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## Similar but different: Polyplacophoran (Mollusca) tail valve – what is it? An attempt to find answers

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**ABSTRACT.** The extant polyplacophoran tail valve is traditionally considered as a unity despite its clear separation into two distinct regions, which were in relation to the delimiting point – the mucro – termed the antemucronal area for the front part and the postmucronal area for the hindermost region. However, earlier conceptions do exist, which consider the postmucronal area as semiplate, with the antemucronal area as modified “intermediate” plate.

To test the usefulness of the terms “antemucronal” and “postmucronal” in their traditionally sense, three independent attempts were made to demonstrate existing differences between the mucro-separated areas.

*Leptochiton rugatus* was histologically examined allowing the confirmation of a cardial complex-antemucronal relation. Valve morphology of the brood of *Radsia nigrovirescens* not only confirms a tegmental development prior to the building of the articulamentum but shows that the postmucronal area develops to its final shape before the antemucronal area appears. For the first time it is demonstrated that the antemucronal area of *Schizoplax brandtii* shows a delayed splitting of the relevant area, characteristic for the conditions found in the intermediate valves of this species only. That leads to the assumption that the underlying valve build processes are of the same nature as in the intermediate valves. Additionally, literature data on valve characters were compiled that show a stronger relationship (61%) of the antemucronal area to the central area of intermediate valves rather than to the merged postmucronal area. In the light of this evaluation it is suggested that the term “tail valve” should be used to demonstrate the merged condition of two independent zones only, the antemucronal area and the postmucronal area.

Схожие, но различные: что такое хвостовые щитки Polyplacophora (Mollusca)? Попытка найти ответы

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**РЕЗЮМЕ.** Существующий хвостовой щиток полиплакофор традиционно рассматривается как единая структура, несмотря на то, что он четко разделен на две отдельные области, которые в зависимости от точки разграничения – мукро – называются антемукрональной областью для передней части и постмукрональной областью для самой задней области. Тем не менее, существуют более ранние концепции, которые рассматривают постмукрональную область как полушиток, а антемукрональную область как модифицированный «промежуточный» щиток.

Чтобы проверить применимость терминов «антемукрональный» и «постмукрональный» в их традиционном смысле, были предприняты три независимых попытки продемонстрировать существующие различия между областями, разделенными мукро.

*Leptochiton rugatus* был исследован гистологически, что позволило подтвердить связь между комплексом сердечной системы и антемукрональной областью. Морфология щитка ювенилов *Radsia nigrovirescens* не только подтверждает развитие тегмента до формирования артикуламентума, но и показывает, что постмукрональная область развивается до своей окончательной формы до того, как появляется антемукрональная область. Впервые продемонстрировано, что в антемукрональной области *Schizoplax brandtii* наблюдается замедленное расщепление соответствующей области, характерное для условий, обнаруженных в промежуточных щитках только этого вида. Это позволяет предположить, что основные процессы роста щитка имеют ту же природу, что и в промежуточных щитках. Кроме того, были собраны литературные данные о признаках щитков, которые показывают более сильную связь (61%) антемукрональной области с центральной областью промежуточных щитков, а не со слившейся постмукрональной областью. В свете этой оценки предлагается использовать термин «задний щиток», чтобы продемонстрировать объединенное состояние двух независимых зон: антемукрональной и постмукрональной областей.

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## Introduction

Among the speciose molluscs, there is a group of exclusive marine inhabitants that show an amazing autapomorphy within this phylum, an exoskeleton of eight dorsally laying valves, reason enough to call them the *Polyplacophora* Gray, 1821 (or much earlier even the *Octovalvia* des Hayes, 1787). As these valves are most conspicuous (e.g. coloration, sculpturing, zonation) and predominantly contribute to the fossil record, they were generally considered to be the most important structure (in a systematic sense) to delimit polyplacophoran species and higher taxonomic levels. That the valve peculiarities alone do not necessarily reflect the true phylogeny has been demonstrated in various studies [e.g. Sirenko, 2006] and even the status of various species known only from fossilized valves is still unclear [e.g. Van Belle, 1981]. Nevertheless, the valves should be considered the best-studied parts of the chitons, spanning various disciplines (e.g., skeletogenesis, chemical analysis, anatomical). Although the valves may vary chemically in structural details among taxa, they are generally of the calcium carbonate morph. aragonite [e.g. Carter, Hall, 1990; Eernisse, Reynolds, 1994]. Each valve comprises of a set of usually prismatic layers, taxon and regional specific in numbers. For systematic use these complex layering is reduced to the sculpture, coloration, and aesthetes bearing distal layer tegmentum and the proximal articulamentum. Especially the latter is of evolutionary interest as it first occurred in the Silurian [Puchalski *et al.*, 2009] and is a diagnostic feature of the subclass Neoloricata that comprises all extant species. The articulamentum forms structures that much contribute to a better anchoring in the valves surrounding mantle tissue by insertion plates [but see Hoffmann, 1929-1930] and a better protection in length axis by means of apophyses. The eight polyplacophoran valves are encountered from anterior to posterior or may alternatively named the head valve for the first, the tail valve for the last and the six intermediate valves between them. Interestingly, tegmental sculptural patterns can be divided into independent regions. The head valve usually shows the same sculpture as the often distinctly raised lateral areas of the intermediate valves and the mucro delimited posterior part (the postmucronal area) of the tail valve. In these regions the sculpture is mainly radial orientated. The same regions notably overlay the insertion plates (if developed). The remaining parts – the central areas of the intermediate valves as well as the anterior to mucro located antemucronal area of tail valve also resemble each other. Here, however is the main orientation of the sculpture in longitudinal direction and these parts overlay the apophyses forming areas of the articulamentum, and also

the jugal laminae if this zone is developed. In sum, a single homogenous valve – the head valve – is followed by seven valves that show a mixture of varying zonations. The origin of these differences has never been fully answered and requires further study. The present study attempts to help untangling the problem, by focusing on one of the heterogeneous valves, the tail valve, of which Simroth [1892-1894: 249] stated the following: “Während das erste Schalenstück niemals eine area centralis oder einen Kiel zeigt, ist er bei der letzten gewöhnlich in ihrer vorderen Hälfte vorhanden, so dass man dieses Stück mehr als eine Verschmelzung einer Mittelplatte mit einem zur ersten Platte symmetrischen Stück betrachten kann” [While the first valve never contains a central area nor a keel, the latter is usually visible in the front half of the posterior valve, so that this valve may be considered a fusion of an intermediate valve with a piece symmetrical to the head valve]. Thiele [1893: 235] even considered the first seven polyplacophoran valves as simply repetitions of the anterior half of its tail valve. More recently and obviously the last who followed the concept of independent zonation of the tail valve Starobogatov and Sirenko [1975] established a new system, which covers the evolutionary trends from the fossil record to extant species, partly focusing on the particularities of this distinct valve which they identified as comprising VIII-a and VIII-b. To test the value of Simroth’s statement, the tail valve is also chosen as it shows a remarkable, in my opinion yet insufficient studied structure, the above mentioned mucro. In addition the tail valve shows evolutionary trends that are of utmost interest, exemplary underlined by the following points: 1) there is a distinct heterochrony in valve development during ontogenesis, as the tail valve evolves later after larval settlement only, 2) the position of the mucro not only varies considerably among species, but also changes during individual growth [e.g. O’Neill, 1984], 3) the condition of insertion plates may distinctly be different from remaining valves in specific taxa (e.g., representatives of *Hanleya* Gray, 1857, *Juvenichiton* Sirenko, 1975, *Nuttallina* Carpenter MS, Dall, 1871, *Dinoplax* Carpenter MS, Dall, 1882, *Ischnoplax* Carpenter MS, Dall, 1879, *Glyptochiton* de Koninck, 1883), 4) the tail valve may develop caudal sinus (e.g., *Mopalia* Gray, 1847, *Placiphorella* Carpenter MS, Dall, 1879) or even terminal slits (e.g., *Schizochiton* Gray, 1847), 5) the tail valve can show extended callus formation, and 6) the mucro may undergo a remarkable up-lifting (e.g. *Craspedochiton umgaziana* (Koch, 1951)). Further reflections lead to a species, which is unique among extant Polyplacophora by having divided intermediate valves: *Schizoplax brandtii* (von Middendorff, 1847), more recently detailed investigated by Sirenko *et al.*, [2013].

