse pentagonal or oval.

Phyllodes: Short and more or less conspicuous, two or three single pored series per half-ambulacrum; buccal pores present; bourrelets weakly inflated with vertical sides leading to the mouth opening.

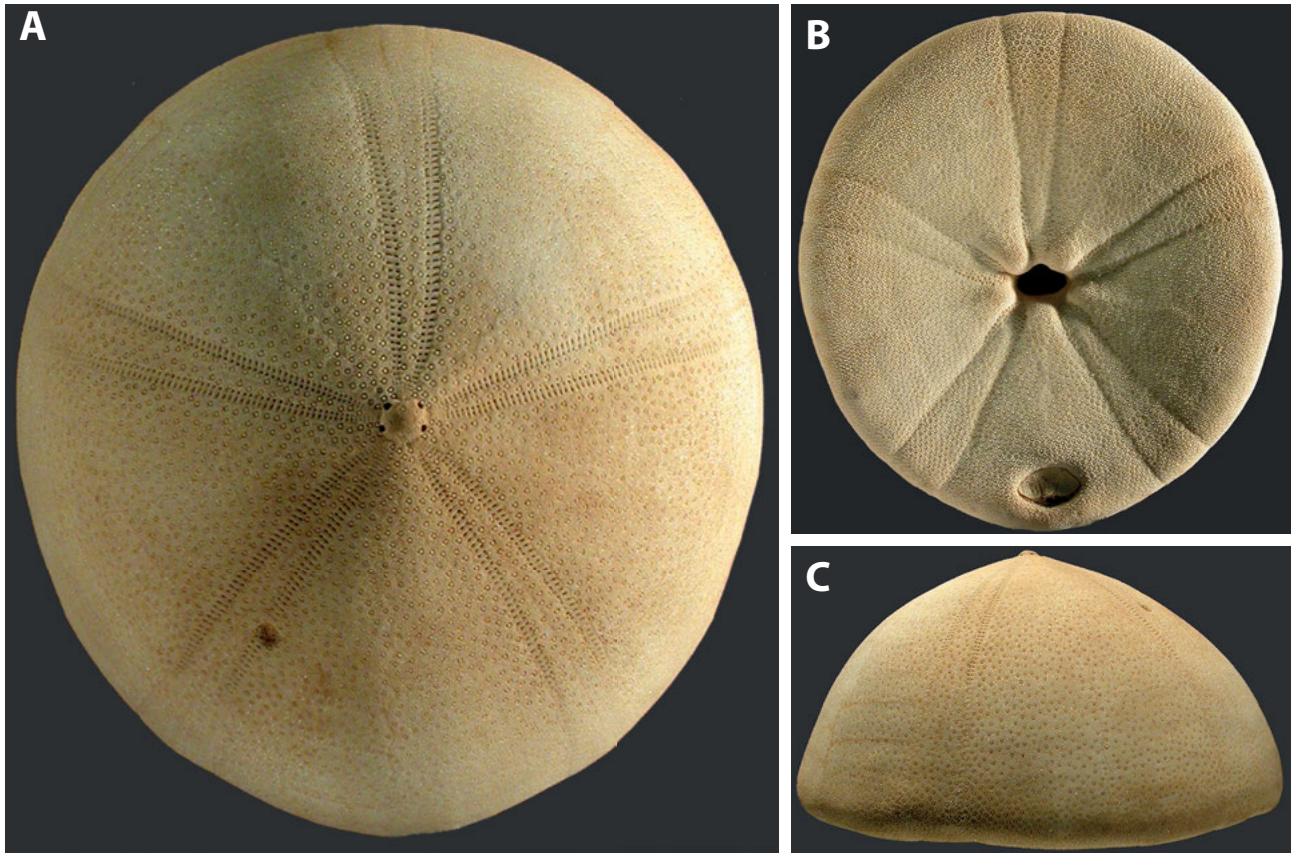


Fig. 3.12: *Conolampas malayana*. Test length 84 mm; off Zamboanga, Philippines. ZMUC. (A) Aboral side. (B) Oral side. (C) Side view: the species has a knob-like apex.

Periproct: Flush with the test, inframarginal, transversely elongated; three valve-like periproctal plates.

Tubercles: Usually of the same size on aboral and oral sides, spines short.

The following 10 extant species are known:

Echinolampas alexandri de Loriol, 1876. Red Sea to Malayan Archipelago, Coral Sea.

Echinolampas chuni Döderlein, 1905. Indonesia.

Echinolampas crassa Bell, 1880. South Africa.

Echinolampas depressa Gray, 1851. Caribbean.

Echinolampas keiensis Mortensen, 1948. Indonesia to Philippines.

Echinolampas koreana H.L. Clark, 1925. Korean Strait.

Echinolampas ovata (Leske, 1778). Red Sea to Western Australia.

Echinolampas rangii Desmoulins, 1837. West Africa.

Echinolampas sternopetala A. Agassiz & H.L. Clark, 1907. Japan.

Echinolampas sumatrana Döderlein, 1905. Indonesia.

A comparison of four species of *Echinolampas* occurring in the Malayan region is shown in Tab. 3.1. Unfortunately, the width of variation within the species is considerable.

The fifth species, *E. keiensis*, is distinguished at first sight by its strongly unequal poriferous zones and the well-developed bourrelets.

Echinolampas alexandri de Loriol, 1876

Test length may reach more than 80 mm.

This species is very similar to *E. ovata* and is not easily distinguished from it. It differs in usually having a flatter, wider and thinner test and less pronounced phyllodes. The peristome is oval, contrary to *E. ovata*, where it is distinctly pentagonal. The two columns of pore pairs in each petal are unequal (Fig. 3.14).

Distribution: Red Sea, Indian Ocean (Mauritius), and Malayan Archipelago; depth 8 to 365 m. The geographic range does not extend to northwest Australia like *E. ovata* (Rowe & Gates 1995), but two dead tests were found in northeast Australia in the Coral Sea (Miskelly 2002).

Echinolampas chuni Döderlein, 1905

Test: Strong, aboral side lowly hemispherical, circumference elongated ovoid, the posterior end being distinctly rostrate; length 75 mm.

