

SONDER-ABDRUCK

aus

PALAEONTOGRAPHICA

BEITRÄGE ZUR NATURGESCHICHTE DER VORZEIT

Pal. A. Bd. 204

STUDIES IN PALEOZOIC CRINOID-COLUMNS AND -STEMS

BY

GALINA A. STUKALINA

With 15 plates, 31 figures and 2 tables in the text



STUTTGART
E. SCHWEIZERBART'SCHE VERLAGSBUCHHANDLUNG
(NÄGELE u. OBERMILLER)
1988

Далее по Учености Кандидат наук с званием
и званием члена. Учености
1.1991.

STUDIES IN PALEOZOIC CRINOID-COLUMNALS AND -STEMS

BY

GALINA A. STUKALINA^{*)}

With 15 plates, 31 figures and 2 tables in the text

Zusammenfassung

Die Komplexität und die Vielfalt der Skelette paläozoischer Crinoiden erweisen sich als außerordentlich vielversprechende Voraussetzung, die Morphogenese und die Evolution dieser Tiergruppe zu untersuchen.

Vom Skelett sind vor allem die Columnalien erhalten. Ihr massenhaftes Vorkommen im Paläozoikum war denn auch der Grund spezieller Studien, die hauptsächlich stratigraphischen Zwecken dienen. Die meisten der adaptiven Trends in der Evolution der paläozoischen Crinoiden liegen in der Ausgestaltung der Bewegungsfunktion. Auf diese Weise entstanden die verschiedenartigsten Artikulationstypen der Stielelemente.

Funktionsmorphologische Analyse und Beobachtung morphogenetischer Muster derartiger Entwicklungen können zu einer möglichen Grundlage einer phylogenetischen Klassifikation der Crinoiden auf der Grundlage ihrer Stiele werden. Allerdings spiegeln solche morphogenetischen Veränderungen der Stiele nicht in allen Fällen die phylogenetischen Zwischenglieder der Crinoidenentwicklung wider, da ähnliche Morphotypen auch konvergent auftreten können.

Die einheitliche Anwendung der erarbeiteten Untersuchungsmethoden auf die Prinzipien der Systematik — unabhängig in welchen Skelettelementen Crinoidenreste im fossilen Zustand vorliegen — ermöglicht es, die Parataxonomie in der Klassifikation aufzugeben und natürliche Gruppen der Crinoiden zu erkennen.

Daraus ergibt sich andererseits aber auch eine verstärkte Berücksichtigung von Crinoiden in Biostratigraphie, Paläoökologie und Paläogeographie.

Schlüsselwörter: Crinoiden — Paläozoikum — Stielglieder — Morphologie.

Abstract

The complex and diverse skeleton structure of Paleozoic crinoids gives an extremely favourable opportunity for studying the morphogenesis and evolution of this faunal group. The complex skeleton of these animals in a fossil state is most frequently represented by columnals. Their abundance in Paleozoic rocks was the cause of special studies, primarily for the purposes of stratigraphy.

Most of the adaptive trends in the evolution of Paleozoic crinoids are characterized by an intensified function of movement, which shows up in various articulation types of the skeletal ossicles of the stems. Morphofunctional analysis and the observed morphogenetic pattern of these changes can serve as a possible basis for a phylogenetic classification of crinoids based on the stems. Morphogenetic changes of the stems do not fully reflect the phylogenetic links of crinoids, since similar morphotypes can appear convergently in different phylogenetic branches; however, each branch may reflect a particular case of morphogenesis. Common methods of studies and principles of crinoid systematics, irrespective of the fact of what skeletal ossicles are represented by in the fossil state, offer a possibility of eliminating parataxonomy in their classification and revealing the most complete evolution pattern of the group in general. This, in its turn, gives an opportunity for the more complete use of crinoids as a faunal group in biostratigraphic, paleoecological, and paleogeographical studies.

Key words: Crinoids — Paleozoic — Columnals — Morphology — Taxonomy.

^{*)} Address of the author: Prof. Dr. G. A. STUKALINA, All-Union Geological Research Institute, Sredny Prospect 74, Leningrad 199026, USSR.

Аннотация

Сложность и разнообразие структуры скелета криноидей палеозоя создает исключительно благоприятную возможность для изучения морфогенеза и эволюции этой фаунистической группы. Сложный скелет этих животных в ископаемом состоянии чаще всего представлен члениками стеблей. Широкое распространение их в породах палеозоя послужило причиной их специального изучения прежде всего в стратиграфических целях.

Большинство адаптивных направлений в развитии палеозойских криноидей, характеризуется интенсификацией функций движения, которая проявляется в различных типах сочленения скелетных элементов стеблей. Морфофункциональный анализ и прослеживаемые морфогенетические закономерности этих изменений могут быть положены в основу филогенетической классификации криноидей по стеблям. Морфогенетические изменения стеблей не отражают полностью филогенетических связей криноидей, так как аналогичные их морфотипы могут конвергентно возникать в различных филогенетических ветвях, но каждая ветвь может отражать частный случай морфогенеза. Единство методов изучения и принципов систематики морских лилий вне зависимости от того, какими скелетными элементами они представлены в ископаемом состоянии, открывает путь к устранению паратаксономии в их классификации и раскрытию наиболее полной картины эволюции группы в целом. Это, в свою очередь, создает перспективу более полного использования морских лилий, как фаунистической группы, в биостратиграфических, палеоэкологических и палеогеографических исследованиях.

Ключевые слова: криноидеи – палеозоология – членики – морфология – таксономия.

Contents

Introduction	2
General remarks	3
Development of views on the classification of Paleozoic crinoid stems	6
Method of studies and principles of systematics in old crinoid stems	9
Morphology and morphofunctional analysis	10
Morphogenesis	13
Ontogeny	24
Taxonomic evaluation of the morphological characters of stems	29
Classification of the Ordovician, Silurian and Lower Devonian crinoids based on the stems ...	32
Phylogenetic relations of higher taxa and major evolutionary trends	35
Conclusion	51
References	51
Explanation of Plates	55

Introduction

Paleontological studies, connected with the use of crinoid stems for the purposes of stratigraphy carried out in the USSR over many years, have presented convincing evidence of their practical value in regional stratigraphy.

Further working-out of methods of studies and systematic principles in this group, undertaken by the author, was connected with the necessity of establishing the role of the objects investigated not only in regional stratigraphic studies, but also in solving problems of stratigraphy on a general scale. This led to the statement and solving of a number of successive interrelated problems. The major problems were 1) working-out the method of studies, consisting in the establishment of the morphogenesis pattern on the basis of morphofunctional analysis of the skeletal ossicles investigated; 2) systematization of stem fragments on the basis of establishing their evolution pattern and possible phylogenetic relations of the taxa distinguished; and 3) use of this systematization for stratigraphic purposes.

The present paper, as its name shows, deals primarily with the method of studies of Paleozoic crinoids on the basis of stem fragments and the principles of their systematics. Therefore, it contains only brief accounts of the stratigraphic use of this group.

Long-term studies accomplished by the author on biostratigraphy of numerous Paleozoic sections in different regions of the USSR (Kazakhstan, Altai, Siberian and East European platforms, Central Asia etc.), are described in the corresponding publications. Due to these studies, numerous specimens were collected, from almost all major regions of the USSR characterizing the stratigraphic and facies associations of various paleontological assemblages, represented by crinoid stem fragments. The general pattern of evolutionary modifications of the taxonomic composi-

tion of crinoids, defined from stems, was amplified considerably due to our acquaintance with collections of specimens which were sent to be identified, and also the collections kept at geological museums in Leningrad, Moscow, Sverdlovsk, Alma-Ata, Novosibirsk, and Tallin.

The analysis of these materials, as well as of numerous publications on paleontological studies of crinoids enabled us to establish the major pattern of evolutionary modifications of skeletal ossicles of crinoids, represented by stems, and gave an exclusive stratigraphic value to these widespread and relatively poorly studied fossils.

Studies on new paleontological objects are commonly connected not only with difficulties which arise when we are looking for the method of investigating them, but also with the overcoming of a certain sceptical attitude to the prospects of scientific and practical value in the new studies. Therefore, at present, we cannot but recall those who pioneered the studies of dissociated fragments of crinoid stems with sincere gratitude. Their keen scientific insight allowed them to see great biostratigraphic value in these paleontological objects. Among these scientists, whose works served as the basis on which the author elaborated the proposed method of studies of dissociated crinoid stem fragments, should be mentioned especially R. MOORE (USA), R. S. YELTYSHEVA and O. S. VYALOV (USSR), H. TERMIER & G. TERMIER (France), and H. SIEVERTS-DORECK (Germany).

The attempts made by the author would not have been so fruitful without the support of many colleagues, who helped in gathering paleontological collections from different areas over the extensive territory of the USSR and took an active part in discussing the results of studies. The author expresses her sincere gratitude to all of them.

Special thanks are due to a constant opponent of the author, Professor R. F. HECKER for his advice and well-wishing criticism.

General remarks

Diverse structures of the crinoid skeleton, like shape, dimensions and adaptive features create extremely favourable conditions for tracing and studying the evolution of this group (MOORE 1950, 1952). As is known, major trends of crinoid evolution in the Early Paleozoic period originally led to differentiation of major skeletal elements, connected with isolation of the stem, consolidation of the cup and development of mobile bifurcating arms. Most of the adaptive trends in the evolution of Paleozoic crinoids are characterized by intensification of the movement function. It affects the articulation type of the skeletal elements of stem and arms. A number of adaptive trends, particularly characteristic of many Late Paleozoic crinoid groups, are noted for a "simplification" of the skeleton structure, loss of stem with transition to swimming or oligomerization of the skeletal ossicles.

