
**Revision of *Acanthopleura* Guilding, 1829 (Mollusca:
Polyplacophora) based on light and electron
microscopy.**

Volume I

**This thesis is presented for the degree of Doctor of Philosophy
of Murdoch University, Western Australia
2003**

Submitted by

Lesley Rita Brooker, B.Sc. (Biology) Murd.

Murdoch University

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I declare that this thesis is my own account of my research and contains, as its main content, work which has not previously been submitted for a degree at any tertiary institution.

Lesley Rita Brooker

Abstract

Light and scanning electron microscopy have been utilized to further resolve the taxonomic status of the genus *Acanthopleura* Guilding, 1829 (Mollusca: Polyplacophora) following Ferreira's 1986 controversial revision, which synonymised four well-established genera and numerous species. Specimens of the 19 nominal species of the genus *Acanthopleura*, together with those from five widely disparate, geographic populations of one of these species (*A. gemmata*), along with specimens of the outgroup, *Onithochiton quercinus* Gould, 1846), have been utilised.

A consideration of gross morphological characters, including features of the valves, girdle armature and gills, clearly separate *A. rehderi* from *Acanthopleura*, aligning it with *Onithochiton*. They also suggest the synonymy of two pairs of species (*A. haddoni*/*A. vaillantii* and *A. testudo*/*A. brevispinosa*), and indicate that *A. loochooana* is closely aligned with species previously assigned to *Squamopleura* (*A. araucariana*, *A. curtisiana* and *A. miles*).

Examination of microstructural characters of the intermediate valve, including features of the tegmental micro architecture, the ocelli, the aesthetes and the central anterior eaves, confirm the conclusions of the gross morphological study, and, in addition, indicate a close relationship between *A. echinata* and *A. nigra*.

Investigation of the girdle armature indicates that *Acanthopleura* can be divided into four groups based on the possession of predominantly scales, spines, spinelets or spicules. However, there is wide intraspecific variation with regard to micro architecture of the girdle elements. This section confirms the close relationships of

A. haddoni/A. vaillantii and *A. testudo/A. brevispinosa*, and suggests affiliations between other species.

A consideration of the morphological and morphometric characters of the radula, including size, shape and orientation of the central, centrolateral, major lateral and uncinal teeth, reveals that there are basically four distinct radula types. The majority of *Acanthopleura* has a similar radula design with dominant, discoid major lateral teeth, and much smaller centrolateral teeth. However, the radulae of *A. echinata* and *A. nigra* have a distinctly robust and angular appearance, those of *A. brevispinosa* and *A. testudo* are long with a greater number of rows of smaller teeth, and that of *A. rehderi* is unique in the shape and orientation of its centrolaterals and the possession of quadricuspid major laterals.

Biom mineralization of the major lateral radular teeth, as determined using energy dispersive spectroscopy, is remarkably consistent for most species of *Acanthopleura*. However, the elemental percentages, and distribution throughout the teeth, indicate a close relationship between *A. loochooana* and the species formerly of the genus *Squamopleura*, while *A. rehderi*, aligns with the outgroup, *O. quercinus*, in its elemental percentages and distribution, and the absence of a lepidocrocite region.

Finally, the total 222 characters examined have been assessed and subjected to cladistic analysis using PAUP (Phylogenetic Analysis Using Parsimony Swofford, 1991), generating a strict consensus tree of 1429 steps in length having a homoplasy index (HI) of 0.6438. However, the high degree of homoplasy in more than 70% of characters has obscured many relationships, preventing a good resolution of the tree. A reassessment of all characters results in a subset of the data containing only characters with unambiguously assigned states, and that have a HI below 0.5. Subsequent cladistic analysis of this data set has resulted in a strict consensus tree of 228 steps in length, having a consistency index of 0.6842 and HI

of 0.3158. When the tree is rooted with *O. quercinus* as the outgroup, *O. quercinus* and *A. rehderi* form sister clades to all other species examined. Hence, on the basis of its separation from all *Acanthopleura* and its conformation to all diagnostic characters for *Onithochiton*, *A. rehderi* is assigned to *Onithochiton*. The consensus tree also depicts a close relationship between *A. echinata* and *A. nigra*, which form a sister clade with all other *Acanthopleura*, while *A. spinosa* forms a sister clade with the remaining species. The tree confirms the close relationship of four of the subpopulations of *A. gemmata*. However, it places the specimens from Guam as a sister clade, supporting separate species status. The Caribbean species, *A. granulata*, is well resolved from *A. gemmata* and confirmed as a valid species. The two Middle Eastern species, *A. vaillantii* from Egypt and *A. haddoni* from Oman, form a tight clade with a limited range of characters separating them, suggesting their synonymy. Similarly, specimens of *A. brevispinosa* from East Africa and *A. testudo* from the Gulf of Oman, also form a tight clade, and the presence of *A. brevispinosa* so far north extends its traditionally recognised range. In support of Ferreira's (1986) synonymy of *Clavarizona*, *Liolophura* and *Squamopleura* with *Acanthopleura*, all species previously assigned to these genera comprise a large clade within *Acanthopleura*.

Fifteen species of *Acanthopleura* Guilding, 1829 are here recognised, of which one is new to science: *A. granulata* (Gmelin, 1791), *A. spinosa* (Bruguère, 1792), *A. gemmata* (Blainville, 1825), *A. hirtosa* (Blainville, 1825), *A. gaimardi* (Blainville, 1825), *A. loochooana* (Broderip & Sowerby, 1829), *A. brevispinosa* (Sowerby, 1840), *A. japonica* (Lischke, 1873), *A. vaillantii* (Rochebrune, 1882), *A. curtisiana* (Smith 1884), *A. miles* (Carpenter in Pilsbry, 1893), *A. araucariana* (Hedley, 1898), *A. tenuispinosa* (Leloup, 1939), *A. arenosa* Ferreira, 1986, *Acanthopleura* spec. nov. The genus *Enoplochiton* Gray, 1847 is comprised of *E. niger* (Barnes, 1824) and *E. echinatus* (Barnes, 1824) (type *Chiton niger* Barnes, 1824 by monotypy). Finally, *A. rehderi* Ferreira, 1986 is assigned to *Onithochiton* as *O. rehderi* (Ferreira, 1986).

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Figure 5.1 Light micrographs showing the variation in the development of the insertion plate of the posterior valve of *Acanthopleura* species.

A, *Acanthopleura spinosa* showing the toothed insertion plate (ip) with distinct slits (dashed arrows) and transverse callus (c).

B, *A. japonica* showing the broad flat insertion plate with round callus just below it.

C and **D**, *A. brevispinosa* and *A. arenosa* displaying an intermediate condition with the insertion plate poorly developed, but not flat, and few slits (dashed arrows) that are degenerate in the centre of the valve.

E, **F** and **G**, specimens of *A. gaimardi*, *A. japonica* and a juvenile *A. hirtosa* exhibiting two small symmetrical notches either side of the valve (arrows).

All scale bars = 2mm.

Figure 5.2: Light micrographs of *Acanthopleura spinosa*.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by a wide girdle covered in long spines. Scale bar = 30mm.

B, dorsal view of an intermediate valve showing smooth tegmentum interrupted by concentric growth lines. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing smooth lateral and plural tegmentum. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing the centro-posterior position of the mucro (solid arrow) and convex post mucral slope (dashed arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing tooth slits and external pectination of the insertion plate. Scale bar = 5mm.

G, ventral view of the round anterior valve. Scale bar = 5mm.

H, ventral view of the whole specimen showing uniform dark cream girdle. Scale bar = 30mm.

Figure 5.3: Light micrographs of *Acanthopleura gemmata* from Okinawa, Japan.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by a banded girdle covered in brown and white spinelets. Erosion of the jugum reveals a dark inner layer of shell. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing tegmental colour pattern. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture of the lateral and plural regions consisting of elongate pustules. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing the posterior position of the mucro (solid arrow) and convex post mucral slope (dashed arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing tooth slits and external pectination of the insertion plate. Scale bar = 5mm.

G, ventral view of the oval anterior valve. Scale bar = 5mm.

H, ventral view of the whole specimen showing ventral girdle that is pale medially with a dark peripheral band and anal wedge. Scale bar = 10mm.

Figure 5.4: Light micrographs of *Acanthopleura gemmata*, from Queensland, Australia.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by a banded girdle covered in brown and cream spinelets. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing tegmental colour pattern. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture of the lateral and plural regions consisting of granules coalesced into raised pustules. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing the posterior position of the mucro (solid arrow) and convex post mucral slope (dashed arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing tooth slits and external pectination of the insertion plate. Scale bar = 5mm.

G, ventral view of the oval anterior valve. Scale bar = 5mm.

Figure 5.5: Light micrographs of *Acanthopleura gemmata*, from Western Australia.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by an irregularly banded girdle covered in brown and cream spinelets. Erosion of the jugum reveals a dark inner layer of shell. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing tegmental colour pattern with dark jugal band and pale parajugal bands. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture of the lateral and plural regions consisting of granules coalesced into round pustules. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing the posterior position of the mucro (solid arrow) and convex post mucral slope (dashed arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing tooth slits and external pectination of the insertion plate. Scale bar = 5mm.