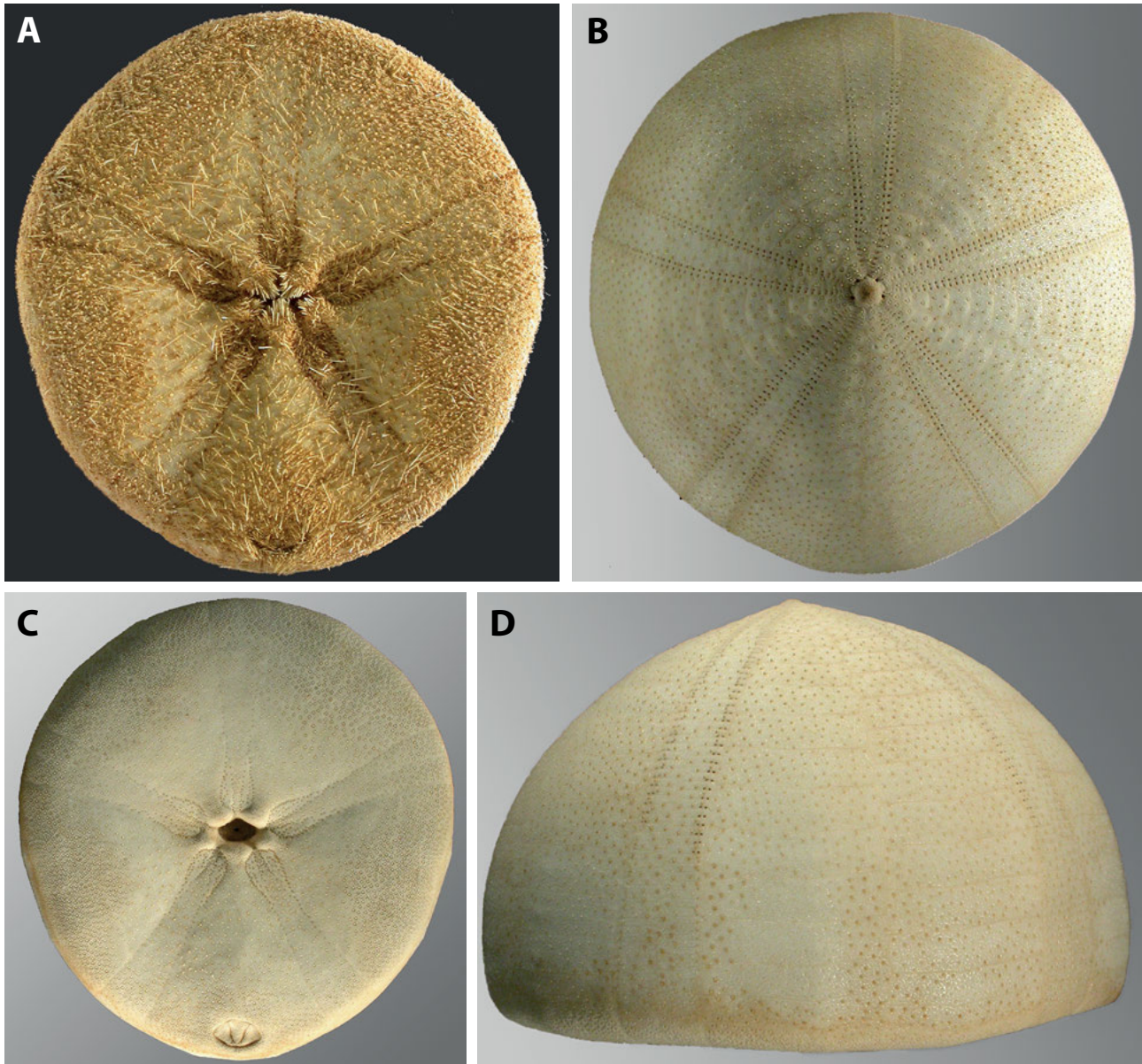
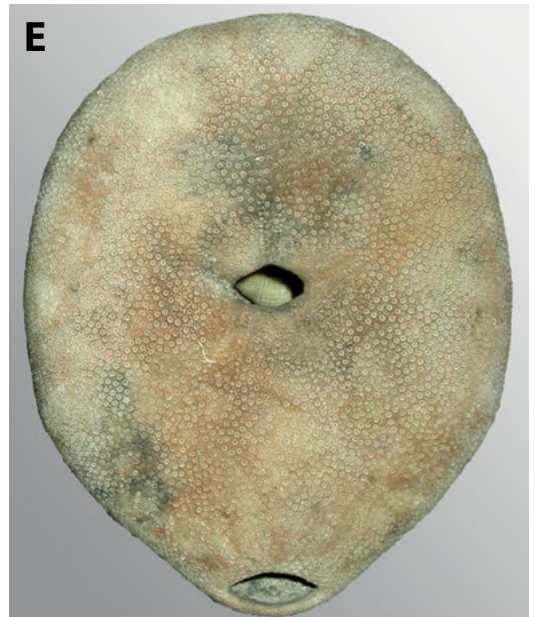


Fig. 3.13: *Conolampas sigsbei*. (A) Specimen with spines, oral side. Test length 79 mm; Cuba. ZMUC. The bourrelets are well developed, set with specialized spines, which spread over the peristome like a fan. (B–D) Specimen without spines. Test length 81 mm; Cuba. ZMUC. (B) Aboral side: the pore pairs are rather distant from each other and not at all conjugate. (C) Oral side: the floscelle is well developed. (D) Side view: the apical system forms a distinct knob.

Tab. 3.1: Four species of *Echinolampas* in comparison.

<i>E. alexandri</i>	<i>E. chuni</i>	<i>E. ovata</i>	<i>E. sumatrana</i>
Test rather broad, low, rounded margin	Test elongated, rostrate, low margin	Test elongated, high with rounded margin	Test rather broad, subconical with low margin
Thin, but robust	Very strong	Solid	Very strong
Apical system anterior	Apical system anterior	Apical system anterior	Apical system subcentral
Petals hardly bowed	Petals narrow, parallel-sided	Petals broad, bowed	Petals broad, parallel-sided
Peristome transversely oval	Peristome transversely subpentagonal	Peristome transversely pentagonal	Peristome transverse and lowly pentagonal



Apical system: Distinctly anterior.

