SPIXIANA	**33**	2	171–194	München, November 2010	ISSN 0341–8391

Illustrated summary of chiton terminology

(Mollusca, Polyplacophora)

Enrico Schwabe

Schwabe, E. 2010. Illustrated summary of chiton terminology (Mollusca, Polyplacophora). Spixiana 33 (2): 171-194.

The aims of the present paper are to summarize and offer a standard set of terminology used to describe morphological and partly anatomical (e. g. the radula) characters of Polyplacophora. To make the understanding of some previously misused terms easier, the identification and description of relevant parts of the animal are illustrated and discussed in context of additional literature.

Enrico Schwabe, Bavarian State Collection of Zoology, Muenchhausenstr. 21, 81247 Munich, Germany; e-mail: enrico.schwabe@zsm.mwn.de

Introduction

Chitons are a group of basal, exclusively marine molluscs, which have not significantly changed their bauplan during more than 300 million years of evolution. Their more or less solid, dorsal plates have been preserved in numerous fossil records and allow researchers a direct comparison with living species, and accordingly there is a high number of described fossil and recent taxa. At present we count for about 930 recent species (see Schwabe 2008, + recently described taxa) and 430 described fossil species (Puchalski et al. 2008).

Due to the vast amount of available literature on these molluscs, there is an inconsistent use of introduced terms for describing characters in Polyplacophora, especially if they were translated from German into different languages. Even within the same country different expressions are in use, e. g. the German "Zwischenplatte" (= intermediate valve) may be found in German language literature as "Segment" (e. g. Janssen 1978), or "Spange" (e. g. Sauer 1992). In addition, despite their simple organisation chitons are sometimes inaccurately described. Recently the author discovered the following sentence in a modern biology textbook (Willmann 2002, pp. 1-39) describing the gross morphology of chitons: "An den Tentakeln des Kopfes befinden sich Riechorgane [On the tentacles of the head there are olfactory organs.]." However, chitons do not have cephalic tentacles at all, and certainly not olfactory tentacles!

This short contribution intends to clarify the terminology of chitons and to present a detailed general description of chiton morphology, to summarise for amateurs, students or scientists the present stage of scientific knowledge of a fascinating group of animals.

For a better understanding, as many relevant taxonomic terms as possible are illustrated and/or described. Where jargon and unusual words are not defined within the present text, the reader should refer to Stachowitsch (1992) who provided a detailed thesaurus, and to Mizzaro-Wimmer & Salvini-Plawen (2001) who illustrated in detail the morphology and anatomy of chitons. Terms for internal anatomy, except for the radula, are not included here. In the framework of the present brief paper, it is impossible to illustrate every combination of characters or terms, and so the reader is requested to imagine other possibilities that occur in the world of chitons.

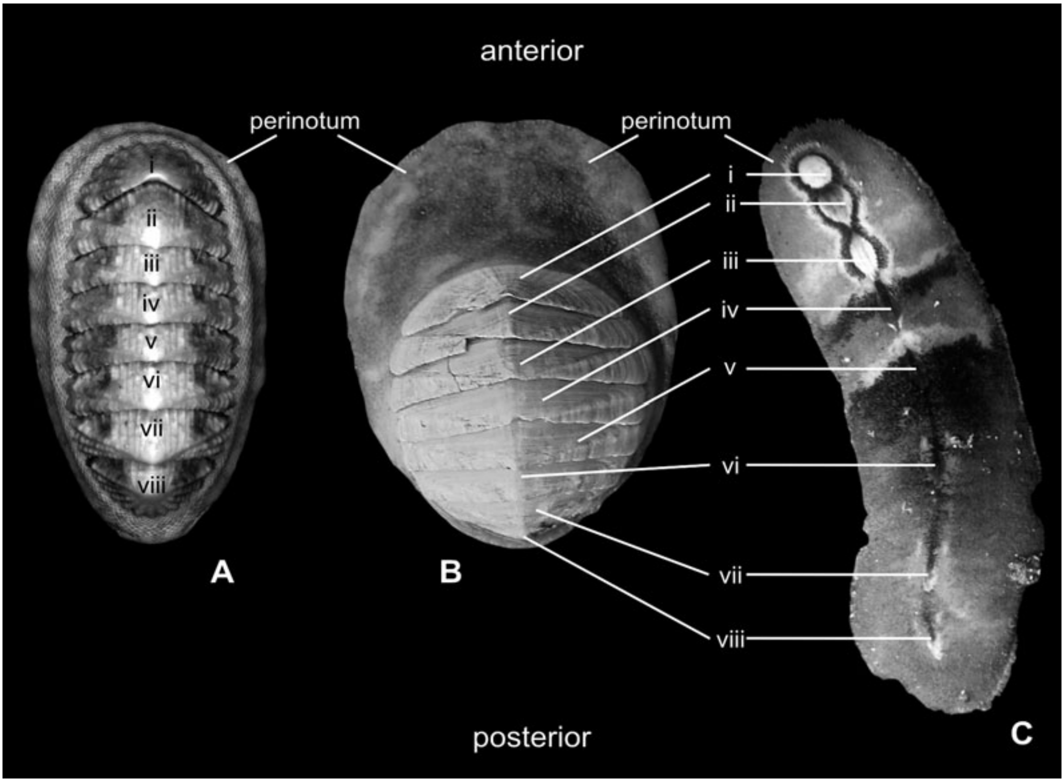


Fig. 1. Dorsal view of selected chitons. **A.** *Chiton (Rhyssoplax) affinis* Issel, 1869, Djibuti (MNHN). **B.** *Placiphorella* sp., Chile (ZSM). **C.** *Cryptoplax oculata* (Quoy & Gaimard, 1835), Indonesia (ZSM).

Materials and methods

The illustrated specimens are, if not otherwise explained, part of the mollusc collection of the Bavarian State Collection of Zoology (ZSM). Methods for the preparation of the animals, either for light or scanning electron microscopy follow Schwabe (2006). To avoid confusion in the plates, no scale bars are given, and the author refrains from additional (collection) data for the relevant taxa. As a non-taxonomic work, the authors of the taxa are not included in the running text. The descriptive part is organized hierarchically, starting from a general body outline and progressing through the characteristics of the taxonomic relevant parts such as girdle elements and radula.

Abbreviations

AMS	Australian Museum, Sydney, Australia
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NM	Natal Museum, Pietermaritzburg, Republic of South Africa
SAMA	South Australian Museum, Adelaide, Australia
UF	University of Florida, Florida, United States of America
ZISP	Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia
ZMB	Natural History Museum Berlin (formerly Zoologisches Museum Berlin), Germany

Body

Dorsal view

Fig. 1

Chitons are unsegmented (in the sense of an annelid-like metamerism), bilateral symmetric, dorsoventrally flattened, and show eight dorsal calcareous **valves** (or plates). The valves usually overlap, with the more anterior valve overlaying the next. In *Cryptoplax*, most valves are separated (Fig. 1C). The valves are surrounded, but may be also completely covered (*Cryptochiton stelleri*, not illustrated) by the tissue of the mantle. This marginal ring of tissue is also called girdle. It is usually of more or less the same width around the body perimeter, but in some genera (e. g. *Placiphorella*, *Craspedochiton*) there is a distinct anterior extension (Fig. 1B).

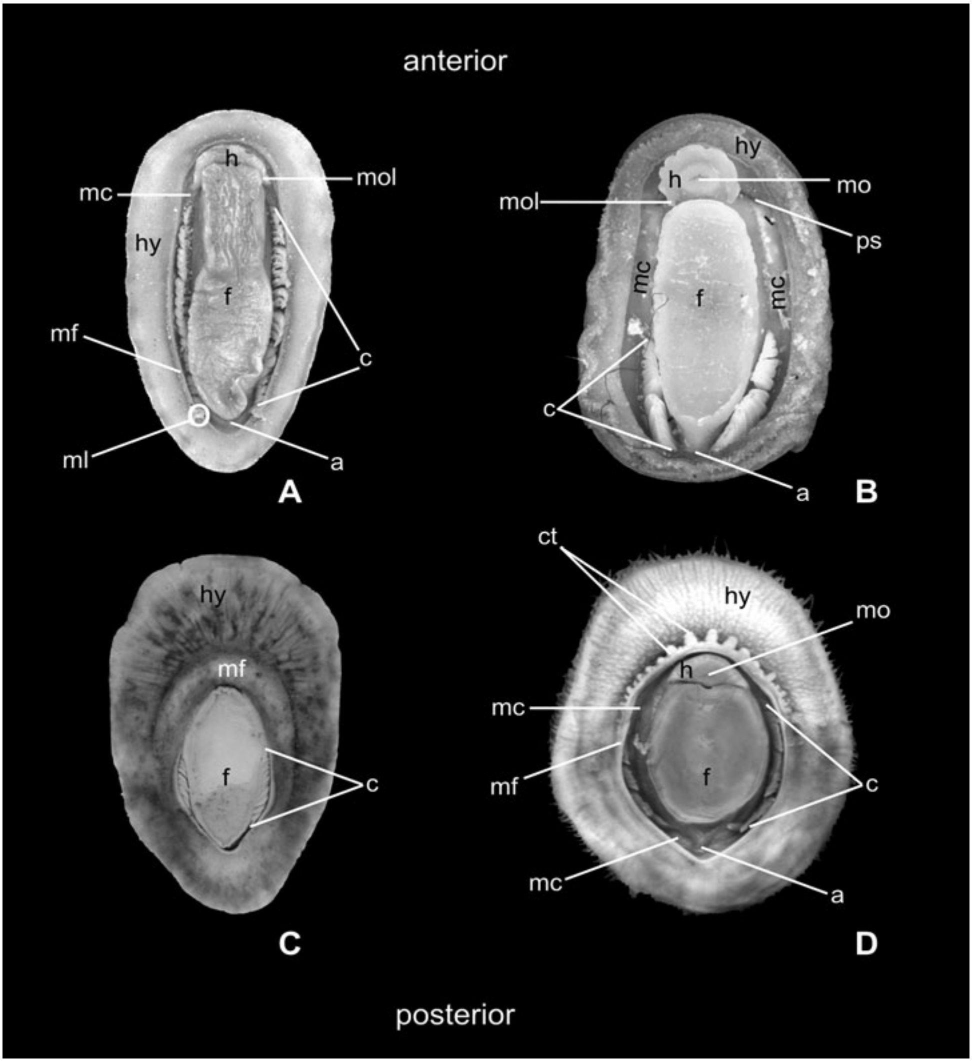


Fig. 2. Ventral view of selected chitons. **A.** *Chiton (Rhyssoplax) affinis* Issel, 1869, Djibuti (MNHN). **B.** *Leptochiton algesirensis* (Capellini, 1859), France (ZSM). **C.** *Craspedochiton isipingoensis* (Sykes, 1901), South Africa (NM). **D.** *Placiphorella stimpsoni* (Gould, 1859), Japan (ZSM). **a**, anus; **c**, ctenidia (holobranchial type in Fig. 2A, merobranchial type in Fig. 2D); **ct**, precephalic tentacles; **f**, foot; **h**, head; **hy**, hyponotum; **mc**, mantle cavity; **mf**, mantle fold; **ml**, mantle lappet; **mo**, mouth; **mol**, mouth lappets; **ps**, pigmented stripe.

Chiton valves are counted from the anterior on and usually noted by Roman numerals (i-viii); the first valve (i) is also called **head valve**, while the posterior most (viii) is called the **tail valve**. Valves ii to vii are called the **intermediate valves**. As the intermediate valves are difficult to distinguish from each other they are often referred to collectively and as distinct from the **terminal valves** (head and tail) (Fig. 1).

Ventral view

Fig. 2

On their ventral body side, chitons have a large and fleshy **foot** and a separated **head**, with a centrally laying **mouth** opening (Figs 2B,D “mo”). The head has no eyes and no tentacles. Members of the genus *Dinoplax* show an anteriorly extended foot that may cover the mouth opening. The head shows lateral extensions, the so-called **mouth lappets** (velum)

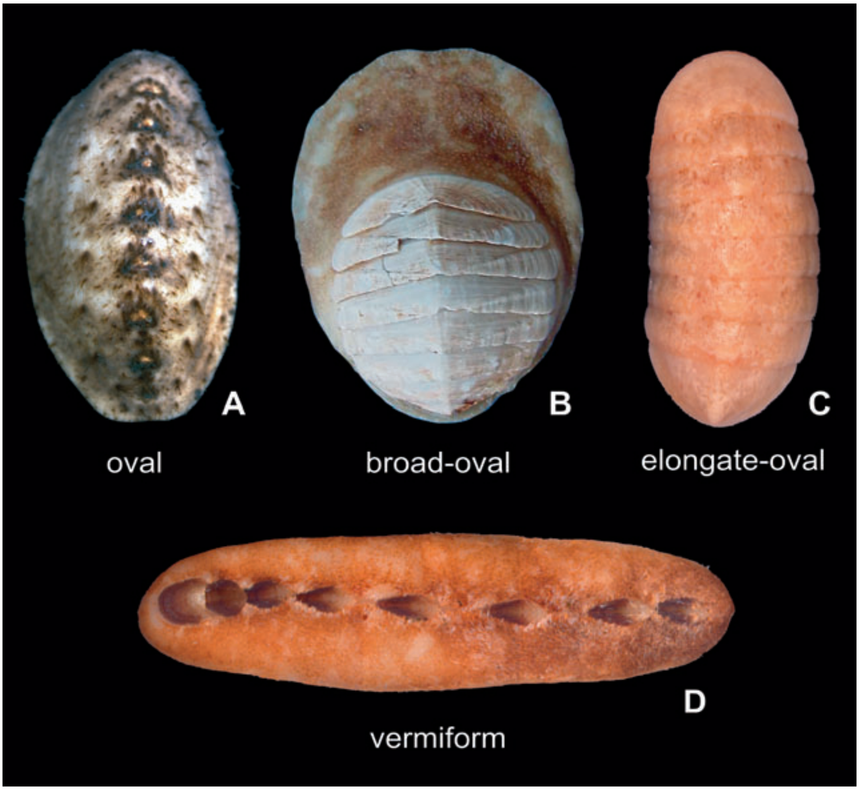


Fig. 3. Dorsal view of selected chitons to show the variety in body shapes. **A.** *Amicula vestita* (Broderip & Sowerby, 1829), Russia (ZSM). **B.** *Placiphorella* sp., Chile (ZSM). **C.** *Parachiton puppis* Hull, 1923, Fiji (UF). **D.** *Cryptoplax caledonicus* de Rochebrune, 1882, New Caledonia (MNHN).