G, ventral view of the oval anterior valve. Scale bar = 5mm.

Figure 5.6: Light micrographs of *Acanthopleura gemmata* from Tanzania.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by an irregularly banded girdle covered in brown and cream spinelets. Erosion of the jugum reveals a dark inner layer of shell. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing tegmental colour pattern with dark jugal band and pale parajugal bands. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture of the lateral and plural regions consisting of flat-topped round to elongate pustules. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing the centro-posterior position of the mucro (solid arrow) and convex post mucral slope (dashed arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing tooth slits and external pectination of the insertion plate. Scale bar = 5mm.

G, ventral view of the oval anterior valve. Scale bar = 5mm.

H, ventral view of the whole specimen showing ventral girdle that is pale medially with a dark peripheral band and anal wedge. Scale bar = 10mm.

Figure 5.7: Light micrographs of *Acanthopleura gemmata* from Pago Bay, Guam.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by a wide girdle covered in long white spines. The distinctive ridged pattern on the lateral triangles is clearly visible on all intermediate valves (arrows). Scale bar = 10mm.

B, dorsal view of an intermediate valve showing tegmental colour pattern. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture of the plural region consisting of parallel ridges and troughs. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing the central position of the mucro (solid arrow) and straight post mucral slope (dashed arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing tooth slits and external pectination of the insertion plate. Scale bar = 5mm.

G, ventral view of the fan-shaped anterior valve. Scale bar = 5mm.

H, ventral view of the whole specimen showing ventral girdle that is pale medially with a narrow dark peripheral band and small anal wedge. Scale bar = 10mm.

Figure 5.8: Light micrographs of *Acanthopleura vaillantii* from Egypt.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by a banded girdle covered in black and white spinelets. The extensive erosion of the valves extends across the jugal, lateral and plural region of the shell. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing tegmental colour pattern. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture of the lateral and plural regions consisting of concentric rows of adpressed granules. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing the posterior position of the mucro (solid arrow) and convex post mucral slope (dashed arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing tooth slits and external pectination of the insertion plate. Scale bar = 5mm.

G, ventral view of the semicircular anterior valve. Scale bar = 5mm.

H, ventral view of the whole specimen showing ventral girdle that is dark brown peripherally and pale cream around the foot. Scale bar = 10mm.

Figure 5.9: Light micrographs of *Acanthopleura haddoni* from Masirah Id., Oman.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by a dark girdle covered in short brown spinelets. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing tegmental colour pattern with dark jugal band and pale parajugal stripes. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture of the lateral and plural regions consisting of concentric rows of granules that are adpressed into laminae on the plural region. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing subterminal position of the mucro (solid arrow) and convex post mucral slope (dashed arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing the well-developed insertion plate that is slitted and extensively pectinate but does not project far beyond the broad flat callus (arrow). Scale bar = 5mm.

G, ventral view of the semicircular anterior valve. Scale bar = 5mm.

Figure 5.10: Light micrographs of *Acanthopleura testudo* from the Gulf of Aden.

A, dorsal view of a whole specimen showing solid, beaked, eroded valves, surrounded by a wide girdle covered in white-tipped, black spinelets. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing tegmental colour pattern along the uneroded growth margins. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture of the lateral and plural regions comprised of small round granules aligned in concentric rows. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of an extremely eroded posterior valve showing the convex post mucral slope (dashed arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing the well developed insertion plate that is slitted and pectinate externally. Scale bar = 5mm.

G, ventral view of the semicircular anterior valve. Scale bar = 5mm.

H, ventral view of the whole specimen showing ventral girdle that is predominantly dark brown with a narrow pale cream region adjacent to the foot. Scale bar = 10mm.

Figure 5.11: Light micrographs of *Acanthopleura granulata* from Florida Keys, USA.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by a banded girdle covered in short brown and cream spinelets. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing tegmental colour pattern that is predominantly pale brown with a brown jugal band and broad, salmon pink parajugal bands. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture of the lateral and plural regions comprised of concentric rows of round granules that coalesce into elongate pustules on the lateral triangle. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing the centro-posterior position of the mucro (solid arrow) and convex post mucral slope (dashed arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing the well developed insertion plate that is slitted and pectinate externally. Scale bar = 5mm.

G, ventral view of the fan-shaped anterior valve. Scale bar = 5mm.

H, ventral view of a whole specimen showing ventral girdle that is cream medially and brown peripherally with a dark anal wedge. Scale bar = 10mm.

Figure 5.12: Light micrographs of *Acanthopleura echinata*, from Peru.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by a wide girdle sparsely covered in long, white-tipped, black spines. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing the uniform brown tegmentum. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture consisting of smooth, featureless jugum, plural region covered in oblique, parallel, longitudinal ridges and lateral triangle with four radial rows of well spaced, large, round pustules. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the wide lateral slits (solid arrows) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing the central position of the mucro (solid arrow) and straight post mucral slope (dashed arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing the distinctly pectinate sinus (solid arrow) and finely pectinate insertion plate that has two poorly developed central (dashed arrows). Scale bar = 5mm.

G, ventral view of the subtriangular anterior valve with wide, well defined slits evenly spaced around the insertion plate. Scale bar = 5mm.

H, ventral view of the whole specimen showing the wide, uniform dark cream girdle. Scale bar = 10mm.

Figure 5.13: Light micrographs of *Acanthopleura brevispinosa* from Tanzania.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by a wide girdle covered in white-tipped, black spinelets. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing predominantly chestnut brown tegmentum with pale jugal stripes. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture comprised of round granules aligned in concentric rows over the central and plural regions while on the lateral triangle they are coalesced into round pustules that are aligned in radial rows and separated by concentric troughs. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing the central position of the mucro (solid arrow) and convex post mucral slope (dashed arrow). Scale bar = mm.

F, ventral view of the posterior valve showing the thin, poorly developed insertion plate with weakly defined teeth that are moderately pectinate. Scale bar = 5mm.

G, ventral view of the fan-shaped anterior valve. Scale bar = 5mm.

H, ventral view of the whole specimen showing ventral girdle that is dark brown peripherally and pale cream around the foot. Scale bar = 10mm.

Figure 5.14: Light micrographs of *Acanthopleura tenuispinosa* from Japan.

A, dorsal view of a whole specimen showing extensively eroded, solid, beaked valves, surrounded by an irregularly banded girdle covered in short, brown and tan spinelets. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing tegmentum predominantly pale cream with erosion of the lateral region revealing brown patches of a lower shell layer. The jugum has a pale central stripe with dark parajugal stripes. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture comprised of ill-defined round granules aligned in concentric ridges. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing the subterminal position of the mucro (solid arrow) and convex post mucral slope (dashed arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing the poorly developed insertion plate with lateral pectination and notches that are obsolete in the centre. Scale bar = 5mm.

G, ventral view of the oval anterior valve. Scale bar = 5mm.

H, ventral view of a whole specimen showing the wide, dark cream/brown girdle. Scale bar = 10mm.

Figure 5.15: Light micrographs of *Acanthopleura japonica* from Hong Kong.

A, dorsal view of a whole specimen showing extensively eroded, solid, beaked valves, surrounded by a wide girdle covered in short, brown and white-tipped brown spinelets. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing predominantly dark brown tegmentum with pale region parajugally. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture at the shell margins comprised of ill-defined round granules that align in concentric ridges. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the extensively eroded posterior valve showing the tegmentum (solid arrow) extending beyond the articulamentum (dashed arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing the broad, flat insertion plate (solid arrow) and round callus (dashed arrow). Scale bar = 5mm.

G, ventral view of the semicircular anterior valve. Scale bar = 5mm.

H, ventral view of a whole specimen showing the uniform dark cream girdle and gills with a large interspace separating them from the stalked anus (arrows). Scale bar = 10mm.

Figure 5.16: Light micrographs of *Acanthopleura gaimardi* from NSW, Australia.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by a banded girdle covered in black and white spinelets. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing tegmentum that is predominantly cream and brown with a dark jugal band and pale then dark parajugal stripes. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture comprised of the small granules adpressed into concentric ridges over the central, plural and lateral regions. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing the subterminal position of the mucro (solid arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing the flat insertion plate, devoid of notched or slits. Scale bar = 5mm.

G, ventral view of the semicircular anterior valve. Scale bar = 5mm.

Figure 5.17: Light micrographs of *Acanthopleura arenosa* from Qld., Australia.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by an irregularly banded girdle covered in brown and cream spinelets. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing brown tegmentum with a dark brown jugal band and broad, pale parajugal bands. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture comprised of ill defined, round granules aligned in concentric ridges over the central and plural regions and coalesced into randomly scattered, round to elongate pustules over the lateral regions. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing the centro-posterior position of the mucro (solid arrow) and convex post mucral slope (dashed arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing the thin, poorly developed insertion plate with incomplete slits laterally. Scale bar = 5mm.

G, ventral view of the oval anterior valve. Scale bar = 5mm.

H, ventral view of a whole specimen showing the uniform cream girdle. Scale bar = 10mm.