In Paleozoic crinoids of all major taxonomic units, evolutionary modifications affect practically all structural elements. However, most adequately studied is the pattern of evolutionary modifications observed in the structure of crinoid crowns. It is these studies that form the basis for the systematics of Phanerozoic crinoids.

An extremely complicated structural organization of crinoid skeletal ossicles, which can only be compared with a composite skeleton of vertebrates, their high rate of evolution, the abundance and diversity of evolutionary differentiation trends, all these things determine the great significance of the group for stratigraphic studies. Especially for providing grounds and giving characteristics of stratigraphic units on a general scale, viz. systems, series, and stages, for determination of their boundaries and range.

Calyxes and crowns might be used for the purposes of stratigraphy only in a few regions, where these fossils can be collected in strict stratigraphic succession. In such cases, crinoids are also used for zonal subdivision. Zones in zonal scales based on crinoids are of practical significance, primarily, for regional stratigraphic studies. At the same time, these scales also reflect the general pattern of the historical evolution of crinoids.

Unfortunately, in spite of the known advantages as compared with many other paleontological groups, the use of crinoids in stratigraphic practice is beset by certain difficulties. They are connected with the fact that entire skeletons are only rarely found; commonly, after the death of an animal, they fall into dissociated elements, viz. arm columnals, stem columnals, and cup plates.

Thus, on the USSR territory, in the interval under consideration of the Ordovician, Silurian, and Lower Devonian, only about 70 crinoid species are at present known, which were determined by their calyxes and crowns (Table 1). These localities are confined to certain stratigraphic levels, separated by large "unfossiliferous" intervals. Naturally, these data cannot give a full idea of the stratigraphic range and space distribution of this group in the Early and Middle Ordovician.

It is doubtful whether *Ramseyocrinus* (tetralobate columnals with a tetralobate axial canal), *Ristnacrinus* (columnals with a fulcral ridge on the articular surface) and *Eustenocrinus* (pentapartial articulation type of columnals) should be combined into one family. The pattern of morphogenetic changes of the articular surface of *Hexacrinites* stems confirms phylogenetic links between *Haxacrinites* and *Platycrinites*, which were advocated by YAKOVLEV (YAKOVLEV & IVANOV 1956), and by MOORE & LAUDON (1943). From the viewpoint of morphogenesis of Gasterocomidae stems, the successive phylogenetic links between the families Gasterocomidae and Hypocrinidae, presumed by ARENDT (1970), are not justified. Structural features of Gasterocomidae stems illustrate them as a group of inadunate crinoids, markedly standing apart in Devonian, being in the final stage of evolution, and do not confirm successive phylogenetic links with specialized Hypocrinidae.

An idea of a possible use of the structural features of stems for solving problems of the systematic position of the known crinoid taxa was conveyed by many scientists (BATHER 1900; EHRENBURG 1922 a, 1922 b, etc.; MOORE 1939; MOORE & LAUDON 1943; H. TERMIER & G. TERMIER 1949; UBAGHS 1953 etc.). However, up to the present time, stem characters are not widely used either for establishing phylogenetic links of taxa, or for describing taxonomic categories of crinoids, distinguished on the basis of crowns and their parts. Besides the characteristics of the outer surface of stems, it is also highly important to take into consideration the structural features of articular surfaces of columnals in the proximal and distal parts, viz. dimensions, shape and articulation character of the axial canal and ligamentary field, character of ribbing, disposition of interpentamerous sutures, and other features.

Working out of the general systematics of Paleozoic crinoids should be preceded by an enormous amount of careful work on the study, first of all, on all the collected material of crowns and cups, found together with stems. Basically, the same also concerns other stem-bearing echinoderms, and, primarily, cystoid groups. Many of these materials are kept in museums in different countries. Of paramount interest among them are collections of Ordovician, Silurian and Devonian echinoderms.

With the present state of knowledge about Paleozoic crinoids, the danger of combining taxa, established on the basis of different parts of the crinoid skeleton, will, probably, result in greater losses from the scientific and practical viewpoint, than the recognition and retaining of parataxonomic classifications.

Thus, we come to the following conclusions: 1) about the necessity and practical efficiency of using parallel classifications in the general systematics of Paleozoic crinoids, and 2) establishing taxonomic units on the basis of stems, the relations of which with taxa of the general classification of crinoids, based on cups and crowns, in the vast majority of cases remain unknown.

Regarding the problems of nomenclature in classification of dissociated stem ossicles, one should recognize that it is reasonable to use "crinus" ending in names of generic categories (*Decacrinus*, *Particrinus*, *Apertocrinus* etc.). Use of these names in most present papers indicates a rather high degree of reliability of the fact that the taxa distinguished belong to the class Crinoidea. The use of special names for the stem fragments of *Pentagonopentagonopa* or *Pentagonopentagonalis* in general in advance leads to setting up polyphyletic groupings with a vague systematic position, taking us back to the state of knowledge of the time when terms *Entrochus* and *Trochites* were used in nomenclature.

Development of views on the classification of Paleozoic crinoid stems

The present studies of Paleozoic crinoid stems are mainly aimed at solving stratigraphic problems. Their successful solving is, to a great extent, dependent on the method of studies and principles of systematics of the objects investigated.

An enormous morphological diversity of crinoid stems, not connected with cups in a fossil state, and their abundance in Paleozoic sections has long attracted the attention of scientists. As is indicated by KONINCK & LE HON (1854), these studies began as long ago as the XVI century. During many decades, attempts were made, in certain cases rather successful ones, to use different types of crinoid columnals in regional stratigraphic studies (GOLDFUSS 1862—1866; EICHWALD 1856; SCHULTZE 1867; QUENSTEDT 1874—1876; WAAGEN & JAHN 1899; W. E. SCHMIDT 1932, 1942, etc.). In publications, they were in most cases described as collective groups under different names (*Entrochus*, *Entrochi*, *Entroques*, *Trochites*, *Trochita*, *Trochi* etc.) and were not included in the general crinoid systematics (BIESE 1934).

The revision of this material was accomplished by MOORE in the 30's of this century (MOORE 1939). In this paper was first formulated the object of studies and systematization principles of crinoid stem columnals isolated from cups in a fossil state, as well as for dissociated plates of the cups proper and arm columnals. A special classification, proposed by MOORE for the stem columnals, amounted for their cataloguing with the use of a binary nomenclature for this purpose. The essence of the method proposed for studying stem columnals was determined as follows: "We may compare our task in classifying crinoid columnals to that of arranging a miscellaneous assortment of nuts and bolts into groups having like characters, such as number and pitch threads, without effort to determine the particular machines from which they might have been disassembled" (MOORE 1939, p. 187). MOORE supposed that it was possible to define separate columnals from one stem under different species names. All the diverse crinoid stems in MOORE's classification were subdivided into two collective groups of a taxonomic rank of "genus" and "species". Genus (*Pentagonopentagonopa*, *Cyclocyclopa*, *Pentagonocyclopa* etc.) was defined by a combination of two characters, viz. outline of columnals and outline of the axial canal. The species characters included all other morphological features of a stem. Units of a higher taxonomic order, viz. "major groups" and "groups", had no significance of their own in this classification, since their determining features (outline of columnals, for major groups; and outline of the axial canal columnals, for groups) in their combination give a characteristic of a "genus", which rules out their subordination.

MOORE's paper (1939) is of paramount historical value. It, to a great extent, determined the fate of further studies on Paleozoic crinoid stems and their studies for the purposes of stratigraphy.

In the practice of stratigraphic studies MOORE's classification was used in the description of Carboniferous and Permian crinoids of North America (MOORE & PLUMMER 1940; STRIMPLE 1962 a, b, etc.). Its possible use for systematization of crinoid columnals from the Devonian and Carboniferous deposits of the USSR was discussed by YAKOVLEV (YAKOVLEV & IVANOV 1956) and ANTROPOV (1954). WARREN regarded the transverse section of columnals and the axial canal as major taxonomic characters for the classification of Middle and Upper Devonian crinoid stems in New York State (WARREN 1962). Principles of MOORE's classification were also used in a recent paper by WRIGHT (1983) for systematization and description of the Ordovician crinoid columnals from Northern Wales.

Following MOORE, French scientists, H. TERMIER & G. TERMIER (1949, 1950, 1974), also began studying crinoid stems, separated from calyxes and crowns in a fossil state. The main principle, which they put forward as the guiding one, when describing isolated fragments of old crinoid stems, consists in using names of the general systematics of crinoids for this purpose (of *Hexacrinites*, *Platycrinites*, *Poteriocrinites*-type). Worthy of note is the suggestion made by the French authors to classify old crinoid stems into two large groups, Tenuiproxa and Pachyproxa.

VYALOV (1953, 1977) over a number of years proposed a classification of old crinoid stems which would take into account practically all taxonomic categories of a biological classification, including the class. He distinguished Paleozoic and Mesozoic crinoid stems as an independent class, Caulinaria. A strict system of subdividing Caulinaria into subclasses, orders and families was not used in practice. Probably, this is due to the fact that taxonomic categories of this classification had no strict descriptions. They had a predetermined heterogenous character, since they presupposed integration of morphologically similar forms of different ages from a broad stratigraphic interval, covering both Paleozoic and Mesozoic.

Of the above classification theories of crinoid stem columnals, principles of their systematization, formulated by MOORE (1939) were further developed. They were taken into account in the classification by YELTSHEVA (1955, 1956), who proposed a system of diagnostic keys for 36 conventional genera, defined by possible combinations of the axial canal and columnal outlines (*Cyclocyclicus*, *Cyclopentagonalis*, *Pentagonopentagonalis* etc.). As compared to the suggestions made by MOORE, YELTSHEVA emphasized a greater systematic significance of the feature, referring to the character of the axial canal section. Correlations of generic categories in MOORE's and YELTSHEVA's classifications are shown in Table 2. Major systematic units in YELTSHEVA's system, viz. subgroups and groups, similar to MOORE's classification, have no taxonomic significance of their own, for their characteristic features (outline of columnals, a feature of a subgroup; outline of canal, a feature of a group) in combination give a characteristic of a "genus" (*Pentagonopentagonalis* etc.).