(Figs 2A,B "mol"). In Lepidopleurida, there is a **pigmented stripe** exterior to the mouth lappets, which most probable serve as a chemosensory organ (Fig. 2B "ps").

Posterior to the foot is a small opening, which usually positioned centrally on a small papilla – the **anus** (Figs 2A,B,D "a"). The head and foot are surrounded by the **mantle cavity** (pallial groove) (Figs 2A,B,D "mc"), that also harbours the **ctenidia** (gills). Between mantle cavity and ventral girdle surface (**hyponotum**) is the **mantle fold**, which in special cases (Fig. 2C) may completely cover the mantle cavity. Posteriorly the mantle fold extends laterally and builds a so-called **mantle lappet** (Fig. 2A "ml"), which usually slightly covers some of the posterior ctenidia. In some genera (e.g. *Placiphorella*, Fig. 2D) the mantle fold may build precephalic **tentacles** that help catching small animals.

Shape, size and profile
Figs 3, 4

The majority of chitons are more or less oval in outline, but there is a wide variation in shape (Fig. 3). Some species adapted to a life within crevices and holes are stretched and the valves may be widely separated (e.g. *Cryptoplax*). Usually these forms have a reduced foot and a wormlike (vermiform) body shape.

Von Middendorff (1847, p. 7) proposed the first standardized terms to describe the body outline in chitons. His mathematical definitions were modified by Bergenhayn (1930, p. 13) to the following ratio: maximal animal length/maximal animal width.

shape term	ratio (length/width)
broad oval ("short oval" sensu Bergenhayn 1930)	0-1.5
oval	$1.5 < l/w \leq 3.5$
elongate-oval	$l/w > 3.5$

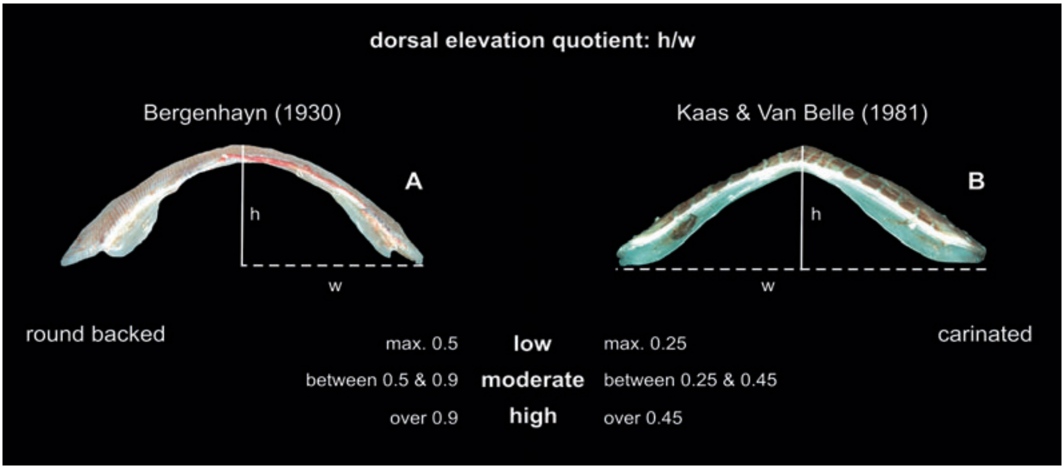


Fig. 4. Frontal view of intermediate valves. **A.** *Parachiton acuminatus* (Thiele, 1909), Western Samoa (ZSM). **B.** paralectotype of *Chaetopleura benaventei* Plate, 1899, Chile (ZMB).

Iredale & Hull (1924, p. 229) defined body size values for chitons. To be exact, they established terms for ischnochitonid species only, but these values are still in use and principally accepted for all chitons.

size term	measurement
small	length ≤ 15 mm
medium	15 mm $<$ length ≤ 30 mm
large	length > 30 mm

Another measurable size is the dorsal **elevation** (Fig. 4). If viewing an intermediate valve from the front, the dorsal shape may be round-backed, or in extreme cases with a distinct keel along the whole mid-line. Usually, if a jugal area (see Fig. 8 “ja”) is present, the valve is carinated (Fig. 4B), peaked on the posterior edge but smooth or rounded on the anterior face. In profile, the shape of lateral areas are called **side slopes**, which may be straight, convex or concave.

Bergenhayn (1930, p. 14) used the following ratio: intermediate valve hight / the half valve width and classified low, moderate, and high valve elevation. Kaas & Van Belle (1981, p. 8) adapted this formula, but applied it for the fourth valve only, and modified the denominator to the whole valve width. As a result Bergenhayn's values must be halved to compare the relevant terms.

elevation (intermediate valve)	sensu Bergenhayn (1930)	sensu Kaas & Van Belle (1981)
low	$(h/0.5w) \leq 0.5$	$(h/w) \leq 0.25$
moderate	$0.5 < (h/0.5w) \leq 0.9$	$0.25 < (h/w) \leq 0.45$
high	$(h/0.5w) > 0.9$	$(h/w) > 0.45$

Valves

A typical polyplacophoran valve consists of two main layers: the dorsal **tegmentum** (Figs 8-10) and ventral **articulamentum** (Figs 5B, 13A-D). However these layers are complex. The uppermost is the very thin **properiostracum**, followed by the tegmentum. The **hypostracum** is composed of the **articulamentum** and the very thin innermost ventral layer, **myostracum**. In some genera, for example in *Acanthopleura*, Bergenhayn (1930, p. 11) discovered another layer between the tegmentum and the articulamentum, which he called **mesostracum**. For species identification only the tegmentum and the articulamentum are relevant.

Tegmentum

Figs 5-9

The **tegmentum** was first described by von Middendorff (1847, p. 9). This visible dorsal aspect of the valves is usually colourful, often with raised shell sculpture (Fig. 9), and divided in different valve zones (Fig. 8). In several genera, this layer may be strongly reduced (e. g. *Choriplax*, *Cryptoplax*, *Amicula*, *Katharina*) or completely absent (in adults of the North Pacific *Cryptochiton*) (Fig. 7). To give an idea about the degree of reduction, usually the percentage of the tegmentum to the whole valve outline is given. Because of its symmetrical form, the head valve is used to calculate this ratio, by estimating the shape of the head valve as a semicircle and calculating semicircular areas of tegmentum and the articulamentum.

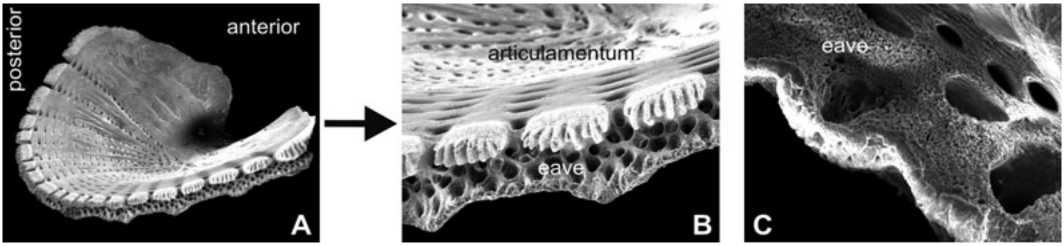


Fig. 5. Eaves in chitons: Ventro-lateral view of selected chiton valves. **A, B.** tail valve of *Chiton (Rhyssoplax) olivaceus* Spengler, 1797, Croatia (ZSM), showing a multi-channel layer, which may termed as "spongy" eaves. **C.** intermediate valve of *Lepidochitona caprearum* (Scacchi, 1836), Croatia (ZSM). Here the eaves are "not spongy" as the tegmentum shows only a single channel layer.

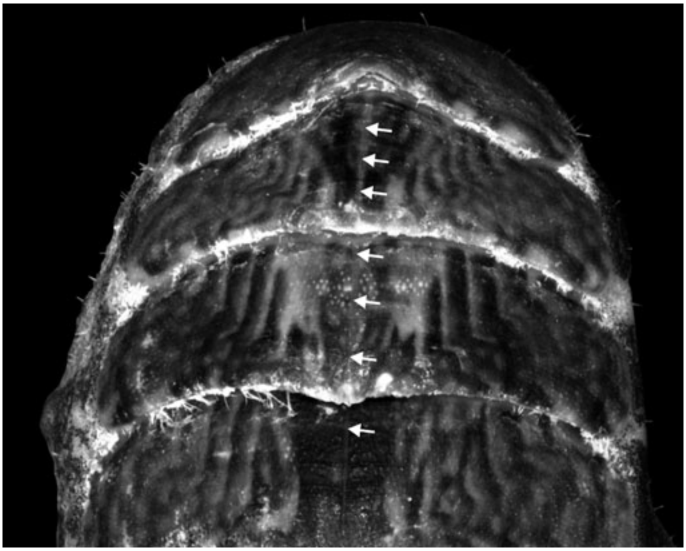


Fig. 6. Anterior portion of *Schizoplax brandtii* (von Middendorff, 1847), USA (ZSM) to show the ligament in chitons. While some fossil chitons are known to have splitted intermediate valves (e. g. *Echinochiton dufoei*), this character is rare in Recent taxa and occurs in the here illustrated *Schizoplax brandtii* only. The intermediate valves of this species are longitudinally interrupted at the jugum, but united by a ligament (arrows).

The tegmentum thickness may vary in different species. As the tegmentum is a distinctly different vertical layer from the articulamentum, it often forms **eaves** (Fig. 5), where the upper tegmentum extends laterally over the attachment point to the articulamentum. The eaves were first mentioned in Dall (1879, p. 283), who cited a term erected by Carpenter. They are visible in the lateral view of the tegmentum (visible in disarticulated valves at the tegmentum margin) as numerous pores, depending how many nerve channels penetrate the tegmentum. The term **spongy eaves**, refers to a morphological condition in some species when this layer appears porous from a high density of nerve channels (Figs 5A,B).

Tegmentum: valve shape
Fig. 8

To describe a species, usually the following terms are used to illustrate the tegmentum:

For the **head valve,** it is important to note the shape of the posterior margin, differentiating between a (nearly) straight and a widely V-shaped type (Fig. 8, upper row). Straight margins may exceptionally show a small central **apex**, while in angle-forming species the corresponding area may show a deep semicircular notch.

Intermediate valves usually show a clear zonation, and are divided primarily into **lateral areas** and a **central area**. The lateral areas are symmetrical triangular fields on either side of the valve, and are more or less elevated. The exterior edges of the lateral areas form the posterior valve margin, which may be straight or angulated (either concave or convex). The posterior valve margin sometimes forms a central apex. The interior faces of the lateral areas cross the middle of the valve, and the wider side reaches the anterior valve margin. The interior edge of the lateral areas is called the **diagonal ridge**. The central area of the valve is the space between the lateral areas; it may be divided with a distinct triangular area in the middle, anteriorly wider and reduced towards the apex. This region is called the **jugal area** (or jugum). In the genus *Cryptoplax* the jugal area it is often nearly parallel-sided rather than triangular (Figs 10H,I). The remaining field in the central area, between lateral area and jugal area is named the **pleural area**.

This means that species without a jugal area nevertheless have a central area. However, in species of the families Acanthochitonidae and Cryptoplacidae (Fig. 8, right column), the tegmentum is significantly reduced. In these cases, the dorsal valve area is divided into the distinct central jugal area and the remaining surface is named the **pleurolateral area**. Although thus only two nominal zones are present, the pleurolateral area may also be bisected by a diagonal ridge.

The head valve and intermediate valves grow in effectively a mixoperipheral pattern, growing outward from the posterior valve margin. However, the tail valve grows in a holoperipheral style, expanding outward in all directions from the centre. The tail valve thus usually shows a small central point or apex, the **mucro** (Figs 10-11, arrows). The position of the mucro is always laterally central but varies in its position on the anterior-posterior axis of the valve, and its prominence and position are relevant to species determination. The mucro is described differentiating from a longitudinally central (or median) position in the tegmentum area, as anterior (antemedian) or posterior. Occasionally (e.g. in *Parachiton*, *Cryptoplax*) the mucro may be posteriorly terminal or the apex of the mucro may even overhang the posterior margin (Figs 10C,E, 11C,E). The mucro divides the tegmentum of the tail valve into an **antemucronal area,** lying anterior to the mucro, and consequently a **postmucronal area**, the area behind the mucro. The antemucronal area is homologous to the central area of the intermediate valves and may show a jugal area. Like in the intermediate valves, the diagonal ridge separates ante- and postmucronal areas. Viewed from the side, the profile of the postmucronal area is named the **postmucronal slope**, which may either be straight, concave (depressed), or convex (domed). The angle of the postmucronal slope relative to the ventral horizontal is also considered, so an obtuse angle is referred to as a steep slope and can approach a vertical angle, but an acute angle is a flat slope.

