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THE VELIGER

A Revision of the Genus *Acanthopleura* Guilding, 1829 (Mollusca: Polyplacophora)

by

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Abstract. Fifteen species of *Acanthopleura* Guilding, 1829 (=*Corephium* Gray, 1847a; *Enoplochiton* Gray, 1847a; *Maugeria* Gray, 1857; *Sclerochiton* Dall, 1881; *Francisia* Dall, 1882; *Rhopalopleura* Thiele, 1893; *Mesotomura* Pilsbry, 1893a; *Amphitomura* Pilsbry, 1893a; *Liolophura* Pilsbry, 1893a; *Squamopleura* Nierstrasz, 1905a; *Clavarizona* Hull, 1923; *Acanthozostera* Iredale & Hull, 1926; *Planispina* Taki, 1962) are here recognized, two of which are new to science. The fifteen species are *A. granulata* (Gmelin, 1791), *A. spinosa* (Bruguière, 1792), *A. echinata* (Barnes, 1824), *A. nigra* (Barnes, 1824), *A. gemmata* (Blainville, 1825), *A. hirtosa* (Blainville, 1825), *A. gaimardi* (Blainville, 1825), *A. loochooana* (Broderip & Sowerby, 1829), *A. brevispinosa* (Sowerby, 1840a), *A. japonica* (Lischke, 1873), *A. curtisiana* (Smith, 1884), *A. miles* (Carpenter *in* Pilsbry, 1893c), *A. araucariana* (Hedley, 1898), *A.* ***arenosa*** Ferreira, spec. nov., and *A.* ***rehderi*** Ferreira, spec. nov. Despite large specimen size, intertidal habitat, and world-wide, mostly tropical distribution, *Acanthopleura* is not represented in the fossil record.

The genus-name *Acanthopleura* Guilding, 1829, began as a grouping of seven heterogeneous "sections," each defined by the girdle characteristics of a given species. Although subsequent authors (SWAINSON, 1840; GRAY, 1847a, 1857; SHUTTLEWORTH, 1853; Carpenter *in* DALL, 1882) altered GUILDING's (1829) concept, it was left to PILSBRY (1893c:213–218) to restrict *Acanthopleura* to the "section" characterized by "zona [=girdle] spinosa," and typified by *Chiton spinosus* Bruguière, 1792. Assigning species without teeth in the posterior valve to a new genus, *Liolophura,* PILSBRY (1893c) divided *Acanthopleura* into four subgenera based upon the characteristics of the insertion plate of the posterior valve: (1) *Acanthopleura s.s.* (type, *C. spinosus* Bruguière), with "a very long insertion plate cut into numerous teeth by short slits," (2) *Maugeria* Gray, 1857 (restricted) (type, *C. piceus* Gmelin), with "the pectinated insertion plate cut into numerous teeth by slits similar to those of the head-valve," (3) *Amphitomura* Pilsbry, 1893a (type, *C. borbonica* Deshayes), with "the insertion-plate very short, with blunt, crenulated edge, interrupted only by a single mopaloid slit on each side," and (4) *Mesotomura* Pilsbry, 1893a (type, *C. echinatum* Barnes), with "the long insertion plate deeply pectinated outside, its edge interrupted only by a single median-posterior slit."

Yet, *Acanthopleura* (*sensu* PILSBRY, 1893c), a widespread, tropical to subtropical group of large, accessible (intertidal to emergent), and abundant specimens, has remained problematical in regard to the biological species involved and their taxonomic arrangement. Complicated by the appearance of several ill-defined nominal genera, subgenera, species, and subspecies much before clear understanding of the whole group had been attained, *Acanthopleura* has been sorely in need of revision. But, likely, the difficulties in assembling sufficient material from exotic areas have been such as to stifle earlier attempts to study the group.

This revision rests upon the examination of material in the museum collections of the California Academy of Sciences, San Francisco (CAS); Los Angeles County Museum of Natural History (LACM); University of Colorado Museum, Boulder, Colorado (UCM); Academy of Natural Sciences of Philadelphia (ANSP); U.S. National Museum of Natural History, Washington, D.C. (USNM); British Museum (Natural History) (BMNH); Muséum National d'Histoire Naturelle, Paris (MNHN); Uppsala Universitets Zoologiska Museum, Sweden (UUZM); The Australian Museum, Sydney (AMS); Western Australian

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Museum, Perth (WAM); National Museum of Victoria, Melbourne (NMV); Institut Royal des Sciences Naturelles de Belgique, Bruxelles (IRScnB); Musée d'Histoire Naturelle, Bucarest, Romania (MHNB); Istituto di Zoologia dell'Universita di Firenze, Italy (MF); and in the personal collections of Dr. John S. Pearse, University of California, Santa Cruz, California; Salle Crittenden, Oakland, California; Clay Carlson and Patty Jo Hoff, Merize, Guam; Ian Loch, Sydney, Australia; Richard A. Van Belle, Sint-Niklaas, Belgium; J. R. Penprase, West Hobart, Tasmania; and J. R. Penniket, Warkworth, New Zealand. Additional material and field observations were obtained by, and are presently in the collection of, A. J. Ferreira (AJF collection station numbers on file at CAS).

An effort was made to study all available type specimens deemed necessary to resolve or clarify taxonomic problems; where type material is mentioned in the literature but no attempt was made here to verify its existence or repository, reference is made only to information at hand regarding types "not examined"; where there is no information in the literature about type specimens and no attempt was made here to examine or locate type material, the types are said to remain "unascertained."

SYSTEMATIC TREATMENT

Polyplacophora Gray, 1821

Neoloricata Bergenhayn, 1955

Ischnochitonina Bergenhayn, 1930a

Chitonidae Rafinesque, 1815

Acanthopleura Guilding, 1829

Description: Mostly large, oval, depressed, round-backed chitons. Valves thick, heavy, beaked. Tegmental sculpture coarsely granular to wrinkled, often obliterated by erosion; tegmentum broadly inflexed at posterior margin of intermediate valves. Mucro central to posterior. Ocelli scattered throughout anterior valve, anterior ⅓ to ⅗ of lateral areas of intermediate valves, and postmucro area of posterior valve. Gills mostly holobranchial (*i.e.*, extending along 90–100% of foot [SIMROTH, 1894:247]). Articulamentum whitish to blue, brown, or black. Strong sutural laminae. Insertion plates markedly pectinate on outside; on posterior valve insertion teeth may be absent in part or in total, often buttressed by transverse callus; slits 8–12 on anterior valve, 1 (2 in one species) on intermediate valves, 0–10 on posterior valve. Girdle thick, muscular, densely covered with calcareous elements, variable in length and in shape from spikes to spines, spinelets, or scales. Radula major lateral teeth with discoid heads (with 4 cusps in one species).

All species of *Acanthopleura* are confined to the intertidal zone. Specimens are often found on the surface of rocks, often exposed at low tide.

Type-species: *Chiton spinosus* Bruguière, 1792, by subsequent designation (GRAY, 1847b).

Synonyms:

Corephium Gray, 1847a (not Browne, 1789)
Type: *Chiton echinatus* Barnes, 1824, by subsequent designation (GRAY, 1847b).

Enoplochiton Gray, 1847a
Type: *Chiton niger* Barnes, 1824, by monotypy.

Maugeria Gray, 1857
Type: *Chiton piceus* Gmelin, 1791 (=*Chiton granulatus* Gmelin, 1791), by subsequent designation (PILSBRY, 1893c).

Sclerochiton Dall, 1881 (not Kraatz, 1859)
Type: *Chiton miles* Carpenter *in* Pilsbry, 1893c, by monotypy.

Francisia Dall, 1882
Type: *Chiton spinosus* Bruguière, 1792, by original designation.

Rhopalopleura Thiele, 1893
Type: *Chiton aculeatus* Linnaeus, 1758 (?=*Chiton echinatus* Barnes, 1824), by monotypy.

Mesotomura Pilsbry, 1893a
Type: *Chiton echinatus* Barnes, 1824, by monotypy.

Amphitomura Pilsbry, 1893a
Type: *Chiton borbonicus* Deshayes, 1863 (=*Chiton brevispinosus* Sowerby, 1840a), by original designation.

Liolophura Pilsbry, 1893a
Type: *Chiton japonicus* Lischke, 1873, by original designation.

Squamopleura Nierstrasz, 1905a
Type: *Chiton miles* Carpenter *in* Pilsbry, 1893c, by subsequent designation (Pilsbry, 1893c).

Clavarizona Hull, 1923
Type: *Chiton hirtosus* Blainville, 1825, by original designation.

Acanthozostera Iredale & Hull, 1926
Type: *Chiton gemmatus* Blainville, 1825, by original designation.

Planispina Is. Taki, 1962
Type: *Acanthopleura (Amphitomura) planispina* Bergenhayn, 1933 (=*Acanthopleura gemmata* [Blainville, 1825]), by original designation.

Remarks: The arrangement of species here allocated to *Acanthopleura* differs significantly from that of PILSBRY (1893c). It is based on the appreciation of over-all similarities among species rather than on modifications of any single character. Most generic names here synonymized under *Acanthopleura* had been defined solely in terms of changes in the girdle elements or in the insertion plate of the posterior valve, ignoring similarities in body plan among species. As a result, species that in most respects appear extremely close, such as *Chiton gemmatus* Blainville, 1825, and *C. gaimardi* Blainville, 1825, had been placed in different genera (even in different subfamilies) on account of modifications in the posterior valve, notwithstanding extreme closeness in all other features. Such situations are here corrected, and 15 species of *Acanthopleura* recognized:

Acanthopleura granulata (Gmelin, 1791)
Acanthopleura spinosa (Bruguière, 1792)
Acanthopleura echinata (Barnes, 1824)
Acanthopleura nigra (Barnes, 1824)
Acanthopleura gemmata (Blainville, 1825)
Acanthopleura hirtosa (Blainville, 1825)
Acanthopleura gaimardi (Blainville, 1825)
Acanthopleura loochooana (Broderip & Sowerby, 1829)
Acanthopleura brevispinosa (Sowerby, 1840a)
Acanthopleura japonica (Lischke, 1873)
Acanthopleura curtisiana (Smith, 1884)
Acanthopleura miles (Carpenter *in* Pilsbry, 1893c)
Acanthopleura araucariana (Hedley, 1898)
Acanthopleura ***arenosa*** Ferreira, spec. nov.
Acanthopleura ***rehderi*** Ferreira, spec. nov.

Acanthopleura has no fossil record. The paleontological literature contains only two possible references to the genus as here understood: SMITH (1960:67) mentioned (but did not cite) *Acanthopleura* in "Pleist., S. Am. (Bol.)"; and COSSMAN (1888:20) allocated one posterior valve from the Eocene of the Paris Basin to *Enoplochiton,* as *E. rochebrunei,* which "is probably no chiton at all" (VAN BELLE, 1983:128).

Acanthopleura spinosa (Bruguière, 1792)

Figures 1 to 6, and 112-S

Chiton spinosus BRUGUIÈRE, 1792:25, pl. 2, fig. 1; LAMARCK, 1819:321; BURROW, 1815:185, pl. 26, fig. 4; MAWE, 1823:1, 3–4, pl. 1, fig. 3; WOOD, 1825:4, pl. 1, fig. 38; BLAINVILLE, 1825:550; SOWERBY, 1840b:1, 10, sp. no. 2, fig. 151; REEVE, 1842:12, pl. 134, fig. 151; 1847, pl. 9, fig. 51; ADAMS & ADAMS, 1858:475; CHENU, 1859: 381, fig. 2868; PAETEL, 1869:66, 1873:80; FISCHER, 1885:881 (in subgen. *Acanthopleura*); ARNOLD, 1901: 322 (fig. only) (reprinted, 1968); LAMY, 1923:260.
Maugeria spinosa: GRAY, 1857:184.
Francisia spinosa: TRYON, 1883:343, pl. 85, fig. 81; HADDON, 1886:30.
Acanthopleura spinosa: PILSBRY, 1893c:220, pl. 45, figs. 80–87; THIELE, 1893:373, pl. 30, fig. 3; HIDALGO, 1905: 272; NIERSTRASZ, 1905a:101, 1905b:152; HORST & SCHEPMAN, 1908:526; HEDLEY, 1910:352; IREDALE, 1910b:158, 1914b:668; ASHBY, 1918:86, 1922a:31–32, 1926:384, 388–389; IREDALE & HULL, 1926:264–265, pl. 38, figs. 1–2 (reprinted, 1927:127–128, pl. 16, figs. 1–2); THIELE, 1929:22; BERGENHAYN, 1930a:32–33; LELOUP, 1933a:24–25, 1933b:2–3; KURODA, 1941:71; LELOUP, 1952:59–61, text fig. 20, pl. 6, fig. 4; ALLAN, 1959:239, fig. 6b; IS. TAKI, 1962:47; IW. TAKI, 1964: 412; ANG, 1967:415–416, pl. 7, figs. 1–4; WU, 1969: 103–104, figs. 1, 7–15; WELLS, 1981:253.
Acanthopleura spinosa montebelloensis ASHBY, 1922a:32.

Type material and type locality:

Chiton spinosus Bruguière, 1792: Type specimens (2) at MNHN (*fide* LAMY, 1923), not examined; locality, not originally stated but presumed to be "isle Maria, baye de l'Est," Australia, according to label accompanying types (LAMY, 1923).
Acanthopleura spinosa montebelloensis Ashby, 1922a: Types' (Ashby coll. No. 5888) whereabouts unknown (not at WAM [WELLS, 1977]); locality "Monte Bello Island," Western Australia (20°25'S, 115°32'E).

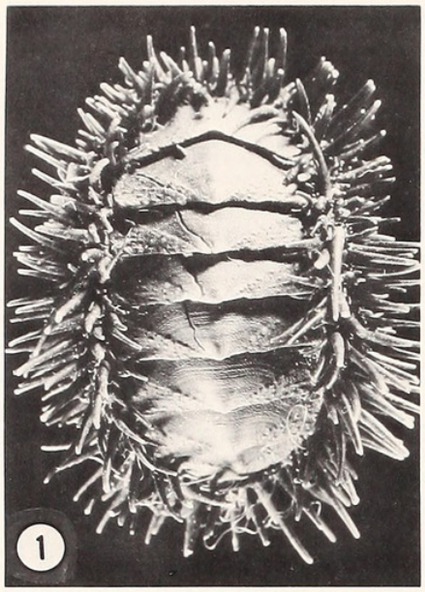
Material examined:

AUSTRALIA: Yardie Creek, North West Cape, 2 specimens (WAM 56-74); Monte Bello Is., 1 specimen (WAM 69-74); Roseman Id., Dampier Arch., 2 specimens (WAM 65-74); Kendrew Is., Dampier Arch., 7 specimens (WAM 1341-78); Port Hedland, 1 specimen (WAM 66-74); Flaccount Bay, 1 specimen (WAM 618-67); Walsh Point, Admiralty Gulf, 3 specimens (WAM 79-78; WAM 1107-78); Pt. Gantheaume, near Broome, 2 specimens (WAM 10884); Riddal Beach, Broome, 2 specimens (WAM 60-74); Broome, 1 specimen (NMV); Kuri Bay, 1 specimen (WAM 55-74); Yampi Sound, 4 specimens (WAM 64-74); Augustus Id., Bonaparte Arch., 2 specimens (WAM 58-74); "N.W. Australia," 4 specimens (WAM 1106-78; NMV); Darwin, 1 specimen (NMV); Nightcliff, Darwin, 1 specimen (WAM 61-74); Fanny Bay, N.T., 5 specimens (NMV); Rainbow Cliffs, Gove, N.T., 1 specimen (I. Loch coll.).
NEW GUINEA: Sowek Soepiori, Schouten Is., 1 specimen, 75 mm long (ANSP 207130).
SULAWESI (=Celebes): 32 km E of Manado, 3 specimens (CAS 009806; CAS 012252).
TAIWAN: Wan-li-tong, Ping-tung Co., 1 specimen (UCM 27522).
PHILIPPINES: Hundred Islands, Lingayen Gulf, Luzon, 16 specimens (AJF 464; AJF 465).

Description: Excellent accounts of *Acanthopleura spinosa* were given by PILSBRY (1893c), IREDALE & HULL (1926), and WU (1969).

Among 60 specimens of *Acanthopleura spinosa* here examined, largest 80 mm long (in alcohol) (WAM 1107-78). Body width/length mean 0.66. Tegmentum uniform dark chestnut in color. Lateral areas hardly defined, not raised (Figures 1, 2). Tegmental sculpture of minute granules on anterior valve, postmucro area of posterior valve, and lateral areas of intermediate valves. Central areas almost smooth except for discrete transverse, concentric growth rugae. Mucro obtuse, moderately posterior; postmucro convex with marked slope. Width of tegmental surfaces of valves i/viii, 1.22. Ocelli round to oval, 40–50 μm in diameter, scattered throughout anterior valve, anterior ⅔ to ⅘ of lateral areas of intermediate valves, and postmucro area. Gills with 50–70 plumes per side.

Articulamentum reddish-brown in middle, lighter to almost white at periphery. On valve viii, tegmentum length/width mean 0.60; articulamentum wider than tegmentum (width of articulamentum/width of tegmentum on valve viii, mean 1.49). Sutural laminae wide; sinus well defined. Insertion plates relatively long, strongly pectinate on outside; on valve i, length of insertion plate/length of tegmentum, mean 0.36. On valve viii (Figures 3, 4), insertion teeth in part (⅔) fused to somewhat rounded, transverse callus; in specimen 50 mm long, insertion teeth (at midline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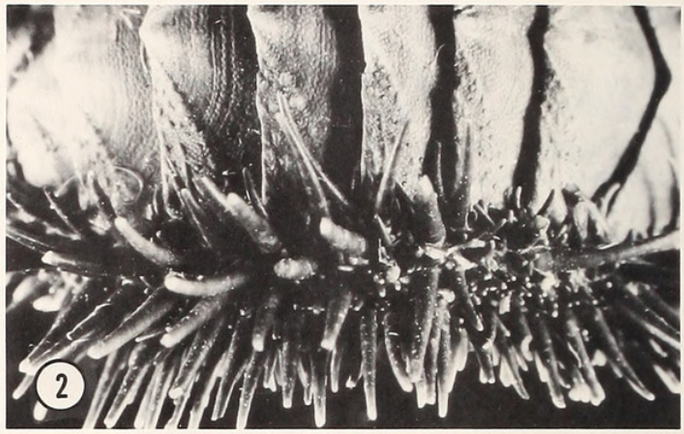
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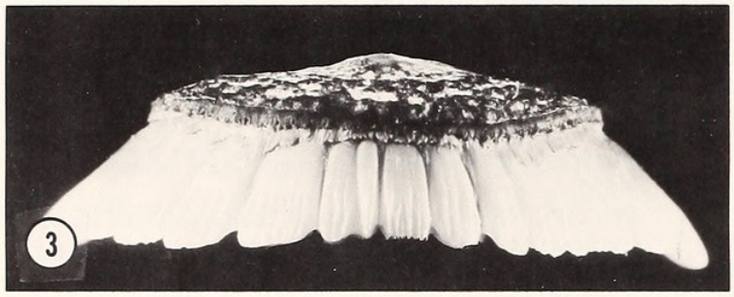
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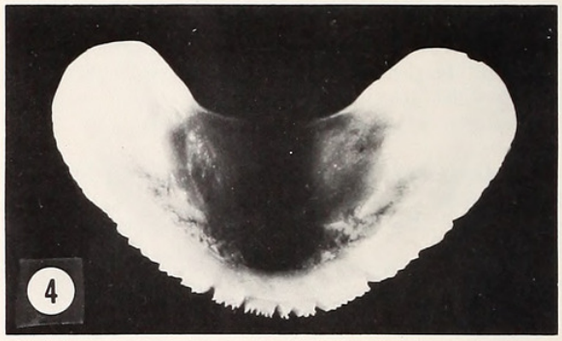
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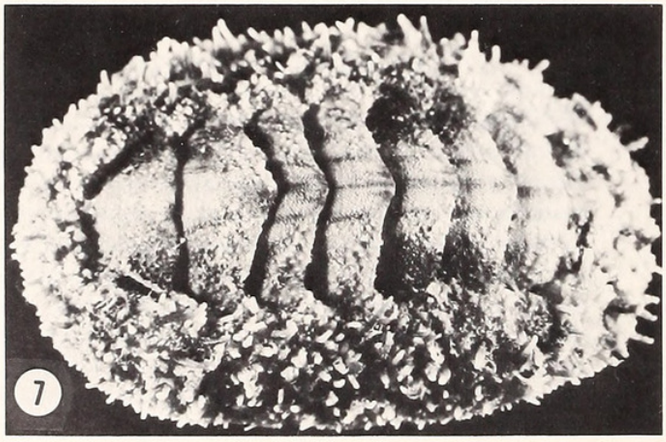
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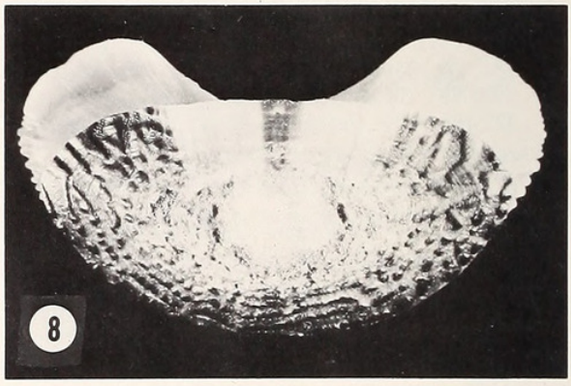
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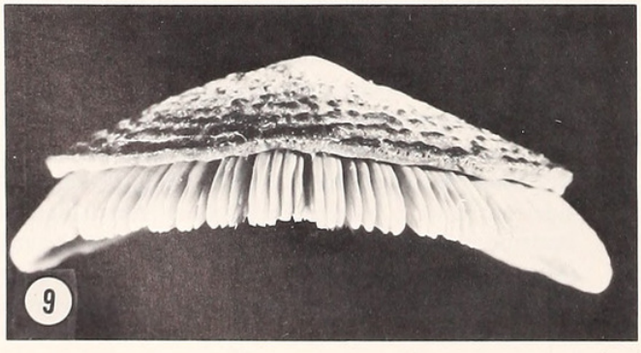
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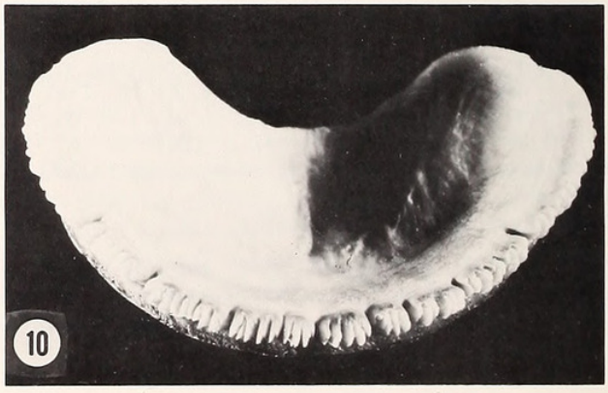
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of valve) 1.3 mm long on outside but extend only 0.4 mm beyond transverse callus on inside of valve. Slit formula 12/16-1-8/12; some intermediate valve(s) (particularly valve II) show 2 slits on one or both sides. Sinusal plate often pectinate on valve ii, but not so on other valves; on valve viii, relative width of sinus (width of sinus/width of sutural plates), mean 1.0.

Girdle upper surface with abundant, dark red, slender spines, sharply pointed, up to 16 mm long, 0.7 mm thick, in large specimens (Figure 5); girdle covered otherwise with dark red elements, translucent to opaque, as small as 30–50 μm long, variable in length and shape, representing all stages of growth from scalelike to spine. Girdle bridges (see Ferreira, 1983a) empty, *i.e.*, without significant elements. Undersurface paved with juxtaposed rows of transparent, squarish scales, 50 × 50 μm, roughly striated, inner edge somewhat convex as if articulating upon concave outer edge of adjacent scale.

Radula averaging 55% of specimen length (range 50–63%, SD = 7.9, n = 5) and 96 rows of teeth (range 80–110, SD = 11.9, n = 5). In specimen 75 mm long (AJF 464: Lingayen Gulf, Philippines), median tooth (Figure 6) 100 μm wide at anterior blade; first lateral teeth somewhat rectangular, outer edge deeply concave, about 220 μm at anterior blade; major lateral teeth with discoid head, 360 μm wide; outer marginal teeth 320 μm long, 350 μm wide (length/width, 0.9).

Distribution: *Acanthopleura spinosa* has been reported from Poulo Dama, Gulf of Thailand (Leloup, 1952), Taiwan (Wu, 1969), Philippines (Hidalgo, 1905; Ang, 1967), Java, Timor (Horst & Schepman, 1908), Pisang Islands (Leloup, 1933b), Amboine Id. [=Ambon] (Horst & Schepman, 1908), New Guinea (Nierstrasz, 1905b; Horst & Schepman, 1908; Leloup, 1933b), and New Caledonia (Iredale & Hull 1926). In Australia it has been reported along the northwestern coast from the Monte Bello Islands (Iredale, 1914b) to Cape York (Haddon, 1886). From the data, *A. spinosa* appears to be confined to the central Indo-Pacific from 25°N to 22°S, and from 105°E to 142°E. The northernmost verified record is Wan-li-tong, Taiwan (25°11′N, 121°41′E) (UCM 27522); the southernmost and westernmost verified record, North West Cape, Western Australia (21°45′S, 114°10′E) (WAM 1107-78); and the easternmost verified record, Gove (12°18′S, 136°55′E). The report of *A. spinosa* in New Caledonia (Iredale & Hull, 1926) requires corroboration; collecting trips to New Caledonia (A. J. Ferreira, July 1980) and eastern New Guinea, Trobriand Is., and New Britain Id. (A. J. Ferreira, August 1981) failed to find the species.

Acanthopleura spinosa is confined to the intertidal zone, with specimens often exposed at low tide.

Remarks: *Acanthopleura spinosa* is very distinct from all other species of *Acanthopleura,* posing no problems in identification. The dark reddish color and the long, thin, sharp girdle spines are diagnostic. It is the only *Acanthopleura* with two slits, though inconstant, on intermediate valves.

Acanthopleura spinosa occurs sympatrically with *A. gemmata* and *A. miles* throughout its range. Field observations show that where *A. spinosa* and *A. gemmata* coexist (AJF 464-465: Gulf of Lingayen, Luzon, Philippines), estimated population sizes are in the proportion of 1:100.

Acanthopleura gemmata (Blainville, 1825)

Figures 7 to 23, and 113-C

Chiton gemmatus Blainville, 1825:544.

Acanthopleura gemmata: Iredale, 1914b:668; Ashby, 1918: 86 (in subgen. *Amphitomura*), 1922b:29–31, 1923b:230, 1926:384, 388–389, 1928:171–172, pl. 12, figs. 6, 7; Way & Purchon, 1981:313; Wells, 1981:253; Chelazzi *et al.*, 1983:115–125; Ferreira, 1983b:278–282, fig. 30.

Acanthopleura gemmata queenslandica Ashby, 1922a:30, 1926: 384, 1928:171–172.

Acanthopleura gemmata maudensis Ashby, 1928:172, pl. 12, figs. 8, 9.

Amphitomura gemmata: Ashby, 1920:291; Hull, 1925:114–115.

Acanthozostera gemmata: Iredale & Hull, 1926:263, pl. 37, figs. 33, 34 (reprinted, 1927:126–127, pl. 15, figs. 33–34); Is. Taki, 1947:1269, fig. 3607, 1960:197, pl. 90, fig. 3, 1962:46–47; Ang, 1967:418–421, pl. 14, figs. 1–5; Wu, 1975:70–71, figs. 14–28.

Chiton spiniger Sowerby, 1840a:287–288, Suppl. pl. 16, fig.

←

Explanation of Figures 1 to 4 and 7 to 10

Figure 1. *Acanthopleura spinosa* (Bruguière, 1792). Gove, N.T., Australia (AJF coll.); specimen 16 mm long.

Figure 2. *Acanthopleura spinosa* (Bruguière, 1792). Same specimen as in Figure 1. Close-up of lateral areas and girdle.

Figure 3. *Acanthopleura spinosa* (Bruguière, 1792). Same specimen as in Figure 1. Posterior aspect of posterior valve.

Figure 4. *Acanthopleura spinosa* (Bruguière, 1792). Same specimen as in Figure 1. Ventral aspect of posterior valve.

Figure 7. *Acanthopleura gemmata* (Blainville, 1825). Bunaken Id., North Sulawesi, Indonesia (AJF 711); specimen 20 mm long.

Figure 8. *Acanthopleura gemmata* (Blainville, 1825). Koror, Palau, Western Caroline Islands (AJF 409); specimen 55 mm long. Dorsal aspect of posterior valve.

Figure 9. *Acanthopleura gemmata* (Blainville, 1825). Same specimen as in Figure 8. Posterior aspect of posterior valve.

Figure 10. *Acanthopleura gemmata* (Blainville, 1825). Same specimen as in Figure 8. Ventral aspect of posterior valve.

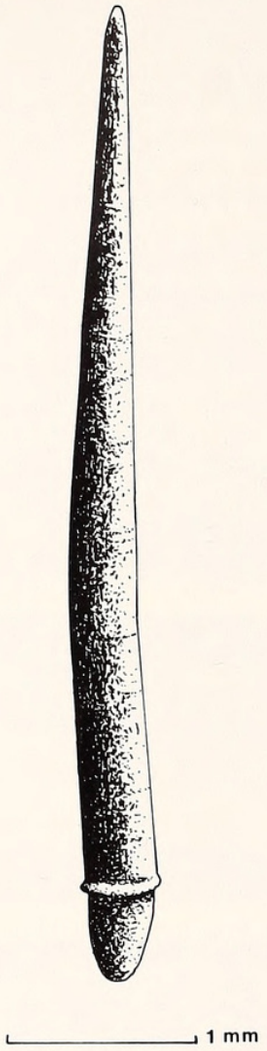


Figure 5

Acanthopleura spinosa (Bruguière, 1792). Hundred Islands, Lingayen Gulf (AJF 464); specimen 35 mm long. Girdle spine.

2, 1840b:1, 10, sp. no. 3, fig. 68, 1841:61; Reeve, 1847, pl. 14, fig. 75; Jay, 1850:99; Adams & Adams, 1854: 475; Chenu, 1859:381–382, fig. 2871; Tillier & Bavay, 1905:176, 179.

Maugeria spinigera: Gray, 1857:184.

Chiton (Acanthopleura) spiniger: Smith, 1884:81; 1891:420; Fischer, 1885:881; Martens, 1887:199.

Acanthopleura spiniger: Dall, 1879:298, fig. 28; Tryon, 1883:343, pl. 86, fig. 94; Moseley, 1884:145; 1885:18, pl. 6, figs. 1–3, 6–9; Haddon, 1886:23–25; Pilsbry, 1893c:221–226, pl. 48, figs. 22–32, pl. 49, figs. 33, 34; Pelseneer, 1899:8, 24–25; Sturany, 1904:267, 280; Hidalgo, 1905:272; Iredale, 1910b:158; Odhner, 1919:21, 42; Ashby, 1922a:31; Dautzenberg, 1923: 58, 1929:552; Bucknill, 1930:529, fig. 10; Leloup, 1933a:19–23, 1933b:1–2, 1952:41, text fig. 15, pl. 2, 1981:9–10, fig. 3.

Acanthopleura spinigera: Horst & Schepman, 1908:526–527; Thiele, 1893:372, pl. 3, fig. 30; Melvill & Standen, 1899:180; Thiele, 1909:8, 1911:398–399; Nierstrasz, 1905a:99–101, 1905b:151–152 (in part), 1906:511–513; Sykes, 1907:34; Smith, 1910:211; Ashby, 1923a:226; Pallary, 1926:28, pl. 4, figs. 4a, 4b; Tomlin, 1927:291; Bergenhayn, 1930a:32–33, pl. 8, fig. 75, pl. 9, fig. 84, 1930b:39–42, pl. 3, figs. 55–61, 70–74; Lamy, 1938:88; Solem, 1953:215; Greenfield, 1972:37–47.

"*Chiton aculeatus* Gmelin" Quoy & Gaimard, 1835:373–376; (Atlas, 1833), pl. 74, figs. 1–5.

Chiton (Acanthopleura) macgillivrayi Adams, 1855:120; Pilsbry, 1893c:224–225 (as syn. of *A. spiniger*).

Acantopleura [sic] *vaillantii* Rochebrune, 1882:192.

Acanthopleura rawakiana Rochebrune, 1882:195–196.

Acanthopleura balansae Rochebrune, 1882:197; Lamy, 1923: 265.

Acanthopleura glareosa Smith, 1884:81, *nomen nudum* (as syn. of *A. spiniger*).

Acanthopleura haddoni Winckworth, 1927:206, pl. 28, figs. 1–4; Leloup, 1937a:172–176, figs. 17–19; Rees & Stuckey, 1952:185; Leloup, 1960:38–39; Bosch & Bosch, 1962:145; Pearse, 1978:92–101, 1979:50, fig. 9; Leloup, 1980b:6.

Acanthopleura planispina Bergenhayn, 1933:36–38, text fig. 12, pl. 1, fig. 11, pl. 3, figs. 51–52, 54–59 (in subgen. *Amphitomura*).

Planispina planispina: Is. Taki, 1962:47.

Acanthopleura bergenhayni Leloup, 1937b:3, 1980c:1–5, figs. 1–3.

Acanthozostera virens Ang, 1967:421–422, pl. 15, figs. 1–5.

"*Acanthopleura brevispinosa* (Sowerby)" Ang, 1967:416–417, pl. 13, figs. 1–5.

Type material and type locality:

Chiton gemmatus Blainville, 1825: Type material from "New Holland" presumed lost (Ashby, 1928, *loc. cit.*); neotype, designated by Ashby, 1928:172, pl. 12, fig. 6 (=holotype of *Acanthopleura gemmata queenslandica* Ashby, 1922a), "in coll. Ashby" (*fide* Iredale & Hull, 1926:264), not examined; locality of neotype, Dunk Island, Queensland, Australia (17°56′S, 146°06′E).

Chiton spiniger Sowerby, 1840a: Lectotype (BMNH 1842.5.10.1654) and paralectotype (BMNH 1842.5.10.1652) designated herein; locality "Cagayan . . . Misamis, Island Midinao" and "island Siquijor," Philippines (Sowerby, 1841:61), here restricted to Siquijor Id. (9°10′N, 123°33′E).

Chiton macgillivrayi Adams, 1855: Types unascertained; locality Fiji Islands.

Acantopleura vaillantii Rochebrune, 1882: Lectotype and paralectotype (at MHNH) designated herein; locality "Canal de Suez," Egypt.

Acanthopleura rawakiana Rochebrune, 1882: Lectotype (at MHNH) designated herein; locality "Rawak. Terre des Papous" (? Rawak, Sumba Id., Lesser Sunda Islands, 9°55′S, 119°50′E).

Acanthopleura balansae Rochebrune, 1882: Lectotype and 3 paralectotypes (at MHNH) designated herein; locality "Australie . . . Nouvelle Caledonie," here restricted to New Caledonia.

Acanthopleura gemmata queenslandica Ashby, 1922a: Holotype, "in coll. Ashby" (*fide* Iredale & Hull, 1926: 264), not examined; locality Dunk Island, Queensland, Australia (17°56′S, 146°06′E).

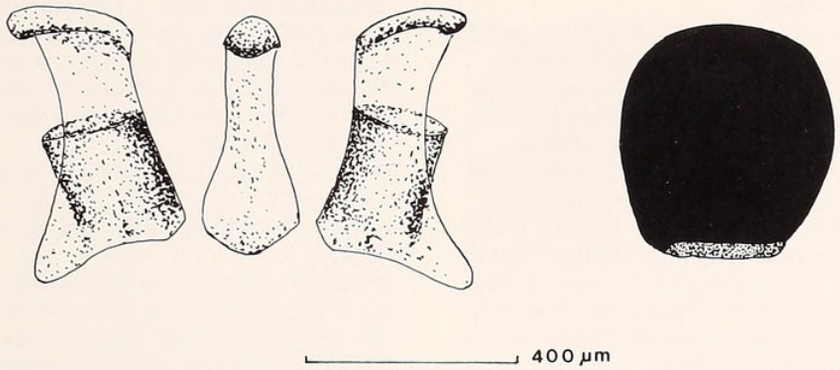


Figure 6

Acanthopleura spinosa (Bruguière, 1792). Hundred Islands, Lingayen Gulf, Philippines (AJF 464); specimen 75 mm long. Radula median and first lateral teeth, and head of major lateral tooth.

Acanthopleura haddoni Winckworth, 1927: Types unascertained; locality Aden (12°45′N, 45°12′E).

Acanthopleura gemmata maudensis Ashby, 1928: Holotype, "Ashby Coll." (*fide* ASHBY, 1928), not examined; locality Maud's Landing, Western Australia (23°06′S, 113°48′E).

Acanthopleura planispina Bergenhayn, 1933: Holotype (UUZM no. 114a) and 4 paratypes (UUZM no. 114b); locality Bonin Islands (27°00′N, 142°10′E).

Acanthopleura bergenhayni Leloup, 1937b: Holotype (BMNH 19823); locality "N. C. Australia."

Acanthozostera virens Ang, 1967: Holotype (University of the Philippines, U.P. Am.-112), not examined; locality, Philippines, but exact "locality, collector, date not recorded" (ANG, 1967:422).

Material examined:

AUSTRALIA, W.A.: Dorre Id., Shark Bay, 8 specimens (WAM 469-74); Maud's Landing, 3 specimens (AMS 112352; WAM 9326); Ningaloo, Point Cloates, 1 specimen (WAM 34-74); Yardie Creek, North West Cape, 7 specimens (WAM 23-74; WAM 1743-78; WAM 1749-78); Exmouth Gulf, 1 specimen (WAM 26-74); Hermite Id., Monte Bello Is., 5 specimens (WAM 19-74; WAM 27-74); Long Id., near Onslow, 1 specimen (AMS C69355); "West Australia," 1 specimen, 65 mm long (AMS C44883); Monte Bello Id., 5 specimens (WAM 5887); Kendrew Id., Dampier Arch., 1 specimen (WAM 74-7); Barrow Id., 2 specimens (WAM 24-74; WAM 605-67); Whitnell Bay, Dampier Penins., 1 specimen (WAM 1111-78); Wood Id., 2 specimens (WAM 36-74); Cockatoo Is., 3 specimens (WAM 18-74); Broome, 8 specimens, largest 50 mm long (AMS C69100; WAM 8987; NMV); Buccaneer Arch., 36 specimens (AMS C42222); Lacepede Is., 1 specimen (WAM 30-74).

