

Structure of the arm-spine articulation ridges as a basis for taxonomy of Ophiuroidea (a preliminary report)

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ABSTRACT: In the present study taxonomical and in a lesser degree phylogenetic significance of the structure of articulation ridges are investigated. Fourteen families of the traditional order Ophiurida and three families of the traditional order Euryalida, about 70 genera (about 27% of all ophiuroid generic diversity) in all, are studied with use of SEM. It was discovered that structure of articulation ridges is conservative character and that almost each family (or group of genera) has a unique shape of the ridges. A classification of articulation ridges is suggested.

1 INTRODUCTION

Currently ophiuroid taxonomy is based mostly on a combination of external characters like disk structure, oral papillae, peculiarities of arms etc (Fell, 1960). Various attempts to use new characters, e.g. shape of vertebral ossicles, genital shield and radial shield articulation, jaws morphology and tooth plate (Lyman, 1882; Matsumoto 1915, 1917; Murakami, 1963; Irimura, 1988; Smith et al., 1995; Litvinova, 1989a,b, 1996) almost have not affected taxonomy of family level. Despite this, LeClair (1996) considered vertebrae as family conservative feature and Irimura & Fujita (2003) described some new features of vertebrae restricted to particular taxa. At the same time, not rarely, ophiuroid genera are transferred between distantly related families – for instance, genus *Amphilimna* Verrill, 1899 from Amphiuroidae to Ophiacanthidae and even to Ophiuridae (Thomas, 1967; Liao, 1983), whereas genus *Ophiambix* was placed in different times in three different family (Paterson & Baker, 1988). Prima facie well-defined families like Ophiacanthidae are considered as paraphyletic groups. These facts require rethinking of traditional characters and involving of new ones both for ophiuroid taxonomy and phylogeny. A certain crisis of taxonomy of ophiures was noted by Paterson & Baker (1988), Smith et al. (1995), Dearborn et al., (1996), Hottenrott (1998) and others. At the same time in paleontological studies (Hess, 1962 and following papers; Jagt & Kutscher, 1998; Jagt, 2000) shape of dissociated plates of ophiures was used, including lateral plates and arm spine articulation ridges, for identification of some taxa. On recent material conservatism of the articulation ridges shape within family Ophiacanthidae for the first time was showed by Paterson (1985). Morphology of the ridges in the family Ophiocomidae was used by Devaney (1970), in the family Ophiomyxidae by Byrne & Hendler (1988), in the genus *Ophiosparte* Koehler, 1922 by Dearborn et al. (1996), in the genus

Astrophiuira Sladen, 1878 by Fujita & Hendler (2001), in the families Amphiuroidae and Ophiactidae by Stöhr (2003) and Stöhr & Segonzac (2005) and in the family Ophiacanthidae by O'Hara & Stöhr (2006). General morphology of the ridges was described by Stauber & Märkel (1988) and Byrne (1994). Thus, this character may be a potentially promising feature for all the ophiuroid taxa.

Despite this until now shape of articulation ridges is considered for description only of particular taxa and is not valid character for ophiuroid taxonomy.

2 MATERIAL AND METHODS

Articulation ridges of ophiuroid specimens from Institute of Oceanology RAS, Moscow and Zoological Museum of Moscow University were studied using SEM after bleaching of the lateral arm plates. From each family several genera, preferably distantly related, are chosen.

3 DESCRIPTION OF ARTICILATION RIDGES

A following classification of articulation ridges is suggested. Gorgonocephalidae (Plate 1, Figures 1–4) and Asteronychidae: a slit-shaped or round large muscle opening with low border. At the basis of the border there is a small simple nerve opening. There are separate tubercles each with a single opening for hook (if any). Ophiuridae (Plate 1, Figures 5–9): an irregularly round large muscle opening on elevation and a nerve opening at the basis of this knob, placed on the miter in relation to the nerve opening. Sometimes, especially in small species, one of the openings is undistinguished. Ophioleucidae (Plate 1, Figures 10–14): an irregularly rhombic, with high borders ridges, bounded large opening for muscle, extended in dorsoventral direction. A small nerve opening is situated ventrally from the ridges. Ophiomyxidae

