Bollettino Malacologico, Roma, Supplemento 5: 83-104, [2003] 2004 - Società Italiana di Malacologia

Phylogenetic significance of the radula in chitons, with special reference to the Cryptoplacoidea (Mollusca: Polyplacophora)

Hiroshi Saito

Department of Zoology, National Science Museum, 3-23-1 Hyakunin-cho, Shinjuku-ku, Tokyo 169-0073, Japan, e-mail: *h-saito@kahaku.go.jp*

ABSTRACT Polyplacophoran radular characters are reviewed and their usefulness in systematics is re-evaluated. The results suggest that radular characters are useful not only for recognition of species but also for assessment of phylogenetic relationships among species, genera or even higher taxa. In particular, the petaloid process of the major lateral tooth may have taxonomic significance at family or higher levels, and the accessory process of the centro-lateral tooth is another possibly important character at higher taxonomic levels. Radular characters may be most useful in evaluation of the phylogenetic relationships within a genus and/or a family. The present study outlines the characteristics of radulae of the following cryptoplacoid genera: *Craspedoplax, Craspedochiton, Notoplax, Cryptoconchus, Leptoplax, Bassethullia, Pseudotonicia, Acanthochitona, Choneplax, Cryptoplax, Hemiarthrum* and *Cryptochiton*. Morphological comparison implies close relationships between *Notoplax* and *Cryptoconchus* and among *Acanthochitona*, *Choneplax* and *Cryptoplax*; paraphyly of *Cryptoconchus*, the presence of a number of species-groups or genera in *Acanthochitona*, and parallel reduction of the tegmentum within the Cryptoplacoidea.

RIASSUNTO Vengono riviste le caratteristiche della radula nei poliplacofori e ne viene rivalutato l'utilizzo in sistematica. I risultati suggeriscono che i caratteri della radula sono utili non solo per il riconoscimento delle specie, ma anche per la valutazione delle relazioni filogenetiche tra specie, generi o taxa di livello superiore. In particolare, il processo petaloide del secondo dente laterale può assumere un significato tassonomico a livello di famiglia o superiore, e il processo accessorio del primo dente laterale e' un altro importante carattere a livelli tassonomici elevati. I caratteri della radula possono essere molto utili nella valutazione delle relazioni filogenetiche all'interno di un genere e/o di una famiglia. Il presente studio evidenzia le caratteristiche della radula dei seguenti generi criptoplacoidi: *Craspedoplax, Craspedochiton, Notoplax, Cryptoconchus, Leptoplax, Bassethullia, Pseudotonicia, Acanthochitona, Choneplax, Cryptoplax, Hemiarthrum* e *Cryptochiton*. I confronti morfologici implicano: una stretta parentela tra *Notoplax* e *Cryptoconchus* e tra *Acanthochitona*, *Choneplax* e *Cryptoplax*; la parafilia di *Cryptoconchus*; la presenza di un certo numero di gruppi di specie o generi in *Acanthochitona*, e un parallelismo nella riduzione del tegmentum all'interno dei Cryptoplacoidea.

KEY WORDS: Polyplacophora, Cryptoplacoidea, radula, morphology, phylogeny.

INTRODUCTION

The confused and unstable state of the phylogeny of the chitons led Sirenko (1997) to state that taxonomy of the class was in a "crisis situation". He reviewed traditional characters, such as gill arrangement, egg hull morphology and articulamentum development, and explored some new ones. Similar attempts to establish new characters were also made, among others, by Haszprunar (1987: ultrastructure of the hypobranchial organ) and Buckland-Nicks (1995: sperm morphology). In order to establish more accurate phylogenetic hypotheses, further useful morphological characters should be sought to complement recent molecular studies.

I am convinced that the radula is one such character, and that it should be re-evaluated via thorough review and extensive studies of fine morphology. Because of its structural complexity and conservative nature, the radula has not been fully employed in chiton taxonomy, although it is widely used in gastropod systematics. The radula is also expected to prove useful in the systematic study of scaphopods, as pointed out by Lamprell and Healy (1998: 8: "Comparative radular morphology may yet prove a most rewarding avenue for further taxonomic research…"). Radular characters are also a promising tool for tackling the phylogeny of chitons, but not merely on the basis of morphological characters of individual species. By review of radular characters using scanning electron microscopy, this paper demonstrates how careful comparisons of radular characters can clarify phylogenetic relationships in chitons. As a test case, the radular morphology of the superfamily Cryptoplacoidea is described and illustrated, and its phylogenetic significance is discussed.

MATERIAL AND METHODS

Most of the material used in this study was from museum or private collections and was preserved in ethanol or formalin. There were also a few dried specimens. Animal size is here defined as body length (BL).

As the radulae of chitons have a complicated, three-dimensional structure, scanning electron microscopy (SEM) is essential for examination of the fine morphology of each tooth. For examination by SEM, the following procedure was adopted: dissected radulae were boiled in KOH solution for one to two minutes, and rinsed with tap water; they were then cleaned with an ultrasonic cleaner (except for some examples that were set aside for examination of the petaloid process and accessory process), and dehydrated using a series of ethanol concentrations. Most of the radulae were then immersed in t-butyl alcohol and dried with a JEOL JFD-300 freeze dryer, while a portion were air dried (AD). All samples examined by SEM were observed in high vacuum mode with gold or gold-palladium coating.

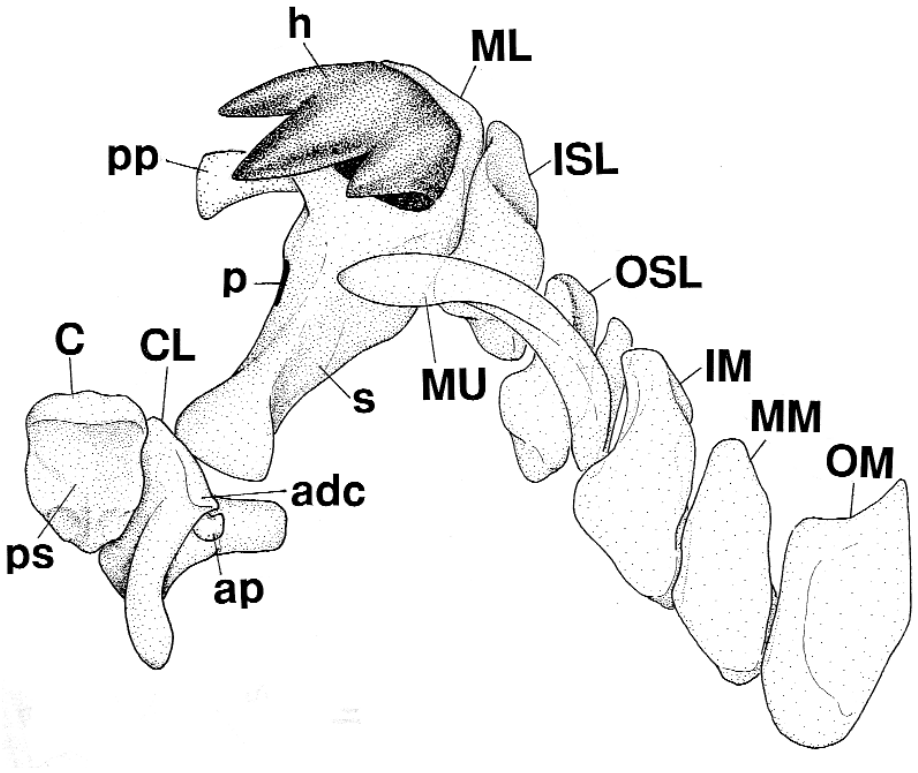

Fig. 1. Terminology for radular teeth of chitons.
C, central tooth; CL, centro-lateral tooth; ML, major lateral tooth; ISL, inner small lateral tooth; OSL, outer small lateral tooth; MU, major uncinus tooth; IM, inner marginal tooth; MM, middle marginal tooth; OM, outer marginal tooth; ps, posterior surface of the central tooth; adc, antero-dorsal corner of the centro-lateral tooth; ap, accessory process; h, head; pp, petaloid process; p, pore; s, shaft.
Fig. 1. Terminologia per i denti radulari nei chitoni.
C, dente centrale; CL, dente centro-laterale (o primo laterale); ML, dente laterale maggiore (o secondo laterale); ISL, piccolo dente laterale interno (o terzo laterale); OSL, piccolo dente laterale esterno (o quarto laterale); MU, dente laterale uncinato (o quinto laterale); IM, dente marginale interno; MM, dente marginale mediano; OM, dente marginale esterno; ps, superficie posteriore del dente centrale; adc, angolo antero-dorsale del dente centro-laterale; ap, processo accessorio; h, testa; pp, processo petaloide; p, poro; s, parte basale.

The terminology of the radular teeth used in this paper basically follows that of Is. Taki, (1938) and Bullock (1988a) **(Fig. 1)**.

Abbreviations for names of institutions used in the text are as follows.

FSBC: Florida Marine Research Institute;
NSMT: National Science Museum, Tokyo;
SAM: South Australian Museum;
USNM: National Museum of Natural History, Smithsonian Institution.

Morphology of Polyplacophoran Radula

The polyplacophoran radular ribbon is cylindrical at the posterior portion and flat at the anterior portion, essentially conforming to the "cylinder model" proposed by Morris & Hickman (1981) for the archaeogastropod radula. The working movement of the chiton radula is also the same as that of the archaeogastropods (Matsukuma & Tsubaki, 1995).

The radular teeth on the radular membrane are arranged in a complex three-dimensional layout. The teeth are either interlocking or actually attached to each other (between the shaft of the major lateral and the inner small lateral teeth) to transmit pressure from the cutting edge and to distribute stress in the same manner as demonstrated for the gastropod radula by Solem (1972) and Hickman (1984). Some genera such as *Callochiton* and *Notoplax* have skewed radular rows.

Radular teeth within the Polyplacophora show a considerable range of morphological variability, though in many cases the radula is less variable among species in the same genus, or even between genera. Some genera in current use contain species with essentially different kinds of radulae and should be re-assessed. The occurrence of considerable ontogenetical variability (O'Neill, 1984; Sirenko, 1974, 1992) and polymorphism (Bullock, 1988b) should also be noted.

General tooth morphology

Central: The central tooth shows a broad range of morphology within the class, from large to small and broad to narrow. It usually consists of a main plate with or without a cusp at the apex and a prop plate at the anterior base. The main plate is sometimes thick, and the prop plate cannot be separated from it. The central tooth is asymmetrical in those genera which have skewed radular rows. Usually the features of the central tooth are fairly consistent within species, but they may vary to some extent in certain species, such as members of the genus *Acanthochitona*.

Centro-lateral: This tooth also displays a wide range of morphology within the class. In many species it consists of two parts: a plate surrounding the central tooth, and prop plate extending between the shafts of the adjoining centro-lateral teeth. In some genera, like *Notoplax*, the centro-lateral tooth is smaller and lower than the central tooth and lacks a cusp, while in other genera such as *Ischnochiton* it is taller than the central tooth and has well developed cusp.

There is a minute process called the "accessory process" or "pad" near the antero-dorsal corner **(Figs. 1, 2, ap)**. The distribution of the accessory process among chitons is unclear because of its minute size and deciduous nature, and it has thus not attracted much attention from past workers. So far, it has been confirmed as occurring in many species in the Chitonina, but not for example in *Radsia barnesii* (Gray, 1828) (Bullock, 1988b). A similar process has also been found in some species of the Lepidopleurina, namely *Leptochiton longispina* Saito, 2001 and *Nierstraszella lineata* (Nierstrasz, 1905) **(Fig. 2A, B)**. Sirenko (1992) supposed that the family Nierstraszellidae, which comprises single species *N. lineata*, is an intermediate link between the orders Lepido-

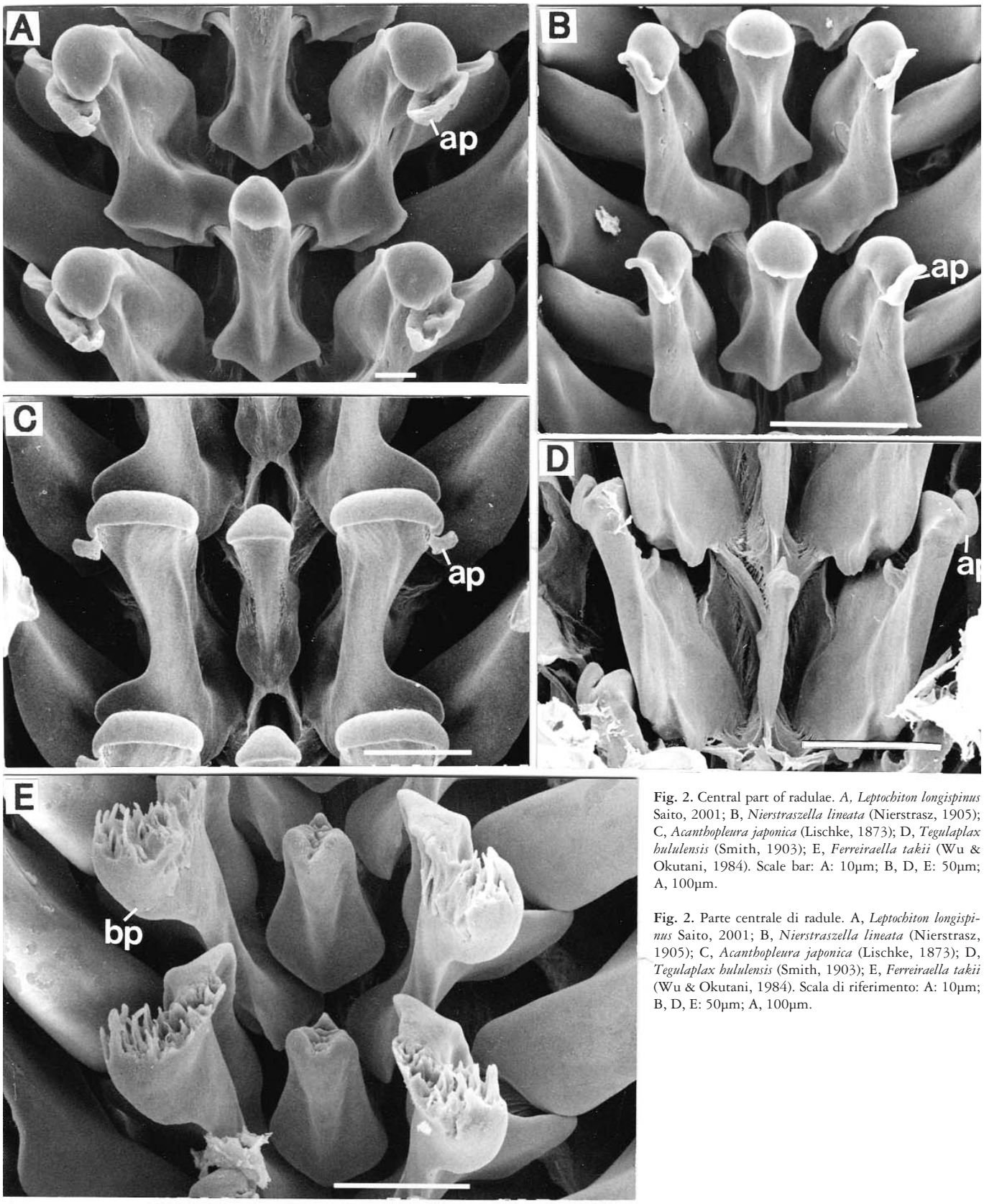

Fig. 2. Central part of radulae. *A, Leptochiton longispinus* Saito, 2001; B, *Nierstraszella lineata* (Nierstrasz, 1905); C, *Acanthopleura japonica* (Lischke, 1873); D, *Tegulaplax hululensis* (Smith, 1903); E, *Ferreiraella takii* (Wu & Okutani, 1984). Scale bar: A: 10µm; B, D, E: 50µm; A, 100µm.