Petals: Parallel sided, shorter and narrower than in *E. sumatrana*.

Oral side: Pore zones depressed; peristome subpentagonal; phyllodes inconspicuous, bourrelets rudimentary.

Tuberculation: Coarser than in *E. sumatrana*.

Remarks: During the “Valdivia” Expedition 1898/1899, the only two specimens of *Echinolampas chuni* were dredged in one and the same haul together with a single specimen of *Echinolampas sumatrana* at Station 192, west of Sumatra from a depth of 371 m. Because they differed conspicuously, Döderlein (1906) described them as two species.

The specimens were old, naked tests, rather worn and set with encrusting organisms. No spines, podia, or pedicellariae were left.

Echinolampas crassa Bell, 1880.

Test: Strong; high and subconical with rather sharp edges; length up to 125 mm.

Apical system: Subcentral (Fig. 3.15).

Petals: Long; the pore zones in a petal being of subequal length.

Oral side: Peristome pentagonal, bourrelets and phyllodes distinct.

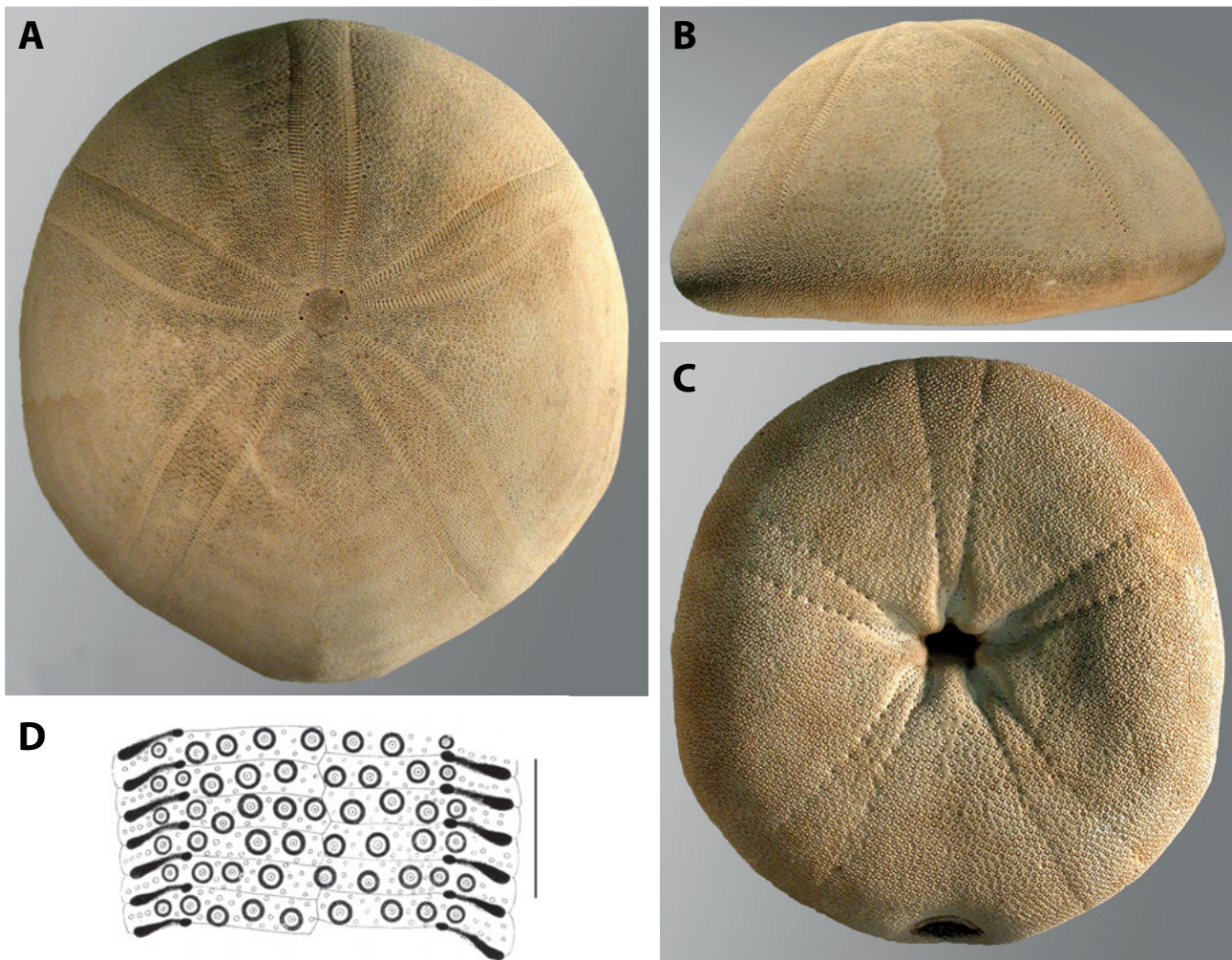


Fig. 3.15: *Echinolampas crassa*. Length of test 121 mm, South Africa. ZMUC. (A) Aboral side: the posterior end may sometimes be slightly rostrate. (B) Side view: the test is high and subconical. (C) Oral side: the bourrelets and phyllodes are well developed. (D) Ambulacral plates. Scale bar is 4 mm; after Mortensen (1948).

◀ **Fig. 3.14:** (A–F) Species of *Echinolampas*. *Echinolampas alexandri*. Test length 55 mm, Philippines. Photos courtesy of H. van Noordenburg. (A) Aboral side. (B) Oral side: the peristome is transversely oval. (C) Side view. The test is lower and the upper surface is more flattened than in *Echinolampas ovata*. (D–F) *Echinolampas chuni*. Test length 75 mm, Siberut Strait, west of Sumatra, Indonesia. MFN Berlin, Holotype, Ech Nr. 5846. (D) Aboral side: the apical system is anterior. (E) Oral side: the posterior end is rostrate. (F) Side view: the upper side is hemispherically vaulted with a low margin.