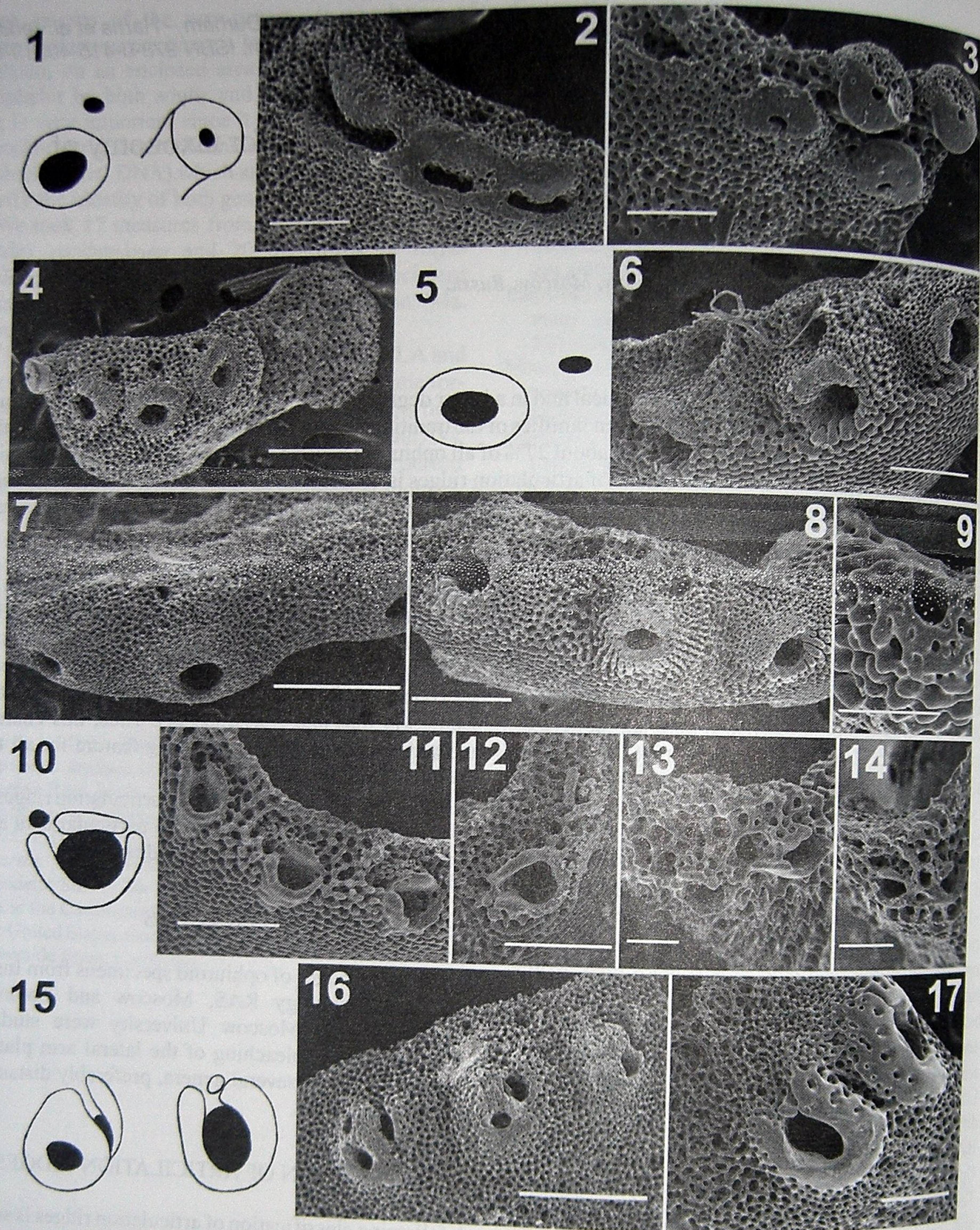


Plate 1. SEM of arm spine articulation ridges. 1. Scheme of articulation ridges for Euryalida. 2-3. *Gorgonocephalus eucnemis* (Müller et Troschel, 1842). 2. Proximal segments. 3. Middle segments. 4. *Astrotoma agassizii* Lyman, 1875. 5. Scheme for Ophiuridae. 6. *Ophiura sarsii* Lütken, 1855. 7. *Ophiosparte gigas* Koehler, 1922. 8. *Ophionotus victoriae* Bell, 1902. 9. *Ophiomisidium irene* Fell, 1952. 10. Scheme for Ophioleucidae. 11. *Ophiopallas paradoxa* Koehler, 1904. 12. *Ophioleuce brevispina* (H.L. Clark, 1911). 13. *Bathylepta pacifica* Belyaev et Litvinova, 1972. 14. *Uriopha ios* Paterson, 1980. 15. Scheme for Ophiomyxidae. 16. *Ophiomyxa brevirima* H.L. Clark, 1915. 17. *Ophioscolex glacialis* Müller et Troschel, 1842. Scale bars: 2-200 μm ; 3-120 μm ; 4-300 μm ; 6-300 μm ; 7-600 μm ; 8-400 μm ; 9-80 μm ; 11-120 μm ; 12-150 μm ; 13-40 μm ; 14-60 μm ; 16-300 μm ; 17-200 μm .

(Plate 1, Figures 15-17): two main types can be distinguished. First, with a chelate, asymmetrically elevated knob with two nearly equal openings in genus *Ophiomyxa*. Second, with a single opening, sometimes horseshoe-shaped with a broad low border (e.g. in genus *Ophioscolex* Müller et Troschel, 1842 s.str.).

In *Ophiomyxa* Müller et Troschel, 1842 there are the same ridges on the distal lateral plates. Ophiacanthidae (Plate 2, Figures 1-5): volute-shaped ridges with large muscle opening and a small slit-shaped nerve opening. The ridges are proximally closed or semi-closed. On distal plates ridges may become