Fig. 2. Parte centrale di radule. A, *Leptochiton longispinus* Saito, 2001; B, *Nierstraszella lineata* (Nierstrasz, 1905); C, *Acanthopleura japonica* (Lischke, 1873); D, *Tegulaplax hululensis* (Smith, 1903); E, *Ferreiraella takii* (Wu & Okutani, 1984). Scala di riferimento: A: 10µm; B, D, E: 50µm; A, 100µm.

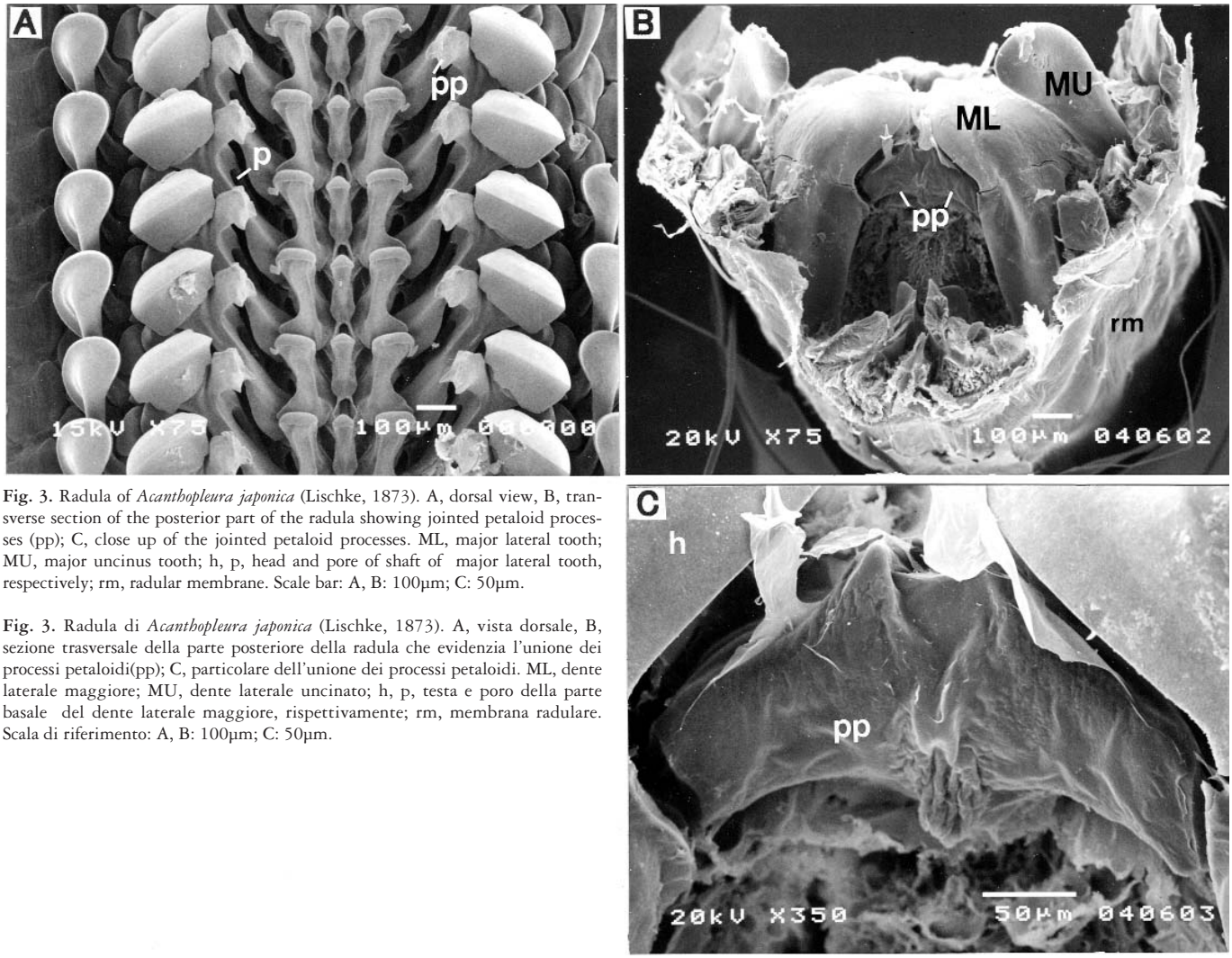

Fig. 3. Radula of *Acanthopleura japonica* (Lischke, 1873). A, dorsal view, B, transverse section of the posterior part of the radula showing jointed petaloid processes (pp); C, close up of the jointed petaloid processes. ML, major lateral tooth; MU, major uncinus tooth; h, p, head and pore of shaft of major lateral tooth, respectively; rm, radular membrane. Scale bar: A, B: 100µm; C: 50µm.

Fig. 3. Radula di *Acanthopleura japonica* (Lischke, 1873). A, vista dorsale, B, sezione trasversale della parte posteriore della radula che evidenzia l'unione dei processi petaloidi(pp); C, particolare dell'unione dei processi petaloidi. ML, dente laterale maggiore; MU, dente laterale uncinato; h, p, testa e poro della parte basale del dente laterale maggiore, rispettivamente; rm, membrana radulare. Scala di riferimento: A, B: 100µm; C: 50µm.

pleurida and Chitonida. The genus *Ferreiraella* has a peculiar "bud-like" process at the antero-dorsal corner **(Fig. 2E, bp)**. It is still unclear whether or not these processes are homologous between these two suborders. Extensive study is needed to fully assess this character. The central and the centro-lateral teeth do not differentiate in the Juvenichitoninae.

Major lateral: The major lateral tooth is the dominant element of the radula and the major scraping unit (Bullock, 1988a). It consists of a large, long shaft and a mineralized black head of dense magnetite. In many species the shaft has been shown to house a large cavity which opens as a small pore or narrow slit on the inner lateral wall **(Figs. 1, 3A, p)**, though the pore could not be found in *Leptochiton assimilis* (Thiele, 1909) at least. The distribution of this feature within the class and its function are unknown at present. A small process called the "petaloid process" or "wing" **(Figs. 1, 3, pp)** is present in certain groups. The function of this process is also unclear (Bullock, 1988a), but it may help maintain the "cylinder" shape of the radula and thus enable efficient grazing, as each pair of processes is brought together in the "cylinder" **(Fig. 3B, C)**. Thiele (1909-1910, 1929) used the presence of the petaloid process as a defining character of the families Ischnochitonidae and Chitonidae. This may support the monophyly of the suborder Chitonina proposed in the latest system (Sirenko, 1997), if the family Callochitonidae, which lacks this process, is removed.

The mineralized head is conspicuous and widely variable in shape, and has thus been treated as an important character for the recognition of species or definition of genera. Beside the "tab" used as an important character in taxonomy of the genus *Chiton* by Bullock (1988a), there are many smaller structures that await examination, e.g. grooves on the posterior surface, minute pores between the tricuspid cusps, and the translucent part of the basal portion. Polymorphism of the head was demonstrated by Sirenko (1974) for *Tonicella* species and for *Sypharochiton* by Bullock (1988b).

Small laterals: The small laterals consist of two teeth on each side. They are usually thick, "boss-like" teeth and the inner one is firmly attached to the lateral depression in the major lateral tooth. The inner small lateral of *Leptochiton tenuidontus* Saito & Okutani, 1991 is elongate, like a toothpick. *Thermochiton undocostatus* Saito & Okutani, 1991 has elongate inner small laterals with two spatula-shaped processes, and prow-shaped outer small laterals.

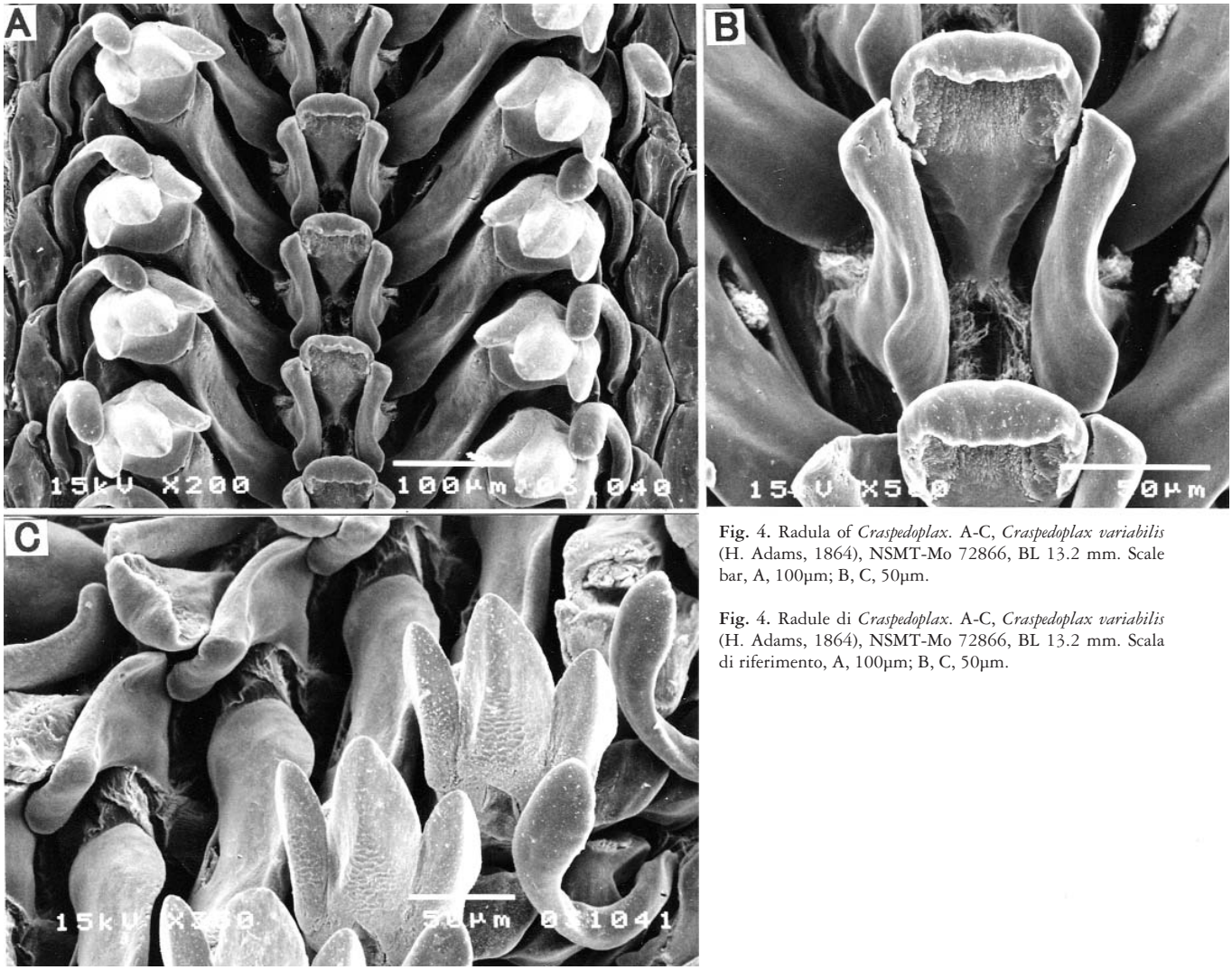

Fig. 4. Radula of *Craspedoplax*. A-C, *Craspedoplax variabilis* (H. Adams, 1864), NSMT-Mo 72866, BL 13.2 mm. Scale bar, A, 100µm; B, C, 50µm.

Fig. 4. Radule di *Craspedoplax*. A-C, *Craspedoplax variabilis* (H. Adams, 1864), NSMT-Mo 72866, BL 13.2 mm. Scala di riferimento, A, 100µm; B, C, 50µm.

Major uncinus: The major uncinus is usually tall and spoon-like in shape; however, it is reduced to a small piece of plate in *Callochiton* and *Cryptochiton* **(Fig. 18)**. In the genera *Ferreiraella* and *Tonicella* there is a rake-like blade at the apex, though the fine morphology is different.

Marginals: The marginals consist of three flat teeth on each side. These teeth have attracted less attention than the others, but they also have important characters. Species with a large number of transverse rows of teeth, such as those of *Stenosemus*, *Connexochiton*, *Thermochiton* and certain species of *Leptochiton* (as outlined below) have wide, short outer marginal teeth and small inner marginals which articulate to the major uncinus. The marginal teeth of *Amicula gurjanovae* Yakovleva, 1952 have serrated edges (Yakovleva, 1952; Okutani & Saito, 1987).

Number of transverse rows: Variation in the number of transverse rows of teeth is usually small within a genus; however, considerable differences are recognized in some genera. For example, in the genus *Leptochiton*, some species, such as *L. assimilis* (Thiele, 1909), *L. surugensis* Saito, 1997, and *L. tenuidontus* Saito & Okutani, 1991, have more than 150 rows, while others have fewer than 40. The morphology of radular teeth of these species is also different from that of others, and a critical review of their taxonomic position is needed.

The Cryptoplacoid Radula as a Test Case

Superfamily CRYPTOPLACOIDEA H. & A. Adams, 1858
Family ACANTHOCHITONIDAE Pilsbry, 1893
Subfamily ACANTHOCHITONINAE Pilsbry. 1893

Genus ***Craspedoplax*** Iredale & Hull, 1925

Type species. *Hanleya variabilis* H. Adams & Angas, 1864

Material examined. *Craspedoplax variabilis* (H. Adams & Angas, 1864), NSMT-Mo 72866, 2 specimens, BL. 7.6 mm & 13.2 mm, Edithburg, South Australia.