Figure 5.18: Light micrographs of *Acanthopleura hirtosa* from Western Australia.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by a banded girdle covered in black and white scales. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing tegmentum that is predominantly black and brown with a dark jugal band and creamy yellow parajugal stripe. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture comprised of low profile elongate pustules that form into concentric ridges on the central region, and aligned in concentric rows on the lateral and plural regions. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing the subterminal position of the mucro (solid arrow) and convex post mucral slope (dashed arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing the flat insertion plate (dashed arrow) with a thin ridge along the posterior margin (arrow). Scale bar = 5mm.

G, ventral view of the fan-shaped anterior valve. Scale bar = 5mm.

H, ventral view of a whole specimen showing the uniform cream girdle. Scale bar = 10mm.

Figure 5.19: Light micrographs of *Acanthopleura loochooana* from Okinawa, Japan.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by a girdle covered in variously shaped scales. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing tegmentum predominantly cream and brown with a dark brown jugal band. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture comprised of small, raised, round granules aligned in concentric rows on the central region, coalesced into wavy ridges over the plural region and formed into randomly scattered, round pustules on the lateral regions. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing the subterminal position of the mucro (solid arrow) and convex post mucral slope (dashed arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing the poorly developed insertion plate with moderately pectinate teeth and two to four slits restricted to the lateral region. Scale bar = 5mm.

G, ventral view of the fan-shaped anterior valve. Scale bar = 5mm.

H, ventral view of a whole specimen showing the uniform cream girdle. Scale bar = 10mm.

Figure 5.20: Light micrographs of *Acanthopleura nigra* from San Bartolo, Peru.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by a wide girdle covered in large subrectangular scales. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing light brown tegmentum with darker brown patches. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture that is smooth over the central region and forms distinctive deep furrows that are oblique on the plural region and concentric on the lateral triangle. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the pectinate sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing terminal position of the mucro (solid arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing the broad, flat, featureless insertion plate. Scale bar = 5mm.

G, ventral view of the oval anterior valve. Scale bar = 5mm.

H, ventral view of a whole specimen showing the uniform cream girdle and holobranchial gills that extend posteriorly to meet beyond the anus (solid arrow) and anteriorly beyond the head/foot junction (dashed arrow). Scale bar = 10mm.

Figure 5.21: Light micrographs of *Acanthopleura araucariana* from New Caledonia.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by a wide girdle covered in large, separate scales. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing tegmentum predominantly cream and tan with a black/brown jugal band. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture comprised of round, raised granules aligned in concentric rows on the central and plural regions and coalesced into rows of pustules on the lateral regions. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing the centro-posterior position of the mucro (solid arrow) and convex post mucral slope (dashed arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing the well developed insertion plate with strongly pectinate teeth. Scale bar = 5mm.

G, ventral view of the fan-shaped anterior valve. Scale bar = 5mm.

H, ventral view of a whole specimen showing the uniform cream girdle and holobranchial gills with a large interspace. Scale bar = 10mm.

Figure 5.22: Light micrographs of *Acanthopleura curtisiana* from Western Australia.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by a wide girdle, banded in brown and yellow small, imbricating scales. Scale bar = 5mm.

B, dorsal view of an intermediate valve showing predominantly tan tegmentum with a dark brown jugal band. Scale bar = 2mm.

C, higher magnification of the valve in **B** showing tegmental sculpture comprised of oval, raised granules aligned in longitudinal rows over the central and plural regions and randomly scattered on the lateral triangle. Scale bar = 2mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 2mm.

E, lateral view of the posterior valve showing the centro-posterior position of the mucro (solid arrow) and convex post mucral slope (dashed arrow). Scale bar = 2mm.

F, ventral view of the posterior valve showing the poorly developed insertion plate with weakly pectinate teeth. Scale bar = 2mm.

G, ventral view of the fan-shaped anterior valve. Scale bar = 2mm.

H, ventral view of a whole specimen showing the uniform cream girdle and holobranchial gills with a large interspace. Scale bar = 5mm.

Figure 5.23: Light micrographs of *Acanthopleura miles* from Indonesia.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by a girdle covered in cream and black, imbricating scales. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing tegmentum predominantly cream and brown. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing tegmental sculpture comprised of concentric rows of round to elongate, raised granules over the central and plural regions with large irregular pustules randomly scattered over the lateral triangle. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the smooth sinus (solid arrow) and subtriangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing the centro-posterior position of the mucro (solid arrow) and convex post mucral slope (dashed arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing the thin, poorly developed insertion plate with weakly pectinate teeth that are obsolete in the centre. Scale bar = 5mm.

G, ventral view of the fan-shaped anterior valve. Scale bar = 5mm.

H, ventral view of a whole specimen showing the uniform cream girdle. Scale bar = 10mm.

Figure 5.24: Light micrographs of *Acanthopleura rehderi* from the Cook Is.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by a banded girdle covered in minute, white and brown spinelets. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing tegmental colour pattern. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing the smooth central tegmentum, raised parallel ridges on the plural region and concentrically orientated elongate pustules on the lateral triangle. There is a single, radial row of round ocelli. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the pectinate sinus (solid arrow) and triangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing the terminal position of the mucro (solid arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing the porcelaneous texture of the articulamentum, and the insertion plate (arrow) merged with the round transverse callus (dashed arrow). Scale bar = 5mm.

G, ventral view of the fan-shaped anterior valve. Scale bar = 5mm.

H, ventral view of a whole specimen showing the uniform cream girdle and the distinctive mantle flap (arrows) either side of the anus. Scale bar = 10mm.

Figure 5.25: Light micrographs of *Onithochiton quercinus* from Western Australia.

A, dorsal view of a whole specimen showing solid, beaked valves, surrounded by a girdle covered in minute orange and white spinelets. Scale bar = 10mm.

B, dorsal view of an intermediate valve showing the glossy, orange and cream tegmentum. Scale bar = 5mm.

C, higher magnification of the valve in **B** showing the essentially smooth central and plural region and concentric furrows that dominate the lateral triangle. Scale bar = 5mm.

D, ventral view of an intermediate valve showing the pectinate sinus (solid arrow) and triangular sutural laminae (dashed arrows). Scale bar = 5mm.

E, lateral view of the posterior valve showing the terminal position of the mucro (solid arrow). Scale bar = 5mm.

F, ventral view of the posterior valve showing the porcelaneous texture of the articulamentum, and the insertion plate (arrow) merged with the round transverse callus (dashed arrow). Scale bar = 5mm.

G, ventral view of the fan-shaped anterior valve. Scale bar = 5mm.

H, ventral view of a whole specimen showing the uniform cream girdle. Scale bar = 10mm.

Figure 6.1: Scanning electron micrographs of the intermediate valve of *Acanthopleura spinosa*.

A, lateral area of the shell viewed from the jugum showing the microtexture consisting of thin transverse furrows following the contours of the shell (arrowhead) and subdivided by finer, perpendicular grooves (dashed arrow). A single round, raised ocellus is surrounded at its base by numerous pores (solid arrows). Scale bar = 50 μ m.

B, lateral area of the shell viewed from the lateral margin showing the pores surrounding the ocellus (solid arrow), which are intermediate in size to the micro- (dashed arrow) and megalopores (arrow head) in the remainder of this region of the shell. Note that each megalopore is encircled by numerous micropores in this region. Scale bar = 100 μ m.

C, central region of the shell with sparse megalopores (solid arrow) and few micropores (dashed arrows) associated with them. Scale bar = 20 μ m.

D, central eaves comprised of two distinct layers: the thick suprategmentum (su) perforated by sparse, oval, channel openings (solid arrows), overhanging the subtegmentum (sb) to such an extent that it is shadowed. Scale bar = 50 μ m.

E, lateral eaves in region of slit-ray notch, showing several, circular, horizontal channel openings (solid arrow) in the subtegmentum. Scale bar = 500 μ m.

F, central eaves with aesthete body under construction, comprised of a short narrow neck (arrowhead) that bulges sharply into a broad chamber (solid arrow), with micraesthete channels opening at the top of the chamber (dashed arrows). Scale bar = 20 μ m.

Figure 6.2: Scanning electron (SEM) and light micrographs (LM) of the intermediate valve of the intermediate valve of *Acanthopleura gemmata*, specimen from Okinawa, Japan.

A, SEM of the central region showing raised, round topped, close-packed, microgranules (dashed arrows) that are uniform in size and generally distributed in an offset pattern in consecutive rows, but occasionally occur in continuous rows (solid arrow). Scale bar = 200 μ m.

B, SEM of the lateral region showing regular arrangement of fine grooves that run both transversely and longitudinally, criss-crossing the entire tegmentum including the granules (solid arrows). Scale bar = 50 μ m.

C, SEM of the lateral region showing random distribution of ocelli in anterior three quarters and location in depressions between the large pustules (solid arrows). Scale bar = 1mm.

D, LM of same region of shell as in **C** showing highly refractive, round ocelli (solid arrows point to the same ocelli as in **C**). Scale bar = 1mm.

E, SEM of the lateral region viewed from lateral side showing distinctly convex, somewhat round ocelli, that tend towards triangular in shape (solid arrows), having a slightly flattened medial edge and distinctly tapering lateral edge. Scale bar =100 μ m.