## Material and methods

Polyplacophoran material used for this study belongs to the Bavarian State Collection of Zoology (ZSM Mol). Specimen data are as follows:

*Leptochiton rugatus* (Carpenter in Pilsbry, 1892) (ZSM Mol 20140440) Canada, British Columbia, Vancouver Island, Victoria, Chinese Cemetery (48°24'21"N, 123°19'16"W), intertidally, leg. Gavin Hanke, 08.2008. (Specimen treatments for histology are described in Sigwart *et al.*, [2014]).

*Radsia nigrovirescens* (de Blainville, 1825) (ZSM Mol 20050849)

Republic of South Africa, Western Cape, Mostbaai (34°22'49"S, 18°49'53"E), under stones, at low tide, 0.5 m, leg. E. Schwabe 18.01.2005.

*Schizoplax brandtii* (von Middendorff, 1847) (ZSM Mol 20080124) Russia, Kamchatka, Kronotsky Bay, leg. O. Kussakin 13.08.1970.

The image procedure and specimen treatments for scanning electronic microscopy follow Schwabe [2006].

Further images of *S. brandtii* were kindly produced on the authors request by Dr. Boris Sirenko and colleagues at the Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (ZISP), where the samples are also located: Sb13 (Russia, Kurile Islands, Urup Id., intertidal, body length [BL] 13 mm); Sb 18 (Russia, Kamchatka, Kronotsky Bay, BL 18 mm); Sb 22 (Russia, Kamchatka, Olutorskiy Bay, BL 22 mm).

The systematics follows with slight alterations Sirenko [2006]. The higher systematics of *S. brandtii*, however, is in accordance with Irisarri *et al.* [2014].

## Results

Class Polyplacophora Gray, 1821  
Subclass Neoloricata Bergenhayn, 1955  
Order Lepidopleurida Thiele, 1909  
Suborder Lepidopleurina Thiele, 1909  
Family Leptochitonidae Dall, 1889

*Leptochiton rugatus*  
(Carpenter in Pilsbry, 1892)  
(Figs 1, 2)

From serial sections through this species the relevant slides of the tail valve reveal some morphological details, which may be interpreted in relation to the mucro. The valve thickening of this particular area occurs at the same level of the most posterior ctenidium (Fig. 1B), the anus papilla with anus (Figs 1 B-C) and overlaying suprarectal commissure (Figs 1D; 2A). While the postmucronal area immediately behind the mucro (Fig. 1A) does not show noteworthy anatomical details, the antimucronal area from the mucro anteriorwards (Fig. 2),

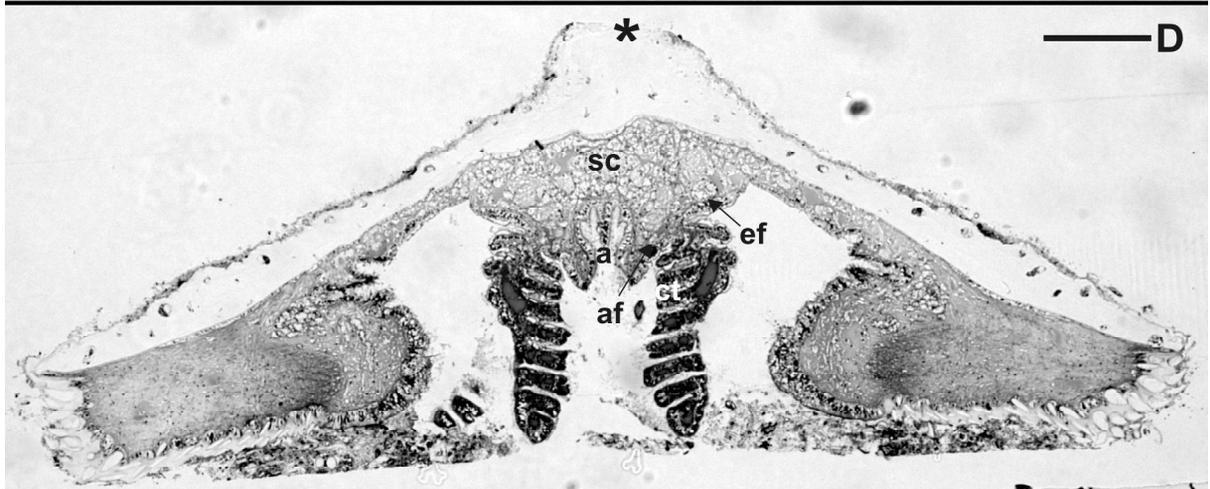
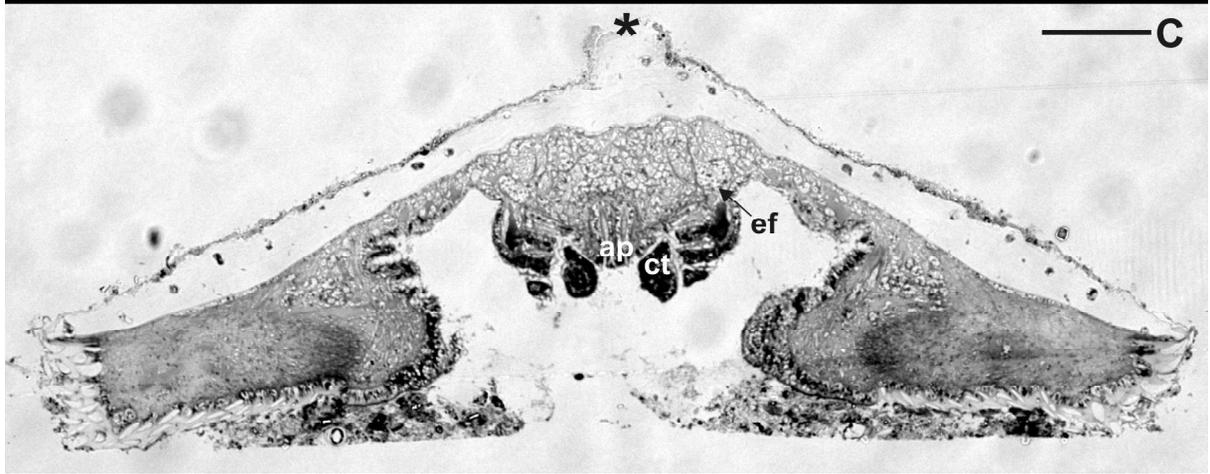
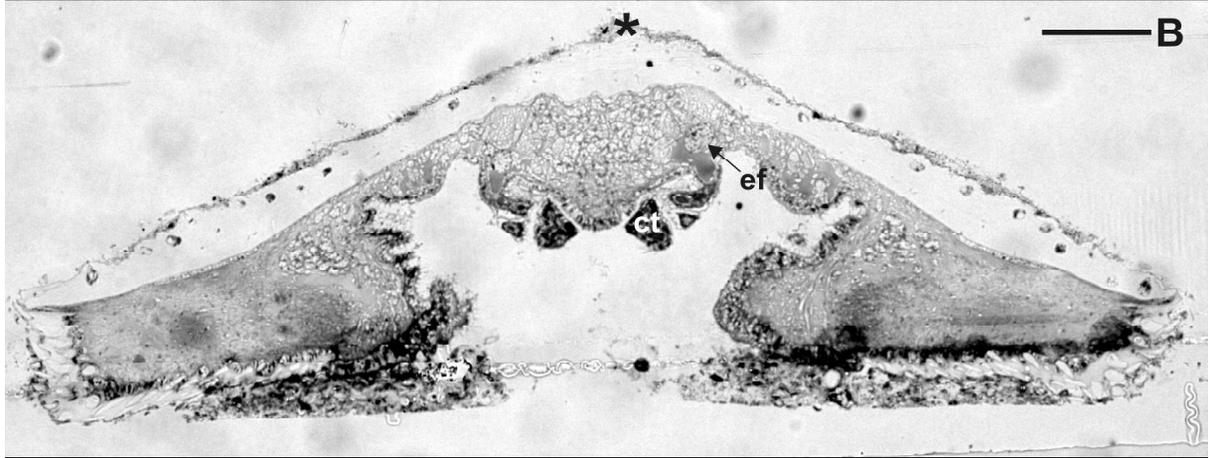
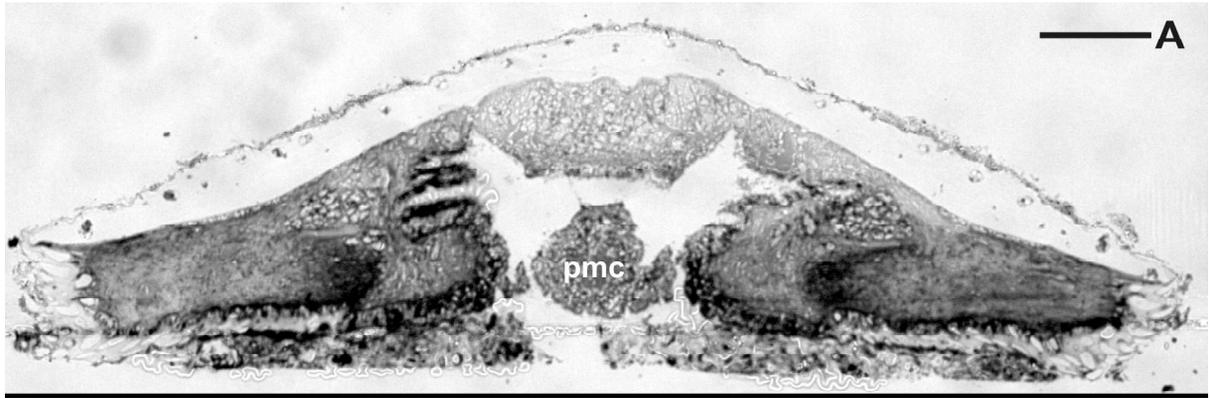
however, indicates the area where the parallel running lateral nerve cords unite to the suprarectal commissure (Fig. 2A), the auricle occurs (Figs 2 C-D), and the spacious pericardium terminates. Additionally, the foot is here enlarged and glandular cells occur. The latter fact as well as the occurrence of the posteriormost ctenidium must be declined from a relation to the mucro, as other taxa (e.g. non Lepidopleurid species for ctenidia arrangement; *Placiphorella* and *Craspedochiton* Shuttleworth, 1853 species with reduced foot) show that these conditions may not generalize. The position of the anus also does not reflect such a relation, as it occurs at the foot's terminal part, which as shown, does not necessarily attain to such extends. Furthermore, such a relation would make the development of anterior directed supporting structures like caudal slits in the postmucronal area (e.g. *Schizochiton*) for an enhanced defecation meaningless. The suprarectal commissure is also not relevant for the relation to the mucro, as it overlays the rectum and thus more related to the anus [e.g., Faller *et al.*, 2012]. From the given conditions the mucro seems therefore related to the dimensions of the cardiac complex, more precise of the length of the pericardium. The latter was also observed by Pelseneer [1898] and finds further support by the fact that the pericardium develops like the tail valve earliest after the settlement of the larvae as described by Hammarsten and Runnström [1926].