Distribution: This species is restricted to South Africa; bathymetric range 12 to 500 m.

Biology: This echinoid feeds on detritus by lifting particles into the mouth using the oral podia and the bourrelet spines. The size of the particles is limited, larger grains are rejected because of the fixed size of the peristome, and smaller ones are obviously difficult to handle. The species lives in ripple beds, burrowing during feeding about 30 to 50 mm deep. As the estimated growth rate per year is approximately 5 mm, this sea urchin is likely to be long living (Thum & Allen 1975).

Echinolampas depressa Gray, 1851

Test: High, upper side more or less flattened; length may reach 50 mm.

Petals: Short, pore zones of strongly different length.

Oral side: Phyllodes hardly widened, bourrelets inconspicuous.

Distribution: The species is found in eastern Central America, southeast USA, and the West-Indies to French Guyana; living between 30 and 310 m (Fig. 3.16).

Echinolampas keiensis Mortensen, 1948.

Test: Broadly ovoid, aboral side subconical, oral side flat; length up to 83 mm.

Apical system: Slightly anterior (Fig. 3.17).

Ambulacra: Pore zones in petals very unequal and curved; pore pairs conjugate.

Oral side: Peristome pentagonal and sunken; phyllodes well-developed, bourrelets distinctly inflated.

Distribution: Kei Islands, Indonesia and off Zamboanga, Philippines; 245 to 400 m.

Remarks: *Echinolampas keiensis* and *E. sternopetala* are very similar in having strongly unequal pore zones. However, in the former, the pore pairs are conjugate but not in the latter.

Echinolampas koreana H.L. Clark, 1925.

Test: High, length of holotype 52 mm.

Petals: Moderately short, pore zones unequal in length.

Peristome: Small and sunken.

Occurrence: Korean Strait and West Japan at a depth of 73 m.

Remarks: This species has a higher test with broader petals than *E. sternopetala*.

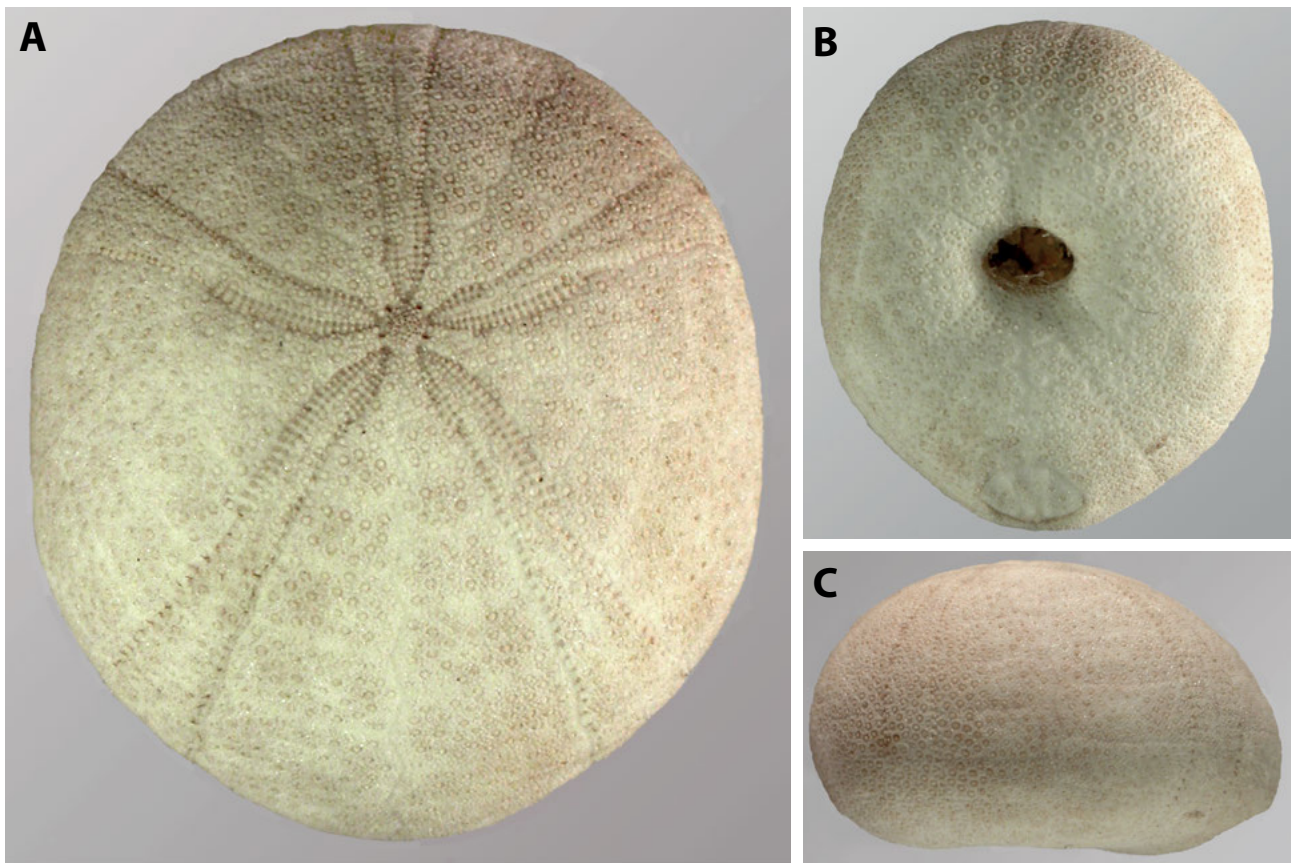


Fig. 3.16: *Echinolampas depressa*. Test length 37.5 mm, height 22 mm; Florida, USA. ZMUC. (A) Aboral side and (B) oral side. The petals are short and the peristome transversely oval with poorly developed phyllodes and bourrelets. (C) Side view: the test is highly convex.