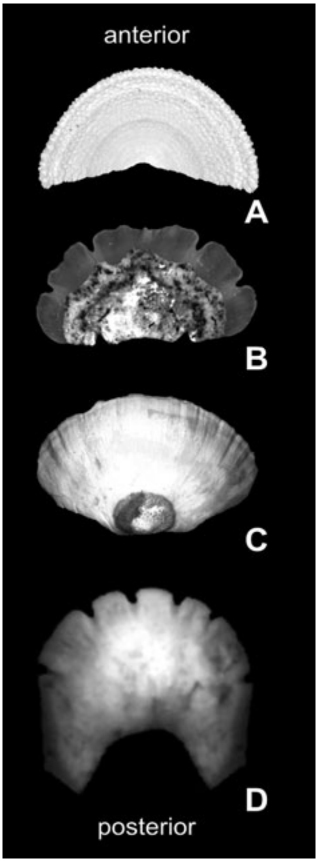


Fig. 7. Dorsal view of selected chiton head valves, to demonstrate the tegmentum reduction in chitons. **A.** *Ischnochiton mawlei* Iredale & May, 1916, Tasmania (AMS), belongs to the species with a **complete covering**, which is common in the orders Lepidopleurida and (with exceptions) Chitonida and thus in the majority of chitons. **B.** *Craspedochiton isipingoensis* (Sykes, 1901), Zululand (NM) with **much reduced tegmentum**. This condition is mainly to be found in genera of the Cryptoplacidae and Acanthochitonidae: e.g. *Cryptoplax*, *Acanthochitona*, *Choneplax*, *Craspedochiton*. **C.** *Choriplax grayi* (H. Adams & Angas, 1864), Australia (SAMA) shows a **nearly complete reduced tegmentum**, which is otherwise only known for the genera *Katharina*, *Amicula* and *Cryptoconchus*. **D.** The **complete reduction** of the tegmentum is only known from the adults of *Cryptochiton stelleri* (von Middendorff, 1847), USA (ZSM).

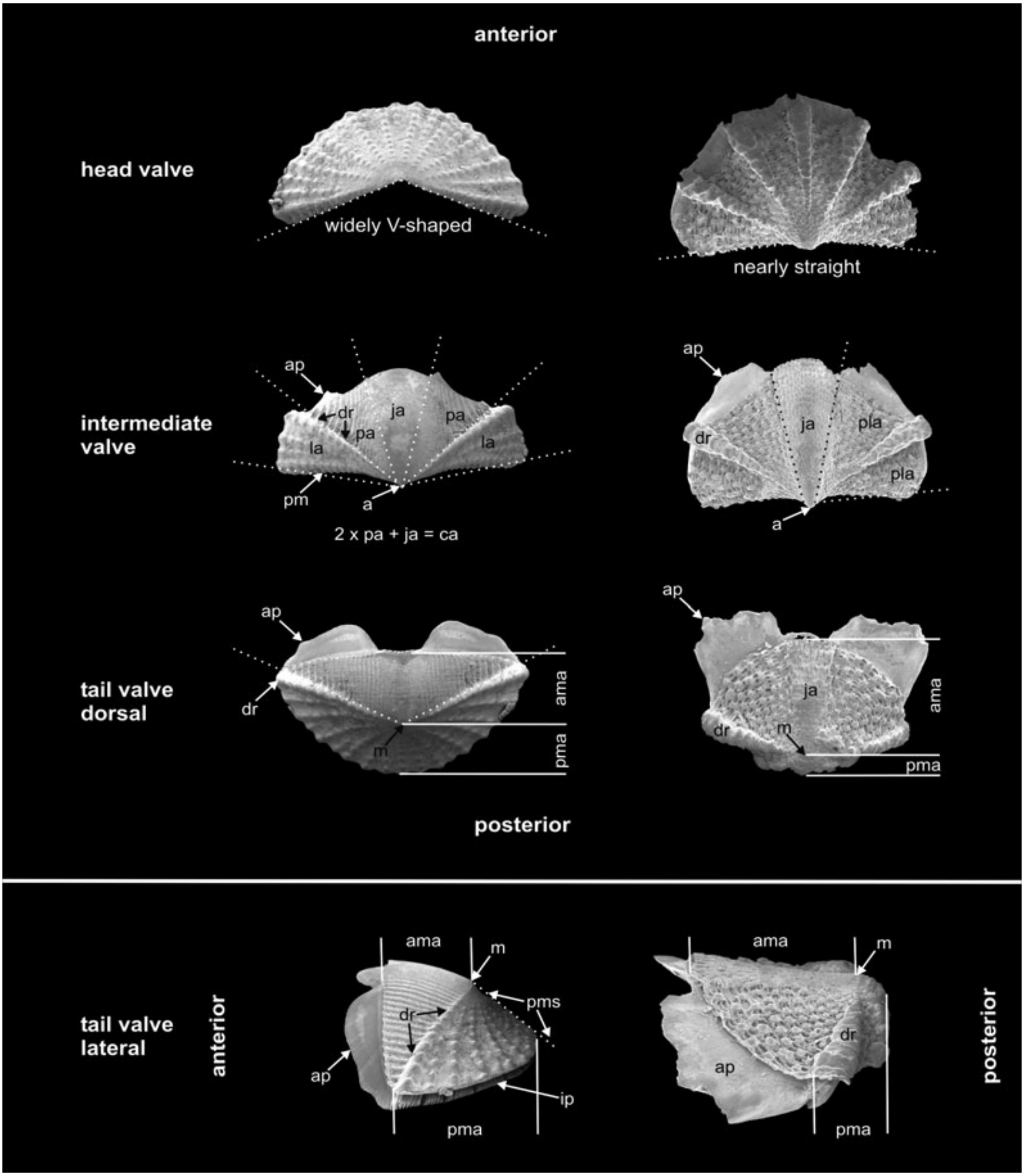


Fig. 8. Dorsal and lateral views of selected chiton valves. **Left column,** *Chiton (Rhyssoplax) ectypus* (de Rochebrune, 1884), New Caledonia (MNHN). **Right column**, *Notoplax tridacna* (de Rochebrune, 1881), New Caledonia (MNHN). **a**, apex; **ama**, antemucronal area; **ap**, apophysis; **ca**, central area; **dr**, diagonal ridge; **ip**, insertion plate; **ja**, jugal area (jugum); **la**, lateral area; **m**, mucro; **pa**, pleural area; **pla**, pleurolateral area; **pm**, posterior valve margin; **pma**, postmucronal area; **pms**, postmucronal slope.

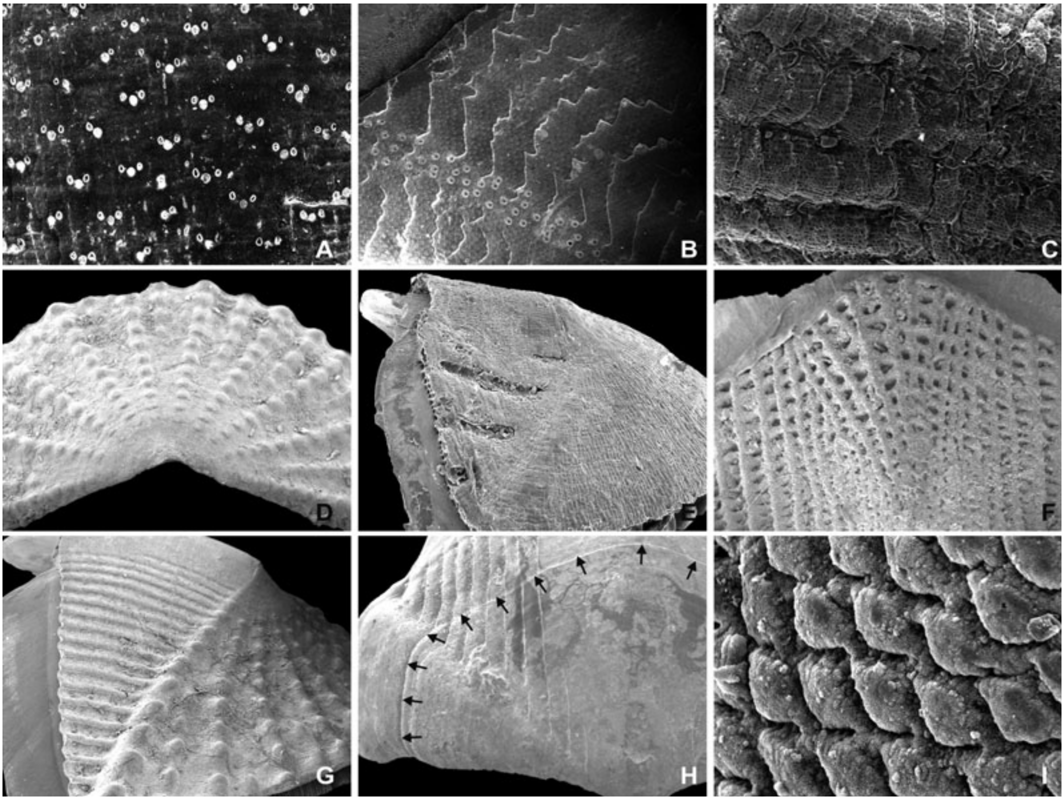


Fig. 9. Dorsal and lateral views of selected chiton valves showing the variety of tegmentum ornamentation. **A.** *Parachiton* sp., New Caledonia (MNHN) with a smooth tegmentum. **B.** *Lucilina lamellosa* (Quoy & Gaimard, 1835), New Caledonia (MNHN) with wavy lines. **C.** *Chiton (Tegulaplax)* sp., New Caledonia (MNHN) with lamellouse granules. **D, G.** *Chiton (Rhyssoplax) ectypus* (de Rochebrune, 1884), New Caledonia (MNHN). **D.** granulated radial ribs on the head valve. **G.** tail valve with longitudinal ribs (at left) and granulated radial ribs (at right side). **E.** *Callochiton neocaledonicus* Kaas & Van Belle, 1990, New Caledonia (MNHN) with deep grooves or sulci. **F.** *Callistochiton mawlei* Iredale & May, 1916, Tasmania (AMS) with cancellated ribs. **H.** *Chiton (Rhyssoplax) rhynchotus* (de Rochebrune, 1884), New Caledonia (MNHN) with longitudinal ribs (at the upper left) and commarginal growth marks (arrows). **I.** *Connexochiton* sp., New Caledonia (MNHN) with quincuncially arranged granules.

Tegmentum: sculpture
Fig. 9

Usually chiton valves are sculptured in different degrees. A single valve may include varying ornamentations that differentiate the valve areas. Truly "smooth" valves are scarce and still show microstructure (Fig. 9A). As a rule, there are two main sculptural arrangements within a species: Radial structures, ribs or series of raised granules, are found in the head valve, lateral areas and postmucronal area only, radiating from a valve apex or the mucro to the valve margin. Longitudinal structures are in the central areas and in the antemucronal area, running parallel to the length axis of the body. Often this structure becomes wider and oblique towards the jugal area. If a pattern of lattice-like structures, for example coalescing granules or raised cross-structures, occurs the shell surface is **cancellate**. A **commarginal** arrangement refers to concentric ornamentation (symmetrical from a central point to all sides), usually reflecting the former (younger) valve margin (Fig. 9H). A surface is **lamellose** if it presents very thin, raised plate-like structures (Fig. 9C). Small elongate, depressions in longitudinal rows in the central areas or in the antemucronal area are **sulci** or may also be termed "**grooved**" (Fig. 9E). A structure is **wavy** if a line is not straight, but consistently well rounded curved (Fig. 9B). Discrete raised **granules** occur not only in different sizes, from microgranulation to globose pustules, but may also be well rounded, drop-shaped, elongate and

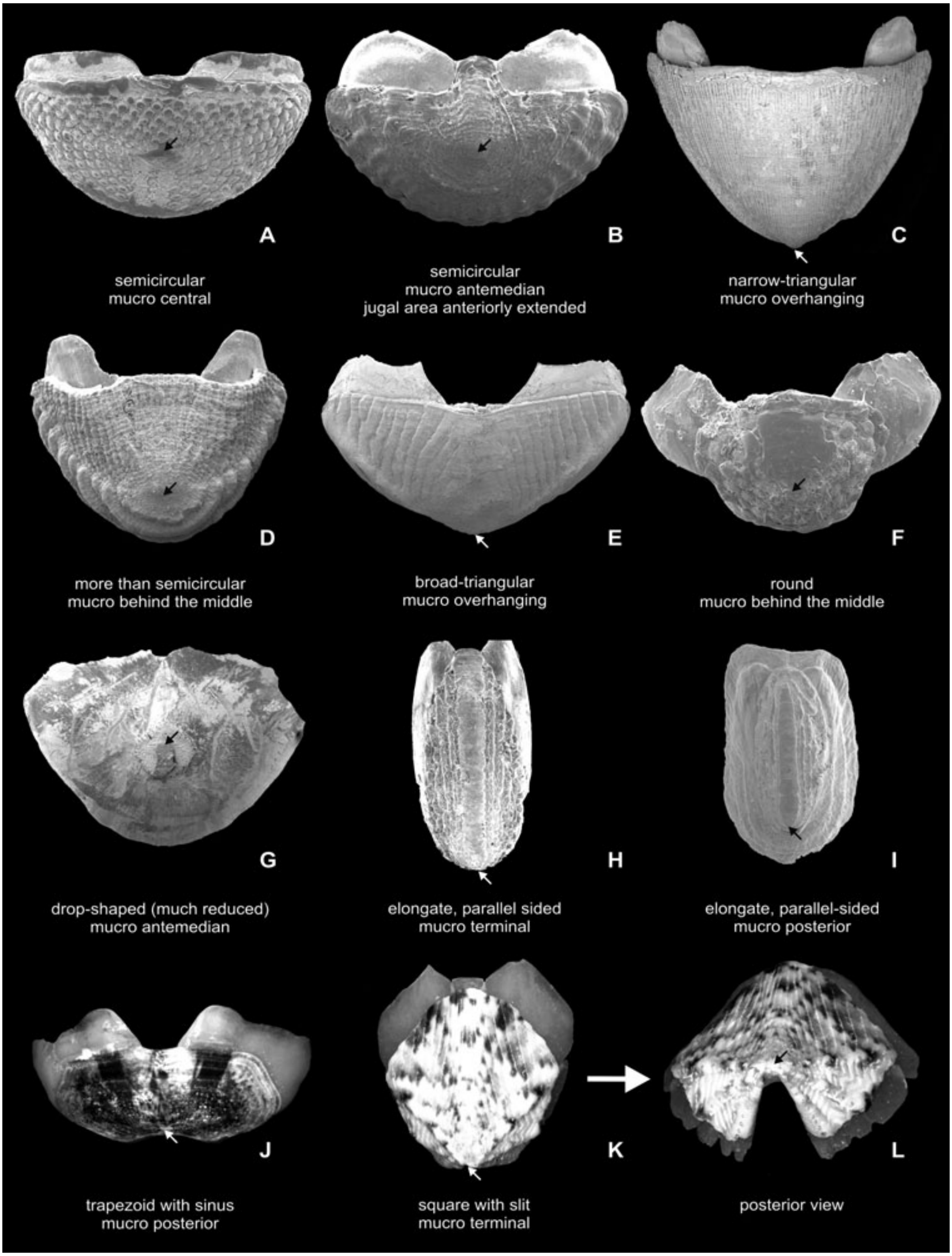


Fig. 10. Dorsal views of selected chiton tail valves, small arrows indicate the position of the mucro. **A.** *Connexochiton platynomenus* Kaas, 1979, Bay of Biscay (MNHN). **B.** *Oldroydia percrassa* (Dall, 1894), USA (ZSM). **C.** *Parachiton acuminatus* (Thiele, 1909), Samoa (ZSM). **D.** *Lepidopleurus cajetanus* (Poli, 1791), Croatia (ZSM). **E.** *Onithochiton* sp., Guam, (UF). **F.** *Choneplax littlerorum* Sirenko, 2003, Fiji (ZSM). **G.** *Choriplax grayi* (H. Adams & Angas, 1864), Australia (SAMA). **H.** *Cryptoplax caledonicus* de Rochebrune, 1882, New Caledonia (MNHN). **I.** *Cryptoplax elioti* Pilsbry, 1901, New Caledonia (MNHN). **J.** *Mopalia swanii* Carpenter, 1864, USA (ZSM). **K, L.** *Schizochiton incisus* (Sowerby, 1841), Indonesia (ZSM).

