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THE MORPHOLOGY AND SYSTEMATIC POSITION OF LOWER ORDOVICIAN SEA LILIES

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ABSTRACT: Four monotypic genera, three of them new, from the Lower Ordovician in the Leningrad region are described. They are assigned to the monocyclic inadunates of the superfamily Myelodactylacea. A new interpretation of the morphology of certain previously known genera is proposed, a comparison is made, and their phylogenetic relationships are noted. The representatives of the iocrinid-eustenocrinid stem of the disparid inadunates are shown to be the predominant taxa among the Lower Ordovician crinoids.

* * *

Calyces and crowns of the oldest sea lilies from the Lower Ordovician are rare, but are of great importance for understanding the origin and development of the main groups of crinoids and their relation to the other echinoderms [24]. By now, 16 Lower Ordovician genera of sea lilies in which the calyces are known have been described, including three new genera here described: *Proexenocrinus* Strimple et McGinnis, 1972 (Al Rose formation, California, USA), *Perittocrinus* Jaekel, 1902 (Kundas horizon, northwestern USSR), *Tetracionocrinus* Ubaghs, 1971 (Kundas horizon, northwestern USSR), *Hybocrinus* Billings, 1857 (Filmore formation, Utah, USA), *Aethocrinus* Ubaghs, 1969 (Tremadocian or Arenigian stage, southern France), *Compagicrinus* Jobson et Paul, 1979 (Arenigian stage, northern Greenland), *Acolocrinus* Kesling et Paul, 1971 (Benbolt formation, Virginia and Tennessee, USA), *Agostocrinus* Kesling et Paul, 1971 (Benbolt formation, Virginia and Tennessee, USA), *Vosecocrinus* Jaekel, 1918 (Lower Ordovician, Czechoslovakia), *Pariocrinus* Rozhnov, gen. nov. (Volkhov horizon, Leningrad region), *Maennilicrinus* Rozhnov, gen. nov. (Volkhov horizon, Leningrad region), *Tetragonocrinus* Yeltyschewa, 1964 (Volkhov horizon, Leningrad region, Estonia and Ukraine), *Ramseyocrinus* Bates, 1968 (Bay Ogof Hên formation, England and Wales), *Pogocrinus* Kelly et Ausich, 1978 (Filmore formation, Utah, USA), *Inyocrinus* Ausich, 1986 (Al Rose formation, California, USA), and *Putilovocrinus* Rozhnov, gen. nov. (Volkhov horizon, Leningrad region). This list by no means exhausts the entire variety of the oldest sea lilies, as is shown, for example, by the multitude of various sea lily stems described by Yeltysheva [2] from the Lower Ordovician of Estonia and the Leningrad region.

Only one of these Early Ordovician genera, *Proexenocrinus*, belongs to the camerates. It is initially considered to be monocyclic, but restudy of the holotype and and of a located paratype show that it is in fact dicyclic. This genus, therefore, is now among the rhodocrinitids of the diplobathridic camerates [8]. Three genera, *Hybocrinus*, *Perittocrinus* and *Tetracionocrinus*, must be considered hybocrinoids. Although in the Treatise on Invertebrate Paleontology [20] the last two genera are combined in the family Perittocrinidae Abel, 1920, were placed among the disparids, I believe that Ubaghs' view [22] that they are closely related to the hybocrinids is better justified. I am engaged in the study of a vast amount of material on the perittocrinids and Early Ordovician hybocrinids from the Volkhov and Kundas horizons of the Leningrad region. The results will be published in another article and therefore need not be discussed here.

The other 12 genera are inadunates. Two of these, *Aethocrinus* and *Compagicrinus* are dicyclic and the other 10 monocyclic. Thus, the largest number of Lower Ordovician crinoids belong to the order Disparida. Morphologically, two genera, *Acolocrinus* and *Agostocrinus*, stand sharply apart from the others [14] and are characteristic of younger deposits, to which, according to R. M. Mannil (pers. com.) is confined a new

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Middle Ordovician species of *Acolocrinus* from Estonia. It will therefore be more appropriate to analyze the morphology and systematic position of these genera in a planned treatment of the Middle Ordovician disparids.

The eight remaining Lower Ordovician sea lilies, although sometimes differing so considerably in morphology that they are distributed among several families, are nevertheless close in origin and form a single phylogenetic line. I shall attempt to substantiate this conclusion. The disparid inadunates have a special structure of their C ray (the anal tube emerging from the brachial plate or here the presence only of the anal tube), while the other four rays are all similar in structure. The disparid inadunates are phylogenetically unified and are with full justification combined into the superfamily Myelodactylacea [18]. The new genus *Pariocrinus* belongs to one of the families of this group, the Iocrinidae. *Pariocrinus* is morphologically very close to the other three genera of this family and reliably shows that the iocrinids appeared at least as early as the Arenigian. All four genera are characterized by a branching of the anal tube from the brachial plate located directly above the radial C plate. This brachial, or brachianal, plate [15] is regarded as an upper radial homologous with that in the other families of disparids, if it is considered as being within the dorsal cup, whose distal boundary is higher than in the other ambulacra. The boundary of the calyx in the iocrinids can be delineated by including all the first brachials in the dorsal cup, as happens in *Caleidocrinus*: the first brachials of all five rays are mutually linked by interbrachial plates [18]. This again underscores the origin and homology of the upper radial plates and the anal tube in the disparids, whose dorsal skeleton represents the first left branching on arc C (in some cases the dorsal skeleton of the entire arm C) [3, 15].

Maennilicrinus gen. nov. should also be assigned to the iocrinids. In this genus the exact structure of the anal interradius is unknown, but the form of the calyx, the indivisibility of the radial plates into upper and lower, and the size and shape of the facets for the attachment of the arms enable its assignment with confidence to the iocrinids. On the same basis, although less reliably, *Vosecocrinus*, now known only from one picture and an inadequate description by Jaekel [11], should also be assigned to the iocrinids. The author of this genus placed it close to *Caleidocrinus*, and thereby also to the iocrinids.

