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Reassessment of the classification of the Ophiuroidea (Echinodermata), based on morphological characters. I. General character evaluation and delineation of the families Ophiomyxidae and Ophiacanthidae

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Key to species of the genus *Ophiophrura*

1(2) Oral shields have distinct distal lobe; oral shield proximal edge triangular..... ..... *O. liodisca* H.L. Clark, 1911, North Pacific, off Japan, at 864–919 m
2(1) Oral shields without distinct distal lobe
3(4) Oral shield broadly traiangular, distal edge almost straight, proximal edge convex..... ..... .*O. imperfecta* (H.L. Clark, 1915) **comb. nov.,** Caribbean, off St. Vincent, at 771 m
4(3) Oral shields elongated lozenge-shaped..... .....*O. tripapillata* (Stöhr & Segonzac, 2005) **comb.nov.,** North Atlantic, at 1015–1400 m

***Ophioplexa* gen. nov.**

Diagnosis. The disk covered with numerous small, uniform scales covered by a thin skin layer, not evident when dried. The radial shield and adradial genital plate are small and externally inconspicuous. The articulation surface of the radial shield is distinctly excavated ventrally, distally with a groove. The abradial genital plate is absent. The genital slits are small. The oral frame bears numerous oral papillae similar in shape to the cluster of the ventralmost teeth (apical papillae). Several adoral shield papillae, which do not differ considerably from the oral papillae, are placed around the second tentacle pore. The jaws are slightly elongated. The adradial sides of the jaws distally bear a few sharp straight folds. The dental plate is large with rounded sockets and irregular folds. The teeth are spiniform and numerous, ventralmost teeth of similar shape. The dorsal and ventral arm plates are well developed. The arm spine articulations are compressed transversally. Some proximal articulations may have a distinct nerve opening. The sigmoidal fold is absent. The arm spines are hollow, relatively short and flattened, not hooked distally. The vertebrae are distinctly keeled and with zygospondylous articulation.

Etymology. *Ophio-* (after ophiuroid) and *plexus* (Latin, noun, feminine), braided, in current usage meaning also a complicated combination of elements in a system, in reference to an intricate relationship of the new genus combining traits of both ophiomyxids and ophiacanthids.

Remarks. (see also under Discussion below). The new genus shows some similarities to the genus *Ophiocymbium* in the presence of a poorly developed adradial genital plate and radial shield, but possesses several important differences. The genus *Ophiocymbium* has distinct block-shaped distal oral papillae as adult and few apical papillae, whereas *Ophioplexa* **gen. nov.** is characterized by numerous spiniform oral papillae, both proximally and distally. The numerous apical papillae of *Ophioplexa* **gen. nov.** are placed in a dense cluster, whereas *Ophiocymbium* has only a few apical papillae. The arm spine articulations of *Ophioplexa* **gen. nov.** are dorso-ventrally compressed with distinct nerve and muscle openings, whereas *Ophiocymbium* has a typical rounded muscle opening, but the nerve opening, if conspicuous, has a different appearance. The dental plate of *Ophioplexa* **gen. nov.** has a remarkable appearance, with a combination of several articulations and numerous small openings (Fig. 55M–N), whereas the dental plate of *Ophiocymbium* has a few round openings and completely lacks articulation (Fig. 12E–H).

***Ophioplexa condita* gen. et sp. nov.**
Figures 4J, K, N, P–S; 17L–O; 54A–E; 55A–H; 56; 67F

Material. Holotype, dried, ZMMU D-788, R/V " Akademik Kurchatov", cruise 11, sta. 896, 05.12.1971, 56° 52' S 24° 59' W – 56° 51' S 24° 59' W, depth 5651–5530 m, Sigsbee trawl. One paratype, dried, ZMMU D-789, same sta. as holotype. One paratype, ethanol, ZMMU D-790, same sta. as holotype. One paratype, mounted on SEM stub, ZMMU D-791, same sta. as holotype. One paratype disarticulated and mounted on SEM stub, ZMMU D-792, same sta. as holotype. Two paratypes, dried, ZMMU D-793, R/V "Akademik Kurchatov", cruise 11, sta. 870, 29.11.1971, 55° 7' S 25° 2' W – 55° 8' S 25° 1' W , depth 4704–4680 m, Sigsbee trawl.