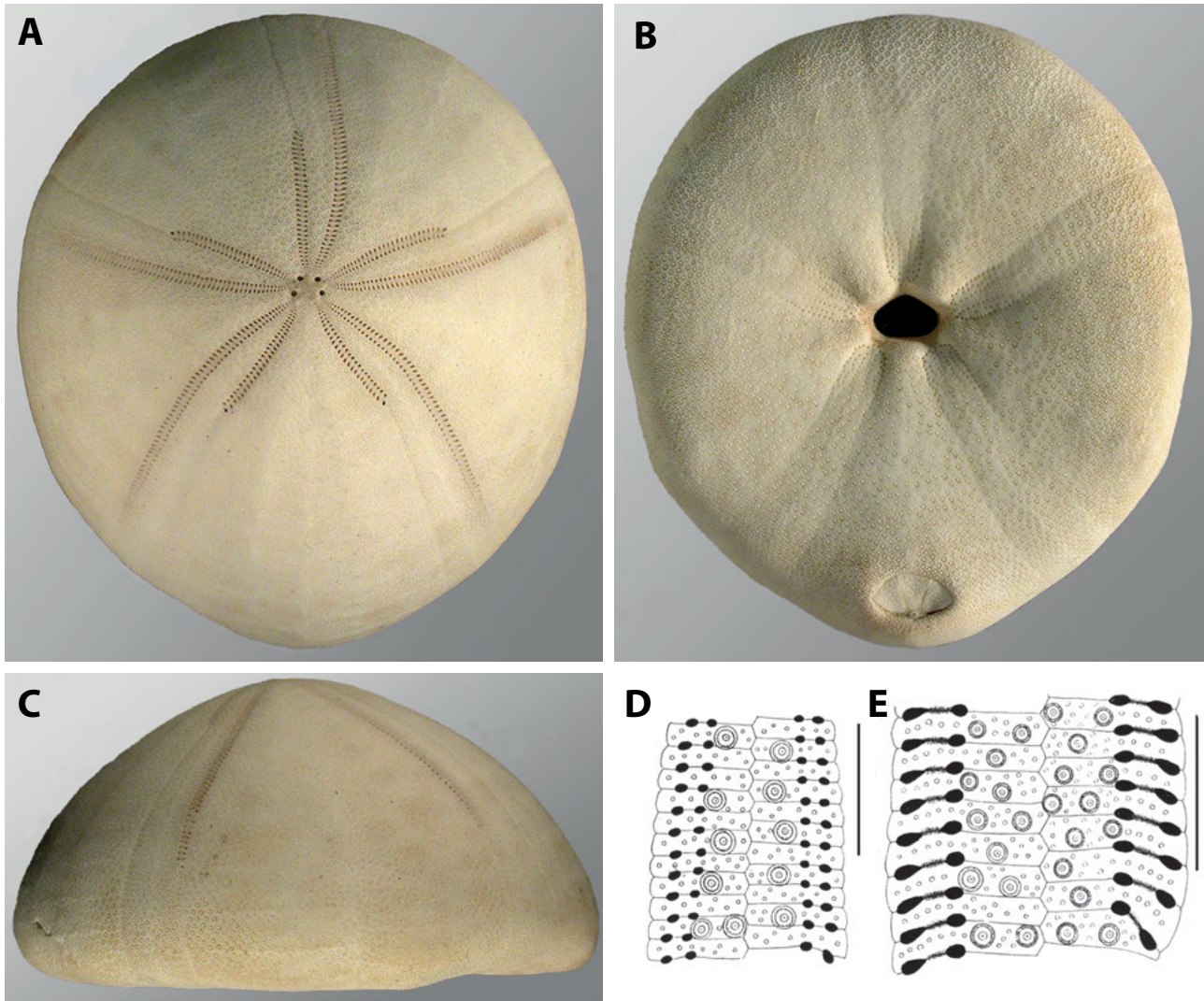


Fig. 3.17: (A–C) *Echinolampas keiensis*. Test length 62 mm; Kei Islands, Indonesia. ZMUC. (A) Aboral side of test: one pore zone has half the length of the other. (B) Oral side of test: phyllodes and bourrelets are well developed. (C) Side view: the test is subconical. (D, E) *Echinolampas*: ambulacral plates: (D) *Echinolampas sternopetala* with very few primary tubercles, pore pairs not conjugate. (E) *Echinolampas keiensis* with distinctly more primary tubercles, pore pairs conjugate. Scale bar is 3 mm. After Mortensen (1948).

Echinolampas ovata (Leske, 1778)

Test: Strong, highly domed with thick margin; circumference egg-shaped; maximum length about 80 mm.

Apical system: Distinctly anterior.

Ambulacra: Petals well-developed, narrow pore zones, pore zones in the paired petals of different lengths (Fig. 3.18).

Oral side: Deeply depressed toward the large, pentagonal mouth, bourrelets vertical and rather inconspicuous, phyllodes small.

Periproct: Transversely elongated, just beneath the posterior margin.

Spines: Uniformly short on the aboral side, longer and thicker on the oral side.

Color: In life, light to chestnut brown, denuded test grayish. After death, the color of the sea urchin turns a bright green, which fades over time.

Distribution: This species is known in the tropical Indian Ocean from the Red Sea to Ceylon, Mauritius, and Western Australia at depths between 9 and 75 m.