The genera *Pogocrinus*,[1] in spite of the incomplete preservation of their representatives, also are placed among the myelodactylaceans, but in the family Eustenocrinidae. This is indicated primarily by the presence, although not always well established, of double radials in all five rays [8, 13].

Thus, these six Lower Ordovician genera unambiguously belong to families well known from younger deposits. If there is some doubt in certain cases, it is due only to incomplete preservation. But the other two Lower Ordovician genera, *Tetragonocrinus* and *Ramseyocrinus*, are evidently closely related to the iocrinid-eustenocrinid line of development; their very distinctive morphology cannot be unambiguously interpreted, so that their supposed phylogenetic relationships are not obvious.

The crown of *Tetragonocrinus*, previously known only from stem fragments, was first described in 1985 [1]. I cannot fully agree with the interpretation of the structure of this genus proposed at that time. From this interpretation [1] it follows that *Tetragonocrinus* is morphologically not related to the disparids, but stands sharply apart from them. It is not clear, however, why its base and stem should have a primary tetraradial structure. The suggestion that its closest ancestor had four arms is no more likely than that it had five or three, because the order of symmetry of the basal and radial crowns often does not coincide. Similarly unconvincing is the supposition that one of the ambulacral food grooves (the third, in the author's terminology) "began to serve for the removal of excreted material, perhaps with the atrophy of a barely developed arm" [1, p. 703]. The ambulacral food groove on the tegmen connects the mouth and the beginning of the arm on the margin of the calyx. The posterior intestine in all ancient sea lilies opens outward at the boundary of the tegmen with the dorsal cup near the C ray. This means that topographically and in the direction of operation of the ciliary epithelium, the ambulacral food groove on the tegmen (the arm, as the author supposes, being atrophied) could remove excreted material only from the anus toward the mouth, which is, of course, nonfunctional. Such a structure does not occur in the sea lilies, although in the disparids the posterior intestine, using for support the dorsal skeleton of the left branching of arm C (more rarely the entire arm C), is located in the groove of the skeleton of the arm, but not the tegmen. The ambulacral food groove as an organ for food transmission is not developed in this branch. Of course, it is possible that the ancestor

[1] In Ausich [8], this genus is figured as *Pogonipocrinus*.

of *Tetragonocrinus* had four arms, but if so, in *Tetragonocrinus* one arm has disappeared without a trace, but in no way did it serve as a means for removing excreta. It is simply not present in the known specimens, just as there are no traces in the calyx of anything for the attachment or derivation of attachment of the anal plates. The anus, therefore, was most likely at the end of the small anal pyramid at the side on the tegmen of the calyx. Another suggestion -- that the posterior intestine encompassed the left branching of one of the arms -- must be rejected, because all the branches above the first auxillary plate also branch, even if only once. To be sure, the nonbranching of the anal tube in the disparids shows that its skeleton serves for the support of the posterior intestine, which cannot branch, and not as an ambulacral food groove that has acquired the function of removing the excreta from the anus.

The location of the anus on the calyx can thus far be determined only indirectly by the somewhat larger gap between the first brachials, by the same orientation of the buried crowns and by the unique morphology of the interradius. The anus, as indicated earlier [1] and, as seen from outside, is evidently to the right of the facet for the attachment of the arm with three sutures. Therefore, one can introduce the designation of the rays and plates adopted for the five-armed forms, on the assumption that the succession of formation and development of the rays in the phylogeny of the crinoids is the same as in their ontogeny. For the disparids, such a succession is quite definitely established: the first formed are the three rays C, E and B, followed by the dyad of rays D and A [5]. These three rays in *Tetragonocrinus* will be C, E and B, counting clockwise, beginning with the arm in front of the anal interradius (although in the case of an incomplete circle described by the intestine, the arm C may be located after the anal interradius). In this designating the radial plates, we can also unambiguously homologize three of the four basals. The fourth may be either EA or AB. But keeping in mind that the succession of formation of the basal plates is like that of the radials, this plate must be designated AB (Fig. 1a).

In this interpretation of the structure of our form, it seems most likely that *Tetragonocrinus* is a completely neotenic disparid. This fully explains all the distinctive morphological features of the genus and establishes its relationships with the other disparids. If *Tetragonocrinus* is a neotenic form, it corresponds to the stage of individual development of the skeleton of a five-rayed sea lily in which only some plates of the basal crown (four) and antimeres of the stem (also only four) have been formed. The radial crown is formed just after the basal, and by the time four basals have appeared, only three radials (C, E and B) have been formed. From this moment on the development of the *Tetragonocrinus* larva followed a different path from that of its five-rayed ancestor. In this not fully differentiated stage were formed the structures required for the functioning of the sexually mature organism. The basal plates grew, forming a small calyx on a four-rayed stem. The radial plates were not mutually interconnected, but acquired a ligamental linkage to the basals. Such a linkage of the basal and radial plates is not unique--it occurs widely among the disparids of the calceocrinacean superfamily, which also has some juvenile features. Above the radial plates appear brachial plates forming the arms, in which the radial plates function only as brachials (Fig. 1b).

Now suppose that the neotenization process did not occur and that the larvae developed as they would in the typical five-rayed forms. What would be the appearance of the mature sea lily in this case? In the stem and base there would be five antimeres, and two more radial plates would have appeared. The basal and radial plates would have grown together into a single capsule forming a larger calyx. The posterior intestine would have encompassed the left branch of the first branching of the C ray, using it for a support, as in all the disparids. If it is supposed that there was a bonding of only the most proximal "radial-brachials," which here is very likely because of their great height, the adult sea lily would have all the features of the representatives of the iocrinid family. Therefore, Stukalina'a [6] monotypic family Tetragonocrinidae should, it seems, be placed next to the family Iocrinidae in the same superfamily Myelodactylacea S. A. Miller, 1883. It is inappropriate to distinguish it as a separate superfamily [1], since this makes the *Tetragonocrinus* too distinctive and masks its genetic relationships. Another argument in favor of the interpretation of *Tetragonocrinus* proposed here is the finding of the attachment structure with part of the stem: the four-lobed rather than cruciform axial canal in the dististele, the almost circular section through the stem, and the larger denticles--that is, the differences from the iocrinid stem are actually only in the order of symmetry.