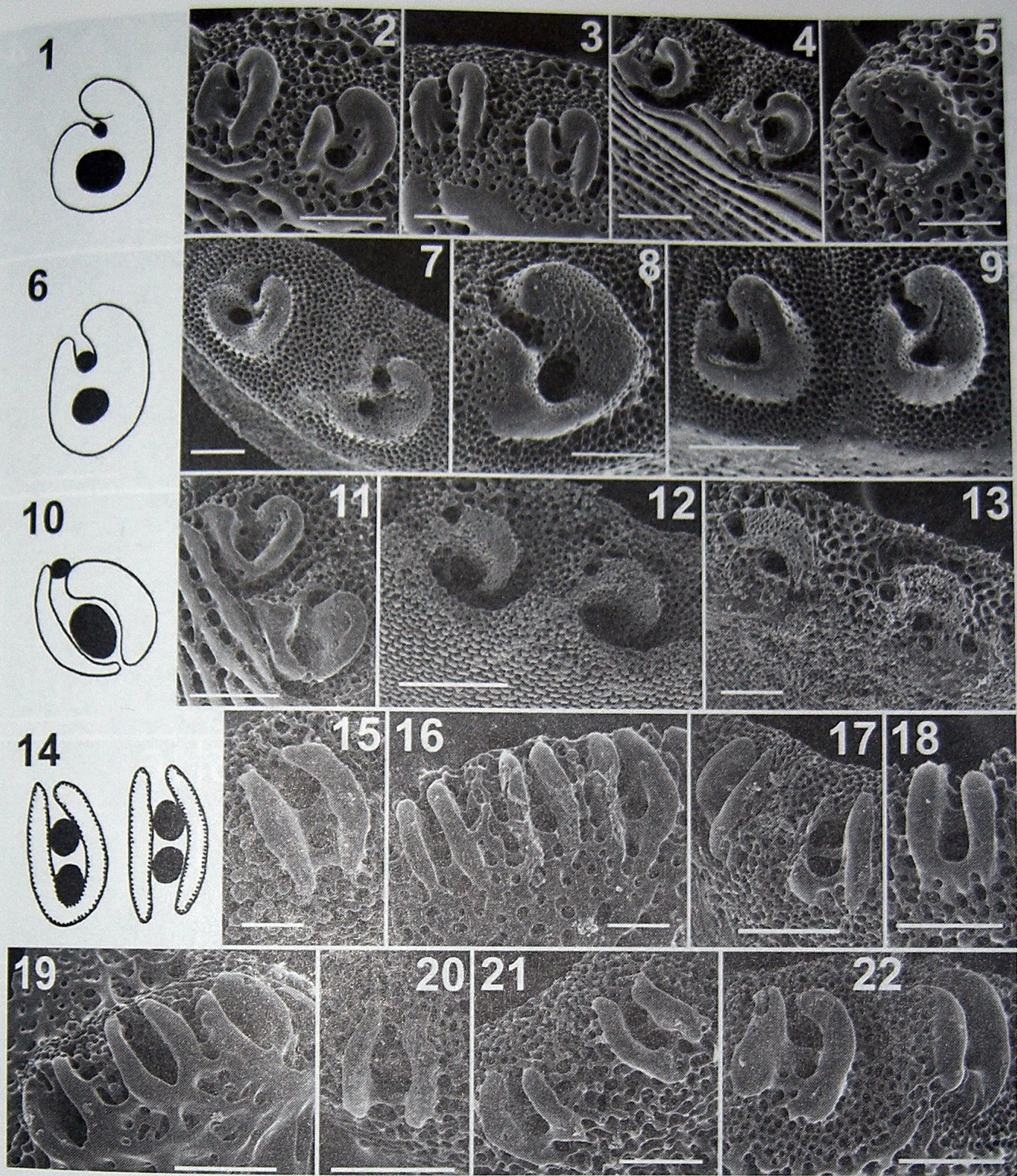


Plate 2. SEM of arm spine articulation ridges. 1. Scheme of articulation ridges for Ophiacanthidae. 2. *Ophiacantha pentagona* Koehler, 1897. 3. *Ophiochondrus convolutus* Lyman, 1869. 4. *Ophiolimna bairdi* (Lyman, 1883). 5. *Ophiosemones* sp. 6. Scheme for Ophiocomidae. 7. *Ophiocoma erinacea* Müller et Troschel, 1842. 8. *Ophiocoma pica* Müller et Troschel, 1842. 9. *Ophiomastix caryophyllata* Lütken, 1869. 10. Scheme for Ophiodermatidae. 11. *Ophioconis forbesi* (Heller, 1863). 12. *Pectinura maculata* (Verrill, 1869). 13. *Ophioderma* sp. 14. Scheme for Amphiuridae and Ophiactidae. 15. *Amphiodia craterodmeta* H.L. Clark, 1911. 16. *Amphilimna multispina* Koehler, 1922. 17. *Amphiura carchara* H.L. Clark, 1911. 18. *Amphilimna olivacea* (Lyman, 1869). 19. *Ophiotholia montana* Litvinova, 1981. 20. "*Ophiothamnus*" *acantophorus* (H.L. Clark, 1911). 21. *Ophiopus arcticus* Ljungman, 1867. 22. *Ophiactis abyssicola* (M. Sars, 1861). Scale bars: 2–120 μm ; 3–100 μm ; 4–150 μm ; 5–80 μm ; 7–200 μm ; 8–150 μm ; 9–300 μm ; 11–100 μm ; 12–300 μm ; 13–100 μm ; 15–60 μm ; 16–40 μm ; 17–120 μm ; 18–100 μm ; 19–100 μm ; 20–100 μm ; 21–100 μm ; 22–150 μm .

more parallel but always retain volutes. Ophiocomidae (Plate 2, Figures 6–9): strong, volute-shaped, always proximally closed ridges with a slightly immersed to the lateral plate, and two openings nearly equal in size. Ophiodermatidae (Plate 2, Figures 10–13): ridges with one large bending lobe and small second, often considerably reduced. There are two openings

nearly equal in size. The ridges often are considerably immersed to the lateral plate. Ophiactidae and Amphiuridae (Plate 2, Figures 14–22): nearly parallel, quite often slightly bending (especially in Ophiactidae) high ridges, extended in proximal-distal direction, bounding two openings nearly equal in size (sometimes one large opening due to reduction of the septa). The