Order Chitonida Thiele, 1909  
Suborder Chitonina Thiele, 1909  
Superfamily Chitonoidea Rafinesque, 1815  
Family Chitonidae Rafinesque, 1815

*Radsia nigrovirescens* (de Blainville, 1825)  
(Figs 3, 4)

One of the roughly 45 brooding chiton species [Sirenko, 2015; Ituarte, Arellano 2016] known to date is the present South African species [Thiele, 1910]. The species was investigated in detail by Bullock [1988] who characterized adult specimen's tail valve having a central mucro, up to 19 teeth in the insertion plate and wide trapezoidal apophyses. Data on the ontogenesis in general and specific on skeletogenesis of this species are unknown. Smith [1966: 441] after a detailed but unpublished examination however noted that he found the demarcation line between the last two valves (vii-viii) in metamorphosed young *R. nigrovirescens* hardly to detect. The young are generally considered to be about 0.7-0.75 mm in length [Smith, 1966].

Here for the first time data on the metamorphosed young shell plates is presented. The examined specimens were more or less of the same size



measuring 380 x 337  $\mu\text{m}$  (Figs 4 C-D), thus about half the size Smith [1966] indicated. At this stages the eight valves are clearly indicated, a well-developed radula is visible, large larval eyes occur, and the mantle is very small with isolated spicules (not scales as in the adults) visible (Figs 4 B-D).

Although the tegmentum is already well developed it shows apart from a weak striation (radial in the terminal valves, longitudinal in the central area of the intermediate valves) and some pores of varying sizes hardly any structures (Figs 3 A, C, E; 4B). Tegmental areas covered by the hind margin of the preceding valve are more or less smooth. The articulamentum develops as in other polyplacophoran young [e.g. Heath, 1899; Hammarsten, Runnström, 1926] delayed after the tegmentum and occurs obviously first as apophysal plate, prior to form insertion plates (Figs 3D; 4A), as the latter are not visible in any of the plates, while different developmental stages of apophyses already occur. In a very tiny tail plate (Fig. 3E) the apophyses are even not building although firstanlagen may be adumbrated. *In situ* observations of the tail valve (Fig. 4B) show that the postmucronal part strongly resembles its final shape (but very small) without a visible anterior part and the supposed mucro underlays the hinder part of the preceding valve. Such condition was also observed by O'Neill [1984] for another brooding species, and the author further demonstrated the steady transforming of the tail valve due to increasing of the antemucronal area.

Suborder Acanthochitonina Bergenhayn, 1930  
Superfamily Mopalioida Dall, 1889  
Family Lepidochitonidae Iredale, 1914

*Schizoplax brandtii* (von Middendorff, 1847)  
(Figs 5, 6)

As earlier stated this species takes an exceptional position among the living Neoloricata by having divided intermediate plates, which are connected with a ligament-like filling. The species was the subject of a recent study by Sirenko *et al.*, [2013], who also illustrated the tail valve (their figs 4 C-D).

After their illustrations the tail valve differs in no way from a "typical" tail valve with more or less centric mucro (Fig. 5A). This however does not fit own observations (Figs 5 B-D) and is not reflecting the whole information. A ventral view on the species' tail valve tells another story (Figs 5 B-D; 6 B-D). On my request Dr. Boris Sirenko kindly provided SEM images of the tail valve of a selected growths series of this species. His largest specimen (Sb22) shows in dorsal view a tegmental splitting of the anterior region to the level of the mucro (= antemucronal area), a condition also met in the ventral view (Figs 6 A-B, respectively). A slightly smaller specimen (Sb18) has the antemucronal area lesser divided, the ligamental furrow does not reach the mucro, neither in dorsal nor in ventral view (Figs 6 C-D). The smallest specimen (Sb13) does not show any traces of division of the antemucronal area. Moreover, it might be that the splitting of the antemucronal area is somehow related to a thickening of the apophysal plate of the articulamentum. Although ultrastructural data are lacking to support this, there are ontogenetic data available [Kussakin, 1960] which might confirm this. Kussakin illustrated a full metamorphosed young of this brooding species (his fig. 2.6), of approx. 765  $\mu\text{m}$  in length, which in general outline corresponds well to the young here illustrated of the preceding species, but for a clear longitudinal splitting of the intermediate valves. Both terminal valves are present, but it remains unclear, if the posterior valve already shows any evidence of the mucro and those a division of these particular valve into an anterior and posterior region. If we expect similar conditions in terms of articulamentum development like in the preceding species, apophyses at least in the intermediate plates might be developed and articulamentum thickening in this region is ongoing. According to Kussakin's figure the "tail valve" is semicircular and entire. This would fit the present observations of the postmucronal area. A splitting of the antemucronal area is neither mentioned nor figured, and would, if the present observations are applicable for a general trend, not be expected at this early stage.