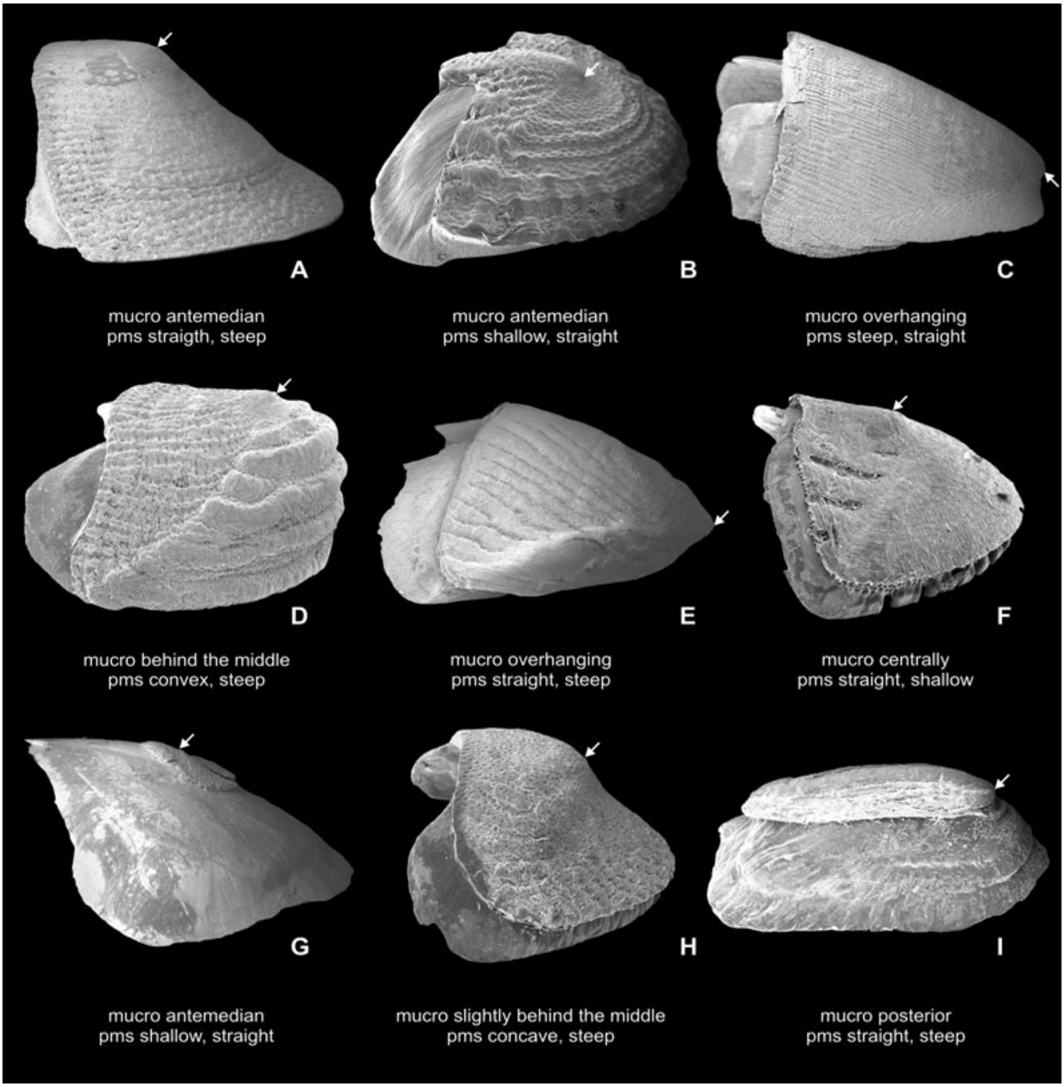


Fig. 11. Left lateral views of selected chiton tail valves, small arrows indicate the position of the mucro. **A.** *Leptochiton algesirensis* (Capellini, 1859), Corse (ZSM). **B.** *Oldroydia percrassa* (Dall, 1894), USA (ZSM). **C.** *Parachiton acuminatus* (Thiele, 1909), Samoa (ZSM). **D.** *Lepidopleurus cajetanus* (Poli, 1791), Croatia (ZSM). **E.** *Onithochiton* sp., Guam, (UF). **F.** *Callochiton neocaledonicus* Kaas & Van Belle, 1990, New Caledonia (MNHN). **G.** *Choriplax grayi* (H. Adams & Angas, 1864), Australia (SAMA). **H.** *Weedingia alborosea* Kaas, 1988, Tuámotu Archipelago (MNHN). **I.** *Cryptoplax elioti* Pilsbry, 1901, New Caledonia (MNHN). **pms**, postmucronal slope.

arranged from irregular to **quincuncial** (in groups of five, on quincunx) (Fig. 9I).

Tegmentum: tail valve

Figs 10, 11

The tail valve holds a special position in regard to characters for species identification. Not only does it show similar structures and sculpture as in intermediate valves, but it also provides the additional features of the mucro (Figs 10-11 arrows). This

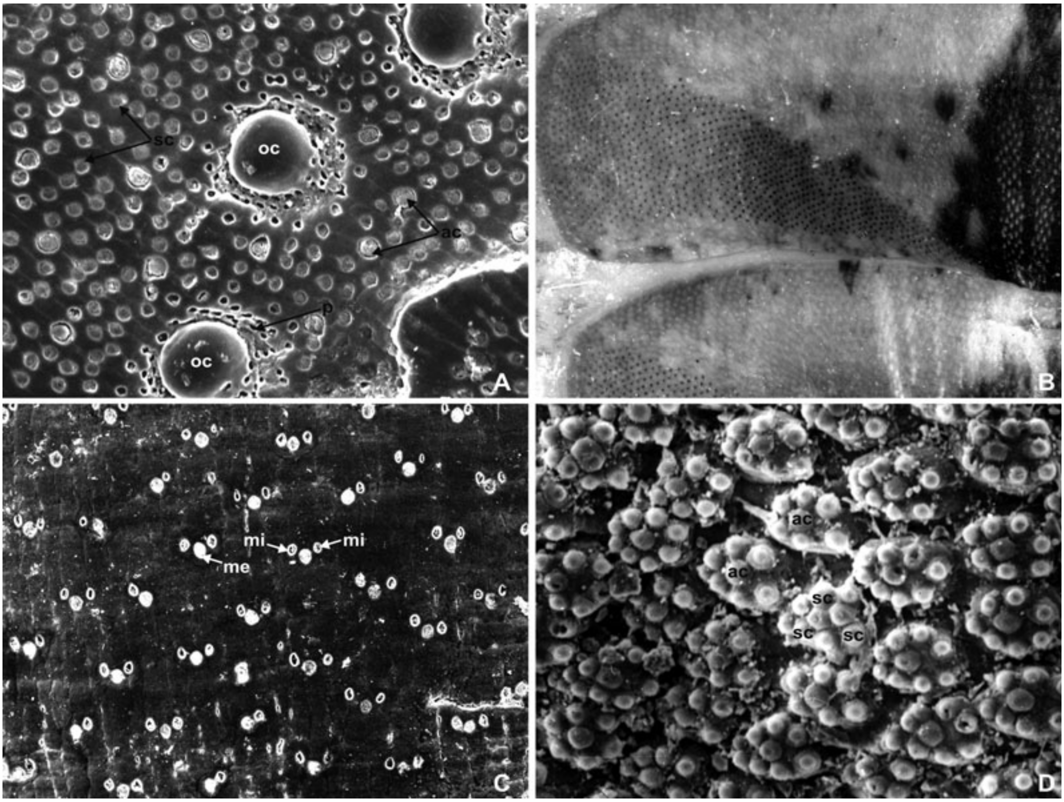


Fig. 12. Dorsal view of selected chiton valves showing different forms of aesthetes. **A.** *Lucilina lamellosa* (Quoy & Gaimard, 1835), New Caledonia (MNHN) with large intrapigmented aesthetes, which are also termed ocelli. **B.** *Callochiton dentatus* (Spengler, 1797), South Africa (ZSM) with blackish extrapigmented aesthetes. **C.** *Parachiton* sp., New Caledonia (MNHN) shows centrally lying megalaesthetes, which are surrounded by two micraesthetes. **D.** Aesthetes of the holotype of *Leptochiton boucheti* Sirenko, 2001, Vanuatu (MNHN) with apical caps (centrally on the nodules) and surrounding elevated subsidiary caps. (image kindly provided by Dr. B. Sirenko, ZISP). **ac**, apical cap; **me**, megalaesthete; **mi**, micraesthete; **oc**, ocelli; **p**, perforation; **sc**, subsidiary cap.

modified form often allows for a fast determination of a species from the tail valve alone. As mentioned above, the position of the mucro in relation to the valve length is important, and whether it is elevated (prominent) or not. According to the general body form, the tail valve may be short and wide, or rather long. Another very interesting aspect is the presence in some species of slits or shallow notches (sinus) at its posterior end (Figs 10J-L, 13D).

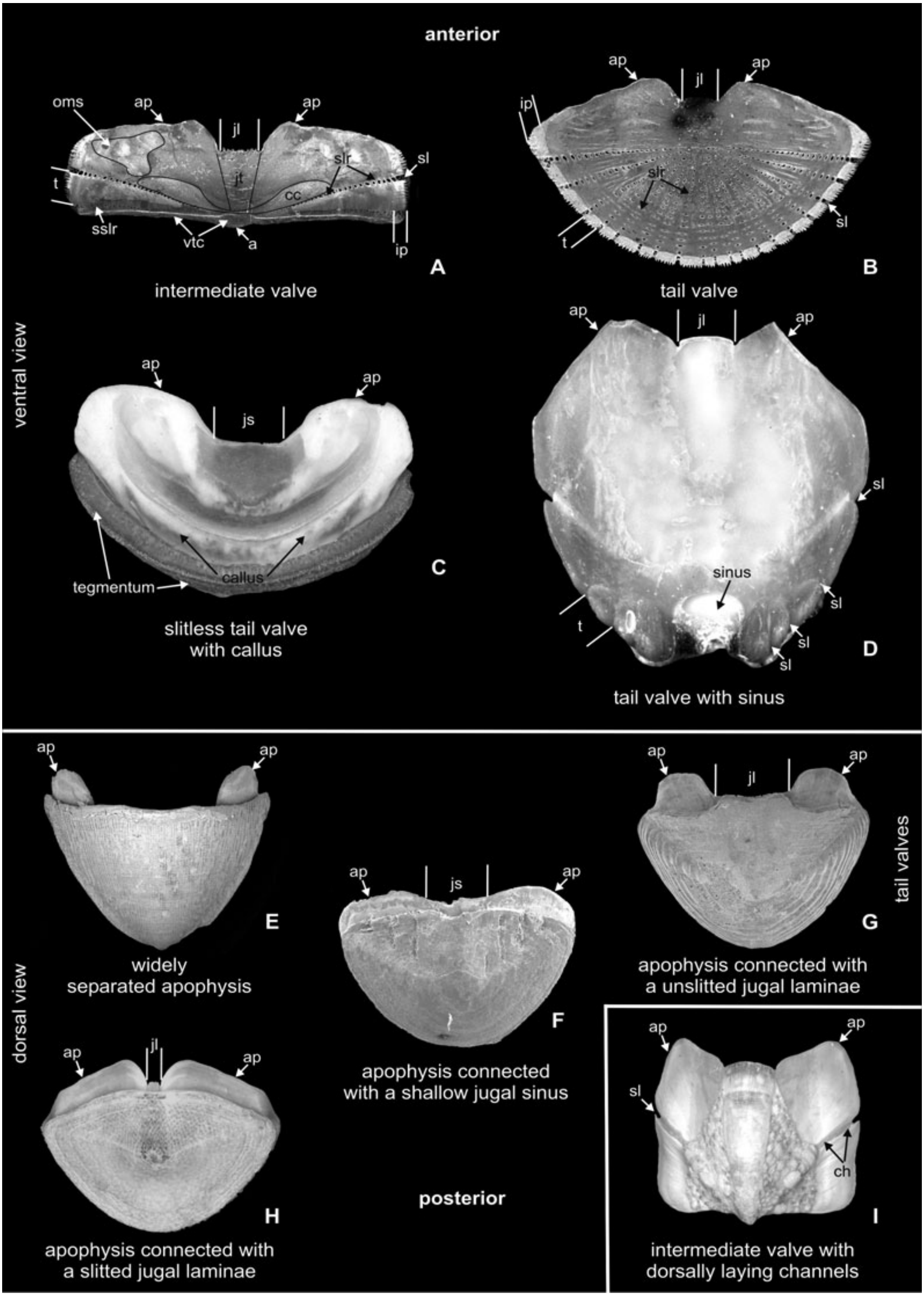
Aesthetes

Fig. 12

Chiton valves are known to contain sensory pores in the tegmentum. These vary in size within a single valve and are termed micropores and macropores. They open into an underlying complex canal system (see "eaves", Fig. 5B) and cavities, which are filled with sensory tissue. This innervated canal

Fig. 13. Dorsal and ventral views of selected chiton valves. **A, B.** *Chiton (Rhyssoplax) olivaceus* Spengler, 1797, Croatia (ZSM). **C.** *Liolophura hirtosa* (Péron MS, de Blainville, 1825), Australia (AMS). **D.** *Schizochiton incisus* (Sowerby, 1841), Indonesia (ZSM). **E.** *Parachiton acuminatus* (Thiele, 1909), Western Samoa (ZSM). **F.** *Callochiton neocaledonicus* Kaas & Van Belle, 1990, New Caledonia (MNHN). **G.** *Chiton (Tegulaplax) hululensis* (E. A. Smith in Gardiner, 1903), Papua New Guinea (ZSM). **H.** *Chiton (Rhyssoplax) translucens* Hedley & Hull, 1909, Australia (AMS). **I.** *Notoplax costata* (H. Adams & Angas, 1864), Australia (AMS). **a**, apex; **ap**, apophysis; **cc**, central callus; **ch**, channel; **ip**, insertion plate; **jl**, jugal laminae; **js**, jugal sinus; **jt**, jugal tract; **oms**, oblique muscle scar; **sl**, slit; **slr**, slit ray; **sslr**, secondary slit ray; **t**, tooth; **vtc**, ventral tegmental callus.