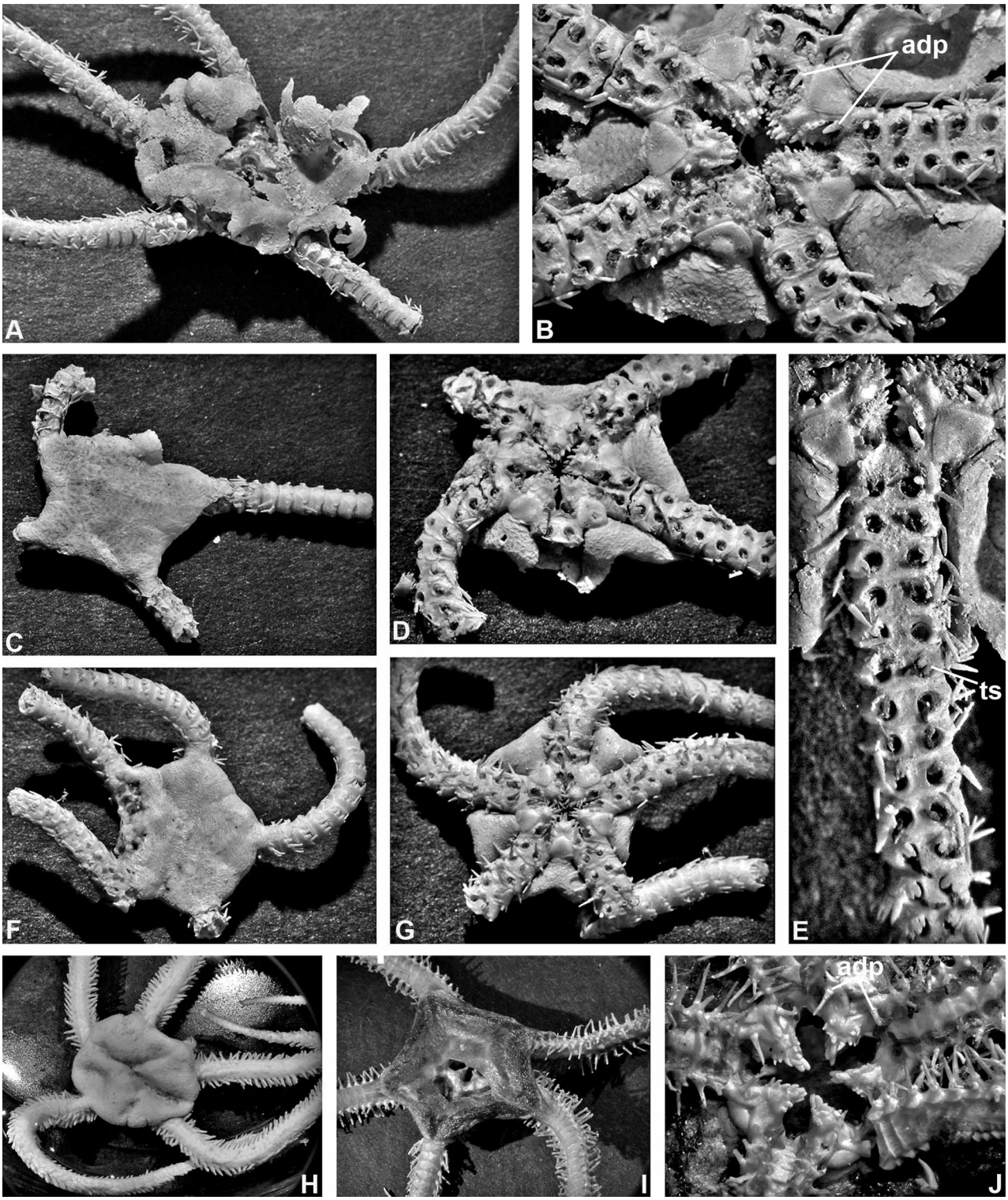

FIGURE 54. ***Ophioplexa condita*** **gen. nov., sp. nov.** and *Ophioscolex glacialis* Müller & Troschel, 1842, external views. A. ***Ophioplexa condita*** **gen. nov., sp. nov.,** external view of the holotype ca. 18 mm dd, dorsal, ZMMU D-788, B. same ventral; C. a paratype 11.8 mm dd, dorsal view, ZMMU D-789; D. same, ventral view; E. holotype, ventral view of the arm; F. a paratype 8 mm dd , dorsal view, ZMMU D-793; G. same ventral; H. *Ophioscolex glacialis* Müller & Troschel, 1842, ZMMU D-118, ethanol specimen 34 mm dd; I. *Ophioscolex glacialis*, ZMMU D-866, dried specimen 22 mm dd, showing changing in the external appearance compare to living and ethanol specimens; J. same, oral frame. Photos: Tatiana Korshunova.