AUSTRALIA, N.T.: 1 specimen (AMS C77617); Anson Bay, 3 specimens, largest 54 mm long (AMS C31532); Fannie Bay, Darwin, 1 specimen (WAM 29-74); "N.C.," holotype of *A. bergenhayni* (BMNH 19823); Darwin, 14 specimens (WAM 38-74; NMV; AMS C112353; AMS C10722); Cape Wessel, 1 specimen (AMS C77821); Port Essington, 3 specimens, largest 70 mm long (AMS C85096; AMS C90471); Cape Arnhem, 1 specimen, 50 mm long (AMS C135475).

AUSTRALIA, Qld.: Swears Id., South Wellesby Is., Gulf of Carpentaria, 3 specimens (AMS C15820); Albatross Bay, Weipa, 1 specimen (AMS C109287); Darnley Id., 1 specimen (AMS C517900; Bamfield Point, Prince of Wales Id., Torres Strait, 1 specimen, 36 mm long (AMS C110626); Murray Id., Torres Strait, 9 specimens (AMS C29619; AMS C112345); Cape York, 1 specimen (Penprase coll.); Campwin Beach, 2 specimens, largest 45 mm long (AMS C135481); Lizard Id., 1 specimen (AMS C135478); Darnby Is., 1 specimen (AMS C51790); Cooktown, 1 specimen (C109286); Two Isles, 2 specimens (AMS C109286); Hope Id., 1 specimen (WAM 27990); Port Douglas, 3 specimens (Van Belle coll.; AMS C76027); Low Isles, 3 specimens (AJF 603); Michaelmas Cay, off Cairns, 1 specimen (AMS C53575); Alma Bay, Magnetic Id., 2 specimens (NMV); Armit Is., 5 specimens (NMV); Bowen, 1 specimen (AMS C109288); Palm Id., 4 specimens (AMS C9303); Brampton Id., Whitsunday Passage, 4 specimens (AMS C109290); Linderman Id., Whitsunday Passage, 13 specimens (AMS C109293); Heron Id., Capricorn Group, 3 specimens (AMS C109189; AMS C109292; CAS 012261); Wilson Id., Capricorn Group, 2 specimens, largest 110 mm long (AMS C135519); Hillsborough Channel, 1 specimen (AMS C125472); Gatecombe Head, 3 specimens, largest 75 mm long (AMS C18778); Keppel Bay, 2 specimens (AMS C109191; AMS C109295); Fairfax Id., Bunker Group, 1 specimen (AMS C69053); Port Curtis, 1 specimen (AMS C109294).

PAPUA NEW GUINEA: Manubada Id., Port Moresby, 6 specimens (AJF 608); Madang, 1 specimen (AJF 623); Kaibola, Kiriwina Id., Trobriand Is., 2 specimens (AJF 611); Rabaul, New Britain Id., 2 specimens (AJF 615); Blanche Bay, New Britain Id., 1 specimen, 35 mm long (AMS C3160); Gigira Id., Louisiade Arch., 6 specimens (AMS C82857); Misima Id., Louisiade Arch., 9 specimens (AMS 112348); Schouten Is., 16 specimens, largest 40 mm long (ANSP 207593; ANSP 207128); Yule Id., 3 specimens, largest 70 mm long (ANSP 84007).

INDONESIA NEW GUINEA: Padaido Is., 2 specimens, largest 30 mm long (ANSP 206192; ANSP 205047); Japen Id., 7 specimens, largest 53 mm long (ANSP 205227; ANSP 208964); Biak Id., 7 specimens, largest 30 mm long (ANSP 206295).

SULAWESI (=Celebes): Utara, 3 specimens, 48 mm long (CAS 009875; CAS 012252); Bunaken Id., 58 specimens (AJF 706; AJF 711); Manado Tua Id., 23 specimens (AJF 708); Manado Bay, 10 specimens, largest 48 mm long (AJF coll., *leg.* S. Motley).

THAILAND: Lower Siam, Butang Arch., 1 specimen (NMV); Hey Id., S of Phuket, 3 specimens (AJF 865).

MALAYSIA: Telor Id., 22 specimens (AJF 719); Kedah, 1 specimen (Penprase coll.).

SUMATRA: Padang, 1 specimen, ca. 50 mm long (ANSP 84316); Pagai, Mentavi Is., 1 specimen (NMV 4055; NMV 4056).

BALI: 5 specimens (AMS C60813).
BORNEO: Marudu Bay, 2 specimens (ANSP 255743; ANSP 255742); Sapi Id., 1 specimen, 62 mm long (ANSP 275040).
SOLOMON IS.: 1 specimen (Van Belle coll.); Tulagi, 9 specimens (AMS C30640); Florida Id., 2 specimens (AMS C11109); Skutland Id., 1 specimen, ca. 60 mm long (ANSP 310058).
NEW CALEDONIA: 23 specimens (AMS C112346; AMS C112347; NMV); Ihio, 1 specimen (NMV); "Hargraves Coll.," 1 specimen (AMS 11314); Noumea, 4 specimens (AJF 530; AJF 534); Baie des Citrons, Noumea, 2 specimens (AMS C72643); Roche al la Voile, Noumea, 1 specimen (AMS C72650); Bourail, 4 specimens (AJF 539); Poindimie, 5 specimens (AJF 537); Faden Reef, Heinghene, 1 specimen (AMS C112344); Ile des Pins, 22 specimens (AJF 532; AMS C4343).
PHILIPPINES: Rita Id., Ulugan Bay, Palawan (South China Sea), 3 specimens (AJF 822); "Auson" Id., off Port Barton, Palawan (South China Sea), 8 specimens, largest 56 mm long (AJF 820); Binumsalian Bay, Palawan, 4 specimens (AJF 814); Tawitani, Sulu Arch., 6 specimens (CAS 002383; CAS 009881); Laminusa Id., Siasi Group, Sulu, 3 specimens (CAS 009877); Luuk, Sulu, 2 specimens (CAS 0122200; Juruck Bay, Cagayan Sulu Id., Sulu, 7 specimens (CAS 012245); Cebu, 1 specimen (Van Belle coll.); Nonoc, 25 specimens (CAS 012795); Siquijor Id., 1 specimen disarticulated (AMS C135473), Maloh, Negros Id., 36 specimens (AJF 451); Sumillon Id., 10 specimens (AJF 453); Liloan Point, Cebu Id., 7 specimens (AJF 454); Apo Id., 2 specimens (AJF 455); San Jose, Negros Id., 6 specimens (AJF 456); Punta Cruz, Bohol Id., 14 specimens (AJF 459); Loon Id., off Bohol Id., 20 specimens (AJF 460); Inamora Id., off Bohol Id., 1 specimen (AJF 461); Mactan Id., off Cebu Id., 21 specimens (AJF 462); Sulpha Id., off Cebu Id., 10 specimens (AJF 463); Ambulong Id., Mindoro, 15 specimens (AJF 791; AJF 793); Ilin Point, Ilin Id., Mindoro, 4 specimens (AJF 797); Hundred Islands, Lingayen Gulf, Luzon, 34 specimens (AJF 464; AJF 465).
TAIWAN: Orchid Id., near Hungtou Rock Formation, Taitung Co., 2 specimens, largest 41 mm long (UCM 28842); Keelung, 17 specimens (CAS 009880; CAS 016698).
OKINAWA, Japan: Cape Ata, 32 specimens (CAS 002383; CAS 012253); Buckner Bay, 1 specimen, 25 mm long (CAS 002163); Okuma, 3 specimens (CAS 012221; S. Crittenden coll.); Meijo, 1 specimen (CAS 012242); White Beach, 2 specimens, largest 62 mm long (AMS C135474).
BONIN IS., Japan: Holotype and 4 paratypes of *Acanthopleura planispina* Bergenhayn) (UUZM Nos. 104, 104a); 2 specimens (CAS-SU 2871).
PALAU: Koro, 55 specimens (AJF 409); Ngesil, 5 specimens (Carlson & Hoff coll.).
YAP: 4 specimens (NMV; Crittenden coll.).
GUAM: Pago Bay, 2 specimens (Carlson & Hoff coll.); Bile Bay, 4 specimens (Carlson & Hoff coll.).
FIJI: 1 specimen, 50 mm long (AMS C135477); Tai Id., Nadi Bay, Viti-levu, 2 specimens (AJF 284); Naindi Bay, near Savusavu, Vanua-levu, 5 specimens (AJF 528); 1 specimen (NMV); Yasawa Is., 1 specimen (Van Belle coll.); Namuya Levu, Yasawa Group, 1 specimen (Penprase coll.); Vambia, Ono, 5 specimens (AMS C112349).
TONGA: Tongatapu, N coast, 16 specimens, largest 55 mm long (CAS 046669; AJF coll., *leg.* M. Wolterding, Apr. 1984); Fanga Tavi Beach, Eva Id., 5 specimens (CAS 046670); Pangaimotu Id., 3 specimens, largest 48 mm long (AJF 766); Fafa Id., 5 specimens, largest 55 mm long (AJF coll., *leg.* M. Wolterding, May 1984); Afa Id., 1 specimen, 58 mm long (AJF 768); Tongatapu Id. and Valitoa Id., 2 specimens (CAS 009883); Vava'u Id., 2 specimens (Penprase coll.).
MARQUESAS: Eiao, 1 specimen (AJF coll., *ex* C. Richard, École Pratique des Hautes Études, Paris).
ISRAEL: Elat, Gulf of Aqaba, 2 specimens (Van Belle coll.); Na'ama Bay, Sinai Peninsula, 31 specimens (AJF 434).
EGYPT: Wadi-el-Dom, Gulf of Suez, 6 specimens (AJF coll., *leg.* Dr. J. Pearse).
OMAN: Masqat, 11 specimens, largest 45 mm long (K. Gudnason coll.).
AFARS ET ISSAS: Djibouti, 4 specimens (MHNB; CAS 009874).
SOMALIA: Gesira, 5 specimens, largest 50 mm long (MF 4106); Sar Uanle, 4 specimens, largest 50 mm long (MF 4107).
COMORO IS.: Grand Comore Id., 1 specimen (CAS 001263).
KENYA: Mombasa Beach, 5 specimens (AJF 593); Malindi, 17 specimens (AJF 594); Wamatu, 10 specimens (AJF 595); Twiga, 15 specimens (ANSP 276916; ANSP 287347); Wassini Id., 7 specimens (AJF 597).
TANZANIA: Mbudya Id., 6 specimens (MHNB); Chumbe Id., 4 specimens (ANSP 213823); Tumbatu Id., 1 specimen (ANSP 212991); Zanzibar Is., 19 specimens (ANSP 212326; ANSP 213024; ANSP 213319; ANSP 214527); Dar-es-Salaam, 19 specimens (Van Belle coll.; CAS 9882; ANSP 283100).
MADAGASCAR: Pointe de Tafondro, 3 specimens (ANSP 258101); Nossi Be, 136 specimens (ANSP 257344; ANSP 257601; ANSP 258553; ANSP 258627; ANSP 258911; ANSP 25864; ANSP 258965); Nossi Iranja, 35 specimens (ANSP 257084; ANSP 257085).

Description: BLAINVILLE's (1825) original description of *Chiton gemmatus* would have been quite sufficient to identify the species were it not for uncertainties developed on account of its considerable intraspecific variation, very wide geographic distribution, and the presence of several other closely related species. Even PILSBRY's (1893c) and IREDALE & HULL's (1926) accounts, good as they are, fail to characterize the species unequivocally.

Among over 1,210 specimens of *Acanthopleura gemmata* here examined, largest 110 mm long (dry) (AMS C135519: Wilson Id., Capricorn Group, Australia) (largest reported, 120 mm long [live] [IREDALE & HULL, 1926]). Specimens (Figures 7–10) depressed, round-backed, large; live specimen 82 mm long observed to shrink to 70 mm after two week preservation in 10% formalin in seawater followed by three months in isopropyl alcohol. Body width/length, mean 0.66. Intermediate valves beaked; posterior edge of valve ii forming 100–120° angle. Tegmentum grayish-green to grayish-brown, usually extensively eroded. Lateral areas poorly defined, hardly raised, sculptured with low-profile, irregular, round to elongate granules, sometimes coalesced into arched wrinkles; anterior valve and postmucro area of posterior valve similarly sculptured. Central areas almost featureless except for smaller to obsolete granules in pleural areas, and thin, ill-defined, transverse lamellae appressed across jugal areas. Mucro central (in small specimens) to somewhat posterior (in larger ones); postmucro strongly convex, at 45–90° slope. Ocelli round to oval, 50–70 μm in diameter, randomly distributed throughout anterior valve, postmucro area of posterior valve, and anterior ⅓ to ⅘ of lateral areas of intermediate valves. On valve i, tegmentum length/width,

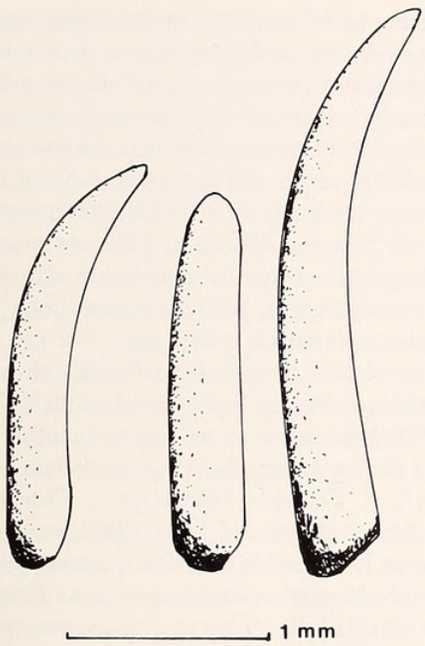


Figure 11

Acanthopleura gemmata (Blainville, 1825). Yeppoon, Qld., Australia; specimen 40 mm long. Girdle spines.

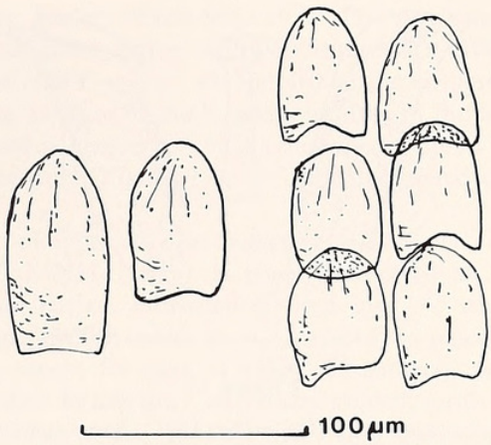


Figure 12

Acanthopleura gemmata (Blainville, 1825). Same specimen as in Figure 11. Scales of girdle undersurface.

mean 0.5. On valve viii, articulamentum often wider than tegmentum; tegmentum length/width, mean 0.5. Widths of tegmental surfaces of valves i/viii, mean 1.1. Gills with 40–60 plumes per side.

Articulamentum color fairly constant for specimens from a given locality, but varying with locality from bluish-white to brown. Sutural laminae well developed, relatively long, subtriangular on valve ii to subrectangular on valve viii. Sinus well formed; sinusal plate mostly smooth; relative width of sinus (width of sinus/width of sutural lamina) on valve viii, 0.9. Insertion plates strongly pectinate on outside. On valve i, insertion teeth irregularly spaced, sometimes fused together; in midline, length of insertion plate/length of tegmentum, mean 0.2. On valve viii, pectinations extremely variable, resulting in incomplete slitting and poor definition of teeth, particularly towards midline; teeth often recurved forward, anteriorly fused to but extending beyond buttressing, transverse, round callus. Slit formula (not always clearly determinable), 8/11-1-6/10. Eaves thick (0.5 mm on midline of valve viii of specimen 50 mm long), moderately spongy.

Girdle thick, musculous, wide, often banded, shrinking appreciably with preservation; at level of valve iv, girdle may measure 75% of width of valve in live specimens, 50% of valve in alcohol preserved specimens, 30% in dry specimens. Upper surface crowded with white to dark gray, brown, or black spinelets (Figure 11), pointed to blunt, straight to curved, somewhat conical, about 3 × 0.6 mm in average-sized specimen (up to 7 × 1 mm in large specimens), with smaller to minute spinelets in between; in some specimens, pointed, crystalline, needle-like elements (up to 200 × 30 µm) may be seen, isolated or in clusters interspersed amidst spinelets. Girdle bridges, empty. Undersurface paved with imbricate, transparent, squarish scales (Figure 12), about 40 × 40 µm (becoming elongate towards outer margin), with 8–10 coarse striations radiating from outer edge of scale.

Radulae averaging 45% of specimen length (range 37–57%, SD = 7.2%, n = 13) and 63 rows of mature teeth (range 45–85, SD = 11.5, n = 13). Radular features (Figure 13) rather constant in 23 specimens examined: in specimen 52 mm long (AJF 594: Malindi, Kenya) median tooth 80 µm wide at anterior blade; first lateral teeth about 450 µm long, 230 µm wide at anterior blade; major lateral teeth with tubercle 170 µm long at anterior part of inner edge, and discoid head 350 µm wide; outer marginal teeth 300 µm long, 210 µm wide (length/width, 1.5).

Distribution: Among intertidal chiton species, *Acanthopleura gemmata* seems to have the widest range (Figure 113-C). It has been recorded, albeit by synonymous names, from about 32°E to 140°W, an east-west range of some 20,000 km. In the western Indian Ocean, it has been reported from the gulfs of Aqaba and Suez in the Red Sea (Rochebrune, 1882; Nierstrasz, 1905b; Tillier & Bavay, 1905; Sykes, 1907; Horst & Schepman, 1908; Leloup, 1933a; Pearse, 1978) down the east coast of Africa, from Djibouti (Leloup, 1933a) through Somalia, Kenya, to Dar-es-Salaam, Tanzania (Ferreira, 1983b), the Comoros Is. (Nierstrasz, 1905a, 1906), and the west coast of Madagascar (Odhner, 1919; Dautzenberg, 1923, 1929), as well as at Aden and Barim Id., Yemen (Winckworth, 1927), and Oman (Leloup, 1937a; Bosch & Bosch, 1962). It has been reported at the Andaman Is. (Leloup, 1952), west coast of Malaysia (Way & Purchon, 1981), Sumatra (Bergenhayn, 1930a; Leloup, 1952), Java (Horst & Schepman, 1908; Bergenhayn,

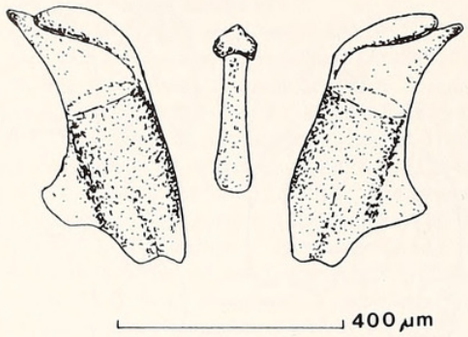


Figure 13

Acanthopleura gemmata (Blainville, 1825). Same specimen as in Figure 11. Radula median and first lateral teeth.

1930a; Leloup, 1933a), Sunda Is. (Bergenhayn, 1930a; Leloup, 1933a), Lombock, Flores, Borneo (Nierstrasz, 1905a), Timor (Lamy, 1923), Amboine, Morotai, Sangi Is. (Horst & Schepman, 1908), Sulawesi (Nierstrasz, 1905a; Leloup, 1933a, b), Halmahera Id., New Guinea (Quoy & Gaimard, 1835; Nierstrasz, 1905a; Horst & Schepman, 1908; Leloup, 1933a), New Ireland and Tonga (Quoy & Gaimard, 1835); Philippines (Sowerby, 1841; Hidalgo, 1905; Leloup, 1933b; Ang, 1967), Taiwan (Is. Taki, 1947, 1962; Wu, 1975), Yaeyama Is. (Is. Taki, 1938), Bonin Is. (Bergenhayn, 1933, as *Acanthopleura planispina*), Solomon Is. (Leloup, 1933a), Fiji (Adams, 1855; Pilsbry, 1893c; Bergenhayn, 1930a; Leloup, 1933a, 1952), and New Caledonia (Rochebrune, 1882; Pilsbry, 1893c; Lamy, 1923). In Australia, *A. gemmata* was reported from the "Torresian Region, . . . the whole coastline from Darwin east and south to Port Curtis, and west and south to Bunbury" (Iredale & Hull, 1926:264); but Ashby (1928:171) pointed out that, on the west coast, the species occurs southward not to Bunbury but to "a point between Carnarvon and Maud's Landing, north of Shark Bay." Reports of the species at the Society Is. (Leloup, 1933a) and Hong Kong (Bergenhayn, 1930a) have not been corroborated (Van Belle, 1980, 1982; A. J. Ferreira, field trips to Society Is. [Moorea, Sept. 1974, Tahiti, Aug. 1980 and Dec. 1983, Bora-Bora, Dec. 1983], and Hong Kong, Sept. 1982, Jan. 1983). The report of *A. gemmata* at Cape of Good Hope, South Africa (Nierstrasz, 1905b, 1906) is obviously in error.

In the Indian Ocean, the northernmost verified record is Elat, Gulf of Aqaba, Red Sea (29°33′N, 34°57′E); the southernmost verified record is Nossi Iranja, 50 km SW of Nossi Be, Madagascar (13°20′S, 48°15′E). Reported records from Mahakamby (=Mahajamba) and Tulear, Madagascar (23°21′S, 43°40′E) (Odhner, 1919, as *A. spiniger*) require confirmation (Kaas, 1979). On the mainland of Africa, the species has been found as far south as Dar-es-Salaam, Tanzania (6°48′S, 39°17′E) (Ferreira, 1983b, and herein).

There seems to be a wide distributional gap between the Red Sea and western Indian Ocean population on one side, and the Indo-Pacific population on the other. *Acanthopleura gemmata* has not been reported between Oman and the Andaman Is.; the species was not found on South Male Atoll, Maldives, or the southwest coast of Sri-Lanka (A. J. Ferreira, field trip, Feb. 1983). The recording gap, approximately between 58°E and 92°E, does not seem to be a collecting artifact due to inadequate sampling but a distributional disjunction, perhaps intermittent, for which no reasonable explanation is at hand.

In the central and eastern Indo-Pacific, *Acanthopleura gemmata* ranges from the Andaman Islands (92°45′E) to Tonga (175°W). It seems to be absent (another distributional gap?) in the Society Is. (A. J. Ferreira, above) and Samoa Is. (A. J. Ferreira, field trips to Tutuila Id. and Upolu Id., March 1976 and Dec. 1983), reappearing in the Marquesas Islands (9°S, 139.5°E), its easternmost record. The northernmost verified record is the Bonin Islands (27°00′N, 142°10′E). In Australia, the southernmost verified record on the east coast is Port Curtis, Qld. (24°00′S, 151°30′E); on the west coast, Dorre Island, Shark Bay, W.A. (25°09′S, 113°07′E).

Acanthopleura gemmata is confined to the intertidal and low subtidal zones, 0–2 m, with specimens often exposed at low tide. Reports of the species at subtidal depths (Haddon, 1886, at 11 m; Nierstrasz, 1905a, at 27 m) are obviously in error.

Remarks: As should be expected from a species with such a wide geographical distribution, *Acanthopleura gemmata* shows considerable intraspecific variation, particularly in the color of the tegmentum (from lighter grays to darker browns), color of the articulamentum (from blue to brown), tegmental sculpture (from granules to wrinkles, variable in shape and disposition), and in the girdle spinelets (from white to gray, brown, or black; from short and stubby to long and pointed). In regard to the latter, there seems to be some positive correlation between the length of the spinelets of a given specimen and the degree of erosion of the valves; specimens with the tegmentum uneroded tend to have longer spinelets, a phenomenon which seems to vary with locality but not necessarily with habitat (*i.e.*, exposure to surf).

The type material of *Chiton spiniger* consists of 2 syntype specimens, well preserved, dry, and flat. The specimen here designated lectotype (Figures 14–16) is accompanied by a pink museum label which says, in part, "Figured Syntype / Loc. — ? [Philippines] / Coll. — ? Purch. of H. Cuming." The specimen, dirty brown, 58 mm long, 35 mm wide; tegmentum clean, not encrusted or significantly eroded, shows abundant coarse, irregular granules in both central and lateral areas as well as in the anterior valve and postmucro of the posterior valve where they are arranged in concentric rows. Ocelli round to oval, 40–60 µm in diameter, throughout anterior valve, postmucro area of posterior valve, and anterior ½ to ⅗ of

lateral areas of intermediate valves. Mucro central, prominent; postmucro convex, with sharp, near vertical slope. Girdle with abundant calcareous spinelets up to 2.4 mm long, 0.4 mm thick. Soft parts absent; articulamentum dark brown; the number "42.5.10.1654" is written in black ink on underside of girdle. The other syntype specimen (BMNH 1842.5.10.1652), here designated paralectotype, 73 × 58 mm, has very similar features. Two other specimens, dry, flat, well preserved, part of the H. Cuming collection, were examined. The larger specimen (BMNH 19824/1), 80 × 47 mm, with yellow museum label, corresponds to the figured specimen in REEVE (1847: pl. 14, sp. & fig. 75); the smaller specimen (BMNH 19825/1), 35 × 19 mm, carries yellow museum label stating in part "Loc. Island of Siquijor [Philippines] found under stones at low water."

Pilsbry (*in* ASHBY, 1922a:29) recognized *Acanthopleura gemmata,* apparently as senior synonym of *A. spiniger*; but ASHBY (1922a) recommended retaining the name *spiniger* for the Sumatra specimens he had examined, reserving *gemmata* for the Australian population. Further, ASHBY (*loc. cit.*) postulated that specimens from Dunk Id., on account of differences in the tail valve, belonged to "a distinct geographical race" for which he proposed the name *A. gemmata queenslandica* (not *queenslandica* Pilsbry, 1894b) (see Remarks on *A. arenosa*).

As noted by HADDON (1886), the specimen(s) cited by QUOY & GAIMARD (1835) as "*Chiton aculeatus*" are of *A. gemmata.*

The type material of *Acantopleura vaillantii* Rochebrune, 1882, consists of two specimens, dry, curled, soft parts removed, 45 and 40 mm in (estimated) length, showing remnants of glued paper. Accompanying label reads "rec. Vaillanti—Types [on red background] / *Acanthopleura vaillanti* Rochbr. / = *A. spinigera* Sow. / Mer rouge / Bull. Soc. Philom. 1882:192." The specimens agree with ROCHEBRUNE's (1882) description of the species; the larger is here designated lectotype, the smaller (Figure 17) paralectotype.

The type material of *Acanthopleura rawakiana* Rochebrune, 1882, consists of a single specimen (Figure 18). The label reads, in part, "Syntype [on red background] / *Acanthopleura rawakana* [sic] ROCH. 1882 / Terre des Papous / Bull. Soc. Philom. Paris 1882 p. 195." The specimen, here designated lectotype, agrees with ROCHEBRUNE's (1882) description, but the alleged locality, Rawak, could not be found on maps of New Guinea, new or old (Judy Kelly, National Library Service, Boroko, Papua New Guinea, *in litt.* 4 Dec. 1981), and is presumed to refer to a village of that name at Sumba Id., Lesser Sunda Islands.

The type material of *Acanthopleura balansae* Rochebrune, 1882, comprises 4 specimens, dry, somewhat curled, estimated lengths from 40 to 50 mm, showing bits of glued paper. Accompanying label reads, "rec. Balansa 1872. XIV-221 — Types [on red background] / *Acanthopleura balansae* Roch. / = *A. Spinigera* Sow. / rec.: Caledonie / Bull. Soc. Philom. Paris 1882:197." The specimens, with soft parts intact, agree with ROCHEBRUNE's (1882) description of the species, the published dimensions corresponding to those of the largest specimen in the lot, here designated as lectotype; the 3 other specimens in the lot, one illustrated (Figure 19), are here designated paralectotypes.

The holotype of *Acanthopleura bergenhayni* Leloup, 1937b (BMNH 19823), is poorly preserved in alcohol; somewhat curled, estimated 60 mm long, 45 mm wide (including girdle); valves iii, v, vi, and vii in place, others missing except for part of valve viii showing pectinate teeth; valves bluish-gray, extremely eroded; girdle almost denuded of spinelets; spinelets white or grayish-black. Accompanying museum label reads, in part, "Holotype / *Acanthopleura bergenhayni* / 1 specs. Acc. no.: / Leloup, 1937 / Loc. N. C. Australia / Coll. Antartic Exped., the Admiralty." The specimen (Figures 20, 21) agrees with LELOUP's (1937b:3) description, except in dimensions (Leloup [*loc. cit.*] described it as 53 × 40 mm), and corresponds to the current concept of *A. gemmata.*

The type material of *Acanthopleura planispina* Bergenhayn, 1933 (at UUZM) consists of holotype and 4 paratypes, well preserved in alcohol. With holotype, type-written label reads, "Uppsala Univ. Zool. Mus. / Typesamlingen / nr. 144a / Molluscaa"; three other handwritten labels add, ". . . Type—ex. J. R. M. Bergenhayn 1933 . . . Prof. Sixten Bocks Japan—Ex. 1914 / Bonin Islands (Ogasawara) / Taki ura Ebbestrand 28.7 / formal konserv . . . ." Holotype (Figure 22), well preserved, flat, 36 mm long, 22 mm wide (including girdle); pulling down girdle (which, obviously, had been done before) shows pectinate insertion plate and single, well defined slit in midline. Contrary to BERGENHAYN's (1933) assertion, girdle spinelets do not appear distinct in any particular way. Paratypes, the anterior valve of one here illustrated (Figure 23), very similar to holotype; largest about 44 mm long, disarticulated, missing valve viii; second largest 39 mm long, with valves v, vi, and vii in place, but others missing; third largest curled, estimated 25 mm long, missing valve i; smallest 16 mm long, with all valves in place. The material corresponds to that described and illustrated by BERGENHAYN (1933) and to specimens of *A. gemmata* from other localities.

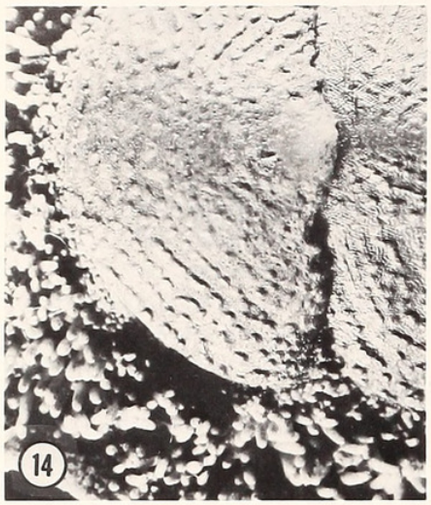
From the description and illustrations, *Acanthozostera virens* Ang, 1967, agrees clearly with the present understanding of *Acanthopleura gemmata.*

A number of other species regarded by authors as synonyms of *Acanthopleura gemmata* are here cast aside as insufficiently characterized:

(1) *Chiton aculeatus* LINNAEUS, 1758:667, no. 3, from "Asia," is unrecognizable (HANLEY, 1855; DODGE, 1952).

(2) *Chiton magnificus* SOWERBY, 1840b:2, sp. 11, fig. 52 (not Deshayes, 1827), is a *nomen nudum.*

(3) *Chiton granatus* REEVE, 1847: pl. 5, sp. & fig. 24, of unknown locality, is inadequately described. Carpenter (*in* PILSBRY, 1893c:224–225, pl. 48, figs. 29, 30) stated of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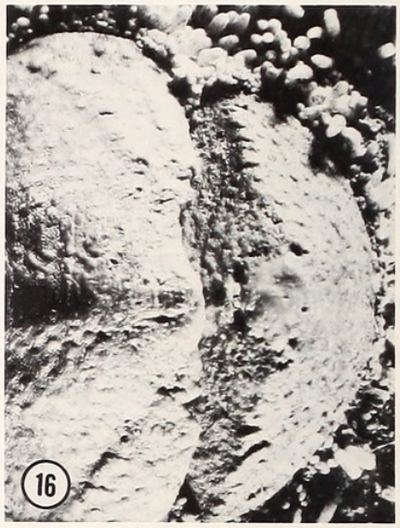
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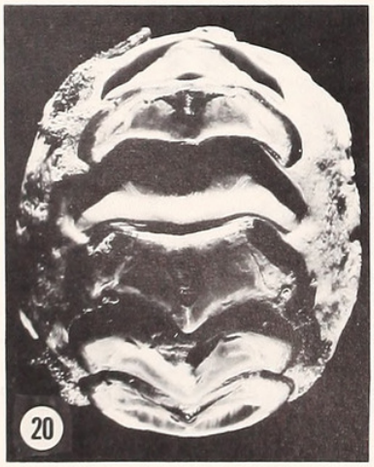
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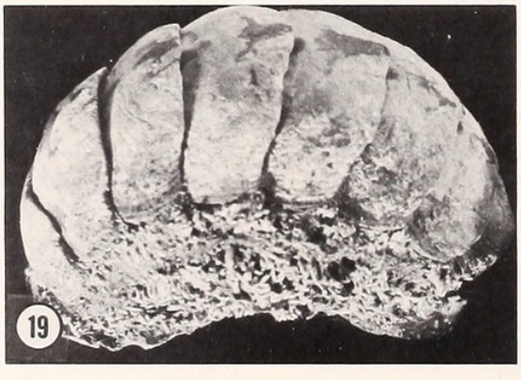
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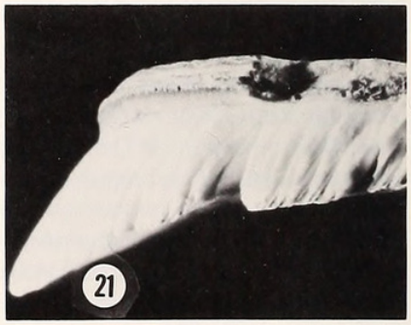
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the tail-valve of the type "should be examined in order to tell whether it is a specimen of spiniger or of borbonica . . . ." It is a *nomen dubium.*

(4) *Chiton piceus* REEVE, 1847: pl. 13, sp. & fig. 70, from "New Holland" (=Australia) (not Gmelin, 1791, from St. Thomas, West Indies) may apply to several similar species of *Acanthopleura* in Australia. Carpenter (*in* PILSBRY, 1893c:226, pl. 49, figs. 37, 38) examined "four specimens from Australia" regarded as types, but left no diagnostic clues. It remains a *nomen inquirendum.*

(5) *Chiton obesus* SHUTTLEWORTH, 1853:61, 69, is a *nomen nudum.*

(6) *Chiton cunninghami* REEVE, 1847, is here regarded as a *nomen inquirendum.* The holotype (BMNH 1951.1.25.6) (Figures 24–27), accompanied by a pink museum label which reads, in part, ". . . Loc. Australia, on the rocks / leg. Cunninghami / Coll. Cuming Acc. 1829," comprises 8 disarticulated valves which, reassembled, suggest a living specimen (with girdle) about 110–120 mm long, 70–80 mm wide. Valves thick, beaked; tegmentum dark brown with whitish midline band; anterior valve with irregular, round granules about 300–400 μm in diameter, in concentric rows; lateral areas hardly defined, with similar granules; central areas with similar granules in pleural regions, somewhat fused into anteroposterior riblets; jugum smooth, almost shiny; valve viii moderately inflated, posterior edge slightly sinused in middle third; mucro not prominent, somewhat posterior; postmucro convex; ocelli round to oval, 60 μm in diameter; articulamentum bluish-gray, darker in middle; sutural laminae subtriangular (on ii) to subrectangular (on viii); sinus well defined, sinusal plate coarsely pectinate; insertion teeth on valve viii, teeth very underdeveloped, as if sunken in middle third; slit formula 10-1-6. Radula and girdle not available. Carpenter (*in* PILSBRY, 1893c:225) described the specimen's girdle (apparently still available at the time) as "dried in around the valves, and the hairs are worn off except in the sutures, where they are short, crowded and black." The species was regarded by Carpenter (*in* PILSBRY, 1893c) as a synonym of *A. spiniger* (=*A. gemmata*), a possibility that may be seriously considered if a pathologic posterior valve is assumed; IREDALE & HULL (1926) and KAAS & VAN BELLE (1980) considered it a synonym of *A. brevispinosa,* a supposition that goes contrary to the objective evidence.

In the western Indian Ocean, *Acanthopleura gemmata* is sympatric through much of its range with *A. brevispinosa.* In the central Indo-Pacific, *A. gemmata* is sympatric with *A. spinosa, A. araucariana, A. miles, A. curtisiana,* and *A. loochooana*; and is parapatric in the north with *A. japonica,* in the south with *A. gaimardi, A. arenosa,* and *A. hirtosa.*

In some localities, as personally observed in Fiji, Philippines, Palau, and at the Trobriand Islands, Papua New Guinea, specimens of *Acanthopleura gemmata* are often the object of human predation, and are so actively searched by the natives as a delicacy that entire populations have been nearly wiped out.

Acanthopleura brevispinosa (Sowerby, 1840)

Figures 28 to 34, and 112-B

Chiton brevispinosus SOWERBY, 1840a:287, Suppl. pl. 16, fig. 1, 1840b:1, 10, sp. no. 4, fig. 136; REEVE, 1847, pl. 9, sp. & fig. 52.

Acanthopleura brevispinosa: PLATE, 1898:167, pl. 11, figs. 111–112; PILSBRY, 1893c:231–232, pl. 47, figs. 18–21 (in subgen. *Amphitomura*); NIERSTRASZ, 1905a:102, 1906:511–515; ASHBY, 1931:49, pl. 7, fig. 82; (?) FISCHER, 1939:36; BARNARD, 1963:344; KAAS, 1979:868; LELOUP, 1980c:8–11, figs. 5, 7, map 1 (in part); CHELAZZI *et al.,* 1983:115–125.