F, SEM of the lateral triangle viewed from the jugal side showing three ocelli each with a single large medial pore (solid arrow). The aesthetes are mainly distributed in the valleys between pustules but do extend to a limited degree over the pustules themselves (dashed arrows). Scale bar =100 μ m.

Figure 6.3: Scanning electron micrographs of the intermediate valve of specimens of *Acanthopleura gemmata*. **A-C**, specimen from Okinawa, Japan; **D**, specimen from Misali Id., Tanzania.

A, damaged region of the central eaves showing thick suprategmentum overhanging thinner subtegmentum, the latter layer being perforated by a row of small, vertically compressed, channel openings (solid arrows) that are restricted to the region immediately dorsal to the articulamentum. Scale bar = 500 μ m.

B, central eaves with two aesthete bodies under construction (solid arrows), comprised of a flared megalopore that narrows into a long neck, prior to bulging into a broad round chamber and showing micraesthete channels (dashed arrow) penetrating the tegmentum vertically for some distance before angling towards the megal aesthete and opening into the lower half of the chamber. Scale bar = 50 μ m.

C, lateral eaves showing ocellus formation, with thin, bi-convex lens (solid arrow) fully formed and clearly visible below a dorsal covering that is contiguous with the tegmental surface. Scale bar = 50 μ m.

D, a section of shell that has been broken in the central region, perpendicular to the eaves and parallel to the growth of the shell, showing two aesthete bodies in cross section (solid arrows). The flared apical pore narrows into a short neck, prior to flaring into a wide chamber, which almost immediately angles obliquely towards the eaves. The dashed line represents a perpendicular section through the aesthete body that would result in a shape similar to that for the Okinawa specimen in **B**. Scale bar = 100 μ m.

Figure 6.4: Scanning electron (SEM) and light micrographs (LM) of the intermediate valve of a specimen of *Acanthopleura gemmata* from Pago Bay, Guam.

A, SEM of the lateral region showing ocelli (dashed arrows) and barely raised granules (solid arrows). Scale bar = 100 μ m.

B, SEM of the central region of the shell devoid of granules and with megalopores (solid arrows) flush with the tegmentum. Scale bar = 50 μ m.

C, SEM of the lateral ocelli (solid arrows) viewed from the jugal side each with a small, round, medial pore (dashed arrow) and with associated subsidiary pores arranged in rows. Scale bar = 50 μ m.

D, LM of an intermediate valve showing parajugal band of diamond shaped pustules (solid arrows), comprised of numerous smaller granules, longitudinal sulcate ribs (dashed arrows) of the pleural region and small discrete roundish pustules covering the lateral region (top right). Scale bar = 1mm.

E, SEM of the lateral region with a large pustule (solid arrow) that is devoid of aesthete pores (cf. Fig. 6.2F). Scale bar = 100 μ m.

F, SEM of the central region of shell showing wide eaves with reduced porosity compared to other *A. gemmata* specimens (cf. Fig.6.2B), and upper layer of suprategmentum with only occasional pores. Scale bar = 100 μ m.

G, SEM of the lateral eaves showing megal aesthetes (solid arrows) in formation with micraesthetes (dashed arrow) entering just below the neck. Scale bar = 100 μ m.

H, SEM of the section of shell broken in the central region perpendicular to the eaves showing aesthete bodies in longitudinal section (solid arrows) that extend for some distance vertically prior to angling towards the eaves. Scale bar = 200 μ m.

Figure 6.7: Scanning electron (SEM) and light micrographs (LM) of the intermediate valve of *Acanthopleura testudo* from Djibouti, Gulf of Aden.

A, LM of the central region of an intermediate valve showing extensive tegmental erosion over all but the shell margin, with micro-granulose structure near the margins (solid arrow). Scale bar = 1mm. **B,** SEM of the central region of a valve broken perpendicular to the eaves and parallel to the growth of the shell, showing an aesthete body in longitudinal section (solid arrow) with all micraesthete channels (dashed arrows) entering the megal aesthete body just as the narrow neck widens into the aesthete chamber. Scale bar = 20 μ m.

C, SEM of the central region showing flat-topped granules arranged in quincunx (solid arrows). Scale bar = 100 μ m

D, SEM of the lateral region showing elongate ocelli (solid arrows), with a single central megalopores (dashed arrow) situated atop the barely raised granules. Scale bar = 100 μ m

E, low power SEM of lateral region showing concentric arrangement of round pustules. Scale bar = 1mm

F, LM of lateral region of an eroded shell showing round reflective ocelli arranged in roughly concentric over the periphery of the lateral region (solid arrow). Scale bar = 1mm

G, SEM of the central eaves showing polygonal microstructure of upper supra-tegmental layer with sparse, large channel openings (solid arrows) and a single aesthete body under construction with flared opening, narrow neck and a ring of micraesthete openings (dashed arrow). Scale bar = 50 μ m

H, SEM of the central region of a valve, broken perpendicular to the eaves, showing two megal aesthete chambers in longitudinal section (solid arrows) penetrating the tegmentum for a substantial distance before angling acutely towards the eaves. Scale bar = 100 μ m

Figure 6.8: Scanning electron (SEM) and light micrographs (LM) of the intermediate valve of *Acanthopleura granulata* from Florida Keys.

A, LM showing the shell to be micro-granulose over its entirety, with a tendency for the granules to coalesce into concentric rows, forming adpressed lamellae across the central region (solid arrows). The ocelli are randomly distributed over the anterior 1/3 of the lateral region (dashed arrow), and in addition are found in a narrow band on the plural region of the intermediate valves of some specimens (arrowhead). Scale bar = 5mm

B, SEM of the lateral region showing a single oval to egg-shaped ocelli with a distinctly tapering lateral edge (solid arrow), with the exception of one large medial pore, the micropores associated with each ocellus are predominantly clustered around the base of the lateral half (dashed arrows). Scale bar = 50µm

C, SEM of the central eaves showing the suprategumentum consisting of two distinct layers: a smooth upper layer (up), constituting the raised mounds of the microgranules, and a coarsely honeycombed lower layer (lw) that is perforated by a moderate amount of round to oval oblique channel openings (solid arrows). Scale bar = 100µm

D, SEM of the lateral eaves showing aesthete bodies under construction that are similar in shape to those of *A. gemmata* (cf. fig: 6.4B) consisting of a short neck that widens abruptly into a rounded chamber. Scale bar = 100µm

Figure 6.9: Scanning electron (SEM) and light micrographs (LM) of the intermediate valve of *Acanthopleura echinata* from San Bartolo, Peru.

A, LM showing the smooth, barely raised lateral triangle, clearly delineated by a row of large, round, smooth pustules along its anterior border (solid arrows), and two or three additional radial rows of round pustules (dashed arrows). Numerous minute, blue, teardrop shaped ocelli are distributed throughout the lateral triangle. Scale bar = 2mm.

B, SEM of the lateral region viewed from the lateral side showing oval, barely raised ocelli that have a wider lateral (solid arrows), and more tapered medial side (dashed arrows). Megalopores and micropores are flush with the tegmental surface and aligned in parallel longitudinal rows, with the latter evenly spaced and the former offset in consecutive rows. Scale bar = 50µm

C, SEM of the central eaves showing the extension of the tegmentum into a “V” shape, making it much thicker in the central than the parajugal region. The suprategmentum (su) consists of a smooth upper layer (up) and granulose lower layer (lw) and overhangs the subtegmentum (sb). Both regions are perforated by numerous holes, with the relative size of pores becoming progressively larger ventrally. Scale bar = 100µm.

D, SEM of the central region showing “V” shaped central eaves (solid arrow) and distinctively toothed sinus plate (dashed arrow), compare to the smooth plate of most other species (e.g. Figs. 6.4.A, 6.6.D). Scale bar = 500µm

E, SEM of the central eaves with a megalaesthete under construction, comprised of a long narrow tube (solid arrow) that does not widen into the chamber (typical of other species), micraesthetes are even narrower tubes (dashed arrows) that descend vertically and do not merge into the megalaesthete. Scale bar = 20µm.

F, SEM of the lateral eaves showing megalaesthetes (solid arrows) similar in structure and arrangement to those of the central eaves, however, with occasional micraesthetes (dashed arrow) that angle to enter the megalaesthete tubes. Scale bar = 100µm.

G, SEM of the lateral eaves showing an ocellus under construction with aesthete channels from numerous earlier rows entering the ocellus chamber (dashed arrows). Scale bar = 20µm.

H, SEM of an ocellus with a relatively thick, double convex, oval lens (solid arrow), (compare with the thinner round lens of other species (e.g. Fig. 6.3C)). Scale bar = 20µm.

Figure 6.10: Scanning electron (SEM) and light micrographs (LM) of the intermediate valve of *Acanthopleura brevispinosa* from Unguja Id., Tanzania.

A, SEM of central region showing pyramidal formations of granules in the parajugal region (solid arrows). Scale bar = 100 μ m.

B, SEM of the lateral region showing distinctly triangular shaped ocelli (solid arrows), crater-like megalopores (dashed arrow) situated atop the raised granules and surrounded by a ring of micropores. Scale bar = 100 μ m.