On the other hand, returning to the analysis of the logical possibilities in the transformation of the morphogenesis of *Tetragonocrinus* without neoteny, one can imagine that the fusion of the plates in the calyx is on the level of the second brachials, and that the brachials above the later formed rays A and D appear above the boundary of the calyx. The result is a typical representative of the homocrinacea. But homocrinacea are not in the Lower Ordovician and are altogether unknown

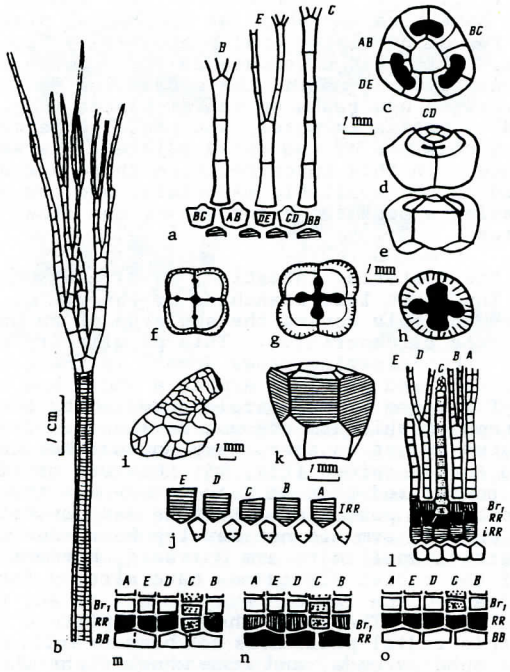

Fig. 1. Representatives of families Tetragonocrinidae, Eustenocrinidae and Ramseyocrinidae; a, b) Spec. 4125/8: a) expansion of proximal part of crown and stem; b) crown with fragment of stem in side view (interradius CD); c-e) Spec. 4125/113, calyx in top and side views--rays B and E; f-h) structure of articular surface of segments: f) in proximal part of stem (diagram); g) Spec. 4125/327, in middle part of stem; h, i) Spec. 4125/321: h) in distal part of stem; i) formation for attachment with distal part of stem, side view; j, k) *Putilovocrinus fundatus* sp. nov; Holotype PIN 4125/1: j) expansion of calyx, k) calyx from above (ray C); l) *Eustenocrinus springeri*, expansion of crown after [15]; m-o) *Ramseyocrinus* Bates, 1968: m) expansion of calyx, after [9], n) after [10], o) in form adopted here. Legend: radial plates, ligamental depressions on facets for attachement of arms, and axial canal of stem are black, anal plates are dotted; brachial plate is cross hatched; fixed first brachials are vertically hatched; lower radials (IRR) are horizontally hatched, and remaining plates are left white. A, B, C, D and E are rays; AB, BC, CD, DE and EA are designations of successive basalt plates; BB are basal plates; RR are radial plates, Br_1 are brachials, and X is anal X.

in Europe. Assuming somewhat more complicated transformations of the skeleton, one can also relegate this genus to certain other superfamilies. This, it would seem, testifies not to its possible concrete genetic relationships, but to the phylogenetic unity of all the disparids. The morphological commonality of the order is clearly based on the similar ontogenesis of its representatives. The basic morphological variety on the extensive development of neoteny and heterochrony in the formation of the organs and skeletal elements in the development of the superfamilies and families. The proposed interpretation of the *Tetragonocrinus* is the most possible at the present level of study of the disparids. Its validity can be more persuasive only by studying in sufficiently abundant material the variability of this genus and the genera compared with it.

Such an approach, it would seem, can also explain the morphology of *Ramseyocrinus*, a distinctive genus with a predominant four-rayed symmetry. This last assertion is not completely true, as will be shown below. There are two interpretations of the structure of the calyx in this genus, which differ in which crown is the radial crown. According to one interpretation [9], the second crown from the bottom is

considered the radial (Fig. 1m). It consists of four plates and a split intercalary anal plate, almost the same size and shape as the radial plates. This anal plate, designated X, bears a row of overlying anal plates--that is, the anal tube--and itself rests on a basal plate. This last circumstance led Donovan [10] to propose another interpretation. He considered as radial the underlying row of plates, so that the anal plate X in this version now rests on radial plates (Fig. 1n). In the latter case the number of radial plates is three, but can also be considered to be four, because one of the plates consists of two fused adjacent plates, as seen from the preserved trace of a suture. In this interpretation there are no basal plates or else they cannot be observed on the available materials, and the calyx also has fixed brachials. Before indicating a preference for one or the other interpretation, we must consider the anal plates.