[*Non:* ROCHEBRUNE, 1882:240; LAMY, 1936:267 (=*Plaxiphora mercatoris* Leloup, 1936); FISCHER, 1978:49 (in part); ANG, 1967:416–417, pl. 13, figs. 1–5 (=*A. gemmata*).]

Chiton borbonicus DESHAYES, 1863:37, figs. 12–13; MARTENS, 1880:300 (in subgen. *Acanthopleura*); VIADER, 1937:58.

Acanthopleura borbonica: PILSBRY, 1893a:105, 1893c:230–231, pl. 45, figs. 76–79 (in subgen. *Amphitomura*); THIELE, 1893:372, pl. 30, fig. 31; NIERSTRASZ, 1905a:102–103;

←

Explanation of Figures 14 to 22

Figure 14. *Acanthopleura gemmata* (Blainville, 1825): *Chiton spiniger* Sowerby, 1840a; lectotype (BMNH 1842.5.10.1654). Dorsal aspect of valves i and ii.

Figure 15. *Acanthopleura gemmata* (Blainville, 1825): *Chiton spiniger* Sowerby, 1840a; lectotype (BMNH 1842.5.10.1654). Dorsal aspect of valves iii and iv.

Figure 16. *Acanthopleura gemmata* (Blainville, 1825): *Chiton spiniger* Sowerby, 1840a; lectotype (BMNH 1842.5.10.1654). Dorsal aspect of valves vii and viii.

Figure 17. *Acanthopleura gemmata* (Blainville, 1825): *Acanthopleura vaillantii* Rochebrune, 1882; paralectotype (MNHN).

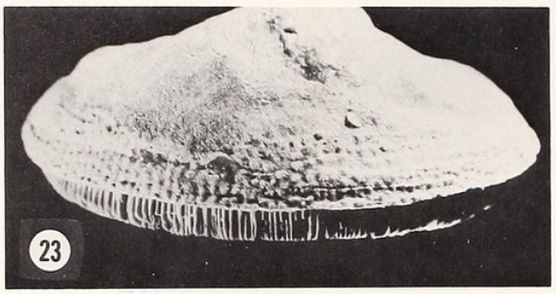
Figure 18. *Acanthopleura gemmata* (Blainville, 1825): *Acanthopleura rawakiana* Rochebrune, 1882; lectotype (MNHN).

Figure 19. *Acanthopleura gemmata* (Blainville, 1825): *Acanthopleura balansae* Rochebrune, 1882; paralectotype (MNHN).

Figure 20. *Acanthopleura gemmata* (Blainville, 1825): *Acanthopleura bergenhayni* Leloup, 1937b; holotype (BMNH 19823). Dorsal aspect of specimen with only valves iii and v in place.

Figure 21. *Acanthopleura gemmata* (Blainville, 1825): *Acanthopleura bergenhayni* Leloup, 1937b; holotype (BMNH 19823). Fragment of posterior aspect of posterior valve.

Figure 22. *Acanthopleura gemmata* (Blainville, 1825): *Acanthopleura planispina* Bergenhayn, 1933; holotype (UUZM).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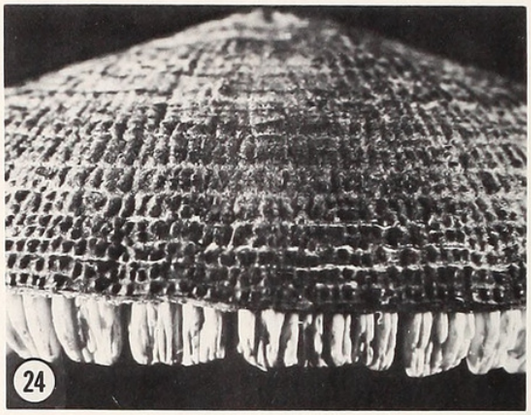
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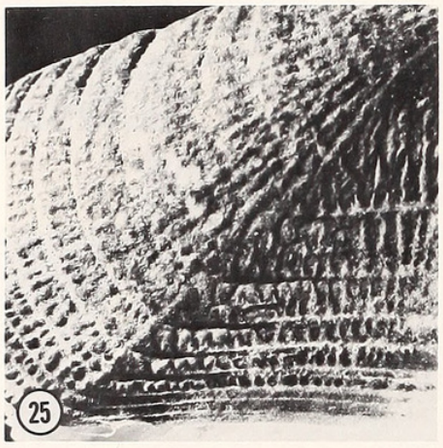
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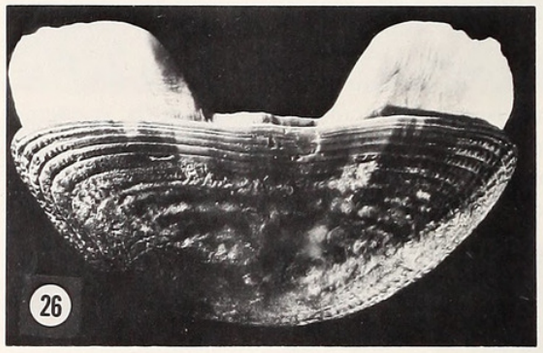
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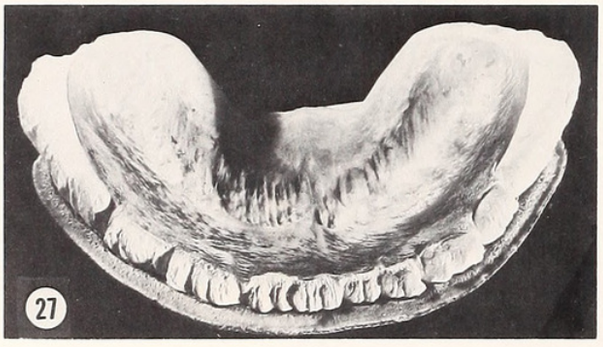
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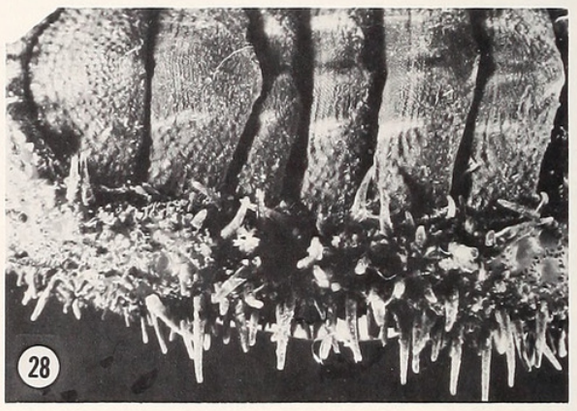
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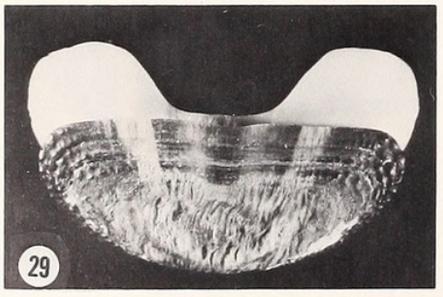
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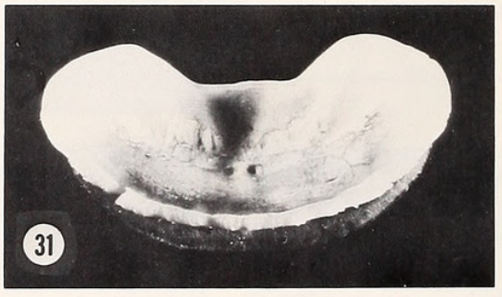
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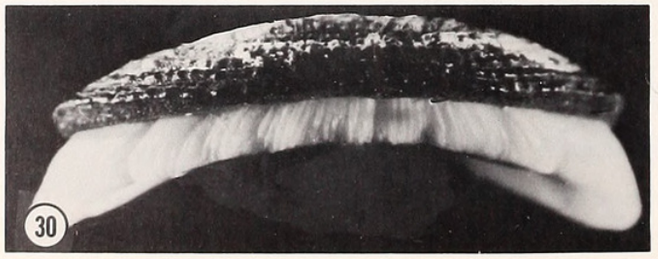
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Melvill, 1909:119; Leloup, 1941:9 (in subgen. *Amphitomura*), 1980c:5–8, figs. 4–6, map 1 (in part).
Acanthopleura afra Rochebrune, 1882:192.

Type material and type locality:

Chiton brevispinosus Sowerby, 1840: Types unascertained; locality "Ins. Johanna [=Anjouan Id., Comoro Is.], E. Africa" (12°13′S, 44°29′E).
Chiton borbonicus Deshayes, 1863: Types unascertained; locality Reunion Id. (21°06′S, 55°38′E).
Acanthopleura afra Rochebrune, 1882: Lectotype and paralectotype (MNHN) here designated; locality Madagascar (Rochebrune [1882:192] gave "Cap de Bonne Espérance . . . ; Madagascar," as localities, but the first is clearly in error).

Material examined:

SOMALIA: Mogadiscio, 5 specimens, largest 35 mm long (MF 4108); Gesira, 7 specimens, largest 60 mm long (MF 4109).
KENYA: Mombasa Beach, 10 specimens, largest 67 mm long (AJF 593); Malindi, 6 specimens (AJF 594); Wamata, 13 specimens (AJF 595); Wassini Id., 5 specimens (AJF 597).
TANZANIA: Fumba, Zanzibar, 3 specimens (ANSP 213319); Mbudy Id., 3 specimens (M. Bacescŭ coll.).
SEYCHELLES: 2 specimens (ANSP 310686); Port Ternary, Mahé Id., 1 specimen, 53 mm long (ANSP 311232); Anse Étoile, Mahé Id., 1 specimen, 50 mm long (ANSP 310382); North West Bay, Mahé Id., 10 specimens (AJF 564).
COMOROS: 1 specimen (ANSP 220840); Pamandzi Id., 2 specimens (*ex* Van Belle coll.); Grand Comore Id., 4 specimens (CAS 000489, CAS 001253, CAS 009876).
MADAGASCAR: Syntypes (2) of *Acanthopleura afra* Rochebrune, 1882 (MNHN); 1 specimen disarticulated, estimated 50 mm long, valves and radula (IRScNB I.G. 9247); 1 specimen, ca. 70 mm long, cited by Leloup (1980c) (IRScN I.G. 9247).
MAURITIUS: 3 specimens (ANSP 35915; ANSP 35952); Souillac, 3 specimens 26–32 mm long (ANSP 274063); Gris-Gris, 4 specimens, 18–33 mm long (ANSP 274088); Pte. Fayette, 8 specimens, 25–45 mm long (ANSP 273693); Vacoas Pt., 5 specimens (ANS 274168); Pointe-aux-Roches, 9 specimens (*ex* B. Smith, March 1979), 26 specimens (AJF 586).
REUNION: St. Gilles-les-Bains, 3 specimens (*ex* Van Belle coll.).

Description: Sowerby (1840a) described specimens of *Chiton brevispinosus* as "rather flat, oval, narrowed in front; the valves are rounded and smooth at the beaks, and granulated at the sides, in undulating, concentric ridges; . . . the numerous short black spines studding (the girdle) are tipped with light yellow points . . . a pretty relief to the general black colour of the shell" (p. 287). Pilsbry (1893c) pointed out "the valves concentrically wrinkled-grained at the sides of the central areas, and the ill-defined lateral areas . . . cut into granules by concentric and radiating grooves. End valves finely grooved radially, finely wrinkled concentrically; mucro posterior, prominent and rather acute. [Articulamentum] blackish-brown or purple-brown except [for white] sutural and insertion plates . . . . Sinus broad, deep, rounded. [Slits 7/8-1-2]; anterior teeth moderately long, finely pectinated outside; posterior teeth very short, blunt, obsoletely pectinated . . . . [Girdle] narrow, clothed with white-tipped black spinelets . . ." (p. 231).

Among 138 specimens of *Acanthopleura brevispinosa* here examined, largest 67 mm long (in alcohol) (AJF 593: Mombasa Beach, Kenya). Body width/length, mean 0.61 (SD = 0.05; n = 25). Specimens (Figures 28–31) oval, depressed, round-backed. Intermediate valves beaked; posterior edge of valve ii forming 120–160° angle. Tegmentum purple-brown to dark brown or black, often with two parajugal cream-white bands. Tegmental sculpture of coarsely round granules, larger (up to 250 μm in diameter) and better defined at periphery, arranged in radial rows. Anterior valve with 30–50 rows of granules. Central areas featureless except for dull shagreened surface and, occasionally, some fine transverse, concentric rugae. Lateral areas not elevated, poorly defined except for 6–10 rows of granules. Mucro central to slightly posterior; postmucro convex, at 45–90° slope. Ocelli round to oval, 50 μm in diameter, randomly distributed throughout anterior valve, postmucro area of posterior valve, and anterior ½ to ⅕ of lateral areas of intermediate valves. Ratio of tegmental surfaces of valves i/viii, mean 1.06. On valve viii, length of tegmentum/width of tegmentum, mean 0.37 (SD = 0.04; n = 11).

Articulamentum dark brown to black, or bluish-white with dark brown area in middle of valve. Sutural laminae

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Explanation of Figures 23 to 31

Figure 23. *Acanthopleura gemmata* (Blainville, 1825): *Acanthopleura planispina* Bergenhayn, 1933; paratype (UUZM). Anterior aspect of anterior valve.

Figure 24. *Chiton cunninghami* Reeve, 1847; holotype (BMNH 1951.1.25.6). Anterior aspect of anterior valve.

Figure 25. *Chiton cunninghami* Reeve, 1847; holotype (BMNH 1951.1.25.6). Dorsal aspect of intermediate valve.

Figure 26. *Chiton cunninghami* Reeve, 1847; holotype (BMNH 1951.1.25.6). Dorsal aspect of posterior valve.

Figure 27. *Chiton cunninghami* Reeve, 1847; holotype (BMNH 1951.1.25.6). Ventral aspect of posterior valve.

Figure 28. *Acanthopleura brevispinosa* (Sowerby, 1840a). Wamatu, Kenya (AJF 595); specimen, 23 mm long.

Figure 29. *Acanthopleura brevispinosa* (Sowerby, 1840a). Malindi, Kenya (AJF 594); specimen, 43 mm long. Dorsal aspect of posterior valve.

Figure 30. *Acanthopleura brevispinosa* (Sowerby, 1840a). Same specimen as in Figure 29. Posterior aspect of posterior valve.

Figure 31. *Acanthopleura brevispinosa* (Sowerby, 1840a). Same specimen as in Figure 29. Ventral aspect of posterior valve.

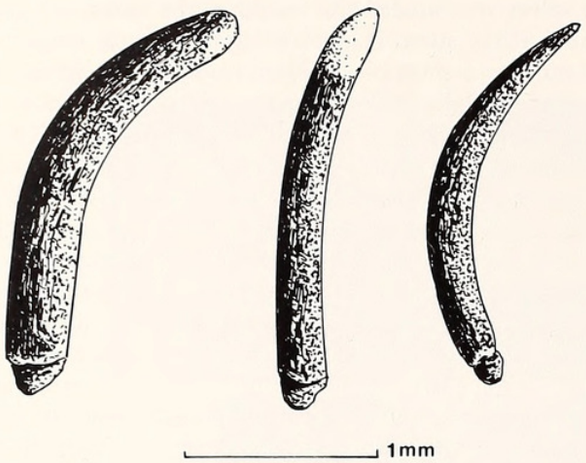


Figure 32

Acanthopleura brevispinosa (Sowerby, 1840a). Wamatu, Kenya (AJF 595); specimen 26 mm long. Girdle spines.

well developed, relatively long, subtriangular on valve ii to subrectangular on valve viii. Insertion plates strongly pectinate on outer surface. On valve i, length of insertion plate/length of tegmentum, mean 0.17; insertion teeth irregularly spaced. On valve viii, relative width of sinus, 0.8; teeth poorly defined by incomplete and irregular slitting and underdevelopement of middle third of insertion plate; often only 2 slits, symmetrically placed; insertion teeth supported anteriorly by buttressing transverse, round, variably developed callus. Slit formula 7/11-1-2/6. Eaves moderately spongy. Gills with some 50 plumes per side.

Girdle wide, muscular, mostly black, usually not banded. Upper surface profusely beset with calcareous, dark brown to black, blunt spinelets (Figure 32), often tipped with yellowish-white, up to 3 mm long, 0.3 mm thick, amidst much smaller to minute ones. Girdle bridges empty. Undersurface covered with transparent, rectangular scales, about 50 μm long, 35 μm wide, with few, coarse longitudinal striations.

Radulae averaging 62% of specimen length (range 53–68%, SD = 6.6%, n = 6) and 93 rows of mature teeth (range 80–110, SD = 12.3, n = 6). In specimen 42 mm long (M. Bacescŭ coll.: Mbudy Id., Tanzania) median tooth 130 μm wide at anterior blade; first lateral teeth 170 μm at anterior blade, outer edge deeply concave, outer posterior angle sharply pointed, inner posterior angle very elongate (Figure 33); major lateral teeth with discoid head 210 μm in diameter; outer marginal teeth 170 μm long, 250 μm wide (length/width, 0.7).

Distribution: *Acanthopleura brevispinosa* is confined to the western Indian Ocean (Figure 112-B). Its range, as here verified, extends from the east coast of Africa to the Seychelles, Comoros, Madagascar, Reunion, and Mauritius; and from Gesira, Somalia (1°58′N) to Santa Carolina Id. (Kaas, 1979) and Bazaruto Id., Mozambique (21°40′S) (Barnard, 1963). Fischer's (1939) report of the species at "mer d'Oman" (? Gulf of Oman) and Aden requires confirmation. Reports of the species at Cabo Verde Arch. (Rochebrune, 1882; Pilsbry, 1893c; Leloup, 1980c), Cape of Good Hope (Rochebrune, 1882; Pilsbry, 1893c; Nierstrasz, 1905a, 1906; Ashby, 1931), Philippines (Ang, 1967; Fischer, 1978), Indochina and Hong Kong (Fischer, 1978), as well as at Rio de Janeiro (Brazil), Ile du Prince (Gulf of Guinea), Poulo Condor (Con Son Is., Vietnam), Moluccas (Indonesia), and Fiji (Leloup, 1980c) are not credible and must be considered in error. Possibly in error, too, is the report of the species in the Red Sea (Nierstrasz, 1905a).

Acanthopleura brevispinosa is confined to the intertidal zone, with specimens often exposed up to 2 m above low tide level.

Remarks: The type material of *Acanthopleura afra* Rochebrune, 1882 (MNHN), is accompanied by a museum label which reads, in part, "rec. Verreaux. XIV 230 Types [on red background] / *Acanthopleura afra* Rchb. 1882 / = *A. borbonica* / Cap de Bonne Espérance . . . ." It consists of 2 specimens, dry, curled, estimated length 60 and 50 mm, soft parts removed, showing indications of having been glued to cardboard. Girdle spinelets of smaller specimen mostly fallen off. The specimens agree with Rochebrune's (1882) description of the species. The larger specimen is here designated lectotype, the smaller, paralectotype (Figure 34). Of the two given localities, Cape of Good Hope is in error, and Madagascar, therefore, must be regarded as type locality.

Chiton nebulosus Wood, 1828, figured (pl. 1, fig. 4), from "Isle of France," but undescribed, is here considered a *nomen dubium*; on subjective grounds, Kaas & Van Belle (1980) suggested the figured specimen might be of *Acanthopleura borbonica* (=*A. brevispinosa*).

Throughout its range, *Acanthopleura brevispinosa* is sympatric with *A. gemmata* from which it must be, therefore, carefully differentiated. Distinctions based on size, color, shape, tegmental sculpture, or girdle elements are potentially deceiving, given the intraspecific variation of the two species. The study of the radula is indispensable, particularly in questionable specimens. The radula of *A. brevispinosa* differs from that of *A. gemmata,* as well as from all other species of *Acanthopleura,* in (1) relatively longer size, (2) much greater number of rows of mature teeth, (3) wide, parallel-sided median teeth, (4) narrow, posteriorly pointed first lateral teeth with sharper outer edge protuberance, (5) relatively smaller head of major lateral teeth, and (6) proportionally shorter outer marginal teeth. Ratio between width (at anterior blade) of median tooth and width of head of major lateral teeth in *A. brevispinosa,* mean = 0.83 (n = 8; SD = 0.11; range 0.73–1.00); in specimens of 12 other species of *Acanthopleura* pooled together, mean = 0.32 (n = 33; SD = 0.08; range 0.21–0.43) ($P < 0.001$).

Acanthopleura araucariana (Hedley, 1898)

Figures 35 to 40, and 115-K

Ischnochiton araucarianus Hedley, 1898:100–101, figs. 3–6; Nierstrasz, 1905a:21, 1908:145 (in subgen. *Heterozona*); Iredale & Hull, 1926:261–262 (as syn. of *Squamopleura miles*) (reprinted, 1927:123–124); Leloup, 1939b:1–6 (as syn. of *S. miles*); Kaas & Van Belle, 1980:19 (as syn. of *S. miles*).
Sclerochiton araucarianus: Thiele, 1910a:96.

Type material and locality:

Ischnochiton araucarianus Hedley, 1898: Holotype (AMS C.4344); locality "Isle of Pines, New Caledonia" (22°37'S, 167°30'E).

Material examined:

NEW CALEDONIA: Pines Id., holotype of *Ischnochiton araucarianus* Hedley, 1898 (AMS C.4344); Pines Id., Kuto Beach, 55 specimens, largest 52 mm long (AJF 532).
LOYALTY IS.: Lifou Id., 1 specimen (NMV).
TONGA: Ha'alafu Beach, Tongatapu, 1 specimen, 25 mm long (AJF 767, *leg.* A. J. Ferreira & M. Wolterding, 3 Dec. 1983); Eua Id., intertidal zone up to 0.8 m above mid-tide water level, 16 specimens, largest 27 mm long (AJF coll., *leg.* M. Wolterding, 9 May 1984).

Description: Hedley (1898) gave an excellent description of *Ischnochiton araucarianus*: "Shell oval, depressed, valves rounded posteriorly, but the anterior ones more pointed. Colour greenish-grey, each valve shading posteriorly into cream, with a median wedge of black, which is sometimes split with a central white stripe. Interior dull purple, shading posteriorly into brown. Girdle . . . chequered black and cream. Lateral areas elevated with about three obscure, diverging lines of granules, more prominent on the anterior valves. Central areas finely and evenly corded transversely. Anterior valve radiately tuberculated. Posterior valve . . . with subcentral mucro, anterior area concentrically striated, posterior concentrically tuberculated, the mucro is eroded in specimens studied. Anterior and posterior valves with eight slits, median with one; teeth finely pectinated and roughened with minute grains. Scales of girdle radiately furrowed, somewhat apart, large and small intermingled, with a series of very small next the valves and along the margin. Gills extending along five-sixths of the foot. Length 38, breadth 22 mm" (Hedley, 1898:100–101).

The holotype (AMS C.4344), is accompanied by a pink museum label that reads, in part, ". . . Loc.: Isle of Pines, New Caledonia / Ref.: Fig'd. P. L. S., NSW, 1898, pt. 1, pg. 100 / Oct. 1897, Coll. C. Hedley." The specimen (Figures 35–38)—preserved dry, soft parts in place, partly disarticulated, valves ii, iii, and iv in place, others loose, plus fragment of girdle—agrees with Hedley's (1898) description and illustration of the species.

Among 74 specimens of *Acanthopleura araucariana* here examined, largest 52 mm long. Body width/length, mean

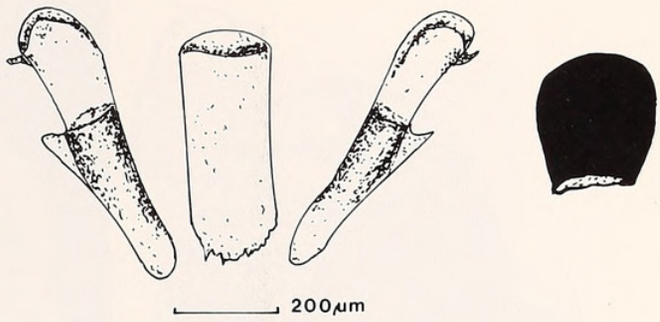


Figure 33

Acanthopleura brevispinosa (Sowerby, 1840a). Same specimen as in Figure 32. Radula median and first lateral teeth, and head of major lateral tooth.

0.60 (SD = 0.05; n = 10). Specimens depressed, round-backed, often markedly eroded. Shell in tones of light grays. Lateral areas of intermediate valves markedly raised, with few, robust, coarse granules, up to 350 μm in diameter. Anterior valve and postmucro area of posterior valve similarly sculptured. Central areas with appressed, transverse lamellae, featureless otherwise. Mucro somewhat posterior; postmucro convex. Ocelli round to oval, 50–60 μm in diameter, on anterior ½ of lateral areas, anterior valve, and postmucro area of posterior valve. Gills holobranchial, 40–50 plumes per side.

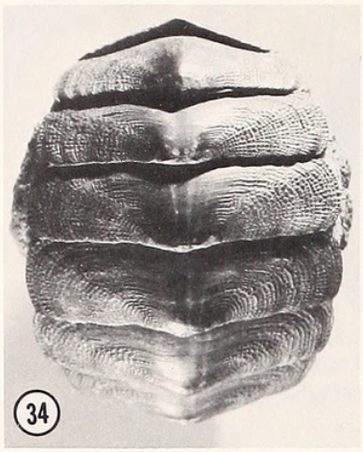
Articulamentum white with dark brown discolorations at apex of valves. Sutural laminae well developed; sinus well defined. Insertion plates pectinate on outside. On valve viii, sinus relative width, 0.7; pectinations appreciably reduced in middle third, and 2 symmetrical slits at outer thirds; well developed transverse callus. Slit formula 8/9-1-2.

Girdle thick, musculous, light gray, often with few symmetrical black bands. Upper surface covered with coarsely striated scales (Figure 39), quite variable in size, up to 1300 μm long, lightly imbricated or, more often, separated from each other by "nude" girdle; occasional hyaline spicules, single or bunched, amidst scales. Girdle bridges empty. Undersurface paved with transparent, squarish scales, 40 × 40 μm, outer edge convex, inner edge concave, arranged as if articulated in rows.

In specimen 32 mm long (AJF 532: Pines Id., New Caledonia), radula 10 mm in length, comprises 50 rows of mature teeth. Median tooth (Figure 40) 60 μm wide at anterior blade; first lateral teeth, 120 μm wide at anterior blade; head of second major lateral teeth, discoid, 200 μm wide; outer marginal teeth, 200 μm long, 180 μm wide (length/width, 1.1).

Distribution: *Acanthopleura araucariana* is known only from Pines Id., adjacent Lifou Id., New Caledonia, and Eua Id. and Tongatapu Id., Tonga (21°10'S, 175°10'W) (Figure 115-K).

It is confined to the upper intertidal zone, having been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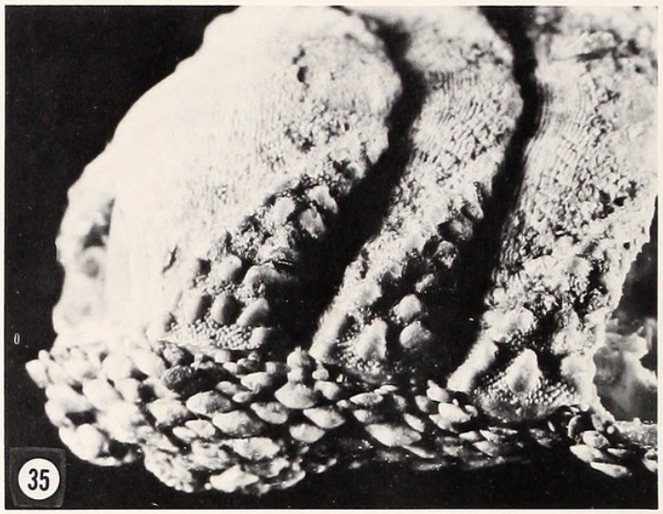
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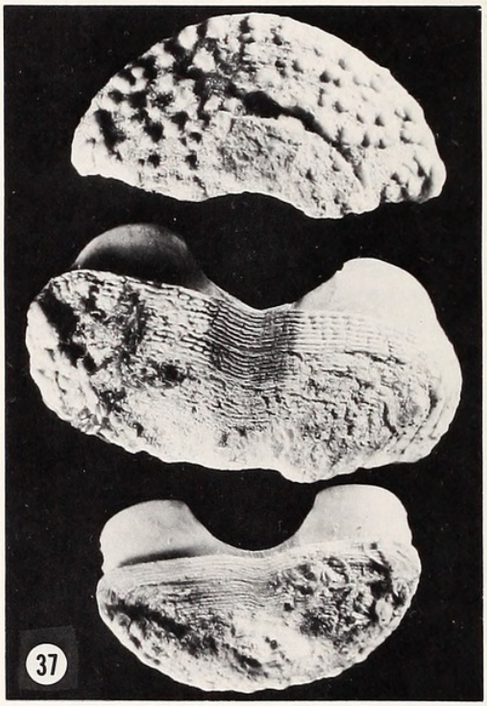
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observed up to 2 m above water level, often exposed to the sun, immediately above the area occupied by the sympatric *Acanthopleura gemmata* (A. J. Ferreira, field observations at Kuto Beach, Pines Id., New Caledonia, 22–24 July 1980).

Remarks: The irregularity in the size of the girdle scales in *Acanthopleura araucariana* was noted by Hedley (1898), Nierstrasz (1905a) (who proposed a subgenus, *Heterozona,* on that account), and Leloup (1939b).

Iredale & Hull (1926), having examined the type of *Acanthopleura miles* and specimens of *A. araucariana* from New Caledonia, regarded them as conspecific. Yet, differences between *A. araucariana* and *A. miles* are apparent in (1) the lateral areas (markedly elevated in *A. araucariana*; hardly raised in *A. miles*), (2) the granules in lateral areas and end valves (large, elevated, coarse in *A. araucariana*; small, subdued, well defined in *A. miles*), and (3) the girdle scales (irregular in size, up to 1300 μm long, often separated by naked girdle in *A. araucariana*; relatively regular in size, up to 700 μm long, often imbricated in *A. miles*). These differences seem sufficient to justify separation at the species level.

Acanthopleura miles (Carpenter *in* Pilsbry, 1893)

Figures 41 to 47, and 115-M

Chiton (Sclerochiton) miles Carpenter *in* Pilsbry, 1893b: 189, pl. 46, figs. 1–5; Smith, 1903:619; Hedley, 1910: 352.

Sclerochiton miles: Ashby, 1923d:231, pl. 18, fig. 3.

Squamopleura miles: Leloup, 1939c:1–6, figs. 1–4, 1940:1–7 (in part).

Chiton (Squamopleura) miles: Smith, 1960:66.

Squamopleura imitator Nierstrasz, 1905a:102–103, pl. 8, figs. 212–218, 1905b:153–154; Horst & Schepman, 1908:527; Leloup, 1933a:19, pl. 1, fig. 4, 1939d:4–8, figs. 3, 4, 10, 11, 20–27.

Sclerochiton imitator: Thiele, 1910:95, pl. 10, figs. 24–28.

Sclerochiton thielei Ashby, 1923e:233.

Squamopleura carteri Iredale & Hull, 1926:260, pl. 27, figs. 18, 20, 28 (reprinted, 1927:123, pl. 15, figs. 18, 20, 28).

Squamopleura stratiotes Leloup, 1939d:9–12, figs. 5–7, 12–15, 28.

Squamopleura salisburyi Leloup, 1939d:9–12, figs. 8, 9, 16–19, 29.

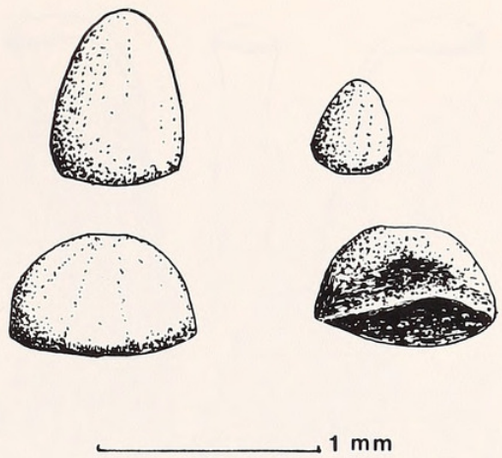


Figure 39

Acanthopleura araucariana (Hedley, 1898). Kuto Beach, Pines Id., New Caledonia (AJF 532); specimen 35 mm long. Girdle scales, outer side and inner side.

"*Sclerochiton curtisianus* (Smith)" Ashby, 1922a:34 (*fide* Ashby, 1923d:232); Ang, 1967:412–414, pl. 9, figs. 1–5.

"*Squamopleura curtisiana* (Smith)" Leloup, 1933a:18–19, pl. 1, figs. 1, 2 (in part: specimen from Mansfield Id., *fide* Leloup, 1939d:1–2, footnote); Wu, 1975:69–70, figs. 1–13.

Type material and type locality:

Chiton (Sclerochiton) miles Carpenter *in* Pilsbry, 1893b: Holotype (BMNH 198017); locality "Torres Strait" (Australia).

Squamopleura imitator Nierstrasz, 1905a: Types unascertained, in Zoologischen Museum zu Amsterdam (*fide* Nierstrasz, 1905a); locality "Insel Remarksaja [? Sumatra, Indonesia, 4°52′N, 95°22′E] and Java."

Sclerochiton thielei Ashby, 1923: Types unascertained; locality Sumatra.

Squamopleura carteri Iredale & Hull, 1926: Holotype (WAM 11662); locality Point Cloates, Western Australia (22°43′S, 113°40′E).

Squamopleura stratiotes Leloup, 1939d: Types unascertained; locality Trincomalee, Ceylon (8°34′N, 81°41′E).

Squamopleura salisburyi Leloup, 1939d: Types unascertained; locality Hambantota, Ceylon (6°07′N, 81°07′E).

←

Explanation of Figures 34 to 38

Figure 34. *Acanthopleura brevispinosa* (Sowerby, 1840a): *Acanthopleura afra* Rochebrune, 1822; paralectotype (MNHN).

Figure 35. *Acanthopleura araucariana* (Hedley, 1898): *Ischnochiton araucarianus* Hedley, 1898; holotype (AMS C-4344). Side view of valves ii, iii, and iv.

Figure 36. *Acanthopleura araucariana* (Hedley, 1898): *Ischnochiton araucarianus* Hedley, 1898; holotype (AMS C-4344). Dorsal view of valves ii, iii, and iv.

Figure 37. *Acanthopleura araucariana* (Hedley, 1898): *Ischnochiton araucarianus* Hedley, 1898; holotype (AMS C-4344). Dorsal view of valves i, v, and viii.

Figure 38. *Acanthopleura araucariana* (Hedley, 1898): *Ischnochiton araucarianus* Hedley, 1898; holotype (AMS C-4344). Ventral view of valves i, v, and viii.

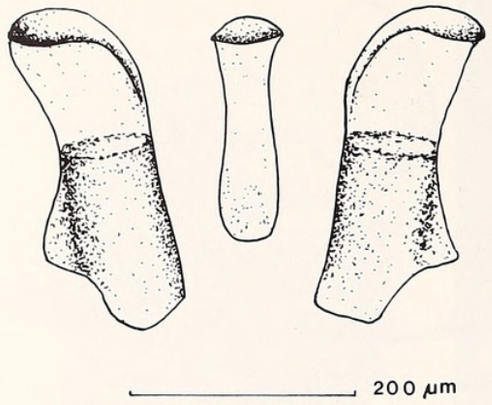


Figure 40

Acanthopleura araucariana (Hedley, 1898). Same specimen as in Figure 39. Radula median and first lateral teeth.

Material examined:

AUSTRALIA, W.A.: Maud's Landing, N of Carnarvon (24°53'S, 113°40'E), 2 specimens, ca. 30 mm long each (NMV); Point Cloates, holotype of *Squamopleura carteri* Iredale & Hull, 1926, ca. 35 mm long (WAM 11662); Dampier Arch., Kendrew Is., 8 specimens, largest 31 mm long (WAM 75-78; WAM 77-78; WAM 1340-78); Broome Bay, 1 specimen (NMV).
NEW GUINEA: Japen Id., Cape Tekopi, 1 specimen, 20 mm long (ANSP 272165).
BORNEO (Sabah, Malaysia): Layang-Layangan, Labuan Id., 19 specimens, largest 36 mm long (AJF 759); Tanjong-Kubong, Labuan Id., 48 specimens, largest 40 mm long (AJF 760).
TAIWAN: Coral reef southeast of Kungting, Pingtung Co., 18 specimens, largest 32 mm long (UCM 28885); Orchid Is., Taitung Hsien, 3 specimens, largest 30 mm long (UCM 28845); Hsiao-liu-chiu Id., Penghu Village, 2 specimens, largest 40 mm long (UCM 28864); Pingtung Hsien, 4 specimens, largest 32 mm long (UCM 28885).
PHILIPPINES: Hundred Islands, Lingayen Gulf, Luzon, 75 specimens, largest 35 mm long (AJF 464; AJF 465); "Auson" Id., off Port Barton, Palawan, 1 specimen, 26 mm long (AJF 820).
JAVA, Indonesia: Udjong Kuton, 1 specimen, 28 mm long (WAM 478-74).
SRI-LANKA (=Ceylon): Trincomalee, 4 specimens, largest 31 mm long (CAS 001203); Dondra Head, 22 specimens, largest 22 mm long (AJF 734); Dondra, 21 specimens, largest 22 mm long (AJF 735); Tangala, 58 specimens, largest 26 mm long (AJF 736; AJF 738); Galle, 22 specimens, largest 21 mm long (AJF 740).