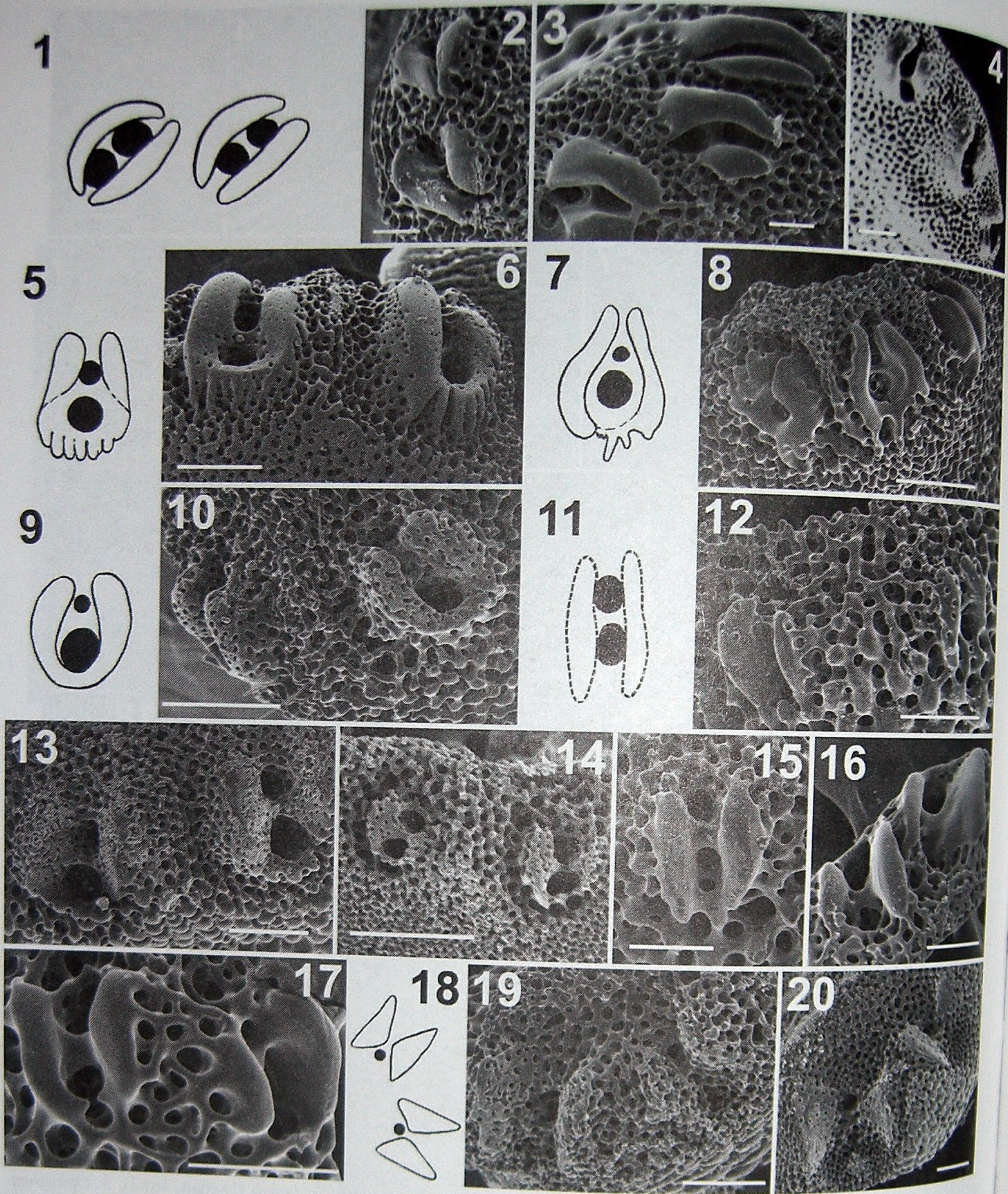


Plate 3. SEM of arm spine articulation ridges. 1. Scheme of articulation ridges for Ophiothricidae. 2. *Ophiopsammium rugosum* Koehler, 1905. 3. *Ophiopteron elegans* Ludwig, 1888. 4. *Gymnolophus obscura* (Ljungman, 1867). 5. Scheme for Ophionereidae. 6. *Ophionereis schayeri* (Müller et Troschel, 1844). 7. Scheme for Amphilepididae. 8. *Amphilepis* sp. 9. Scheme for Ophiochitonidae. 10. *Ophiochiton ternispinus* Lyman, 1883. 11. Scheme for Ophiolepididae. 12. *Ophiozonella alba* (Lütken et Mortensen, 1899). 13. *Ophioplocus imbricatus* (Müller et Troschel, 1842). 14. *Ophiolepis elegans* Lütken, 1859. 15. *Ophiopenia tetracantha* H.L. Clark, 1911. 16. *Ophiambix aculeatus* Lyman, 1880. 17. *Abyssura brevibrachia* Belyaev et Litvinova, 1976. 18. Scheme for Hemieuryalidae. 19. *Hemieuryale pustulata* Martens, 1867. 20. *Sigsbeia murrhina* Lyman, 1878. Scale bars: 2–40 μm ; 3–40 μm ; 4–30 μm ; 6–150 μm ; 8–120 μm ; 10–150 μm ; 12–150 μm ; 13–150 μm ; 14–150 μm ; 15–100 μm ; 16–60 μm ; 17–100 μm ; 19–120 μm ; 20–150 μm .