In the disparids the posterior intestine, as already noted, is usually supported by the skeleton of the first left branching of the arm C. But in certain cases the posterior intestine entirely covers the skeleton of an unbranching arm C. This is especially clear in the calceocrinids. This peculiarity is evidently due to neoteny and heterochrony: the intestine grows upward in the C ray until it has made a complete circle in its coil and until an arm as a whole has been formed here. As a result, the skeleton of the arm C is entirely occupied by the posterior intestine, and the remaining systems of this arm are not developed. In the calceocrinids this phenomenon is complicated by yet another, very unusual heterochrony, and in *Ramseyocrinus* (Fig. 1o) as in *Eustenocrinus* (Fig. 1*l*) this was manifested in more "pure" form. Thus it can be considered that in *Tetragonocrinus* the skeleton of the arm C is completely occupied by the posterior intestine and constitutes an anal tube, while the remaining systems of this arm did not develop here, due to neoteny and heterochrony. Yet this assertion applies to arm C itself, but not to the radial plate C. Actually, the crown of the radial plates may have already formed when the spirally growing intestine approached the ray C. But if this is so, the radial crown was formed as a five-rayed crown. Therefore the radial plate C should be designated as a radial plate. But this radial plate does not bear an axillary plate, from whose left shoulder the anal tube extends, and from whose right shoulder the arm proper extends (as, for example, in the iocrinids), but it has only the anal tube, whose most proximal plate is homologous with the anal tube of the other disparids. As a result, *Tetragonocrinus* can be characterized as a sea lily with a five-rayed radial crown but with four arms and an anal tube in place of the fifth arm. There are four basal plates, although two of them, judging by the traces of a suture, are intergrown in mature specimens. The symmetries of the stem and basal crown in this case coincide--both are four-rayed. In this interpretation *Tamseyocrinus* differs from *Eustenocrinus* almost exclusively in the number of basals, the symmetry of the stem and the unfixed first brachials in the calyx. Consequently the difference between these two genera is not as great as was thought earlier.

It follows from all the above that the families Iocrinidae Moore et Laudon, Eustenocrinidae Ulrich, Tetragonocrinidae Stukalina, and Ramseyocrinidae Donovan, whose representatives are most characteristic of the Lower Ordovocian, are phylogenetically very close.

Thus, the above Lower Ordovician sea lilies can relatively easily, although sometimes only on the assumption of a neotenic origin, be inscribed in the existing system of the sea lilies. The situation is different with the Lower Ordovician *Aethocrinus* Ubaghs, from France [21]. There are four interpretations of its structure (Fig. 2a-c) which attempt to fit it into the morphology of the typical dicyclic inadunates [12, 17, 19, 21, 23]. But each of these interpretations encounters serious contradictions, evidently indicating that the morphology of this genus does not correspond to that of the dicyclic inadunates, although individual features of similarity do exist between them. To explain the discrepancy, one must image the morphogenesis of *Aethocrinus* and compare it to the morphogenesis of the inadunates. To begin with, the radial plates of the sea lilies are the most proximal parts of the arms. This is shown by the morphogenesis of the Recent sea lilies and confirmed by the structure of *Tetragonocrinus* considered above, in which the proximal brachials are not transformed into radial plates. In *Aethocrinus*, therefore, the radial plates must be considered the most proximal plates of the arms, as in the reconstruction of Philip and Strimple [19]. In the inadunates the anal series of plates, as indicated above, is derived from the arm C. Have we sufficient basis for saying the same about *Aethocrinus*? Evidently not, because such an interpretation, for all its internal consistency, does not agree with the surrounding structures, especially in this case with the interradial disposition of the arms. It is, therefore, more reliable and convincing to regard the upper anal plates as plates of the tegmen that have become part of the calyx, and the lowermost anal plate as a plate of special origin that is not homologous with the anal plates of most late inadunates. Thus the anal plates of *Aethocrinus* cannot by any means correspond to the anal plates of the inadunates, but the upper anal plates may be homologous with the anal plates of certain hybocrinids [4, 5]. In such an interpretation, perhaps, one can see their homology with the anal plates of the camerates.

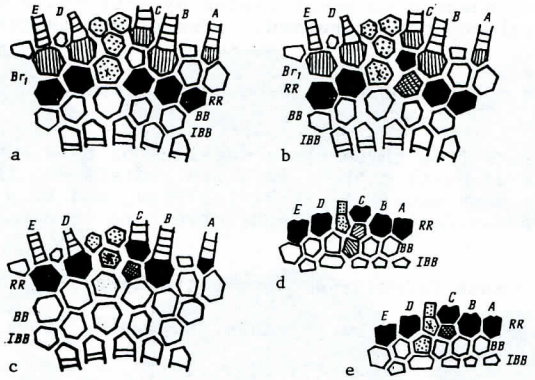

Fig. 2. Various interpretations of structure of calyx in *Aethocrinus* and *Compagicrinus*; a-c) different interpretations of *Aethocrinus* calyx: a) after [21]; b) after [17]; c) after [19]; d, e) different interpretations of structure of calyx in *Compagicrinus*: d) after [12]; e) as proposed here. Legend: IBB - infrabasal plates; oblique hatching - lower and upper radial plates; oblique crosshatching - radial plate; for remainder of legend, see Fig. 1.

In the interpretation of the structure of *Aethocrinus* proposed here, there are three more crowns of plates between the stem and the radial crown. Which of these three crowns corresponds to the one crown in the monocyclic and the two in the dicyclic sea lilies? This question, like the phylogenetic relationship between mono- and dicyclicity, is very complicated [25] especially in view of the strialate--in Stukalina's terminology [7]--structure of the stem in the genus under consideration. and requires special study.

Nevertheless, only the recognition of an "excess" crown below the radials in *Aethocrinus* (and a corresponding interpretation of the anal plates) can serve as the basis for the supposition [16] that this genus has features ancestral of all inadunates. In all the other hypotheses expressed earlier, this genus can be only an unusually and highly specialized dicyclic sea lily, but never their ancestral form. This conclusion suggests the idea of the neotenic origin of the sea lilies from some multicrowned forms in which the five-rayed symmetry of the food-gathering apparatus and accordingly of the oral and radial plates and of the lowest crown of the theca was already formed, whereas the intermediate crowns may have been poorly formed and lack a clear five-rayed symmetry. The above considerations compel us to assign the genus *Aethocrinus* to a considerably higher rank than family within the superfamily Mastigocrinacea of the cladid inadunates. But a convincing substantiation of this will require much additional and new material of the oldest sea lilies.