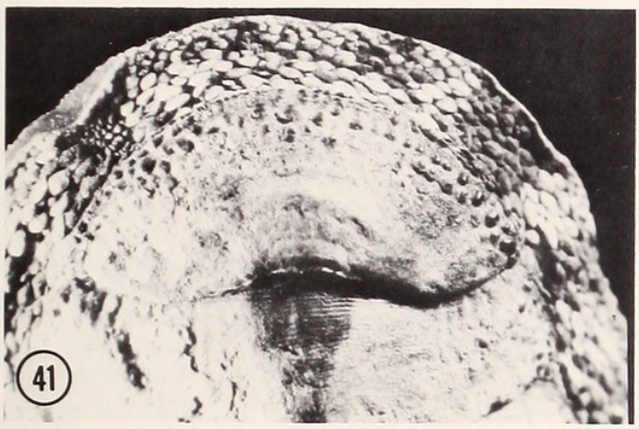
Description: The original description of *Chiton (Sclerochiton) miles* is quite adequate to identify the species: "Shell . . . rugose, oval, depressed . . . dorsal ridge rounded . . . mucro [posterior], nearly flat; apices of the valves prominent, obtuse . . . . Central areas transversely pretty regularly rugulose, the wrinkles appressed; lateral areas hardly elevated, moderately well defined, conspicuously rugose, rugae subradiating, granose; the end valves similarly sculptured . . . [slits, 11-1-9/11] . . . . Teeth of posterior valves directed forward, strongly callosed inside above the slits, sulcate outside; the rest of the valves having the teeth sulcate outside and pectinated at the margins . . . . Eaves moderate, solid . . . . Sinus deep, wide, wavy, smooth . . . . Girdle [with] large, solid, more or less separated scales which are striated outside . . ." (Carpenter *in* PILSBRY, 1893b:189).

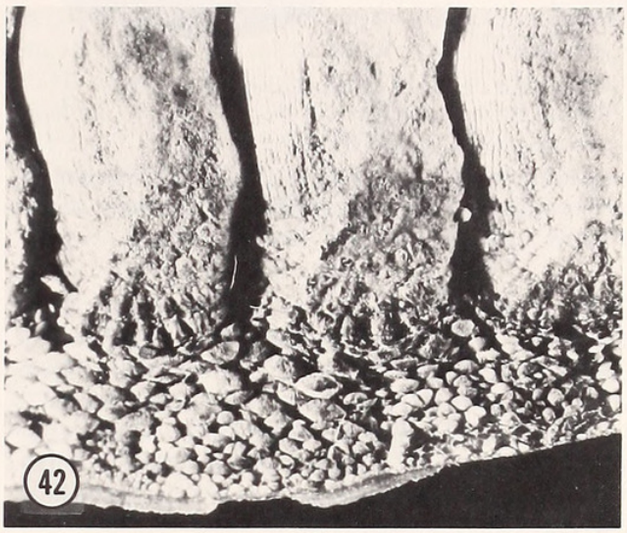
Holotype (BMNH 198017), dry, in excellent condition, flat, 30 mm long, 18 mm wide, 5 mm high, shows evidence of having been glued to cardboard; soft parts removed, posterior valve disarticulated; girdle scales variable in size, up to 600 μm long, discretely striated. Accompanying label reads, in part, "*Chiton (Sclerochiton) miles* (Carpenter MS) Pilsbry / HOLOTYPE / Torres Straits / H. Cuming coll. No. 42 / 1 specs Acc. no: 1829 . . . ." The specimen (Figures 41–44) agrees with Carpenter's (*in* PILSBRY, 1893b) description and illustrations.

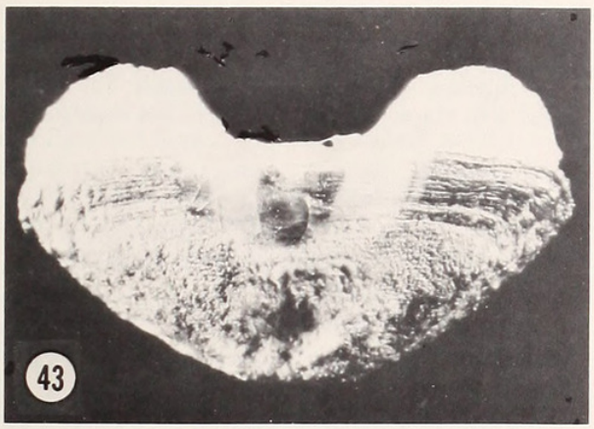
Among 176 specimens of *Acanthopleura miles* here examined, largest 40 mm long (live) (AJF 760: Labuan Id., Borneo). Body width/length, mean 0.63 (SD = 0.05; n = 30). Specimens round-backed, often depressed; valves moderately beaked, posterior edge angled (130–150° on valve ii). Tegmentum brownish-gray usually with dark jugal stripe. Lateral areas variably raised, from flat (in Sri-Lanka specimens) to elevated (in Taiwan specimens), with relatively small, round, well defined granules; diagonal line of lateral areas often defined by row of granules; tegmental surface between granules coarsely microgranular. Central areas featureless except for some 30 transverse, appressed trabeculae, 60–100 μm thick, often interrupted on pleural areas by 4–6 poorly defined oblique riblets. Similar granules on end valves. Mucro central to slightly posterior; postmucro convex, at 30–45° slope. Widths of tegmental surfaces of valves i/viii, mean 1.2. On valve i, tegmentum length/width, mean ratio 2.1. On valve viii, tegmentum's length/width, mean 1.9. Eaves thick (0.5 mm at midline of valve viii of specimen 30 mm long), relatively solid. Ocelli round to oval, 50–60 μm in diameter, randomly distributed amidst granules of anterior valve, postmucro area of posterior valve, and anterior ⅓ to ⅘ of lateral areas of intermediate valves. Gills with 40–50 plumes per side.

Articulamentum brown to white. Insertion plates strongly pectinate on outside. On valve i, length of insertion plate/length of tegmentum, mean 0.14; insertion teeth irregularly spaced. On valve viii, insertion plate with irregular pectinations becoming smaller to obsolete in middle ⅓, often with only 2 symmetrical slits (but in some specimens with as many as 5); well defined transverse round callus. Slit formula 5/10-1-1/5. Sutural laminae well developed, subtriangular on valve ii to subrectangular on valve viii. Sinus well defined; sinusal plate, smooth; relative width of sinus (width of sinus/width of sutural lamina) on valve viii, 0.5.

Girdle thick, musculous, often all black. Upper surface covered with calcareous, opaque, oval, strongly convex scales (Figure 45), more or less separated (evident in live or wet preserved specimens) to somewhat imbricate, variable in size, often up to 600–700 μm long (largest measured, 1100 μm long), with 6–15 discrete striations; amidst







Explanation of Figures 41 to 44, and 47

Figure 41. *Acanthopleura miles* (Carpenter *in* Pilsbry, 1893c): *Chiton (Sclerochiton) miles* Carpenter *in* Pilsbry, 1893c; holotype (BMNH 1951.2.1.2). Dorsal aspect of valves i and ii.

Figure 42. *Acanthopleura miles* (Carpenter *in* Pilsbry, 1893c): *Chiton (Sclerochiton) miles* Carpenter *in* Pilsbry, 1893c; holotype (BMNH 1951.2.1.2). Side view of valves iii, iv, and v.

Figure 43. *Acanthopleura miles* (Carpenter *in* Pilsbry, 1893c): *Chiton (Sclerochiton) miles* Carpenter *in* Pilsbry, 1893c; holotype (BMNH 1951.2.1.2). Dorsal aspect of posterior valve.

Figure 44. *Acanthopleura miles* (Carpenter *in* Pilsbry, 1893c): *Chiton (Sclerochiton) miles* Carpenter *in* Pilsbry, 1893c; holotype (BMNH 1951.2.1.2). Ventral aspect of posterior valve.

Figure 47. *Acanthopleura miles* (Carpenter *in* Pilsbry, 1893c): *Squamopleura carteri* Iredale & Hull, 1926; holotype (WAM 11662).

scales, occasional bunches of hyaline spicules, up to 100 × 30 μm. Girdle bridges empty. Undersurface covered with transparent, rectangular scales, 50 × 30 μm, with slightly convex outer edges, slightly concave inner edges; at outer margin, fringe of translucent spicules, up to 150 × 40 μm, vaguely striated longitudinally.

In a specimen 25 mm long (AJF 464: Lingayen Gulf, Philippines), radula measures 10 mm in length (40% of

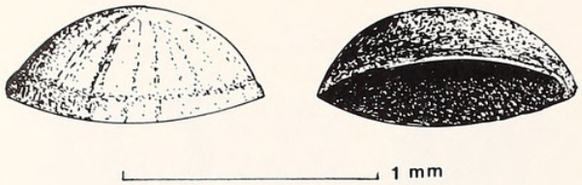


Figure 45

Acanthopleura miles (Carpenter *in* Pilsbry, 1893c). Hundred Islands, Lingayen Gulf, Philippines (AJF 464); specimen 25 mm long. Girdle scales, outer side and inner side.

specimen length), comprising 40 rows of mature teeth; median tooth, 40 μm wide at anterior blade, bulging posteriorly to 60 μm wide (Figure 46); lateral teeth 75 μm wide at anterior blade, with outer edge deeply concave, outer-posterior corner protruding almost to a knob; major lateral teeth with discoid head, 160 μm in width; outer marginal teeth 140 μm long, 100 μm wide (length/width, 1.4).

Distribution: Widely distributed in the central Indo-Pacific (Figure 115-M), from 25°S to 27°N, and from 73°E to 142°E, *Acanthopleura miles* has been recorded, albeit by synonymous names, at Atu Atoll, Maldives Is. (SMITH, 1903), Ceylon (LELOUP, 1939c, as *Squamopleura stratiotes* and *S. salisburyi*), Andaman Is. and Nicobar Is. (LELOUP, 1939c), Raja Id., Java, and Timor (NIERSTRASZ, 1905a, b; THIELE, 1909), Sumatra (THIELE, 1909; ASHBY, 1923d, as *S. thielei* Ashby, 1923d), Bali (LELOUP, 1933a, as *S. imitator*), Philippines (ANG, 1967, as *S. curtisiana*), Lanshu Id., Taiwan (WU, 1975, as *S. curtisiana*), Mansfield Id. (LELOUP, 1933a, as *S. curtisiana*), Torres Strait, Australia (Carpenter *in* PILSBRY, 1893b, type locality), Carnarvon, W. Australia (ASHBY, 1923d), Point Cloates, W. Australia (IREDALE & HULL, 1926, as *S. carteri*). The species is here recognized also at Taiwan, Philippines (Lingayen Gulf), Borneo, and New Guinea (AJF coll.).

Acanthopleura miles is confined to the intertidal zone, 0–0.5 m, often on rocks exposed at low tide.

Remarks: The identity of *Acanthopleura miles* has been much confused in the literature. IREDALE (1914b:125), noting that "Nothing like . . . *miles* has yet been seen from Torres Straits," assumed the locality in error, a gratuitous assumption later echoed by ASHBY (1923) and IREDALE & HULL (1926). LELOUP (1939c) introduced *Squamopleura stratiotes* and *S. salisburyi*, from Ceylon, which he immediately (in the same paper!) synonymized as geographic forms of a single species, later (LELOUP, 1940) regarded simply as a variety ("*forma*") of *S. miles*.

As observed here, *Acanthopleura miles* differs from *A. araucariana* in (1) lateral areas (very elevated in *A. araucariana*; hardly raised in *A. miles*), (2) tegmental granules (coarse, large in *A. araucariana*; well defined, small in *A. miles*), and (3) girdle scales (larger and separated in *A. araucariana*; smaller and often imbricated in *A. miles*).

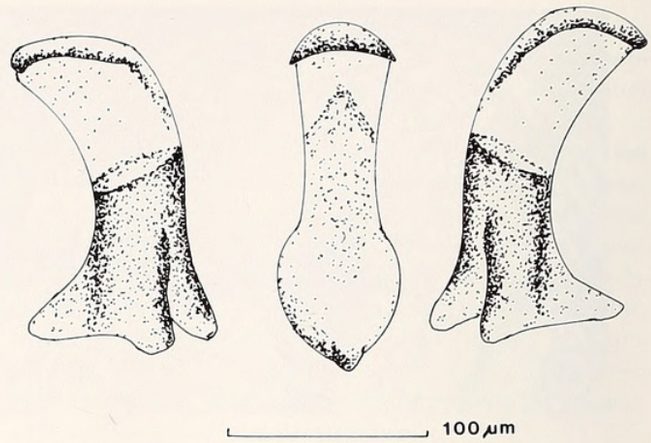


Figure 46

Acanthopleura miles (Carpenter *in* Pilsbry, 1893c); same specimen as in Figure 45. Radula median and first lateral teeth.

In the field, *Acanthopleura miles* was observed sharing the intertidal zone with *A. gemmata,* and *A. spinosa* (AJF 464, AJF 465, Lingayen Gulf, Philippines).

Acanthopleura curtisiana (Smith, 1884)

Figures 48 to 54, and 115-T

Chiton (Ischnochiton) curtisianus SMITH, 1884:78, pl. 6, fig. D.
Ischnochiton curtisianus: PILSBRY, 1892b:97, pl. 24, fig. 6.
Liolophura curtisiana: PILSBRY, 1893c:242; HEDLEY & HULL, 1909:265.
Sclerochiton curtisianus: THIELE, 1910:96, pl. 10, figs. 29–35; IREDALE, 1910a:103–104, 1914b:125; ASHBY, 1922a: 34.
Squamopleura curtisiana: HULL, 1923:160, 1925:114; IREDALE & HULL, 1926:259–260, pl. 37, figs. 5, 26–27 (reprinted, 1927:122–123, pl. 15, figs. 5, 26–27); MACKAY, 1930:292–295; LELOUP, 1933b:17–19, pl. 1, fig. 3 (in part: specimens from Aru Id.), 1939d:1–4, figs. 1–2.
[*Non:* LELOUP, 1933a:17–19, pl. 1, figs. 1–2; ANG, 1967: 412–414; WU, 1975:69–70, figs. 1–13.]
Enoplochiton torri BASTOW & GATLIFF, 1907:27–30, pls. 3–4, figs. 1–12.
Sclerochiton aruensis THIELE, 1910:96, pl. 10, figs. 36–41.

Type material and locality:

Chiton (Ischnochiton) curtisianus Smith, 1884: Holotype (BMNH 1881.11.10.32); locality Port Curtis, Queensland, Australia (24°00′S, 151°30′E).
Enoplochiton torri Bastow & Gatliff, 1907: Types unascertained; locality Queensland, Australia.
Sclerochiton aruensis Thiele, 1910: Types unascertained; locality Aru Is., Indonesia (6°00′S, 134°30′E).

Material examined:

AUSTRALIA, Qld.: Utinga, Cape York, 15 specimens, largest 23 mm long (NMV); Port Curtis, holotype of *Chiton (Ischnochiton) curtisianus* Smith, 1884 (BMNH 1881.11.10.32); Port Curtis, 9 specimens, largest 23 mm long (NMV); Cid Id., W of

Whitsunday Id., 1 specimen, 18 mm long (CAS 044790); Shelly Beach, near Townsville, 10 specimens, largest 25 mm long (NMV); Gill's Beach, Hinchinbrook Id., 5 specimens (*ex* J. R. Penprase coll.); Broad Sound, 17 specimens, largest 18 mm long (NMV); Moreton Bay, 8 specimens, largest 24 mm long (NMV).
AUSTRALIA, N.T.: Port Darwin, 2 specimens (CASG-SU 3389).
AUSTRALIA, W.A.: Point Cloates, 4 specimens, largest 40 mm long (cited by ASHBY, 1922a) (WAM 9336); Bay of Rest, Exmouth Gulf, 3 specimens, largest 25 mm long (WAM 1746-78); Dampier Arch., 2 specimens, largest 16 mm long (WAM 82-78; WAM 1079-75; Barrow Id., 1 specimen, 19 mm long (WAM 605-67); Cape Preston, 1 specimen, 17 mm long (WAM 1113-78); Broome, 1 specimen, 19 mm long (NMV).

Description: SMITH (1884) described *Chiton (Ischnochiton) curtisianus,* based on a specimen 16 × 9 mm (excluding girdle), as "Shell . . . dark greyish . . . [with] black broadish line from end to end down the middle of the back . . . with strong, concentric lines of growth . . . . [Girdle] alternately light and dark . . . . Valves arched, not carinate . . . very indistinct lateral areas . . . mucro probably near the centre . . . . [Articulamentum] greenish blue, stained dark brown in the middle . . . [slits 10-1-0] . . . . [Anterior valve insertion teeth] different-sized . . . striated on both sides but more strongly externally, their edges being sharp, but not smooth . . . . [Posterior valve] much thickened within along the posterior edge, which is roughened by fine cross striae, there being no prominent teeth, and of course no notches . . . . [Girdle] covered with small subimbricating oval [scales] . . . . The granules of the surface have an irregular disposition, following to some extent the lines of growth" (SMITH, 1884:78–79).

The holotype (BMNH 1881.11.10.32) consists of 8 disarticulated valves; no girdle, no radula. Reassembled, the valves add up to 18 mm, indicating a live specimen (with girdle) about 20 mm long (larger than, but compatible with length given by SMITH [1884]). Museum pink label reads, in part, ". . . Holotype / *Chiton (Ischnochiton) curtisianus* Smith, 1884 . . . / Loc. Port Curtis . . . / leg. Coppinger / Pres. The Admiralty." The specimen (Figures 48, 49) agrees with SMITH's (1884: pl. fig. D) description and illustration: light brown, with darker jugal band flanked by lighter bands. Valves considerably eroded, round-backed; beak distinct on valve ii, indistinct on others; posterior edge angulate at 130° on valve ii, less so on valve iii, almost straight on valves iv–vii. Tegmentum on valve i sculptured with concentric rows of round to oval granules, 100–150 μm in diameter, often coalesced into minute ridges. Lateral areas of intermediate valves slightly raised, poorly defined otherwise; sculpture with similar granules. Central areas with similar granules, more noticeable in pleural areas (particularly on valve ii) where they align into longitudinal rows; jugal areas with similar granules, though less well defined, and few coarse, transverse growth rugae. Posterior valve somewhat flattened, much eroded; mucro central (?). Width of valve i/width of valve viii, 1.15. Ocelli round to oval, 70–90 μm in diameter, throughout anterior valve, lateral areas of intermediate valves, and postmucro area of posterior valve.

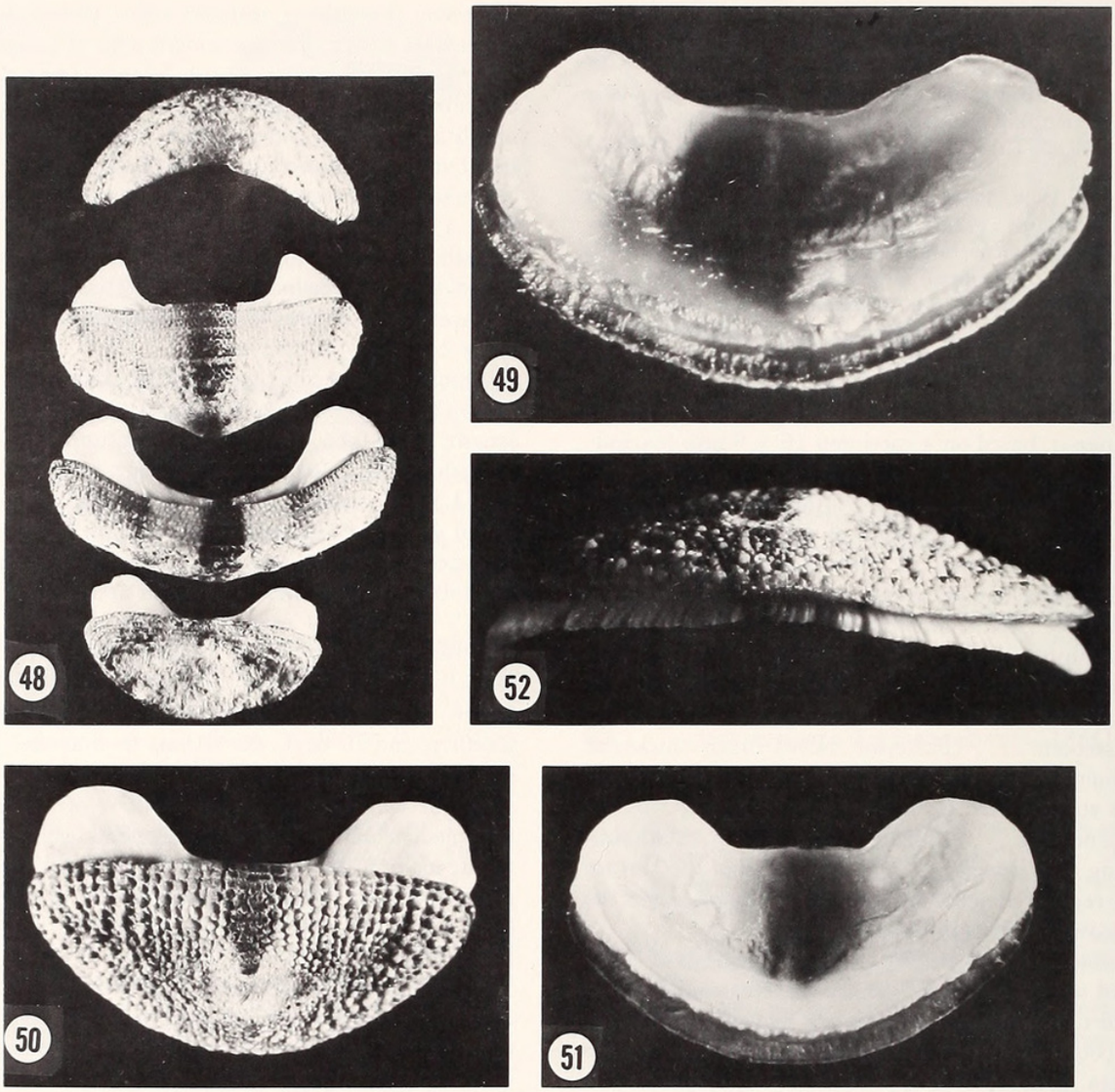
Articulamentum white with intense, large, brown discoloration in the middle. Sutural laminae, subtriangular on all intermediate valves, more so on ii; sinus very wide in all valves; on valve viii, width of sinus/width of sutural laminae, 0.9. Insertion plates pectinate on outside. On valve i, 10 slits, teeth 0.4 mm long. Intermediate valves uni-slit. On valve viii, insertion teeth almost obsolete, reduced to small pectinations on posterior aspect of round, transverse callus; only 2 (? 3) vestigial slits. Eaves relatively compact, 0.3 mm wide.

Among 78 specimens examined, largest 40 mm long (dry) (WAM 9336: Pt. Cloates, Australia). Body width/length, mean 0.66 (n = 20). Tegmentum grayish-green to grayish-brown, often with wide dark brown band at jugum. Lateral areas poorly defined, hardly elevated, with round to elongate granules, 100–200 μm in diameter, often in concentric rows. Central areas with smaller granules, 80–150 μm in diameter in pleural areas, often aligned in 10–15 longitudinal rows, much less apparent at jugum. Intermediate valves clearly beaked on valve ii, less so posteriorly; posterior edge of valve ii forming 130–140° angle. Mucro central; postmucro moderately convex (Figure 50). Ocelli round to oval, 60–80 μm in diameter, randomly distributed throughout anterior valve, postmucro area of posterior valve, and anterior ⅓ to ½ of lateral areas of intermediate valves. Widths of tegmental surfaces of valves i/viii, mean 1.08. On valve i, tegmentum length/width, mean 0.48. On valve viii, tegmentum length/width, mean 0.48. Eaves thick (0.4 mm in midline of valve viii), relatively solid. Gills 25–30 plumes per side.

Articulamentum white with diffuse light brown discolorations in middle. Sutural laminae well developed, subtriangular on valve ii to subrectangular on valve viii. Sinus wide. Insertion plates pectinate on outside. On valve i, length of insertion plate/length of tegmentum, mean 0.13. On valve viii (Figures 51, 52), insertion plate markedly underdeveloped to obsolete, often reduced to weak pectinations on posterior aspect of thick, smooth, transverse callus; 2 slits symmetrically placed at outer fourth of plate, weakly defined to obsolete. Slit formula 8/10-1-0/2.

Girdle thick, musculous, wide, often banded. Upper surface with oval, vaguely striated, opaque, calcareous scales (Figure 53), up to 300–400 μm in length in middle of girdle, progressively smaller to minute at margins; in living and alcohol preserved specimens, girdle scales are clearly separated from each other by about half of their width; occasional bunches of small, translucent spicules, up to 70 × 15 μm, amidst the scales. Girdle bridges empty. Undersurface covered with transparent, rectangular scales, 40 × 20 μm, with coarse striations.

In a specimen 17 mm long (NMV: Utinga, Cape York, Australia), radula 6 mm in length (35% of specimen length), comprising 35 rows of mature teeth. Median tooth (Figure 54), 35 μm wide at anterior blade, parallel-sided,



Explanation of Figures 48 to 52

Figure 48. *Acanthopleura curtisiana* (Smith, 1884): *Chiton curtisianus* Smith, 1884; holotype (BMNH 1881.11.10.32). Dorsal aspect of valves i, ii, v (?), and viii.

Figure 49. *Acanthopleura curtisiana* (Smith, 1884): *Chiton curtisianus* Smith, 1884; holotype (BMNH 1881.11.10.32). Ventral side of posterior valve.

Figure 50. *Acanthopleura curtisiana* (Smith, 1884). Cape York, N.T., Australia (NMV); specimen 17 mm long. Dorsal aspect of posterior valve.

Figure 51. *Acanthopleura curtisiana* (Smith, 1884). Same specimen as in Figure 50. Ventral aspect of posterior valve.

Figure 52. *Acanthopleura curtisiana* (Smith, 1884). Same specimen as in Figure 50. Posterior aspect of posterior valve.

globose posteriorly; first lateral teeth 65 μm wide at well developed anterior blade; second lateral teeth with discoid head 130 μm in diameter; outer marginal teeth, 130 μm long, 80 μm wide (length/width, 1.6).

Distribution: *Acanthopleura curtisiana* is confined to tropical northern Australian waters (Figure 115-T). It has been recorded in Queensland at Port Curtis (SMITH, 1884; IREDALE, 1910a; HULL, 1923), Gladstone (HEDLEY & HULL, 1909), Keppel Bay, Broad Sound, Magnetic Id. (MACKAY, 1930), Cape York (LELOUP, 1939c), Thursday Id. (IREDALE, 1910a), and (herein) at Moreton Bay (27°20′S), its southernmost record; in the Northern Territory, at Port Darwin (ASHBY, 1922a; and herein); in Western Australia at Point Torment, and Point Cloates (22°43′S), its southernmost record on the western coast. Reports of the species at Aru Is., Indonesia (6°S) (THIELE, 1909; LELOUP, 1933a), may constitute northernmost records. LELOUP's (1933a) report of the species at Mansfield Id. was later retracted (LELOUP, 1939d). Reports of *A.*

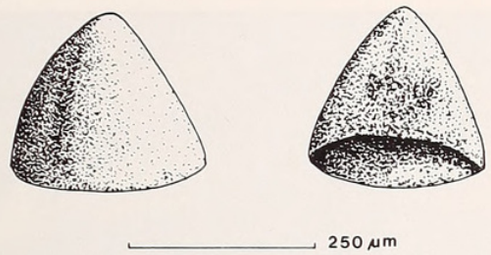


Figure 53

Acanthopleura curtisiana (Smith, 1884). Exmouth Gulf, W.A., Australia (WAM 1746-78); specimen 23 mm long. Girdle scales, outer and inner sides.

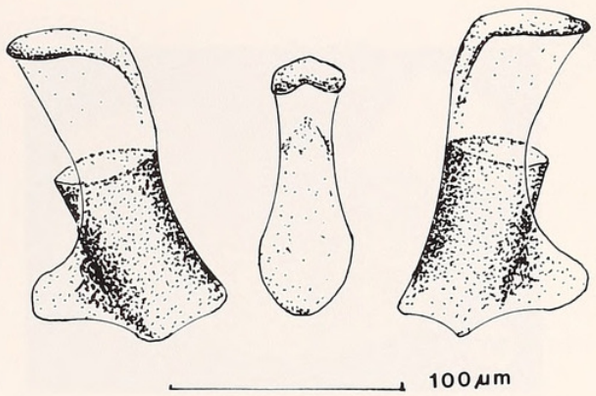


Figure 54

Acanthopleura curtisiana (Smith, 1884). Same specimen as in Figure 53. Radula median and first lateral teeth.

curtisiana in the Philippines (Ang, 1967) and Taiwan (Wu, 1975) are presumed in error for *A. miles*.

Bathymetric range 0–1 m, on rocks often exposed at low tide.

Remarks: *Acanthopleura curtisiana* has often been confused with *A. miles*. The two species, hitherto assigned to *Squamopleura,* are identical in size, shape, color, and habitat, but they differ in (1) size of girdle scales (up to 400 µm long in *A. curtisiana*; up to 800 µm long in *A. miles*), (2) central areas (with longitudinal rows of granules on pleural areas in *A. curtisiana*; without granules, featureless except for fine, appressed, transversal lamellae at jugal areas in *A. miles*), (3) radula (median tooth parallel-sided in *A. curtisiana*; bulging posteriorly in *A. miles*).

Thiele's (1910) illustration of the median tooth of the radula of *Acanthopleura curtisiana* shows a two-pointed posterior end, instead of a globose end as here illustrated (Figure 54); the discrepancy may reflect intraspecific variation or the difficulties in properly visualizing radular teeth under ordinary microscopy.

Acanthopleura loochooana (Broderip & Sowerby, 1829)

Figures 55 to 61, and 114-L

Chiton loochooanus Broderip & Sowerby, 1829:368.
Liolophura loochooana: Pilsbry, 1893c:244; (?) Is. Taki, 1938: 411, 1962:46 (with *Liolophura gaimardi platispinosa* Leloup, 1939a, as syn.); Kaas & Van Belle, 1980:76.

Type material and locality:

Chiton loochooanus Broderip & Sowerby, 1829: Neotype (CAS 044306) here designated; locality "shore of Loo Choo Is." (=Ryukyu Islands, Japan), here restricted to Buckner Bay, Okinawa, Japan (26°17′51.5″N, 127°54′26″E), intertidal zone.

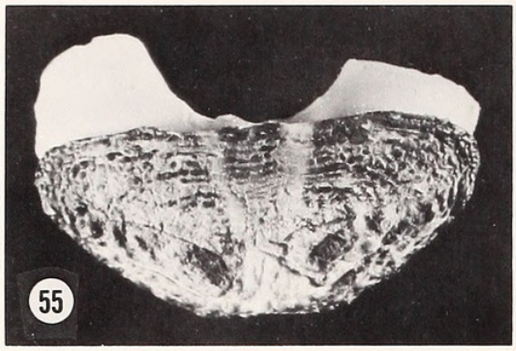
Other material examined:

OKINAWA, Japan: Buckner Bay, at rocky intertidal zone, neotype lot, 14 specimens, largest 26 mm, smallest 8 mm long, *leg.* E. V. Iverson, 23 Apr. 1975 (CAS 001627); Nagahama, 2 specimens, largest 25 mm long (CAS 019919; CAS 040204); Okuma, 1 specimen, ca. 50 mm long (S. Crittenden coll.).
TAIWAN: Penghu Is., south of Chienshan Village, Penghu Co., 4 specimens, largest 28 mm long (UCM 28893); Keelung, 18 specimens, largest 26 mm long, *leg.* F. B. Steiner, Oct. 1963 & Sept. 1968 (CAS 009880; CAS 016698).
HONG KONG: Repulse Bay, Hong Kong Id., 2 specimens, largest 18 mm long (AJF 686); Cheung-Sha, Lantau Id., 7 specimens, largest 34 mm long (AJF 685).

Description: *Chiton loochooanus* was described as "*Ch. valvis subscabrosis, areis marginalibus radiatim granosis, margin coriaceo superne granoso, granielevatis; long. 15/20, lat. 3/10 poll. Hab. in mari Sinensi, ad littora Insulae Loo-Choo.* A very pretty little Chiton, whose margin is covered with small grains resembling very short, blunt spines" (Broderip & Sowerby, 1829:368).

Among 48 specimens here referred to *Acanthopleura loochooana,* largest 50 mm long (in alcohol) (S. Crittenden coll.: Okuma, Okinawa). Body width/length, mean 0.65. Round-backed; intermediate valves beaked; posterior edge of valve ii forming 140–160° angle. Tegmentum grayish-white to brown, often with dark gray jugal stripe. Lateral areas elevated, well defined, crowded with low, round granules which tend to align radially and coalesce; anterior valve and postmucro area of posterior valve similarly sculptured. Central areas with ill-defined sculpture of appressed transverse lamellae, often broken into irregular granules or rugosities which, on pleural areas, tend to form forward-converging riblets. Mucro central (in small specimens) to posterior (in larger ones); postmucro slightly to markedly convex, slope varying with size of specimen (Figure 55). Ocelli round to oval, 60–70 µm in diameter, throughout anterior valve, postmucro area of posterior valve, and anterior half of lateral areas. On valve i, tegmentum length/width, mean 0.48. On valve viii, tegmentum length/width, mean 0.42. Widths of tegmental surfaces of valves i/viii, mean 1.2. Gills with 35–40 plumes per side.

Articulamentum brown with white discoloration at sutural laminae and insertion plates. Sutural laminae well developed, relatively long, subtriangular on valve ii to subrectangular on valve viii. Sinus well formed; sinusal plate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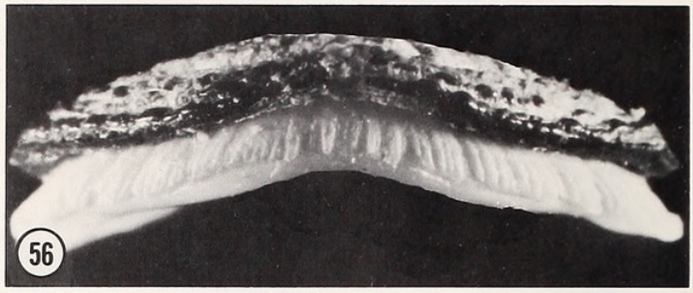
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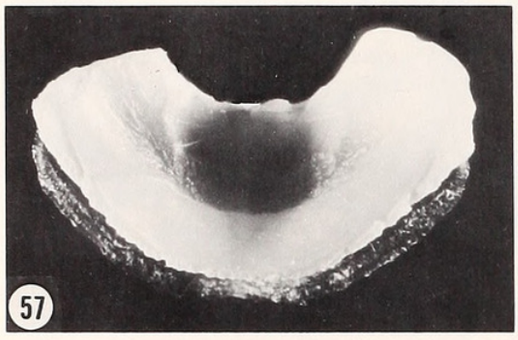
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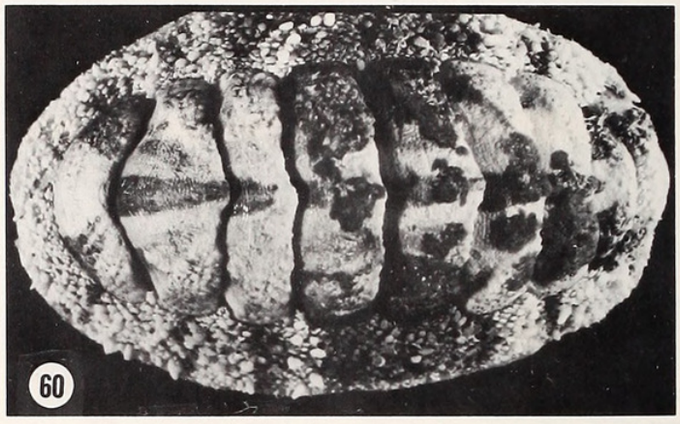
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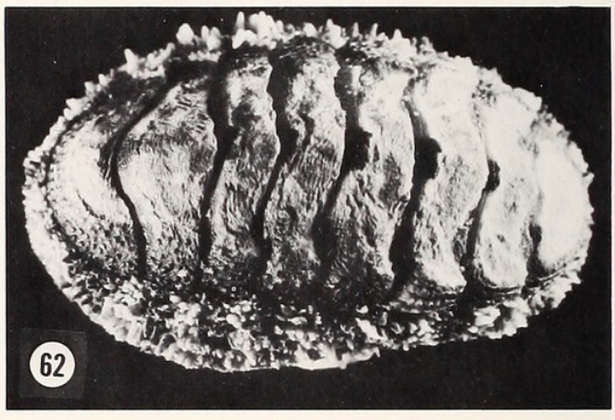
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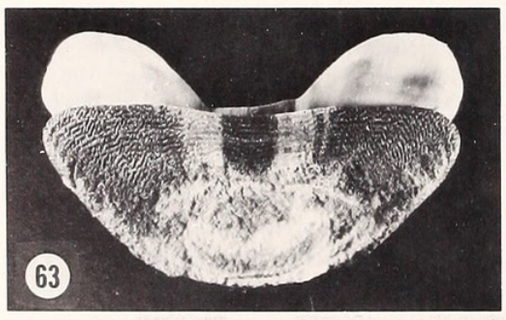
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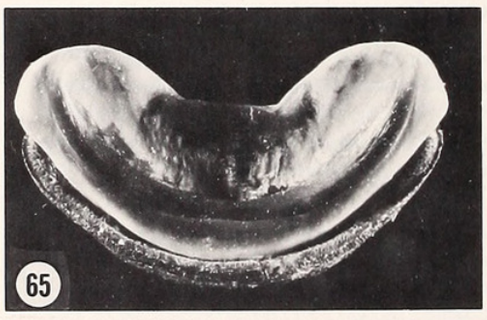
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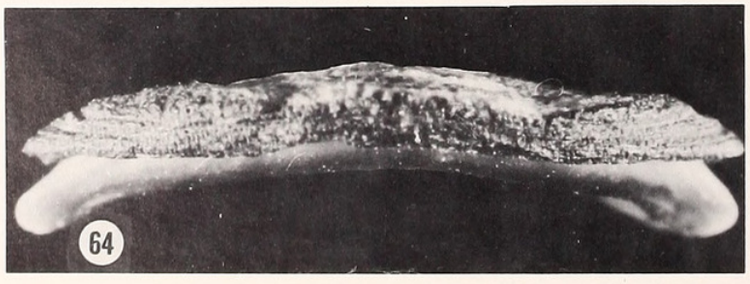
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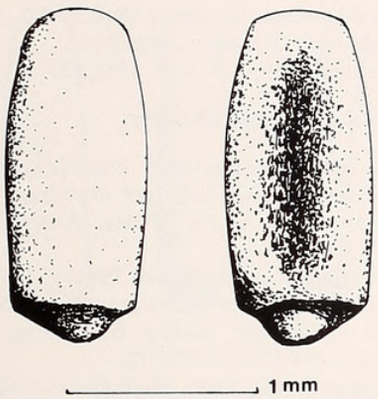


Figure 58

Acanthopleura loochooana (Broderip & Sowerby, 1829). Keelung, Taiwan (CAS 009880); specimen 29 mm long. Girdle scales, outer and inner sides.