Radula. The radula is symmetrical. The central tooth is moderate in size and inverse teardrop-shaped in outline. The posterior surface is concave below the fairly large cusp and flat in the middle portion, with a keel forming towards the

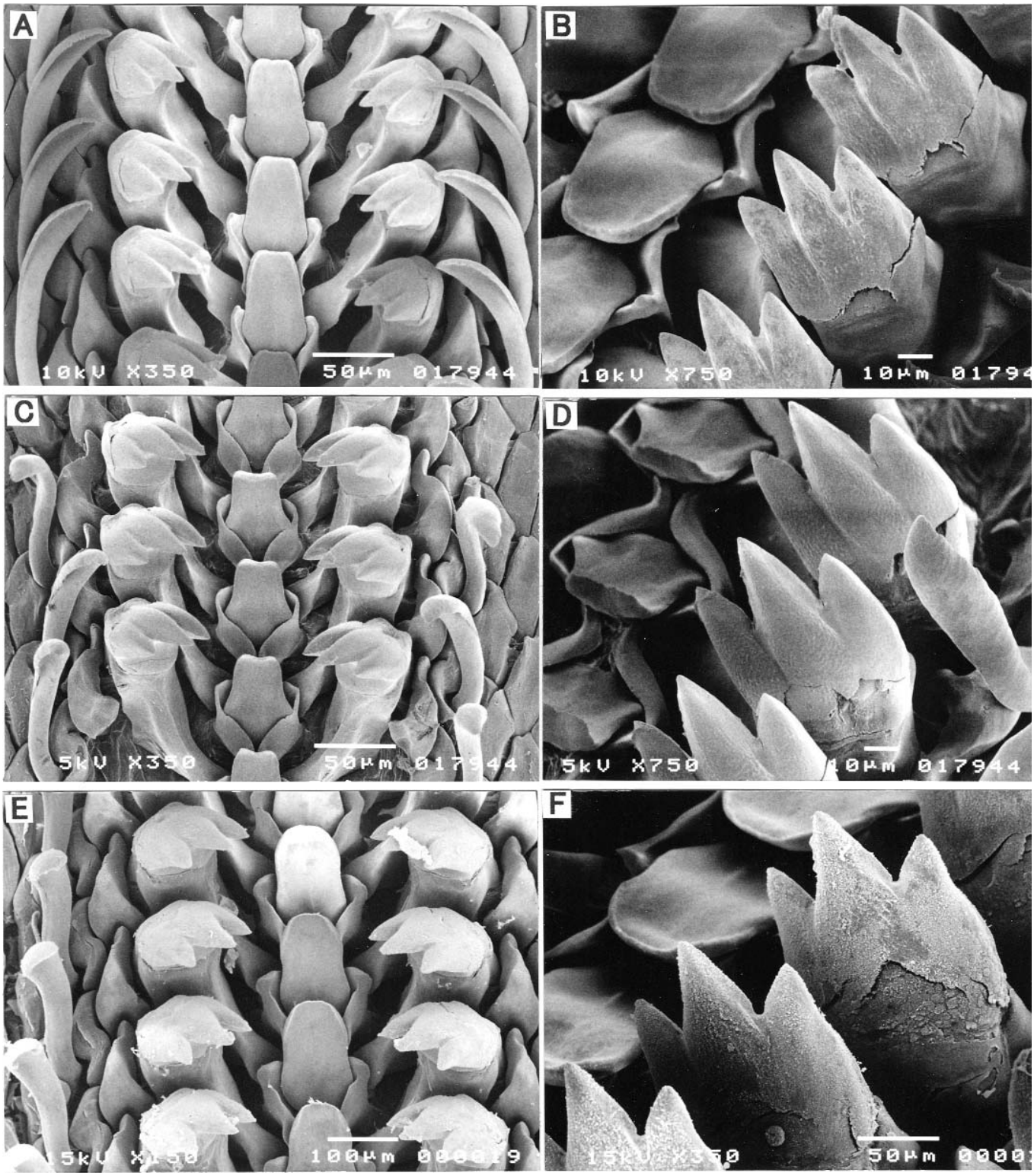

Fig. 5. Radulae of *Craspedochiton*. A, B, *C. laqueatus* (Sowerby, 1842), NSMT-Mo 71180, BL 17.3 mm; C, D, *C. pyramidalis* (Is. Taki, 1938), NSMT-Mo 70043, BL ca. 18 mm (AD); E, F, *C. productus* (Carpenter in Pilsbry, 1892), NSMT-Mo 72867, BL 41.8 mm. Scale bar: A, C, F, 50µm; B, D, 10µm; E, 100µm.

Fig. 5. Radule di *Craspedochiton*. A, B, *C. laqueatus* (Sowerby, 1842), NSMT-Mo 71180, BL 17.3 mm; C, D, *C. pyramidalis* (Is. Taki, 1938), NSMT-Mo 70043, BL ca. 18 mm (AD); E, F, *C. productus* (Carpenter in Pilsbry, 1892), NSMT-Mo 72867, BL 41.8 mm. Scala di riferimento: A, C, F, 50µm; B, D, 10µm; E, 100µm.

base. The centro-lateral tooth has a thickened antero-lateral corner bearing a narrow, indistinct cusp. The head of the major lateral tooth has rather thin cusps. The central cusp is apparently wider than the others, which splay slightly outwards, and the anterior surface has an irregular reticulate sculpture. The major uncinus tooth is narrow (**Fig.** 4).

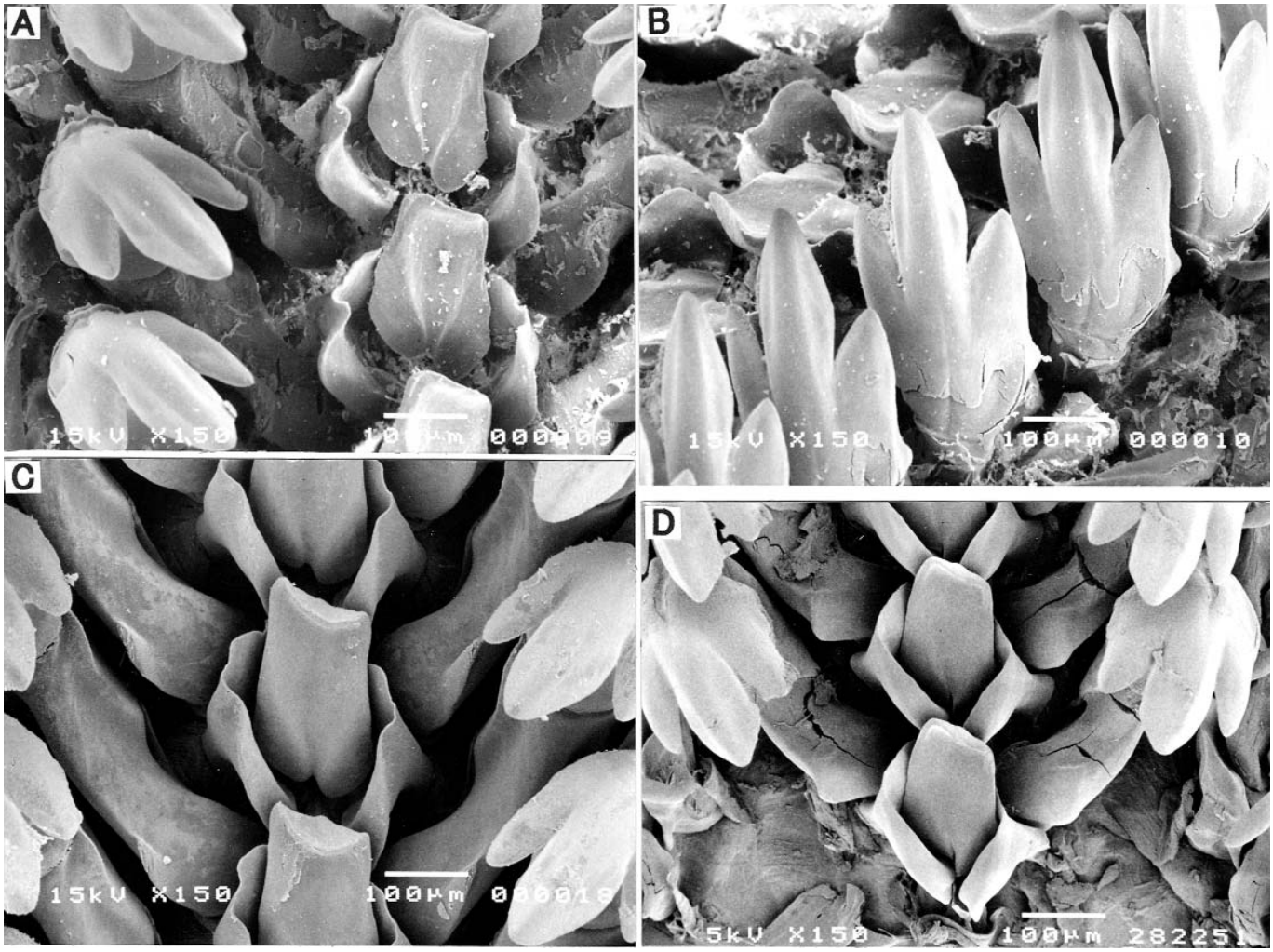

Fig. 6. Radulae of *Notoplax*. A, B, *N. speciosa* (H. Adams, 1861), SAM D 16073, BL ca. 29 mm, (dried material), C, *N. addenda* Iredale & Hull, 1925, SAM D 17944, BL 56.3 mm; D, *N.* sp., NSMT-Mo 70061, BL ca. 60 mm (AD). Scale bar: A-D, 100µm.

Fig. 6. Radule di *Notoplax*. A, B, *N. speciosa* (H. Adams, 1861), SAM D 16073, BL ca. 29 mm, (materiale a secco), C, *N. addenda* Iredale & Hull, 1925, SAM D 17944, BL 56.3 mm; D, *N.* sp., NSMT-Mo 70061, BL ca. 60 mm (AD). Scala di riferimento: A-D, 100µm.

Remarks. *Craspedoplax* Iredale & Hull, 1925 has been treated as a distinct genus chiefly by Australian authors (e.g. Cotton, 1964; Gowlett-Holmes, 1998), but elsewhere it has been synonymised with *Craspedochiton* (e.g. Smith, 1960; Van Belle, 1983; Kaas & Van Belle, 1981, Slieker, 2000). The radula of *Craspedoplax variabils* (H. Adams, 1864) is quite different from that of *Craspedochiton* species **(Fig. 5)**, especially in possessing a central tooth with a large cusp and narrow base, and the thickened antero-dorsal corner of the centro-lateral tooth. These differences in the radula together with those in other external features such as the tegmental sculpture, girdle, spicules etc. confirm the validity of the genus.

Genus ***Craspedochiton*** Shuttleworth, 1853

Type species. *Chiton laqueatus* Sowerby, 1842

Material examined. *Craspedochiton laqueatus* (Sowerby, 1842), NSMT-Mo 70040, 1 specimen, BL ca. 24 mm, Off Amakusa Islands, Japan (AD); NSMT-Mo 71180, 1 specimen, BL 17.3 mm, Goto Islands, Japan. *C. pyramidalis* (Is. Taki, 1938), NSMT-Mo 70043, 1 specimen, BL ca. 18 mm, Off Izu-Oshima Island, Japan (AD). *C. productus* (Carpenter in Pilsbry, 1892), NSMT-Mo 72867, 1 specimen, BL 41.8 mm, South Africa.

Radula. The radula is small and symmetrical. The central tooth is large and squarish in outline. The posterior surface is mildly concave, weakly keeled and convex near the weakly bilobed base. The antero-lateral corner of the centro-lateral tooth is obtuse and smooth, thin or slightly thickened. The head of the major lateral tooth is small and has pointed cusps. The major uncinus tooth has a narrow blade **(Fig. 5)**.

Remarks. The radula of *Spongiochiton productus* Carpenter in Pilsbry, 1892, the type species of *Spongiochiton* is essentially the same as that of *Craspedochiton* species. The other characters of *Craspedochiton*, such as the peculiar tegmental sculpture, wide expansion of the anterior girdle, and the enlarged,

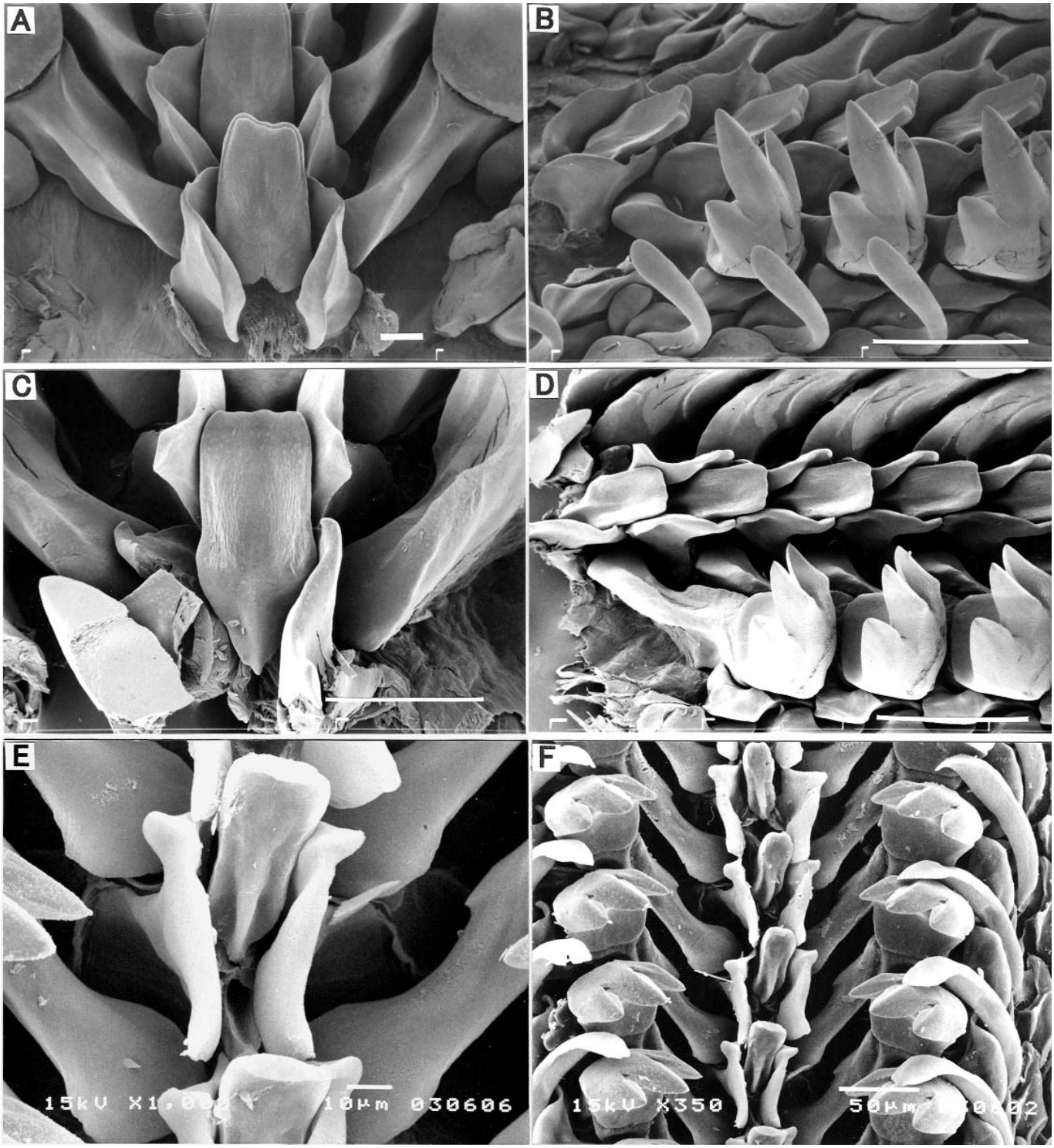

Fig. 7. Radulae of *Cryptoconchus*. A, B, *C. porosus* (Blainville MS, Burrow, 1815), NSMT-Mo 72868, 1 specimen, BL. 43.5 mm, (AD); C, D, *"Cryptoconchus" burrowi* Nierstrasz, 1905, NSMT-Mo 70111, BL ca. 18 mm (AD); E, F, *"Cryptoconchus" floridanus* (Dall, 1889), FSBC I 32081, BL 13.6 mm. Scale bar: A, D, 100µm; B, 500µm; C, F, 50µm; E, 10µm.

Fig. 7. Radule di *Cryptoconchus*. A, B, *C. porosus* (Blainville MS, Burrow, 1815), NSMT-Mo 72868, 1 esemplare, BL. 43.5 mm, (AD); C, D, *"Cryptoconchus" burrowi* Nierstrasz, 1905, NSMT-Mo 70111, BL ca. 18 mm (AD); E, F, *"Cryptoconchus" floridanus* (Dall, 1889), FSBC I 32081, BL 13.6 mm. Scala di riferimento: A, D, 100µm; B, 500µm; C, F, 50µm; E, 10µm.

leaf-like scales of the hyponotum are also present in *S. productus*. *Spongiochiton* is thus regarded as a synonym of *Craspedochiton*.