C, low power SEM of lateral region showing concentric and radial arrangement of round pustules, tending more elongate along anterior edge and extending slightly into plural triangle (solid arrow). Note also the distinct concentric growth (dashed arrows). Scale bar = 1mm.

D, SEM of the lateral region from medial perspective showing coarse microstructure with concentric grooves and ridges (solid arrow), and featuring a single ocellus with large, slit-like medial pore (dashed arrow). Scale bar = 20 μ m. **E,** LM of the lateral region showing tendency of the oval ocelli to align in the depression between the radial rows of small round pustules (solid arrows). Scale bar = 1mm

F, SEM of lateral region showing arrangement of elongate ocelli (solid arrows) and aesthetes (dashed arrows) in valleys between pustules (arrowheads). Scale bar = 200 μ m.

Figure 6.11: Scanning electron micrographs of the intermediate valve of *Acanthopleura brevispinosa* from Unguja Id., Tanzania.

A, central eaves showing polygonal microstructure of upper layer of suprategmentum. Scale bar = 10 μ m.

B, central eaves showing scarcity of pores in upper region of suprategmentum in comparison to the numerous round, almost vertically, opening channels in the lower region of the suprategmentum as it curves under. Scale bar = 50 μ m.

C, central eaves showing suprategmentum overhanging subtegumentum, which features round, horizontal openings of multi-branched channels (arrows). Scale bar = 200 μ m.

D section of central region of shell, broken perpendicular to eaves, showing megal aesthete chambers with micraesthetes entering just below the narrow neck (arrows). Scale bar = 20 μ m.

E, central region of shell broken perpendicular to eaves showing numerous megal aesthetes with long tubular chambers that are aligned vertically until they join into the horizontal multi-branch channels (arrows). Scale bar = 100 μ m.

Figure 6.12: Scanning electron (SEM) and light micrographs (LM) of the intermediate valve of *A. tenuispinosa* from Ikenma Id., Japan.

A, SEM of the lateral region viewed from the medial side showing regular arrangement of coarse ridges and troughs (solid arrows) running both transversely and longitudinally. An egg-shaped ocellus is present with lens situated medially (dashed arrow), it features numerous micropores around the base and a single central pore on the convex medial surface (arrowhead). Scale bar = 500 μ m.

B, SEM of the central region showing regular arrangement of criss-crossed ridges and troughs and raised, round, micro-granules arranged in quincunx (solid arrows), with a central megalopore and frequently two megalopores merged together (dashed arrows), surrounded by numerous micropores aligned in the troughs (arrowhead). Scale bar = 50 μ m.

C, LM of the lateral and plural region showing distribution of ocelli in two distinct bands over the lateral plural (solid arrow) region and anterior 1/3 of lateral triangle (dashed arrow). Scale bar = 50 μ m.

D, SEM of the lateral region showing randomly distributed apical pores situated atop slightly raised granules (arrows). Scale bar = 100 μ m.

E, SEM of the central eaves showing the thick supratégmentum perforated by sparse, large, round, oblique channel openings, with frequently two or more channels merging into one large opening (solid arrows), This layer extensively overhangs the thinner subtegumentum, which contains much smaller, oval, horizontal openings (dashed arrow). Scale bar = 50 μ m.

F, SEM of the lateral eaves with an ocellus (solid arrow) and an aesthete body (dashed arrow) under construction. The megal aesthete had a short neck that barely widens into a chamber (arrowhead), which penetrates vertically for some distance. Scale bar = 50 μ m.

Figure 6.13: Scanning electron (SEM) and light micrographs (LM) of the intermediate valve of *Acanthopleura japonica* from Cape d'Aguilar, Hong Kong.

A, LM of the lateral and plural region of valve showing extensive erosion typical of all *A. japonica* specimens and distribution of ocelli across three quarters of the lateral triangle (solid arrow) and half of the plural region (dashed arrow) at uneroded margins. Scale bar = 500 μ m

B, SEM of the anterior central region showing barely raised granules, coarsely, criss-crossed micro texture and sparse distribution of megalopores (solid arrow) and micropores (dashed arrow). Scale bar = 100 μ m

C, SEM of a section of the lateral triangle viewed from the medial side showing a single, round ocellus with a lateral fissure (solid arrow), a single large slit-like medial pore, and surrounded by numerous micropores. Scale bar = 50 μ m

D, SEM of the central anterior eaves showing homogeneous nature of the suprategmentum with very few pores (arrows). Scale bar = 520 μ m

E, SEM of the suprategmentum of the lateral eaves comprised of two distinct layers, a coarsely granular upper layer (up), containing an ocellus at a late stage of construction with a lateral cleft present (solid arrow), and a smoother lower layer (lw) containing sparse small, round, oblique holes (dashed arrows). Scale bar = 50 μ m

Figure 6.14: Scanning electron (SEM) and light micrographs (LM) of the intermediate valve of *Acanthopleura gaimardi* from Queensland, Australia.

A, LM of the lateral and plural region showing shell sculpture comprised of granules adpressed into transverse lamellae (solid arrow) and distribution of ocelli in two bands over the lateral plural region (dashed arrow) and anterior 1/3 of lateral triangle (arrowhead). Scale bar = 500 μ m.

B, SEM of the central region showing low profile, flat-topped microgranules adpressed into rows, with at least one, and frequently two megalopores (solid arrows) in the centre of each granule and high density of micropores. Scale bar = 100 μ m.

C, SEM of the lateral region viewed from the medial side showing regular arrangement of fine transverse and longitudinal grooves, presence of numerous micropores arranged in transverse rows (solid arrows) and featuring a two ocelli (arrowhead) that are slightly wider medially than laterally and have a prominent medial pore (dashed arrows). Scale bar = 50 μ m.

D, SEM of the central eaves showing supratsegmentum perforated with a moderate number of large, round to oval, oblique channel openings, with frequently two or more channels merging into one large opening (arrows). Scale bar = 100 μ m.

E, SEM of the lateral eaves showing an aesthete body under construction, comprised of a very short neck that widens into an elongate chamber, into which the preceding megal aesthete channel (solid arrow) and numerous micraesthete channels (dashed arrows) open. Scale bar = 50 μ m.

F, SEM of the lateral eaves showing disjunction (solid arrow) between the upper (up) and lower (lw) supratsegmentum and three ocelli (dashed arrows) at various stages of construction, with two radial rows of micraesthete channels (arrow heads) opening into the chamber beneath the thick, oval, bi-convex lens. Scale bar = 100 μ m.

Figure 6.15: Scanning electron (SEM) and light micrographs (LM) of the intermediate valves of *Acanthopleura arenosa* from Queensland, Australia and *A. gemmata* from Western Australia.

A, SEM of the central region showing tendency for the micro-granules to form into adpressed, concentric lamellae (arrows). Scale bar = 500µm

B, SEM of the central region showing low profile, flat-topped micro-granules with at least one, and frequently two or more megalopores (solid arrow) in the centre of each granule. Note the relatively low density of micropores (compare with *A. gaimardi* Fig. 6.14B). Scale bar = 50µm

C, SEM of the lateral region showing the granules formed into large, smooth-topped, elongate pustules (solid arrows). Scale bar = 200µm

D, LM of the lateral region showing predominantly oval ocelli (arrows). Scale bar = 500µm.

E, LM of the lateral region of an intermediate valve of a specimen of *A. gemmata* from Western Australia, showing the typical round ocelli of this species, surrounded by a thin circle of pigment (arrows). Scale bar = 200µm.

F, SEM of the central eaves of *A. arenosa* showing two rows of oblique channel openings (solid arrows) typical of species whose granules are adpressed into rows. Scale bar = 200µm

Figure 6.16: Scanning electron (SEM) and light micrographs (LM) of the intermediate valve of *Acanthopleura hirtosa* from Perth, Western Australia.

A, LM of the lateral and plural region showing granules formed into adpressed lamellae on central region (solid arrow), concentric rows of elongate pustules on lateral region and ocelli covering anterior 1/3 of lateral triangle (dashed arrows). Scale bar = 500 μ m.

B, SEM of the lateral region showing fine micro-texture of concentric ridges and troughs, large, elongate pustules (arrowheads) pitted by apical pores (solid arrows), granules with central apical pores (diamond arrows) and tear-drop shaped ocelli (dashed arrows) lying in the valleys between pustules. Scale bar = 200 μ m.

C, SEM of the central region of the shell showing a single lamella with numerous apical pores, subsidiary pores are difficult to see at this magnification due to their small size and the fact that the pores are mostly intact, so do not contrast well with the remainder of the tegmentum. Scale bar = 50 μ m.

D, SEM of the lateral region viewed from the medial side showing: a single ocellus with medial pore (dashed arrow) and subsidiary pores roughly aligned in radial rows (solid arrows). Scale bar = 100 μ m.

E, SEM of a broken section of shell in region of lateral eaves showing several megalaesthete (solid arrows) and a single ocellus (dashed arrow) chamber in longitudinal section. The megalaesthete has a narrow neck and widens gradually into the chamber, which penetrates the shell vertically for some distance prior to angling towards the eaves. Scale bar = 50 μ m.

F, SEM of several aesthete complexes in longitudinal section showing the micraesthetes channels penetrating vertically (solid arrows) prior to angling towards the megalaesthete and entering low down in the chamber (dashed arrow). Scale bar = 50 μ m.