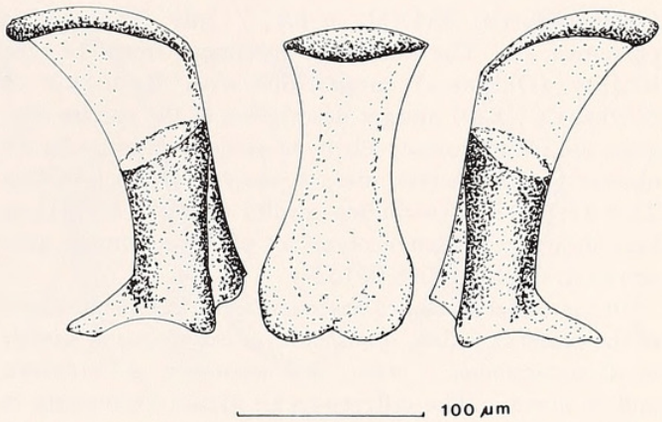


Figure 59

Acanthopleura loochooana (Broderip & Sowerby, 1829). Same specimen as in Figure 60. Radula median and first lateral teeth.

smooth; relative width of sinus on valve viii, 0.8. Insertion plates pectinate on outside. On valve i, insertion teeth irregularly spaced; in midline, length of insertion teeth/length of tegmentum, mean 0.13. On valve viii, pectinations and teeth underdeveloped to obsolete in middle third, hardly extending beyond transverse round callus in outer third; slits of posterior valve not always clearly determinable (Figures 56, 57). Slit formula 8/10-1-2/7. Eaves relatively thick (0.4 mm on midline of valve viii in specimen 20 mm long), moderately spongy.

Girdle banded black and white, thick, musculous. Upper surface girdle elements (Figure 58) irregular in size and shape; most elements spinelet-like, up to 2000 µm long, 600 µm wide, relatively flattened in cross section; other elements scale-like, *i.e.,* much smaller in all dimensions, particularly in height, vaguely striated on outer face; in living or wet preserved specimens, girdle elements often separated by "nude" girdle, with occasional hyaline, needle-like elements, single or bunched, up to 120 × 20 µm. Girdle bridges empty. Undersurface paved with transparent, subrectangular scales, about 40 × 30 µm, becoming elongate to 70 × 30 µm at periphery, with some coarse striations, convex outer edge, concave inner edge. Marginal fringe of 1 or 2 rows of translucent spicules, up to 300 × 50 µm, finely striate.

In specimen 29 mm long (CAS 009880: Taiwan), radula measures 12.8 mm in length (44% of specimen length), comprising 55 rows of mature teeth. Median tooth (Figure 59) 80 µm wide at anterior blade; first lateral teeth 110 µm wide at anterior blade; head of second lateral teeth discoid, 210 µm wide; outer marginal teeth 200 µm long, 150 µm wide (length/width, 1.4).

Distribution: The geographic range of *Acanthopleura loochooana* extends from Okinawa (26°31′N, 127°59′E) to Taiwan and Hong Kong (22°15′N, 114°10′E) (Figure 114-L). Listings of the species at Shizuoka, Japan (Is. Taki, 1938, 1962) cannot be taken at face value.

Acanthopleura loochooana seems to be confined to the intertidal zone, on top of rocks in moderate surf areas.

Remarks: *Chiton loochooanus,* left unfigured, was considered by Pilsbry (1893c:244) as "absolutely unrecognizable . . . but . . . perhaps a member of the genus *Liolophura.*" The original type material could not be found

←

Explanation of Figures 55 to 57, and 60 to 65

Figure 55. *Acanthopleura loochooana* (Broderip & Sowerby, 1829). Specimen from the neotype-lot (CAS 001627). Dorsal aspect of posterior valve.

Figure 56. *Acanthopleura loochooana* (Broderip & Sowerby, 1829). Same specimen as in Figure 55. Posterior aspect of posterior valve.

Figure 57. *Acanthopleura loochooana* (Broderip & Sowerby, 1829). Same specimen as in Figure 55. Ventral aspect of posterior valve.

Figure 60. *Acanthopleura loochooana* (Broderip & Sowerby, 1829); neotype (CAS 044306).

Figure 61. *Acanthopleura loochooana* (Broderip & Sowerby, 1829); neotype (CAS 044306). Close-up of girdle.

Figure 62. *Acanthopleura gaimardi* (Blainville, 1825). Magnetic Id., Qld., Australia (AJF 602); specimen 15 mm long.

Figure 63. *Acanthopleura gaimardi* (Blainville, 1825). Magnetic Id., Qld., Australia (AJF 602); specimen 30 mm long. Dorsal aspect of posterior valve.

Figure 64. *Acanthopleura gaimardi* (Blainville, 1825). Same specimen as in Figure 63. Posterior aspect of posterior valve.

Figure 65. *Acanthopleura gaimardi* (Blainville, 1825). Same specimen as in Figure 63. Ventral aspect of posterior valve.

(Solene Morris, BMNH, *in litt.,* 7 July 1983) and is presumed lost. The finding of specimens from the type locality (Okinawa) compatible with BRODERIP & SOWERBY's (1829) meager description of the species suggests the identification, albeit on subjective grounds. To obviate future uncertainties, a neotype (CAS 044306), 25 × 15 × 7 mm (including girdle) (Figures 60, 61), is here designated from neotype lot of 15 specimens preserved in alcohol (CAS 001627).

In the underdeveloped insertion teeth and pectinations of the posterior valve, *Acanthopleura loochooana* is similar to *A. brevispinosa, A. miles, A. araucariana, A. curtisiana,* and *A. arenosa.* The differences lie almost exclusively in the girdle elements: in *A. miles, A. araucariana,* and *A. curtisiana,* the girdle elements are clearly scales; in *A. brevispinosa,* they are thin and cylindrical spicules; and in *A. arenosa,* they are pointed spicules, almost conical, circular in cross section, and larger at base.

In its relatively limited range, *Acanthopleura loochooana* is sympatric with *A. japonica, A. miles,* and *A. gemmata.* Specimens of *A. loochooana* have been found exposed at low tide, up to 30 cm above water level, sharing habitat with specimens of *A. japonica* (A. J. Ferreira, field observations at Lantau Id. and Repulse Bay, Hong Kong, Sept. 1982).

Acanthopleura loochooana is present in a relatively narrow area in the zone of contact between *A. japonica* and *A. gemmata.* In this respect, *A. loochooana* seems to be related to *A. japonica* and *A. gemmata* in the vicinity of the Tropic of Cancer, as *A. arenosa* is to *A. gemmata* and *A. gaimardi* in the vicinity of the Tropic of Capricorn.

Acanthopleura gaimardi (Blainville, 1825)

Figures 62 to 67, and 114-D

Chiton gaimardi BLAINVILLE, 1825:546.
Liolophura gaimardi: PILSBRY, 1893c:240–241, pl. 53, figs. 30–35; NIERSTRASZ, 1905b:155 (in part: Sydney specimens only); HORST & SCHEPMAN, 1908:528 (in part: Sydney specimens only); ASHBY, 1918c:87, 1922c:581; HULL, 1923b:198, pl. 28, figs. 1–4; ASHBY, 1926b:384; IREDALE & HULL, 1926:262, pl. 37, figs. 13–16, 19, 31 (reprinted, 1927:125, pl. 15, figs. 13–16, 19, 31); BERGENHAYN, 1930a:32, pl. 8, figs. 76–77; ALLAN, 1959: 238, fig. 6a; LELOUP, 1961b:42–44, text figs. 3, 5b, pl. 3, fig. 2; WU, 1969:109, figs. 5a, 5b, 47–58.
[*Non:* NIERSTRASZ, 1905a:108, 1905b:154–155, figs. 20–21; HORST & SCHEPMAN, 1908:528 (in part); LELOUP, 1939a:3–7, fig. 5A.]
Liolophura gaimardi queenslandica PILSBRY, 1894f:87–88; ASHBY, 1918c:87; DAVIS *et al.,* 1979:2, 18.
[*Non:* LELOUP, 1961b:67, fig. 5-B3].
Liolophura queenslandica: HULL, 1923b:199, pl. 28, figs. 5–8, 1925:115; IREDALE & HULL, 1926:263, pl. 37, figs. 23–25, 30, 32 (reprinted, 1927:126, pl. 15, figs. 23–25, 30, 32); ALLAN, 1959:239.
Chiton incanus GOULD, 1846:145 (reprinted, 1862:6), 1861 (Atlas):315, pl. 28, figs. 432, 432a.
Maugeria incana: GOULD, 1862:248.
Chiton (Acanthopleura) incanus: SMITH, 1884:81–82.
Acanthopleura incana: HADDON, 1886:25–30.
Liolophura incana: PILSBRY, 1893a:105.
"*Chiton piceus* Gmelin" ANGAS, 1867:223.

Type material and type locality:

Chiton gaimardi Blainville, 1825: Possible types at MNHN (*fide* ASHBY, 1922c:581), not examined; locality Port Jackson, New South Wales, Australia (33°50′S, 151°16′E).
Liolophura gaimardi queenslandica Pilsbry, 1894f: Lectotype (ANSP 64853) and paralectotype (ANSP 355874) herein designated; locality Bundaberg, Queensland, Australia (24°52′S, 152°21′E).
Chiton incanus Gould, 1846: Holotype (USNM 5823) and paratypes (MCZ 169189); locality "New South Wales," Australia.

Material examined:

AUSTRALIA, Qld. Townsville, 11 specimens, largest 42 mm long (AJF 600); Radical Bay, Magnetic Id., 14 specimens, largest 30 mm long (AJF 602); Yeppoon, 33 specimens, largest 59 mm long (AJF 356; AMS C135480); Stradbroke Id., 9 specimens, largest 36 mm long (AMS C135478; AMS C13008); Port Curtis, Bagara Beach, 1 specimen (AMS C109294); Bundaberg, 13 specimens, largest 45 mm long (AJF coll., *leg.* Gail Chapman); Pt. Cartwright, 1 specimen, 28 mm long (NMV, *ex* Basset Hull coll.); Caloundra, 8 specimens, largest 61 mm long (NMV); Peel Is., Moreton Bay, 1 specimen, 38 mm long (AMS C109296). AUSTRALIA, N.S.W.: Holotype of *Chiton incanus* Gould, 1846 (USNM 5823); Flat Rock, north of Richmond River, 2 specimens, largest 50 mm long (AMS C50821); Byron Bay, 2 specimens, largest 50 mm long (CAS 012387); Sydney, 3 specimens, largest 32 mm long (WAM 1592-78; WAM 1590-78; CASG-SU 2868); Port Jackson, 11 specimens (WAM 1591-78; AMS C135482); Gunnamatta Bay, Port Hacking, 2 specimens, largest 35 mm long (AMS C135479).

Description: BLAINVILLE's (1825) description of *Chiton gaimardi* based on 3 specimens, "un pouce à quinze lignes" (27–34 mm) in length, collected by Quoy and Gaimard at Port Jackson, Australia, stresses the fact that insertion teeth are absent on the posterior valve but present and pectinate on the anterior valve. The species was further described and illustrated by PILSBRY (1893c), HULL (1923b), and IREDALE & HULL (1926), always with significance given to the callused, slitless and toothless posterior valve.

Among 112 specimens of *Acanthopleura gaimardi* here examined, largest 61 mm long (in alcohol) (NMV: Caloundra, Qld., Australia). Specimens (Figures 62–65) depressed, round-backed. Body width/length, mean 0.60. Intermediate valves beaked; posterior edge of valve ii forming 110–140° angle. Tegmentum grayish-green to grayish-brown often with wide black band at jugum. Lateral areas poorly defined, hardly raised, sculptured with inconspicuous, low-profile granules in vaguely defined radial rows, or coalesced into obsolete concentric ridges; anterior valve similarly sculptured. Central areas almost featureless except for transversely appressed lamellae, about 50 μm thick. Posterior valve rather flat, almost triangular

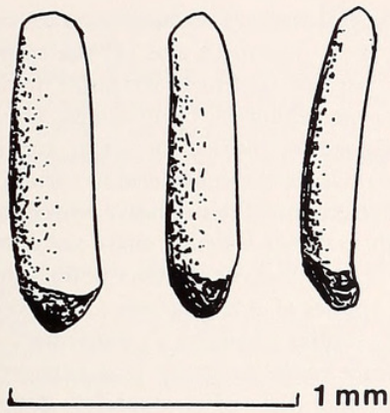


Figure 66

Acanthopleura gaimardi (Blainville, 1825). Yeppoon, Qld., Australia (AJF 356); specimen 45 mm long. Girdle spines.

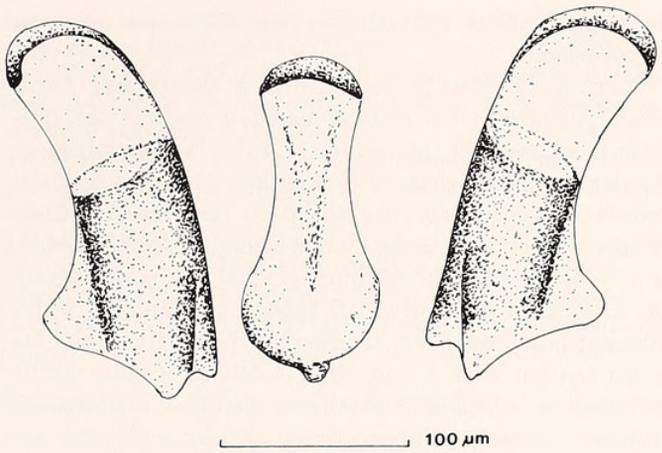


Figure 67

Acanthopleura gaimardi (Blainville, 1825). Same specimen as in Figure 66. Radula median and first lateral teeth.

in some specimens; mucro inconspicuous, decidedly posterior to terminal. Ocelli round to oval, 60–70 µm in diameter, randomly distributed throughout anterior valve, postmucro area of posterior valve, anterior ½ to ⅔ of lateral areas of intermediate valves, and (in about 50% of specimens examined) pleural areas. On valve i, tegmentum length/width, mean 0.5. On valve viii, tegmentum length/width, mean 0.4. Widths of tegmental surface of valves i/viii, mean 1.1. Gills with 35–50 plumes per side.

Articulamentum dark brown, often lighter on sutural laminae. Sutural laminae well developed, subtriangular on valve ii to subrectangular on valve viii. Sinus well formed; sinusal plate mostly smooth. Insertion plates of anterior and intermediate valves, strongly pectinate on outside. On valve i, insertion teeth irregularly spaced, sometimes fused together; in midline, length of insertion plate/length of tegmentum, mean 0.14. Valve viii without insertion teeth; posterior aspect of transverse callus flat, crescentic, smooth, without slits or pectinations. Slit formula 8/12-1-0. Eaves thick, projecting conspicuously beyond articulamentum of posterior valve.

Girdle, thick, musculous, wide, often banded black-brown and white. Upper surface crowded with white to dark brown spinelets (Figure 66), often tipped with white, pointed to blunt, close together, straight to curved, somewhat conical, variable in size, from short and scale-like to 1.5 mm long, with vague to obsolete longitudinal striations; in fresh or wet-preserved material, spinelets often seen standing apart from each other, separated by "nude" girdle; amidst spinelets, in the "nude" girdle, needle-like elements may be found, single or clumped, pointed, hyaline, up to 120 × 25 µm. Girdle bridges empty. Undersurface paved with transparent, squarish to rectangular scales, about 60 × 40 µm, vaguely striate.

Radulae averaging 45% of specimen length, with 50 rows of mature teeth. In specimen 40 mm long (AJF 356: Yeppoon, Australia), median tooth (Figure 67) 50 µm wide at anterior blade; first lateral teeth 80 µm at anterior blade; head of second lateral teeth discoid, 230 µm wide; outer marginal teeth, 220 µm long, 110 µm wide (length/width, 2.0).

Distribution: *Acanthopleura gaimardi* is confined to the eastern coast of Australia between Magnetic Id. (19°08′S) (AJF 602), the northernmost verified record, and Sydney (33°52′S) (Iredale & Hull, 1926; Ferreira, herein), the southernmost verified record (Figure 114-D). The presence of the species southward to Port Hacking (34°05′S) (Hull, 1923b) is credible but requires corroboration. Reports of the species in the Moluccas Is. (Nierstrasz, 1905b; Horst & Schepman, 1908), Japan (Leloup, 1939a), and Taiwan (Wu, 1969) are in error.

Bathymetric range, confined to the intertidal zone, often exposed at low tide.

Remarks: *Acanthopleura quatrefagesi* Rochebrune, 1881a: 42 (misspelled as *quatrefagei* in Rochebrune, 1881b:117), from Table Bay, South Africa, was regarded by Ashby (1931a) as a synonym of *A. brevispinosa* and by Thiele (1910), Leloup (1961b), and Kaas & Van Belle (1980) as a synonym of *A. gaimardi*. Leloup (1939a, fig. 5-B) figured a valve of a supposed "co-type." But type material has not been found at MNHN (A. Tillier, *in litt.* 15 April 1980) and may be presumed lost. Because Rochebrune's (1881a, b) accounts are totally inadequate, the species is here regarded as a *nomen dubium*.

Chiton incanus Gould, 1846, has been regarded as a synonym of *C. gaimardi* since Pilsbry (1893a). The holotype (USNM 5823) is accompanied by museum labels that read, in part, ". . . *Chiton incanus* Gould / New South Wales . . .," and ". . . type . . ."; a handwritten note states "2/8/18 . . . compared to undoubted *Liolophura gaimardi* Blainville 1825 which it certainly is / E. Ashby." The single specimen, disarticulated with fragments of dry girdle, agrees with Gould's (1846, 1852) description and illustration of the species. The report of the species at

Stewart Id., New Zealand (SMITH, 1884) has not been corroborated.

PILSBRY (1894b:87) established a subspecies, *Liolophura gaimardi queenslandica,* based solely on "the uniform black color of the girdle" and the "somewhat more slender [spinelets] than in *Gaimardi*." The type material consists of 2 specimens, dry, soft parts removed. The larger specimen, 42 mm long, 29 mm wide (including girdle), is a 7-valve specimen; the number "64853" is written on the articulamental surface of valve v (?); anterior valve missing; posterior valve, disarticulated showing white articulamentum and broad, flat, toothless callus; girdle spinelets all black and relatively slender. The smaller specimen, curled, estimated length 20 mm, soft parts removed, articulamentum dark brown, is here designated lectotype (ANSP 64853); the larger, partly disarticulated, 7-valve specimen, paralectotype (ANSP 355874). PILSBRY's (1894b) designation of a subspecies, *queenslandica,* cannot be maintained, despite HULL (1923b) having raised it to species rank upon hardly spelled out differences in the tegmental sculpture of specimens collected between Port Hacking (34°05'S) and Broken Bay (33°34'S).

Acanthopleura gaimardi is remarkably similar to *A. japonica.* Yet, neither PILSBRY (1893c) nor subsequent workers devoted much space to contrasting them. Pilsbry stated only that *Liolophura gaimardi* differs from *L. japonica* "in the differently colored interior and sutural plates, in the details of girdle-structure, etc." (PILSBRY, 1893c:241), and that *L. japonica* differs "from *L. incana* [=*A. gaimardi*] by the uniform black color of the inner layer or articulamentum" (PILSBRY, 1893c:243). Diagnostic criteria (besides locality) have been increasingly obscured by subsequent authors. NIERSTRASZ (1905b:154–156, pl. 1, figs. 20–25) reported specimens of both *L. gaimardi* and *L. japonica* (as "var. *tesselata*") at the Moluccas Is., none of which agrees with the concept of *Liolophura* Pilsbry, 1893a. LELOUP (1939) identified Japanese specimens as *L. gaimardi,* and specimens from Indochina as *L. japonica*; and later LELOUP (1961:38) tabulated a single distinction between the two species, the girdle spinelets, said to be "of equal length" in *japonica,* "of different lengths" in *gaimardi.* WU (1969) identified specimens from Taiwan as *L. gaimardi,* with no reference to *L. japonica.*

In this study no reliable differences were found between putative specimens of *Acanthopleura gaimardi* from Australia and *A. japonica* from Japan in habitat, general shape, size, tegmental sculpture, articulamental features, slit formula, gills, girdle undersurface scales, or radula. However, the specimens were seen to differ in (1) the shape of the posterior valve (flat, somewhat triangular, mucro almost terminal in *A. gaimardi*; modestly elevated, somewhat oval, mucro posterior but not terminal in *A. japonica*), (2) the color of articulamentum (dark brown in *A. gaimardi*; almost black in *A. japonica*), (3) the callus of the posterior valve (with no vestiges of teeth or pectinations in *A. gaimardi*; often with some symmetrical pectinations or vestigial teeth, particularly on outermost areas of the callus, in *A. japonica*), and (4) the spinelets of the girdle upper surface (pointed, irregular in size, rather conical in *A. gaimardi*; erect, blunt-ended, regular in size, often white-tipped, cylindrical or wide, and imbricating in *A. japonica*). Given the considerable variation observed in these characters and their relative unreliability, it remains difficult to decide whether there are two species, *A. japonica* and *A. gaimardi,* or disjunct populations of a single biological species of *Acanthopleura.* However, until and unless further studies (cytological, molecular, *etc.*) should produce evidence to the contrary, it is here recommended that the traditional view of two species, *A. japonica* and *A. gaimardi,* be maintained.

Morphologically, *Acanthopleura gaimardi* is also very close to *A. gemmata,* from which it differs only in (1) the shape of the posterior valve (oval, elevated, mucro almost central in *A. gemmata*; triangular, depressed, mucro almost terminal, in *A. gaimardi*), (2) insertion plate of posterior valve (with well developed teeth in *A. gemmata*; without teeth in *A. gaimardi*), (3) the tegmental sculpture of the central areas (an unreliable distinction, particularly considering the often extremely eroded condition of specimens of either species), (4) the presence of ocelli in the pleural areas in *A. gaimardi* (an inconstant feature), not in *A. gemmata,* (5) the smaller average size of *A. gaimardi,* and (6) the geographic distribution.

The differentiation between *Acanthopleura gaimardi* and *A. gemmata* is further complicated by the presence of a "transition" population between the two at their zone of contact, a population here regarded as of a different species, *A. arenosa,* but which further study may prove to be a *gaimardi-gemmata* hybrid (see Remarks on *A. arenosa*).

Liolophura gaimardi platispinosa LELOUP, 1939a:3–7, figs. 2, 5, reported from Japan and Gulf of Tonkin, is here regarded as a *nomen dubium,* because description and illustrations do not permit certain assignment to a known taxon; type material not examined.

Acanthopleura japonica (Lischke, 1873)

Figures 68 to 72, and 115-J

Chiton japonicus LISCHKE, 1873:22–23, 1874:71–72, pl. 5, figs. 8–11.
Chaetopleura japonica: DUNKER, 1882:158.
Acanthopleura japonica: THIELE, 1893:373, pl. 30, fig. 34.
Acanthopleura (Liolophura) japonica: THIELE, 1910a:115.
Liolophura japonica: PILSBRY, 1893c:242–244, pl. 53, figs. 41–44; NIERSTRASZ, 1905b:155, pl. 10, fig. 22; HORST & SCHEPMAN, 1908:528; THIELE, 1929:21; BERGENHAYN, 1933:39–40, pl. 1, fig. 12, pl. 3, figs. 60–67, text figs. 13a–c; IS. TAKI, 1938a:398–404, pl. 15, fig. 3, pl. 32, figs. 15–16, pl. 33, figs. 1–8, pl. 34, figs. 1–4, 1947: 1269, fig. 3606, 1949:287, fig. 904; OKADA *et al.,* 1954: 214, fig. 392; IS. TAKI, 1960:197, pl. 90, fig. 2; LELOUP, 1961:39–42, text figs. 1, 2, 5a, pl. 3, fig. 1; IS. TAKI, 1962:46; IW. TAKI, 1964b:412; VAN BELLE, 1982:473–474; INABA, 1982:32.
[*Non:* NIERSTRASZ, 1905b:155–156, pl. 10, figs. 23–25].

Liolophura japonica tessellata Pilsbry, 1893c:243–244, pl. 53, figs. 45–46.
[*Non:* Horst & Schepman, 1908:528].
Liolophura japonica tenuispinosa Leloup, 1939a:1–3, figs. 1, 3, 4; 1952:59; Van Belle, 1980:33–35.
Liolophura japonica unispinosa Is. Taki, 1962:46 (*nomen nudum*).
Liolophura japonica planispinosa Is. Taki, 1962:46 (*nomen nudum*).
"*Liolophura gaimardi* (Blainville)" Wu, 1969:109, figs. 5a, 5b, 47–58.
Chiton defilippii Tapparone-Canefri, 1874:77; Pilsbry, 1893c:243–244 (as syn. of *Liolophura japonica*).
Nuttallina allantophora Dall, 1919:502; Smith, 1961:82, 1977:253.
[*Non:* "*Nuttallina* sp. cf. *allantophora* Dall, 1919," Steinbeck & Ricketts, 1941:555, pl. 26, fig. 6 (=*Nuttallina crossota* Berry, 1956).]

Type material and type locality:

Chiton japonicus Lischke, 1873: Types unascertained; locality Nagasaki, Japan (32°48′N, 129°55′E).
Liolophura japonica tessellata Pilsbry, 1893c: Lectotype (ANSP 35969) and 2 paralectotypes (ANSP 355873) herein designated; locality Enoshima, Japan (35°18′N, 139°29′E).
Liolophura japonica tenuispinosa Leloup, 1939a: Types unascertained; locality here restricted to Poulo Dama Is., Gulf of Thailand (9°40′N, 104°30′E).
Chiton defilippii Tapparone-Canefri, 1874: Types unascertained; locality Japan.
Nuttallina allantophora Dall, 1919: Holotype (USNM 110360a); locality ? Japan (given in error as "Los Animas Bay," Baja California, Mexico).
Liolophura gaimardi platispinosa Leloup, 1939a: Types unascertained; locality Shikok Kamigari, Toso Pref., Japan.

Material examined:

HONSHU: Japan, Shiriya, Aomori Pref., 2 specimens, largest 48 mm long (LACM 17-82); Takojima, Ishikawa Pref., 1 specimen, 25 mm long (LACM 11-82); Sagami Bay, 21 specimens, largest 37 mm long (CAS 009871; CAS 015103; CAS 12390; CAS 12394; CAS 012395; CAS 012400; CAS 031641; NMV 1026); Awaji, 1 specimen (NMV); Toshijima, Mie Pref., 1 specimen, 48 mm long (UCM 28917); Cape Bansho-zaki, near Seto Marine Biological Station, Wakayama Pref., 20 specimens, largest 47 mm long (LACM 19-82); Wakayama Pref., 2 specimens (*ex* Iw. Taki coll.); Ise Wan, 4 specimens, largest 52 mm long (CAS, acc. no. 1658); Shiju-shima Id., Hiroshima Pref., 2 specimens, largest 62 mm long (*ex* K. Y. Arakawa coll.).
KYUSHU: North Kyushu, 8 specimens, largest 38 mm long (CAS 034180); Taujushima Id., near Amakusa Marine Biological Station, Kumamoto Pref., 4 specimens, largest 60 mm long (LACM 25-82); Amakusa Marine Biological Station, Tamioka Peninsula, 4 specimens, largest 51 mm long (LACM 26-82); Hana, 1 specimen, 18 mm long (CAS 030933); Moji, S of Kabura Shima, 28 specimens, largest 50 mm long (CAS 012370; CAS 012399); Nagasaki, 9 specimens, largest 30 mm long (CAS 012364; CAS 012362; CAS 12362).
SOUTH KOREA: Pusan, 48 specimens, largest 32 mm long (CAS 012396; CAS 034552; CAS 053347); Dadas Po Beach, 15 specimens, largest 35 mm long (CAS 053345); Tanang Mal, 4 specimens, largest 30 mm long (CAS 053346); Seogwipo, 18 specimens, largest 30 mm long (CAS 012391); Chesudo, 1 specimen, 20 mm long (CAS 000973).
HONG KONG: Cheung-Sha, Lantau Id., 1 specimen, 33 mm long (AJF 685); Repulse Bay, Hong Kong Id., 3 specimens, largest 37 mm long (AJF 686).
TAIWAN: Yehliu, Chilung Co., 1 specimen, 57 mm (UCM 27560); Chien-shaw, Pen-hu Co., 3 specimens, largest 23 mm long (UCM 28893).
THAILAND: Sattahip, Gulf of Thailand, 4 specimens, largest 80 mm long (CAS 012397; CAS 030931); Ko-I-lao, 3 specimens, 70 mm long (CAS 012389; CAS 012398); Ko-Phai, 3 specimens, largest 50 mm long (CAS 012358); Ko-Sichang, 14 specimens, largest 55 mm long (CAS 012393; CAS 012403; CAS 012404).

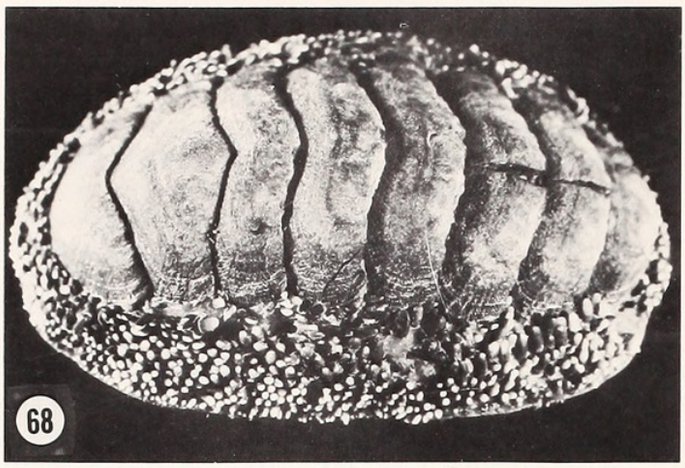
Description: Lischke (1873) described *Chiton japonicus* as "*Testa ovata, parum convexa, atro-fusca, griseo strigata, minutissime rugulosa, granulis parvis concentrice, ad latera interdum radiatim ordinatis sculpta; areae laterales indistinctae; valva postica perbrevis, planata, acutimarginata margo incertus; valvae anticae, incisurisque profundoribus 8 ad 10 irregulariter divisus, valvae posticae integer, valvarum reliquarum minute crenulatus et incisura unica bipartitus; ligamentum spinis calcareis erectis, obtusis, griseis, fuscis et fulvis densissime obtectum; pagina valvarum fusca, paene nigra.—Long. 35, lat. 21 mill.*" (pp. 22–23), distinguishing it carefully from the similar *Chiton spiniger* Sowerby (=*A. gemmata*).

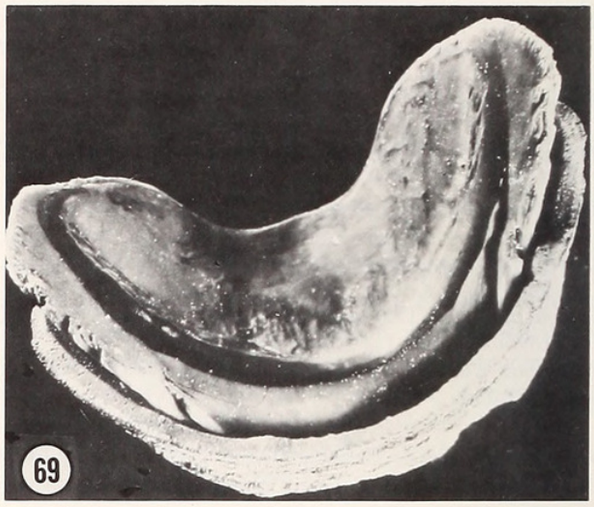
Among 175 specimens of *Acanthopleura japonica* here examined, largest 80 mm long (in alcohol) (CAS 030931: Sattahip, Gulf of Thailand). Body width/length, mean 0.64 (SD = 0.03; n = 10). Tegmentum dark brown. Lateral areas poorly defined, not elevated, sculptured with ill-defined, small granules. Central areas sculptureless except for subdued transverse growth lines. Posterior valve rather flat; mucro poorly defined, posterior to near terminal. Ocelli round to oval, 40–60 μm in diameter, scattered through anterior valve, anterior ⅓ of lateral areas, and postmucro area (Figure 68). Gills with 40–50 plumes per side.

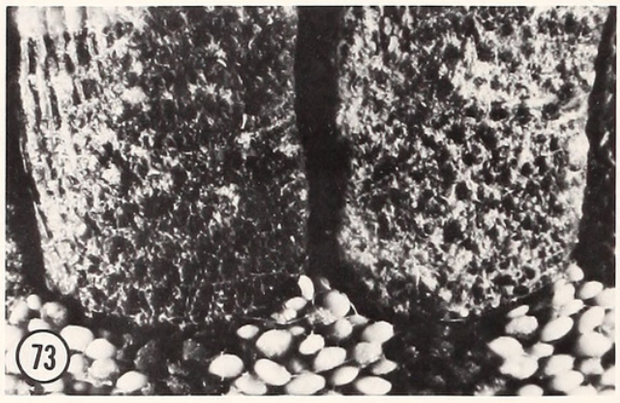
Articulamentum dark brown. Sutural laminae well developed, triangular on valve ii, becoming subrectangular on valve viii. Sinus well defined. Insertion plates pectinate on outside. Posterior valve with no teeth but wide, transverse, flat-surfaced callus (Figure 69); occasionally (particularly in specimens from the Gulf of Thailand), a few, coarse pectinations or teeth seen at outer part of callus (one specimen shows large single tooth in middle of callus). Slit formula 8/11-1-0.

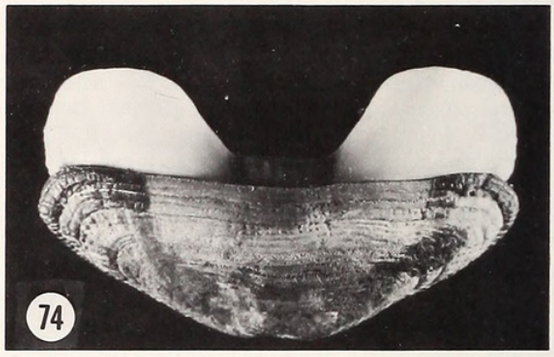
Girdle upper surface often banded brown-white, covered with erect spinelets, all about same size and appearance, usually cylindrical, blunt-ended, white-tipped, up to 700 μm long (Figure 70); in some populations, specimens have variable girdle elements, from "typically" slim and cylindrical spinelets, to flattened, scale-like, imbricate elements (Figure 71). Girdle bridges empty. Undersurface paved with transparent, rectangular to squarish scales, 50 × 40 μm, arranged in rows, with convex outer edge articulating with concave inner edge of adjacent scale.

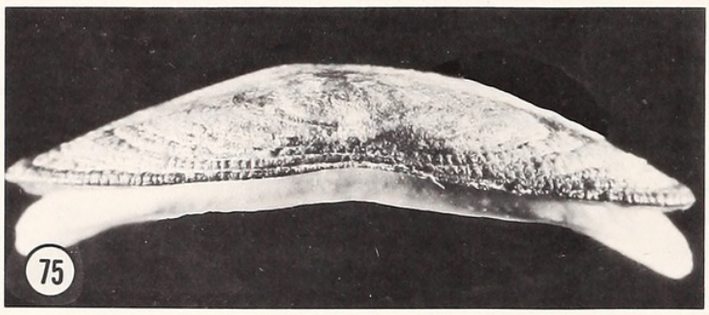
Radula averaging 35% of specimen length and 55 rows

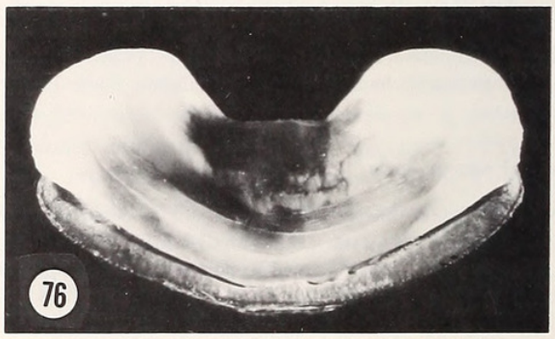












Explanation of Figures 68, 69, and 73 to 76

Figure 68. *Acanthopleura japonica* (Lischke, 1873). Takojima, Ishikawa Pref., Japan Sea, Japan (LACM 82-11); specimen 18 mm long.

Figure 69. *Acanthopleura japonica* (Lischke, 1873). Shiriya. Aomori Pref., Japan (LACM 82-17); specimen 25 mm long. Ventral aspect of posterior valve.

Figure 73. *Acanthopleura hirtosa* (Blainville, 1825). Bremer Bay, W.A., Australia (WAM 47-74); specimen 25 mm long. Close-up of lateral areas of valves iii–iv and girdle.

Figure 74. *Acanthopleura hirtosa* (Blainville, 1825). Cockburn, W.A., Australia (WAM 201-74); specimen 40 mm long. Dorsal aspect of posterior valve.

Figure 75. *Acanthopleura hirtosa* (Blainville, 1825). Same specimen as in Figure 74. Posterior aspect of posterior valve.

Figure 76. *Acanthopleura hirtosa* (Blainville, 1825). Same specimen as in Figure 74. Ventral aspect of posterior valve.

of mature teeth. In a specimen 38 mm long (CAS 012399: Unose Hana, Kyushu, Japan), radula 22 mm in length, comprising 60 rows of mature teeth. Median tooth (Figure 72) 110 μm at anterior blade; first lateral teeth 170 μm wide at anterior blade; head of second lateral teeth discoid, 300 μm in diameter; outer marginal teeth 250 μm long, 230 μm wide (length/width, 1.1).