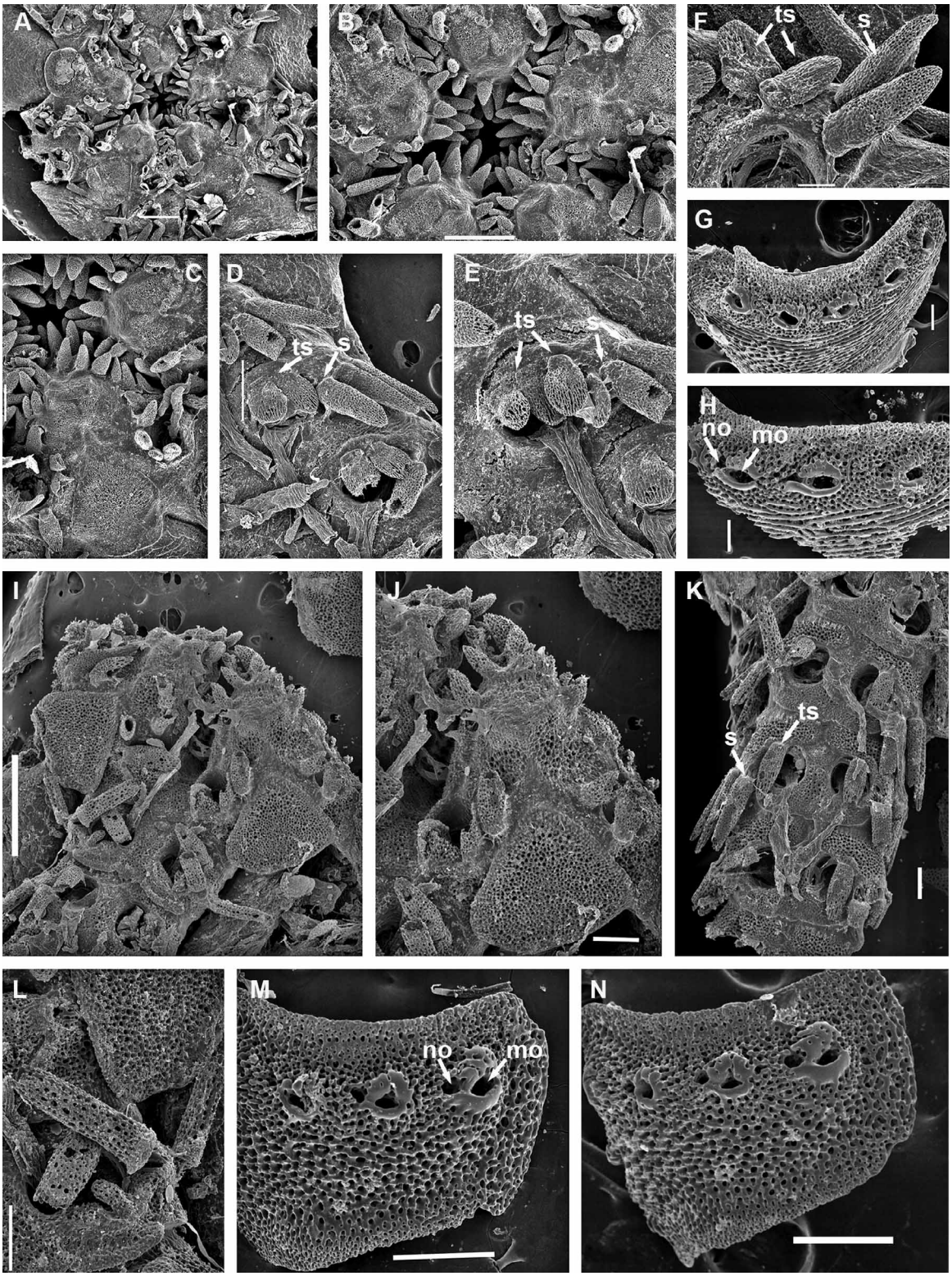

FIGURE 55. ***Ophioplexa condita*** **gen. nov., sp. nov. and** ***Ophiocymbium ninae*** **sp. nov**., details. A. ***Ophioplexa condita*** **gen. nov., sp. nov.,** paratype 19 mm dd, ZMMU D-791, disk ventral view; B. same oral frame showing clusters of the ventral teeth (apical papillae); C. same, one interradius showing apical, oral and adoral shield papillae; D-F, same, most proximal arm segments showing tentacle scales and spines; G-H, arm spine articulations, distal segments; I. ***Ophiocymbium ninae*** **sp. nov**., paratype 5 mm dd, ZMMU D-803, details, part of the oral frame and ventral arm side; J. same, jaw and oral papillae, one interradius; K. ventral arm view showing spines and tentacle scales; L. most proximal segments showing details of tentacle scales and spines; M-N, arm spine articulations, proximal segments; Scale bars: A–B, 1 mm; C–D, 500 μ; E–F, 200 μ; G–H, 100 μ; I, 1 mm; J–N, 300 μ. Photos: Alexander Martynov.