ridges are opened from both sides or closed proximally. Ophiothricidae (Plate 3, Figures 1–4): nearly parallel slightly bending ridges with a low round border, extended in ventro-dorsal direction, bounding opening nearly equal in size. The ridges are opened from both sides. Amphilepididae (Plate 3, Figures 7–8): from

semi-parallel to semi-round ridges, proximally semi-closed with irregular ribs. Ophionereidae (Plate 3, Figures 5–6): horseshoe-shaped, proximally closed ridges, with a saddle-shaped area, which is bounded with a regular ribbed border, a little bit immersed to the lateral plate. There are two openings nearly

equal in size. Ophiochitonidae (Plate 3, Figures 9–10): horseshoe-shaped, not large ridges, closed proximally, without a ribbed border. Muscle opening is a little bit larger than nerve one. Ophiolepididae (Plate 3, Figures 11–17): small, in different degree of reduction, parallel or subparallel ridges opened from both sides, bounding two openings nearly equal in size. The ridges are considerably immersed to the lateral plate in the genus *Ophiolepis* Müller et Troschel, 1842. Hemieuryalidae (s.str.) (Plate 3, Figures 18–20): two parallel ridges placed on the miter to each other, with a single small opening. Inside surfaces of the ridges bear triangle scars – sites of contact with the spine base.

4 ARTICULATION RIDGES AND OPHIUROID TAXONOMY

4.1 General conclusions and some proposed taxonomical changes

Applying of this new character to the ophiuroid systematic confirmed a taxonomical stability of most traditional ophiuroid families. I.e. there is correlation between shape of articulation ridges and other external ophiuroid characters. For instance, within families Ophiuridae not found volute-shaped articulation ridges, within Ophiocomidae not found subparallel ridges and within Ophiacanthidae – there are no simple ridges with elevated muscle opening. At the same time placement of several groups of genera within families e.g. Ophiacanthidae, Hemieuryalidae, Ophiuridae and others are strongly contradictory and inconsistent not only with the present analysis of the shape of articulation ridges but also with the other traditional external characters.

Based on this, at least the following changes to the ophiuroid taxonomy are suggested. The genera *Bathylepta* Belyaev et Litvinova, 1972 and *Uriopha* Paterson, 1980 should be placed in the family Ophioleucidae rather than Ophiuridae. In the family Hemieuryalidae should be retained only taxa, which are close to the type genus, whereas at least genera *Ophiochondrus* Lyman, 1869 and *Ophiomoeris* Koehler, 1904 should be transferred to Ophiacanthidae. Genus *Ophiothamnus* Lyman, 1869 and closely related new genus, based on the species “*Ophiomitra*” *acontophora* H.L. Clark, 1911, and recently described (Stöhr & Segonzac, 2005) genus *Ophienigma* should be transferred to the family Ophiactidae. Subfamily Ophiohelinae also should be placed from Ophiacanthidae to Ophiactidae. Genus *Amphilimna* Verrill, 1899 (= *Sinophiura* Liao, 1983 syn.nov.) should be returned back to the Amphiuroidae. Ophiacanthidae after these transferences is likely well-defined, monophyletic group. Genera *Abysura* Belyaev et Litvinova, 1976, *Ophiambix* Lyman, 1880 and *Ophiophyllum* Lyman, 1878 should be placed in the family Ophiolepididae, whereas genera *Ophiomisidium* Koehler, 1914, *Ophiophycis* Koehler, 1901 and *Astrophiuroida* Sladen, 1878 should be retained in Ophiuridae. Some genera need further analysis.