Distribution: *Acanthopleura japonica* has been recorded at Hakodate, Hokkaido, Japan (41°45′N, 140°43′E) (Is.

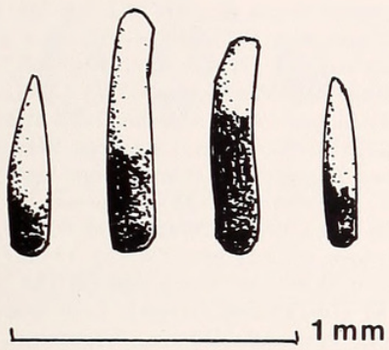


Figure 70

Acanthopleura japonica (Lischke, 1873). Thailand (CAS 018358); specimen 41 mm long. Girdle spines.

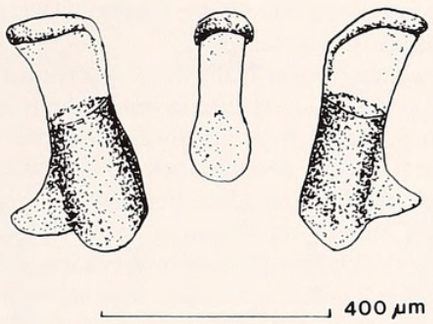


Figure 72

Acanthopleura japonica (Lischke, 1873). Same specimen as in Figure 69. Radula median and first lateral teeth.

Taki, 1938a; Inaba, 1982), its northernmost record, along the coasts of Japan on the Sea of Japan, Inland Sea and Pacific Ocean, to Kyushu, the southern coast of Korea and Cheju-do (Is. Taki, 1938a, 1962), Taiwan (Wu, 1969, as "*Liolophura gaimardi*"), and Hong Kong (22°15′N, 114°10′E) (Van Belle, 1980, 1982; Ferreira, herein). A seemingly disjunct, perhaps relict population is present in the Gulf of Thailand (12°N, 102°E), with records at Poulo Dama Is., Poulo Condor (=Con Son Is.), Cap Saint-Jacques (=Vung-tau), Vietnam (Leloup, 1939a, as *Liolophura japonica platispinosa*), and Sattahip, Thailand (Ferreira, herein) (Figure 115-J). The report of the species in the Moluccas (Nierstrasz, 1905b:155–156, pl. 10, figs. 23–25) is, from the illustrations, in error.

Bathymetric range confined to the intertidal zone, on top of rocks often exposed at low tide.

Remarks: Pilsbry (1893c), segregated *Liolophura japonica tessellata* from the "typical *japonica*" on account of its "much narrower [girdle] . . . conspicuously varied with alternate patches of white and scorched-brown or blackish . . . spinelets [which] are larger . . . [and] vary much in size, being small toward the outer edge of the girdle, large and flattened toward the inner edge . . ." (p. 243). Type material of *L. j. tessellata* (ANSP 35060) consists of 3 dry specimens, curled, soft parts removed, estimated lengths 35–38 mm, eroded; articulamentum black; insertion plate of posterior valves inaccessible for inspection; girdle spinelets as described and illustrated by Pilsbry (1893c). An old museum label on cardboard marked with a red dot to which the specimen had been glued, reads "Type of var. 35969 / *L. Japonica* Lischke. / var. *tessellata* Pils. / Fr. Stearns. Enoshima, Japan." The least eroded specimen is here designated lectotype (ANSP 35969); the other two as paralectotypes (ANSP 355873).

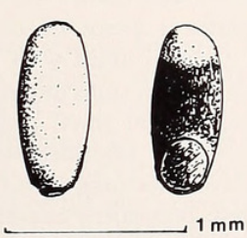


Figure 71

Acanthopleura japonica (Lischke, 1873). Same specimen as in Figure 69. Girdle scale-like spines.

As observed by Taki (1938a:402), *Liolophura japonica* exhibits such wide variations in size, color, and width of girdle spinelets as to render meaningless alleged subspecies based on such variations (yet, Taki [1962] later introduced two such subspecies, *unispinosa* and *planispinosa,* left undescribed). Still, attention must be called to two other phenotypes. Specimens from the Gulf of Thailand differ from those of Japan not only by attaining conspicuously larger sizes, but in the girdle spinelets, which tend to be thinner, clearly cylindrical, closer together, equal-sized, and often white-tipped. Some specimens from Japan (LACM 7-82: Akasaki, Noto Peninsula [37°21.5′N, 137°15′E]; LACM 25-82: Tsujushima Id., Kumamoto [32°33′N, 130°07.7′E]) and from Korea have girdle elements that, being wide, flat, and clearly imbricate, are more properly called scales than spinelets (Figure 71), suggesting a distinct species (perhaps deserving a name such as "*planispinosa,*" left *nudum* by Taki [1938a]) were it not for the presence of spinelets with an intermediate form, and the fact that such specimens do not appear to differ from those of "typical" *Acanthopleura japonica* in any other respect. Further study of these populations is indicated.

Ornithochiton [sic] *caliginosus* Carpenter (*in* Pilsbry, 1893c:243–244, pl. 54, figs. 41–45), based upon specimens from the China Sea and Hong Kong, has been regarded by Kaas & Van Belle (1980) as a synonym of *Acanthopleura japonica.* However, as Taki (1938a:402) pointed out, the specimen illustrated by Pilsbry (1893c) differs from *A. japonica* in the insertion plate of the posterior valve (specimen of *A. loochooana?*). The species-name, unquestionably referring to an *Acanthopleura,* is here suppressed as a *nomen dubium.*

The placement of *Chiton defilippii* in the synonymy of

Liolophura japonica proposed by PILSBRY (1893c) on subjective grounds is here accepted.

Nuttallina allantophora Dall, 1919, was shown to belong in the synonymy of *Liolophura japonica,* the type locality, "Los Animas Bay," Baja California, Mexico, being in error (SMITH, 1977). Examination of color slides of the holotype (CASIZ Color Slide Series Nos. 1992, 1993) substantiates Smith's conclusion.

LELOUP's (1939a) assignment of specimens from Japan and the Gulf of Tonkin to *Liolophura gaimardi platispinosa* and specimens from Indochina and the Gulf of Thailand to *L. japonica tenuispinosa* was left unjustified. The true nature of the former (see Remarks on *Acanthopleura gaimardi*) remains a matter of speculation.

In Hong Kong, *Acanthopleura japonica* is found sharing the intertidal habitat with *A. loochooana* on rocks exposed to mild surf (personal observations, Sept. 1982). In Taiwan, *A. japonica* is sympatric (or at least parapatric) with three other species of *Acanthopleura, A. spinosa, A. loochooana,* and *A. miles.*

Acanthopleura hirtosa (Blainville, 1825)

Figures 73 to 78, and 114-H

Chiton hirtosus BLAINVILLE, 1825:546; PILSBRY, 1894a:106; LAMY, 1923:263.
Acanthopleura (Liolophura) hirtosa: DUPUIS, 1917:533–534.
Liolophura hirtosa: DUPUIS, 1918:531; ASHBY, 1926:384; LELOUP, 1961:44–49, text figs. 4, 5c.
Liolophura (Chiton) hirtosus: ASHBY, 1922b:579–580.
Clavarizona hirtosa: HULL, 1923:199, pl. 28, figs. 9–12; IREDALE & HULL, 1926:261–262, pl. 37, figs. 9–12, 17, 21 (reprinted, 1927:124–125, pl. 15, figs. 9–12, 17, 21).
Liolophura (Clavarizona) hirtosa: THIELE, 1929:21; VAN BELLE, 1983:129–130.
Chiton georgianus QUOY & GAIMARD, 1835:379, pl. 75, figs. 25–30; IREDALE, 1910b:154.
Liolophura georgiana: PILSBRY, 1893c:241–242, pl. 53, figs. 36–40; TORR, 1911:100–101; ASHBY, 1921:45, 1922a: 32.
Acanthopleura (Liolophura) georgiana: THIELE, 1911a:399–400, fig. 3; DUPUIS, 1918:533–534.
Plaxiphora pustulosa TORR, 1911:107, pl. 25, fig. 7.

Type material and type locality:

Chiton hirtosus Blainville, 1825: Type at MHNH (*fide* DUPUIS, 1917; ASHBY, 1922c; LAMY, 1923); locality "mers de l'île King" (in error) corrected to King George Sound, Western Australia (35°03'S, 117°57'E) (ASHBY, 1922c; IREDALE & HULL, 1926).

Chiton georgianus Quoy & Gaimard, 1835: Syntypes (4) at MNHN (*fide* ASHBY, 1922c); locality "port du Roi-Georges," Western Australia (35°03'S, 117°57'E).

Plaxiphora pustulosa Torr, 1911: Type "in coll. Torr" (*fide* IREDALE & HULL, 1926); locality Albany, Western Australia (35°02'S, 117°53'E).

Material examined:

AUSTRALIA, W.A.: Cape Cuvier, 1 specimen, 20 mm long (WAM 48-74); Point Quobba, 2 specimens, largest 35 mm long (WAM 43-74); Point Gregory, Peron Peninsula, Shark Bay, 3 specimens, largest 50 mm long (WAM N4726); Shark Bay, 1 specimen, 30 mm long (WAM 714-79); Dick Hartog Id., 1 specimen disarticulated (NMV, *ex* Ashby coll.); Kalbarri, 1 specimen, 35 mm long (WAM 1864-67, WAM-USNM Barrow Is. Exped., 18 August 1966); Abrolhos Is., 1 specimen, 40 mm long (AMS C31530); Geraldton, 1 specimen 30 mm long (WAM 7125); Dongara, 10 specimens, largest 30 mm long (WAM 6021); "W. Austr.," 2 specimens (NMV); Carnac Is., 3 specimens, largest 55 mm long (WAM 50-74; WAM 704-79); Leighton, 2 specimens, largest 40 mm long (WAM 13446/7); Cockburn Sound, 6 specimens, largest 60 mm long (WAM 200-74; WAM 201-74; WAM 476-74); Port Gregory, 1 specimen, 40 mm long (WAM 46-74); Fremantle District, 1 specimen, 20 mm long (AMS C31531); Fitzgerald Inlet, 2 specimens (WAM 42-74); Point Peron, 4 specimens, largest 60 mm long (WAM 45-74; WAM 278/9-1938); Bunbury, 1 specimen, 20 mm long (WAM 49-74); Lucky Bay, 1 specimen, 50 mm long (WAM 710-79); Geographe Bay, 3 specimens, largest 30 mm long (AMS C18012); Cottesloe, 1 specimen, 24 mm long (NMV); Bunker Bay, 1 specimen, 40 mm long (WAM 713-79); Rottnest Id., 1 specimen 35 mm long (AMS C32119); Foul Bay, 1 specimen (AMS C121194); Garden Id., 2 specimens, largest 45 mm long (WAM 706-79, with label "ident. as *Liolophura gaimardi* by E. Ashby"); Coweramup Bay, 1 specimen, 40 mm long (WAM 705-79); Augusta, 1 specimen, 50 mm long (WAM 708-79); Cape Leeuwin, 1 specimen disarticulated (NMV, *ex* Gatliff coll.); Nornalup, 2 specimens, largest 50 mm long (WAM 15568/69, *leg.* E. Ashby, August 1929); King George Sound, 8 specimens, largest 56 mm long (NMV, *ex* Basset Hull coll.); King George Sound, 5 specimens (NMV); Middleton Beach, King George Sound, 1 specimen, 42 mm long (AMS C69338); Albany, 4 specimens, largest 40 mm long (WAM N3272); Frenchman's Bay, 1 specimen, 25 mm long (WAM 707-79); Bremer Bay, 4 specimens, largest 40 mm long (WAM 47-74); Hopetown, 2 specimens, largest 17 mm long (WAM 495-74); Esperance, 1 specimen, 37 mm long (WAM 51-74); Seven Mile Beach, Esperance, 6 specimens, largest 40 mm long (NMV); Dempster Head, Esperance (NMV, *ex* Basset Hull coll.); Duke of Orleans Bay, 1 specimen, 40 mm long (WAM 709-79); Wilson Id., 1 specimen, 40 mm long (WAM); Mondrain Id., 5 specimens, largest 70 mm long (WAM 44-74; WAM 712-79).

Description: *Acanthopleura hirtosa* is adequately characterized in the descriptions of BLAINVILLE (1825), PILSBRY (1893c), and IREDALE & HULL (1926).

Among 96 specimens of *Acanthopleura hirtosa* here examined, largest 70 mm long (dry) (WAM 44-74: Mondrain Id.). Body width/length, mean 0.62. Tegmentum olive-green to brown, often with black patches and whitish band in jugal area. Anterior valve covered with round granules which tend to align in radial rows. Lateral areas of intermediate valves moderately elevated, with somewhat elongate granules in about 10–15 ill-defined radial rows (Figure 73). Central areas with transverse, juxtaposed lamellae on jugal area superimposed by round granules in parallel longitudinal rows, particularly well defined on pleural areas. Intermediate valves beaked; posterior edge of valve ii forming 100–110° angle. Mucro posterior to terminal; postmucro convex, sharply sloped. Ocelli round to oval, 20–50 μm in diameter, throughout anterior valve, postmucro area of posterior valve, and anterior ½ of lateral areas of intermediate valves. Widths of tegmental surfaces of valves i/viii, mean 1.17. On valve i,

Figure 77

Acanthopleura hirtosa (Blainville, 1825). Bayonet Head, Albany, W.A., Australia (WAM N3272); specimen 32 mm long. Girdle scales.

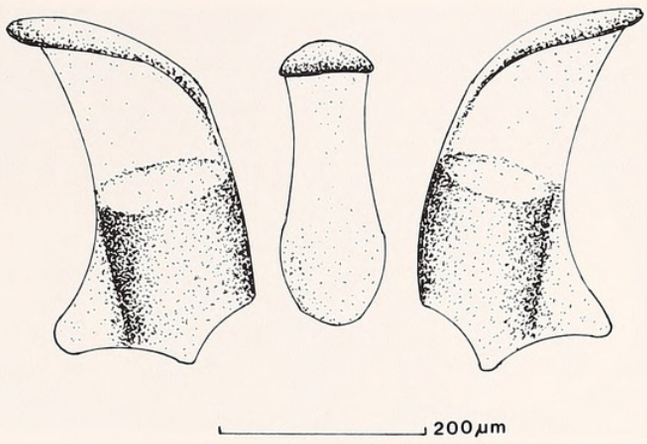


Figure 78

Acanthopleura hirtosa (Blainville, 1825). Same specimen as in Figure 77. Radula median and first lateral teeth.

tegmentum length/width, mean 0.51. Posterior valve somewhat triangular in outline (Figure 74); tegmentum length/width, mean ratio 0.38; articulamentum not wider than tegmentum. Eaves thick (0.5 mm in midline of valve viii of specimen 32 mm long), somewhat spongy. Gills with 25–35 plumes per side.

Articulamentum dark brown and white. Sutural laminae well developed, subtriangular on valve ii to subrectangular on valve viii. Insertion plates pectinate on outside. On valve i, insertion plate hardly extends beyond tegmental surface (measured in midline, length of insertion plate/length of tegmental surface, mean ratio, 0.10). On valve viii, insertion plate absent but with conspicuous, toothless, flat, wide callus (Figures 75, 76). Slit formula 8/11-1-0.

Girdle banded black-white in most specimens; at valve iv, girdle width up to 36% of width of valve in alcohol preserved specimens. Upper surface covered with calcareous, somewhat conical scales (Figure 77), irregular in size, averaging 400 μm in length, 500 μm in height, 200 μm in thickness, with 8–12 fine, converging striae; clusters of 3–8 relatively opaque spicules 100–200 μm long, 20–30 μm thick, may be seen amidst scales. Girdle bridges empty. Undersurface covered with transparent, subquadrangular scales, 60 × 50 μm, vaguely striate.

In specimen 40 mm long (WAM 201-74: Cockburn, SW Australia), radula measures 22 mm in length (55% of specimen length), comprising 68 rows of mature teeth. Median tooth (Figure 78) 100 μm wide at anterior blade; first lateral teeth 150 μm wide at anterior blade; head of second lateral teeth discoid, 260 μm in diameter; outer marginal teeth 270 μm long, 190 μm wide (length/width, 1.4).

Distribution: *Acanthopleura hirtosa* is confined to southwestern Australia (Figure 114-H) from Cape Cuvier (WAM 48-74) (24°14′S, 113°22′E), the northernmost verified record, to Mondrain Id., Recherche Arch. (WAM 44-74; WAM 712-19) (34°08′S, 122°15′E), the easternmost verified record on the south coast of Australia. Hull (1923) recorded the species from Point Cloates to Eyre.

Bathymetric range 0–2 m.

Remarks: *Acanthopleura hirtosa* is the only species of the genus in southwestern Australia. It is remarkably similar to *A. gaimardi* from which it mainly differs in the girdle elements—conical scales in *A. hirtosa,* spinelets in *A. gaimardi.* Hull (1923) separated the two species at the generic level, erecting *Clavarizona* for *hirtosa,* but his action was refuted by Ashby (1926) and Leloup (1961). Smith (1960:67) placed *Clavarizona* in the synonymy of *Liolophura.*

Acanthopleura ***arenosa*** Ferreira, spec. nov.

Figures 79 to 85, and 114-A

Diagnosis: Specimens quite similar to those of *Acanthopleura gaimardi* except for a moderately inflated (*i.e.,* not as flat) posterior valve, with a rounder posterior edge, and insertion teeth definitely present although underdeveloped to obsolete.

Type material:

Holotype (CAS 044305) and 11 paratypes (CAS 044304; BMNH 1985065; USNM 848001; ANSP A10648; LACM 2107; AJF coll.).

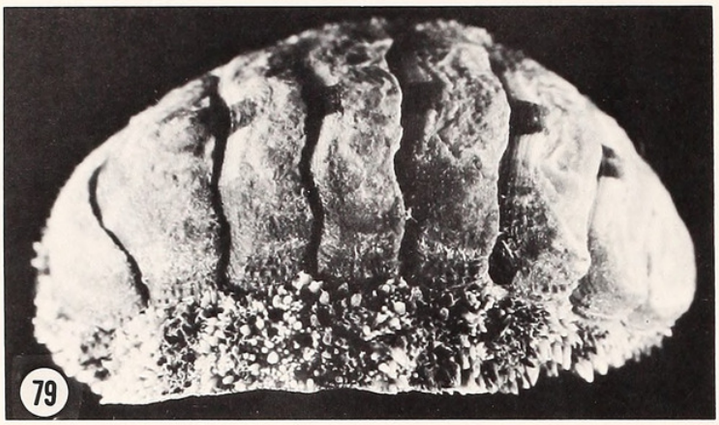
Type locality:

Pebbly Beach (about 25 km south of Port Douglas), Queensland, Australia (16°35′S, 145°22′E), 0.5 m below to 1 m above low tide water (AJF 604, *leg.* A. J. Ferreira & Sandy Motley, 14 Aug. 1981).

Other material:

AUSTRALIA, Qld.: Buchan's Point (30 km N of Cairns), 0 to 1 m above low tide water, 4 specimens, largest 25 mm long (AJF 605); Trinity Beach (some 15 km N of Cairns), 0 to 1 m above low tide water, 4 specimens, largest 28 mm long (AJF 606).

Description: Holotype (Figures 79, 80) preserved in alcohol, intact (except for disarticulated posterior valve), somewhat curled, 22 m long (if flattened), 14 mm wide (including girdle); dark brown on side, and well defined jugal band, whitish otherwise; valves somewhat beaked, round-backed. Tegmentum eroded at apex of valves; an-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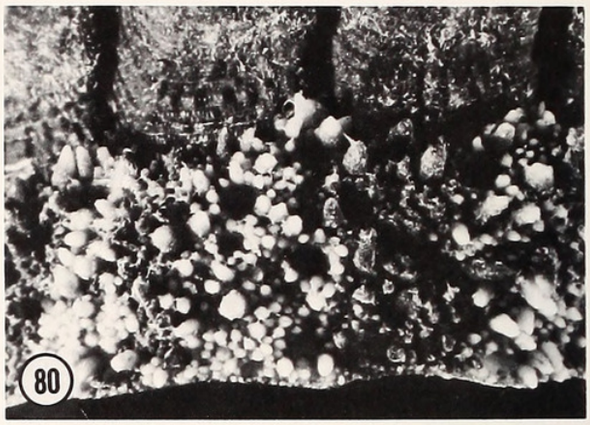
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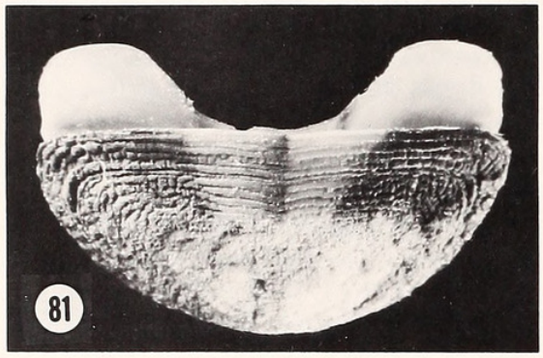
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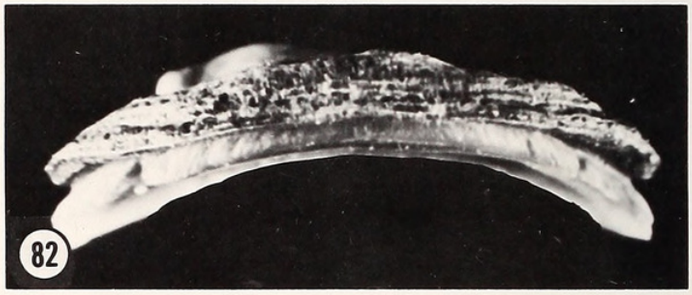
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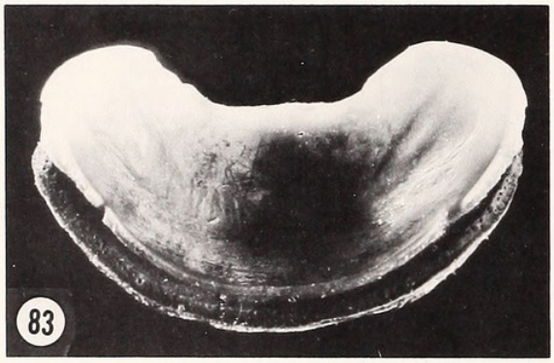
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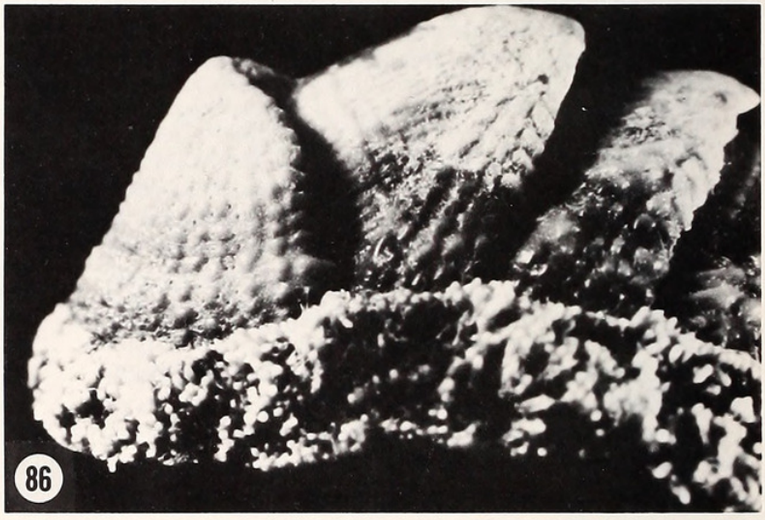
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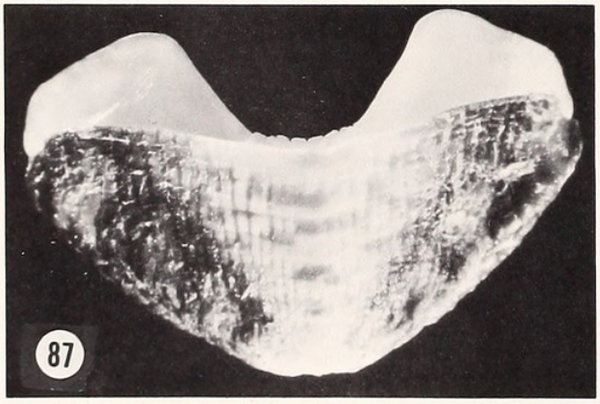
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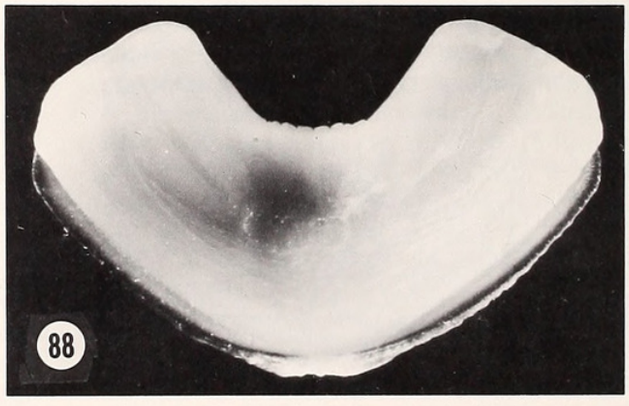
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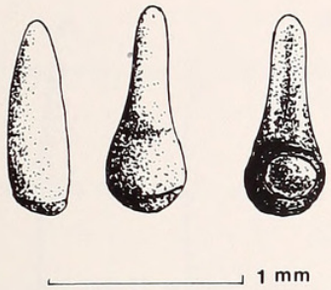


Figure 84

Acanthopleura ***arenosa*** Ferreira, spec. nov. Paratype (AJF coll.), 24 mm long. Girdle spinelets, outer and inner sides.

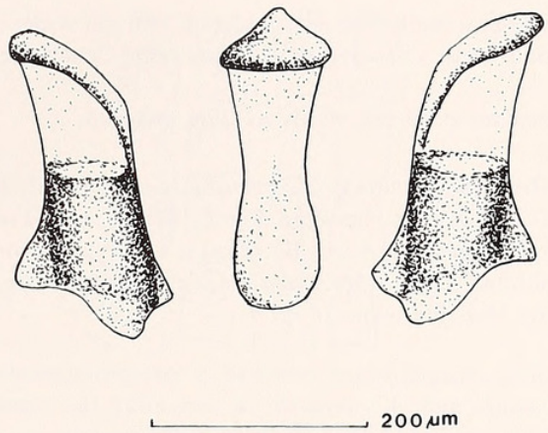


Figure 85

Acanthopleura ***arenosa*** Ferreira, spec. nov. Same paratype as in Figure 84. Radula median and first lateral teeth.

terior valve with roundish, poorly defined granules; lateral areas slightly elevated, with similar granules; central areas with weak, transversely appressed lamellae; posterior valve with tegmental surface semicircular, 7.5 mm wide, 3.6 mm long, with mucro (eroded) slightly post-central; gills holobranchial. Articulamentum of disarticulated posterior valve dark brown in middle, white at sutural laminae; sutural laminae subrectangular, about 2.8 mm wide, 1.5 mm long; sinus well defined, smooth, about 1.5 mm wide at anterior edge of tegmental surface; insertion plate reduced to transverse, roundish callus, pectinations clearly cut in outer ⅓ but progressively ill-defined to absent in middle ⅓, showing symmetrical slit on each side; eaves solid. Girdle banded black and white, crowded with pointed but short spinelets.

Paratypes (Figures 81–83) dark brown, most with brown jugal band flanked by white areas; largest 30 mm long (live). Body width/length, 0.65. Valves beaked, round-backed. Anterior valve with concentric rows of small, irregular, round to ovate granules 100–200 µm in diameter. Lateral areas poorly defined, hardly raised, similarly sculptured. Central areas (markedly eroded) featureless except for ill-defined, appressed, transverse lamellae. Posterior valve somewhat inflated (*i.e.,* not flat), with semicircular posterior edge; mucro not prominent, central to slightly posterior; postmucro convex, sloping. On valve i, tegmentum length/width, 0.5. On valve viii, tegmentum length/width, 0.4. Widths of tegmental surfaces of valves i/viii, 1.1. Ocelli round to oval, 50–60 µm in diameter. Gills with 30–35 plumes per side.

Articulamentum brown to bluish-white. Sutural laminae well developed, subtriangular to subrectangular; sinus well formed; sinusal plate smooth; relative width of sinus, 0.6. Insertion plates strongly pectinate on outside. On valve i, insertion teeth irregularly spaced; in midline, length of insertion teeth/length of tegmentum, 0.18. On valve viii, pectinations and insertion teeth extremely subdued, vestigial to absent in middle ⅓; single, well cut, symmetrical slits on each outer ⅓. Slit formula 9/10-1-2. Eaves thick (0.5 mm on midline of valve viii), somewhat spongy.

Girdle thick, musculous, banded blackish-brown and white. Upper surface with calcareous spinelets (Figure 84), somewhat pointed, straight to slightly curved, conical in outline, up to 1000 µm high, 300 µm thick at base. Undersurface with transparent scales, vaguely striate, squarish (40 × 35 µm) to elongate (60 × 30 µm) at periphery.

In paratype (AJF coll.) 24 mm long, radula 9 mm long (45% of specimen length), comprising 45 rows of mature teeth. Median tooth (Figure 85) 70 µm wide at anterior blade; first lateral teeth 120 µm wide at anterior blade;

←

Explanation of Figures 79 to 83 and 86 to 88

Figure 79. *Acanthopleura* ***arenosa*** Ferreira, spec. nov. Holotype (CAS 044305).

Figure 80. *Acanthopleura* ***arenosa*** Ferreira, spec. nov. Holotype (CAS 044305). Close-up of lateral areas of valves iii–v and girdle.

Figure 81. *Acanthopleura* ***arenosa*** Ferreira, spec. nov. Paratype (AJF coll.), 20 mm long. Dorsal aspect of posterior valve.

Figure 82. *Acanthopleura* ***arenosa*** Ferreira, spec. nov. Same paratype as in Figure 81. Posterior aspect of posterior valve.

Figure 83. *Acanthopleura* ***arenosa*** Ferreira, spec. nov. Same paratype as in Figure 81. Ventral aspect of posterior valve.

Figure 86. *Acanthopleura* ***rehderi*** Ferreira, spec. nov. Holotype (USNM 842113).

Figure 87. *Acanthopleura* ***rehderi*** Ferreira, spec. nov. Paratype (USNM 842114). Dorsal aspect of posterior valve.

Figure 88. *Acanthopleura* ***rehderi*** Ferreira, spec. nov. Same paratype as in Figure 87. Ventral aspect of posterior valve.

major lateral teeth with discoid head, 180 μm wide; outer marginal teeth 150 μm long, 140 μm wide (length/width, 1.1).

Other material essentially as type material.

Distribution: *Acanthopleura* ***arenosa*** is known only from the 80 km of coast between Peebly Beach and Trinity Beach, Queensland, Australia (Figure 114-A). Specimens are confined to the intertidal zone, exposed on rocks 0–1 m above low-tide water level.

Remarks: *Acanthopleura* ***arenosa*** is extremely similar to *A. gemmata* and *A. gaimardi*; in fact, only the posterior valve shows reliable distinctions in configuration and particularly in the characteristics of its insertion plate. The posterior valve of *A.* ***arenosa*** differs from that of *A. gaimardi* in being rounder (*i.e.*, not subtriangular), somewhat inflated (*i.e.*, not as flat), with central to moderately posterior (*i.e.*, not as terminal) mucro, and in the presence of insertion teeth and pectinations (completely absent in *A. gaimardi*) at the outer ⅓ of the insertion plate; and it differs from that of *A. gemmata* in the underdevelopment (to obsolescence) of the insertion teeth. Otherwise, specimens of *A.* ***arenosa*** conform well with what *gemmata-gaimardi* hybrids might be expected to be. Since, in addition, specimens of ***arenosa*** have been found exclusively in the zone of contact and overlap between *A. gemmata* and *A. gaimardi*, the possibility that they might be part of a hybrid population must be considered.

Hybridization in mollusks has been known in a few instances—in the prosobranch gastropods *Cypraea* (Schilder, 1962) and *Haliotis* (Owen, 1961; Owen *et al.*, 1971), the pulmonate gastropod *Cerion* (Mayr & Rosen, 1956), and the pelecypods *Ostrea (Crassostrea)* (Davis, 1950; Imai & Sakai, 1961), *Pinctada* (Matsui, 1958), *Mercenaria* (Menzel, 1962; Menzel & Menzel, 1965), and *Tellina* (Boss, 1964)—but not in chitons. Thus, unless further investigation should show otherwise, it seems appropriate to treat this population as a new species, which, judging from the abundance and relative uniformity of its specimens at the localities studied, is viable and self-reproductive.

The species is here named ***arenosa*** for the sandy beaches where it was found, and after Cecily "Sandy" Motley, Davis, California, who assisted in the collecting.

Acanthopleura ***rehderi*** Ferreira, spec. nov.

Figures 86 to 92, and 113-R

Diagnosis: Specimens small (to 2 cm) for the genus. Anterior valves with radial rows of round tubercles alternating with rows of ocelli. Lateral areas similarly sculptured. Central areas with well defined, parallel, longitudinal riblets. Posterior valve flat, subtriangular, mucro posterior to terminal. Slit formula 8/9-1-0. Girdle with spinelets. Radula with 4-cuspid major lateral teeth.

Type material:

Holotype (USNM 842113) and paratypes (USNM 842114; CAS 060405).

Type locality:

Palmerston Id., Cook Islands (18°04'S, 163°10'W).

Other material:

NIUE: Avatolo, 1 specimen, ca. 22 mm long, *leg.* R. Sixberry (USNM 685399); Alofi, 2 specimens, largest ca. 18 mm long, *leg.* R. Sixberry (USNM 685343).

Description: Holotype (Fig. 86), well preserved, dry, moderately curled, estimated 18 mm long (if flattened), 10 mm wide (including girdle), 4 mm high. Valves subcarinate, posterior edge beaked and angled at about 150°. Tegmentum (somewhat eroded) light tan with grayish-green suffusions towards margin and brown stripe along jugal area. Anterior valve with about 24 radial rows of ground granules. Lateral areas of intermediate valves raised, with 3 or 4 similar rows of round granules better defined at sutural edge, rendering it crenulate. Central areas with 18–20 longitudinal, parallel riblets, close together, as wide as interstices in between. Posterior valve rather flat, subtriangular; mucro posterior, almost terminal, somewhat pointed. Ocelli mostly oval, 50–60 μm maximum diameter, aligned in radial rows on anterior valve and most of lateral areas. Gills with 35–40 plumes per side.

Girdle upper surface covered with white, calcareous spinelets, close together, rather uniform in size, up to 700 μm long, 130 μm thick.

Paratypes quite similar to holotype. Disarticulated paratype (Figures 87, 88) ca. 20 mm long: Articulamentum white with brown discolorations at apex of valves; tegmentum reflected forward along posterior edge of valves; width of valve i/width of valve viii, 6.6 mm/6.2 mm = 1.1; sinus well defined, wide, deep, with pectinate sinusal plate; sutural laminae subrectangular; insertion plates pectinate on outside; slit formula 8-1-0; posterior valve with no teeth but well developed callus. Girdle upper surface with regular, straight, gently tapered, calcareous spinelets (Figure 89), mostly white, up to 900 μm long, 140 μm thick, with transverse "growth" striations and relatively abundant, glassy, sharply pointed spicules, up to 200 × 15 μm, scattered in between. Undersurface covered with transparent, rectangular, coarsely striate scales (Figure 90), about 40 × 30 μm, each with convex outer side that articulates into concave inner side of adjacent scale. Radula 5 mm long (25% of specimen length), comprising 45 rows of mature teeth; median teeth (Figure 91) elongate, 40 μm wide at anterior blade; first lateral teeth with elongate, bladed, anterolateral corner; second lateral teeth with basically discoid head, 140 μm wide, but with four short, rounded cusps (unique feature among *Acanthopleura*); spatulate teeth (Figure 92) with subrectangular spatula; outer marginal teeth elongate, 125 × 80 μm.

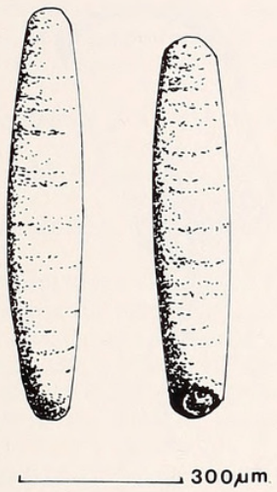


Figure 89

Acanthopleura ***rehderi*** Ferreira, spec. nov. Same paratype as in Figure 87. Girdle spinelets.

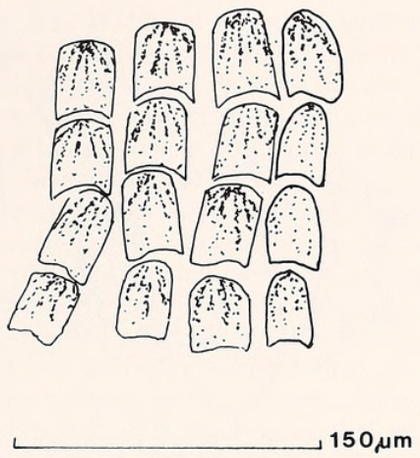


Figure 90

Acanthopleura ***rehderi*** Ferreira, spec. nov. Same paratype as in Figure 87. Girdle undersurface scales.

Specimens from Niue (USNM 685399; USNM 685343) agree in every respect with the types except for the slit formula, 9-1-0, of an 18 mm long specimen.

Distribution: The species is known only from Palmerston, Cook Islands ("outside reef nr. village," *leg.* R. Sixberry), type locality, and Niue (19°02'S, 169°52'W) (Figure 113-R), presumably in the intertidal zone.