Echinolampas rangii Desmoulins, 1837

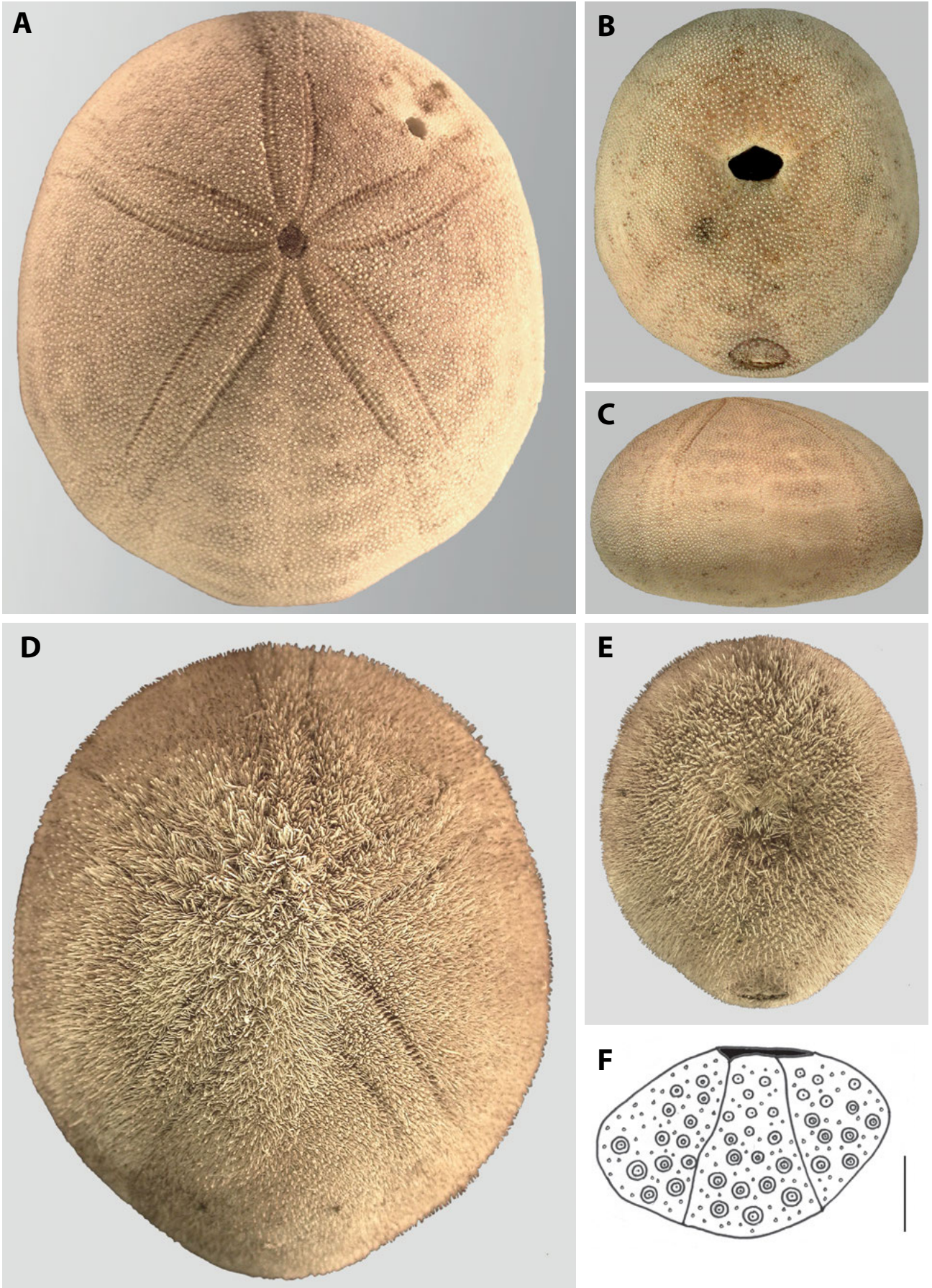
Test: Broadly ovoid, aboral side moderately vaulted; margin rounded; maximum length 103 mm.

Apical system: Slightly anterior, slightly knob-shaped (Fig. 3.19).

Petals: Broad, narrowing distally, but not closed; pore zones of unequal length, especially in the anterior pair; pores unequal, outer pore slit-like, inner one round.

Oral side: Sunken toward the pentagonal peristome; phyllodes and bourrelets well-developed.

Tuberculation: Aborally dense and uniform.