Genus *Notoplax* H. Adams, 1861

Type species. *Cryptoplax (Notoplax) speciosa* H. Adams, 1861

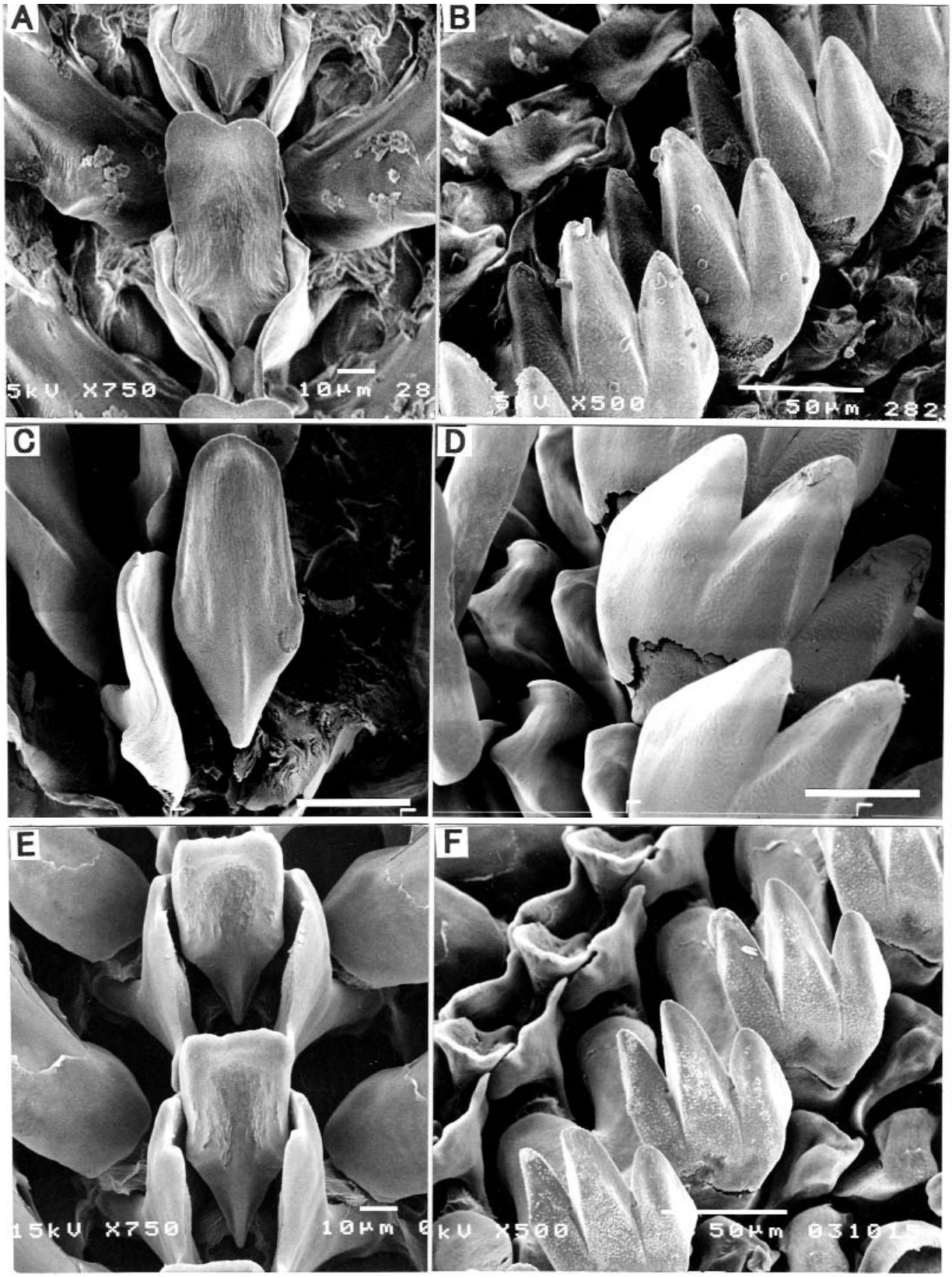

Fig. 8. Radulae of *Leptoplax*. A, B, *Leptoplax coarctata* (Sowerby, 1841), NSMT-Mo 70109, BL 15.2 mm (AD); C, D, *L. doederleini* (Thiele, 1909), NSMT-Mo 70088, BL ca. 25 mm, Boso Peninsula, Japan (AD); E, F, *L. curvisetosa* (Leloup, 1960), NSMT-Mo 72869, BL. 9.0 mm, Aqaba, Jordan. Scale bar: A, E, 10µm; B-D, F, 50µm.

Fig. 8. Radule di *Leptoplax*. A, B, *Leptoplax coarctata* (Sowerby, 1841), NSMT-Mo 70109, BL 15.2 mm (AD); C, D, *L. doederleini* (Thiele, 1909), NSMT-Mo 70088, BL ca. 25 mm, Boso Peninsula, Japan (AD); E, F, *L. curvisetosa* (Leloup, 1960), NSMT-Mo 72869, BL. 9.0 mm, Aqaba, Jordan. Scala di riferimento: A, E, 10µm; B-D, F, 50µm.

Material examined. *Notoplax speciosa* (H. Adams, 1861), SAM D 16073, 1 specimen; BL ca. 29 mm, (dried material), Clenery, South Australia. *N. addenda* Iredale & Hull, 1925, SAM D 17944, 1 specimen; BL 56.3 mm, Eyre Peninsula, South Australia. *N.* sp., NSMT-Mo 70061, 1 specimen, BL ca. 60 mm, Amakusa Islands, Japan (AD).

Radula. The radula is asymmetrical; the teeth on the left

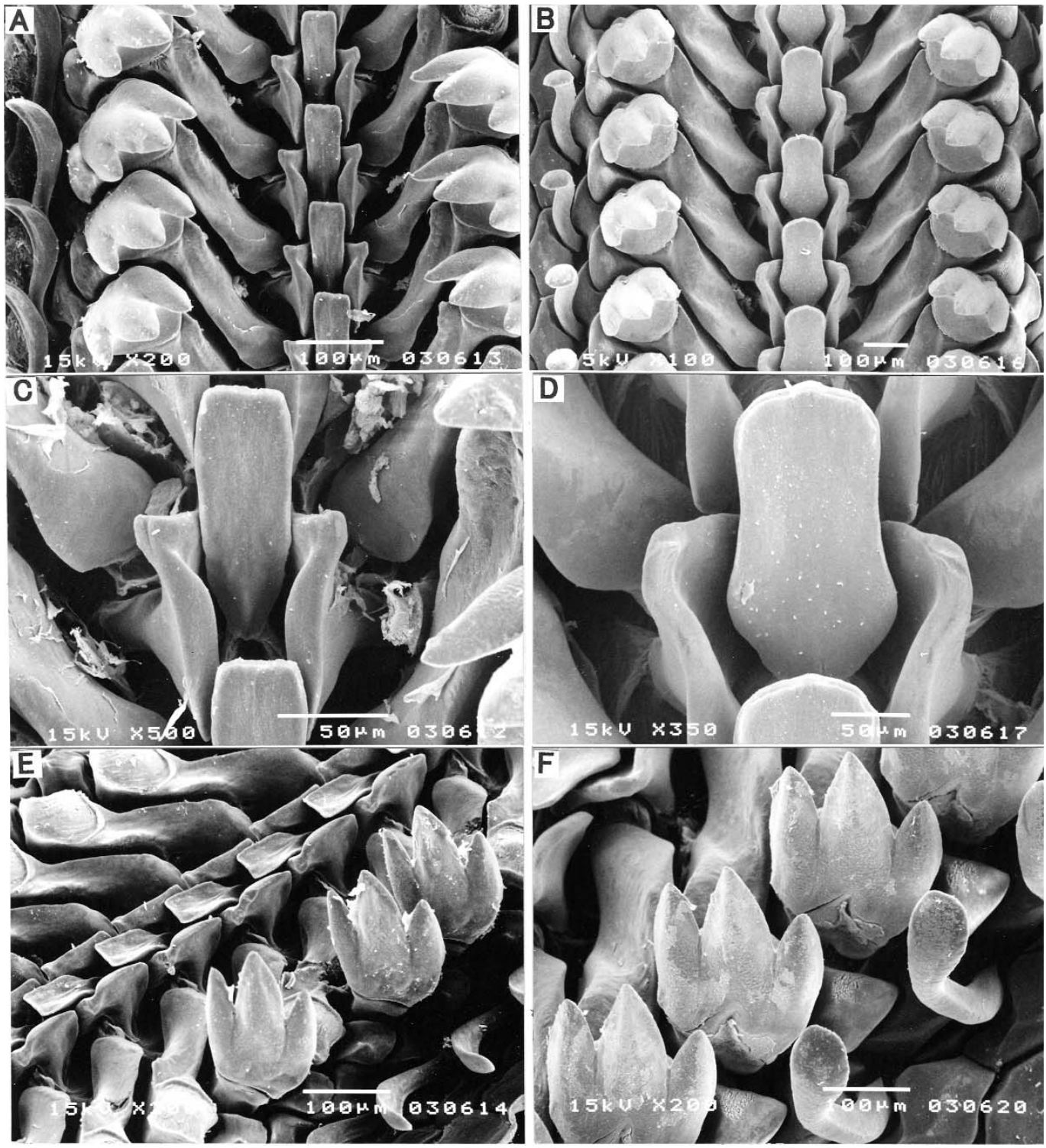

Fig. 9. Radulae of *Bassethullia* and *Pseudotonicia*. A, C, E, *Bassethullia matthewsi* (Bednall & Pilsbry in Pilsbry, 1894), NSMT-Mo 72870, BL. ca. 25 mm; B, D, F, *Pseudotonicia cuneata* (Suter, 1908), SAM D 18604, 1 specimen, BL 54.5 mm. Scale bar: A, B, E, F, 100µm; C, D, 50µm.

Fig. 9. Radule di *Bassethullia* e *Pseudotonicia*. A, C, E, *Bassethullia matthewsi* (Bednall & Pilsbry in Pilsbry, 1894), NSMT-Mo 72870, BL. ca. 25 mm; B, D, F, *Pseudotonicia cuneata* (Suter, 1908), SAM D 18604, 1 esemplare, BL 54.5 mm. Scala di riferimento: A, B, E, F, 100µm; C, D, 50µm.

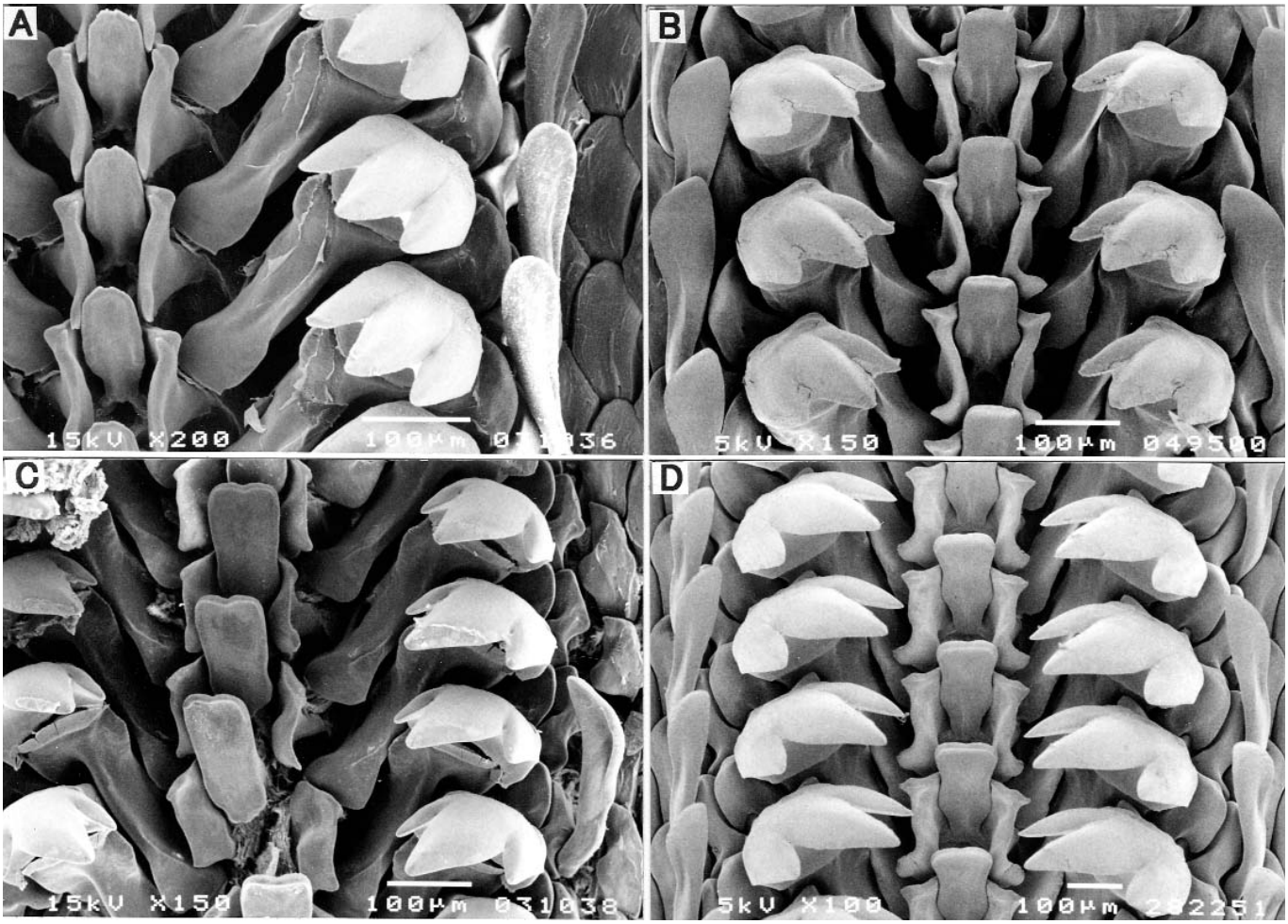

Fig. 10. Radulae of *Acanthochitona fascicularis* species-group. A, *A. fascicularis* (Linné, 1767), NSMT-Mo72871, BL 29.4 mm; B, *A. achates* (Gould, 1859), NSMT-Mo72879, BL 25.5 mm, (AD); C, *A. exquisita* (Pilsbry, 1893), NSMT-Mo 72872, BL 24.6 mm; D, *A. defilippii* (Tapparone-Canefri, 1874), NSMT-Mo 72882, BL ca. 43 mm, (AD). Scale bar: A-D, 100µm.

Fig. 10. Radule delle specie appartenenti al gruppo *Acanthochitona fascicularis*. A, *A. fascicularis* (Linné, 1767), NSMT-Mo72871, BL 29.4 mm; B, *A. achates* (Gould, 1859), NSMT-Mo72879, BL 25.5 mm, (AD); C, *A. exquisita* (Pilsbry, 1893), NSMT-Mo 72872, BL 24.6 mm; D, *A. defilippii* (Tapparone-Canefri, 1874), NSMT-Mo 72882, BL ca. 43 mm, (AD). Scala di riferimento: A-D, 100µm.

side are higher or staggered behind those on the right side. The central tooth is asymmetrical, large, squarish, mildly concave in the distal half and bilobed at the base. The centro-lateral tooth has a thin, weakly notched antero-dorsal corner. The head of the major lateral tooth is large, with a long median denticle and a dorsal groove. There are orange, translucent, triangular portions on both basal sides of the head. The major uncinus tooth is very slender **(Fig. 6).**

Remarks. This genus has hitherto been considered endemic to Australian and New Zealand waters (Gowlett-Holmes, 1991). The characters of the valves, girdle, and the radula of the Japanese species examined in this study agree well with the redefinition of *Notoplax* by Gowlett-Holmes (1991). However, the Japanese species has a tubular stomach that lacks a ventral pouch. The Australian species *Notoplax addenda* Iredale & Hull, 1925 has a large pouch, but no pouch was observed in a dried specimen of *N. speciosa* (H. Adams, 1861).