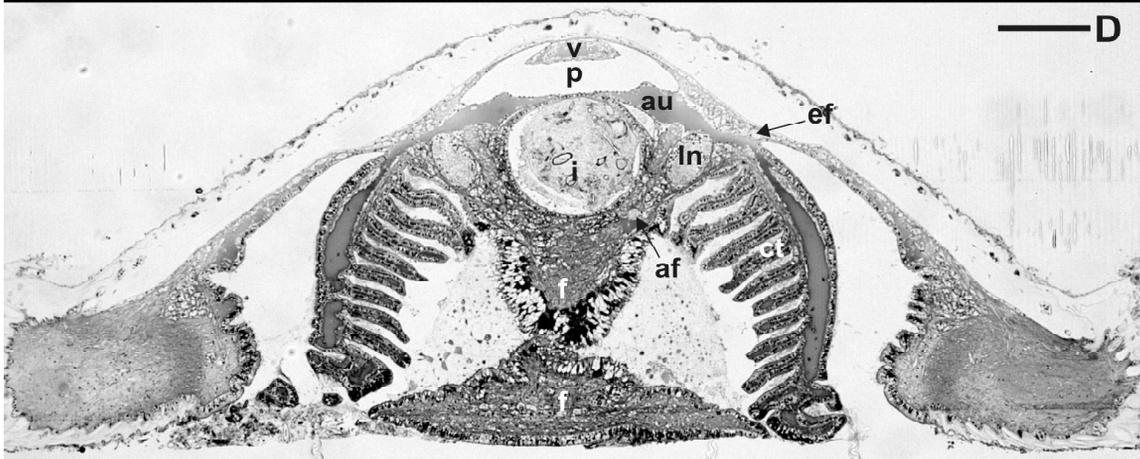
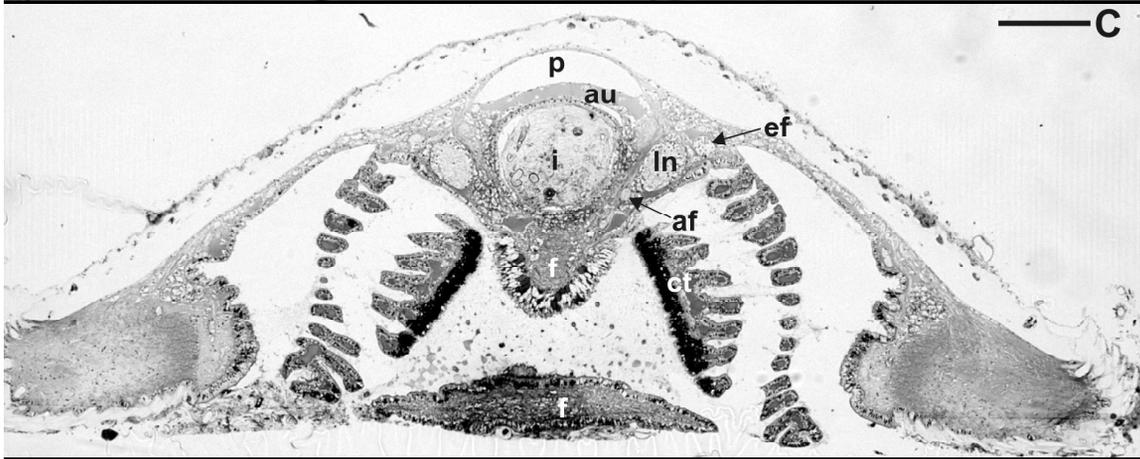
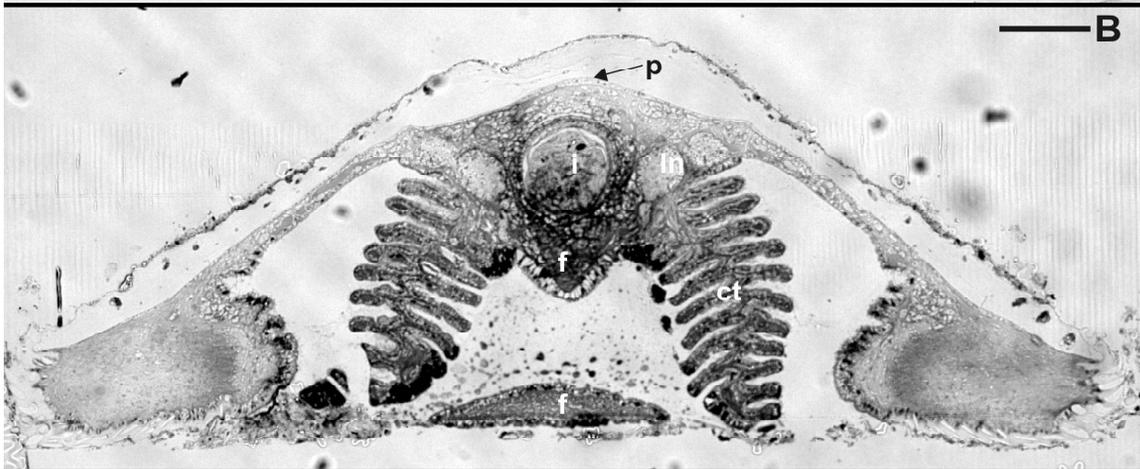
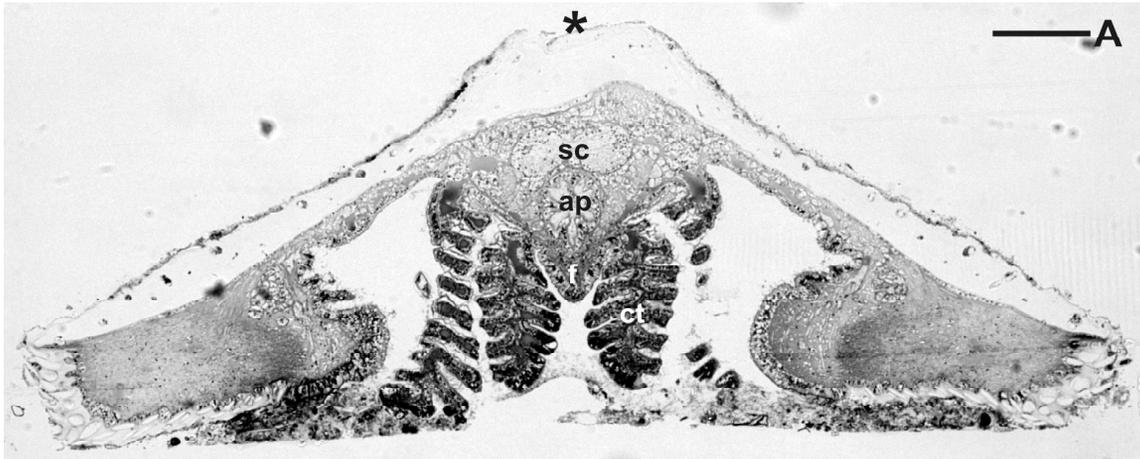
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FIG. 1. *Leptochiton rugatus* (Carpenter in Pilsbry, 1892) (ZSM Mol 20140440) serially sectioned at a thickness of 1.5  $\mu\text{m}$  and stained using Richardson's solution, showing various regions of the postmucronal area. **A.** Region of posterior most part of mantle cavity (behind last ctenidia); **B.** Region of last ctenidia; **C.** Region of anus papilla; **D.** Region of suprarectal commissure. **B-D** show a remarkable size increase of the mucro (marked by asterisk). All scales 200  $\mu\text{m}$ .