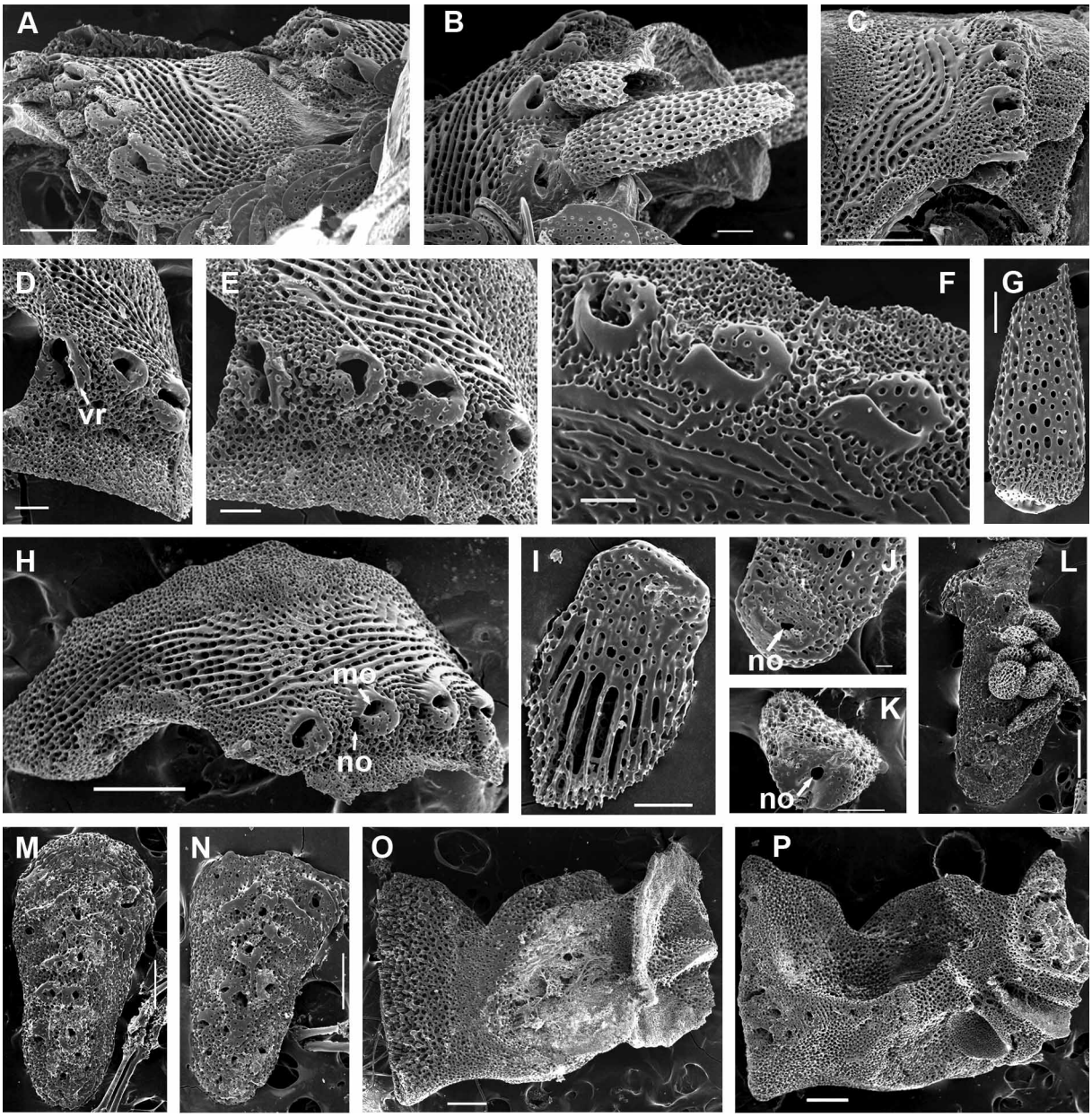

FIGURE 56. ***Ophioplexa condita*** **gen. nov., sp. nov.** Arm spine articulations, spines, tentacle scales, dental plates and jaws of a paratype of ca. 17 mm dd, ZMMU D-792. A. two proximal arm segments adjoining disk; B. same, showing hollow spines; C. ventral view of the artciulations of the most proximal segments under the disk in situ including attaching area of the tentacle scales; D. separate lateral arm plate of the most proximal segments showing distinct shape of the ventralmost ridge; E. same, showing variability of following articulation; F. articulations of a middle segment; G. spine of a middle segment; H. separate lateral arm plate of the proximal segment showing more typical pattern of the articulation; I. a separate tentacle scale of the most proximal segment; J. same, basal part showing a small opening, presumably for nerve; K. basal part of a spine showing an opening for nerve; L. dental plate with several teeth; M, N, dental plates; O. jaw, abradial view; P. jaw, adradial view. Scale bars: A, 300 ; B, 100 μ; C, 300 μ; D, 100 μ; E, 100 μ; F,G, 100 μ; H, 300 μ; I,J, 100 μ; K, 30 μ; L–P, 300 μ. Photos: Alexander Martynov.

Etymology. from Latin *conditus*, hide, concealed, in reference to some morphological (small concealed radial shields and genital plates) and ecological (abyssal environment) features of the new species.

Description of the holotype. The disk is damaged, approximately 18 mm dd, presumably flattened when alive, round and not indented interradially. The disk plates are numerous, most of them elongated and narrow, irregular-rhomboidal and polygonal, entirely devoid of spines and granules. There is a thin skin layer, which is conspicuous in ethanol specimens, but almost undetectable when dried. Radial shields are very small and

entirely concealed under disc scales (see a detailed radial shield description under internal and other characters below). The interradii are slightly swollen, ventrally covered with numerous scales similar to the dorsal ones. Each jaw bears three to five irregularly placed, narrow, spiniform ventralmost teeth, which are not distinguished from more dorsally placed teeth, nor from adjacent lateral oral papillae. Distal oral papillae and adoral shield papillae are similar in size and shape, and placed along both edges of a jaw in a characteristic slightly curved row around the second tentacle pore, approximately 5–6 in number (including 2–3 adoral papillae in the strict sense). Thus there is a continuous series of papillae from the teeth to the adoral shield papillae. Deeper in the mouth opening on the jaws there is a distinct group of papillae, placed laterally to the other oral papillae, 2–4 in number. Numerous spiniform teeth are arranged in a dorsalwards tapering cone-shape on the dental plate. There are 17–20 teeth (including "apical papillae"). The oral shield is