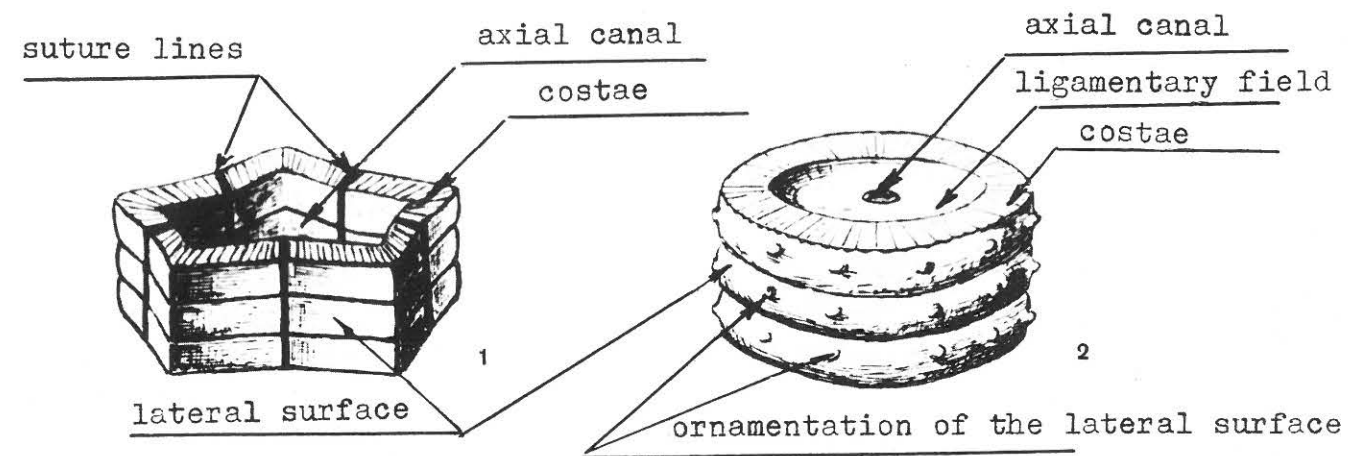
In the USSR, the classification by R. S. YELTSHEVA marked the beginning of purposeful collections and systematic studies of Paleozoic crinoid stems. In the 50's and 60's, this classification was widely used in stratigraphic practice in the Soviet Union. It served the basis for systematizing abundant specimens (several hundred species) collected from the Ordovician, Silurian, Devonian, Carboniferous and Permian deposits. Besides R. S. YELTSHEVA, also participating in collecting and studies were T. V. SHEVCHENKO (a series of papers from 1959 to 1985), YU. A. DUBATOLOVA (a series

with changes in crinoid crowns, and in certain cases, particularly in Early Paleozoic, determine various adaptive trends of crinoids. Thus, the development of a long flexible stem is correlated with consolidation of the calyx plates and their regular disposition at the calyx base; atrophy of the stem results in a disturbance of the regular structure of the base; development of a short fixed bent stem is connected with a bilaterally symmetrical disposition of the crown plates etc.

Morphology and morphofunctional analysis

The exceptional diversity of morphotypes of crinoid stems is due to the high evolution rate of this group and diverse adaptive trends of its evolution. Skeletal ossicles, composing the stem, viz. columnals (Text-fig. 1), in their morphology reflect the change of functions of the stem proper at different stages of its evolution. In primitive forms it is supporting the cup, and in more advanced ones it has a function of active movement.

In attached benthic forms, which make up the most abundant group of Paleozoic crinoids, the stem is made up of dozens, and sometimes, hundreds of columnals. It is commonly divisible into three parts, viz. 1) upper, proximal, adjacent to the cup; 2) lower, distal, and 3) holdfast. The proximal part of the column is, as a rule, characterized by alternating columnals of different orders: nodals, internodals, and infranodals. WEBSTER (1974) proposed special terms "proxistele", "mesistele", and "dististele" for different parts of a column. However, their practical use for all types of columnals is difficult, since the boundary between the proximal and distal parts of the column is not always distinct.



Text-fig. 1. Morphological features of crinoid columnals: 1. pentamerous columnals; 2. monolithic columnals (after STUKALINA 1964).

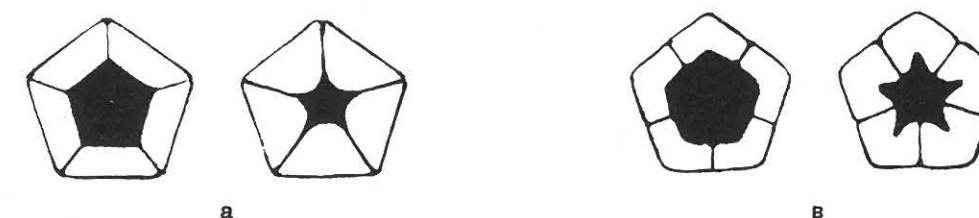
Columnals differ in their morphology depending on their position within the stem. In the lower, distal part, they commonly retain the morphological features, characteristic of older primitive forms.

In Ordovician and Early Silurian crinoids, columnals are usually made up of pentameres. Attachment areas of pentameres are marked by suture lines (interpentamerous suture lines). According to the author's observations, two essentially different types of pentamerous structure of crinoid stems are distinguished (Text-fig. 2) (STUKALINA 1966, 1967): 1) The first type — Angulata, the most widespread, is observed in the vast majority of the known Ordovician and Silurian crinoids. Interpentamerous suture in this type of stems connect angles of the axial canal with those of columnals. 2) The second type — Strialata, of a pentamerous structure, known in inadunate Ordovician crinoids, *Aethocrinus* and *Grenprisia* is less frequent and has a lower species diversity. Interpentamerous suture lines in the second type of stems are perpendicular to the walls of lumen and the sides of columnals.

The axial canal runs along the stem axis, and its cavity is in the proximal part connected with the calyx cavity. The axial, or central, canal encloses the connective tissue, which lines walls of the canal and axial cords. In most primitive forms, soft body organs were enclosed in a broad axial canal cavity. It is assumed that this soft body might have been a chambered organ (BATHER 1900; UBAGHS 1953, etc.). The dimensions and a transverse shape of the axial

canal are highly diverse and correlated both with the character of columnals outline, and the morphology of the articular surface. Most widespread in Paleozoic were crinoids the stems of which display a pentactinal symmetry of the transverse shape of the axial canal. Relatively primitive forms have a broad pentagonal canal. It should be noted that the diameter of the axial canal of the stem frequently exceeds one half of the columnal diameter (Text-fig. 1,1). In more advanced forms, the axial canal has a stellate, or quinquelobate shape. Lobes of the axial canal are commonly directed into the angles of columnals. In different morphological types of columns, lobes of the axial canal have different outlines, from broad bulb-like to narrow slit-like. Columns with a very small "point" axial canal belong to highly advanced morphofunctional types (Text-fig. 1,2).

Columnals adjoin each other by articular facets or articular surface. The attachment surface is ornamented by a system of radial, pinnate, multiple bifurcating costae and short costae of different length. Costae and short costae are separated by grooves. They are so arranged that costae on the articular surface of one columnal enter grooves in the articular surface of an adjacent columnal. Thus, there is a rigid union of columnals, which might counteract the torque of the column. High torsional stresses should, probably, be expected in long, flexible stems. Coarse costae on the articular surfaces of columnals in such stems are abruptly widened towards the peripheral margin of a columnal, and thin low costae are bifurcating. For the zone of the articular surface of columnals, covered by costae and short costae, separated by grooves, MOORE & JEFFORDS (1968) proposed good term "crenularium". In very low columnals, a rigid union is effected not only by fine bifurcating costae, but also by the articular surface proper. In this case, this surface may be undulated.



Text-fig. 2. Two types of a pentamerous structure of crinoid columnals: a) Angulata type: suture lines branch off from the axial canal angles; b) Strialata type: suture lines are normal to the axial canal walls (after STUKALINA 1966).

Stems, made up of columnals, the articular surface of which is covered overall by costae, belong to passive mobile morphofunctional types of stems. Their bending and tilt is, apparently, due to the active mobile arms of the crown. In highly advanced active mobile morphofunctional types of stems, deepened areas, devoid of costae, are traced on the articular surface of columnals. These areas point to a development of elastic connective commissure, which connect the columnals. Connective commissure are, of course, not preserved in the fossil state; and, thus, there are different theories as to their nature. It is commonly assumed that they were an elastic ligamentary connective commissure (Ligament-Bündel). However, for highly organized forms of *Hexacrinus*, *Arthroacantha*, *Platylateum*, *Platycrinus*, *Camptocrinus*, *Stomiocrinus*, *Neocamptocrinus*, *Myelodactylus*, *Ammonocrinus* types, the existence of muscle commissure is also possible. The indefinite nature of the ligamentary connective commissure in fossil crinoids, tissue which lay between columnals, is also reflected in the different names of these deepened areas, lacking costae. Quite a number of synonymic terms for them are known from publications, viz. ligamentary depression, deepening zone (YAKOVLEV & IVANOV 1956), central area (MOORE 1939), central facet (YELTSYSHEVA 1955, 1956, etc.) deepening field, inner field, central field, rosette (VYALOV 1953), areola (MOORE, JEFFORDS & MILLER 1968). Admitting the possible presence of a muscle, commissure serving as a connective tie between columnals in highly advanced specialized crinoids, it might be assumed that in more primitive (simple) morphofunctional types of stems, these depressions in the articular surface of columnals are also muscle scars. In the present paper, deepening areas in the articular surface of columnals are termed ligamentary fields, though this might not always strictly correspond to their meaning. This term was introduced by the author (STUKALINA 1964, 1965, 1966). Ligamentary fields may be of a pentagonal, stellate, quinquelobate, decempartite, round or oval outline. They have different dimensions and deepening degrees. Less advanced forms have a smooth ligamentary field. Highly advanced forms display a costate surface of the ligamentary field (*Divisicrinus*, *Sibiricrinus*, *Scyphocrinites*), or a granulose shagreen surface (*Kojvicrinus*, *Pinegicrinus*, *Floricyclus*,

Mooreanteris, etc.). These costae and granules increase the total attachment area of muscle commissures. On the articular surface of highly advanced forms there is often a low ridge, which surrounds the axial canal in the form of a papilla (*Altimarginalicrinus*, *Scalaricrinus*, *Asperocrinus*, *Nimioocrinus*, *Hexacrinites*, *Lampterocrinus*, *Gilbertocrinus*, *Laudonomphalus*, etc.). MOORE, JEFFORDS & MILLER (1968) introduced a good term "perilumen" for designating this ridge.