*a* – anus, *af* – afferent branchial sinus, *ap* – anus papilla, *ct* – ctenidium, *ef* – efferent branchial sinus, *pmc* – posterior wall of mantle cavity, *sc* – suprarectal commissure.

РИС. 1. *Leptochiton rugatus* (Carpenter in Pilsbry, 1892) (ZSM Mol 20140440), серийные срезы толщиной 1.5 мкм, окрашенные раствором Ричардсона, показывающие различные участки постмукрональной зоны; **A.** Участок самой задней части мантийной полости (позади последнего ктенидия); **B.** Участок последнего ктенидия; **C.** Участок анальной папиллы; **D.** Участок супраректальной коммисуры; **B-D** демонстрируют значительное увеличение размеров мукро (отмечено звездочкой). Масштаб 200  $\mu\text{m}$ .

*a* – анус, *af* – афферентный жаберный синус, *ap* – анальная папилла, *ct* – ктенидий, *ef* – эфферентный жаберный синус, *pmc* – задняя стенка мантийной полости, *sc* – супраректальная коммисура.



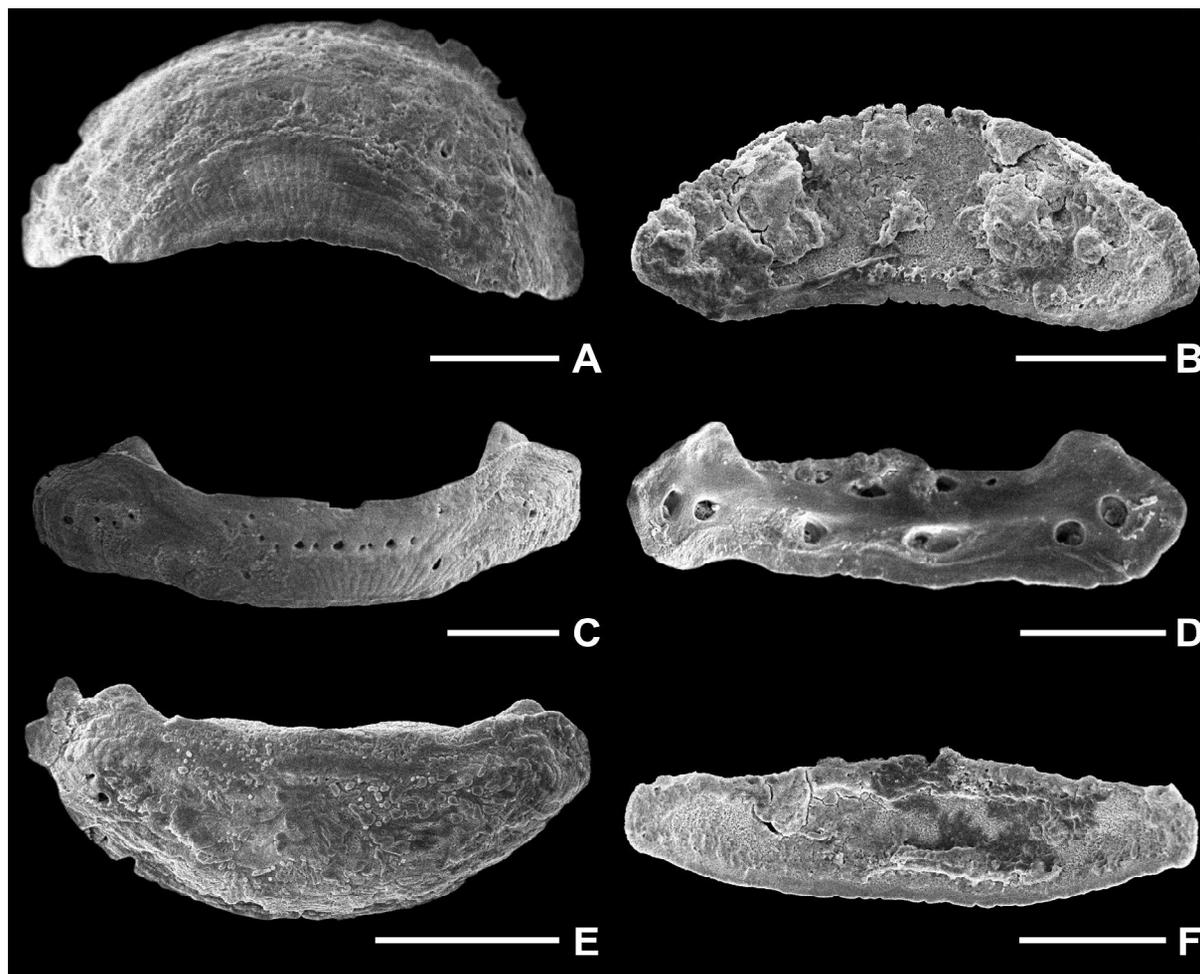


FIG. 3. *Radsia nigrovirescens* (de Blainville, 1825) (ZSM Mol 20050849): SEM illustrations of isolated valves of two randomly selected juveniles from the brood, left column dorsal views, right column ventral views. A–B. Head valves. C–D. Unspecific intermediate valves. E–F. Tail valves. All scales 100  $\mu$ m.

РИС. 3. *Radsia nigrovirescens* (de Blainville, 1825) (ZSM Mol 20050849): скановые фотографии изолированных щитков двух случайно выбранных ювенильных особей из вынашиваемых в жаберной борозде; левая колонка – дорсальный вид, правая колонка – вентральный вид. A–B. Головные щитки; C–D. Произвольно выбранные промежуточные щитки; E–F. Хвостовые щитки. Масштаб 100  $\mu$ m.

## Discussion

Three polyplacophoran species belonging to different families were chosen to demonstrate that the tail valve as whole includes two independent areas,

which are delimited by the mucro. In traditional systematics these parts are named antemucronal and postmucronal area in relation to the anterior-posterior orientation in reference to the mucro, that is why Starobogatov and Sirenko [1975] additional-

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FIG. 2. *Leptochiton rugatus* (Carpenter in Pilsbry, 1892) (ZSM Mol 20140440) serially sectioned at a thickness of 1.5  $\mu$ m and stained using Richardson's solution, showing various regions of the antemucronal area.: A. Region of anterior most part of mucro (marked by asterisk), suprarectal commissure divides to lateral nerve cords. B. Hindmost region of antemucronal area, pericardium appears. C. Region of auricle. D. Posterior region of ventricle. All scales 200  $\mu$ m.

*af* – afferent branchial sinus, *ap* – anus papilla, *au* – auricle, *ct* – ctenidium, *ef* – efferent branchial sinus, *f* – foot, *i* – intestine, *ln* – lateral nerve cord, *p* – pericardium, *sc* – suprarectal commissure, *v* – ventricle.

РИС. 2. *Leptochiton rugatus* (Carpenter in Pilsbry, 1892) (ZSM Mol 20140440) серийные срезы толщиной 1.5 мкм, окрашенные раствором Ричардсона, показывающие различные участки антеромукрональной зоны; A. Участок самой передней части мукро полости (отмечен звездочкой), супраректальная коммисура разделяется на латеральные нервные стволы; B. Самый отдаленный участок антеромукрональной зоны, появляется перикардий; C. Район предсердия; D. Задний участок желудочка. Масштаб 200  $\mu$ m.

*af* – афферентный жаберный синус, *ap* – анальная папилла, *au* – предсердие, *ct* – ктенидий, *ef* – эфферентный жаберный синус, *f* – нога, *i* – интестина, *ln* – латеральный нервный ствол, *p* – перикард, *sc* – супраректальная коммисура, *v* – желудочек.