wide, triangular, with straight or slightly convex, distal edge, about as long as wide, completely separated from the first lateral arm plate by the adoral shields. Distally the oral shield is contiguous with a supplementary oral shield in form of a narrow elongated plate or just an elevation formed by adjacent interradial scales. The madreporite is similar in shape to the others, but slightly larger and has a swollen round area in the middle, conspicuously smaller than the entire shield. Adoral shields wing-like laterally, widely adjoining the arm, rapidly narrowing towards the jaws, thus retaining only a narrow bar between jaws and oral shield. True genital slits are small openings under the adoral shields, but long furrows between the proximalmost arm segments and the ventral disk interradius form false slits. Arm length is about 1.4 times the disk diameter.

The dorsal arm plates are well developed but thin, fan-shaped, moderate in size. Few proximal plates are wide, rapidly narrowing towards the middle of the arm, contiguous along most of the arm length. The proximal edge of the dorsal arm plate is almost straight throughout the length of the arm, but triangular on the basal segments. A few proximal dorsal plates have a pointed proximal angle, whereas the majority of them possess a short straight proximal edge. Two arms show irregular bands of numerous elongated scales intermingled with the lateral and dorsal plates. These proximal scales are similar to dorsal disk scales. The second dorsal arm plate near the disk is narrow, elongated transversally, bar-shaped or oval. On two arms the proximalmost dorsal plates are absent for 4–5 segments, whereas in one arm small scales almost entirely conceal the first two proximal segments. Arms are weakly noded and form a low lateral ridge on which the arm spine articulations are placed. There are two or four arm spines on the most proximal segments under the disk, six to seven rather adpressed spines on the free proximal and middle segments, and five distally. Dorsal and ventral spines are similar in size. Arm spines are flattened, pointed apically. The proximal edge of the ventral arm plate is straight, whereas the distal edge is convex with a small pit in the middle. Ventral plates throughout the length of the arm are contiguous. The tentacle pores are larger and more conspicuous proximally than towards the distal end of the arm. Basally on the part of the lateral plate that encircles the tentacle pores, three flattened, apically rounded tentacle scales are placed. The tentacle scales are shorter than the arm spines, but conspicuous and large enough to cover the whole tentacle pore. Many of the tentacle scales are broken or have fallen off. Towards the distal end of the arm the number of tentacle scales is reduced to two, and the inner scale is shorter than the outer one. The ventral arm plates do not bear any tentacle scales.