▷


anterior
ventral view
oms
ap
ap
jl
jt
slr
sl
t
cc
sslr
vtc
a
ip
A
intermediate valve
ap
ap
jl
ip
slr
sl
t
B
tail valve
ap
ap
js
tegmentum
callus
C
slitless tail valve
with callus
ap
ap
jl
sl
sinus
sl
t
sl
sl
D
tail valve with sinus
dorsal view
ap
ap
E
widely
separated apophysis
ap
ap
js
F
apophysis connected
with a shallow jugal sinus
ap
ap
jl
G
tail valves
apophysis connected with
a unslitted jugal laminae
ap
ap
jl
H
apophysis connected with
a slitted jugal laminae
posterior
ap
ap
sl
ch
I
intermediate valve with
dorsally laying channels

system and its dorsal surface openings are called **aesthetes**, a term first erected by Moseley (1885). It is possible to morphologically differentiate **micraesthetes** and **megalaesthetes**, corresponding to small and larger surface pores. Within the shell interior, megalaesthetes and micraesthetes occur in bundles, usually with a large central megalaesthete and a radiating network of micraesthetes which may be highly modified. Further, there are different types of megalaesthetes, which are used in identification. Moseley (1885) discovered that in certain species these pores form light-sensing structures. Such specialised megalaesthetes can be differentiated between lens-bearing **ocelli** (e. g. *Acanthopleura*, *Onithochiton*, *Schizochiton*, *Lucilina*, *Tonicia*) (Fig. 12A) and pigmented "**shell eyes**" (e. g. *Callochiton*, *Leloupia*, *Eudoxochiton*, *Choriplax*, and at least some species in the genera *Chiton*, *Stenochiton*, *Tonicella* and *Ischnochiton*) (Fig. 12B). Aesthetes are **extrapigmented** when their pigmentation occurs in the tegmentum (not in the aesthete itself) and the lens is a modified apical cap (Scheitelkappe). This extrapigmented form was the type of shell eyes described by Moseley (1885) and the term was first used by Plate (1901). Similarly, the term **intrapigmented** refers to aesthetes where the pigmented cells occur within the aesthete body and a lens is present with a separate apical cap. Extrapigmented ocelli are always symmetrically arranged at least on the lateral areas. Whereas intrapigmented aesthetes are irregularly arranged on lateral areas and in some genera they occur radially (Nowikoff 1909).

One peculiarity within aesthete morphology was first mentioned by Gowlett-Holmes & Jones (1992). They discovered that in some deep water lepidopleurans (e. g. *Ferreiraella xylophagus*) the micraesthetes protrude fleshy **subsidiary caps** (Fig. 12D). The complexity of aesthetes has been used in phylogenetic analysis and may serve a strong character for the classification of chitons (e. g. Vinther 2006, Fernandez et al. 2007, Vendrasco et al. 2008).

Articulamentum

Fig. 13

As a name for the ventral valve layer, the articulamentum was first mentioned by von Middendorff (1847, p. 9). This valve layer is absent in fossil taxa in the Paleoloricata, and its presence as a feature differentiates the recent chitons (Neoloricata) although its morphology is variable. A typical articulamentum is porcelain-like and white, often with a different colouration in the central part.

With the exception of the head valve, chiton valves have a large, bilobed anterior extension of the articulamentum that usually underlies the preceding valve. The two lobes of this enlargement are known as **apophyses** (sutural laminae) (Fig. 13 "ap"). If the lobes are connected the central bridge is called a **jugal lamina** (Fig. 13 "jl"), which either may be fused with the apophyses or separated by lateral slits. The edge of the jugal lamina may be sharp and solid, sawed, or exceptionally may show a small centrally laying beak. In the posterior region of the apophyses are the attachment site of the oblique body muscles and accordingly there are often large visible **muscle scars** (Fig. 13A).

Usually the articulamentum forms a raised thickened area that sits transversally and extends for the width between the lateral margins of the dorsal tegmentum. This thickening is known as a **central callus** (see also Bullock 1988a, p. 144) (Fig. 13A). Accordingly, the shallower regions in front and behind this bulbous area on the articulamentum are termed the **anterior depression** and **posterior depression**. Observing an intermediate valve from the ventral side one may observe at the posterior margin an area of "overhanging" tegmentum. This area is known as **ventral tegmental callus** (Fig. 13A).

In the majority of recent chitons the articulamentum may form extensions beyond the margin of the tegmentum. These extensions, called **insertion plates** occur on the lateral margins of intermediate valves, on the anterior margin of the head valve and posteriorly on the tail valve. In some species (e. g. *Ferreiraella*) there are insertion plates on the terminal valves only. The distal edge of the insertion plates may be slitted or solid in different taxa. The bridges between the **slits** (or incisions) are called **teeth** (Figs 13A,B,D) and may either be smooth at their outside, roughened, or even strongly pectinate.

The number of slits in the insertion plates differs between the terminal and intermediate valves, and is frequently used as a determinational character. Again it was von Middendorff (1847, p. 16) who established a standard notation to illustrate the slit numbers of the chiton valves, but only using the terminal valves. Unfortunately, he assumed that all intermediate valves have only one marginal slit per side (p. 10, as incisura lateralis), and that is why he did not include intermediate valves in his original formula. The **slit formula** reads as follows: (number of slits in) head valve / slit(s) per side of one intermediate valve / tail valve. For example slit formula: "8/1/10" describes a species with 8 slits in the insertion plate of the head valve, 1 per side in an intermediate valve, and 10 in the tail valve. In some cases the terminal valves may be without slits and may show instead a callus, or sinus. In this case its value is "0" and the relevant explanatory term is added in brackets (e. g. *Plaxiphora mercatoris*: 8/1/0 (callus)) (Fig. 13C).

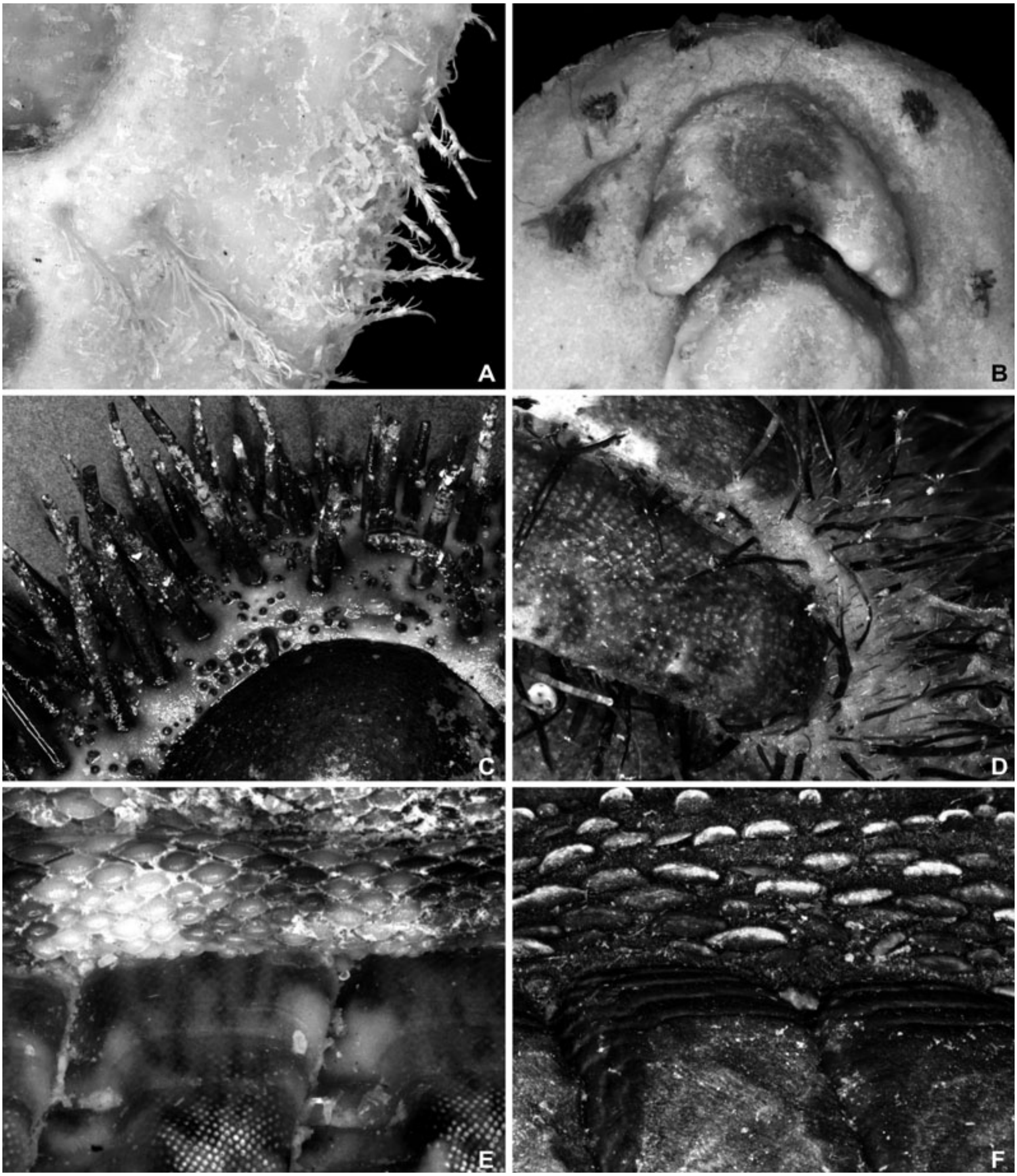


Fig. 14. Dorsal view of selected chiton perinotum zones. **A.** *Mopalia spectabilis* Cowan & Cowan, 1977, USA (ZSM) with corneous bristles. **B.** *Choneplax lata* (Guilding, 1829), Dominican Republic (ZSM) has tufts with calcareous spicules. **C.** *Acanthopleura spinosa* (Bruguière, 1792), Indonesia (ZSM) with large calcareous spines. **D.** *Chaetopleura peruviana* (Lamarck, 1819), Colombia (ZSM) with corneous hairs. **E.** *Chiton (Rhyssoplax) olivaceus* Spengler, 1797, Croatia (ZSM) is covered with imbricated calcareous scales. **F.** *Enoplochiton niger* (Barnes, 1824), Peru (ZSM) has calcareous scales, which are quite wide separated.