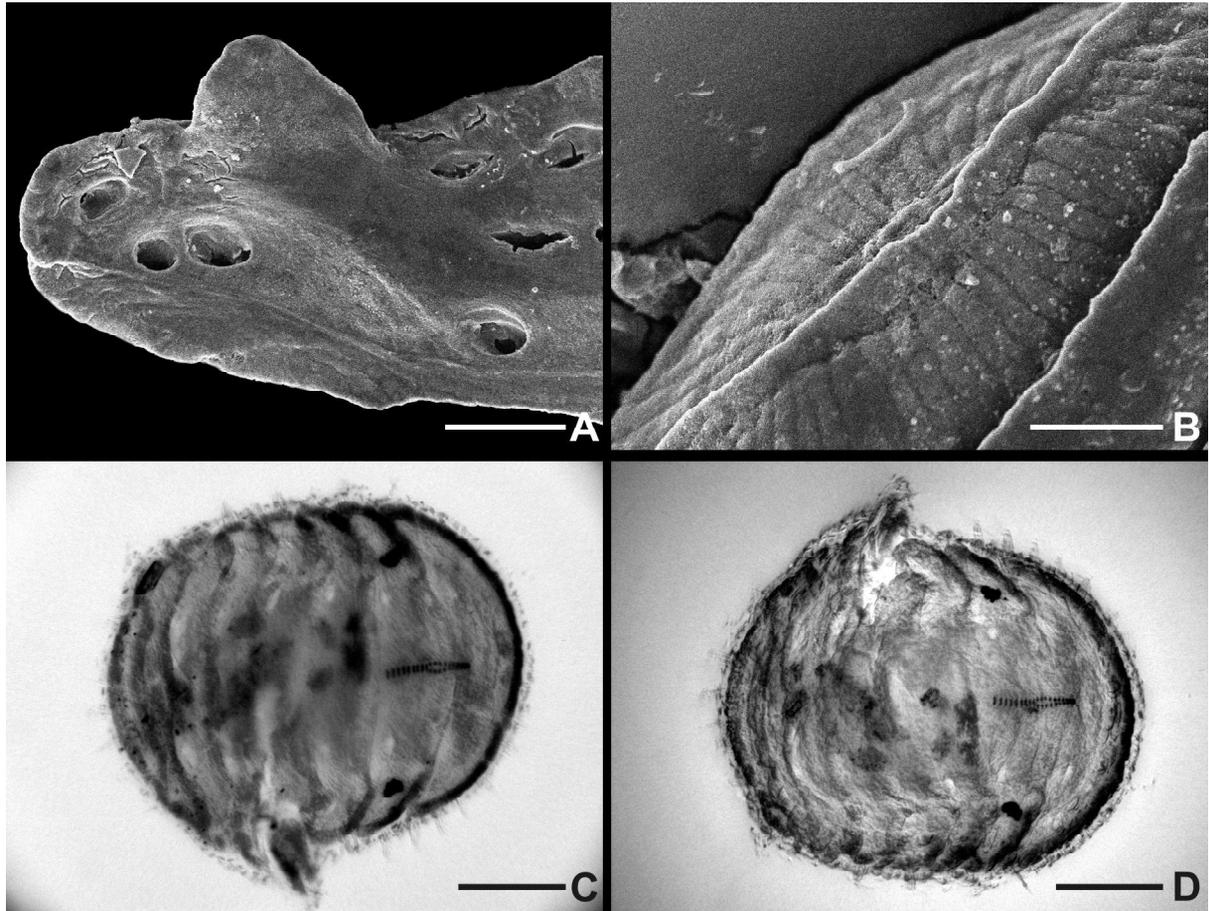


FIG. 4. *Radsia nigrovirescens* (de Blainville, 1825) (ZSM Mol 20050849): images of three randomly selected juveniles from the brood. **A.** SEM illustration of the ventral view of an intermediate valve to show the occurrence of the apophysal plate prior to insertion plate. **B.** *In situ* dorsal view of the last three valves. **C.** Whole juvenile in dorsal view. **D.** Whole juvenile in ventral view. Scale bars: A 50  $\mu\text{m}$ , B 30  $\mu\text{m}$ , C–D 100  $\mu\text{m}$ .

РИС. 4. *Radsia nigrovirescens* (de Blainville, 1825) (ZSM Mol 20050849): изображения трех случайно выбранных ювенильных особей из жаберной борозды; **A.** Сканирующая фотография вентральной стороны промежуточного щитка показывающая появление апофиз раньше образования инсерционной пластинки; **B.** Вид с дорсальной стороны трех последних щитков *in situ*; **C.** Целая ювенильная особь, вид с дорсальной стороны; **D.** Целая ювенильная особь, вид с вентральной стороны. Масштабы: A 50  $\mu\text{m}$ , B 30  $\mu\text{m}$ , C–D 100  $\mu\text{m}$ .

ly introduced the term “semiplate” to delimitate morphological the postmucronal area (their “VII-Ib”) [see also Sirenko, Starobogatov, 1977]. The traditionally still valid [e.g. Schwabe, 2010] naming makes sense in a comparative description of this particular valve only. Morphological, functional and ontogenetic the combination of both zones, however, may lead to misinterpretations. For example, generally it is considered that the “tail valve” occurs latest in ontogeny, definitively appearing at the earliest at a point after larval settlement [e.g. summary in Strathmann, Eernisse, 1987]. That is simple an overstatement if we take into account the limited studies of embryogenesis in chitons in general and the available information on tail plate formation in particular [e.g., Sirenko, 1986]. The peculiarities of the tail valve examined here from metamorphosed young of the brooding species *Radsia nigrovires-*

*cens* indicate that such statement may refer to the so called postmucronal area only, as the antemucronal area starts to grow with some delay [see also O’Neill, 1984]. Hull and Risbec [1930: 286] probably observed a similar trend in the larvae of *Ischnochiton acomphus* Hull et Risbec, 1930, as they stated: “Behind the furrow six faint lines indicate the divisions between the valves in formation. The rear-most of these lines seems to correspond to the posterior part of the last valve.” There is some evidence that the growth and enlargement of the antemucronal area is closely related to the development of the cardiac complex as it also starts to shape after larval settlement [Hammarsten, Runnström, 1926] and terminates under the mucro (e.g. Pelseneer, [1898]; herein for *Leptochiton rugatus*). The skeletogenesis was studied by various authors [e.g. Lovén, 1855; Kowalevsky, 1883; Heath,