In other forms, the articular surface is symmetrically divided by a longitudinal ridge or fulcral ridge (*Ristnacrinus*, *Platyplateum*, *Eucladocrinus*, *Camptocrinus*, *Neocamptocrinus*, etc.).

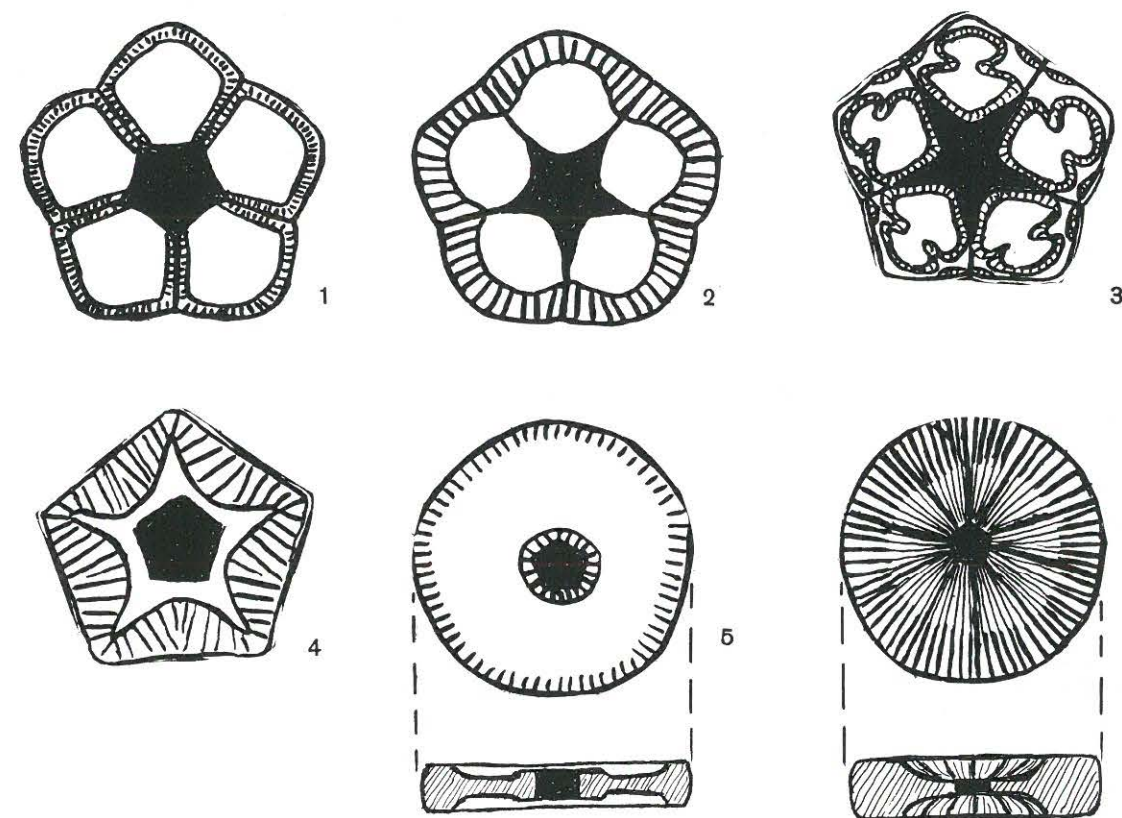
The lateral surfaces of columnals, as well as their other morphological characters are rather diverse. In many instances their shape is correlated with the articulation type of columnals. Thus, in forms with well-developed ligamentary fields, the lateral surface is commonly abruptly convex. Columnals proper acquire a barrel-like shape. In stems with a broad axial canal cavity, lateral surfaces are commonly flat. There are columns with a concave lateral surface. The lateral surface of columnals is frequently ornamented by sculptural formations, viz. granules, spines, tubercles. In the proximal part of stems, ornamentation is commonly more distinct in nodals. It is common knowledge that the ornamentation of columnals and calyx plates is frequently the same (MOORE 1939; YAKOVLEV & IVANOV 1956; UBAGHS 1953 etc.). The functional role of sculptural formations is not quite clear, though they may be, in a number of cases, regarded as a protective device.

One of the important morphological characteristics in the description of columnals is the characteristic of their absolute and relative dimensions. In the practice of descriptions, the Russian specialists commonly make ample use of such parameters as diameters of columnals, axial canal, and ligamentary field, height of columnals, and ratios of these values. Noteworthy is a system of quantitative characteristics of morphological elements of columnals and their indexing, worked out by MOORE, JEFFORDS & MILLER (1968) and amplified by WEBSTER (1974), HAUDE (1981), BRISKEY (1981), and LE MENN (1983). In future, this system of quantitative characteristics may appreciably expand the species characteristics available. This is well illustrated in the description of stems of Permian crinoids *Neocamptocrinus* (WILLINK 1980), stems of Ordovician crinoids in Wales (DONOVAN 1983, 1984 a, b) and Norway (BRISKEY 1981), stems of Middle and Upper Paleozoic crinoids from Poland (GLUCHOWSKU 1981 a, b, 1982) and Lower and Middle Devonian of the Armorican Massif (LE MENN 1983).

In recent years, the scanning microscope has been increasingly used in practice, allowing studies on the microstructure of the column stereom. Working-out the procedure of these investigations is described in the papers by ROUX (a series of papers from 1970 to 1978), MACURDA & MEYER (1975), LANE & MACURDA (1975), SEVASTOPULO & KEEGAN (1980) etc. This procedure is more acceptable for studying skeletal ossicles of recent and Meso-Cenozoic crinoids. It is less acceptable for the study of Paleozoic crinoids, because of secondary diagenetic changes in the skeleton structure of old crinoids. At the same time, studies on the microstructure of skeletal elements of crinoids are, undoubtedly, of great cognitive significance, and in future may, probably, be used in taxonomy.

For establishing the morphogenesis pattern of Paleozoic crinoid stems, morphological elements of the articular surface of columnals are of paramount significance. Among all the diverse morphological types of articulation, MOORE, JEFFORDS & MILLER distinguished five types, viz. zygosynostosis, synostosis, synarthry, cryptosymplexy, symplexy and syzygy (MOORE, JEFFORDS & MILLER 1968). This classification of the articulation of columnals was continued by the author (STUKALINA 1979, 1982 b). New terms were introduced, viz. pentapartial, bullial, comptial, mamillial, divisial, and rosalia (Text-fig. 3). By a pentapartial type of articulation we mean the articulation of columnals typical for many Ordovician and Early Silurian crinoid species (*Particrinus*, *Baltocrinus*, *Pulchellocrinus*, etc.). The articular surface of pentameres is covered by ligamentary relief pits, the outlines of which coincide with those of the pentameres. A bullial type of articulation is a rather rare in Ordovician crinoid stems composite articulation type of pentameres, making up columnals (*Mirabilicrinus*, *Kalgacrinus*, *Ramulicrinus*, *Bulbocrinus*, etc.). Most of the articular surface of each pentamere is taken up by a bulla, a distinct elevated area, which in its shape approaches an ellipse. The central part of the oval is taken up by one or two ligamentary pits. A characteristic feature of the comptial type is a relief ligamentary field with a distinct stellate outline (*Comptocrinus*, *Pennatocrinus*, etc.); that of the rosalia type, a relief ligamentary field of a quinquelobate outline with low, semicircular lobes (*Rugulosocrinus*, *Rookulaecrinus*, etc.). A mamillial type of articulation is characteristic of highly advanced morphofunctional stem types (*Altimarginalicrinus*, *Scalaricrinus*, *Asperocrinus*, *Nimioocrinus*, *Hexacrinites*, etc.). Its specific feature is, primarily, the central circular ridge, lying in a ligamentary field depression. The divisial type of articulation is noted for coarse radial costae, dividing the articular surface of columnals into sectors (*Divisicrinus*, *Sibiricrinus*, etc.).

Classification of the most characteristic articulation types of columnals reflects the difference between morphofunctional types of stems, which relate to different adaptive trends in the evolution of Paleozoic crinoids. It should be emphasized once again that morphofunctional types of stems do not represent specific taxa in crinoid classification based on stems. They may be compared only with categories of adaptive ecological groups, which are not regarded as synonyms of taxa in the classification based on phylogenetic principles. In this case, the distinguishing of morphological types is justified by the fact that they are convenient categories. Such categories might be used in morphofunctional analysis and for establishing the major morphogenesis pattern.



Text-fig. 3. Articulation types of columnals: 1. pentapartial; 2. rosalia; 3. bullial; 4. comptial; 5. mamillial; 6. divisial (after STUKALINA 1979, 1982).