The only strictly dicyclic genus among the Lower Ordovician inadunate sea lilies is *Compagicrinus* which has certain features similar to *Aethocrinus* -- six plates in the crown below the radial plates [12]. However, the overlying part of the anal area more closely resembles that of the typical inadunates (Fig. 2d-e). It can, therefore, be suggested that the sixth plate in the basal crown of *Compagicrinus* (not the right one, however, as the authors of the genus believe, but the left one) is the anal plate as inferred from the shape of the underlying plates. This anal plate is homologous with that in *Aethocrinus*, but is absent in the typical inadunates. The radial plate, the anal X and the overlying plate, to judge by the large anal sac above them, may perhaps be homologous with the corresponding plates in the cladids (Fig. 2e).

SUBCLASS INADUNATA WACHSMUTH ET SPRINGER, 1885

ORDER DISPARIDA MOORE ET LAUDON, 1943

SUPERFAMILY MYELODACTYLACEA S. A. MILLER, 1883

FAMILY TETRAGONOCRINIDAE STUKALINA, 1980

Diagnosis. Stem of four rows of antimeres. Calyx small, and of only four basal plates. Three radial plates (B, C, E), not part of calyx, being most proximal

elements of arms, and connected to basal plates by distinctly manifested ligaments. Anal structure in dorsal cup not expressed. Arms branch isotomously, without pinnules.

Composition. One monocyclic genus from Lower Ordovician of Leningrad region, Estonia and Ukraine.

Comparison. Differs from three other families of this superfamily in having calyx constructed only of basal plates, to which radials are linked by ligaments, being functionally the most proximal brachial plates, and also in absence of radials A and D and in lack of manifestation of anal structure in dorsal cup.

Genus *Tetragonocrinus* Yeltyschewa, 1964

Tetragonocrinus pygmaeus (Eichwald, 1860)

Pl. VI, figs. 1-10

Synonyms. See Yeltysheva, 1964; Stukalina, 1980; and Arendt, 1985.

Description (Fig. 1a-i). Small sea lilies with long narrow crown. Stem in transverse section has square outline with rounded corners, up to 3.8 mm in diameter but usually comewhat less. Proximal part of stem becomes sharply thinner. It consists of segments of two orders, which differ in height and, in some cases, in presence of spines. But this order is often broken. Each segment consists of four antimeres; levels of upper and lower surfaces of adjacent antimeres differ somewhat, so that articular surface of segments is stepped. Narrow rim present on perifery of each antimere; this rim bears several very small ribs, which are sometimes barely discernible. On inner side, rim borders on lower even area. Through center of segment runs axial canal, and approximately in middle of sutures separating adjacent antimeres are four peripheral canals. In proximal part of stem, axial and peripheral canals are separated and have square or rhombic outline. Corners of axial canal are on sutures, instead of pointing toward corners of segment. In middle part of stem, axial and peripheral canals are connected to form single cruciform canal that widens in middle and at ends. In distal part of stem, this canal becomes wider and approaches four-lobed outline. Lower areas on surface of antimeres are very small, and large and rare denticles occupy almost entire articular surface of segment. Attachment structure has form of small base made up of plates of irregular shape. Surface of most proximal segment, for linkage with calyx, has four marginal depressions in which peripheral canals begin, and central elevation with axial canal in middle.

Calyx is very small and in shape of inverted truncated cone. It widens slightly upward and bears three facets for attachment of arms, which are separated from each other by distal protuberances of calyx. Calyx consists only of four basal plates. In the middle of one plate (symmetrical), is distal protuberance separating facets for attachment of arms. Two plates adjacent to it (right and left, asymmetrical) have distal protuberance shifted toward margin. Fourth plate lacks protuberance, but has slightly convex distal surface. Stem facet has four gentle depressions, separated by elevated bosses. There are three facets for attachment of arms. Two of these are the same--made up of lateral parts of two plates, in such a way that in middle of each of these two facets is suture between plates. Third facet occupies three plates at once, and it has two sutures; middle part of this facet is somewhat convex. Along each of facets runs longitudinal depression whose greatest depth is confined to suture; "double-suture" facet thus has two maximal depths. No place for

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KEY TO PLATE VI

Figs. 1-10. *Tetragonocrinus pygmaeus* (Eichwald): 1) Spec. 4125/113, calyx (× 13); 1a) top view; 1b) side view, radius B; 1c) side view, anal interradius; 1d) side view, radius E; 1e) bottom view; 2) Spec. 4125/111, calyx (× 13): 2a) top view; 2b) side view, radius B; 2c) bottom view; 3) Spec. 4125/112, calyx in side view, showing basal plates AB and DE (× 13); 4) Spec. 4125/8, crown with fragment of stem in side view, showing anal interradius (× 1.5); 5) Spec. 4125/323, articular surface of segment (× 13); 6) Spec. 4125/320, proximal part of stem: 6a) side view (× 6); 6b) top view (× 13); 7) Spec. 4125/322, proximal part of stem in side view (× 6); 8) Spec. 4125/325, small stem with spines (× 13); 9) Spec. 4125/324, stem with spines (× 6); 10) Spec. 4125/321, attachment formation (× 6); all specimens from Volkhov horizon in Leningrad region: 1-3, 7, 8) from Putilovo quarry; 4, 5, 9 [sic]) from quarry near Babino settlement on right bank of Volkhov River; 6, 9 [sic]) from Lava River.

Fig. 11. *Putilovocrinus fundatus* sp. nov.; Holotype PIN 4125/1, calyx: 11a) top view; 11b) side view, radius C (× 13); Putilovo quarry; Volkhov horizon.