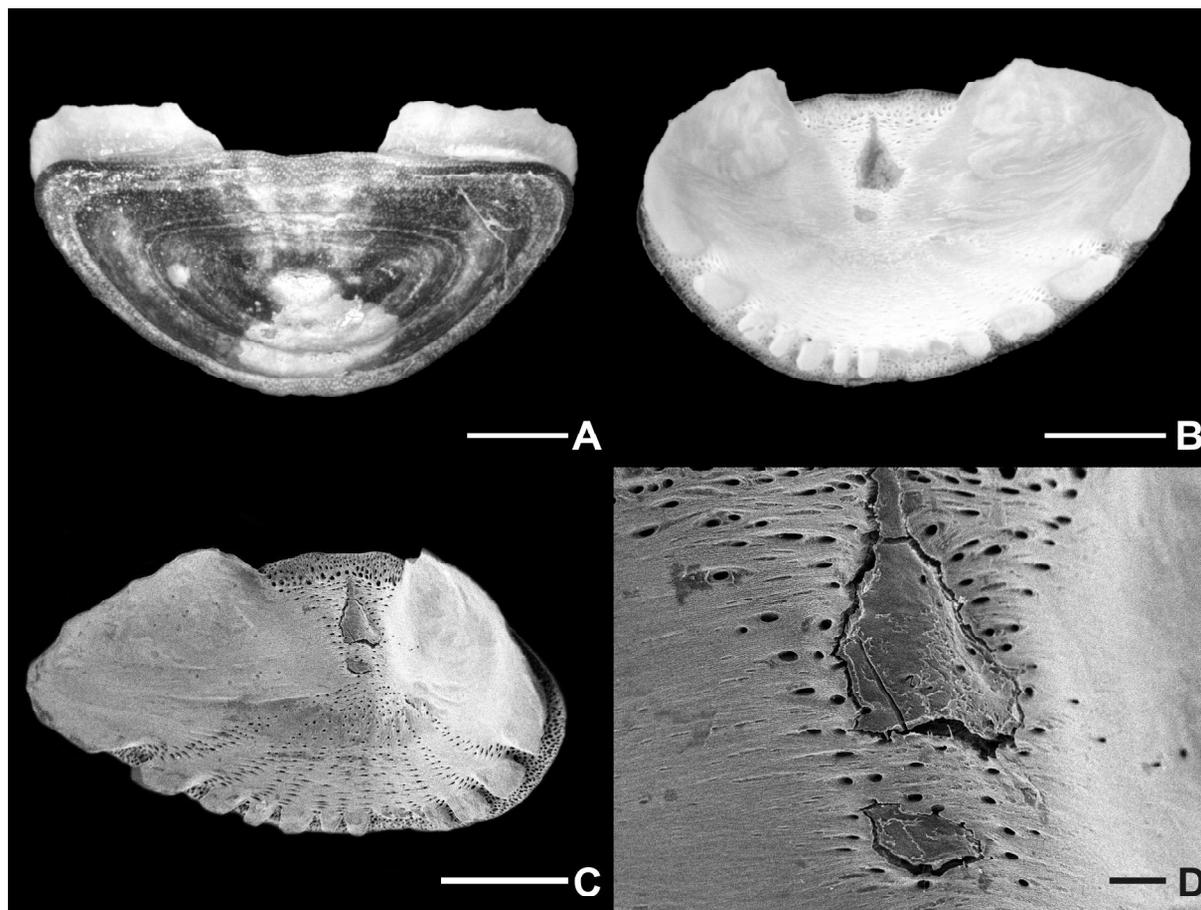


FIG. 5. *Schizoplax brandtii* (von Middendorff, 1847) (ZSM Mol 20080124): light microscopically images (A–B) and SEM images (C–D) of tail valve. **A.** Dorsal view. **B–C.** Ventral views. **D.** Detail of the ventral ligament region. Scale bars: A–C 1000  $\mu\text{m}$ , D 100  $\mu\text{m}$ .

РИС. 5. *Schizoplax brandtii* (von Middendorff, 1847) (ZSM Mol 20080124): фотографии хвостового щитка на световом (A–B) и сканирующем (C–D) микроскопе; **A.** Вид с дорсальной стороны; **B–C.** Вид с вентральной стороны; **D.** Деталь района вентрального лигамента. Масштабы: A–C 1000  $\mu\text{m}$ , D 100  $\mu\text{m}$ .

1899; Hammarsten, Runnström, 1926; Hull, Risbec, 1930; Grave, 1932; Okuda, 1947; Christiansen, 1954; Kussakin, 1960; Watanabe, Cox, 1975; Haas *et al.*, 1979; Kniprath, 1980; Sirenko, Kashenko, 1990; Sirenko, 1991; Minichev *et al.*, 1996; Lord, 2011] but detailed studies on the development of the posteriormost valve is lacking although several authors examined growth series until the final metamorphosis (e.g., older records summarized in Sirenko, 1986: table 1). Minichev *et al.* [1996] stated that the terminal valves are built as unit, while the intermediate valves are formed by coalescence of mineralized centres. Such coalescence agrees with observations of some earlier researchers, but was declined by Kniprath [1980]. Thus, detailed investigation of the definitive development of the tail valve in particular is in need, especially covering a broader range of taxa. Interesting in this content could be the region of the posterior valve's underlying cell structure, which according to the figures of Kowalevsky [1883: fig. 71] and Kniprath

[1980: fig. 3a] differs from those of the intermediate valves [see also Jacobs *et al.*, 2000, fig. 3B]. The above mentioned is not new, but was obviously overlooked or ignored in last decades. Starobogatov and Sirenko [1975] mentioned that the semiplate evolved “as in ontogenesis” later (after the occurrence of *Scanochiton* Bergenhayn, 1943, which falls in the Cretaceous, see Sirenko [2006]). The authors relate the development of the semiplate with the appearance of the articulamentum, which however is known since the Silurian (see above). Or do they especially refer to the insertion plates? These structures would indeed lie below their semiplate, but for example the Permian *Ochmazochiton* Hoare et Smith, 1984 already show such structures. Additionally, even older paleoloricate (defined by the absence of an articulamentum!) polyplacophorans (e.g. *Aulochiton sanmerae* Pojeta, Vendrasco et Darrough, 2010) show tail valves that comprise of mucro delimited zones as in traditionally senses.

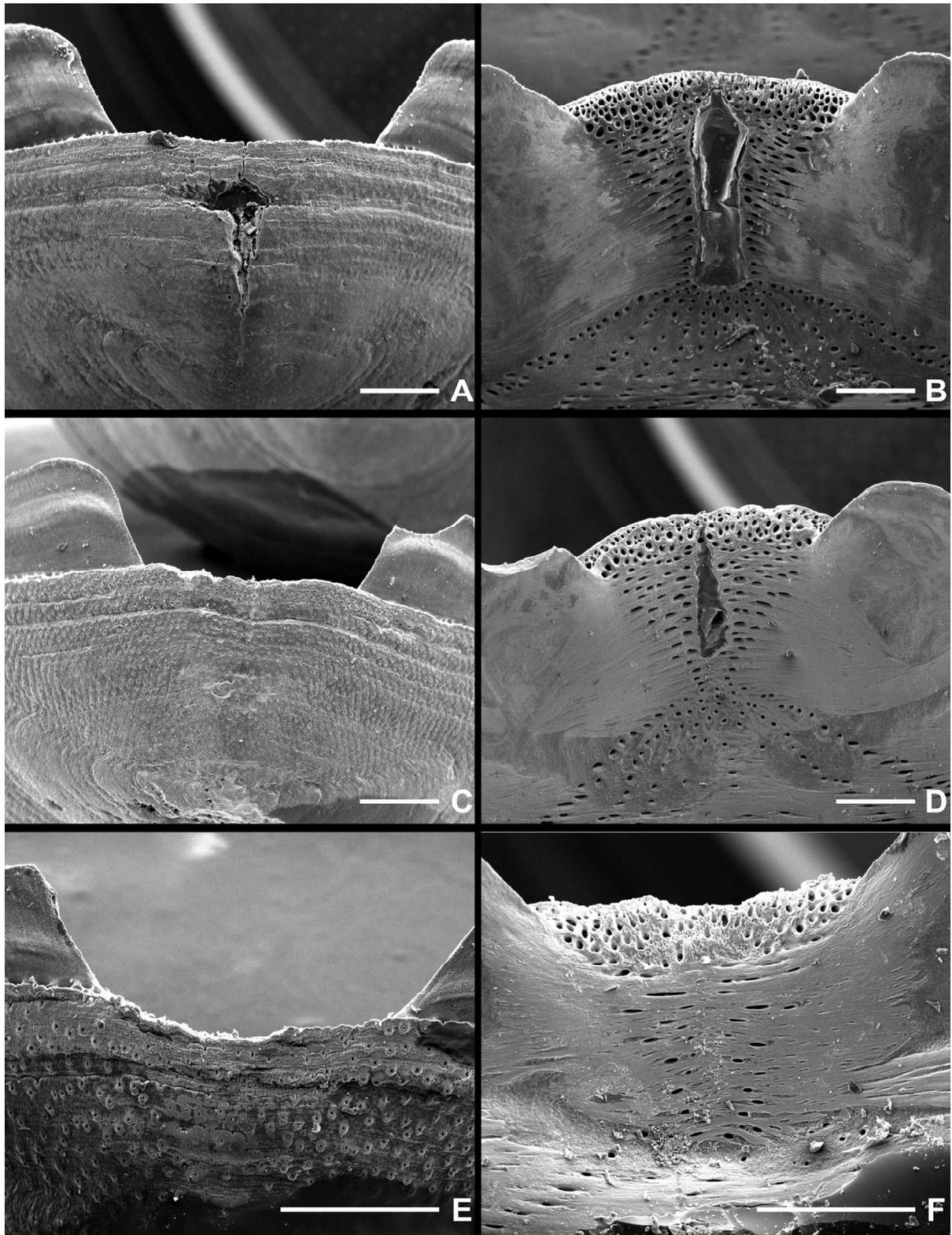


FIG. 6. *Schizoplax brandtii* (von Middendorff, 1847) (ZISP): antemucronal aspects of tail valves of three specimens of varying sizes [A–B, Sb 22; C–D, Sb 18; E–F, Sb 13]. Left column dorsal views, right columns ventral views to highlight the different degrees of ligament building. All scales 500  $\mu\text{m}$ .