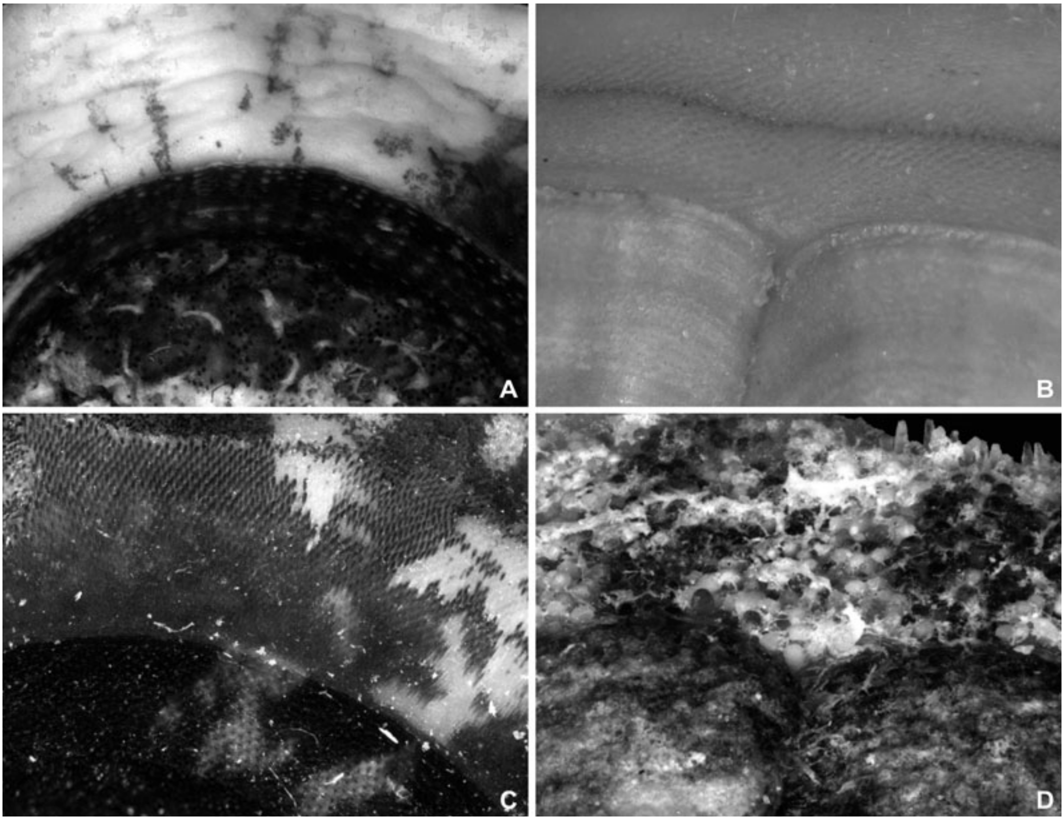


Fig. 15. Dorsal view of selected chiton perinotum zones. **A.** *Tonicia forbesii* Carpenter, 1857, Panama (ZSM) has a naked appearing perinotum**. B.** *Tonicina zschaui* (Pfeffer in von Martens & Pfeffer, 1886), South Georgia (ZSM) shows besides the calcareous corpuscles a distinct median surrounding groove. **C.** *Callochiton dentatus* (Spengler, 1797), South Africa (ZSM) with inwardly directed calcareous spicules. **D.** *Lepidochitona caprearum* (Scacchi, 1836), Croatia (ZSM) with calcareous corpuscles.

In some cases there are perforated lines, extending radially from the apical area towards the slit incisions. These structures are called **slit rays** (Fig. 13B) and they reflect older growth stages of the valve, and are often associated with the ventral termination of the aesthetes. In addition, some species show a highly porous area in the middle field of the valves, which shows the openings of the innervation channels. This area on the ventral valve surface is called the **jugal tract** (Fig. 13A). In species with reduced tegmentum, the articulamentum may show channels that are visible from the dorsal side of the dissected valve and which level off towards the slits (Fig. 13I).

The mantle: girdle and girdle covering
Figs 14-18

The tough and thick tissue that surrounds the chiton plates is the girdle; the entire dorsal surface of the girdle is called the **perinotum** (Fig. 1). Simroth (1892-94, p. 244 as "perinotaeum") initially introduced this term for the mantle edge only. It is covered by various calcareous or corneous **spines**, **hairs**, **scales**, **spicules**, **needles** or **bristles** (Figs 14-16), which are important taxonomic characteristics. Among these surface structures occur **sensory organs** that may serve as mechano- and/or photoreceptors. In some genera (e. g. *Choriplax*, *Tonicia*, *Tonicella*) the perinotum elements are so minute that the dorsal girdle surface appears naked without significant magnification. The illustrations highlight the variability of perinotum elements and structures between different taxa.

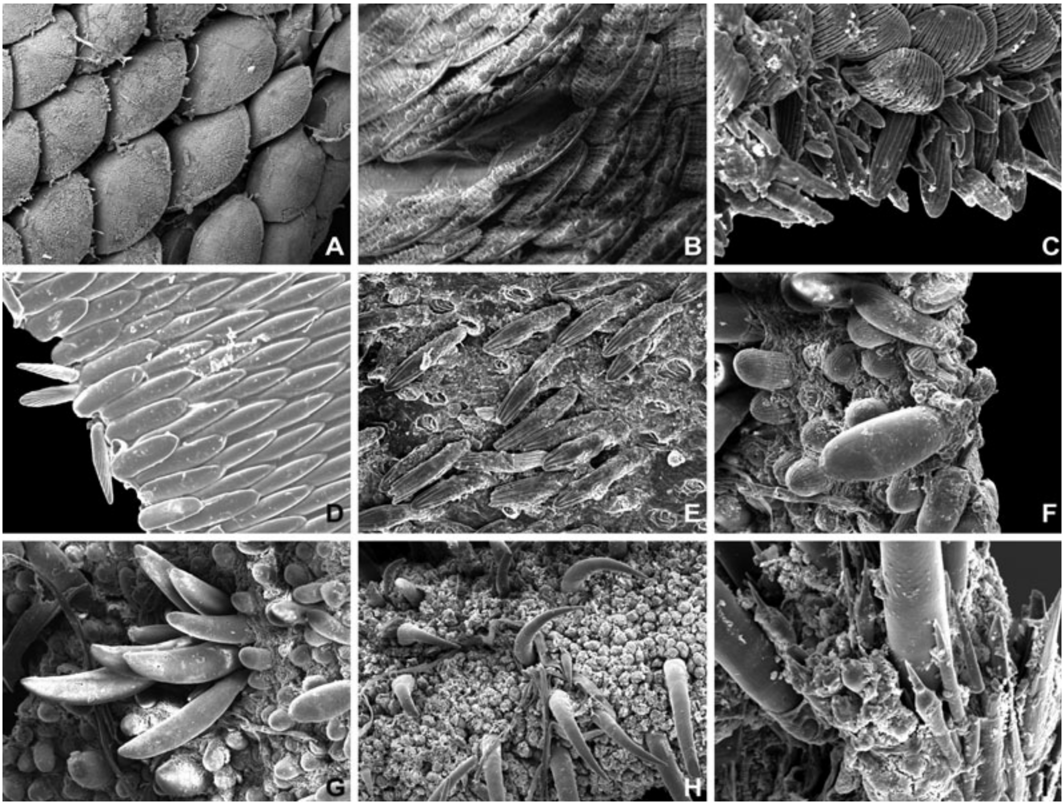


Fig. 16. Perinotum elements of selected chitons. **A.** *Chiton (Rhyssoplax) ectypus* (de Rochebrune, 1884), New Caledonia (MNHN) with smooth, imbricating calcareous scales. **B.** *Ischnochiton albinus* Thiele, 1911, Indonesia (ZSM) with fine-ribbed, imbricating scales with spherules. **C.** *Ischnochiton acomphus* Hull & Risbec, 1930, New Caledonia (MNHN) with fine-ribbed, bent scales (above) and a marginal fringe of straight, obtusely pointed spicules (below). **D.** *Callochiton* sp., New Caledonia (MNHN) with smooth, conical, inward-directed spicules. **E.** *Cryptoplax caledonicus* de Rochebrune, 1882, New Caledonia (MNHN) with straight, radial ribbed, obtusely pointed spicules. **F, G.** *Cryptoplax larvaeformis* (de Blainville MS, Burrow, 1815), New Caledonia (MNHN) with solid, club-shaped, radially fine-ribbed spicules (F) and solid, slightly curved, smooth spicules (G). **H, I.** *Acanthochitona* sp., New Caledonia (MNHN) with large, strongly curved spines among minute corpuscles (H) and smooth, straight, sliletto-like, sharp pointed spines (I).

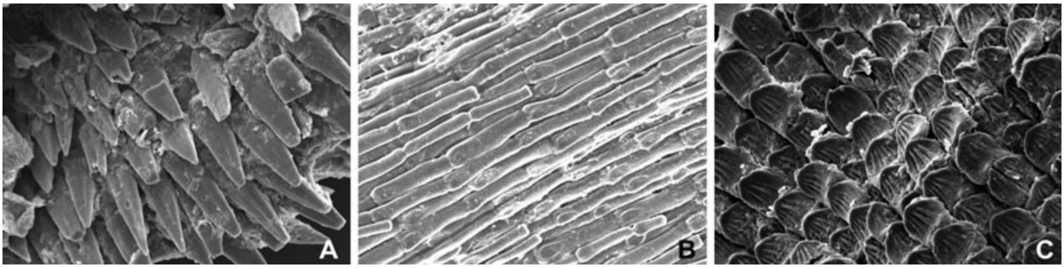


Fig. 17. Hyponotum elements of selected chitons. **A.** *Plaxiphora obscurella* (Souverbie in Souverbie & Montrouzier, 1866), New Caledonia (MNHN) with spicule-like scales of irregular arrangement. **B.** *Chiton (Rhyssoplax) rhynchotus* (de Rochebrune, 1884), New Caledonia (MNHN) with radial rows of smooth, elongate scales. **C.** *Onithochiton societatis* Thiele, 1909, New Caledonia (MNHN), with radial rows of squarish, strong ribbed scales.

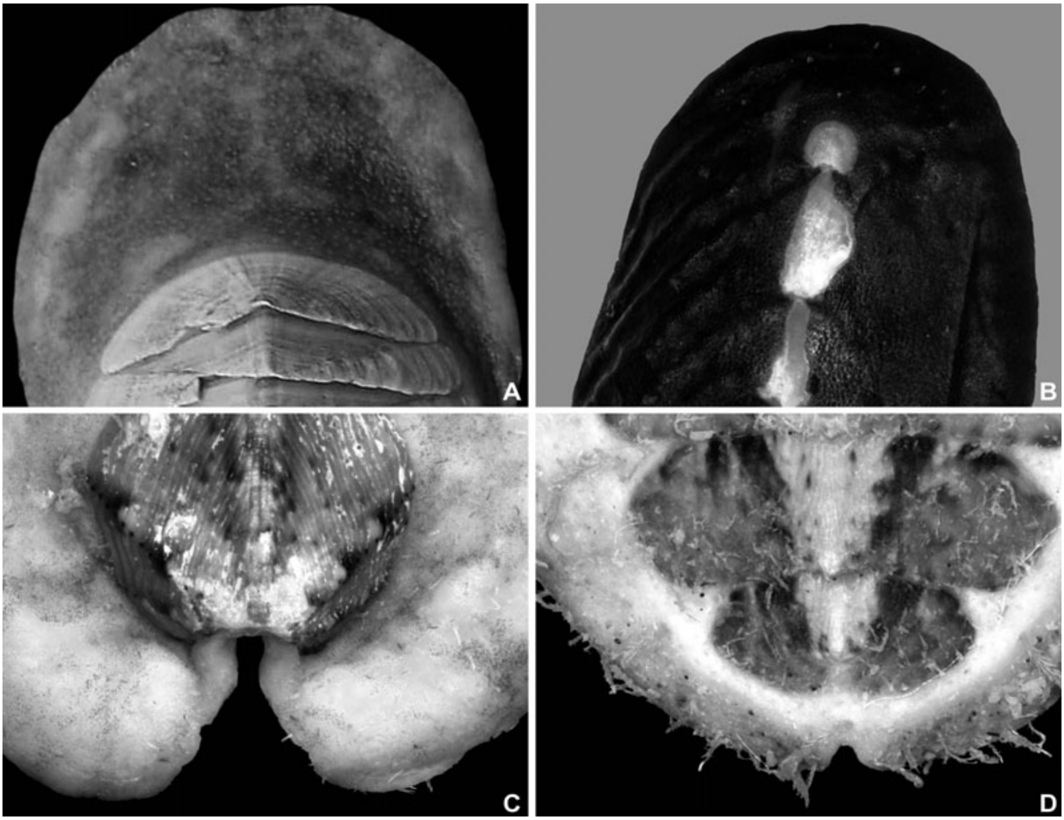


Fig. 18. Perinotum of selected chitons. **A.** *Placiphorella* sp., Chile (ZSM) with anteriorly extended perinotum. **B.** The perinotum of *Cryptoconchus floridanus* (Dall, 1889), Dominican Republic (ZSM) is partly expanded over the valves. **C.** *Schizochiton incisus* (Sowerby, 1841), Indonesia (ZSM) with a posterior deeply notched perinotum. **D.** *Mopalia spectabilis* Cowan & Cowan, 1977, USA (ZSM) shows posterior a shallow sinus in the perinotum**.**

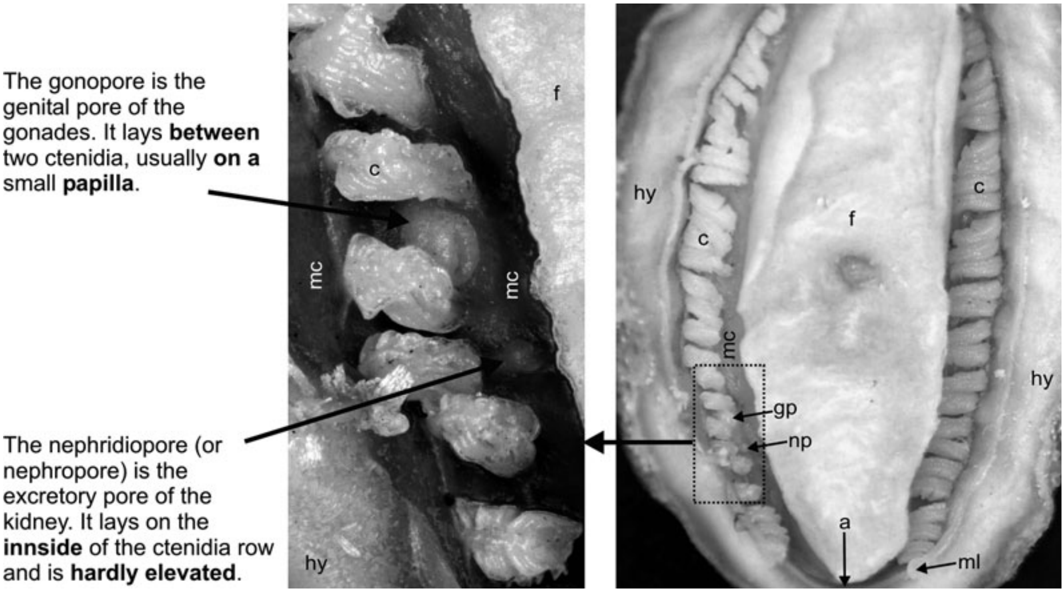
The ventral side of the girdle (Fig. 17), which is known as **hyponotum** (Simroth 1892-94, p. 245 as "hyponotaeum"), is usually covered with flat **scale-like spicules** or small rectangular **scales**. The hyponotum is completely **naked** only in the deep-water genus *Ferreiraella*, although there are a few rows of scales with a hyponotum like morphology on the distal margin (Kaas and Van Belle 1985 p. 115-116, fig. 50.7).