There are several species which have basically the same radula as that of *Notoplax* described above, e.g. *"Notoplax" conica* Is. & Iw. Taki, 1929 and *"N" hilgendorfi* Thiele, 1909 but in these cases the other morphological characters do not match well.

Genus ***Cryptoconchus*** Blainville MS, Burrow, 1815

Type species. *Chiton porosus* (Blainville MS) Burrow, 1815

Material examined. *Cryptoconchus porosus* (Blainville MS, Burrow, 1815), NSMT-Mo 72868, 1 specimen, BL. 43.5 mm, Katai Bay, New Zealand (AD). *"Cryptoconchus" floridanus* (Dall, 1889), FSBC I 32081, 1 specimen, BL 13.6 mm. Key Vaca, Florida Keys. *"Cryptoconchus" burrowi* Nierstrasz, 1905, NSMT-Mo 70111, BL ca. 18 mm, Amami-Oshima Id., Japan (AD).

Radula. The radula of *Cryptoconchus porosus* (Dall, 1889) **(Fig. 7a, b)** is essentially the same as that of *Notoplax* **(Fig. 6).**

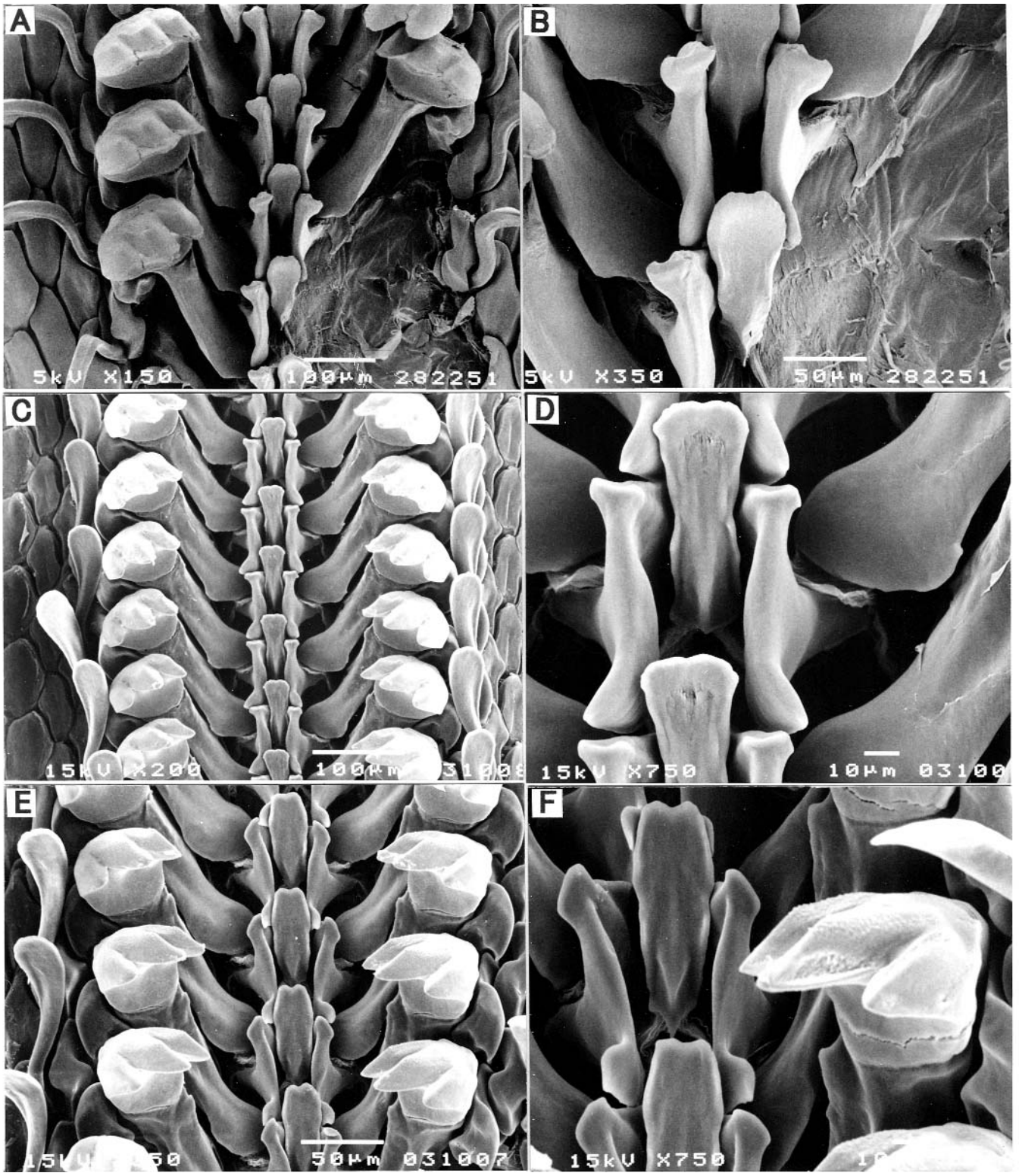

Fig. 11. Radulae of *Acanthochitona intermedia* species-group. A, B, *A. intermedia* (Nierstrasz, 1905), NSMT-Mo 72878, BL ca. 23 mm, (AD), C, D, *A. penicilata* (Deshayes, 1863), NSMT-Mo 72873, BL 11. 8 mm (dried specimen), E, F, *A. mastalleri* Strack,1989, NSMT-Mo 72874, BL 6.6 mm (dried specimen). Scale bar: A, C, 100µm; B, E, 50µm; D, F, 10µm.

Fig. 11. Radule delle specie appartenenti al gruppo *Acanthochitona intermedia*. A, B, *A. intermedia* (Nierstrasz, 1905), NSMT-Mo 72878, BL ca. 23 mm, (AD), C, D, *A. penicilata* (Deshayes, 1863), NSMT-Mo 72873, BL 11. 8 mm (esemplare a secco), E, F, *A. mastalleri* Strack,1989, NSMT-Mo 72874, BL 6.6 mm (esemplare a secco). Scala di riferimento: A, C, 100µm; B, E, 50µm; D, F, 10µm.

Remarks. In addition to the radula, similarities in valve morphology, such as the outline of the valves, suggest a close relationship between *Cryptoconchus* and *Notoplax*.
The other two species, which have been placed in *Cryptoconchus*, namely, *"C." floridanus* (Dall, 1889) and *"C." burrowi* Nierstrasz, 1905 have quite different radulae **(Fig. 7c-f)**. The radula of *"C." floridanus* is symmetrical. The central tooth is small, with a prominent keel. The centro-lateral has a thickened, nodulous antero-dorsal corner. The head of the major lateral has rather thin cusps, which have a minute pore between them. The major uncinus is moderate in width. These radular characters and certain aspects of valve morphology, especially the two slits in the tail valve, suggest a closer relationship between *"C." floridanus* and *Acanthochitona* than between the former and *Cryptoconchus*. The radula of *"C." burrowi* is essentially the same as that of *Leptoplax* **(Fig. 8).** The characters of the valves and the girdle also suggest a close relationship with *Leptoplax*. These two species should clearly be removed from *Cryptoconchus*, but as they are also different from related genera as outlined above, further study is needed to determine their correct generic assignment.

Genus ***Leptoplax*** Carpenter MS, Dall, 1882

Type species. *Chiton coarctatus* Sowerby, 1841

Material examined. *Leptoplax coarctata* (Sowerby, 1841), NSMT-Mo 70109, 2 specimens, BL ca. 10 mm & 15.2 mm, Iriomote Island, Japan (AD). *L. doederleini* (Thiele, 1909), NSMT-Mo 70088, 1 specimen, BL ca. 25 mm, Boso Peninsula, Japan (AD); NSMT-Mo 70089, 1 specimen, BL ca. 15 mm, Izu Peninsula, Japan (AD), *L. curvisetosa* (Leloup, 1960), NSMT-Mo 72869, 1 specimen, BL. 9.0 mm, Aqaba, Jordan
Radula. The radula is symmetrical. The central tooth is spatula-shaped, pointed and keeled in the basal portion. There is no cusp at the tip. The centro-lateral tooth has a slightly thickened antero-dorsal corner. The head of the major lateral tooth is large, with blunt cusps having a flat anterior surface. The major uncinus is narrow to moderate in width **(Fig. 8)**.

Remarks. The genus *Leptoplax* was treated as a synonym of

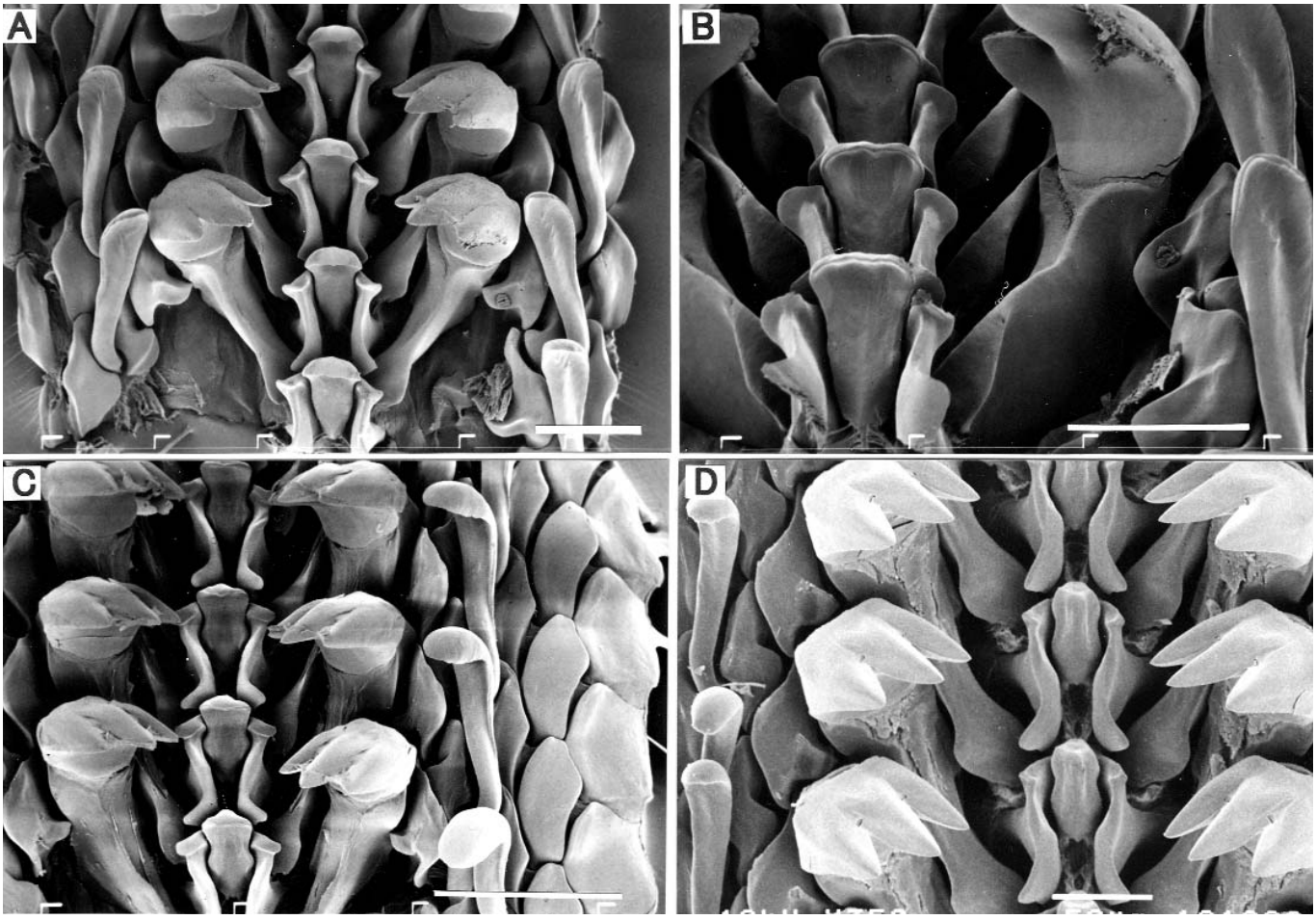

Fig. 12. Radulae of *Acanthochitona dissimilis* species group. A, B, *A. sueurii* (Blainville, 1825), NSMT-Mo 72877, BL 16.5 mm, (AD); C, *A.* sp., NSMT-Mo 72875, BL ca. 7 mm, Chichijima Island, Japan (AD); D *A. dissimilis* Is. & Iw. Taki, 1931, NSMT-Mo 73023, BL 13.7 mm. Scale bar: A-C, 100µm; D, 50µm.

Fig. 12. Radule delle specie appartenenti al gruppo *Acanthochitona dissimilis*. A, B, *A. sueurii* (Blainville, 1825), NSMT-Mo 72877, BL 16.5 mm, (AD); C, *A.* sp., NSMT-Mo 72875, BL ca. 7 mm, Chichijima Island, Japan (AD); D *A. dissimilis* Is. & Iw. Taki, 1931, NSMT-Mo 73023, BL 13.7 mm. Scala di riferimento: A-C, 100µm; D, 50µm.

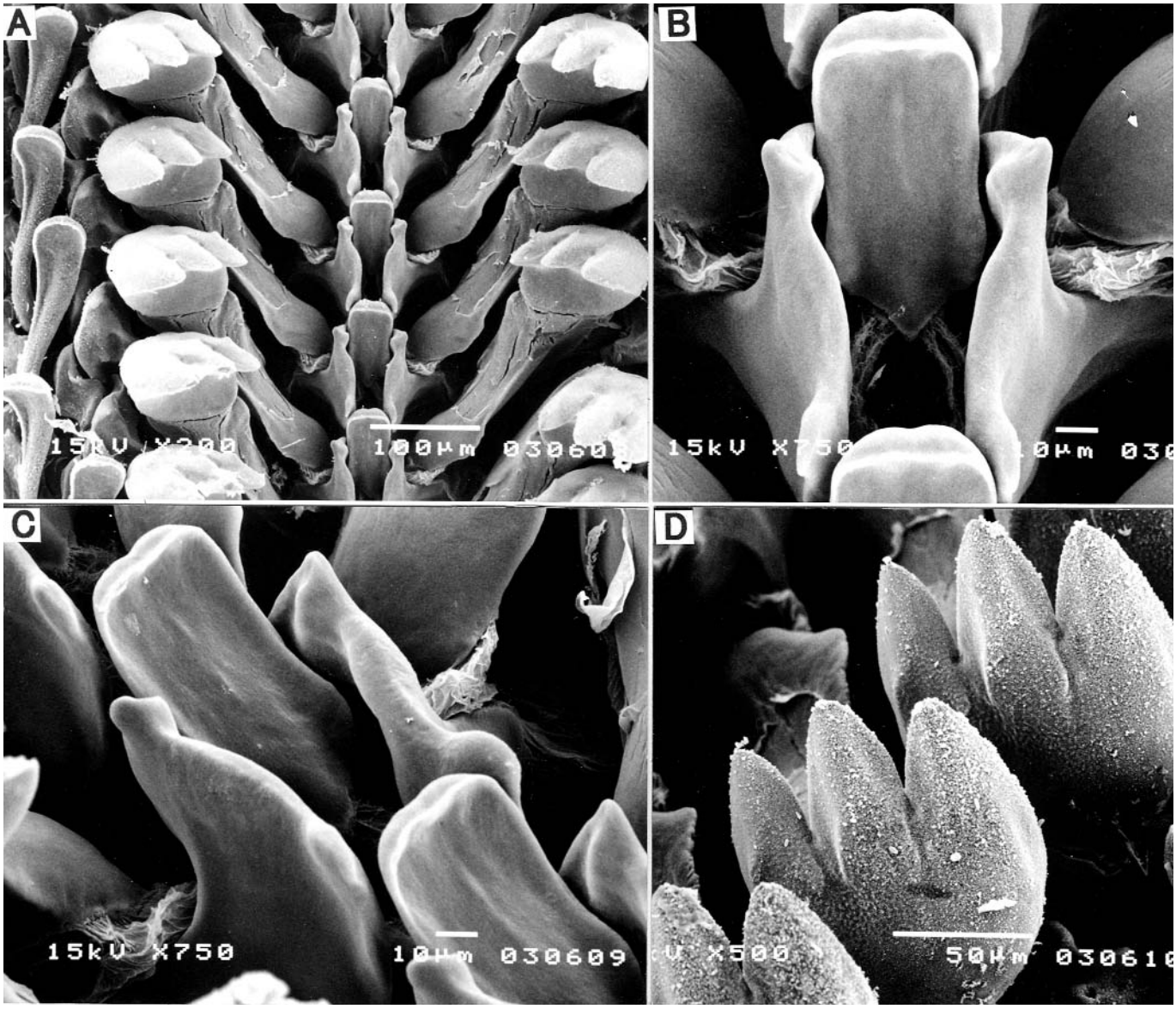

Fig. 13. Radula of *Choneplax*. A-D, *C. lata* (Guilding, 1829), FSBC I 32548, BL 25.2 mm. Scale bar: A, 100µm; B, C, 10µm; D, 50µm.