Morphogenesis

One of the possibilities of phylogenetic studies of crinoids based on stems is connected with studies of their morphogenesis (STUKALINA 1964, etc.).

The establishment of the morphogenesis pattern consists in the explanation of the genesis of various morphofunctional types of stems and their evolutionary trends. Morphogenetic changes do not fully reflect phylogenetic links between crinoids based on their stems; similar morphofunctional types of stems might appear convergently in different phylogenetic branches. However, each branch might be a particular case of morphogenesis.

Crinoids, similar to many other groups of invertebrates, at the beginning of Paleozoic, took the road of idioadaptive evolution (SEVERTSOV 1949). This resulted in the greater complexity of their skeletal ossicles without any appreciable change of the general organization level, which might result in aromorphosis. Aromorphosis is understood as an appearance of a new group or a new class.

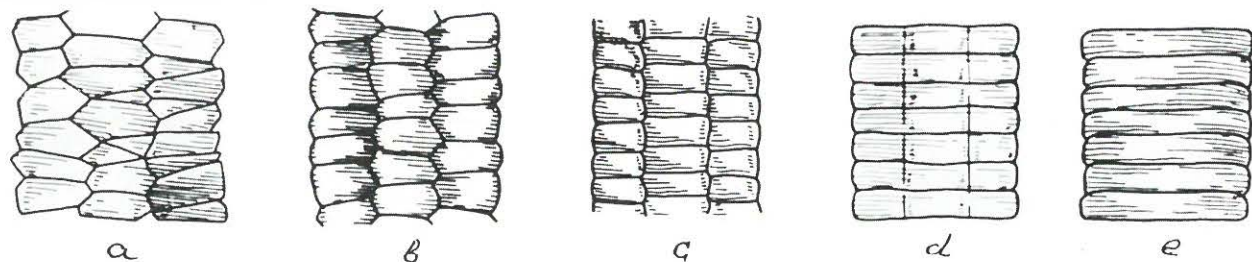
As is known, idioadaptive evolutionary changes in crinoids within a class, generally, consisted in an increase of the cup dimensions, its consolidation, development of flexible multiserial arms and a long flexible stem. In the studies of various evolutionary trends of crinoids, attention is commonly focused on phylogenetic constructions, which are

based on the studies of skeletal ossicles of the cup and arms. These studies resulted in the known crinoid classifications (WACHSMUTH & SPRINGER 1897, etc.; BATHER 1900; JAEKEL 1894, 1918; SPRINGER 1926; MOORE & LAUDON 1943; MOORE & TEICHERT 1978, etc.). Contradictory opinions as regards phylogenetic relations of taxa frequently consist of different evaluations of the taxonomic significance of various cup and arm ossicles. Stems are usually not used in phylogenetic studies of crinoids. Rare exceptions are only groups of specialized crinoids, as, for example, *Crotalocrinites*, *Myelodactylus*, *Ammonocrinus*, *Platycrinites*, *Camptocrinus*, *Neocamptocrinus*, etc.

At the same time, even from the viewpoint of general evolutionary development, it is quite obvious that crinoid stems play a significant role in the formation and isolation of this group of echinoderms as an independent class. The appearance and evolution of a flexible stem promoted the formation of the crinoid cup, consolidation and a regular disposition of its plates and the development of flexible multiserial arms.

Even the presence of a stem determined a regular disposition of the plates at the calyx base. As is known, this is regarded as a major taxonomic feature in crinoid classification. And conversely, the atrophy of a stem or its transformation into a rudimentary organ has a reverse result, i. e. disturbance of the regular disposition of plates at the calyx base.

Special attention should also be given to the fact that the function of stems in crinoid evolution did not remain constant.

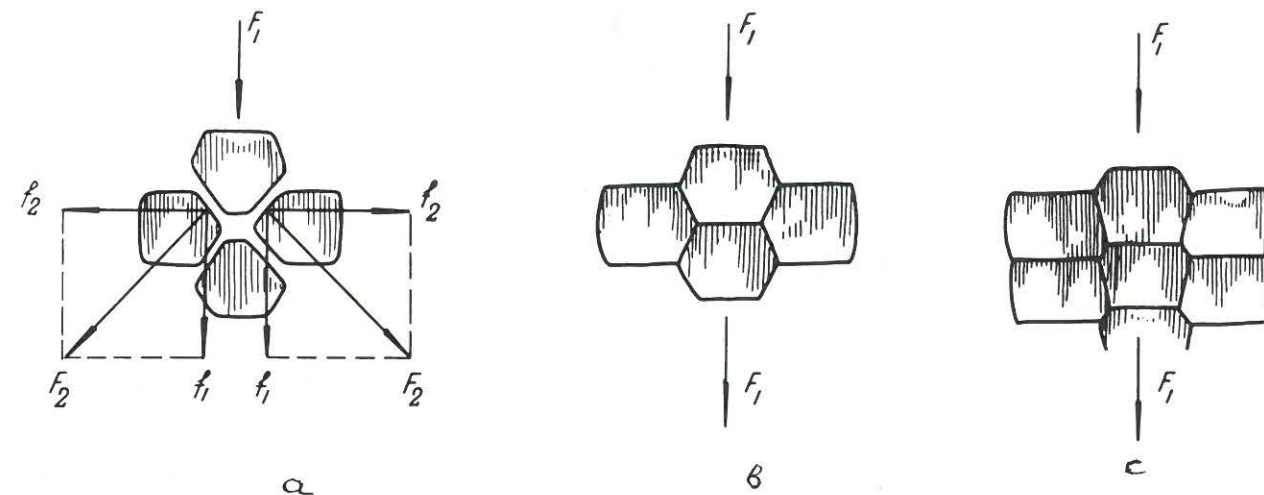


Text-fig. 4. A general scheme of evolutionary development of Paleozoic crinoid stems: a) plates-segments randomly arranged in a stem; b, c) plates-segments (pentameres) arranged in vertical rows in a stem; d) plates-segments (pentameres) arranged in vertical and horizontal rows in a stem; e) the stem is composed of monolithic columnals (after STUKALINA 1967).

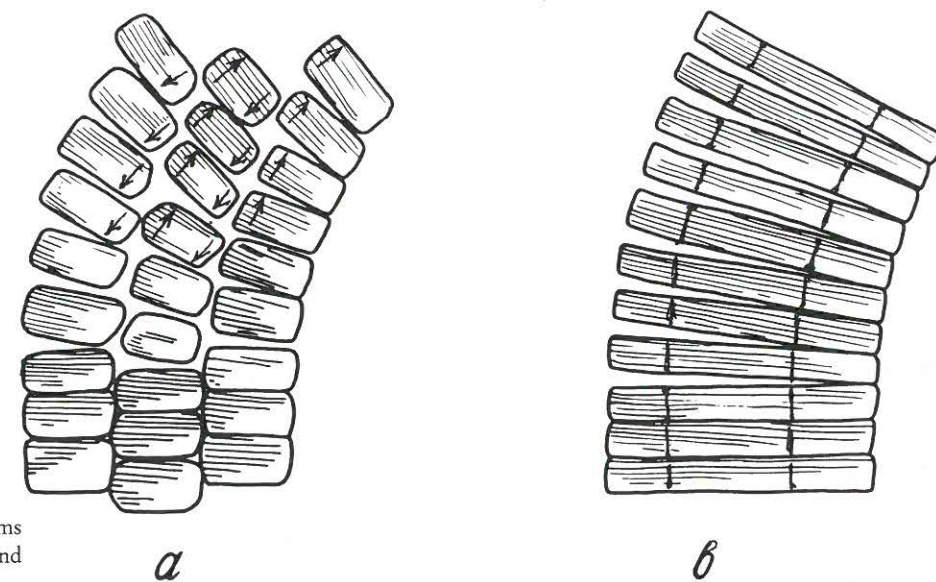
Though up to now there is no common viewpoint as regards the origin of crinoids, most workers tend to draw the conclusion that their ancestral forms were stemless. Their theca was composed of randomly arranged plates and was attached directly to the substrate. Generation of primitive stem on crinoids according to JAEKEL (1984) and BATHER (1900) illustrated by SPRINKLE (1973) as exemplified by other stem-bearing echinoderms, was due to the thecal skeleton differentiation. Originally, the protruding lower part of the theca represented a rudimentary stem. Functionally it differed but slightly from the theca proper and was also made up of randomly arranged thin plates with a movable articulation (Text-fig. 4 a). During later stages of the stem evolution, connected with the increase of its length, the lower protruding part of the theca is constricted and grades into a stem. Its major functions consisted in supporting theca above the substrate and protecting some organs of the animal's soft body, which were enclosed in its broad cavity.

The morphology of all stages of the stem evolution was, to a great extent, determined by the pressure of theca, which was gradually differentiated into the cup and arms. Short primitive stems of the initial evolution stages were made up of randomly arranged plates. They illustrate a low strength of the general stem construction, since under a downward pressure, the composing plates underwent both horizontal, and vertical displacements (Text-fig. 5). The low strength of their construction was also due to a broad cavity of the canal, which formed a single whole with the calyx cavity. Further evolution of the stem and its separation from the theca (crown) was connected with an increase of the strength of its skeletal ossicles. This showed up as a constriction of the stem cavity (axial canal) and a regular arrangement of the composing plates (pentameres). The constriction of the axial canal promoted the thickening of stem walls and the increase of the articular surface of plates-pentameres. The plates-pentameres proper gradually acquired a regular disposition; they were first grouped into vertical, and then horizontal rows according to the "brickwork" (Text-fig. 4 b, c, d) principle. This eliminated their possible sideward displacement under downward pres-

sure (Text-fig. 5 b, c). In the case of such disposition of plates-pentameres, stems might have a certain tilt (Text-fig. 6), indicative of their new function, viz. function of movement. At the same time, possible vertical displacements of plates-pentameres made the structure of stems in general not strong.