Paratype variations. A paratype, from sta. 870, 8 mm dd, differs from the holotype in having an almost undamaged irregularly-pentagonal disk, evenly covered with numerous, mostly elongated scales, which continue dorsally onto 1–2 proximal arm segments. Almost all dorsal arm plates, except for the 1–2 most proximal, have a pointed, narrowly triangular proximal edge, and are separated by lateral plates, to a small degree proximally, but up to half of the dorsal plate length distally. The pattern of the oral papillae is similar to the holotype, but the papillae are significantly fewer, and the curved row of oral papillae around the second tentacle pore is evident only in some interradii. Numerous spiniform teeth do not differ from the 3–4 apical papillae. Two, rarely three papillae on the adoral shield. Oral shields are more lengthened than in the holotype, and the madreporite is just an inconspicuous spot within the oral shield. Most of the oral shields have a remarkable feature of one or two rather conspicuous scales overlapping the shield distally, as a continuation of the supplementary oral shield – several scales adjacent distally to the oral shield. In other characters the paratype is similar to the holotype.

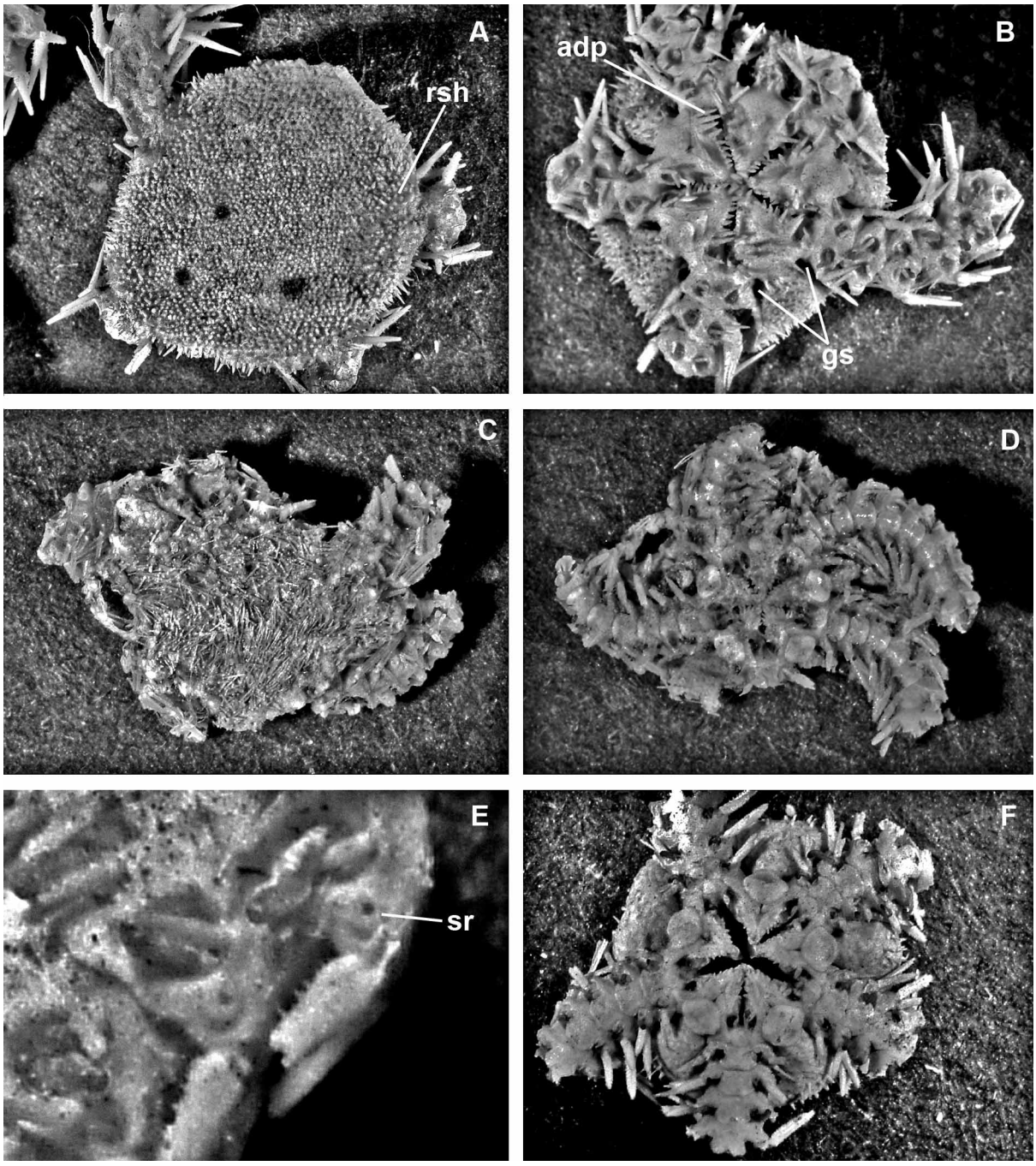

FIGURE 57. Genera *Ophioprium* and *Ophiopristis*, external views. A-B, *Ophioprium cervicornis* (Lyman, 1883), holotype MCZ 2043, 10 mm dd, dorsal and ventral views respectively; C-D, *Ophiopristis hirsuta* (Lyman, 1875), holotype MCZ 1950, 5.8 mm dd, dorsal and ventral views respectively; E. *Ophioprium cervicornis* (Lyman, 1883), holotype MCZ 2043, arm spine articulations, proximal segments; F. *Ophiopristis hirsuta* (Lyman, 1875), paratype MCZ 1951, 5 mm dd, ventral view. Photos: Alexander Martynov.

Another paratype, also from sta. 870, 5.5 mm dd, differs from the holotype and other paratype in size, an irregularly pentagonal disk, evenly covered with numerous polygonal and oval scales, which are continued dorsally on 2–3 proximal arm segments. The pattern of the oral papillae is also distinct from the holotype and from the paratype from the same station (870), but these differences clearly reflect the juvenile nature of the present specimen. The papillae are significantly smaller in number, and the curved row of oral papillae around the second tentacle pore is indistinct and can be traced only in two interradii. One or two distalmost oral papillae are block shaped. At least one papilla on the adoral shields is present in one interradius, whereas in