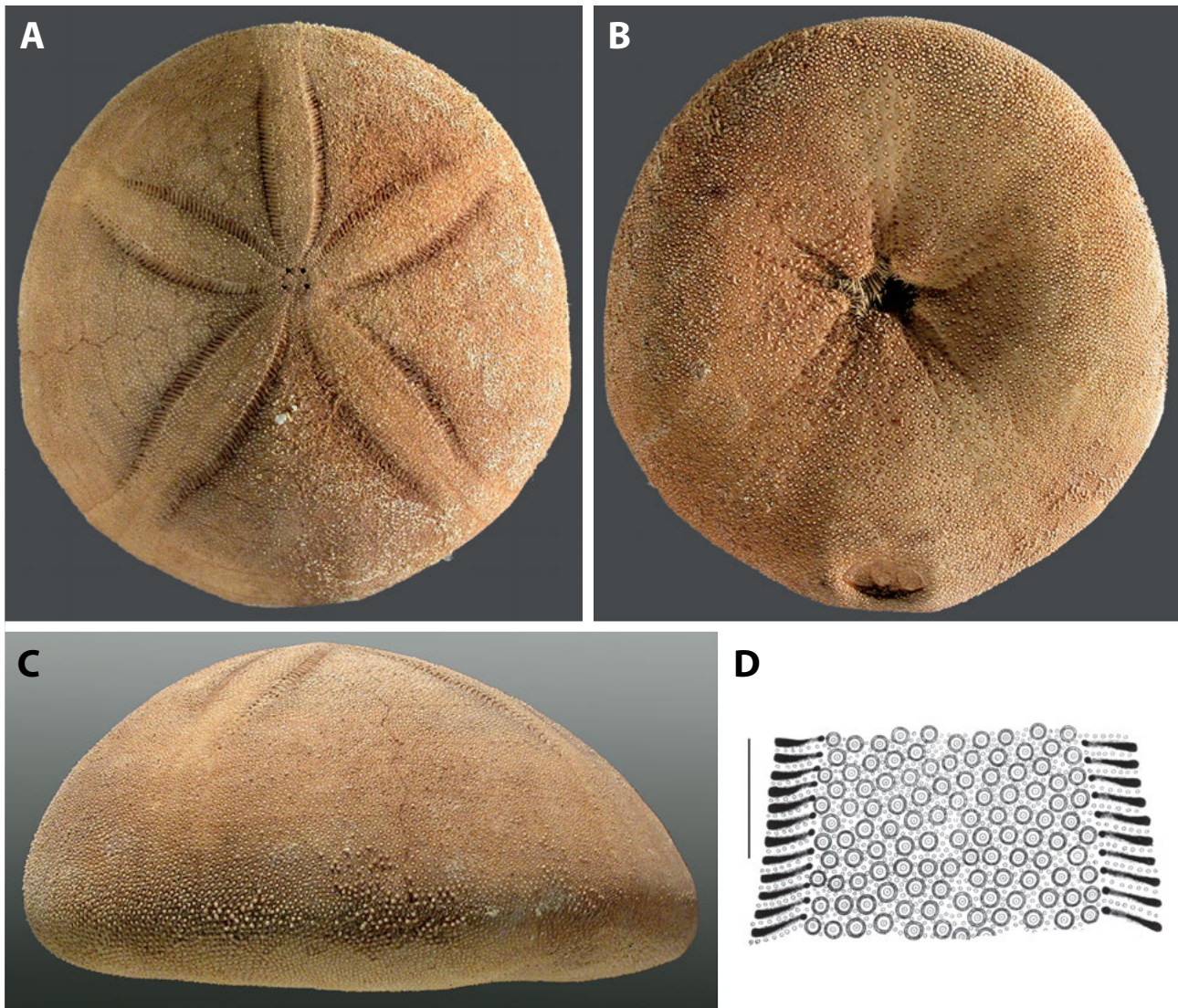


Fig. 3.19: (A–C) *Echinolampas rangii*. Test length 79 mm; Dakar, Senegal. ZMUC. (A) Aboral side: the petals are broad and rather bowed, distally open. (B) Oral side: Phyllodes and bourrelets are distinct. (C) Side view: in profile, the test is subconical. (D) Ambulacral plates of *E. rangii*. The petals are broad, the interporiferous zone densely set with primary tubercles. The pore pairs are strongly conjugate. Scale bar is 4 mm. After Mortensen (1948).

Color: Test and spines are light brownish, cleaned tests are whitish.

Distribution: This species is recorded from the Cape Verde region and Senegal, West Africa. The bathymetric range reaches from 1,570 to 1,670 m, but Mortensen (1948) also reported findings from “shallow waters”.

Echinolampas sternopetala A. Agassiz & H.L. Clark, 1907.

Test: Fairly strong, ovoid in outline, slightly tapering toward the posterior end; length may reach up to 79 mm.

Apical system: Anterior to subcentral (Fig. 3.20).

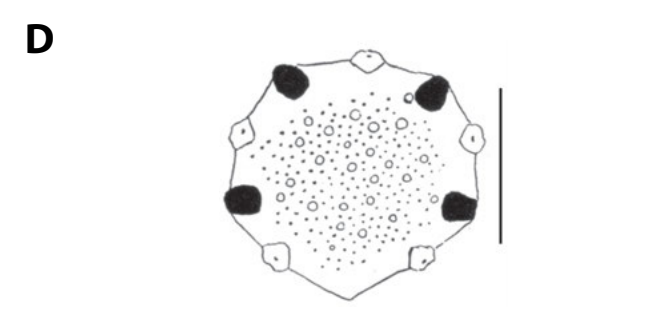
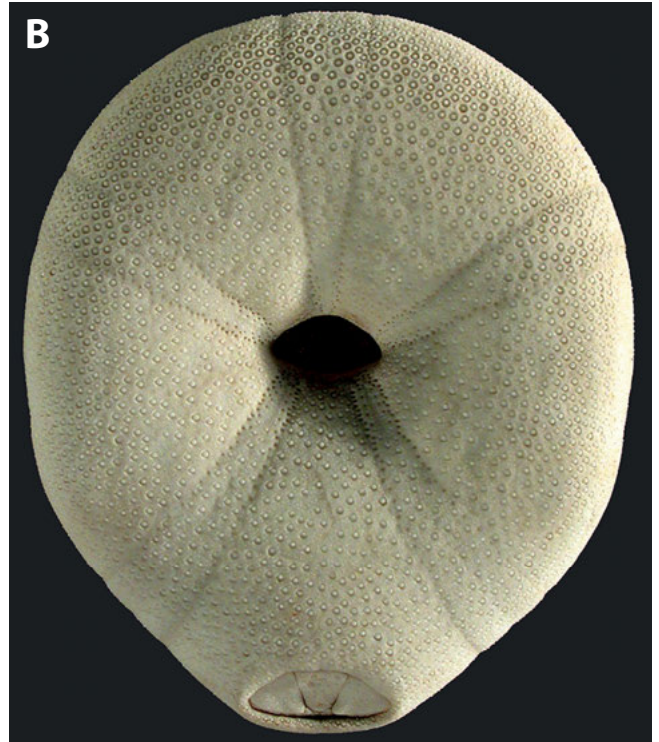
Petals: Narrow, pore zones very unequal in length and curved, anterior ambulacrum shortest; pore pairs not conjugate.

Oral side: Nearly flat, sunken toward the transversely oval peristome; phyllodes short and not widened, bourrelets rudimentary.

Periproct: Broader than the peristome, positioned obliquely below the posterior end, the distal edge nearly straight.

Primary tuberculation: Rather sparse.

◀ **Fig. 3.18:** *Echinolampas ovata*. (A–C) Test length 65 mm; Dahab, Gulf of Aqaba, Red Sea. (A) Aboral side: in the paired petals, the pore zones are of different lengths. The specimen has been drilled by a predating snail and died. (B) Oral side: the pentagonal mouth is deeply depressed. (C) Side view of test. (D, E) Test length 56 mm; Dahab, Gulf of Aqaba, Red Sea. (D) Aboral side: the test is covered by short and dense spines. (E) Oral side. (F) The periproct is built by three plates. Scale bar is 1 mm. After Mortensen (1948).



Color: In living specimens, the test and spines have a yellow tinge.

Distribution: This species is endemic to Japan, known only from Sagami Bay southward to the Kagoshima Gulf; bathymetric range: 100 to 500 m.