Figure 6.17: Scanning electron (SEM) and light micrographs (LM) of the intermediate valve of *Acanthopleura loochooana* from Okinawa, Japan.

A, LM showing the granules arranged into transverse lamellae on the central region (dashed arrow), arranged into parallel rows on the plural region (arrowheads) and coalesced into larger pustules on the lateral triangle (solid arrows). Scale bar = 100 μ m.

A, SEM of the central region showing granules coalesced into concentric ridges (arrows) on the central region. Scale bar = 200 μ m.

C, SEM of a section of the lateral triangle showing the extensive erosion that has resulted in the loss of most of the apical caps, leaving large holes in the tegmentum (arrows). Scale bar = 200 μ m.

D, SEM of a single ocellus with the periostracum removed and outer tegmentum eroded revealing the ocellus lens (solid arrow), while some of the subsidiary pores associated with the ocellus are eroded (dashed arrow), the apical pores are relatively intact (diamond head arrow). Scale bar = 20 μ m.

E, SEM of a section of the central, anterior eaves showing well-spaced, oval, oblique channel opening in the suprategmentum (solid arrows) and small, vertically compressed openings in the subtegumentum (dashed arrows). Scale bar = 100 μ m

Figure 6.18: Scanning electron (SEM) and light micrographs (LM) of the intermediate valve of *Acanthopleura nigra* from San Bartolo, Peru.

A, LM of the lateral region showing the smooth tegmentum, with deep concentric furrows separating rounded plateaus (solid arrows) that are covered in numerous minute, blue, oval ocelli. Scale bar = 1mm.

B, SEM of the lateral region featuring a single, oval, barely raised, ocellus (solid arrow) displacing and distorting the subsidiary pores that are otherwise evenly spaced along longitudinal rows (dashed arrows), with apical pores offset from each other in adjacent rows (arrowheads). Scale bar = 20 μ m.

C, SEM of the central region showing arrangement and density of subsidiary and apical pores and the distinct extension of the suprategmentum into a “V” shape (arrow). Scale bar = 500 μ m.

D, SEM of the central eaves showing two distinct layers of the tegmentum with the suprategmentum (su) overhanging the recessed subtegumentum (sb). The suprategmentum is further divided into three layers: a smooth upper layer (up) containing numerous vertical micra- and megalaesthete channels in longitudinal section; a more coarse middle layer (m) that is perforated with numerous oblique channel openings, and finally a coarse lower layer (lw) containing large, horizontally projecting plates (solid arrows). Scale bar = 100 μ m.

E, SEM of a section of the suprategmentum showing long narrow tube-like megalaesthetes (solid arrows) with numerous micraesthete channels extending horizontally for some distance and often converging prior to angling towards, and opening into, the aesthete complex (dashed arrows). Scale bar = 20 μ m.

Figure 6.21: Scanning electron (SEM) and light micrographs (LM) of the intermediate valve of *Acanthopleura miles* from Western Australia.

A, LM showing granules arranged in concentric rows across the central and plural region (solid arrows) and coalesced into large round pustules on the lateral triangle (dashed arrows). Scale bar = 500 μ m

B, SEM clearly showing the large, round, discrete pustules (solid arrows) aligned in a row delineating the lateral and plural triangles and in radial rows on the lateral region (dashed arrows). Scale bar = 500 μ m

C, SEM of the central region showing apical pores atop the granules that are coalesced into concentric ridges (arrows). Scale bar = 200 μ m

D, SEM of the lateral region showing tegmentum crowded with prominent, raised granules (solid arrows); apical pores (dashed arrows) atop the granules and over the large pustule (top right); subsidiary pores covering the entire tegmentum and a round, raised ocellus (arrow head). Scale bar = 50 μ m.

E, SEM of the lateral region viewed, from the jugal side, showing an ocellus with a distinctive pore on the medial side (arrow). Scale bar = 50 μ m.

F, SEM of the central, anterior eaves showing channel openings. Note that the apical pores atop the raised granules penetrate the tegmentum for some distance prior to opening into a wide, round chamber (arrows). Scale bar = 50 μ m

G, SEM of the central eaves of a worn valve showing sparse, round to oval channel openings (solid arrows) in the suprategmentum and smaller, oval, horizontal openings (dashed arrows) in the recessed subtegmentum. Scale bar = 100 μ m.

Figure 6.22: Scanning electron (SEM) and light micrographs (LM) of the intermediate valve of *Acanthopleura rehderi* from Palmerston Id., Cook Is.

A, SEM of the lateral and plural region showing longitudinal riblets (solid arrows) on the plural region and slightly raised lateral area with radial rows of round to oval pustules (dashed arrows). Scale bar = 1mm.

B, LM of the lateral area of an intermediate valve showing a single row of small, round ocelli (arrows). Scale bar = 1mm.

C, SEM of the lateral region showing subsidiary pores evenly spaced along parallel, longitudinal rows (solid arrows), and apical pores offset from each other in consecutive rows (dashed arrows). A single round convex ocellus (arrowhead) lies in a tegmental depression. The surrounding subsidiary pores are distorted in shape by the depression around the ocellus, which also displaces them out of their linear alignment. Scale bar = 50µm.

D, SEM of the central region showing arrangement of subsidiary and apical pores in parallel rows. The eaves are thick with several aesthete chambers in longitudinal section while the subtegmenum contains a row of horizontally projecting, articulamental teeth (solid arrows).

Scale bar = 200µm.**E,** SEM of the anterior central eaves in the parajugal region showing: the smooth, upper (up) suprategmenum (su) with an aesthete complex (arrowhead) under construction, which has a long vertical micraesthete channel (dashed arrow) angling to enter the megalaesthete chamber and channels from previous rows of aesthetes entering the chamber below this (solid arrows). The coarse, lower suprategmenum (lw) has several oblique aesthete channel openings and vertical openings under the overhang. Horizontal openings can also be seen in the subtegmenum (sb). Scale bar = 50µm.

Figure 6.23: Scanning electron (SEM) and light micrographs (LM) of the intermediate valve of *Onithochiton quercinus* from Perth, Western Australia.

A, LM of the lateral and plural region showing the smooth, polished tegmental surface. Fine transverse lines extend across the central and plural regions of the valve and the scarcely raised lateral triangle is marked by coarse longitudinal furrows (dashed arrows). The oval ocelli (solid arrows) are aligned in radiating rows along the anterior diagonal of the lateral area. Scale bar = 500 μ m

B, SEM of the lateral region viewed from the medial side showing: two oval, rather flat ocelli (solid arrows) set in a tegmental depression and surrounded by slit-like subsidiary pores that have been distorted in shape and displaced from their linear arrangement. A large round to elliptical pore lies on the tegmental surface medial to the ocellus (dashed arrows). Apical and subsidiary pores are flush with the tegmental surface and aligned in parallel longitudinal rows, with the subsidiary pores evenly spaced, and the apical pores (arrowheads) offset from each other in consecutive rows. Scale bar = 50 μ m.

C, SEM of the anterior central eaves showing the suprategmentum perforated by numerous oblique aesthete channel openings. The subtegmentum contains many horizontal channel openings (dashed arrow) and intercalated within it is an articulamental plate divided into several horizontally projecting teeth (solid arrows). Scale bar = 200 μ m.

D, SEM of the anterior central eaves showing the suprategmentum consisting of a smooth upper layer containing numerous aesthete complexes (solid arrows) under construction in longitudinal section. The megalaesthete bodies are comprised of a flared opening and short narrow neck that widens abruptly into a large vertical chamber, the micraesthete channels penetrate vertically for some distance prior to angling towards the chamber, forming a ring of holes (dashed arrow) at approximately the same depth in all complexes. The coarsely granular lower layer of the suprategmentum contains numerous round channel openings (arrowheads). Scale bar = 50 μ m.

Figure 7.25 Scanning electron micrographs of the girdle elements of a number of species of *Acanthopleura*, showing the shape of the base.

A, spine of *A. brevispinosa*, showing the convex base. Scale bar = 500 μ m.

B, spinelet of *A. japonica*, with a convex base. Scale bar = 100 μ m.

C, scale-like elements of *A. hirtosa*, all with a convex base. Scale bar = 500 μ m.

D, spinelet of *A. rehderi*, with a convex base. Scale bar = 50 μ m.

E to **H**, Scales of *A. araucariana*, *A. curtisiana*, *A. miles* and *A. loochooana* respectively, all displaying a basal concavity.

All scale bars = 100 μ m.

Figure 7.26 Scanning electron micrographs of the girdle elements of a number of species of *Acanthopleura*, showing minor variations in the design of the apical complex.

A, distal tip of a spinelet of *A. arenosa*, showing widely separated lateral shoulders (dashed arrows), five prominent dorsal ridges (solid arrows) and a small apical plate (diamond head). Scale bar = 50 μ m.

B, spinelet of *A. vaillantii*, with a small apical complex that displays seven dorsal ridges. Scale bar = 20 μ m.

C, spinelet of *A. gaimardi* with five prominent dorsal ridges and a large reflexed apical plate. Scale bar = 20 μ m.

D, lateral view of a spinelet of *A. tenuispinosa* with well pronounced dorsal ridges. Scale bar = 20 μ m.