the other interradii it has most probably fallen off. Oral shields are more elongated in length than in the holotype, and the madreporite is just an inconspicuous spot within one oral shield. Most of the oral shields are overlapped by a conspicuous scale distally. On the most proximal lateral arm plates under the disk there are 2 spines, on the proximal lateral plates 4–5 spines, towards the middle 5–6. Spines are flattened, all similar in size. Tentacle scales are similar to the holotype, but many are broken or have fallen off. In the middle part of the arm the number of tentacle scales is reduced to two.

Internal and microstructural characters. Radial shield and genital plate articulate very tightly, unlike most extant ophiuroids, and have the appearance of an entire plate broken by a fissure (Figs 4J, K, P). The articulation surface of the radial shield is distinctly excavated ventrally, with a distal groove (Figs 4R, S). The articulation surface of the adradial genital plate lacks distinct condyles (Fig. 4Q). The abradial genital scale is absent. Jaws are slightly elongated (Figs 56O, P). Adradial sides of the jaws distally bear few sharp straight folds (Fig. 56P). The dental plate is large with rounded sockets and irregular folds (Figs 56M, N). Arm spine articulations compressed transversally (Figs 55G–H; 56A–H). Some proximal articulations may have a distinct nerve opening (Figs 56D–E). Few ventralmost articulations on the proximalmost segments have a distinctive slit-shaped appearance (Figs 56C–E). Vertebrae short, distinctly keeled and with well developed zygospondylous articulation (Figs 17L–O). Vertebral dorsal median groove almost indistinct (Fig. 17L). Podial basins are large (Fig. 17M).

Genus *Ophiopristis* Verrill, 1899

Figures 57C–D, F; 58–60

Ophiopristis Verrill, 1899: 39, 40
Type species: *Ophiacantha hirsuta* Lyman, 1875, by original designation