4.2 Placement of the genus *Ophiosparte*

Combination of the shape of articulation ridges with internal, rarely used in ophiuroid taxonomy characters may be an additional test for their taxonomical and phylogenetic value. Large Antarctic *Ophiosparte* *gigas* Koehler, 1922 traditionally included into the family Ophiacanthidae, currently is showed as having affinities to the Ophiomyxidae (Dearborn et al., 1996). However, unlike Ophiomyxidae, *Ophiosparte* possesses articulation ridges typical for the family Ophiuridae and Euryalida. Besides, *Ophiosparte* has such a distinctive for family Ophiuridae character as true arm comb. Type of articulation between radial shield and genital plate are more similar to ophiurid rather to ophiomyxid or Euryalida. Tooth plate with many rows of openings is similar to another Antarctic ophiurid, *Ophionotus* Bell, 1902 rather than ophiomyxid. Thus, *Ophiosparte* can be considered as an archaic member of the family Ophiuridae.

4.3 Relationship between Amphiuroidae and Ophiolepididae

Very similar in articulation ridges families Ophiactidae and Amphiuroidae possess similar radial shield-genital plate articulation as well as shape of tooth plate openings. Moreover, obscure family Ophiolepididae possesses articulation ridges similar to the Amphiuroidae. It may be caused by the convergence due to a possibility of independently emerging parallel ridges. However, oral papillae of Ophiolepididae are similar to the Amphiuroidae. Tooth plate of some Ophiolepididae also similar with amphiuroid and ophiactid type (in present study it is revealed from the *Ophiozonella alba* (Lütken et Mortensen, 1899). So family Ophiolepididae becomes more well defined and appears as a derivate of Amphiuroidae with massive arms and reduced spines.

4.4 Origin of the group Ophiohelinae

Based on the present study, a hypothesis of the origin of the aberrant group Ophiohelinae from *Ophiothamnus*-like ancestors is suggested. Ophiohelinae share with “*Ophiomitra*” *acontophora* H.L. Clark, 1911 and genus *Ophiothamnus* shape of articulation ridges and easily detached disk, covered with spines. Paterson (1985) for the first time mentioned inconsistency of the shape of articulation ridges of Ophiohelinae with the family Ophiacanthidae but nevertheless he maintained this subfamily within ophiacanthids. Aberrant flat mouth papillae of Ophiohelinae placed on the jaws dorsally and not laterally are similar to true spines in shape and also in having articulation ridge with large opening.

4.5 Relationship between Euryalida and Ophiuridae

Phylogenetically it is possible that the shape of articulation ridges of *Ophiomyxa* type is a basic construction for ophiacanthid ridges, which modifications appeared

afterwards in Ophiocomidae and Ophiidermatidae. Simultaneously, the shape of articulation ridges is found typical for Ophiuridae with except of absent tubercles for hooks, is similar to the euryalids. These facts, along with similarity of Ophiomyxidae dental plate and articulation between genital plate and radial shield with Ophiacanthidae, for instance, suggest that gap between traditional Euryalida and Ophiurida is lesser than proposed. Unification of the Ophiomyxidae with Euryalida and their opposition to Ophiurida is likely artificial. Rather, there are several lines where "ophiuridisation" takes place, from taxa with a thick skin to taxa with a more or less massive uncovered stereom. The genus *Ophiosparte* is one of the archaic representatives of such lines, from one side it has an euryalid and ophiomyxid character – thick skin, but from other side it possesses unique features for family Ophiuridae – arm comb and articulation between genital plate and radial shield.

5 LIMITS OF THE SHAPE

As is shown in present study stability of the shape of articulation ridges to a great extent depends on shape and size of spine rather than on modifications, even considerable, of the lateral plate. Then, the ridges lost their usual shape under aberrant, flat, fused proximal spines in species of the genus *Amphilimna*, entirely disappeared traces of ridges under bristle-like spines in the genus *Ophiernus* Lyman, 1878 and very short spines in the genus *Ophiomusium* Lyman, 1869. Such cases are restrictions of the approach here suggested. Nevertheless, most of the studied taxa retain characteristic shape of the ridges of their family even in cases of considerable differences in morphology of lateral plates and sizes of spines. For instance, both large ophiurid *Ophionotus victoriae* Bell, 1902 and tiny *Ophiotjalfa vivipara* Mortensen, 1913 from the same family have similar pattern of articulation ridges. Thus, under the stipulation that spines are not changed considerably, articulation ridges retain their conservative shape within a group of related taxa, usually within family and below, in some cases within a group of closely related families. Present approach allows to determine family or generic placement by lateral plates, equally useful in recent and extinct taxa, and potentially valued for phylogenetic studies.

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