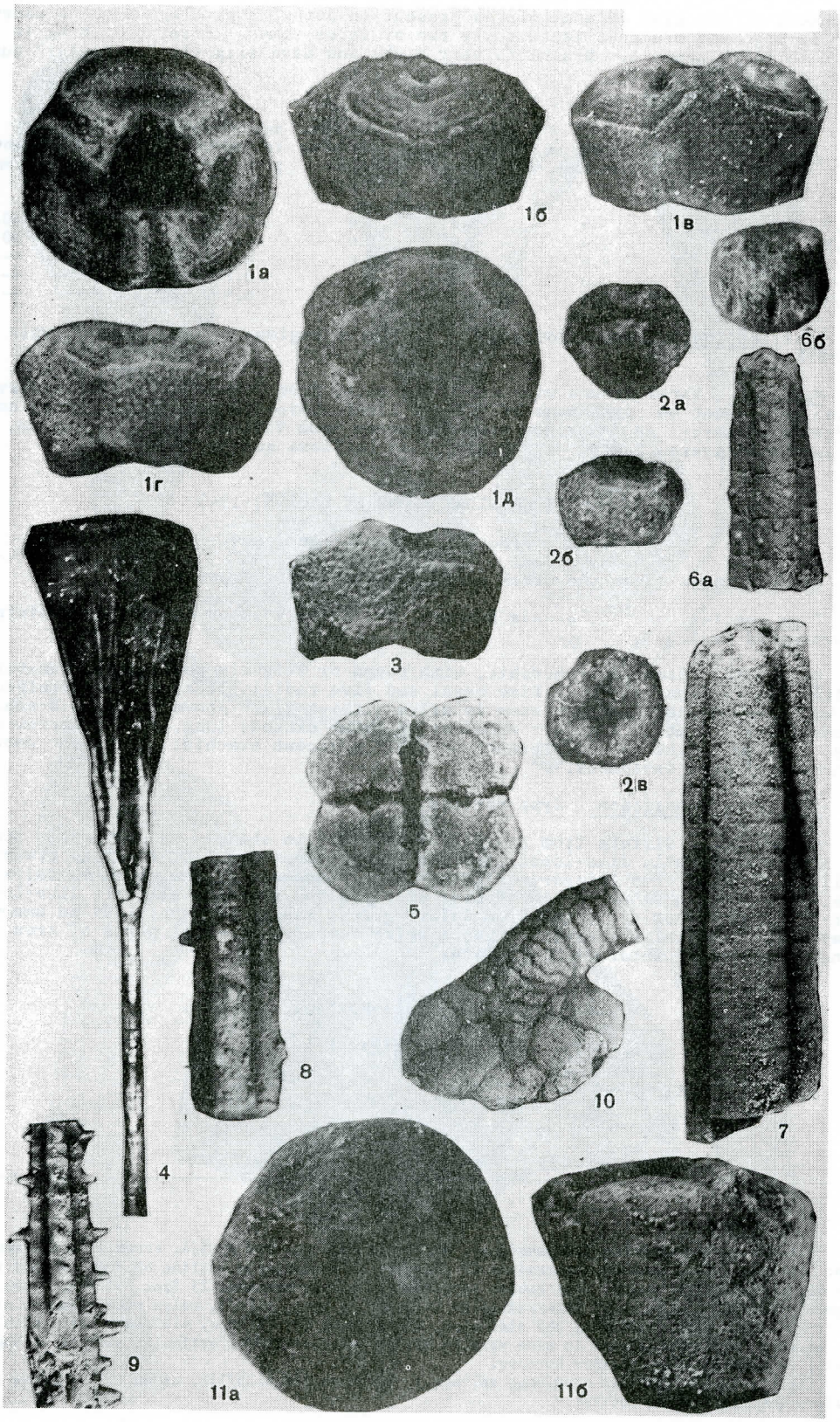

PLATE VI

attachment of any kind of anal plates present in dorsal cup. Tegmen not preserved. Crown is high and branches isotomously two or three times. First branching is after second to fifth segment. Brachials very high, and have slightly "vesicular" surface.

Dimensions in mm:

Spec. No.	Width of stem	Diameter of calyx base	Width of calyx at level of facets	Height of calyx (with protuberances)	Height of calycate protuberances	Width of arm facets	Height of arms
4125/7	2.1	2.6	3.0	1.8	0.3	1.6	40
4125/8	2.2	2.4	3.0	2.0	0.3	1.7	40
4125/111	--	1.0	1.3	1.0	0.2	0.7	--
4125/112	--	2.0	2.5	1.5	0.4	1.3	--
4125/113	--	2.5	3.0	1.8	0.5	2.0	--

Distribution. Lower Ordovician of Leningrad region, Estonia and Volhynia (UkrSSSR).

Material. Three crowns with stem fragments, from Volkov horizon in quarry near Babino settlement on right bank of Volkhov River, three calyces from Volkhov horizon in Putilovo quarry; and numerous stem fragments from Volkhov horizon on Lynna, Volkhov and Lava rivers, quarry near Babino, and Putilovo quarry.

FAMILY IOCRINIDAE MOORE ET LAUDON, 1943

Genus *Pariocrinus* Rozhnov, gen. nov.

Generic name. From the Greek *para* ("next to") and *Iocrinus*.

Type species. *P. ladogensis* Rozhnov, sp. nov.; Volkhov horizon in eastern part of Leningrad region.

Diagnosis. Stem heteromorphic, with round or slightly pentagonal transverse outline. Calyx conical, with five basal and five radial plates without sculpture and with even transition from stem to calyx without rim. Above radial C brachial (upper radial) plate, from left shoulder of which extends long, fairly narrow anal tube, and from right shoulder branch of arm. Adjacent brachial plates not connected. Branching of arms isotomous.

Specific composition. Type species.

Comparison. Differs from *Iocrinus* Hall, 1866 in sharply heteromorphic stem and its round or slightly five-lobed, but not sharply pentagonal or stellate transverse outline. Differs from *Peltacrinus* Warn, 1982 in absence of sculpture on calyx, narrower anal tube, absence of rim at base of calyx and round or slightly five-lobed (not ten-lobed) stem. Differs from *Caleidocrinus* Waagen et Jahn, 1899 in unconnected adjacent brachials, whereas in genus being compared proximal parts of arms are connected by small interbrachial plates.

Pariocrinus ladogensis Rozhnov, sp. nov.

Pl. VII, figs. 1-5

Specific name. From Lake Ladoga.