Fig. 13. Radula di *Choneplax*. A-D, *C. lata* (Guilding, 1829), FSBC I 32548, BL 25.2 mm. Scala di riferimento: A, 100µm; B, C, 10µm; D, 50µm.

Notoplax which had been considered a heterogeneous genus characterised by multiple slits in the tail valve. Since Gowlett-Holmes (1991) redefined the genus *Notoplax*, those heterogeneous genera have once more been divided. The genus *Leptoplax* has previously also been regarded as a distinct genus (Gowlett-Holmes, 1998; Saito, 2001), although sufficient definition of the genus has not yet been provided. The peculiar radular morphology of *Leptoplax* supports separation at generic level.

Genus ***Bassethullia*** Pilsbry, 1928

Type species. *Acanthochites matthewsi* Bednall & Pilsbry in Pilsbry, 1894

Material examined. *Bassethullia matthewsi* (Bednall & Pilsbry in Pilsbry, 1894), NSMT-Mo 72870, 1 specimen, BL. ca. 25 mm, Moana Reef, South Australia.

Radula. The radula is symmetrical. The central tooth is narrow, spatula-shaped and keeled near the base. The apical edge has no blade. The centro-lateral tooth has a thickened and somewhat nodulous antero-dorsal corner. The head of the major lateral tooth has rather thin cusps. The central cusp is apparently wider than the others, which splay slightly outwards. The major uncinus tooth is moderate in width **(Fig. 9A, C, E)**.

Remarks. The radulae of the other two species of *Bassethullia*, *B. glypta* (Sykes, 1896) and *B. porcina* (Ashby, 1919), which were illustrated by Gowlett-Holmes (1990), have essentially the same morphology as that of *B. matthewsi.* The

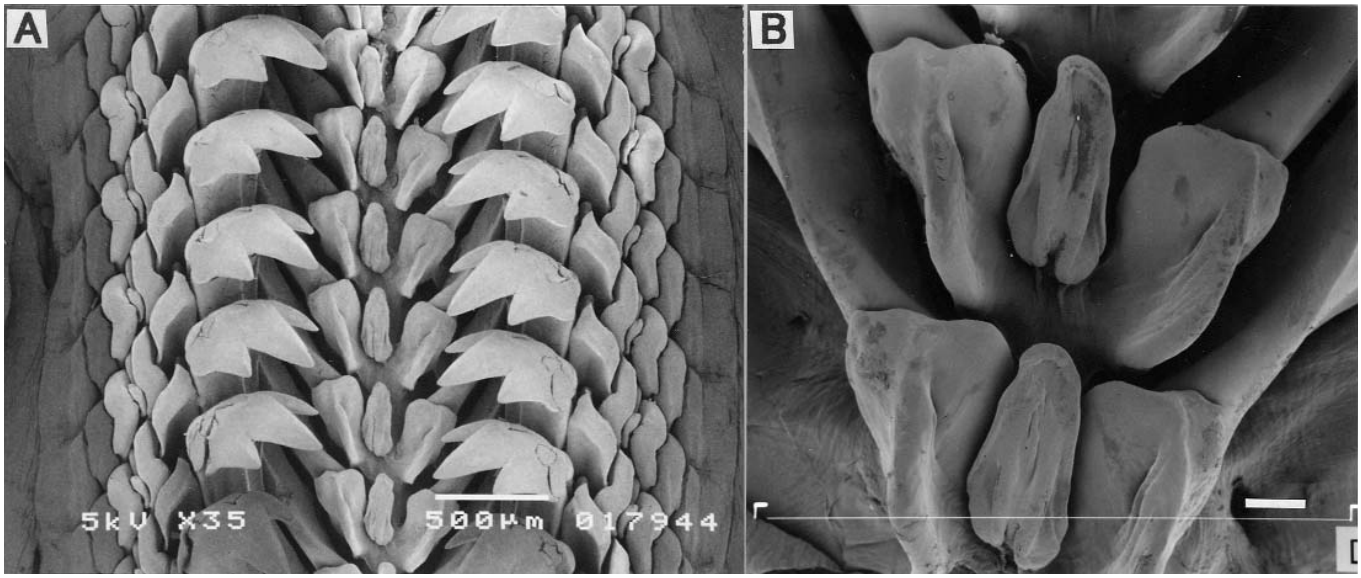

Fig. 14. Radula of *Cryptochiton*. A, B, *C. stelleri* (Middendorff, 1847): NSMT-Mo 72887, BL 125 mm (AD). Scale bar: A, B, 100µm.

Fig. 14. Radula di *Cryptochiton*. A, B, *C. stelleri* (Middendorff, 1847): NSMT-Mo 72887, BL 125 mm (AD). Scala di riferimento: A, B, 100µm.

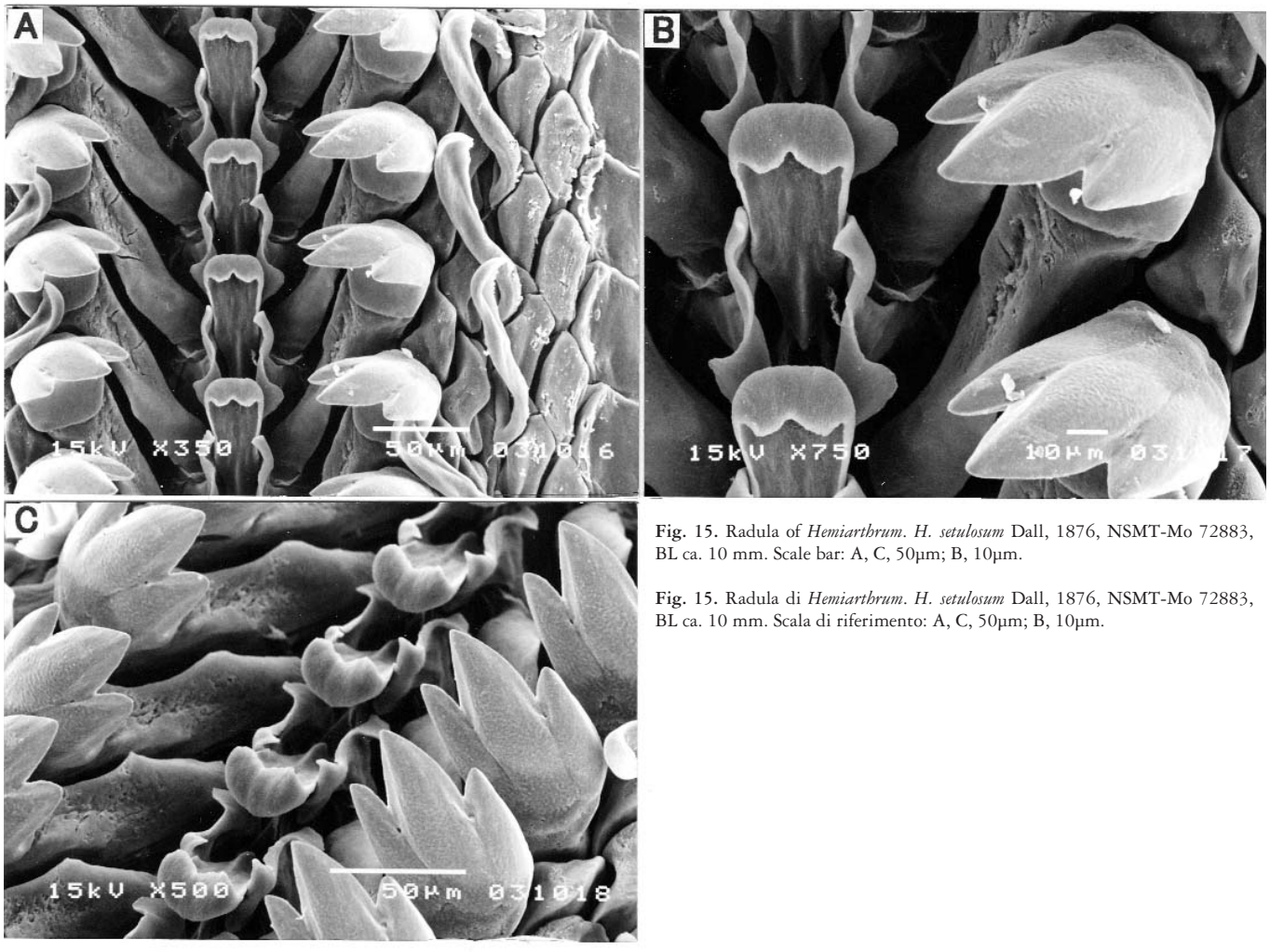

Fig. 15. Radula of *Hemiarthrum*. *H. setulosum* Dall, 1876, NSMT-Mo 72883, BL ca. 10 mm. Scale bar: A, C, 50µm; B, 10µm.

Fig. 15. Radula di *Hemiarthrum*. *H. setulosum* Dall, 1876, NSMT-Mo 72883, BL ca. 10 mm. Scala di riferimento: A, C, 50µm; B, 10µm.

morphology of the central and the centro-lateral teeth of *Bassethullia* is somewhat similar to that of *Leptoplax*, while the head of the major lateral tooth, with its rather thin cusps and wider central cusp, is similar to those of *Craspedoplax* and *Pseudotonicia*.

Genus ***Pseudotonicia*** Ashby, 1928

Type species. *Tonicia cuneata* Suter, 1908

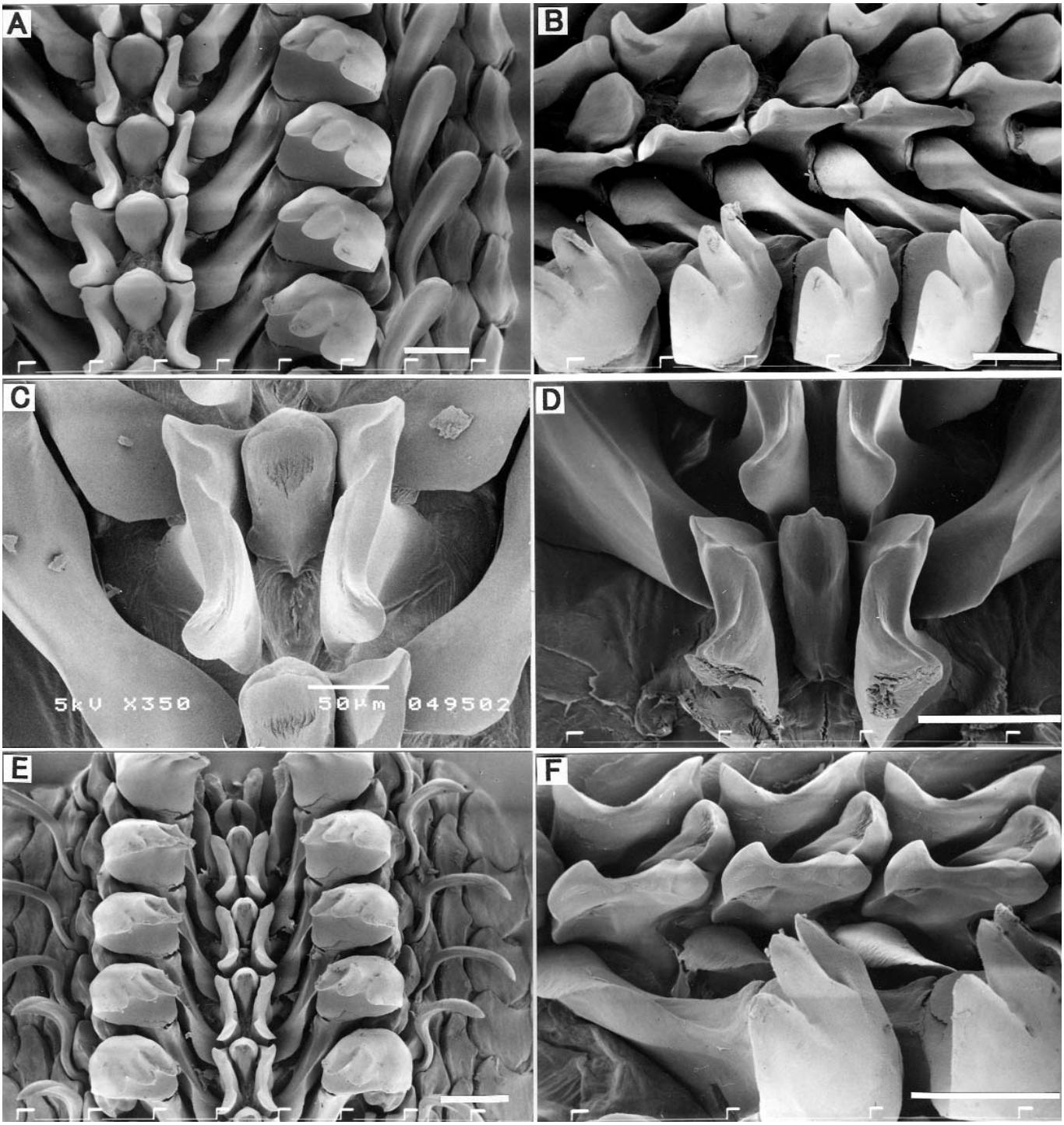

Fig. 16. Radulae of *Cryptoplax*. A, B, *C. larvaeformis* (Blainville MS, Burrow, 1815), NSMT-Mo 72885, BL ca. 40 mm (AD); C, *C. japonica* Pilsbry, 1901, NSMT-Mo 72884, BL ca. 100 mm (AD); D, *C. striata* (Lamarck, 1819), NSMT-Mo 72887, BL ca. 50 mm, (AD); E, F, *C. elioti* Pilsbry, 1901, NSMT-Mo 72886, BL 76.0 mm (AD). Scale bar: A, B, E, F, 100µm; C, D, 50µm.

Fig. 16. Radule di *Cryptoplax*. A, B, *C. larvaeformis* (Blainville MS, Burrow, 1815), NSMT-Mo 72885, BL ca. 40 mm (AD); C, *C. japonica* Pilsbry, 1901, NSMT-Mo 72884, BL ca. 100 mm (AD); D, *C. striata* (Lamarck, 1819), NSMT-Mo 72887, BL ca. 50 mm, (AD); E, F, *C. elioti* Pilsbry, 1901, NSMT-Mo 72886, BL 76.0 mm (AD). Scala di riferimento: A, B, E, F, 100µm; C, D, 50µm.