Remarks: The specimens here referred to *Acanthopleura* ***rehderi*** are clearly distinct from those of *A. nigropunctata* Carpenter, 1865, described from the nearby Society Islands. Examination of the lectotype (USNM 19297) of the latter, here designated—an incomplete specimen missing valves vii and viii but conforming well to CARPENTER's (1865) account of *nigropunctata,* which indicated the presence of slits in the posterior valve—corroborated its current generic assignment (since Carpenter *in* PILSBRY, 1893b:207) to *Tonicia.*

Acanthopleura ***rehderi,*** like *A. japonica, A. hirtosa, A. gaimardi,* and *A. nigra,* has no insertion teeth in the posterior valve, and, as such, it would fit in *Liolophura* Pilsbry, 1893a. However, despite articulamental similarities, *A.* ***rehderi*** clearly differs from the other four "*Liolophura*" in tegmental sculpture, girdle elements, and, above all, in its unique radula.

The radula of *Acanthopleura* ***rehderi*** with 4-cuspid major lateral teeth constitutes a departure from all congenerics (and, to my knowledge, from all other chitonids), although the cusps seem to be based upon (or cut into) the discoid head characteristic of *Acanthopleura.* The possible evolutionary significance of such a radular modification is unknown, but it is tempting to speculate that it may represent an adaptive response to a new set of dietary conditions, perhaps presaging a new line of speciation. The question deserves further investigation.

The species is here called ***rehderi*** after Dr. Harald A. Rehder, Professor Emeritus, National Museum of Natural History (Smithsonian Institution), Washington, D.C., who generously provided the specimens for study.

Acanthopleura granulata (Gmelin, 1791)

Figures 93 to 97, and 113-G

Chiton granulatus GMELIN, 1791:3205; WOOD, 1815:9; BLAINVILLE, 1825:545; ORBIGNY, 1853:200.

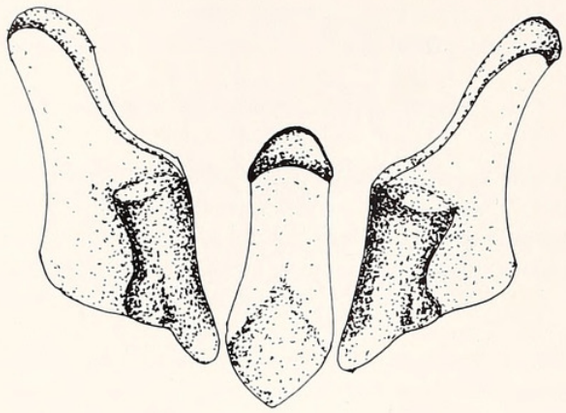
Acanthopleura granulata: HADDON, 1886:24–28; PILSBRY, 1893c:227–230, pl. 50, figs. 39–49 (in subgen. *Maugeria*; DAUTZENBERG, 1900:220–221; DALL & SIMPSON, 1901:454; HAMILTON, 1903:138; NIERSTRASZ, 1905a: 102, 1905b:152 (in part); HORST & SCHEPMAN, 1908: 527 (in part); THIELE, 1909:3, 1910b:112; REMINGTON, 1922:121; BERRY, 1925:173–175, pl. 12, figs. 1, 2; (?) PEILE, 1926:74; NIERSTRASZ, 1927:163; THIELE, 1929: 21; HUMMELINCK, 1933:303, 306; JOHNSON, 1934:14; LELOUP, 1937a:146–150, figs. 13–15a (in part), 1941: 44–45, pl. 1, fig. 1; SALISBURY, 1953:42; HIDALGO, 1956: 4–8, pls. 3, 4; OLSSON & MCGINTY, 1958:23; LEWIS, 1960:398, 410, fig. 8; WARMKE & ABBOTT, 1961:220, fig. 33f; CONDE, 1966:287; ALTENA, 1969:37; GLYNN, 1970:1–21; KAAS, 1972:117–122, text figs. 239–244, pl. 9, figs. 1–3; GÖTTING, 1973:251, text fig. 2, pl. 11, fig. 14; ABBOTT, 1974:406, fig. 4755; BABOOLAL *et al.,* 1981: 43, fig. 5; MOOK, 1983:101–105.
[*Non:* SUTER, 1905:70, 1913:44–45, 1915, pl. 2, fig. 21, pl. 5, fig. 2.]

Chiton piceus GMELIN, 1791:3205; BLAINVILLE, 1825:545; SOWERBY, 1840b:1, 10, sp. no. 10, fig. 147; SAUSSAYE, 1853:416; SHUTTLEWORTH, 1853:78–79 (in subgen. *Acanthopleura*); SCHIFF, 1858:12–47, pls. 1–2.
[*Non:* REEVE, 1847, pl. 13, sp. & fig. 70; ANGAS, 1867: 223.]

Acanthopleura picea: MOSELEY, 1885:18, pl. 6, figs. 8, 9; DALL, 1889:174; THIELE, 1893:373, pl. 30, fig. 32.

Chiton salamander SPENGLER, 1797:80–81.

Acanthopleura salamander: THIELE, 1893:373, pl. 30, fig. 35.



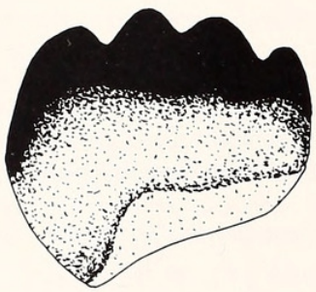


Figure 91

Acanthopleura ***rehderi*** Ferreira, spec. nov. Same paratype as in Figure 87. Radula median tooth, first lateral teeth, and head of major lateral tooth.

Chiton convexus Blainville, 1825:544.
Chiton occidentalis Reeve, 1847, pl. 14, sp. & figs. 76; Saussaye, 1853:416.
Chiton (Acanthopleura) mucronulatus Shuttleworth, 1853: 79.
Acanthopleura granulata mucronulata: Dall & Simpson, 1901: 454.
Chiton (Acanthopleura) blauneri Shuttleworth, 1856:170–171.

Type material and type locality:

Chiton granulatus Gmelin, 1791: Based upon Chemnitz, (1785:fig. 806); locality "Oceano americano" (St. Thomas, West Indies, Caribbean Sea).
Chiton piceus Gmelin, 1791: Based upon Chemnitz (1785: figs. 807, 810); locality "mari americano & rubro" (St. Thomas, West Indies, Caribbean Sea).
Chiton salamander Spengler, 1797: Based upon Chemnitz (1785:fig. 806); locality St. Thomas, West Indies.
Chiton convexus Blainville, 1825: Types unascertained; locality "mers de l'archipel american."

Figure 92

Acanthopleura ***rehderi*** Ferreira, spec. nov. Same paratype as in Figure 87. Radula spatulate tooth.

Chiton occidentalis Reeve, 1847: Types unascertained; locality "Savannah-le-mer, West Indies."
Chiton (Acanthopleura) mucronulatus Shuttleworth, 1853: Types unascertained; locality Puerto Rico, West Indies.
Chiton (Acanthopleura) blauneri Shuttleworth, 1856: Types unascertained; locality Puerto Rico, West Indies.

Material examined:

BAHAMAS: Grand Bahamas Id., 15 specimens (AJF coll., *leg.* A. J. Ferreira *et al.*, May 1971); Bimini Id., 15 specimens, largest 86 mm long (AJF 290; AJF 291); Long Island, 10 specimens (AJF 248); San Salvador Id., 15 specimens (AJF 439); New Providence Id., 24 specimens (CAS 010094); Nassau, 4 specimens, largest 40 mm long (CAS 034777); Chub Cay, 2 specimens, largest 8 mm long (IRCZM 61:066); Gun Cay, 3 specimens, largest 65 mm long (IRCZM 61:016).
FLORIDA KEYS: Bonefish Key, 18 specimens (AJF 426); Crawl Key, 2 specimens, largest 60 mm long (CAS 012259); between Windley and Plantation Keys, 4 specimens, largest 80 mm long (IRCZM 61:010).
BONAIRE: 50 specimens (AJF 210; AJF 208; AJF 264).
CURAÇAO: 20 specimens (AJF 260; AJF 263).
PANAMA: Galeta, 2 specimens (AJF coll., *leg.* H. Bertsch, Sept. 1974; IRCZM 61:013); Bocas del Toro, 10 specimens (AJF 216); Caledonia Bay, 5 specimens (LACM-AHF A 1-39).
HONDURAS: Roatan Id., 24 specimens, largest 74 mm long (AJF 309; CAS 012137; CAS 012138; CAS 012148; CAS 012149; CAS 021294).
NICARAGUA: Corn Id., 3 specimens (AJF coll., *leg.* B. Keagan, Sept. 1975).
JAMAICA: Montego Bay, 20 specimens (AJF 253; AJF 254); Negril, 10 specimens (AJF 256).
DOMINICAN REPUBLIC: Caracoles, 8 specimens (AJF coll., *leg.* B. Keagan, Jan.–Oct. 1976); Playas Bayabibe, 1 specimen (AJF coll., *leg.* B. Keagan, Sept. 1977).

BRITISH VIRGIN ISLANDS: Virgin Gorda Id., 1 specimen (AJF 297); Cooper Id., 4 specimens (AJF coll., *leg.* S. Motley, Feb. 1983); Peter Id., 3 specimens (AJF coll., *leg.* S. Motley, Feb. 1983).
ANTIGUA: 14 specimens (CAS 012135; CAS 012136; CAS 012150).
ST. LUCIA: Pigeon Id., 2 specimens (AJF coll., *leg.* B. Keagan, May 1977).
DOMINICA: Anse de Mai, 3 specimens (AJF coll., *leg.* B. Keagan, May 1977).
VENEZUELA: Puerto Mara, 2 specimens (AJF 347); Tortuga Id., 5 specimens, largest 102 mm long (LACM-AHF A20-39).
CAYMAN ISLANDS: Grand Cayman Id., 34 specimens, largest 65 mm long (AJF 420; AJF 421; IRCZM 61:030; IRCZM 61:031); Cayman Brac, 5 specimens (AJF 424).
TURK & CAICOS: Grand Turk Id., 20 specimens (AJF 443; AJF 444).
MEXICO: Cozumel Id., 35 specimens (AJF 511; AJF 512; AJF 514).
TOBAGO: Courland Point, 6 specimens (AJF 670); Bateau Bay, 2 specimens (AJF 672); Mt. Irvine Bay, 8 specimens (AJF 674); Store Bay, 12 specimens, largest 52 mm long (AJF 678).
BARBADOS: Paradise Beach, 6 specimens (AJF 679); River Bay, 5 specimens (AJF 680); St. Lawrence, 1 specimen, 50 mm long (AJF 684); Bathsheba, 4 specimens, largest 39 mm long (CAS 012260).
TRINIDAD: Maracas Beach, 3 specimens, largest 39 mm long (AJF 668).

Description: Because there is only one *Acanthopleura* in the Caribbean, GMELIN's (1791) description of *Chiton granulatus* in "Oceano Americano," based upon a figure in CHEMNITZ (1758:fig. 806), has proved adequate to identify the species: "*Ch. piceus supra planus, punctis elevatis numerosis in series digestis, limbo lato coriaceo spinoso; areis nigris albisque alternis.*" The species has been repeatedly described by authors working with the Caribbean chiton fauna, and little remains to be added to such accounts (*e.g.,* KAAS, 1972).

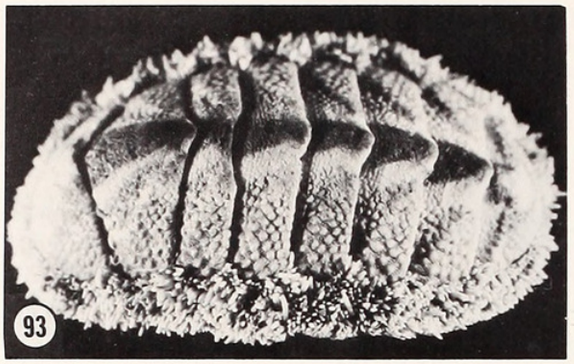
Among 472 specimens of *Acanthopleura granulata* examined, largest 102 mm long (in alcohol) (LACM-AHF A 20-39: Tortuga Id.,Venezuela). Body width/length, mean 0.64. Specimens (Figure 93) depressed, round-backed, large, beaked; posterior edge of valve ii forming 100–120° angle. Tegmentum grayish-green to grayish-brown, often with dark longitudinal stripe in midline. Lateral areas poorly defined, hardly raised, sculptured with low, mostly round, coarse granules; anterior valve and postmucro area of posterior valve similarly sculptured. Central areas almost featureless except for smaller to obsolete granules in pleural areas, and thin, ill-defined, transverse lamellae appressed across jugal areas. Mucro central (in young specimens) to somewhat posterior (in older, larger ones); postmucro strongly convex, at 30–90° slope. Ocelli round to oval, 50–70 μm in diameter, throughout anterior valve, postmucro area of posterior valve, and anterior ⅓ to ⅘ of lateral areas of intermediate valves. On valve i, length of tegmentum/width of tegmentum, mean 0.6. On valve viii, articulamentum not wider than tegmentum; length of tegmentum/width of tegmentum, mean 0.6. Widths of tegmental surfaces of valves i/viii, mean 1.2. Gills with 40–80 plumes per side.

Articulamentum blue to blue-green, often with purplish-brown spot at apex of valves. Sutural laminae well developed, relatively long, subtriangular on valve ii to subrectangular on valve viii. Sinus well formed; sinusal plate mostly smooth; relative width of sinus on valve viii, 0.7. Insertion teeth irregularly spaced, sometimes fused together; in midline, length of insertion plate/length of tegmentum, mean 0.2. On valve viii (Figures 94, 95), pectinations of insertion plate variable, often with incomplete slitting and poor definition of teeth (usually better defined than in *Acanthopleura gemmata*); teeth recurving forward, extending considerably beyond (more so than in *A. gemmata*) transverse callus. Slit formula 6/17-1-7/16. Eaves thick (0.5 mm wide on midline of valve viii of specimen 45 mm long), moderately spongy.

Girdle, often banded, thick, musculous, wide, shrinking appreciably with preservation; at level of valve iv, girdle may measure 60% of valve in live specimens, 40% in alcohol preserved specimens, 10% or less in dry specimens. Upper surface crowded with white or blackish, pointed to blunt, straight to curved, calcareous spinelets (Figure 96), up to 1.5 mm long in average specimens (up to 2.2 mm long in larger ones); occasional needle-like elements, pointed, crystalline, 200 × 30 μm, interspersed amidst spinelets. Girdle bridges empty. Undersurface paved with imbricated, transparent, squarish scales, about 40 × 40 μm, becoming elongate towards outer margin, showing some 8–10 coarse striations and riblets that seem to radiate from outer edge of scale.

Radulae averaging 43% of specimen length (range 38–55%, SD = 8.4%, n = 7) and 58 rows of mature teeth (range 40–70, SD = 9.3, n = 7). In specimen 43 mm long (AJF 248: Long Island, Bahamas), median tooth (Figure 97) 80 μm wide at anterior blade; first lateral teeth 220 μm wide at anterior blade; head of major lateral teeth discoid, 280 μm wide; outer marginal teeth 250 μm long, 180 μm wide (length/width, 1.6).

Distribution: *Acanthopleura granulata* is limited to the Caribbean Sea, having been recorded at practically every island or cay from the Florida Keys, Mexico, Central America coast to the Leeward Islands, from the Bahamas to the northern coast of South America (Figure 113-G). The northernmost verified record is Grand Bahama Id., Bahamas (26°40'N) (AJF coll., *leg.* A. J. Ferreira, May 1971); the report of *A. granulata* in Bermuda (PEILE, 1926) has not been corroborated in field work (A. J. Ferreira & W. E. Daily collecting trip to Bermuda, May 1977; Dr. John S. Pearse, personal communication upon field trip to Bermuda, July 1980) or museum material (Bermuda Aquarium, Natural History Museum, and Zoo, David D. Lonsdale, Curator: chiton collection on loan, Sept. 1979). The southernmost record is Trinidad (10°39'N) (BABOOLAL *et al.,* 1981; Ferreira, herein); the westernmost record, Cozumel Id., Mexico (86°55'W) (HIDALGO, 1956;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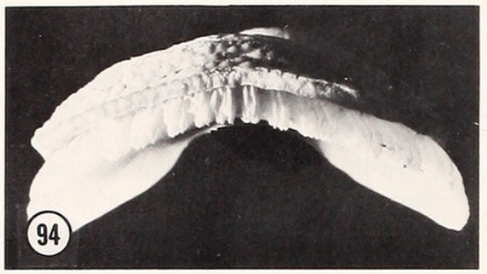
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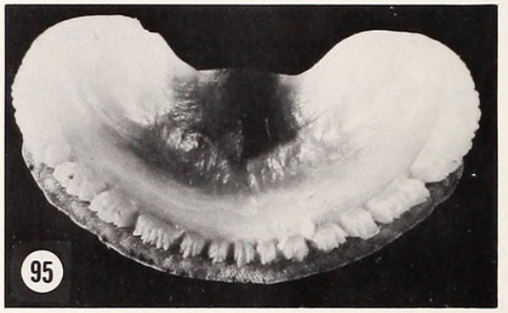
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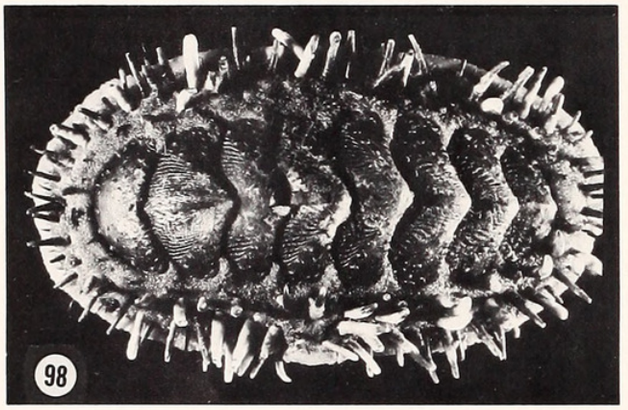
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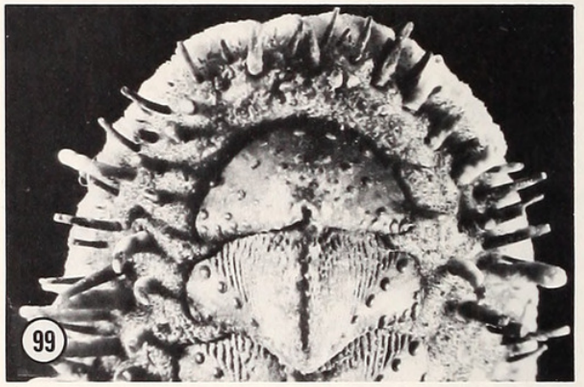
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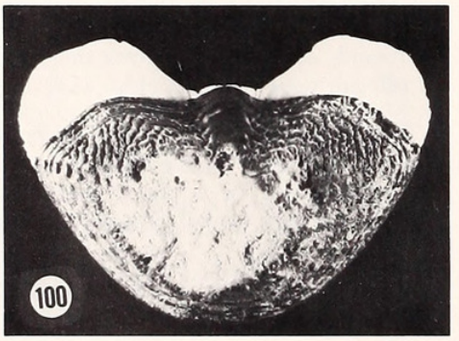
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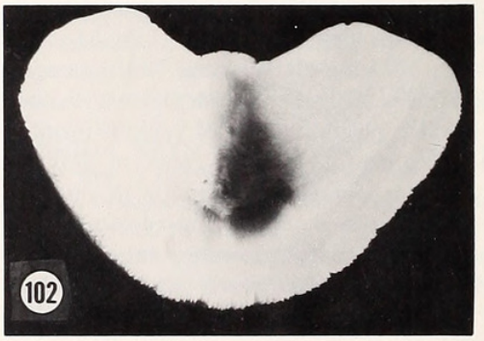
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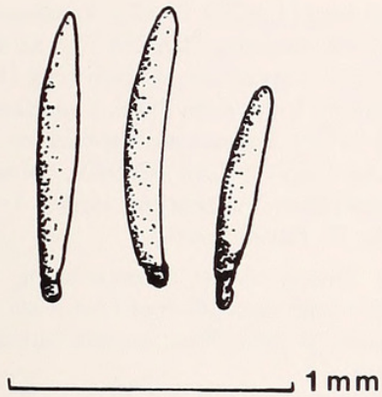


Figure 96

Acanthopleura granulata (Gmelin, 1791). Barbados (AJF 609); specimen 35 mm long. Girdle spinelets.

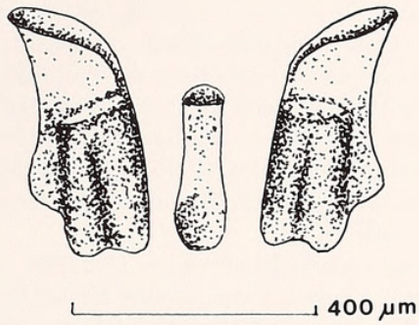


Figure 97

Acanthopleura granulata (Gmelin, 1791). Long Island, Bahamas (AJF 248); specimen 45 mm long. Radula median and first lateral teeth.

Ferreira, herein); the easternmost record, Barbados Id. (59°32'W) (Thiele, 1910b; Lewis, 1960; Conde, 1966; Kaas, 1972; Ferreira, herein). Reports of *A. granulata* in the Magellan Strait (Nierstrasz, 1905a, b) and at the Cape of Good Hope (Nierstrasz, 1905b) are obviously in error.

Acanthopleura granulata is confined to the intertidal zone, 0–1 m, often exposed, in crevices on coral limestone up to 1 m above low tide level.

Remarks: *Acanthopleura granulata* is the only species of the genus in the Atlantic Ocean. Likely, *A. granulata* and *A. gemmata* stem from the same ancestral species separated by the emergence of the Panama Isthmus. Still, *A. granulata,* a geographical isolate (Mayr, 1969), has not achieved sufficient phenotypic distance from *A. gemmata* to dispell the question of conspecificity. Although the question has not been previously addressed in the literature—and Pilsbry (1893c) went as far as allocating *A. granulata* and *A. gemmata* to different subgenera—the fact is that character-by-character comparison of Indo-Pacific specimens of *A. gemmata* with Caribbean specimens of *A. granulata* has failed to differentiate them in size, color, shape, tegmental sculpture, articulamental features, girdle elements, radula, and habitat.

Admittedly, when compared with the Indo-Pacific *Acanthopleura gemmata,* a few, subtle, and variable characters do seem to earmark the Caribbean *A. granulata*: (1) the more regular and less often coalesced tegmental granules, (2) the somewhat recticular appearance of the pleural areas, (3) the less conspicuous lamellar sculpture of the central areas, (4) the brighter blue or bluish-green articulamentum, often with an apical dark brown spot, but never wholly brown, (5) the better defined teeth of the posterior valve, less recurved forward, extending farther beyond the callus, (6) the less well defined transverse callus of the posterior valve, and (7) the girdle spinelets not quite as long as sometimes seen in *A. gemmata.* But, considering the large intraspecific variation and wide geographic range of the respective populations, these equivocal distinctions can hardly be accepted as specific. Still, whether they are sibling species (*sensu* Mayr, 1969:183) or a single species cannot be decided on morphology alone and must await further and more sophisticated (electrophoretic, immunologic, genetic, *etc.*) studies. Thus, given their total geographic separation, it is here recommended that the traditional view be accepted, and the Caribbean and Indo-Pacific populations continue to be addressed as different species.

Chiton magellanicus Gmelin, 1791:3204, was based upon

←

Explanation of Figures 93 to 95 and 98 to 102

Figure 93. *Acanthopleura granulata* (Gmelin, 1791). Caracoles, Dominican Republic (AJF coll.); specimen 15 mm long.

Figure 94. *Acanthopleura granulata* (Gmelin, 1791). Villa del Mar Beach, Dominican Republic (AJF coll.); specimen 41 mm long. Posterior aspect of posterior valve.

Figure 95. *Acanthopleura granulata* (Gmelin, 1791). Villa del Mar Beach, Dominican Republic (AJF coll.); specimen 41 mm long. Ventral aspect of posterior valve.

Figure 98. *Acanthopleura echinata* (Barnes, 1824). Los Colorados, Chile (LACM 75-19); specimen 23 mm long.

Figure 99. *Acanthopleura echinata* (Barnes, 1824). Same specimen as in Figure 98. Close-up of anterior valves.

Figure 100. *Acanthopleura echinata* (Barnes, 1824). Tumbes, Chile (AJF coll.); specimen ca. 70 mm long. Dorsal aspect of posterior valve.

Figure 101. *Acanthopleura echinata* (Barnes, 1824). Same specimen as in Figure 100. Posterior aspect of posterior valve.

Figure 102. *Acanthopleura echinata* (Barnes, 1824). Same specimen as in Figure 100. Ventral aspect of posterior valve.

an illustration in CHEMNITZ (1785, 8:279, pl. 95, figs. 797, 798) with Magellan Strait as locality. PILSBRY (1983c), KAAS (1972), and KAAS & VAN BELLE (1980) assigned the figured specimen to the West Indies (*i.e.,* to *Acanthopleura granulata*); ROCHEBRUNE (1889) assigned it to Australia; NIERSTRASZ (1905b, 1906) to the Cape of Good Hope, South Africa. The name is here suppressed as a *nomen dubium.*

Chiton unguiculatus BLAINVILLE, 1825:544, is regarded here also as a *nomen dubium,* having no locality, no illustration, and lacking descriptive elements to differentiate it from other species of *Acanthopleura.*

Acanthopleura echinata (Barnes, 1824)

Figures 98 to 105, and 113-E

Chiton echinatus BARNES, 1824:71–72, pl. 3, figs. 4a, 4b; SOWERBY, 1840b:1, 9, sp. 1, fig. 47.
Corephium echinatus: GRAY, 1847a:68, 1847b:169, 1857:184; DALL, 1879:280, fig. 30 (radula).
Acanthopleura echinata: PILSBRY, 1893a:105, 1893c:217–219, pl. 47, figs. 6–17 (in subgen. *Mesotomura*); PLATE, 1898: 5–167, pls. 1–10, figs. 1–110; NIERSTRASZ, 1905a:102; SCHWEIKART, 1905:384–386, figs. 20, 26–28; HORST & SCHEPMAN, 1908:526; DALL, 1909:180, 248, pl. 23, fig. 6; AYRES, 1916:335; BERGENHAYN, 1930a:8, 31, 33; pl. 8, fig. 74; GIGOUX, 1934:281; BOUDET, 1945:130; LELOUP, 1956:55–58, figs. 28, 29; STUARDO, 1959:145–146, 1964:82; MARINCOVICH, 1973:43, fig. 100; LELOUP, 1980a:1.
Rhopalopleura echinata: THIELE, 1893:374 (as syn. of "*Rhopalopleura aculeata* Linnaeus"), 1909:6.
Mesotomura echinata: THIELE, 1929:22.
Chiton tuberculiferus SOWERBY, 1825:29 (*nomen nudum*).
Chiton spiniferus FREMBLY, 1827:196–197, 1832 (plates):pl. 16, fig. 1; STEARNS, 1892:334 (in subgen. *Corephium*).
Acanthochiton spinifera: STEARNS, 1894b:449.
"*Chiton aculeatus* Linnaeus" REEVE, 1847:pl. 9, fig. 49 (with *C. spiniferus* and *C. tuberculiferus* as syn.).
[*Non:* Linnaeus, 1758 (*fide* DODGE, 1952:20–21).]
"*Rhopalopleura aculeata* Linnaeus" THIELE, 1893:373–374, pl. 30, fig. 37, 1909:6.
"*Corephium aculeatum* Linnaeus" MOSELEY, 1885:18–19, pl. 5, fig. 8, pl. 6, figs. 10–12 (aesthetes).

Type material and type locality:

Chiton echinatus Barnes, 1824: Types unascertained; locality "Coast of Peru," here restricted to Callao, Peru (12°02'S, 77°05'W).

Material examined:

PERU: Talara, 4 specimens (CAS 010147); Paita, 8 specimens, largest 100 mm long (CAS 010145; LACM 72-86); Lobos de Tierra Id., 1 specimen (LACM 74-10); Lobos de Afuera Id., 10 specimens, largest 75 mm long (LACM 74-5; LACM 74-6); Guanape Id., 2 specimens (LACM 74-2); Callao, 1 specimen (CAS 012793).
CHILE: Arica, 2 specimens (CASG-SU 33761); Iquique, 1 specimen, 110 mm long (CAS 010146); Cumbres Borascosas, Tarapaca Prov., 1 specimen, 45 mm long (LACM 75-14); Los Colorados, Antofagasta Bay, 4 specimens, largest 42 mm long (LACM 75-19); Antofagasta, 7 specimens, largest 100 mm long (LACM 75-15); Los Molles, Aconcagua Prov., 1 specimen, 44 mm long (LACM 75-28); Islota Concon, Valparaiso Prov., 1 specimen, 132 mm long (LACM 75-31); Valparaiso, 9 specimens, largest 112 mm long (CAS 030914; CAS 030942); Punta Tumbes, Bahía de Concepcion, 7 specimens, largest 105 mm long (AJF coll., *leg.* E. Bay-Schmith).

Description: Owing to the accompanying illustration, BARNES' (1824) brief description of *Chiton echinatus,* based upon two specimens from Peru, is quite sufficient to identify the species.

Among 59 specimens of *Acanthopleura echinata* here examined, largest 132 mm long (in alcohol) (LACM 75-31: Islota Concon, Valparaiso Prov., Chile) (largest specimen reported, 200 mm long [PLATE, 1898: Pajaros Id., off Coquimbo, Peru]). Specimens (Figures 98–102) depressed, subcarinate. Body width/length, mean 0.57 (SD = 0.06; n = 17), specimens becoming relatively wider with growth (width/length ratio *vs.* specimen length, $r = 0.58$, $P < 0.02$, n = 17) (Figure 103). Tegmentum smooth to shiny (but often eroded), dark reddish-brown, with occasional small blue spots. Lateral areas hardly raised, smooth except for two radial rows, one of 5–9 round granules along diagonal line, another of 5–9 elongate granules indenting sutural edge. Anterior valve with some 10 radial rows of round granules; space between rows smooth. Central areas with raised, well defined, smooth jugal band bordered by shallow, longitudinal grooves with short, wavy, longitudinally oriented riblets on pleural areas. Mucro elevated, prominent, central to posterior; postmucro sharply sloped. Ocelli round to oval, 40–50 μm in diameter, throughout anterior valve, postmucro area of posterior valve, and lateral areas of intermediate valves. Eaves somewhat spongy. Gills with 50–70 plumes per side.

Articulamentum white, often with red discolorations at apex of valves. Central part of all valves show conspicuous, transverse, strongly engraved lines. Sutural laminae subrectangular; sinus well defined, pectinate; on valve viii, relative width of sinus, 0.44. Insertion plates strongly pectinate on outside; sinus minutely pectinate. Posterior valve with pectinate insertion plate with 1–3 slits (none in small specimens), irregularly and variably arranged, often with one particularly better defined on or near midline. Slit formula 8-1-0/3. Width of valves i/viii, 0.87. Valve viii tegmental surface length/width, 0.61.

Girdle upper surface with erect, strong, spikelike spines (Figure 104), round in cross section, up to 8 mm long in large specimens (longer if not broken), often encrusted; in addition, abundant spinelet-like elements averaging 300 × 80 μm, separated by about 100–200 μm or more of "nude" girdle. Girdle bridges empty. Undersurface with transparent scales, about 35 × 35 μm, with convex outer edge, concave inner edge, vaguely striate.

In specimen 70 mm long (AJF coll.: Tumbes, Chile), radula 31 mm long (44% of specimen length), comprising 65 rows of mature teeth. Median tooth (Figure 105) 130

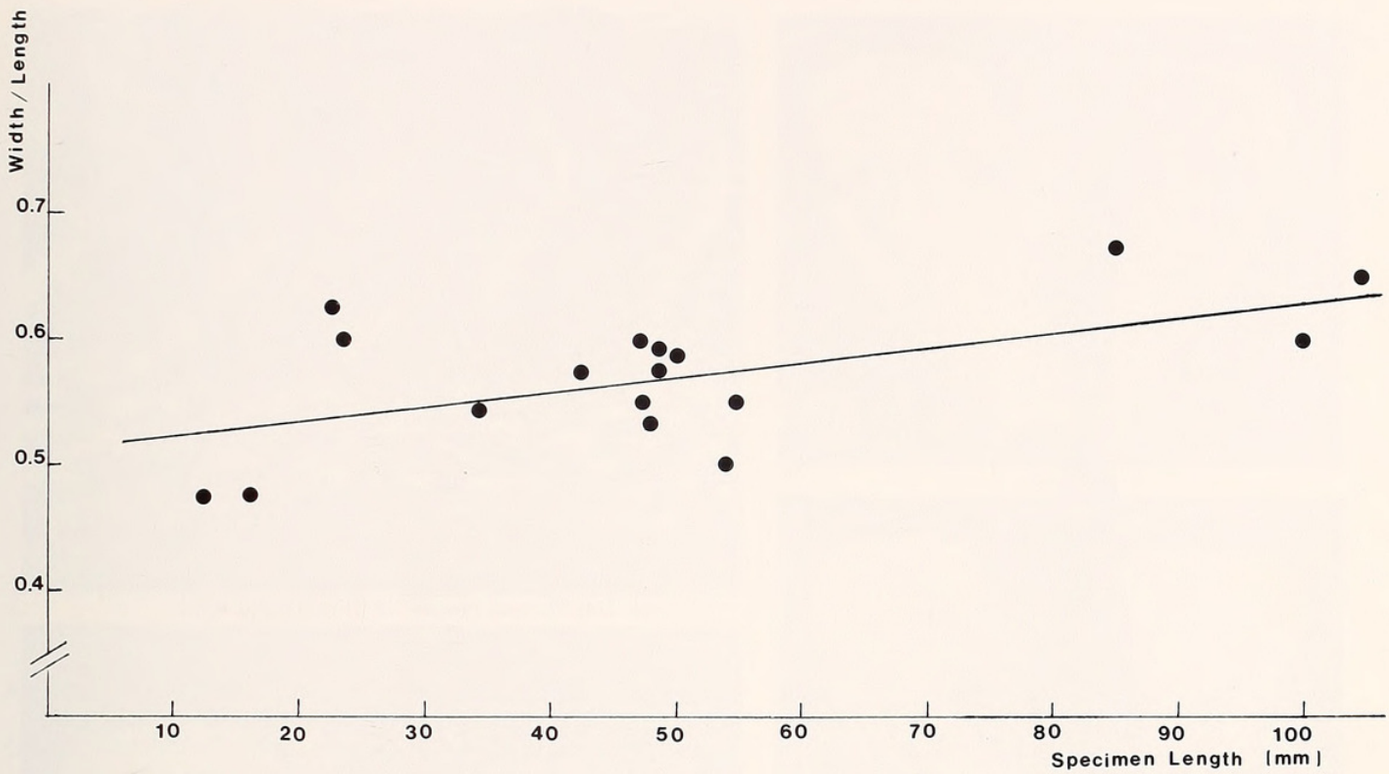


Figure 103

Acanthopleura echinata (Barnes, 1824). "Wideness" of specimen (body width/length ratio) as a function of specimen length (mm): Large specimens are relatively wider than smaller ones ($r = 0.58$; $n = 17$; $P < 0.02$).

μm wide at anterior blade; first lateral teeth 200 μm wide at anterior blade; head of second lateral teeth discoid, 550 μm wide; outer marginal teeth 350 μm long, 350 μm wide (length/width, 1.0).

Distribution: *Acanthopleura echinata* is confined to the western coast of South America (Figure 113-G), from Talara, Peru (4°35'S), the northernmost verified record (CAS 010147), to Punta Tumbes, Bahía de Concepcion, Chile (36°37'S), the southernmost verified record (AJF coll., *leg.* E. Bay-Schmith, Feb.–Sept. 1977). Reports of the species at the Galápagos Islands, Ecuador (Pilsbry, 1893c; Stearns, 1894; Nierstrasz, 1905a; Dall, 1909), have not been confirmed (see Smith & Ferreira, 1977).

Acanthopleura echinata is limited to the intertidal zone and shallow subtidal, 0–4 m, on rocks often exposed to heavy surf.

Remarks: Among early authors, *Chiton echinatus* Barnes, 1824, occasioned some taxonomic confusions. Sowerby (1825:29) named the species *Chiton tuberculiferus* as a replacement for "*Aculeatus,* Barnes" (!), apparently confusing the name *echinatus* with *aculeatus,* for nowhere did Barnes (1824) use the latter name. Frembly (1827) described and illustrated "*tuberculiferus,*" which Sowerby (1825) had left as a *nomen nudum,* and renamed it *spiniferus* "because the name *aculeatus* given to it by Barnes [!] was long since previously occupied; that of *tuberculiferus* [Sowerby, 1825] was given from an old specimen, in which the spines were reduced in length by being broken, so that it is not applicable [!]; we have therefore now called it *spiniferus*" (p. 197). Reeve (1847b) compounded the confusion by stating that "the *C. spiniferus* of Frembly . . . is the old Linnaean *C. aculeatus* in fine condition . . . [and figured] in Chemnitz, Conch. Cab. v. 10. pl. 173. f. 1692." It must only be added that the cited figure 1692 in Chemnitz (1788) does not conform at all, in morphology or locality (Nicobar Is.), to *echinatus* Barnes, 1824!

Chiton echinatus was first allocated to *Acanthopleura* by Pilsbry (1893a) in the monotypic subgenus *Mesotomura* Pilsbry, 1893a (=*Corephium* Gray, 1847a [not Browne, 1827]). The material here examined shows that Pilsbry's (1893c) "single median-posterior slit," characterizing *Mesotomura,* is not a constant feature of *A. echinata,* which may have 1 to 3 slits (none, in small specimens) on the posterior valve, and not necessarily in the midline.

In the uniqueness of its tegmental sculpture, articulamentum, and girdle *A. echinata* differs sharply from all other species of *Acanthopleura.* It is a curious fact, then, that workers since Pilsbry (1893c) have easily accepted *echinata* as a member of the genus *Acanthopleura* while relegating species much closer to its type (*A. spinosa*), such as *A. gaimardi, A. japonica, A. miles,* or *A. curtisiana,* to other genera.