Text-fig. 5. Distribution scheme of forces (F_1 , F_2 , f_1 , f_2) under a vertical pressure, affecting stems with a pentamerous structure (after STUKALINA 1967).



Text-fig. 6. Scheme of tilt of crinoid stems composed of mobile pentameres (a) and monolithic columnals (b).

A growing possibility of the stem bending (development of the movement function) with its elongation should, naturally, be connected with the higher strength of the skeletal ossicles. This is reflected in a gradual constriction of the axial canal cavity which was accompanied by the pushing-out of the soft body organs into the calyx cavity. Thus, the axial canal cavity encloses only blood vessels, nerve tissue and axial connective, commissure which plays the major role in the articulation of columnals. An increase of the stem strength is also promoted by a regular arrangement of the plates-pentameres into horizontal rows. The natural completion of this process is the fusion of the plates-pentameres into monolithic plates, i. e. appearance of new stem ossicles-columnals (Text-fig. 4 e). Plates-pentameres fused into horizontal rows, in case of stem tilting, behave as monolithic columnals, for in this case, the possibility of their vertical displacement is eliminated (Text-fig. 6 b). The process of the ordering and arrangement of the plates-pentameres in stems is, apparently, similar to the process, taking place at the calyx base (YAKOVLEV 1947 a, b, 1949;

YAKOVLEV & IVANOV 1956, etc.). Here also the pressure exerted by their upper part and arms on the calyx base, results in an ordered disposition of the composing plates according to the "brickwork" principle. They are grouped into one or two small horizontal circlets with a trend towards fusion inside the circlet.

Thus, the evolution of stems consists in a regular arrangement of the composing plates-pentameres into vertical and horizontal rows with their subsequent fusion into monolithic columnals. This is connected with a successive elongation of stems and their assuming independent functions, different from those of theca. Almost all soft body organs of the animal are displaced into a cup, and the stem not only supports the cup above the substrate, but also imparts to it a certain mobility, thus, expanding the alimentation areas of the animal (Text-fig. 9a).

A pentamerous structure of stems is observed in most Ordovician crinoids known. In Early Silurian, the abundance of pentamerous forms is abruptly decreased, and in higher beds of Silurian, Devonian, Carboniferous, and Permian, pentamerous stems are found only in single crinoid species (SIEVERTS-DORECK 1957; MOORE & JEFFORDS 1968; STUKALINA 1967; WARN 1973).

At the same time, as the material studied shows, the character of a pentamerous structure of Ordovician and Silurian crinoid stems is indicative of their rather high evolutionary stages. Already in the Early and Middle Ordovician species displaying an incomplete arrangement of the stem pentameres into horizontal rows (an abrupt stepped articular surface, and zigzag-like interpentamerous suture lines on the lateral surface), are found comparatively rarely (*Apertocrinus privus* (YELT.), *Morkokacrinus morkokaensis* (YELT.), *Parvicrinus parvus* STUK., *Mirabilicrinus mirabilis* (YELT.), *Dwortsowaecrinus sculptus* STUK., *D. korjikensis* STUK., *Fascicrinus concavus* STUK., *F. fasciculatus* STUK., etc.). In the vast majority of cases, pentamerous stems of Ordovician crinoids have flat articular surfaces and smooth continuous vertical interpentamerous suture lines on the lateral surface of stems.

It is of interest that in the case of a final fusion of pentameres into horizontal rows, traces of a pentamerous structure do not disappear immediately from the stem columnals. As the material investigated shows, they first "disappear" from the lateral surface of columnals. Their former presence might be deduced only from thin sections of the lateral surface of the stems, or from a characteristic arrangement of sculptural formations (excrescences, spines, tubercles, etc.). Relics of a pentamerous structure on the articular surfaces of columnals turn out to be more stable. They are found in many Silurian forms, and in certain phylogenetic lineages among Devonian and Carboniferous crinoids (*Clavaticrinus*, *Anthinocrinus*, *Bazarcrinus*, *Floracrinus*, *Floripilla*, *Floricyclus*, *Pentamerostella* etc.).

The appearance of stems with monolithic columnals is recorded as early as the Middle and Late Ordovician (*Ristnacrinus*, *Altimarginalicrinus*, *Rosulicrinus*, *Simplocrinus*). In the Early Silurian, the number of crinoid species, having stems made up of monolithic columnals, is markedly increased. However, this feature of the stem structure is most pronounced in the Middle and Late Paleozoic crinoids.

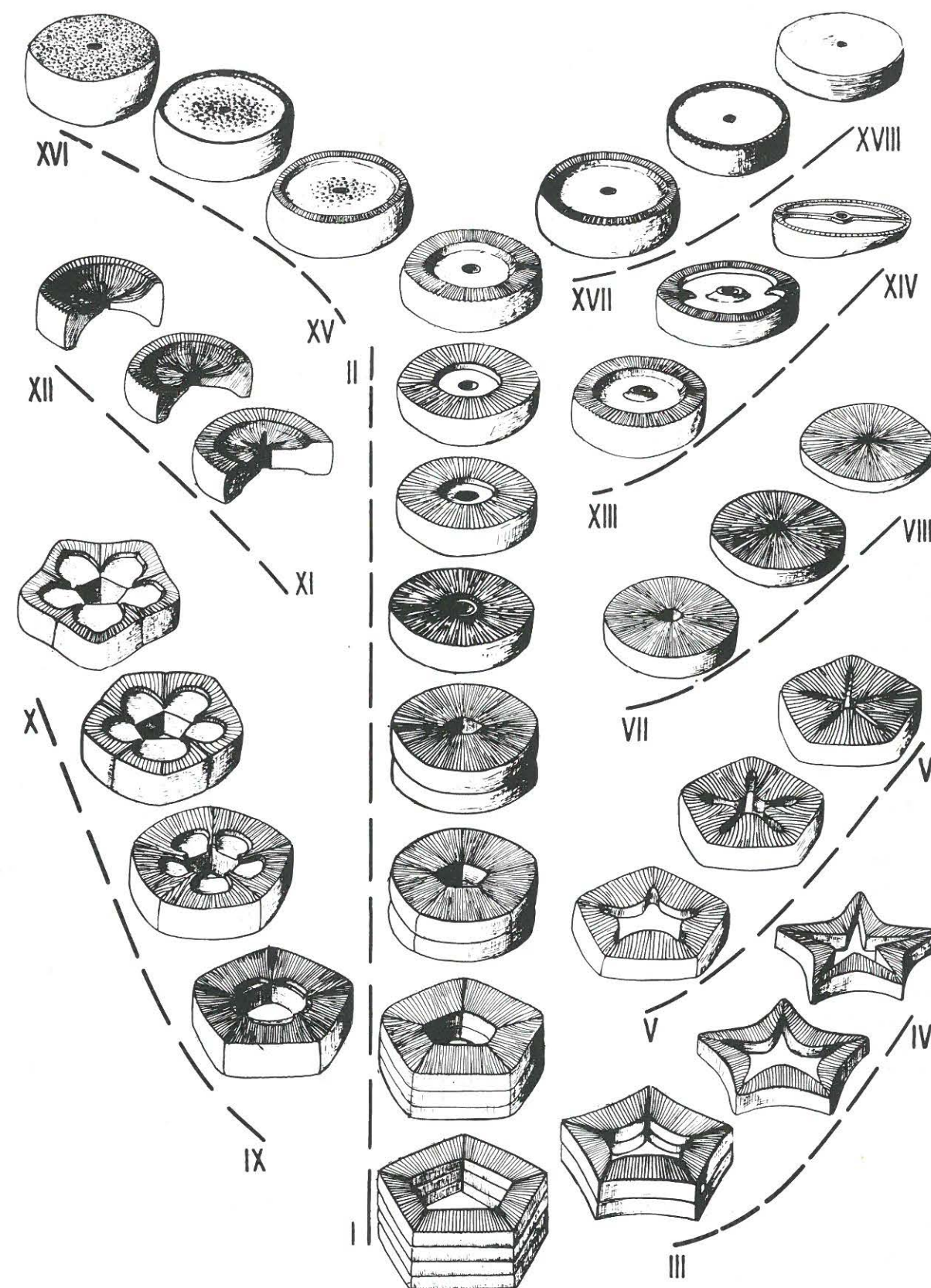
A gradual change of the stem structure, from pentamerous to monolithic columnals, may also be observed within one stem. In this case, features of a more primitive structure are confined to the distal part of the stems.

Subsequent trends of evolutionary modifications of crinoid stems, composed of monolithic columnals, are characterized by an exceptional diversity of adaptive trends. Here, only the basic general scheme of morphogenesis of crinoid stems is considered, which reflects the most characteristic adaptive trends of their evolution (Text-fig. 7).

Most of them are characterized by a gradual constriction of the axial canal cavity, which is correlated with the thickening of the stem walls and an increase of the general articular surface of adjacent columnals.

There are two main trends in the constriction of the axial canal cavity.

One of them, which turned out to be least progressive, is associated with differentiation of the axial connective commissure, a gradual decrease of the central part of the axial canal and formation of lobes, directed towards angles of columnals (genera *Compositocrinus*, *Webericrinus*, *Bakanasocrinus*, *Eqiasarowicrinus*, *Bystrowicrinus*, *Flexicrinus*, *Klunnikovicrinus*, *Clavaticrinus*, *Mediocrinus*, etc.) (Text-fig. 7, V—VI). Lobes are directly connected with the central part of the canal. In certain instances, they might, apparently, be regarded as relics of a broad overgrowing canal. This process, probably, expresses a trend towards preservation of a broad axial connective commissure, while the articular surface of columnals is increasing and, thus, their strength is also mounting up. If the central part of the canal is broad, its lobes are, usually, short and have a bulb-like or digitate shape. When stems with such structure of the axial displayed a tilt towards angles of a columnal, or towards its sides, the tension of the axial connective remained practically the same. However, the divergence angles of columnals were different. Thus, becomes clear the persistence of a pentagonal outline of columnals in representatives of *Compositocrinidae*, *Webericrinidae*, *Flexicrinidae*, and *Eqiasarowicrinidae*.