The girdle is adapted to specific lifestyles of chitons and accordingly some interesting modifications occur. Several carnivorous species (e. g. *Placiphorella*, *Loricella*) show a considerable **anteriorly extended girdle**, which functions to trap prey (Fig. 18A). Species with a slit or a caudal sinus in the tail valve may show a corresponding adaptation at the posterior girdle edge, allowing the animal a more effective channel for excreting faecal pellets (Figs 18C-D). Many species of the suborder Acanthochitonina show tegmentum reduction and the parallel expansion of the perinotum over the valves (Fig. 18B); the most extreme form of this is complete coverage of the valves in adult *Cryptochiton stelleri*.

Ctenidia

At both sides of the foot, suspended from the roof of the mantle cavity, is a serial arrangement of single-file **ctenidia** (or gills). The ctenidial number shows considerable variability between species, even within a genus. The number of ctenidia on each side also depends on the age of the individual, as additional gill structures are added during growth. The direction of the extension of the gill rows is relevant to taxonomy, as is the position of the last ctenidium in relation to the anus and the number of ctenidia extending behind the **nephridiopore**.

At present (Sirenko 1993, but see Sigwart 2008) gill arrangements are classified as **abanal** or **adanal**.


The gonopore is the genital pore of the gonades. It lays **between** two ctenidia, usually **on a** small **papilla**.

The nephridiopore (or nephropore) is the excretory pore of the kidney. It lays on the **innside** of the ctenidia row and is **hardly elevated**.

Fig. 19. Ventral view of *Chiton (Rhyssoplax) kurodai* Is. & Iw. Taki, 1929, Japan (ZSM) to show the positions of the nephridiopore and gonopore**.** The species has a holobranchial and adanal arrangement of the ctenidia as the gonopore is situated between the ctenidia 9-10 (counted from posterior) and the nephridiopore is on a level with ctenidium 8. **a**, anus; **c**, ctenidia; **f**, foot; **gp**, gonopore; **hy**, hyponotum; **mc**, mantle cavity; **ml**, mantle lappet; **np**, nephridiopore.

If only one ctenidium is posterior to the nephridiopore this is an **abanal** arrangement. In contrast, the **adanal** type has at least two post-renal ctenidia (as defined in Yonge 1939, p. 369). These definitions differ considerably from the terms coined by Plate (1896, p. 170). The terms **metamacrobranch** and **mesomacrobranch** of Pelseneer (1898, p. 25) are synonyms of Plate's abanal and adanal, respectively. Pelseneer (1898) termed ctenidia that become larger towards the anus as abanal, while adanal ctenidia are smaller towards the anus. This usage was also employed by Kaas and Van Belle (1985).

Ctenidia that extend along the whole length of the foot are termed **holobranchial** (Simroth 1892-94,

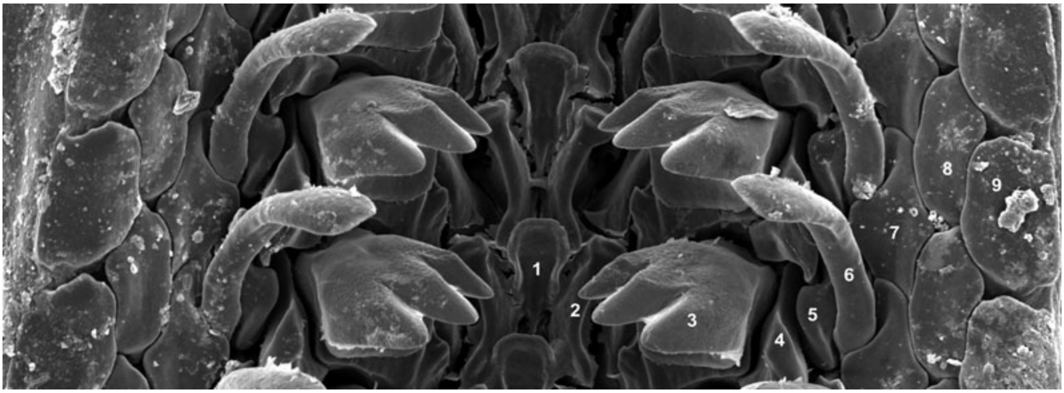


Fig. 20. Radula of *Acanthochitona noumeaensis* Leloup, 1941, New Caledonia (MNHN). **1**, rhachidian or central tooth; **2**, first or minor lateral tooth; **3**, second or major lateral tooth; **4**, first uncinal tooth; **5**, second uncinal tooth; **6**, third or major uncinal tooth; **7**, first or inner marginal tooth; **8**, second or middle marginal tooth; **9**, third our outer marginal tooth.

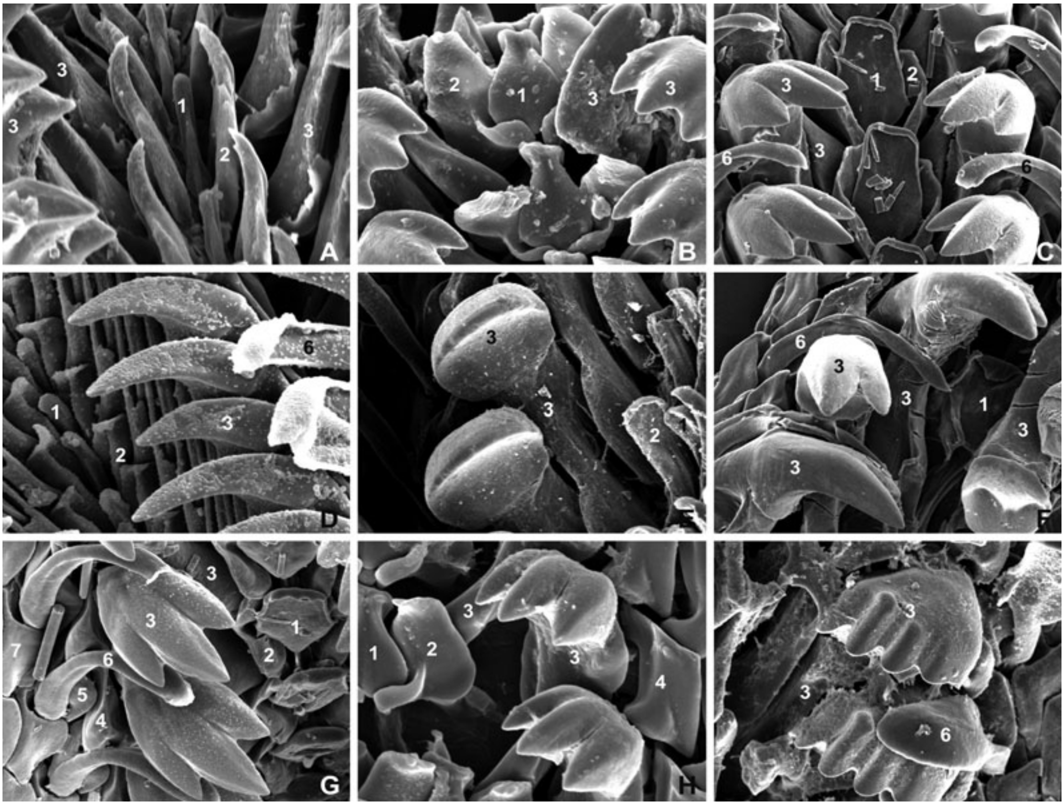


Fig. 21. Close-ups of chiton radulae to show the central teeth (A-C) and the heads of the second lateral teeth (D-I). **A.** *Parachiton* sp., New Caledonia (MNHN), long and slender central tooth with anterior keel. **B, H.** *Callochiton neocaledonicus* Kaas & Van Belle, 1990, New Caledonia (MNHN). **B.** tulip-shaped central tooth with extended and slightly covered shaft. **H.** second lateral tooth with tricuspidate blade with similar sized denticles. **C, G.** *Notoplax tridacna* (de Rochebrune, 1881), New Caledonia (MNHN). **C.** broad rectangular central tooth with forward bent straight blade. **G.** head of the second lateral tooth tricuspidate with central denticle largest. **D.** *Connexochiton platynomenus* Kaas, 1979, Bay of Biscay (MNHN), head of the second lateral tooth unicuspidate with a slender blade. **E.** *Liolophura hirtosa* (Péron MS, de Blainville, 1825), Australia (AMS), second lateral tooth discoid with a unicuspidate blade. **F.** paralectotype of *Chaetopleura benaventei* Plate, 1899, Chile (ZMB), head of the second lateral tooth bicuspidate. **I.** *Lucilina* sp., Guam, (ZSM), head of the second lateral tooth fourcuspidate with the outermost denticle being the smallest. **1**, rhachidian or central tooth; **2**, first or minor lateral tooth; **3**, second or major lateral tooth; **4**, first uncinal tooth; **5**, second uncinal tooth; **6**, third or major uncinal tooth; **7**, first or inner marginal tooth.

p. 247) (see Fig. 19); when the gill row is restricted to the posterior half it is **merobranchial** (Simroth 1892-94, p. 247; example here figured in Fig. 2B). The basal order Lepidopleurina is usually characterized by merobranchial, ctenidia that reach the anus, with many species having ctenidia in a **circumanal** continuous semicircular curtain, and the stems of individual ctenidia at the posterior arising from the flesh of the anal papilla. All other recent chitons have a distinct space between the last ctenidium and the anus.

Radula

Figs 20-24

A typical chiton radula is comprised of 17 teeth per transverse row, with a half row numbered here (Fig. 20).

The chiton radula differs from other molluscan groups in that the morphology is both relatively simple and, more strikingly, is largely conserved over the entire class. However, morphological features of particular teeth are indicative for taxonomic identification.

By far the best radula descriptions are found in

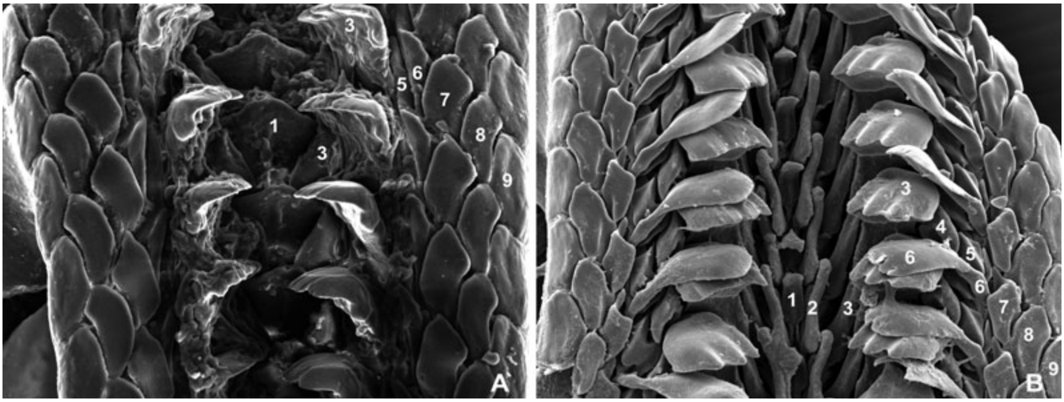


Fig. 22. Close-ups of chiton radulae to show the differences in tooth numbers per transverse row. **A.** *Juvenichiton saccharinus* (Dall, 1878), Kurile Islands (ZSM), with 13 teeth per row. **B.** *Onithochiton societatis* Thiele, 1909, New Caledonia (MNHN), with the usual 17 teeth per row. **1**, rhachidian or central tooth; **2**, first or minor lateral tooth; **3**, second or major lateral tooth; **4**, first uncinal tooth; **5**, second uncinal tooth; **6**, third or major uncinal tooth; **7**, first or inner marginal tooth; **8**, second or middle marginal tooth; **9**, third our outer marginal tooth.

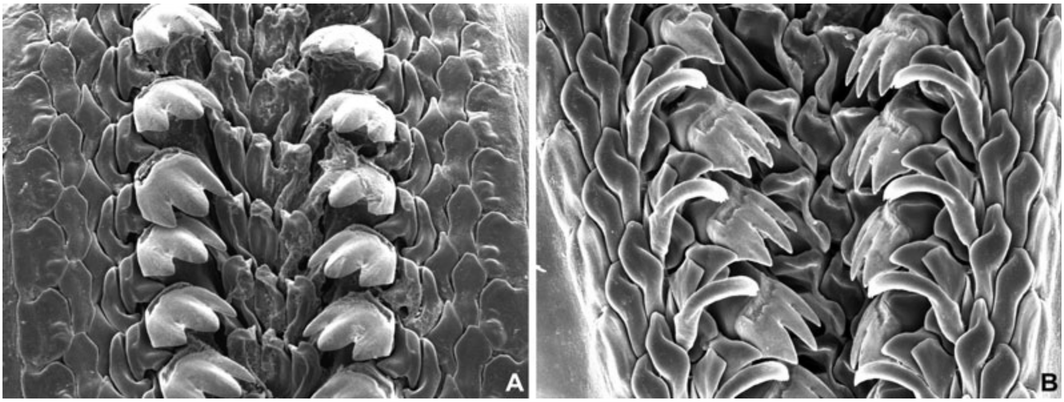


Fig. 23. Close-ups of chiton radulae to show two different cases of radula asymmetrie. **A.** *Callochiton crocinus* (Reeve, 1847), Australia (ZSM) with flat major uncinal teeth. **B.** *Choriplax grayi* (H. Adams & Angas, 1864), Australia (AMS) with long and slender major uncinal teeth.

Bullock (1988a) and Saito (2004), although the terminology of these two authors differs slightly from earlier more taxonomically oriented comprehensive works.