Echinolampas sumatrana Döderlein, 1905

The only known specimen is a rather worn, encrusted, naked test (see also *E. chuni*).

Test: Strong, aboral side rounded conical; outline broadly ovoid, tapering to the posterior end.

Apical system: Subcentral.

Petals: Longer than in *E. chuni* and broader, parallel-sided; the pore zones only slightly unequal in each petal (Fig. 3.21).

Oral side: Depressed, peristome transversely pentagonal, distinct phyllodes, bourrelets hardly inflated; periproct below the posterior margin.

Occurrence: A single specimen found off the west coast of Sumatra, Indonesia, at a depth of 371 m together with two specimens of *E. chuni*.

3.2.1.3 Family Neolampadidae Lambert, 1918

The members of this family are characterized by their apetaloid ambulacra. The plates are simple, each perforated by a single, small pore, which may be in some species aborally rudimentary or even entirely lacking. All species display sexual dimorphism, the females having either large gonopores or a marsupium.

Literature: Mortensen 1948; McKnight 1968; Baker & Rowe 1990; Mooi 1990b; Suter 1994, 1996; Holmes 1995.

Six genera are included in this family, each with a single extant species (Tab. 3.2):

Genus *Anochanus* Grube, 1868. China Sea.

Genus *Aphanopora* de Meijere, 1903. Sulu and Tasman Seas.

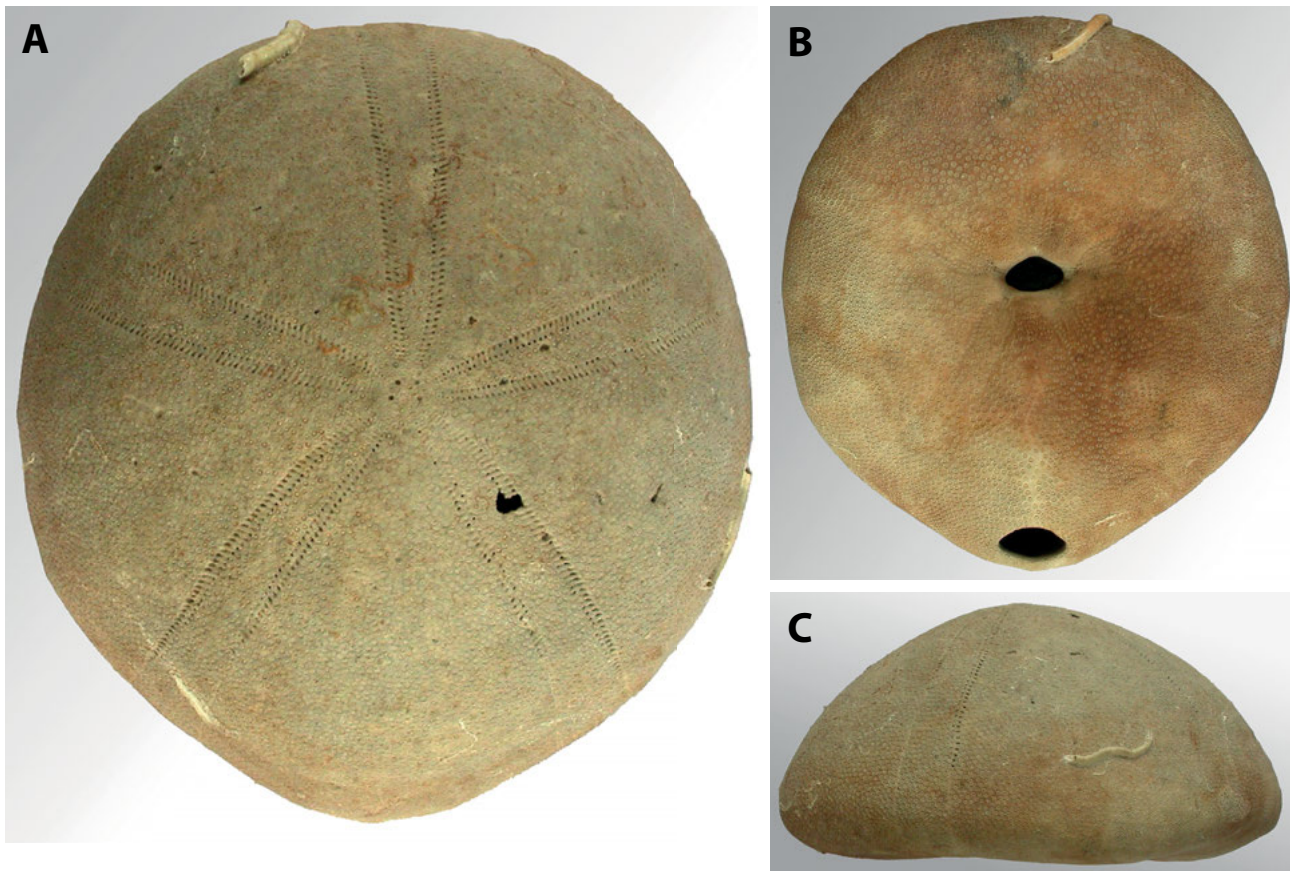


Fig. 3.21: *Echinolampas sumatrana*. Test length 75 mm, Siberut Strait, west of Sumatra, Indonesia. MfN Berlin Holotype, Ech Nr. 5845. (A) Aboral side. (B) Oral side: the phyllodes are conspicuous. (C) Side view.

◀ **Fig. 3.20:** *Echinolampas sternopetala*. (A–C) Test length 68 mm, Sagami Bay, Japan. ZMUC. (A) Aboral side: the narrow ambulacra with strongly unequal pore zones widen conspicuously toward the margin. (B) Oral side: the peristome is deeply sunken. (C) Side view. (D) Monobasal apical system: there is a single large, fused plate with hydropores, four gonopores, and five small ocular plates. Scale bar is 2 mm; after Mortensen (1948). (E, F) Specimen with spines. Test length 71 mm, Sagami Bay, Japan. ZMUC. (E) Aboral side: the spination is dense and uniform. (F) Oral side.