Text-fig. 7. General scheme of morphogenesis of Paleozoic crinoid stems (after STUKALINA 1966).

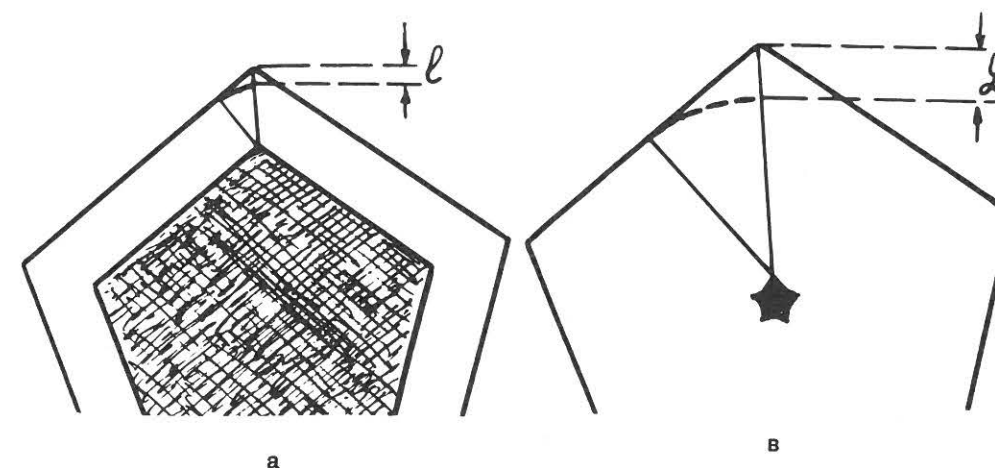
Quite a different situation is observed in morphofunctional types of stems, in which the central part of the canal is constricted abruptly. An abrupt constriction of the central part of the axial canal is usually accompanied, first, by the generation of long lobes, and then, of short ones. This may be well illustrated by the known representatives of the families Bystrowicrinidae, Flexicrinidae, and Klunnikowicrinidae. Long lobes of the axial canal have different dimensions and shapes. For instance, in Bystrowicrinidae representatives, they remain narrow through the entire length, or are constricted at the base and widened abruptly in the distal part; or expanding in the central part, are again constricted abruptly near the distal edge. In spite of a different shape of lobes, they are all united by a common tendency towards broadening. This is mainly observed near the distal edge of lobes. Broadening of lobes, on the one hand, increases the attachment area of the axial connective commissure and on the other hand, when the distal edge of the lobes is broadened, an equal divergence angle of columnals becomes possible if there is a similar tension of the axial connective commissure. This is correlated with the outline of columnals, which in the case of a given axial canal structure, loses its distinct pentagonal section and gradually acquires a rounded shape. Short lobes of the axial canal Bystrowicrinidae, Flexicrinidae, etc., representatives display an even more distinct tendency towards broadening of the distal edge. Columnals, frequently have a rounded outline. In the case of short lobes of the axial canal with a broadened distal edge, the axial connective commissure experienced the same tension when the stem bent in different directions, and the divergence angles of columnals were also identical.

Another trend, the most common, of a gradual constriction of the axial canal is characterized by preservation of its initial shape (Text-fig. 7, III—IV). This eventually results in an increase of the articular surface, a phenomenon similar to that discussed above. A regular trend towards an increase of the articular surface becomes clear, if account is taken of the fact that one of the major adaptive trends of crinoids consists in elongation of the stem due to an increase in the number of the constituent columnals. Thus, the role of a "hinge", i.e. articular surface should grow. Most "beneficial" in this case is the increase of the articular surface due to a gradual constriction of the axial canal, but not due to increase of the columnal diameter with that of the axial canal remaining constant. A gradual constriction of the axial connective commissure and, thus, of the axial canal, commonly results in changing the shape of columnals, namely the rounding of their angles and their transformation into columnals with a round outline (Text-fig. 7; I—II). This may be traced in numerous examples of Paleozoic crinoids, where different stages of this process may be observed. Here we shall give only two examples. Thus, columnals of Silurian crinoids *Medinecrinus lenitus* SruK. with a broad cavity of the pentagonal axial canal, more than one third of the columnal diameter, have a distinct pentagonal outline. In the case of a narrow axial canal cavity, constituting one third or less than one third of the columnals diameter, the columnals have a round outline. The same holds true for columnals of other Silurian crinoids, viz. *Medinecrinus subradialis* SruK. When the axial canal cavity is broad, which is often accompanied by distinct relics of a pentamerous structure on the articular surface, columnals of the stems have a pentagonal shape. In the case of a smaller axial canal cavity, columnals have a stable round outline. A regular pattern, consisting of a close correlation between a gradually constricted axial canal and the changing of a pentagonal outline of the columnal into a round one, is easily explained by the analysis of schemes contained in this paper (Text-fig. 8). In the case of a broad pentagonal outline of the axial canal and a pentagonal outline of the columnal, the difference in the distance from the axial commissure to the edge of the columnal in the direction of the side and angle of the columnal is not great. Consequently, the tension of the axial (strong) connective commissure is practically the same, whether the stem is bent towards the side of a columnal, or towards its angle. It should be taken into account that stems, made up of such columnals, were short, and the function of their bending was not the major one. Quite a different situation arises, if a strictly pentagonal outline of a columnal is assumed in the case of a narrow (point) axial canal. In this case, the difference between the distances from the axial commissure to the columnal edge in the direction of its side and its angle abruptly. When the tilt of the stem in the direction of the columnal angle equals that in the direction of its side, a sharp difference between tensions of the axial connective commissure is recorded. Or, in the case of a similar tension of the axial commissure (its similar extension), the divergence angles of the columnals relative to each other will be different. Thus, a trend towards a regular tilt of the stem in all directions with a similar tension of the fine axial connective commissure results in a gradual rounding of angles of the pentagonal columnal and a round outline of columnals.

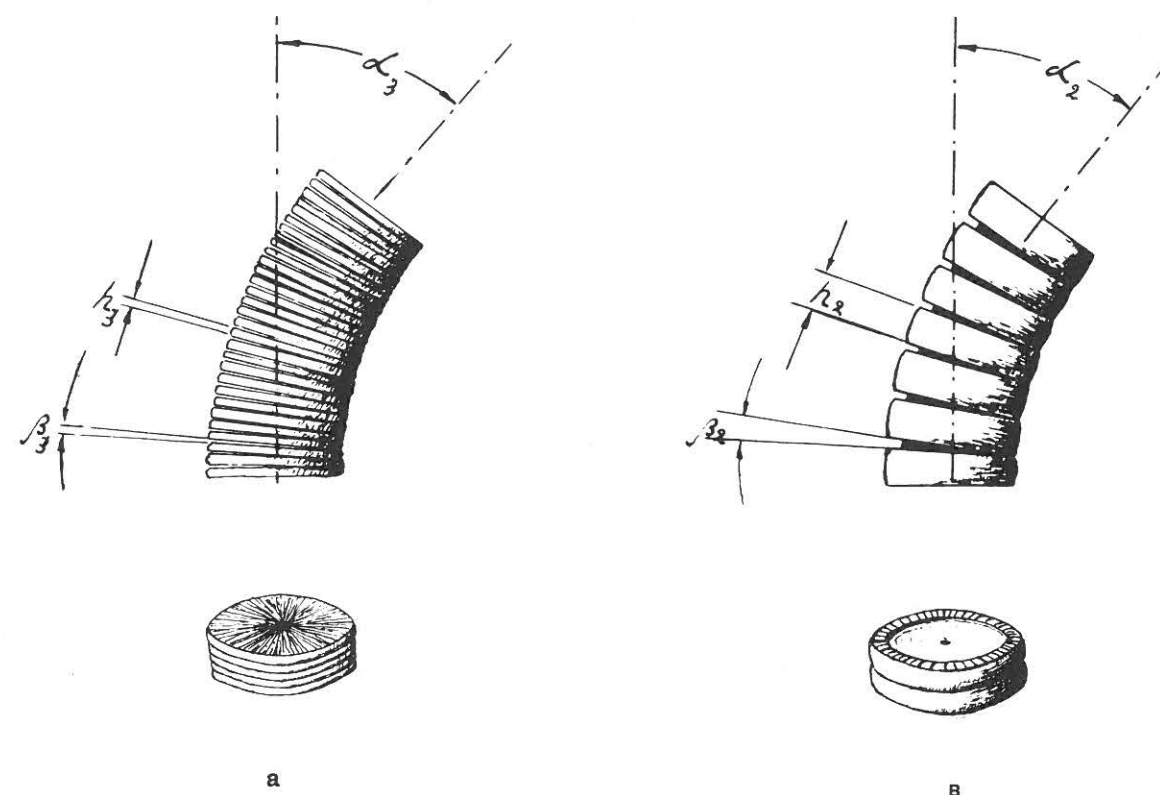
Decreasing dimensions of the axial canal of stems result in elongation of costae on the articular surface. In the central part of the articular surface, they are more closely spaced, than near the periphery. The intervals are filled

in by implanted and bifurcating costae, which makes the distribution of costae and intervals uniform throughout the articular surface and increases the binding strength of the columnals ("hinge") in case of their divergence.