KEY TO PLATE VII

Figs. 1-5. *Pariocrinus ladogensis* sp. nov.: 1) Holotype PIN 4125/4, crown with fragment of stem: 1a) side view, showing interradius CD (× 1.5); 1b) transverse outline of stem (× 13); right bank of Volkhov River, quarry near Babino settlement; Volkhov horizon; 2) Spec. 4125/6, crown with fragment of stem in side view, interradius CD (× 1.5); 3) Spec. 4125/5, calyx with fragment of stem (× 5): 3a) side view, radius A; 3b) side view, interradius CD; 4) Spec. 4125/115, calyx with fragment of stem and bases of arms in side view (× 5); 5) Spec. 4125/326, articular surface of segment (× 13); Putilovo quarry; Volkhov horizon.

Fig. 6. *Maennilicrinus concinnus* sp. nov.: Holotype PIN 4125/114, crown in side view (× 6); Putilovo quarry, Volkhov horizon.

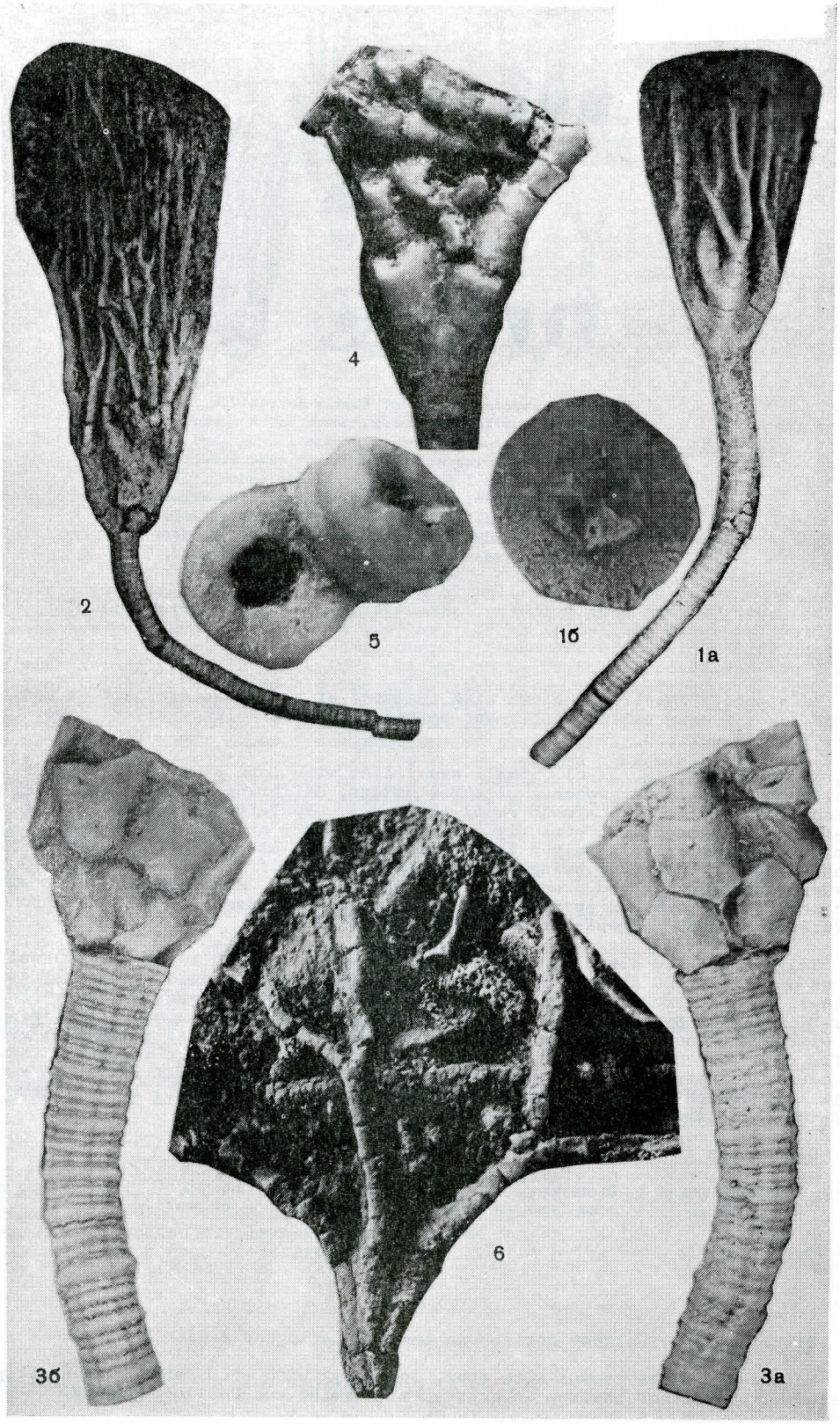

PLATE VII

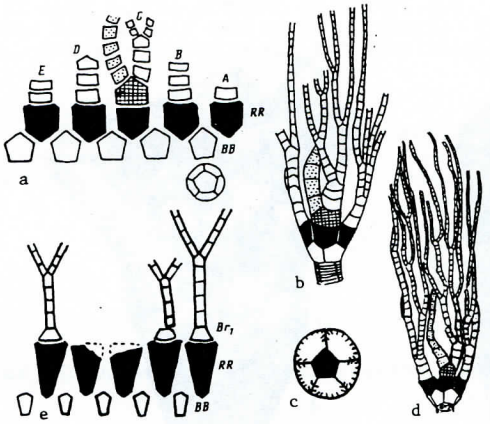

Fig. 3. Representatives of family Iocrinidae; a-c) *Pariocrinus ladogensis* sp. nov.: a, b) Holotype PIN 4125/4: a) expansion of proximal crown and stem; b) crown with stem fragment in side view (interradius CD) (× 1.5); c) Spec. 4125/6, same (× 1); d) Spec. 4125/326, articular surface of stem segment (× 5); e) *Maennilicrinus concinnus* sp. nov.: Holotype PIN 4125/114, expansion of calyx; eastern part of Leningrad region; Volkhov horizon. For legend, see Fig. 1.