Material examined. *Pseudotonicia cuneata* (Suter, 1908), SAM D 18604, 1 specimen, BL 54.5 mm, Tauranga Harbour, New Zealand.

Radula. The radula is symmetrical. The central tooth is fairly large, roughly oblong in outline, convex, and faintly keeled near the base. There is a weak blade at the apex. The centro-lateral tooth is angulate with a faint cusp at the antero-dorsal corner. The head of the major lateral tooth has rather thin cusps. The central cusp is apparently wider than the others, which splay slightly outwards. The major uncinus is narrow **(Fig. 9B, D, F).**

Remarks. Gowlett-Holmes (1991) stated that *P. cuneata* (Suter, 1908) resembles *Bassethullia* in appearance and habitat; however, the similarities between them may be attributable to convergent evolution towards a similar habitat rather than to common ancestry. The general appearance of the radula is different between the two taxa but the similarity of the major lateral tooth may suggest common ancestry.

Genus ***Acanthochitona*** Gray, 1921

Type species. *Chiton fascicularis* Linné, 1767

Material examined. *Acanthochitona fascicularis* (Linné, 1767), NSMT-Mo72871, 1 specimen, BL 29.4 mm, Bretagne, France. *A. achates* (Gould, 1859), NSMT-Mo72879, 1 specimen, BL 25.5 mm, Nagasaki, Japan (AD); NSMT-Mo 72880, 1 specimen, BL 25.5 mm, Muroran, Japan (AD); NSMT-Mo 72881, 1 specimen, BL 41.5 mm, Izu-Oshima Island, Japan. *A. exquisita* (Pilsbry, 1893), NSMT-Mo 72872, 1 specimen, BL 24.6 mm, Baja California, Mexico. *A. defilippii* (Tapparone-Canefri, 1874), NSMT-Mo 72882, 1 specimen, BL ca 43 mm, Aoshima, Japan (AD). *A. intermedia*

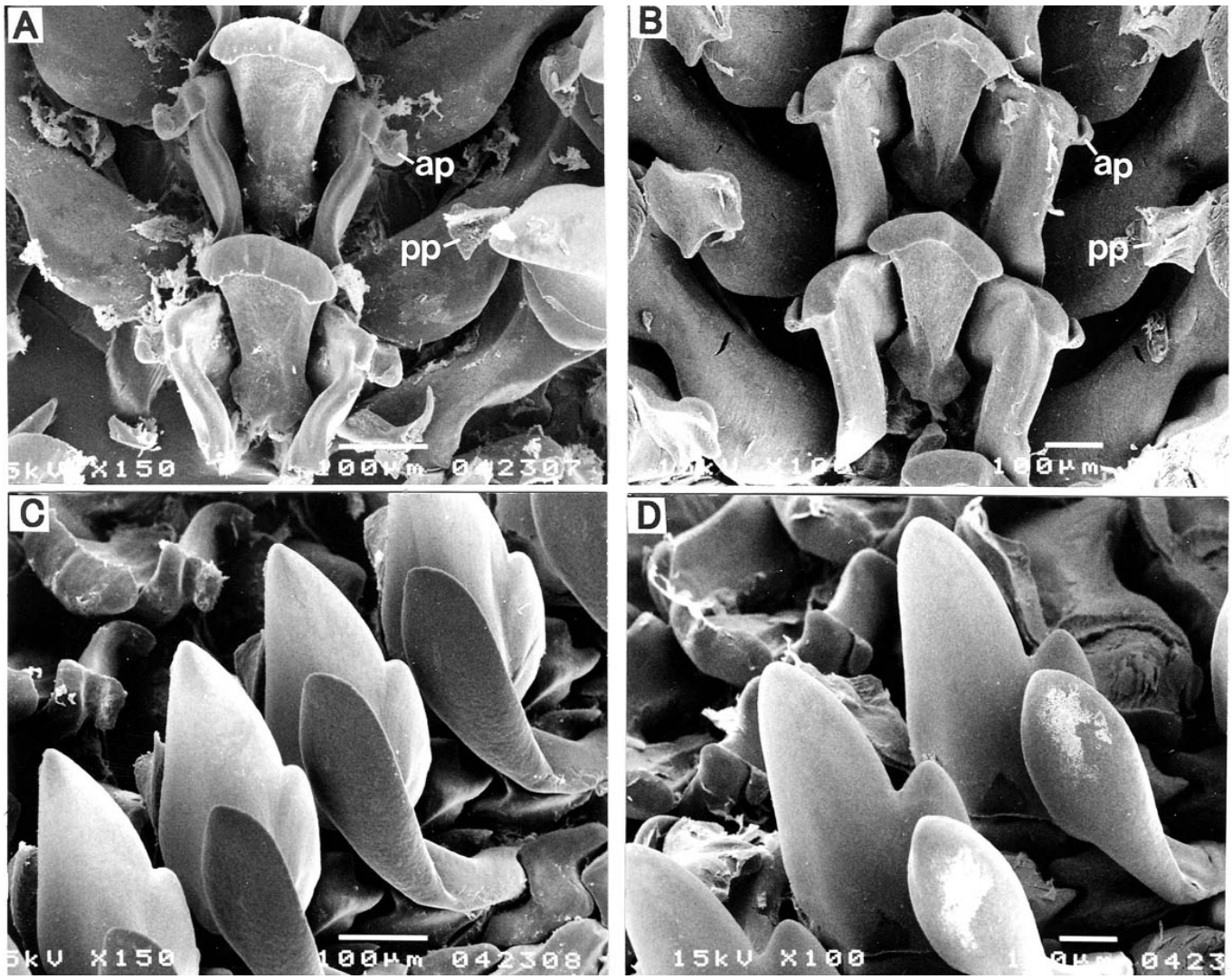

Fig. 17. A,C, Radula of *Lepidozona coreanica* (Reeve, 1847) NSMT-Mo 72891, BL 42.0 mm. B,D, *Lorica cimolia* (Reeve, 1847) NSMT-Mo 72892, BL 46.5 mm. ap, accessory process; pp, petaloid process. Scale bar: A-D, 100µm.

Fig. 17. A,C, Radula di *Lepidozona coreanica* (Reeve, 1847) NSMT-Mo 72891, BL 42.0 mm. B,D, *Lorica cimolia* (Reeve, 1847) NSMT-Mo 72892, BL 46.5 mm. ap, processo accessorio; pp, processo petaloide. Scala di riferimento: A-D, 100µm.

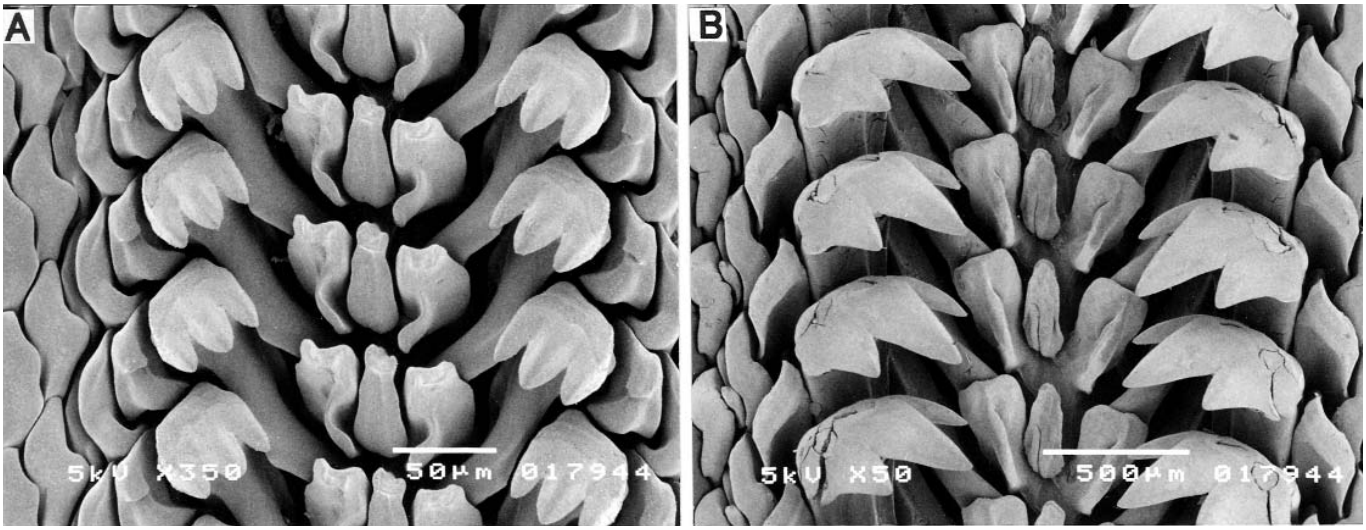

Fig. 18. A, Radula of *Callochiton foveolatus* (Is. Taki, 1938). NSMT-Mo 72890, BL 18.5 mm. B, Radula of *Cryptochiton stelleri* (Middendorff, 1847): NSMT-Mo 72887, BL 125 mm (AD). Scale bar: A, B, 50µm.

Fig. 18. A, Radula di *Callochiton foveolatus* (Is. Taki, 1938). NSMT-Mo 72890, BL 18.5 mm. B, Radula di *Cryptochiton stelleri* (Middendorff, 1847): NSMT-Mo 72887, BL 125 mm (AD). Scala di riferimento: A, B, 50µm.

(Nierstrasz, 1905), NSMT-Mo 72878, 1 specimen, BL ca. 23 mm, Amami-Oshima Island, Japan (AD), *A. penicilata* (Deshayes, 1863), NSMT-Mo 72873, 1 specimen, BL 11. 8 mm (dried specimen), Aqaba, Jordan, *A. mastalleri* Strack,1989, NSMT-Mo 72874, 1 specimen, BL 6.6 mm (dried specimen), Pharaon Island, Egypt. *A. dissimilis* Is. & Iw. Taki, 1931, NSMT-Mo 72876, 1 specimen, BL ca. 13 mm, Boso Peninsula, Japan (AD); NSMT-Mo 73023, 1 specimen, BL 13.7 mm, Boso Peninsula, Japan. *A.* sp., NSMT-Mo 72875, 1 specimen, BL ca. 7 mm, Chichijima Island, Japan (AD). *A. sueurii* (Blainville, 1825), NSMT-Mo 72877, 1 specimen, BL 16.5 mm, Edithburg, South Australia (AD).

At least three species groups featuring different types of radula are recognized within this genus.
1) ***fascicularis*-group.** This group consists of *A. fascicularis, A. exquisita, A. defilippii*, and *A. achates*. They are characterized by a bimorphic perinotum, which gives a heavily spiculous appearance.

Radula. The radula is symmetrical. The central tooth is small and squarish in outline; the posterior surface is mildly concave in the distal half, and somewhat keeled and dilated in the basal half. The anterior process is short and adherent in the basal half. The centro-lateral tooth has a nodulous antero-dorsal corner. The head of the major lateral tooth is large and has a rounded anterior surface; the median denticle is apparently larger than the others. The major uncinus tooth has a fairly wide blade **(Fig. 10)**.

2) ***intermedia*-group.** This group consists of *A. intermedia, A. penicilata*, and *A. mastalleri*. They are characterized by thin, whitish valves and a monomorphic perinotum consisting of slender spicules.

Radula. The radula is symmetrical. The central tooth is small, narrow and spatula-shape in outline; the posterior surface is mildly concave in the distal half and sharply keeled in the basal portion. The anterior process is short and adherent at the base. The centro-lateral tooth has a thick and knobbed antero-dorsal corner. The head of the major lateral tooth is large with a flat anterior surface. Each of the three denticles has an obtuse tip. The major uncinus tooth has a blade of moderate width **(Fig. 11)**.

3) ***dissimilis*-group.** This group consists of *A. dissimilis, A. sueurii*, and *A.* sp. They are characterised by very fine "asbestoid" sutural tufts and fine granular spicules on the perinotum.

Radula. The radula is symmetrical except for the central tooth of *A. dissimilis*, which is slightly asymmetrical. The central tooth is small, narrow in outline, thick, rather deeply concave on the distal half and keeled at the basal portion. The anterior process is long and entirely adherent. The centro-lateral tooth has a thick and knobbed antero-dorsal corner. The head of the major lateral tooth is large and the three denticles are rather narrow and of nearly the same length. The major uncinus tooth has a rather narrow blade **(Fig. 12)**.

Remarks. As shown above, the radula of *Acanthochitona* is variable among species groups; however it is consistently characterised by the nodulous antero-lateral corner of the centro-lateral tooth. The genus *Acanthochitona* contains many species, the morphology of which is little known. The taxonomic status of each species-group must await more extensive study of this genus.

Genus ***Choneplax*** Dall, 1882

Type species. *Chitonellus latus* Guilding, 1829
Material examined. *Choneplax lata* (Guilding, 1829), FSBC I 32548, 1 specimen, BL 25.2 mm, Grand Bahama Island; USNM 886327, 1 specimen, BL ca. 25 mm, Carrie Bow Cay, Belize.

Radula. The radula is symmetrical. The central tooth is oblong in outline, weakly keeled near the base; there is a fairly wide cusp at the apex. The centro-lateral tooth has a nodular antero-dorsal corner. The head of the major lateral tooth has short cusps of almost equal size and a flat anterior surface. The major uncinus tooth is moderate in width **(Fig. 13)**.

Remarks. The valve morphology of *Choneplax* has certain characters in common with both *Acanthochitona* and *Cryptoplax*, and it has thus been placed variously in the Acanthochitonidae/inae (Pilsbry, 1893; Thiele, 1909; 1929; Kaas, 1972; Kaas & Van Belle, 1980; 1998) and in the Cryptoplacidae/inae (Bergenhayn, 1955; Van Belle, 1983; Lyons, 1988; Sirenko, 1997). Thiele (1909) pointed out that the radula of *Choneplax lata* is similar to that of *Cryptoplax striata*. The present study reveals that the radular features are also intermediate in nature; the grooved antero-dorsal corner of the centro-lateral tooth is similar to that of *Cryptoplax*, while in central tooth characters *Choneplax* more closely resembles *Acanthochitona* than *Cryptoplax*.

Subfamily CRYPTOCHITONINAE Pilsbry, 1893

Genus ***Cryptochiton*** Middendorff, 1847

Type species. *Chiton stelleri* Middendorff, 1847

Material examined. *Cryptochiton stelleri* (Middendorff, 1847): NSMT-Mo 72887, 1 specimen, BL 125 mm, Shiretoko Peninsula, Japan (AD); NSMT-Mo 72888, 1 specimen, BL ca. 100 mm, Akkeshi, Japan (AD); NSMT-Mo 72889, 1 specimen, BL 23 mm, Noshappu, Japan (AD).

Radula. The radula shows slight asymmetry, and the rows are skewed. The central tooth is small; the main plate is roughly elongate pentagonal in outline, obtuse at the dorsal edge, and bilobed ventrally with double keels along the medial line in the ventral half. The centro-lateral tooth is expanded laterally at the antero-lateral edge. The head of the major lateral tooth is large but rather thin, and only slightly expanded posteriorly at the juncture with the shaft. The median denticle of the head is apparently larger than the others. The shaft is long and dilated ventrally, and widened and curved dorsally in the anterior portion. The major uncinus tooth is reduced to a basal plate and a minute isolated fragment **(Fig. 14)**.

Remarks. This monotypic genus has been placed in the family Acanthochitonidae, based on the reduced tegmentum, the presence of spinous tufts, and the small number of slits in the head valve. Watters (1991) recommended reconsideration of its taxonomic position. The radula morphology of *Cryptochiton stelleri* (Middendorff, 1847) is quite different from that of other members of the Cryptoplacoidea and this also supports the need for reconsideration of its systematic status.