E, apical view of a spinelet of *A. japonica* with eight prominent ridges that degenerate into rows of pustules not far from the apex. Scale bar = 50 μ m.

F, ventral view of a spinelet of a specimen *A. gemmata* from Karratha with five dorsal ridges (solid arrows), and barely discernable apical shelves (dashed arrows) and apical plate (diamond arrow). Scale bar = 50 μ m.

Figure 7.27: Species with girdle elements that do not display typical architecture of the genus *Acanthopleura*.

A, subrectangular girdle scale of *A. nigra*. Scale bar = 500 μ m

B, spicule of *A. nigra*, essentially smooth except for distal ridges and occasional large, round, ventral, pustules Scale bar = 20 μ m.

C, spicule of *A. echinata*, essentially smooth except for distal ridges and occasional large, round, ventral, pustules Scale bar = 50 μ m

D, spinelet of *A. granulata* with smooth, pointed apex that does not give rise to distal ridges. Scale bar = 50 μ m.

E, spicule of *O. quercinus* with smooth, pointed apex and discontinuity separating it from the dorsal ridges. Scale bar = 20 μ m.

Figure 8.3: Scanning electron micrographs of the radula of *Acanthopleura spinosa*.

A-C, central and centrolateral teeth, top, anterior and lateral views respectively.

A, indicating quadrilobed base of central teeth (solid arrows), and the lateral and medial keels of centrolateral teeth (dashed arrows).
Scale bar = 100µm.

B, showing smooth, rounded anterior surface of central teeth.
Scale bar = 100µm.

C, indicating the central posterior keel of the central tooth (solid arrow), and concave platform below the distal cusp (dashed arrow).
Scale bar = 100µm.

D, top view of radula showing major lateral teeth with chisel-shaped medial wings (arrows). Scale bar = 500µm.

E, posterior view of major lateral teeth Scale bar = 100µm.

F, lateral view of spatulate uncinals (arrowed) showing extent of curled distal and lateral margins. Scale bar = 200µm.

Figure 8.4: Scanning electron micrographs of the radula of specimens of *Acanthopleura gemmata* from Okinawa, Japan (**A-E**) and Queensland, Australia (**F**).

A-C, central and centrolateral teeth, anterior, lateral and posterior views respectively.

A, indicating fine anterior ridge on central tooth (solid arrow), and angle of orientation of lateral flare of centrolateral tooth (dashed arrow). Scale bar = 100µm.

B, indicating prominent central keel along full length of shaft of central tooth (solid arrow), and showing lateral and medial keels of centrolateral teeth (dashed arrows). Scale bar = 100µm.

C, showing bilobed base of central tooth (solid arrow), and large medial pad on centrolateral teeth (dashed arrow). Scale bar = 100µm.

D, posterior view of major lateral teeth with club-shaped medial wings (arrowed). Scale bar = 200µm.

E, lateral view of spatulate uncinals showing curled distal and lateral margin (arrow). Scale bar = 100µm.

F, posterior view of central and centrolateral teeth of a specimen from Australia, exhibiting a more rounded distal cusp (solid arrow) and smaller medial pad (dashed arrow). Scale bar = 100µm.

Figure 8.5: Scanning electron micrographs of the radula of specimens of *Acanthopleura gemmata* from Pago Bay, Guam (**A-D, F**) and Tanzania (**E**).

A, top view of a section of radula showing bluntly squared base of central teeth (arrows). Scale bar = 500 μ m.

B-D, central and centrolateral teeth, posterior, lateral and top views respectively.

B, indicating squared off distal edge of central teeth (solid arrow) and distinctive bulge on medial side of centrolateral teeth (dashed arrow).

Scale bar = 100 μ m.

C, showing restricted central keel (solid arrow), with flat triangular platform below distal cusp (dashed arrows). Scale bar = 200 μ m.

D, showing centrolateral tooth with anteriorly curled lateral flare (solid arrow), and medial bulge (dashed arrow). The solid black line approximates the angle of orientation of the distal cusp for comparison with **E**. Scale bar = 100 μ m.

E, the orientation more typical of *A. gemmata*, in a specimen from Tanzania. Scale bar = 100 μ m.

F, posterior view of major lateral and spatulate uncinal teeth showing the squat tooth cusps of the former teeth (solid arrow), and uncurled margins of the latter teeth (dashed arrow). Scale bar = 200 μ m.

Figure 8.7: Scanning electron micrographs of the radula of *Acanthopleura testudo* from Djibouti, Gulf of Aden.

A-C, central and centrolateral teeth, posterior, top and lateral views respectively.

A, showing the sturdy, squat central teeth with relatively straight sides, distinctly flared base (solid arrow), and somewhat square distal cusp (dashed arrow). Scale bar = 100 μ m.

B, showing the distinctive nodule proximal to the flat triangular platform (dashed arrow), smooth anterior surface (solid arrow) and two small but distinct anterior lobes (arrowheads). Scale bar = 100 μ m.

C, showing the centrolateral teeth with recurved lateral flare (solid arrow) and lateral bulge in place of the usual pad (dashed arrow). Scale bar = 200 μ m.

D, posterior view of major lateral and centrolateral teeth showing the large medially extruded cusps of the former (solid arrow), and lateral bulge of the latter (dashed arrow). Scale bar = 200 μ m.

E, top view of a section of the radula showing the broad, medially extruded blades of the spatulate uncinial teeth. Scale bar = 500 μ m.

F, lateral view of the spatulate uncinals showing the recurved nature of the margins (solid arrow). Scale bar = 200 μ m.

Figure 8.8: Scanning electron micrographs of the radula of *Acanthopleura granulata* from the Florida Keys, USA.

A-C, central and centrolateral teeth, posterior, top and lateral views respectively.

A, showing the long, slender central teeth (solid arrow) with a bilobed base (dashed arrow) that is bifid between the lobes. Scale bar = 100 μ m.

B, showing the absence of an anterior ridge on the central teeth (dashed arrow), and the distinct lateral curling that gives them a bicuspid appearance (solid arrow), and the large lateral pad on the centrolateral teeth (arrow head). Scale bar = 100 μ m.

C, showing the posterior keel present along the full length of the shaft of the central tooth (solid arrow), and the posteriorly cupped distal tip (dashed arrow). Scale bar = 100 μ m.

D, top view of a section of radula showing the reduced lateral flare on the centrolateral teeth (solid arrows), cf. Figs: 8.5F, 8.6D and 8.7B. Scale bar = 500 μ m.

E, posterior view of squat major lateral teeth with club-shaped medial wing with narrow point of attachment to the shaft (solid arrow). Scale = 100 μ m.

F, posterior view of spatulate uncinals with limited curling along the lateral margin (solid arrow). Scale bar = 200 μ m.

Figure 8.9: Scanning electron micrographs of the radula of *Acanthopleura echinata* from San Bartolo, Peru.

A, posterior view showing the long, thin, straight-sided central teeth (solid arrow), with large proximal bulb (dashed arrow), and large, robust centrolateral teeth with chiselled appearance, small, narrow cusp (arrowhead), and distinct furrow inside medial and distal margin (blocked arrow). Scale bar = 200 μ m.

B, lateral view of radula section showing keeled central teeth (arrows). Scale bar = 500 μ m.

C, top view showing tapering base of central teeth (solid arrow), and posterolateral keel of centrolateral teeth devoid of lateral flare typical of other *Acanthopleura* species (compare e.g. with Figs. 8.5F, 8.6D, 8.7B). Scale bar = 200 μ m.

D, top view of radula section showing location of the central tooth (dashed arrow) midway between two rows of centrolateral teeth (solid arrows) (cf. their relative position in other species, e.g. in Fig. 8.5E). Scale bar = 500 μ m.

E, posterior view of major lateral tooth showing medial wing with tapering recurved tip (solid arrow), and spatulate uncinals with strongly curled margin (dashed arrow). Scale bar = 200 μ m.

F, anterolateral view of major lateral teeth showing narrow disjunct band around margin of the cusp (solid arrow), and lateral bulge (dashed arrow). Scale bar = 500 μ m.

Figure 8.10: Scanning electron micrographs of the radula of *Acanthopleura brevispinosa* from Zanzibar, Tanzania.

A and **B**, central and centrolateral teeth, posterior, and lateral views respectively.

A, showing the short, squat, straight-sided (solid arrow), anteroposteriorly flattened central teeth, with a bifid base (arrowhead), and centrolaterals with a very small lateral flare (dashed arrow). Scale bar = 100 μ m.

B, showing concave triangular platform (dashed arrow) below the cusp of the central teeth that extends into a soft, central keel (arrowhead), and a small square lateral pad on the centrolateral teeth (solid arrow). Scale bar = 100 μ m.

C, oblique view of radula section showing major lateral teeth with wedge-shaped medial wing (dashed arrows) and tapering extrusion (solid arrows), and spatulate uncinals with folded margin half way down the shaft (arrowhead). Scale bar = 500 μ m.

D, posterior view of major lateral teeth with small, medially extruded cusps (solid arrow), and spatulate uncinals with limited marginal curling (dashed arrow). Scale bar = 100 μ m.

E, anterior view of major lateral tooth cusps with distinctive lateral bulge (arrow). Scale bar = 100 μ m.