Holotype. PIN 4125/4, crown with fragment of stem; eastern part of Leningrad region, quarry near Babino settlement on right bank of Volkhov River; Lower Ordovician, Volkhov horizon.

Description (Fig. 3a-d). Small sea lilies with long stem consisting of round or slightly five-lobed segments of three orders, differing in width and height. Each segment consists of five almost equal antimeres, separated by sutures. Such pentameres of all segments lie strictly one above another, and sutures between them on stem surface form five straight longitudinal lines. Axial canal of stem is pentagonal and wide, its diameter being somewhat more than half diameter of stem. Sutures between pentameres extend from corners of axial canal. Articular surfaces smooth, with short ribs (7-9) on periphery and side of each pentamere. In short proxistele, difference between segments of different orders is less.

Calyx small and conical, with slight convexity forming cone. Five basal plates are of same size and shape. Sutures between them are in middle of pentameres (alternating). Radial crown somewhat wider than basal. Radial plates slightly convex in center in distal part. Facets for attachment of arms occupy about 3/4 of distal margin of radials and are somewhat inclined outward. Above radial place C is brachial plate, from left part of which extends long (no less than eight segments) anal tube, and from right part branch of arm, in which third segment is axillary. In remaining radii arms branch for first time above third or fourth segment. In all, arms branch three or four times, almost isotomously.

Dimensions in mm:

Spec. No.	Diameter of stem	Diameter of stem facet	Height of calyx	Width of calyx	Length of of arms	Height of basals	Height of radials
Holotype 4125/4	3.0	4.6	5.0	8.1	35	2.4	3.1
4125/5	2.1	2.9	4.2	7.0	--	2.5	3.0
4125/6	2.2	3.1	5.7	9.0	52	3.0	3.5

Distribution. Volkhov horizon in east of Leningrad region.

Material. Three crowns with stem, one calyx with stem, and numerous fragments of stems from Volkhov horizon in quarry rear Babino and Putilovo quarry.

Genus *Maennilicrinus* Rozhnov, gen. nov.

Generic name. In honor of R. M. Mannil.

Type species. *M. concinnus* sp. nov.; Volkhov horizon in eastern part of Leningrad region.

Diagnosis. Well-shaped conical calyx with five low basal plates, five high radial plates, arms branching isotomously once, and spreading out widely toward sides. Structure of anal interradius unknown.

Specific composition. Type species.

Comparison. Differs from other genera of iocrinid family in slender conical calyx, low basal plates, little branching of arms and widely spreading crown.

Remarks. Anal interradius poorly preserved, and its exact structure could not be ascertained. This genus is therefore assigned to family Iocrinidae only on basis of similarity in structure of other rays, shape of calyx and relative size of facets for attachment of arms.

Maennilicrinus concinnus Rozhnov, sp. nov.

Pl. VII, fig. 6

Specific name. From the Latin *concinnus* ("elegant").

Holotype. PIN 4125/114, crown; Putilovo quarry; Lower Ordovician, Volkhov horizon.

Description (Fig. 3e). Calyx has form of well-proportioned cone, 4 mm high and 3.2 mm wide, with stem facets 1 mm in diameter. Basal plates number five, although only three are well-preserved. They are low, 1.1 mm in height, which is about 1/4 height of calyx. Radial plates five in number; these are high, almost 3/4 height of calyx, with strongly convex and thicker median part, so that sutures between them lie in depressions. Three radials are well-preserved. Of other two, only proximal parts are seen, and structure of anal interradius is unknown. Facets for attachment of arms are about 3/4 width of radials. Arms are preserved in three radii; they branch isotomously once, after fifth axillary or sixth (middle of preserved arms) segments. Proximal brachials have massive lower part and narrowing upper part, from which extend high (0.8 mm) and narrow (0.4 mm) brachials. Number of brachials after branching is not less than eight. Height of arms about 12 mm.

Material. Holotype.

FAMILY EUSTENOCRINIDAE ULRICH, 1925

Genus *Putilovocrinus* Rozhnov, gen. nov.

Generic name. From Putilovo settlement.

Type species. *P. fundatus* Rozhnov, sp. nov.; Volkhov horizon in eastern part of Leningrad region.

Diagnosis. Small thick-walled conical calyx with five basal plates, visible from below. First brachials evidently not fixed in calyx.

Specific composition. Type species.

Comparison. Differs from all other genera of family in very thick-walled calyx and is very narrow interior cavity. In addition, differs from *Eustenocrinus* and *Peniculocrinus* in distinctly conical calyx and first brachials not being fixed (?), from *Inyocrinus* in considerably larger size, and from *Pogocrinus* in high conical shape of calyx; also differs from *Ristnacrinus* in basal plates being well visible from side.

Putilovocrinus fundatus Rozhnov, sp. nov.

Pl. VI, fig. 11

Specific name. From the Latin *fundatus* ("solid").

Holotype. PIN 4125/1, calyx; Leningrad region, Putilovo quarry; Volkhov horizon.

Description (Fig. 1j, k). Small calyx of conical form with flat stem facet. Five basal plates of approximately same size and shape. Crown of lower radial plates somewhat higher than basal. Lower radial plate C somewhat lower than others, and lower radial E somewhat higher. Distal surfaces of lower radial plates wide and flat, and without sign of ligamental linkage. Diameter of inner cavity of calyx at level of boundary between lower and upper radial plates in 0.9 mm, which is 1/4 width of whole calyx.

Dimensions of holotype in mm: Diameter of stem facet = 2.0; diameter of axial canal = 0.25; width of calyx = 3.5; height of calyx = 2.5-3.0; height of basals = 1.2; and height of lower radials = 1.7-2.2 mm.

Material. Holotype.

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