Family HEMIARTHRIDAE Sirenko, 1997

Genus ***Hemiarthrum*** Dall, 1876

Type species. *Hemiarthrum setulosum* Dall, 1876

Material examined. *Hemiarthrum setulosum* Dall, 1876, NSMT-Mo 72883, 1 specimen, BL ca. 10 mm, King George Island, Antarctica.

Radula. The radula is symmetrical. The central tooth is fairly large, spatula-shaped, pointed and keeled in the basal portion. The apical edge forms a wide cusp with a central notch. The centro-lateral tooth has a thin, angulate antero-dorsal corner, which curves inward, forming a small cusp. The head of the major lateral tooth has a wide middle cusp and two smaller cusps, separated by faint grooves that reach the basal portion. The major uncinus is narrow **(Fig. 15)**.

Remarks. Sirenko (1997) separated this genus from Hanleyidae and placed it in the new family Hemiarthridae, which he created in the superfamily Cryptoplacoidea based on differences in gill arrangement, articulamentum, innervation to the aesthetes and sutural tufts on the perinotum. The radular characters do not contradict his assignment; on the contrary, no radular character has so far been identified that is common only to the Cryptoplacoidea.

Family CRYPTOPLACIDAE H. & A. Adams, 1858

Genus ***Cryptoplax*** Blainville, 1818

Type species. *Chiton larvaeformis* Blainville MS, Burrow, 1815

Material Examined. *Cryptoplax larvaeformis* (Blainville MS, Burrow, 1815), NSMT-Mo 72885, 1 specimen, BL ca. 40 mm, Iriomote Island, Japan (AD), *C. japonica* Pilsbry, 1901, NSMT-Mo 72884, 1 specimen, BL ca 100 mm, Boso Peninsula, Japan (AD). *C. striata* (Lamarck, 1819), NSMT-Mo 72887, 1 specimen, BL ca. 50 mm, Point Souttar, South Australia (AD). *C. elioti* Pilsbry, 1901, NSMT-Mo 72886, 1 specimen, BL 76.0 mm, Tokashiki Island, Japan (AD).

Radula. The radula is symmetrical. The central tooth is small, thick, and oblong in outline. The posterior surface is clearly concave in the upper half and keeled near the base. The anterior process is short and adherent at the base. The

centro-lateral tooth has a nodulous antero-dorsal corner with a groove on the inner surface. The head of the major lateral tooth has short, almost equal-sized, obtuse cusps, and a flat anterior surface. The major uncinus tooth is moderate in width (**Fig. 16**).

Remarks. The central tooth varies among species, but it is consistently characterised by its small size and keeled, squarish base. The radula of *Cryptoplax* resembles that of *Acanthochitona* in the nodulous antero-dorsal corner of the centro-lateral tooth, but differs by having a groove on the inner wall of the antero-dorsal corner.

CONCLUSIVE REMARKS

Thiele (1893) established a large number of Polyplacophoran genera based on study of the radula; however, those parts of his work based solely on radular characters have seldom been accepted by subsequent authors. Bullock (1988) remarked of the characteristic ischnochitonid radula of the chitonid *Radsia*: "It should be noted that if one were classify the Polyplacophora solely on the basis of the radula, *Radsia* would be placed in the Ischnochitonidae. In fact, Thiele (1893, 1909), who emphasized the radula as a phylogenetic tool, placed *R. nigrovirescens* Blainville, 1825 in the genus *Ischnochiton*". Bullock (*ibid*) also identified similarities in valve characters between *R. nigrovirescens* and the ischnochitonid *Ischnoradsia australis* (Sowerby, 1840). The exact systematic position of *Radsia* is unclear, but his comparison of radular characters provided an important clue to their phylogenetic relationship. A similar example is that of the ischnochitonid *Lepidozona* and the loricid *Lorica* (**Fig. 17**) and an extreme example is the resemblance between the radulae of *Callochiton* and *Cryptochiton* (**Fig. 18**). Morphological characters other than radular are totally different in these two genera and no one at present supports the notion of a close relationship; future study may or may not establish the truth. We should nevertheless explore phylogeny by a holistic approach, and radula should therefore be treated as one character among many and explored to find new characters.

The crucial problem in using radular characters in systematics is the lack of adequate data concerning their fine morphology. Many radular characters have been described and illustrated in the literature, but most were based on optical microscope observation, sometimes, moreover, confined to a few sections such as the three central teeth. To assess phylogenetic relationships, further morphological comparisons using SEM and light microscopy are essential. The latter is still necessary for certain characters, for example the translucent part, the tab on the head of the major lateral and the accessory process of the centro-lateral tooth (which is easily detached during preparation for SEM examination). Accumulation of information on fine radular morphology will enable us to make exact comparisons and will lead us to the discovery of new characters.

Because ontogenetic variation and polymorphism in radula have been established (Sirenko, 1974, 1992; O'Neill, 1984; Bullock, 1988), the exact size, number, and localities of specimens examined in every study should be recorded in the resulting articles. It is interesting that the tricuspid head of the major lateral tooth appears in the early life stage in examples of Lepidopleurida and Chitonida. The initial stages of radular development in several chitons imply an ancestral radular state in the Mollusca (Sirenko & Minichev, 1975; Eernisse & Kerth, 1988). Further research into ontogenetic variation may provide clues into the phylogeny of chitons.

The present study suggests that radular characters may be most effective in evaluating the phylogenetic relationships within a genus and/or a family, as demonstrated here using the example of the superfamily Cryptoplacoidea. Comparisons of radular characters suggest that a significant reduction in the tegmentum occurred in parallel within the Cryptoplacoidea, namely in the lineages of *Notoplax-Cryptoconchus*, *Leptoplax*, *Acanthochitona* and *Cryptochiton*. Radular characters might also be useful at family or higher taxonomic levels. Unfortunately, there are still few established or candidate characters; for example, I have not yet found any radular character common only to the Cryptoplacoidea. This means that assignment of *Hemiarthrum* to the superfamily Cryptoplacoidea (Sirenko, 1997) cannot at present be based on radular characters, however there are some useful established and candidate characters at higher taxonomic levels. For example, the petaloid process of the major lateral tooth may be an "innovative" or a character shared within the suborder Chitonina, and the accessory process of the centro-lateral tooth is possibly a new character useful at higher taxonomic levels. I would like to propose that the radulae of Lepidopleurida be extensively studied to establish useful characters for work at higher taxonomic levels because, although their fine morphology is poorly known, even the limited numbers of species examined in detail so far exhibit wide morphological variation and similar morphology to species in the Chitonida. Any and all efforts to reveal the fine morphology of the radulae and explore new characters are to be greatly encouraged.

ACKNOWLEDGMENTS

I would like to thank Dr. B. Dell'Angelo, the Società Italiana di Malacologia, and the Istituzione Culturale Federico II of Menfi for granting me the opportunity to participate in the 4th International Workshop of Malacology "Systematics, Phylogenesis and Biology of Polyplacophora", and to contribute to this volume of the proceedings.

I must also thank the following people and institutions for generously loaning or donating valuable specimens: Messrs. B. Anseeuw and Y. Terryn, the late Mr. C. Ebreo, Ms. S. L. Farrington and Dr. W. Lyons (FSBC), Ms. K. L. Gowlett-Holmes, Dr. M. G. Harasewych (USNM), Dr. T. Kikuchi, Dr. S. Nishihama, Dr. H. Numanami, Dr. T. Sasaki, Mr. H. Strack, the late Mr. T. Tateshi and Dr. W. Zeidler (SAM),.

Finally, I am grateful to Dr. T. Okutani, Mr. P. Callomon and Dr. L. Cao for their critical reading of the manuscript.

REFERENCES

BERGENHAYN J. R. M., 1955. Die fossilen Schwedischen Loricaten nebst einer vorläufigen Revision des Systems der ganzen Klasse Loricata. *Lunds Universitets Årsskrift*. N. F. *Avd*. 2, **51**(8): 1-46, pls. 1-2.

BUCKLAND-NICKS J., 1995. Ultrastructure of sperm and sperm-egg interaction in Aculifera: Implications for molluscan phylogeny. In: Jamieson, B. G. M., Ausio, J., & Justine, J.-L. (eds), Advances in Spermatozoal Phylogeny and Taxonomy. *Memoires du Museum National d'Histoire Naturelle*, **166**: 129-153.

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

BULLOCK R. C., 1988b. The systematics of the southern hemisphere chiton genera *Radsia* Gray, 1847, and *Sypharochiton* Thiele, 1893 (Mollusca: Polyplacophora: Chitonidae). *Proceedings of the Biological Society of Washington*, **101**(2): 280-299.

COTTON B. C., 1964. *South Australian Mollusca. Chitons. Handbook of the Fauna and Flora of South Australia*. W. L. Hawkes, Government Printer, 151 pp. Adelaide.

EERNISSE D. J. & KERTH K., 1988. The initial stages of radular development in chitons (Mollusca: Polyplacophora). *Malacologia*, **28**(1-2): 95-103.

GOWLETT-HOLMES K. L., 1990. A review of the endemic Australian chiton genus *Bassethullia* Pilsbry 1928 (Mollusca: Polyplacophora: Acanthochitonidae). *Journal of the Malacological Society of Australia*, **11**: 9-28.

GOWLETT-HOLMES K. L., 1991. Redefinition of the genus *Notoplax* H. Adams, 1861, and recognition of the monotypic New Zealand genus *Pseudotonicia* Ashby, 1928 (Mollusca: Polyplacophora: Acanthochitonidae). *Journal of the Malacological Society of Australia*, **12**: 77-88.

GOWLETT-HOLMES K. L., 1998. *Family Acanthochitonidae*. In: Beesley, P. L., Ross, G. J. B. & Wells, A. (eds), *Mollusca: The Southern Synthesis. Fauna of Australia*. Vol. 5, Part A., CSIRO Publishing, Melbourne: 188-189.

HASZPRUNAR G.H., 1987. The fine morphology of the osphradial sense organs of the molluscs. III. Placophora and Bivalvia. *Philosophical Transactions of the Royal Society of London,* (B) **315**: 37-61.

HICKMAN C. S., 1984. Implications of radular tooth-row functional integration for archaeogastropod systematics. *Malacologia*, **25**(1): 143-160.

KAAS P., 1972. Polyplacophora of the Caribbean region. *Studies on the fauna of Curaço and other Caribbean Islands*, **41**(137): 1-162.

KAAS P., & VAN BELLE R. A., 1980. *Catalogue of living chitons*. Backhuys, Rotterdam, 144 pp.

KAAS P., & VAN BELLE R. A., 1998. *Catalogue of living chitons (Mollusca, Polyplacophora) Second, revised edition*. Backhuys Publishers, Leiden, 204 pp.

LAMPRELL K. L. & HEALY J. M., 1998. A revision of the Scaphopoda form Australian waters (Mollusca). *Records of the Australian Museum, supplement* **24**: 1-189.

LYONS W. G., 1988. A review of Caribbean Acanthochitonidae (Mollusca: Polyplacophora) with descriptions of six new species of *Acanthochitona* Gray, 1821. *American Malacological Bulletin*, **6**(1): 79-114.

MATUSKUMA A. & TSUBAKI Y., 1995. Radular morphology and feeding tracks of *Liolophura japonica* (Mollusca: Polyplacophora). *Science Reports, Department of Earth & Planet Sciences., Kyushu University*, **19**(1): 81-92 (In Japanese with English abstract).

MORRIS T. E. & HICKMAN C. S., 1981. A method for artificially protracting gastropod radulae and a new model of radula function. *The Veliger*, **24**(2): 85-90.

OKUTANI T. & SAITO H., 1987. An occurrence of *Amicula gurjanovae* Yakovleva, 1952 (Polyplacophora: Mopaliidae) from Hokkaido with an extended description. *Venus*, **46**(3): 166-172.

O'NEILL M. H. B., 1984. Morphological changes in *Onithochiton neglectus* Rochebrune, 1881 (Mollusca: Chitonidae), and their taxonomic significance. *New Zealand Journal of Zoology*, **11**: 43-48.

PILSBRY H. A., 1893. *Monograph of the Polyplacophora.* In: Tryon, G. W., *Manual of Conchology*, 15, Academy of the Natural Sciences of Philadelphia: 1-64, pls. 1-10.

SAITO H., 2001. *Class Polyplacophora.* In: Okutani, T. (ed.) *Marine Mollusks in Japan*, Tokai University Press, Tokyo: 4-23.

SAITO H. & OKUTANI T., 1992. Carnivorous habits of two species of the genus *Craspedochiton* (Polyplacophora: Acanthochitonidae). *Journal of the Malacological Society of Australia*, **13**: 55-63.

SIRENKO B. I., 1974. Taxonomy of the genus *Tonicella* (Ischnochitonidae). *Zoologicheskij Zhurnal,* **53**(7): 988-997 (In Russian with English Abstract).

SIRENKO B. I., 1992. Nierstraszellidae fam. nov. a new family of chitons (Polyplacophora, Lepidopleurida) from the bathyal of Western Pacific. *Ruthenica*, **2**(2): 81-90.

SIRENKO B. I., 1997. The importance of the development of articulamentum for taxonomy of chitons (Mollusca, Polyplacophora). *Ruthenica*, **7**(1): 1-24.

SIRENKO B. I. & MINICHEV Y., 1975. Dèveloppment ontogènètique de la radula chez les Polyplacophores. *Cahiers de Biologie Marine*, **16**: 425-433.

SLIEKER F. J. A., 2000. *Chitons of the world. An illustrated synopsis of recent Polyplacophora*. Mostra Mondiale Malacologia, Cupra Marittima, Italy: 154 pp.

SMITH A. G., 1960. Amphineura. In: Moore, R. C (ed.), *Treatise on Invertebrate Palaeontology. Part I. Mollusca 1*. Geological Society of America and University of Kansas Press, Lawrence: 41-76.

SOLEM A., 1972. Malacological applications of scanning electron microscopy II. Radular structure and functioning. *The Veliger,* **14**(4): 327-336.

TAKI Is., 1938. Report of the biological survey of Mutsu Bay 31. Studies on chitons of Mutsu Bay with general discussion on chitons of Japan. *Science Report of Tohoku Imperial University*, (4)**12**: 323-423, pls.14-34.

THIELE J., 1893. *Polyplacophora, Lepidoglossa, Schuppenzüngler*. In: Troschel, F. H., *Das Gebiss der Schnecken zur Begründung einer Naturlichen Classification*, 2. Berlin: 355-401, pls. 30-32.

THIELE J., 1909-1910. Revision des Systems der Chitonen. *Zoologica, Stuttgart*, 22(56), part I: 1-70, pls. 1-6 (1909); part II: 71-132, pls. 7-10 (1910).

THIELE J., 1929. Classis Loricata. In: *Handbuch der Systematischen Weichtierkunde*, I. Gustav Fischer, Jena: 397-406.

VAN BELLE R. A., 1983. The systematic classification of the chitons (Mollusca: Polyplacophora). *Informations de la Société Belge de Malacologie*, **11**(1-3): 1-178.

WATTERS G. T., 1991. A review of the Recent Eastern Pacific Acanthochitoninae (Mollusca: Polyplacophora: Cryptoplacidae) with the description of a new genus, *Americhiton. The Veliger*, **33**(2): 241-271.

YAKOVLEVA A. M., 1952. *Shell-bearing Mollusks (Loricata) of the seas of the U.*

S. S. R. Fauna USSR, 45. Zoological Institute, Academy of Sciences, U.S.S.R., Moskva and Leningrad: 107 pp., 11 pls. (Translated into English by the Israel Program for Scientific Translations, Jerusalem, 1965).