Thiele (1893) made the first attempt to use chiton radulae for a systematic classification. Despite the limited value of the characteristics he examined, his work is detailed and a useful resource. His original work in German has led to some confusion about English names for radular elements, even Bieler & Mikkelsen (1992, p. 7) proposed modified "standard terms", which are no longer in use.

radula	Reibplatte
central tooth (rhachidian)	Mittelplatte
first lateral (minor lateral) tooth	Zwischenplatte
major lateral (second lateral) tooth	Hauptzahnplatte
head (cusp) of the major lateral tooth	Hakenplatte
major uncinal (third uncinal) tooth	Seitenplatte
first uncinal, **second uncinal** and **marginal** (lateral) teeth collectively	Randplatten

Thiele (1893, p. 358) introduced the term "lepidoglossate" for the chiton radula to demonstrate its differences from the docoglossate type, but this term is no longer in use. Modern workers (e.g. Wimmer & Salvini-Plawen 2001, pp. 22-23) refer to the arrange-

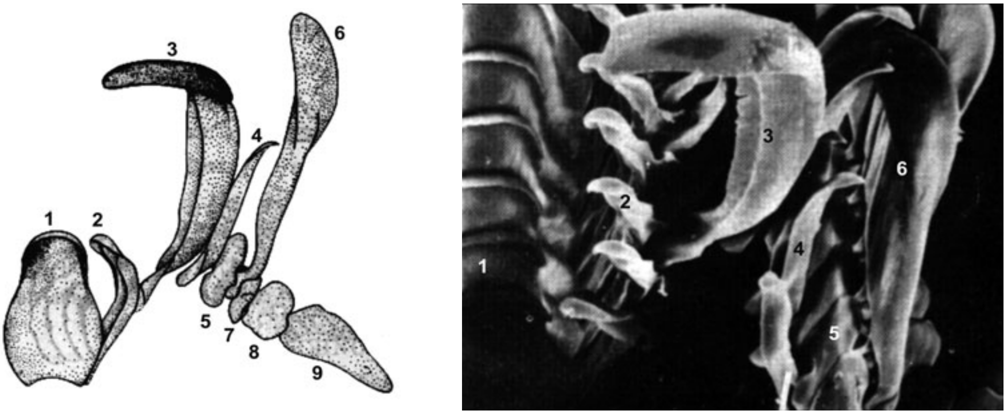


Fig. 24. Toothpick-like first uncinal tooth of *Leptochiton tenuidontus* Saito & Okutani, 1990 (slightly modified after Saito & Okutani 1990). **1**, rhachidian or central tooth; **2**, first or minor lateral tooth; **3**, second or major lateral tooth; **4**, first uncinal tooth; **5**, second uncinal tooth; **6**, third or major uncinal tooth; **7**, first or inner marginal tooth; **8**, second or middle marginal tooth; **9**, third our outer marginal tooth.

ment of the chiton radula teeth as **polyserial**.

Some recent work (e. g. Kaas & Van Belle 1985, p. 16; Kaas et al. 1998, p. 166) uses the term "**spatulate** uncinal tooth" for the third uncinal tooth. However, this designation is misleading, because representatives of the genera *Callochiton* (partim) and *Cryptochiton* do not show such a modified tooth (compare Fig. 23A). So it is recommended to retain the name that was originally introduced by Dall (1879, p. 292): "major uncinus" or **major uncinal** tooth. Dall (1879) also pointed out the difficulties interpreting the more distal teeth as marginal or a combination of marginal and uncinal teeth. The marginal teeth, sometimes also called lateral teeth, are numbered one to three but are also referred to as the inner, middle, and outer marginal teeth.

The most visually distinctive aspect of the chiton radula is the mineralised **head** of the major lateral teeth (Figs 21D-I). The head may have one to four distinct points; the various states are called uni-, bi-, tri- or fourcuspidate. Confusingly the points of the major lateral head may also be referred to as cusps or denticles, but these terms are also sometimes applied to the head as a whole.

Peculiarities and variation in radular morphology

A radula may vary considerably in length (relative to body size) in different genera. As a result, the number of transverse rows can fluctuate considerably between taxa.

In several species of *Callochiton* and in *Cryptochiton* the major uncinal tooth is so much reduced, that it appears as a flat plate (like the other uncinals) (Fig. 23A).

So far, only a single species is known (*Leptochiton tenuidontus* Saito & Okutani, 1990) that shows an elevated, toothpick-like first uncinal tooth (Saito & Okutani 1990) (Fig. 24).

Juvenichiton, *Nanichiton* and *Micichiton* differ from all other genera in having 11-13 teeth per transverse row (Fig. 22A) instead of 17 (Figs 20, 22B). This lower number results from the lack of the first lateral tooth and a decreased number of uncinal teeth. Whether the first lateral tooth is actual lacking per se or if it is fused with the central tooth as in the gastropod family Lepetidae (see Schwabe 2006) has not been investigated. A few genera, such as *Callochiton*, *Cryptochiton*, *Choriplax* and *Notoplax* have **asymmetric radula rows** (Fig. 23).

Bullock (1988b) was the first to point out that the orientation of the distal edge of the first lateral tooth is of taxonomic relevance. He mentioned that the distal edge of this tooth in species of *Rhyssoplax* is parallel to the longitudinal axis, while in other genera (e. g. *Chiton*) it is perpendicular.

Thiele (1893, p. 356) was the only author who has ever mentioned an abnormality in a chiton radula. He found in a specimen of *Tonicella submarmorea* an extra tooth on only one side of the radula.

Conclusions

Chitons as a group are distributed over the entire globe. Consequently they are also studied by a widely-dispersed international group of researchers. Linguistic and historical barriers have in the past caused some confusion about the precise meaning for various anatomical terms, most particularly with regard to soft tissues such as ctenidia. With an increased understanding of chitons in terms of their biological and evolutionary importance, and also the establishment of clearly defined morphological character sets for cladistic analysis, there is a need to agree on standard terms to avoid perpetuating further confusion between different published works. Although no radical changes in usage are proposed in this paper, it is hoped that the standardised terms laid out here may be adopted as an agreement for general morphological descriptions.

Acknowledgements

The author thanks Dr Julia Sigwart (Dublin, Ireland) for helpful comments on an earlier version of the manuscript and for polishing the English.

References

Bieler, R. & Mikkelsen, P. M. 1992. Handbook of systematic malacology, Part 1 (Loricata; Gastropoda: Prosobranchia). XIII + 625 pp., Washington, D.C. (Smithsonian Institution Libraries and The National Science Foundation) (Annotated English-language edition of: Thiele, J., Handbuch der systematischen Weichtierkunde, Teil 1).

Bergenhayn, J. R. M. 1930. Die Loricaten von Dr. Sixten Bocks Pazifik-Expedition 1917-1918, mit spezieller Berücksichtigung der Perinotumbildungen und der Schalenstruktur. Göteborgs Kungliga Vetenskaps- och Vitterhets-Samhälles Handlingar, Ser. B, (12) 1: 1-52, pls 1-3.

Bullock, R. C. 1988a. The genus *Chiton* in the New World (Polyplacophora: Chitonidae). The Veliger 31 (3/4): 141-191.

– – 1988b. Notes on some *Rhyssoplax* from the Pacific Ocean (Mollusca: Polyplacophora: Chitonidae). Proceedings of the Biological Society of Washington 101 (3): 682-692.

Dall, W. H. 1879. Report on the limpets and chitons of the Alaskan and Arctic regions, with descriptions of genera and subspecies believed to be new. Proceedings of the United States National Museum 1: 281-344, pls 1-5.

Fernandez, C. Z., Vendrasco, M. J. & Runnegar, B. 2007. Aesthete canal morphology in twelve species of chiton (Polyplacophora). The Veliger 49(2): 51-69.

Gowlett-Holmes, K. L. & Jones, A. M. 1992. Xylochitonidae fam. n., a new family of deep-water chitons, with descriptions of a new genus and species from New Zealand (Polyplacophora: Lepidopleurina). Journal of the Malacological Society of Australia 13: 35-44.

Iredale, T. & Hull, A. F. B. 1924. A monograph of the Australian loricates (Phylum Mollusca – Order Loricata), II. The Australian Zoologist 3: 227-238, pls 33-34.

Janssen, R. 1978. Revision der Polyplacophora des Oligozäns in Mitteleuropa. Archiv für Molluskenkunde 108 (4-6) 1977: 215-235.

Kaas, P., Jones, A. M. & Gowlett-Holmes, K. L. 1998. Class Polyplacophora. Introduction. Pp. 161-177 in: Beesley P. L., Ross, G. J. B. & Wells, A. (eds). Mollusca: The Southern Synthesis. Fauna of Australia, Vol. 5, Part A. Melbourne (CSIRO Publishing).

– – & Van Belle, R. A. 1981. The genus *Lepidochitona* Gray, 1821 (Mollusca: Polyplacophora) in the northeastern Atlantic Ocean, the Mediterranean Sea and the Black Sea. Zoologische Verhandelingen, Leiden, 185: 1-43.

– – & – – 1985. Monograph of living chitons (Mollusca: Polyplacophora) 1, Order Neoloricata: Lepidopleurina. 240 pp., Leiden (E. J. Brill/W. Backhuys).

Mizzaro-Wimmer, M. & Salvini-Plawen, L. 2001. Praktische Malakologie. Beiträge zur vergleichend-anatomischen Bearbeitung der Mollusken. 188 pp., Wien (Springer-Verlag).

Nowikoff, M. 1909. Über die intrapigmentären Augen der Placophoren. Zeitschrift für Wissenschaftliche Zoologie 93 (4): 668-680, pl. 19.

Pelseneer, P. 1898. Sur la morphologie des branchies et des orifices rénaux et génitaux des chitons (1). Bulletin Scientifique de la France et de la Belgique 31: 23-30.

Plate, L. H. 1896. Über die Organisation einiger Chitonen. Verhandlungen der Deutschen Zoologischen Gesellschaft 6: 168-176.

– – 1901. Die Anatomie und Phylogenie der Chitonen. Fauna Chilensis 2 (2). Zoologische Jahrbücher, Systematik 3, Suppl. 5: 281-600, pls 12-16.

Puchalski, S. S., Eernisse, D. J. & Johnson, C. C. 2008. The effect of sampling bias on the fossil record of chitons (Mollusca, Polyplacophora). American Malacological Bulletin 25: 87-95.

Saito, H. 2004. Phylogenetic significance of the radula in chitons, with special reference to the Cryptoplacoidea (Mollusca: Polyplacophora). Bollettino Malacologico, Suppl. 5: 83-104.

– – & Okutani, T. 1990. Two new chitons (Mollusca: Polyplacophora) from a hydrothermal vent site of the Iheya Small Ridge, Okinawa Trough, East China Sea. Venus 49 (3): 165-179.

Sauer, F. 1992. Meerespflanzen, Meerestiere nach Farbfotos erkannt. 354 pp., Karlsfeld (Fauna-Verlag).

Schwabe, E. 2006. A new species of *Bathylepeta* Moskalev, 1977 (Mollusca: Gastropoda) from the Weddell Sea, Antarctica. Zootaxa 1297: 37-45.

– – 2008. A summary of reports of abyssal and hadal Monoplacophora and Polyplacophora (Mollusca). Pp. 205-222 in: Martínez Arbizu, P. & Brix, S. (eds). Bringing light into deep-sea biodiversity. Zootaxa 1866: 1-574.

Sigwart, J. D. 2008. Gross anatomy and positional homology of gills, gonopores, and nephridiopores in "basal" living chitons (Polyplacophora: Lepidopleurina). American Malacological Bulletin 25(1/2): 43-49.

Simroth, H. 1892-1894. Dr. H. G. Bronn's Klassen und Ordnungen des Thier-Reichs, wissenschaftlich dargestellt in Wort und Bild, 3. Band. Mollusca, I. Abtheilung: Amphineura und Scaphopoda. VIII+467 pp., 22 pls, Leipzig (C. F. Winter'sche Verlagsbuchhandlung).

Sirenko, B. I. 1993. Revision of the system of the order Chitonida (Mollusca: Polyplacophora) on the basis of correlation between the type of gills arrangement and the shape of the chorion processes. Ruthenica 3(2): 93-117.

Stachowitsch, M. 1992. The invertebrates. An illustrated glossary. 690 pp., New York (Wiley-Liss).

Thiele, J. 1893. Polyplacophora, Lepidoglossa, Schuppenzüngler. Pp. 353-401, pls 30-32 in: Troschel, F. H. (ed.). Das Gebiss der Schnecken zur Begründung einer natürlichen Classification. Vol. 2(8). Pp. 336-409, pls. 29-32, Berlin (Nicolaische Verlagsbuchhandlung).

Vendrasco, M. J., Fernandez, C. Z., Eernisse, D. J. & Runnegar, B. 2008. Aesthete canal morphology in the Mopaliidae (Polyplacophora). American Malacological Bulletin 25: 51-69.

Vinther, J. 2006. The esthetal canal system in chitons (Polyplacophora) and sachitids (Lower to Middle Cambrian) – a comparison of canals in a mineralized matrix, their possible homology and phylogenetic implications. Special thesis, 123 pp., Geological and Zoological Museum of Copenhagen.

von Middendorff, A. T. 1847. Beiträge zu einer Malakozoologia Rossica. Mémoires Sciences Naturelles de l'Académie Impériale des Sciences St. Petersburg 6(1): 1-151, pls 1-14.

Willmann, R. 2002. Das System der "Tiere". Pp. 1-1–1-129 in: Munk, K. (ed.). Grundstudium Biologie. Zoologie. I-XII, 1-1–1-33, Heidelberg and Berlin (Spektrum Akademischer Verlag).

Yonge, C. M. 1939. On the mantle cavity and its contained organs in the Loricata (Placophora). Quarterly Journal of Microscopical Science 81(3): 367-390.

Zeitschrift/Journal: Spixiana, Zeitschrift für Zoologie

Jahr/Year: 2010

Band/Volume: 033

Autor(en)/Author(s): Schwabe Enrico

Artikel/Article: Illustrated summary of chiton terminology (Mollusca, Polyplacophora) 171-194