Throughout its range, *Acanthopleura echinata* is sym-

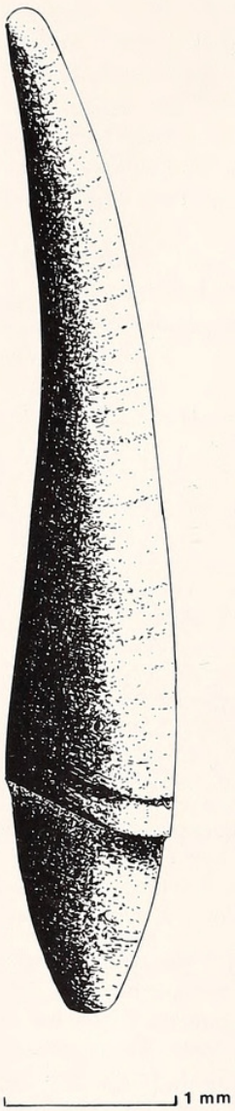


Figure 104

Acanthopleura echinata (Barnes, 1824). Same specimen as in Figure 100. Girdle spikelike spine.

patric with *A. nigra* from which it clearly differs in tegmental sculpture and girdle elements.

Acanthopleura nigra (Barnes, 1824)

Figures 106 to 111, and 113-N

Chiton niger Barnes, 1824:71, pl. 3, fig. 3; Gray, 1828:6 (with *C. coquimbensis* Frembly as syn.).

Enoplochiton niger: Gray, 1847a:69, 1847b:169, 1857:181; Moseley, 1885:19, pl. 4, figs. 6–9; Thiele, 1893:375, pl. 30, fig. 40; Pilsbry, 1893c:252–253, pl. 52, figs. 22–29; Plate, 1898:208–215, pl. 9, figs. 86–88, pl. 12, figs. 135–140; Nierstrasz, 1905a:106; Horst & Schepman, 1908:528; Dall, 1909:181, 248, pl. 23, fig. 8; Thiele, 1929:21; Bergenhayn, 1930a:32–34, pl. 8, figs. 78–79, pl. 9, figs. 81–82; Gigoux, 1934:281; Leloup, 1939b:6–9, figs. 5, 6, 1956:54–55; Stuardo, 1959:144, 146, 1964:82; Marincovich, 1973:43, fig. 99.

Chiton coquimbensis Frembly, 1827:197–198, 1832 (plates): pl. 16, fig. 2; Reeve, 1847, pl. 4, sp. & fig. 22.

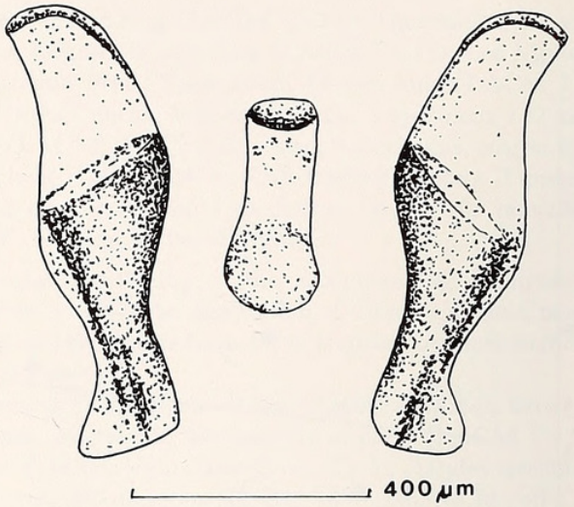


Figure 105

Acanthopleura echinata (Barnes, 1824). Same specimen as in Figure 100. Radula median and first lateral teeth.

Type material and locality:

Chiton niger Barnes, 1824: Types unascertained; locality "Coast of Peru," here restricted to Iquique, Chile (20°13′S, 70°10′W).

Chiton coquimbensis Frembly, 1827: Types unascertained; locality Coquimbo Bay, Peru (29°58′S, 71°21′W).

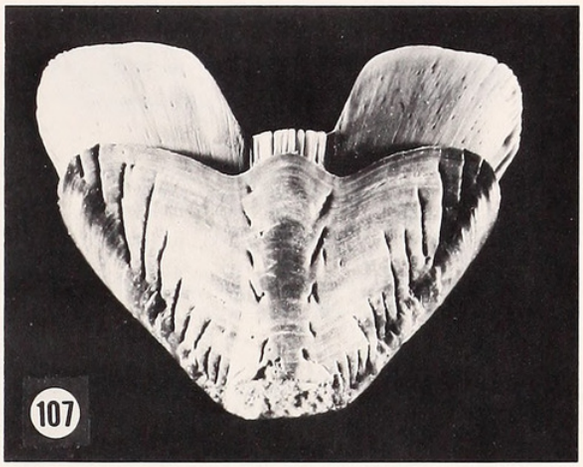
Material examined:

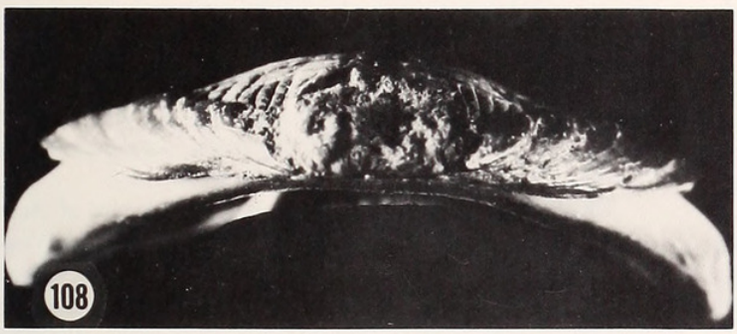
PERU: Talara, 2 specimens, largest 59 mm long (CAS 010148); Pisco, 3 specimens (CASG-SU 35328); Callao, 17 specimens (CAS 012791).

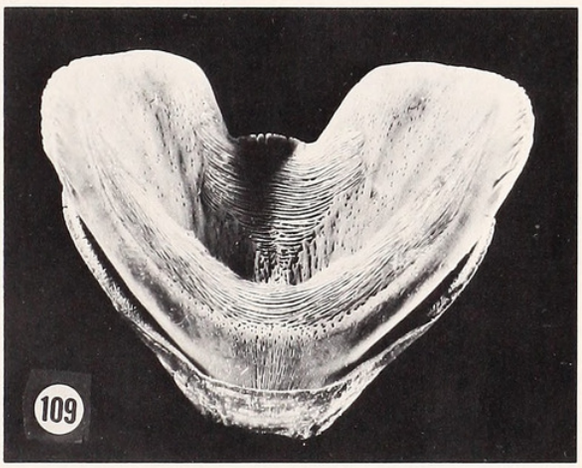
CHILE: Independencia Bay, 2 specimens (LACM-AHF 380-35); Arica, 3 specimens, largest 90 mm long (CASG-SU 33760); Iquique, 5 specimens, largest 131 mm long (LACM 64-16; LACM 75-12; CAS 010144); Cumbres Barascosas, Antofagasta Prov., 1 specimen, 93 mm long (LACM 75-14); Antofagasta, 7 specimens, largest 61 mm long (LACM 75-15); Coquimbo Bay, 1 specimen (CASG-SU 32955).

Description: Barnes' (1824) brief description but good illustration of *Chiton niger* is sufficient to identify the species.

Among 41 specimens of *Acanthopleura nigra* here examined, largest 131 mm long (in alcohol) (LACM 64-16: Iquique, Chile). Body width/length, mean 0.48 (n = 9). Specimens (Figures 106–109) round-backed, depressed. Tegmentum dark chocolate-brown, shiny, but easily eroded. Valves beaked; posterior edge of valve ii forming 110–120° angle. Anterior valve with 4–6 concentric, zig-zagged furrows. Lateral areas elevated, well defined by strong round rib at diagonal line, with zig-zagged furrows as on anterior valve. Central areas well defined, smooth jugum







Explanation of Figures 106 to 109

Figure 106. *Acanthopleura nigra* (Barnes, 1824). Iquique, Chile (LACM 75-12); specimen 32 mm long.

Figure 107. *Acanthopleura nigra* (Barnes, 1824). Same specimen as in Figure 106. Dorsal aspect of posterior valve.

Figure 108. *Acanthopleura nigra* (Barnes, 1824). Same specimen as in Figure 106. Posterior aspect of posterior valve.

Figure 109. *Acanthopleura nigra* (Barnes, 1824). Same specimen as in Figure 106. Ventral aspect of posterior valve.

bordered by narrow, depressed area with irregular, short, oblique furrows; para-jugal area smooth; pleural area with longitudinal, parallel furrows, not usually reaching anterior border of valve. Mucro posterior, almost terminal. Ocelli round to oval, 20–30 μm in diameter, throughout anterior valve and anterior half of lateral areas of intermediate valves. Gills with 70–80 plumes per side.

Articulamentum dark chocolate-brown, with transverse, strongly engraved lines at middle of valves (also seen in *A. echinata* but not in any other *Acanthopleura* species). Sutural laminae somewhat elongate; sinus well defined, sinusal laminae pectinate. Insertion teeth strongly pectinate on outside. Posterior valve without insertion teeth but with well developed transverse callus. Slit formula 8/9-1-0.

Girdle thick, musculous. Upper surface dark brown, conspicuously dotted with light brown scales (Figure 110); scales irregular in size (larger in middle ⅓ of girdle), up to 1.5–2 mm long in specimens 50 mm long (larger in larger specimens), vaguely striate, usually eroded at upper edge, clearly separated from each other by area as wide as scale (in alcohol preserved specimens); on outer ⅕ of girdle, scales much smaller, shorter, dark brown, erect, spine-like; girdle surface completely covered otherwise with minute, dark brown, lanceolate spicules, up to 100 μm long, 25 μm thick. Girdle bridges, empty in middle third, but crowded with small, dark brown spiculoid elements (akin to those on girdle proper) in outer thirds. Undersurface covered with transparent squarish scales, about 40 × 40 μm, in columnar arrangement, with coarse, irregular striations.

In specimen 49 mm long, radula measures 15 mm in length (30% of specimen length) and comprises 60 rows of mature teeth. Median tooth (Figure 111) 100 μm wide at anterior blade; first lateral teeth about 500 μm long, 150 μm wide at anterior blade; head of major lateral teeth

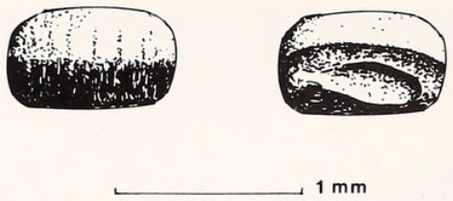


Figure 110

Acanthopleura nigra (Barnes, 1824). Same specimen as in Figure 106. Girdle scales, outer and inner sides.

discoid, 300 μm in width; outer marginal teeth 300 μm long, 250 μm wide (length/width, 1.2).

Distribution: *Acanthopleura nigra* is confined to the western temperate coast of South America, the Peru-Chilean zoogeographic province (Briggs, 1974) (Figure 113-N), from Talara, Peru (4°34′S) (CAS 010148), the northernmost verified record, to Coquimbo Bay, Chile (29°58′S) (CASG-SU 32955), the southernmost verified record.

Bathymetric range limited to the intertidal zone.

Remarks: *Chiton niger* has been generically segregated from *Acanthopleura* by authors since Gray (1847a) and Pilsbry (1893c) on account of three taxonomic characters: (1) the girdle elements, (2) the articulamentum of the posterior valve, and (3) the ocelli.

The girdle elements of *Chiton niger* have made for easy identification of the species; the light-colored, "rude" scales, clearly separated from each other by the fleshy girdle, do confer on *C. niger* a unique appearance. However, close observation of the scales shows that, although in shape, size, and placement (*i.e.*, apart from each other) they have no similarity, they show no major departure from the girdle elements in other species of *Acanthopleura.* In addition, their implantation in the girdle through a rough, irregular, and variously shaped facet (Figure 110) conforms well to that of scales and spinelets in other species of *Acanthopleura.* The conspicuous separation of the scales by the girdle is a feature also seen, though less conspicuously, in other species of *Acanthopleura* (*e.g., A. miles, A. curtisiana, A. araucariana*).

The absence of teeth in the posterior valve of *Chiton niger* led Pilsbry (1983c) to group the species with *Liolophura* and *Onithochiton* Gray, 1847a. Yet, toothless posterior valves are seen not only in other members of *Acanthopleura—A. gaimardi, A. japonica* (the "*Liolophura*"), *A. hirtosa,* and *A.* ***rehderi***)—and in *Onithochiton,* but also in other genera and other families, such as in the acanthochitonid *Cryptoplax* Blainville, 1818, the schizochitonids *Aulacochiton* Shuttleworth, 1853 (=*Lorica* Adams & Adams, 1852, preoccupied by *Lorica* Bronn, 1848, a crustacean) and *Componochiton* Milne, 1963, and the mopaliid *Plaxiphora* Gray, 1847a, indicating that similar modifications of the posterior valve have occurred more than once in the evolution of chitons.

The ocelli in *Chiton niger* were said to be, in contrast

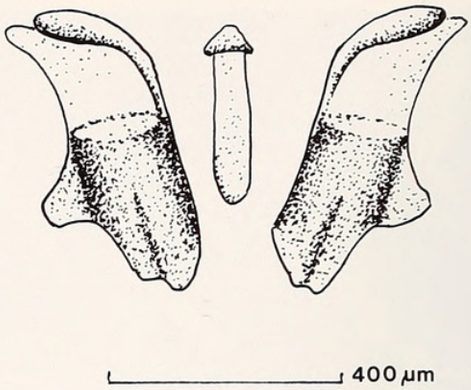


Figure 111

Acanthopleura nigra (Barnes, 1824). Same specimen as in Figure 106. Radula median and first lateral teeth.

to those of *Acanthopleura* species, "excessively minute" (Moseley, 1885:19) and "extremely minute and oval instead of round" (Pilsbry, 1893c:252). These statements are here in part refuted. Careful evaluation of ocelli in *Acanthopleura* shows that in *A. nigra* the ocelli are smaller (average diameter: 25 μm in *A. nigra,* 45 μm in other species of *Acanthopleura*) but not more "oval instead of round" than in other species of *Acanthopleura.*

Thus, except for the fact that the girdle scales of *Acanthopleura nigra* are distinct enough to immediately diagnose the species, there seems to be no compelling reason to segregate the species in the monotypic *Enoplochiton* Pilsbry, 1893c, and so obscure its relationship with other members of *Acanthopleura.*

Acanthopleura nigra is sympatric with *A. echinata* along the Peru–Chile coast.

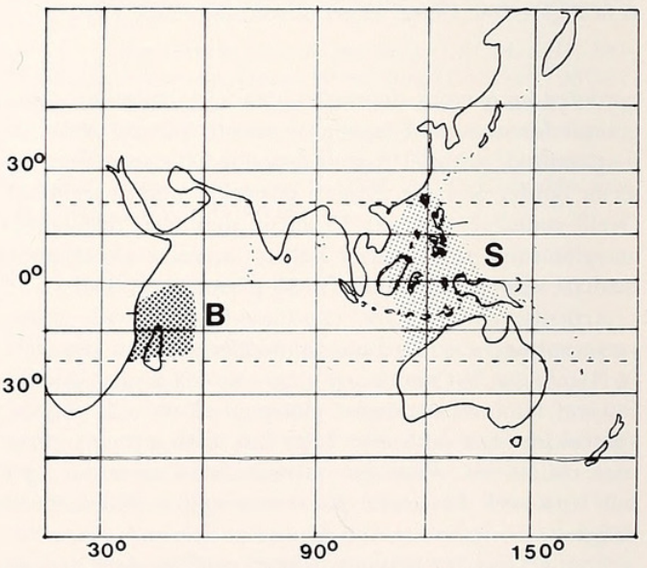


Figure 112

Geographic distribution of: S = *Acanthopleura spinosa* (Bruguière, 1792); B = *Acanthopleura brevispinosa* (Sowerby, 1840).

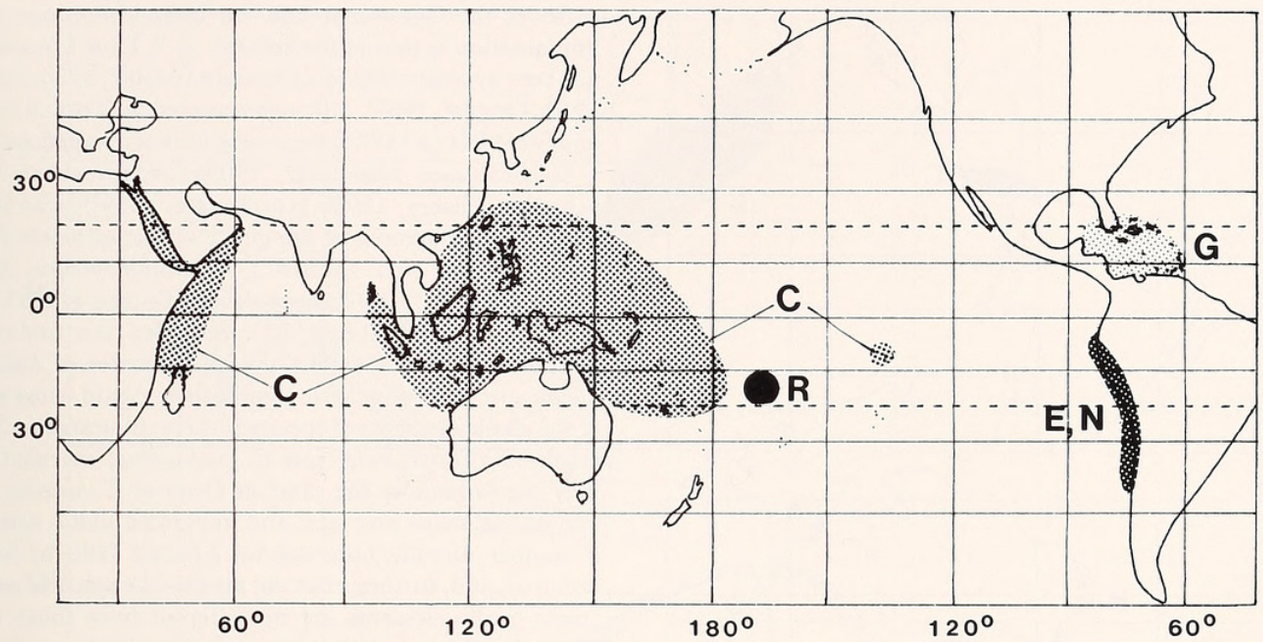


Figure 113

Geographic distribution of: C = *Acanthopleura gemmata* (Blainville, 1825); R = *Acanthopleura* ***rehderi*** Ferreira, spec. nov.; E = *Acanthopleura echinata* (Barnes, 1824); N = *Acanthopleura nigra* (Barnes, 1824); G = *Acanthopleura granulata* (Gmelin, 1791).

DISCUSSION

As here understood, the genus *Acanthopleura* corresponds to the subfamily Acanthopleurinae (*sensu* VAN BELLE, 1983:126–130), with the genera *Liolophura, Enoplochiton,* and *Squamopleura* suppressed as synonyms. Although the particular reasons for such an action were given previously in the account of the respective species, they bear restating here since they may not be immediately apparent to chiton taxonomists.

Liolophura Pilsbry, 1893a, erected to accommodate *Chiton incanus* (=*C. gaimardi*) and *C. japonicus,* was distinguished from *Acanthopleura* by the presence of a "smooth crescentic callus in place of the insertion-teeth" (PILSBRY, 1893a:105) in the posterior valve. Despite obvious affinity with *Acanthopleura,* PILSBRY (1893a) placed the taxon "in the immediate vicinity of *Onithochiton,*" and grouped it, instead, with *Enoplochiton* and *Onithochiton* in the subfamily Liolophurinae Pilsbry, 1893c. Although Liolophurinae was rejected by some chiton workers (NIERSTRASZ, 1905a; THIELE, 1909, 1929; BERGENHAYN, 1930a, 1933), *Liolophura,* as a generic taxon, has remained in general usage.

On introducing *Liolophura,* PILSBRY (1893a, c) assumed that in species of this genus the insertion teeth of the posterior valve had been replaced by a callus. But the interpretation was faulty. Close examination of specimens of *Liolophura* species suggests that the callus in the posterior valve appears not "in place of insertion-teeth" as PILSBRY (1893a:105) asserted, but as a result of their disappearance. In fact, a transverse callus is present in the posterior valve of most other species of *Acanthopleura,* only less developed and "hidden" by the pectinations and teeth on its posterior aspect. In this respect, it may be noted that in specimens of *A. japonica* (previously segregated in *Liolophura*) vestigial insertion teeth are often seen as coarse pectinations or rugosities on the sides (occasionally, even in the middle) of an otherwise smooth, flat-surfaced, crescentic callus, indicating by the irregularity of their presence, position, shape, and size, their vanishing, relict nature. The taxonomic significance of the absence of teeth in "*Liolophura*" is further diminished by the observation that they are absent also in other genera and families (see Remarks on *A. nigra*), and that in several other species of *Acanthopleura* (*A. brevispinosa, A. loochooana, etc.*) the posterior valves show "in between" forms of insertion plates where insertion teeth are present but underdeveloped. Because members of *Liolophura* and *Acanthopleura* (*sensu* Pilsbry) do not seem to differ in any other major character, the two genera are here regarded as synonymous.

Enoplochiton Gray, 1847a, erected to accommodate *Chiton niger,* has been accepted by chiton workers without dissent. Apparently, the unique appearance of *C. niger,* with its conspicuously large, light-colored (*i.e.,* eroded) scales distinctly separated by the "velvety" girdle, has been regarded as demonstration of sufficient evolutionary distance to justify assignment to a distinct genus. However, in the course of this study it became apparent that overall similarities between *C. niger* and members of *Acanthopleura* are greater than generally assumed. The girdle scales of *C. niger,* peculiar looking as they are, cannot be re-

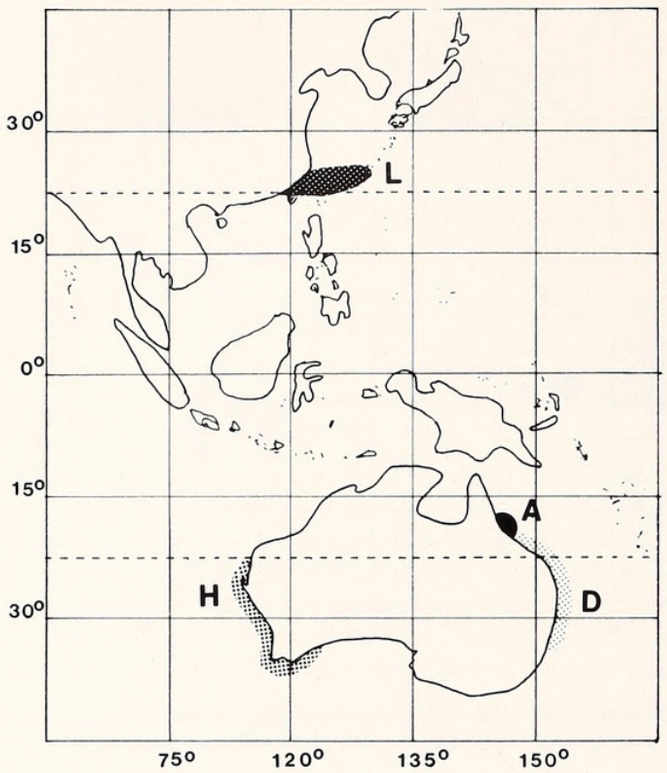


Figure 114

Geographic distribution of: H = *Acanthopleura hirtosa* (Blainville, 1825); L = *Acanthopleura loochooana* (Broderip & Sowerby, 1829); A = *Acanthopleura* ***arenosa*** Ferreira spec. nov.; D = *Acanthopleura gaimardi* (Blainville, 1825).

garded as a "major modification of the girdle armature" (ASHBY, 1929:160) of *Acanthopleura*; in fact, they do not seem to be more evolutionarily "distant" from the spines of *A. spinosa* (type species of *Acanthopleura*) than, say, the spinelets of *A. gemmata,* or the spikes of *A. echinata.* And since the modification in girdle elements is not accompanied by changes in "some more stable character" (ASHBY, *loc. cit.*)—in their large size, oval body shape, heavy and beaked valves, shape and distribution of ocelli (though smaller in diameter), pectinate insertion teeth, radula with discoid major lateral teeth, and intertidal habitat, specimens of *C. niger* do conform well with other *Acanthopleura* species—it seems that segregation of *C. niger* in the monotypic *Enoplochiton* is unjustified.

Acanthozostera Iredale & Hull, 1926, and *Planispina* Taki, 1962, have been long regarded as synonyms of *Acanthopleura* (SMITH, 1960; VAN BELLE, 1983).

Clavarizona Hull, 1923, was erected to accommodate a single species, *Chiton hirtosus,* distinguished from *Liolophura* for "the girdle covering which consists of . . . scales" (HULL, 1923:199). But, as already pointed out by LELOUP (1961:47), the girdle elements in *C. hirtosus* do not differ from those of other *Liolophura* "except in dimensions . . . [they appear] not as scales . . . but as spines . . . [and] their arrangement on the girdle is not regular like that of the scales of the Chitoninae and the Ischnochitoninae; their implantation is that of the spines . . . ." Thus *Clavarizona* has been synonymized to *Liolophura* (ASHBY, 1926; SMITH, 1960; LELOUP, 1961), although accepted by THIELE (1929) and VAN BELLE (1983) as a subgenus of *Liolophura.*

Squamopleura Nierstrasz, 1905a (=*Sclerochiton* Carpenter *in* Pilsbry, 1893b [not Kraatz, 1859]), was introduced also on account of the girdle scales: spinelets ("*kalkigen Stacheln und Dornen*") in *Acanthopleura,* scales ("*Kalkschuppen*") in *Squamopleura.* THIELE (1929), and presently VAN BELLE (1983), regarded the finding of needle-like spicules amidst the girdle scales of *Squamopleura* species as of generic significance. Again, close study of the girdle elements of species hitherto allocated to *Squamopleura* (*Chiton miles* and *C. curtisianus*) revealed that they are essentially the same as those of *C. hirtosus* (*i.e.,* variable in shape and size, and implanted like a spine, in a manner already observed by LELOUP [1961b] for *C. hirtosus*), and, further, that the needle-like spicules amidst larger girdle elements are no different from those to be found in virtually all species of *Acanthopleura.* SMITH (1960), probably overlooking the presence of ocelli in *Squamopleura* species, regarded it as a subgenus of *Chiton* Linnaeus, 1758.

Acanthopleura attains greatest species diversity in the Central Indo-Pacific, in the "fertile triangle" (BRIGGS, 1974:14) of the Indo-Malayan region (EKMAN, 1953), with a "center of origin" at Taiwan where five species (*A. spinosa, A. gemmata, A. japonica, A. miles,* and *A. loochooana*) have been recognized.

In the central Indo-Pacific, the north-south distribution of *Acanthopleura* maps out in a curiously symmetrical manner: *Acanthopleura gemmata,* the most common species, is present virtually everywhere in the tropics. To the north of the Tropic of Cancer (approximately), in Korea, Taiwan, and Japan, *A. gemmata* is replaced in the intertidal zone by *A. japonica*; and to the south of the Tropic of Capricorn (approximately), *A. gemmata* is similarly replaced by *A. gaimardi* on the east and *A. hirtosa* on the west coasts of Australia. What is intriguing is the realization that the three species "replacing" *A. gemmata* in temperate waters, *i.e., A. japonica, A. gaimardi,* and *A. hirtosa,* all differ from *A. gemmata* in a single major feature, the absence of insertion teeth in the posterior valve. It is curious, too, that, in the northern hemisphere, *A. loochooana* (with posterior valve insertion teeth present but considerably underdeveloped) is confined to the zone of contact between *A. gemmata* and *A. japonica*; and, similarly, in the southern hemisphere, *A.* ***arenosa*** (with underdeveloped insertion teeth in the posterior valve) is limited to the zone of contact between *A. gemmata* and *A. gaimardi.* This correlation between the reduction or loss of insertion teeth and high latitude (both north and south) is impressive. It is tempting to speculate that the implied difference in water temperature may be a factor influencing the articulamental changes, although the possible adaptive value of such changes is obscure.

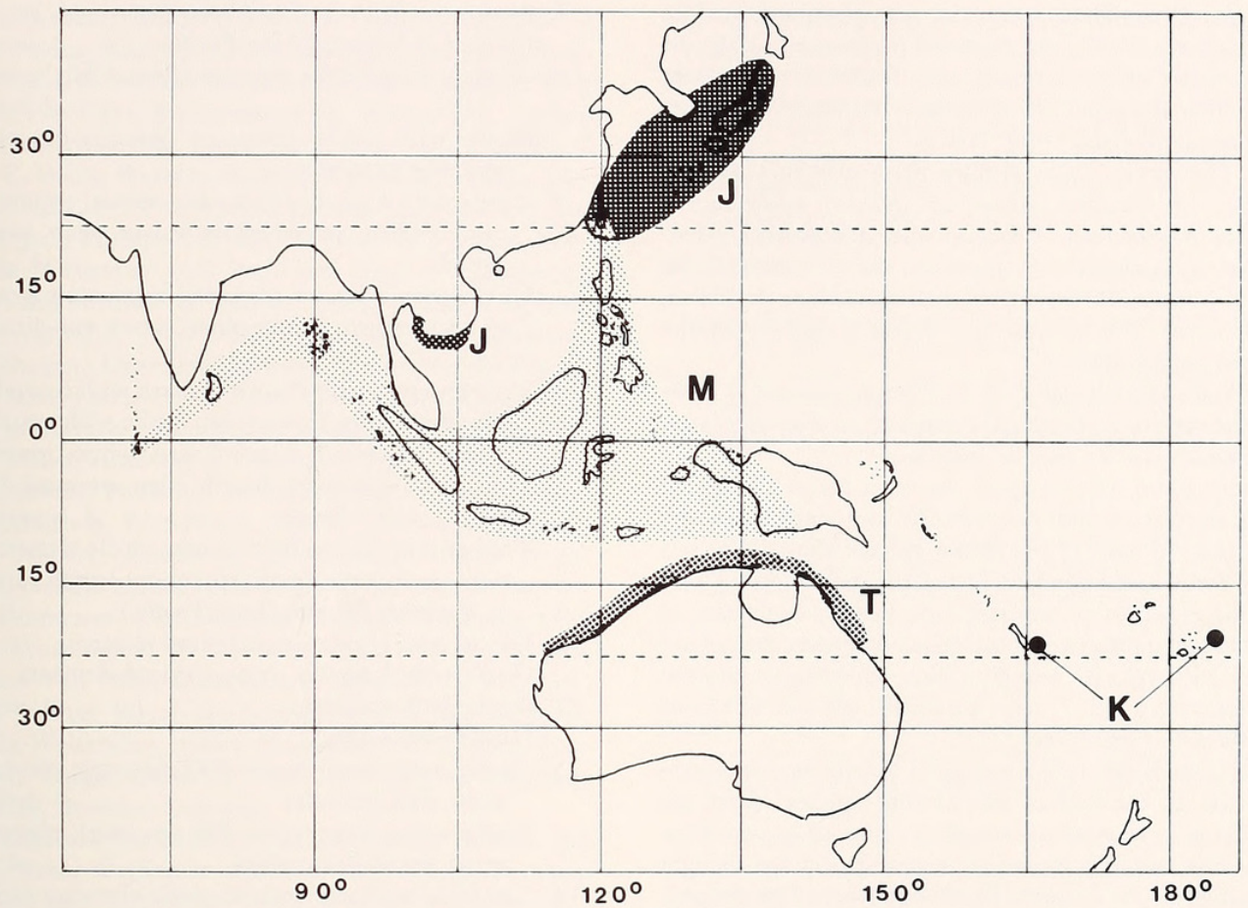


Figure 115

Geographic distribution of: T = *Acanthopleura curtisiana* (Smith, 1884); J = *Acanthopleura japonica* (Lischke, 1873); M = *Acanthopleura miles* (Carpenter *in* Pilsbry, 1893); K = *Acanthopleura araucariana* (Hedley, 1898).

The differential diagnosis of *Acanthopleura* species may be quite difficult at times, particularly when one is faced with dry, and eroded specimens. The fifteen species of *Acanthopleura* here recognized are remarkably similar to each other, bespeaking their congeneracy, and explaining the difficulties encountered in unraveling the group. The following summary of comparative points and comments regarding the morphology of *Acanthopleura* species may be of value:

(1) The relatively large size of the specimens, drab and eroded tegmentum, and intertidal habitat (on top of rocks, beaten by surf, emergent at low tide, often exposed to sun) are common to all *Acanthopleura* species.

(2) The valves, heavy and beaked, are usually (easily?) eroded; but even among pristine, young specimens, interspecific distinctions in the tegmental sculpture are minor and hard to draw out (except in *A. spinosa, A. echinata,* and *A. nigra*), making for difficulties in the differential diagnosis of the species. In all species, the tegmentum recurves forward at the ventroposterior portion of the valve, forming an underfold or hypotyche (see Hoare *et al.,* 1983).

(3) The ocelli are essentially identical in distribution, shape, and size in all species, although somewhat smaller in *A. nigra.* They are assumed to be light-sensitive organs (Boyle, 1969, 1972). In this respect, it is curious to observe that in *Tonicia, Onithochiton,* or *Schizochiton,* whose specimens are hardly ever eroded, the ocelli are likely to remain functional throughout life; but in *Acanthopleura* their usefulness appears short-lived, because they are soon destroyed by erosion (though a few are usually seen at the periphery of the growing shell). The possible sensory function of the hypotyche (Hoare *et al.,* 1983:996), well developed in *Acanthopleura,* may conceivably compensate for the loss of sensory input resulting from erosion of the ocelli. No ocelli have been found in the hypotyche of *Acanthopleura* species.

(4) The significant differential features in the articulamentum of *Acanthopleura* species are limited to the posterior valve, where the insertion teeth may be well developed (*A. spinosa, A. gemmata,* and *A. granulata*), absent (*A. gaimardi, A. japonica, A. hirtosa, A.* ***rehderi***, and *A. nigra*), or poorly and irregularly developed (in the other species). In *A. echinata* and *A. nigra,* sympatric species

along the Peru–Chile coast, the articulamental surface shows an area of strongly engraved transverse lines in the middle of the valves; curiously, this feature is not present in any other species of *Acanthopleura,* but is seen in species of the genus *Mopalia* Gray, 1847a.

(5) The girdle upper surface main elements may be spikelike (*A. echinata*), spines (*A. spinosa*), spinelets (*A. gemmata, A. granulata, A. brevispinosa, A.* ***arenosa***, A. loochooana, A. gaimardi, A. japonica, and *A.* ***rehderi***), or scales (*A. miles, A. araucariana, A. curtisiana, A. hirtosa,* and *A. nigra*). The undersurface shows no significant distinctions among species.

(6) With the exception of *A. brevispinosa* and *A.* ***rehderi***, the radula is remarkably constant in *Acanthopleura,* revealing no species-specific features.

Acanthopleura has no fossil record, a rather intriguing fact for a group so widely distributed, and containing specimens that, in most of the fifteen species known, are relatively large and abundant in the intertidal zone. However, the presence of *Acanthopleura* in the Caribbean, as *A. granulata,* indicates that the genus antedates the closure of the Pacific-Atlantic seaway which, as it may be inferred from GEISTER's (1977) work on corals, did not take place until the late Pleistocene.

A diagnostic key to the species of *Acanthopleura* is here suggested. In the case of very similar species where the question of conspecificity is still at issue (*A. gaimardi vs. A. japonica,* and *A. granulata vs. A. gemmata*) it was thought preferable to use couplets based upon broad geographic localities rather than give artificial importance to some minor and/or inconstant character. In this manner it is hoped the diagnostic key will better fulfill its main purpose: to provide a practical tool for the nonspecialist.

Diagnostic Key of *Acanthopleura* Species

1. Posterior valve with no insertion teeth 2
   Posterior valve with insertion teeth 6
2. Girdle with scales 3
   Girdle with spinelets 4
3. Girdle scales large (1–2 mm long in large specimens), separated from each other by girdle (Peru–Chile coast) ..... *A. nigra*
   Girdle with moderate size scales (less than 0.5 mm long even in large specimens) relatively close together (southwest Australia) ... *A. hirtosa*
4. Radula major lateral teeth with tetracuspid head ..... *A.* ***rehderi***
   Radula major lateral teeth with discoid head .. 5
5. Specimens from north of Tropic of Cancer (or Gulf of Thailand) ..... *A. japonica*
   Specimens from south of Tropic of Capricorn ..... *A. gaimardi*
6. Posterior valve with well developed insertion teeth 7
   Posterior valve with poorly developed insertion teeth 8
7. Specimens from the Caribbean Sea ... *A. granulata*
   Specimens from the Indo-Pacific ..... *A. gemmata*
8. Girdle with spikelike elements (Peru–Chile) coast ..... *A. echinata*
   Girdle with scales, spines or spinelets but not spikelike elements 9
9. Girdle with long, blackish, thin spines; tegmentum reddish; intermediate valves often two-slitted ..... *A. spinosa*
   Girdle with scales or spinelets; tegmentum gray to dark brown; intermediate valves uni-slitted 10
10. Tegmentum purple-brown to black with coarsely round granules throughout; girdle with equal-sized cylindrical, black (often white-tipped) spinelets; specimens length often attaining 50 mm (Indian Ocean) ..... *A. brevispinosa*
    Tegmentum gray to light brown; girdle elements not usually cylindrical; specimens length rarely attaining 50 mm (Indo-Pacific) 11
11. Girdle with regular, equal-sized elements 12
    Girdle with irregular, unequal-sized elements .. 14
12. Girdle with spinelets ..... *A.* ***arenosa***
    Girdle with scales 13
13. Girdle scales small (up to 400 μm long); pleural areas with granules ..... *A. curtisiana*
    Girdle scales large (up to 800 μm long); pleural areas almost featureless ..... *A. miles*
14. Lateral areas hardly raised; girdle elements variable in size and shape but mostly spinelet-like ..... *A. loochooana*
    Lateral areas markedly raised; girdle elements also variable in shape but mostly scale-like .. .. *A. araucariana*

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