РИС. 6. *Schizoplax brandtii* (von Middendorff, 1847) (ZISP): антеромукрональная область хвостовых щитков трех экземпляров различного размера [A–B, Sb 22; C–D, Sb 18; E–F, Sb 13]. Левая колонка – вид с дорсальной стороны, правая – вид с вентральной стороны, чтобы подчеркнуть различную степень роста лигамента. Масштаб 500  $\mu\text{m}$ .

The investigation of regional growth in the antemucronal region of the tail valve of *Schizoplax brandtii* further shows a general agreement of topology with central parts of the intermediate valves, but also functionally with the delayed development of a ligament-like filling in a length axis slitting, which does not occur in the head valve and the postmucronal area of the species. Thus, the anlagen of the antemucronal area seem to be identical with those of the central portions of the intermediate valves.

From the brief investigation here and available literature data (see Tab. 1), it appears attractive considering the antemucronal area as independent from the head valve – like usually semicircular postmucronal area but unfortunately both are merged to a unity which is called “tail valve”. With using the latter, we have the risk that older references of this term might regard to one of the independent zones only (e.g. in ontogenesis for the postmucronal area). If this proportion for independency of the valve areas withstands further researches, it has some phylogenetic consequences (e.g., supporting the origin from a diplacophoran ancestor as discussed by Parkhaev [2017]). The antemucronal area is obviously a crop-upped intermediate valve (more precise, the central area), necessarily developed to cover a delayed enhanced cardiac complex. But what is the mucro? According to Thiele [1893] it is the oldest part of the tail valve, as from here the articulamentum increases in thickness. Taken the above mentioned into account, the mucro seemingly belongs to the postmucronal area. Schwabe [2010, figs 10-11] illustrated several tail valves and pointed to the mucro. According to these images, it is morphologically evident that the mucro is not only the delimitation point between the two independent zones, but also often lays slightly above the antemucronal area. It thus corresponds to the apical region of the head valve and intermediate valves (as indicated above, the present author also does not consider the intermediate plate as a unity – the interpretation of an apical region here refers only to its position, not on its origin!), with the exception that is anteriorly located in the postmucronal area. This interpretation gets further support from aesthete channel distribution, which shows the same pattern in the three regions (compare Baxter and Jones [1981: fig. 4]). Generally, the apical region shows a trend of ventral folding of tegmentum. As this downward folding is blocked by the presence of a further piece of valve, it is likely that this structure contributes to the growing of tegmentum in the new valve part and hence enabling coalescence between these regions. In how far the articulamentum is involved by this process is unknown and needs to be studied under the aspect of current consideration. This is even more necessary as tradi-

tionally studies on polyplacophoran valve structures [e.g. Bergenhayn, 1930; Haas, 1972] hardly comment on tail valve’s fine structure, and if so, do not differentiate between the above mentioned valve zones. Haas [1972: 12] even stated that the conditions for the articulamentum found in the end valves may readily deduced from conditions found in the intermediate valves.

Taken Simroth’s aforementioned statement into account, there is a morphological support. But again, it is here postulated that the lateral areas should be excluded from his interpretation. To get a better understanding of the distinct valve regions it is summarized here, what characterises them (see Table 1).

Of the eighteen characters compiled in their relation to the valves (Table 1) eleven (61%) demonstrate a clear analogy between the antemucronal area and the central area. This is slightly higher as the ten analogies that undoubtedly occur between the head valve, lateral areas and postmucronal area. Noteworthy, except for a general heterochrony in ontogenesis, there is practically no character accordance between the antemucronal area and the postmucronal area! However, the table also shows how unprecise our knowledge is, if we refer to “intermediate” and “tail” valves, only. Future researche(r)s, especially covering ontogenetic studies, should be thus more clearly relate to the particular zonation of individual valves.

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Table 1: The valve groups, their zonation and characters related to them.

Табл. 1. Группы щитков, их зональность и присущие им признаки.

Characters (if developed)	Head valve	Intermediate valve		Tail valve	
		lateral area	central area	antemucronal area	postmucronal area
Main sculpture orientation	radial	radial	longitudinal	longitudinal	radial
Valve layering <sup>1</sup>	less complex	complex		less complex	
Apical region	+	-	+	- <sup>2</sup>	+ <sup>2</sup>
Jugal area	-	-	+	+	-
Lateral area	-	-	+	-	? <sup>3</sup>
Apophyses	-	-	+	+	-
Insertion plates	+	+	-	-	+
Jugal plate	-	-	+	+	-
Longitudinal splitting <sup>4</sup>	-	-	+	+	-
Main aesthete orientation <sup>5</sup>	radial	radial	±longitudinal	±longitudinal	radial
Musculus obliquus d. <sup>6</sup>	-	-	attached	attached	-
Musculus rectus d. <sup>6</sup>	attached	-	attached	attached	-
Musculus transversus <sup>6</sup>	-	-	+	+	-
Musculus longitudinales laterales <sup>6</sup>	+	±	+	+	-
Shell field cell layer <sup>7</sup>	thicker	thin		no data, but relevant region thicker	
Skeletogenesis <sup>8</sup>		prior settlement		after settlement	
Myogenesis of shell plate muscles <sup>9</sup>		prior settlement		after settlement	
Neurogenesis <sup>10</sup> (“aesthete holes”)	+	from available images mainly in central area		no data, images do not show such pores	

<sup>1</sup> data according to Carter and Hall [1990] and Peebles *et al.*, [2017]; <sup>2</sup> unknown, current author’s interpretation; <sup>3</sup> here referred to the diagonal ridge, in accordance to point 2; <sup>4</sup> present study on *Schizoplax brandtii*; <sup>5</sup> own observations, von Knorre [1925], Vinther [2006], Fernandez *et al.*, [2007], Vendrasco *et al.*, [2008]; <sup>6</sup> data according to Sampson [1895], Henrici [1912], Wingstrand [1985]; <sup>7</sup> according to illustrations in: Kowalevsky [1883], Kniprath [1980], Jacobs *et al.*, [2000]; <sup>8</sup> here refers to the best studied reproduction type (trochophore larvae), limited by the fact that the trigger moments for finalization of metamorphoses (e.g. larval settlement) is unknown in brooding species. <sup>9</sup> according to Wanninger and Haszprunar [2002], Scherholz *et al.*, [2013]. <sup>10</sup> available data refer more or less to the central nervous system [e.g. Hammarsten and Runnström, 1926; Friedrich *et al.*, 2002; Voronezhskaya *et al.*, 2002] and demonstrated an irrespective neuronal development from the skeletogenesis, the caudal plexus of the pedal cords develops however after the larval settlement. Shell related sensory structures (aesthetes) are insufficient studied in early development, apart from the so called “aesthete holes” [e.g. Haas *et al.*, 1979]. Interestingly, the diameter of this structure in Haas *et al.*, [1979] is (calculated from their figure) ca. 17.5 µm and thus nearly double the size Baxter and Jones [1981] examined in adults of the same species. Moreover, Hammarsten and Runnström [1926] demonstrated that early aesthetes are more frequent, but may decrease during the development of the articulamentum. So whatever these holes are [positionally they could also be influenced by muscle development], data on them (skeletogenesis references cited earlier), is treated here with caution as neuronal structure (compare also Sirenko and Kashenko, [1990: figs: 4 A-B] versus Voronezhskaya *et al.*, [2002: fig. 4F]).

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