Diagnosis. The disk is covered with numerous small, uniform scales; a skin layer is not evident. The dorsal disk surface is covered with long, densely spaced spinelets. The radial shields are well-defined, elongated, but concealed under the disk plates. The adradial and abradial genital plates are well-defined. The genital slits are long and conspicuous, genital plates border approximately half of the slits. The articulation surface of the radial shield is a broad, low elevation. The jaw bears numerous short conical oral papillae similar in shape to the single (or double) apical papillae. The adoral shield papillae and adjacent oral papillae are slightly longer than other oral papillae. The half-jaws are relatively low. The adradial sides of the half-jaws distally bear a few convoluted folds. The dental plate is elongated without folds and with few elongate narrow slit-shaped sockets, alternately placed. The sockets for the apical papillae are similar in shape to all others. The teeth are broad, conical to rectangular. There are 1–2 ventralmost teeth. Generally all teeth are similar in shape, but the dorsalmost teeth are usually longer. The oral shield is broadly arrow-shaped with a short distal lobe. The adoral shields have distal wings, proximally tapered. Dorsal and ventral arm plates are well developed. The arm spine articulations are placed at a small angle in relation to the lateral plate. The muscle opening is larger than the nerve opening. There is a volute-shaped perforated lobe occupying the dorsal and distal part of the articulation. The sigmoidal fold is well-defined. The proximal edge of the spine articulation is entire but connected with the main part of the lateral arm plate by a short ridge. The arm spines are relatively long, rounded, hollow over almost their entire length, not hooked distally. Tentacle scales are well-defined, oval or lanceolate, single or double. The tentacle pores of moderate size. The vertebrae have a narrow keel that is distally abruptly truncated; the dorsal medial furrow is moderately expressed. The articulation is zygospondylous. Podial basins are moderate in size.

Material studied. *Ophiopristis hirsuta* (Lyman, 1875), Holotype MCZ 1950 (Figs 57C–D, F); USNM 6429, 1 specimen (Fig. 58); *Ophiopristis luctosa* (Koehler, 1904), MNHN EcOs 22978–22979, 2 specimens (Fig. 59); *Ophiopristis procera* (Koehler, 1904), Syntype EcOs 20406 (Fig. 60); *Ophiopristis dissidens* (Koehler, 1905), MNHN EcOs 22478, 4 specimens.

Remarks. O'Hara & Stöhr (2006) recently reviewed the genus *Ophiopristis* and further delineated it from other ophiacanthid genera, initially suggested by Paterson (1985). Among the species included into this genus,

goes to Nina Litvinova (P.P. Shirshov Institute of Oceanology, Moscow), for support of my study and providing numerous materials. The head of the Laboratory of the Electron Microscopy of the Biological Faculty, Moscow State University, Georgy Davidovich, the leading engineer Anatoly Bogdanov, and the staff members Yulia Golubtosva and Alsu Kuznetsova provided excellent SEM facilities. Alexander Mironov and Andrey Gebruk (P.P. Shirshov Institute of Oceanology, Moscow) always supported my study in a friendly way. Special thanks to Sabine Stöhr (Swedish Museum of Natural History) for kind discussions, comments on the manuscript and for improvement of English. I am particularly thankful to Tim O'Hara (Victoria Museum, Melbourne) who generously improved English, made important comments on the manuscript, and also kindly provided some specimens and discussed some points. My special appreciations to curators who have lent me numerous necessarily materials in a very restricted time: David Pawson (Smithsonian Institution, Washington), Nadia Améziane (Muséum national d'Histoire naturelle, Paris), Marc Eléaume (Muséum national d'Histoire naturelle, Paris), Andrew Cabrinovic (British Museum of Natural History, London), Gudmundur Gudmundson (Icelandic Institute and Museum of Natural History, Reykjavik) and Danny Eibye-Jacobsen (Zoological Museum, Danish Museum of Natural History, Copenhagen). Many thanks to Frederick J. Collier (Museum of Comparative Zoology, Harvard University) and Martha Collier, who made possible my visit to the Museum of Comparative Zoology. Daniel Miller (Museum of Paleontology, the University of Michigan) generously made excellent microscopic photographs of paleozoic ophiuroids. For comparative purposes, some ophiuroid specimens, which were studied during my visit to the Museum of Comparative Zoology, Harvard University (supported by The Ernst Mayr Travel Grant in Animal Systematics), were used. Igor S. Smirnov (Zoological Institute RAS, St. Petersburg) kindly provided a specimen of *Ophiosparte gigas.* Frederick Hotchkiss (Marine and Paleobiological Research Institute, Vineyard Haven, MA) kindly discussed some aspects of ophiuroid taxonomy during my visit to the Museum of Comaparative Zoology. The lunch discussion with Seiichi Irimura (Tokyo, Japan) during the 12th International Echinoderm conference is unforgettable. I am also especially gratitude to Grand Chamberlain of the Emperor's Palace (Tokyo, Japan) and Toshihiko Fujita (National Museum of Nature and Science, Tokyo) for sending me rare literature on the Japanese ophiuroids. I am thankful to the late Cynthia Ahearn (National Museum of Natural History, Smithsonian Institution) for lending me some of H.L. Clark's ophiuroid type material. Jessica D. Cundiff (Museum of Comparative Zoology, Harvard University) kindly made photographs of some ophiuroid types.

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