F, anterior view of major lateral tooth cusp removed from shaft, showing incomplete attachment of the lateral bulge at its base (arrow). Scale bar = 100 μ m.

Figure 8.12: Scanning electron micrographs of the radula of *Acanthopleura japonica* from Yamaguchi Province, Japan.

A and **B**, central and centrolateral teeth, posterior and lateral views respectively.

A, showing central teeth with bilobed base that is rounded proximally (solid arrow), has a slight bulge either side of the shaft where it attaches to the base anteriorly (arrowheads) and anterior keel (diamond-head arrow). The centrolateral teeth have very large lateral lobes (dashed arrow). Scale bar = 100 μ m.

B, showing central teeth with concave triangular platform below cusp (solid arrow) extending into a keel proximally (dashed arrow). Scale bar = 100 μ m.

C, posterior view of a major lateral and centrolateral teeth showing slight medial extrusion of the cusp of the former (solid arrow), and curling of the distal and medial margin of the latter (dashed arrow). Scale bar = 100 μ m.

D, top view of a section of radula showing absence of any lateral pads on the centrolateral teeth, and extent of distal and lateral curling of margins of spatulate uncinals (arrows). Scale bar = 500 μ m.

Figure 8.16: Scanning electron micrographs of the radula of *Acanthopleura loochooana* from Okinawa, Japan.

A and **B**, central and centrolateral teeth viewed from posterior and lateral views respectively.

A, showing the central tooth with flattened bulbous base (solid arrow), and flat triangular platform below distal cusp (dashed arrow). Scale bar = 50 μ m.

B, showing smooth anterior surface of central tooth (solid arrow), and centrolateral teeth with lateral flare extended into a lobe that curls up on itself (arrowhead). Scale bar = 100 μ m.

C, posterior view of radula section showing major lateral teeth with wedge shaped wing (solid arrow), and large leaf shaped lateral pad on centrolateral teeth (dashed arrow). Scale bar = 200 μ m.

D and **E**, major lateral tooth cusps, posterior and anterior views respectively.

D, showing round, disc-shaped cusps (arrows). Scale bar = 100 μ m.

E, showing distinctive indentation (solid arrows) on the lateral side of the triangular magnetite tab (dashed arrow). Scale bar = 200 μ m.

F, posterior view of spatulate uncinals showing straight medial side (solid arrow) and tight marginal curling distally and laterally (dashed arrow). Scale bar = 100 μ m.

Figure 8.17: Scanning electron micrographs of the radula of *Acanthopleura nigra* from San Bartolo, Peru.

A-C, central and centrolateral teeth, posterior, top-anterior and top-posterior views respectively.

A, showing the long, thin, straight-sided central tooth with bulbous base (solid arrow) and concave region below cusp (dashed arrow) that extends into a central keel (arrowhead) for most of the shaft. Scale bar = 200 μ m.

B, showing central tooth smooth and convex distally (solid arrow), but keeled for the remainder of the shaft (dashed arrow). Scale bar = 200 μ m.

C, showing tapering base of central tooth (solid arrow), and centrolateral teeth with narrow cusp (arrowhead), deeply furrowed region within the curled distal and medial margins (dashed arrow), and absence of lateral flare. Scale bar = 200 μ m.

D, top view of radula section showing the location of teeth in each row, particularly the midway position of the central teeth (solid arrow) and the relatively large spatulate uncinals (dashed arrow). Scale bar = 500 μ m.

E and F, posterior and anterior views of major lateral teeth showing.

E, tapering tip of medial wing (solid arrow). Scale bar = 200 μ m.

F, cusps with prominent lateral bulge (solid arrow) and narrow disjunct band (dashed arrow). Scale bar = 200 μ m.

Figure 8.20: Scanning electron micrographs of the radula of *Acanthopleura miles* from Latuhalat, Ambon, Indonesia.

A and **B**, central and centrolateral teeth viewed from posterior and lateral views respectively.

A, showing central teeth with quadrilobed base (solid arrows), and lateral flare of centrolateral teeth (dashed arrow). Scale bar = 50 μ m.

B, showing central tooth with central keel (solid arrow) and sharply pointed base (dashed arrow), and curling of the distal and medial margin of the centrolateral teeth (arrowhead). Scale bar = 50 μ m.

C, posterior view of major lateral teeth showing discoid cusps, small, square lateral pad on centrolateral teeth (solid arrow), and slight curling along distal and lateral margin of spatulate uncinals (dashed arrow). Scale bar = 100 μ m.

D oblique-anterior view of radula section and showing smooth anterior surface of central teeth (dashed arrow), and tapering distal tip of wing of major lateral tooth cusps (solid arrow). Scale bar = 100 μ m.

E, top view of radula section showing the large size of spatulate uncinals relative to major lateral teeth (solid arrows). Scale bar = 200 μ m.

Figure 8.21: Scanning electron micrographs of the radula of *Acanthopleura rehderi* from Palmerston Island, Cook Is.

A-C, central and centrolateral teeth viewed from posterior, top-lateral and lateral angles respectively, all showing centrolateral teeth to be substantially larger than the central tooth.

A, showing central teeth with straight distal edge (arrowhead), and relatively straight sides (solid arrow), centrolateral teeth that are distinctly mediolaterally flattened, lacking a prominent central keel and lateral flare, having an anteriorly curled, acutely angled distal edge (dashed arrow) and possessing a wing-like lateral pad (large arrow). Scale bar = 50µm.

B, showing central teeth with wide, straight base (arrowhead), distinctive, pointed central tab (large arrow) and tooth joined to basal membrane proximally by two membranous strands (dashed arrows); centrolateral teeth with small medial keel (solid arrow). Scale bar = 50µm.

C, showing central tooth with small central keel (solid arrow), anteriorly curled distal-lateral edges (dashed arrows) and sharp angle half way up the shaft (arrowhead), resulting in distal half of tooth aligned perpendicular to proximal half. Scale bar = 100µm.

D-F, major lateral teeth viewed from the posterior, posterior and anterior sides respectively.

D, featuring the club-shaped wings (solid arrows). Scale bar = 50µm.

E, showing discoid cusps with three small distal (solid arrows) and one small medial denticle (dashed arrow), also straight-sided spatulate uncinals (arrow head) with limited curling along distal edge (large arrow). Scale bar = 100µm.

F, showing discoid cups with one medial and three distal denticles. Scale bar = 100µm.

Figure 8.22: Scanning electron micrographs of the radula of *Onithochiton quercinus* from Rottnest Island, Western Australia.

A, central and centrolateral teeth viewed from the posterior, showing central teeth with straight distal edge (arrowhead), straight sides and a small central keel (solid arrow), and centrolateral teeth with a small medial keel (dashed arrow). Scale bar = 100 μ m.

B, section of the radula viewed from the anterior side showing central teeth that are distinctly scooped distally and with a right angle bend half way along the shaft giving the teeth a chair-shaped appearance (solid arrows), also centrolateral teeth that are distinctly mediolaterally flattened (dashed arrows). A single broad, stumpy spatulate uncinal does exhibit any tapering of the shaft towards the base (arrowhead). Scale bar = 100 μ m.

C, major lateral teeth viewed from the posterior showing discoid cusps (solid arrows) with one small medial denticle (dashed arrows). Many of the club-shaped wings have broken away from the shaft of the tooth (arrowheads). Scale bar = 200 μ m.

D, section of the radula viewed from the posterior side showing broad spatulate uncinals that are slightly curled distally (solid arrows). Scale bar = 100 μ m.

Figure 9.6 Secondary electron micrographs (SEM) and corresponding energy dispersive spectroscopy (EDS) line scans of iron taken along the transects indicated by the black lines in the micrographs:

A, SEM (a) and EDS line scan (b) of an early black-capped tooth with high iron levels in a wide band (x) along the posterior cutting surface (P). No apatite has yet been deposited in the anterior region of the tooth (z) and the line scan shows that iron levels taper off well into this region.

Scale bar = 4 μm .

B, SEM (a) and EDS line scan (b) of the tenth black-capped tooth. The magnetite region (x) has now been completely infilled, and the distinct shoulder seen in the line scan on the anterior side of this mineral is indicative of lepidocrocite deposition (y). Apatite has still not yet been deposited in the core of the tooth (z), but the iron forms a more discrete boundary than in **A**. Scale bar = 30 μm .

C, SEM (a) and EDS line scan (b) of a fully mature tooth. Note the discrete nature of the mineral deposits in both the micrograph and line scan. The levels of iron throughout the magnetite region (x) are constant, while lower iron concentrations on the anterior surface, correspond to lepidocrocite (y) and the small but distinct shoulder on the posterior surface corresponds to remnant ferrihydrite. The core has now been fully infilled with apatite (z). Scale bar = 20 μm .

Figure 10.1 Four equally parsimonious trees each 1313 steps in length resulting from 100 unordered, unweighted, heuristic searches using PAUP to analyse 222 characters examined in species of *Acanthopleura* and the outgroup *Onithochiton quercinus*.

A, tree 1; **B**, tree 2; **C**, tree 3; **D**, tree 4.

Green lines indicate minor branch length changes, while red lines indicate changes in the structure of the tree. Scale bar = 50 changes.