One of the major evolutionary trends of stems, connected with a gradual constriction of the axial canal cavity (its initial shape being retained), is accompanied by a gradual decrease in the height of the columnals (Text-fig. 7; VII—VIII). A decrease in the height of the columnals seems to compensate the tension of the constricted axial connective

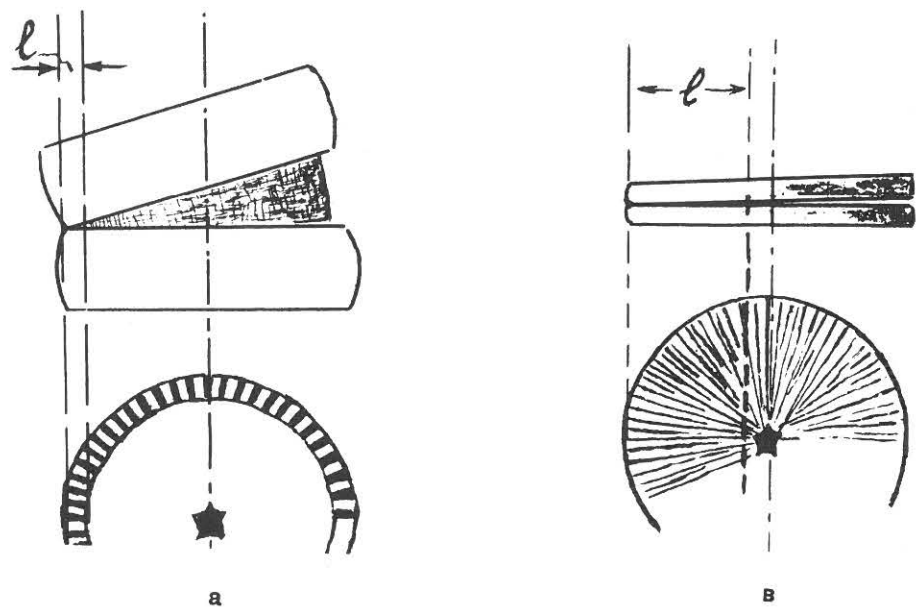


Text-fig. 8. Scheme, illustrating the difference in distances (l , L) from the axial connective commissure to the edge of columnals in case of a broad (a) and narrow (B) axial canal.



Text-fig. 9. Scheme, illustrating the tilt of stems with: a) a fine axial connective commissure; b) a ligamentary attachment of columnals; α , tilt angle of stems; β , divergence angle of columnals; h , height of columnals.

commissure. A general increase in a number of columnals in the stem due to their decreasing height, probably, favoured large tilt amplitudes of stems with small divergence angles of the columnals proper (Text-fig. 9). In this case, the tilt of the stems is made up for by the small divergence angles of the low columnals which a fine axial connective commissure permitted. A decrease in the height of columnals with constriction of the axial canal is also correlated to a development of a dense network of fine bifurcating costae on the articular surface of columnals. This is due to the large contact surface of costae when a stem of such morphofunctional type is tilted. And in fact, in this case, as discussed above, the divergence angles of columnals, if the stem is bent, are small. Thus, even low fine costae contact each other long a considerable part of their length (Text-fig. 10b). A general evolutionary trend of stems, connected with a gradual decrease of the height of columnals, eventually results in the generation of thin foliated columnals. At the same time, this is, probably, accompanied by a partial loss of the stem's strength. Numerous examples (species of *Multifidocrinus*, *Pandocrinus*, etc.) show that the strength increased due to increase of the stem diameter and formation of "undulated" bent columnals. The function of undulated articular surfaces consists not only in increasing the strength of thin broad columnals, but also in their binding in the case of a tilting stem. Thus, in this case, the function of binding columnals is transferred from fine, often almost indiscernible costae to the undulatory, bent articular surface of columnals proper. The final evolutionary stage of the stems in this direction, probably results in the stem atrophy and the appearance of swimming stemless crinoids. The assumptions, repeatedly made in publications that certain Paleozoic crinoids had stems only at a definite stage of individual evolution, might be fully confirmed by the evolutionary modifications of the stems.



Text-fig. 10. Contacting crinoid columnals in case of a ligamentary attachment (a) and a ligamentary-free attachment (b); l , length of the contact of costae in case of a tilting stem.

One of the most important evolutionary trends of flexible and mobile stems consists in the appearance of a new attachment form of columnals with the help of a connective commissure (tie), filling in depressions in the articular surface of columnals. We termed these depressions ligamentary fields (STUKALINA 1964). As may be seen from numerous examples of Early and Middle Paleozoic crinoids, a ligamentary field appears in stems with a narrow axial canal cavity. Thus, the function of attaching columnals in such stems is accomplished by axial connective commissure and commissures located in depressions in the articular surface. With constriction of the axial canal cavity, the function of attaching columnals gradually passes on entirely to the connective commissure (ligamentary connective commissure) which filled in depressions in the articular surface of a columnal. Ligamentary connective commissure, as compared to axial connective commissure, had greater possibilities for a progressive increase of their mass. They were not filling the constricted axial canal cavity, as is the case with axial connective commissure, but were developed in

depressions in the articular surface of rather strong columnals. The developing connective ligaments could allow an ever increasing divergence angle of columnals and, thus, an ever increasing tilt angle of stems (Text-fig. 9b). This is correlated to an increasing height of the columnals, possibly, also, in certain cases, to a decreasing total number of columnals in a stem, and to the development of coarse ribbing on the articular surface. The appearance of coarse high costae was, probably, due to increasing torsional stresses in the case of a high divergence angle of the columnals.

The analysis of evolutionary modifications of a ligamentary field in the known Paleozoic crinoid stems shows that the evolutionary trends of a ligamentary attachment of columnals are highly diverse. However, in spite of the rather specific character of the changes, they have a general tendency in common, which is connected with a gradually increasing total mass of the ligamentary connective tie, which bound the columnals.

The appearance and development of a ligamentary connection can be observed in crinoid stems which have both pentamerous and monolithic columnals (Text-fig. 7; I—II, IX—X; XVII—XVIII).

The ligamentary field in pentamerous forms develops within the articular surface of pentameres. Suture lines are the limits of their distribution. Due to this, a ligamentary field can increase its area, developing only from the centre towards the periphery of pentameres. Depending on the type of pentamerous structure, ligamentary fields might develop from the walls of the axial canal (type *Angulata*), or from its angles (type *Strialata*). In some cases, this is due to a simple increase of the ligamentary field dimensions, its general outline being retained; in other cases, due to the deepening of ligamentary pits, or due to a subdivision of the distal edge of the ligamentary field into lobes. The development of a lobate structure of the ligamentary field is, probably, connected with an increase of the area of attached ligamentary connective commissures and, thus, an increase of their mass. Closely correlated to the development of the ligamentary field is a change in the outline of columnals, the position of the ridges, the framing suture lines and margins of the columnals, the relief of costae on the surface of the ridges, and the height of columnals.

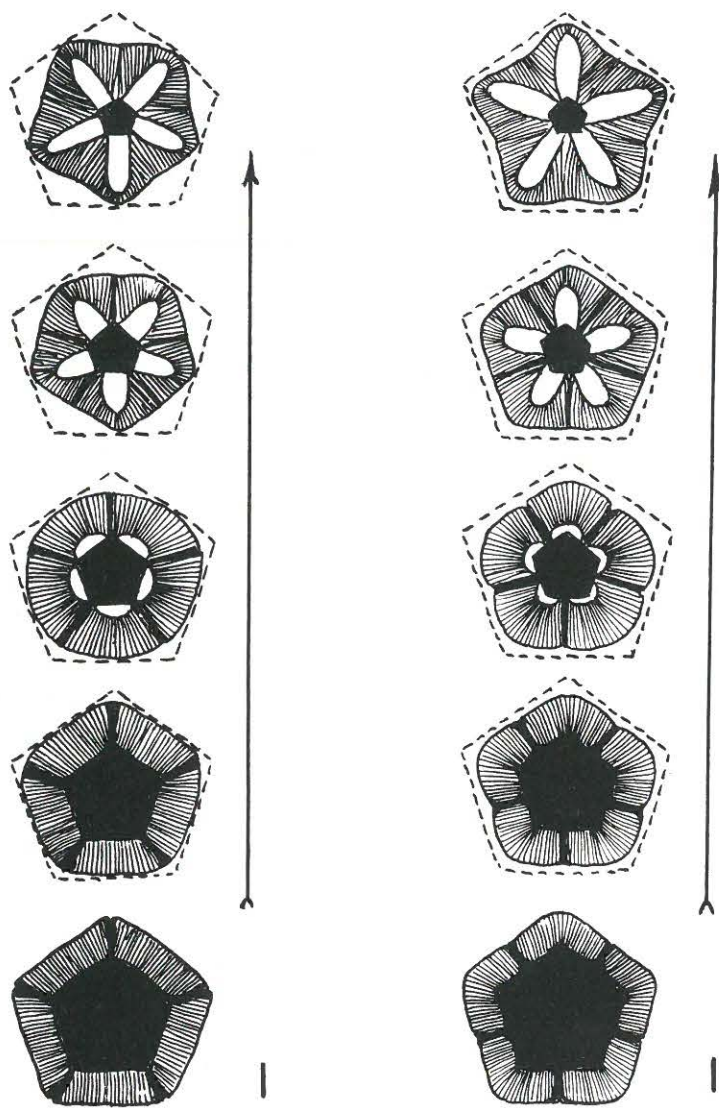
If visible traces of a pentamerous structure are lost, the ligamentary field retains its evolution pattern, increasing its area between "suture" lines from the walls of the axial canal or its angles, depending on the type of the pentamerous structure of the stems of ancestral forms (Text-fig. 11). In the case of development of ligamentary fields which branch off from the axial canal angles to the margins of columnals (type *Strialata*) in the form of separate lobes, a pentagonal outline of columnals is commonly retained. There, a direct analogy might be drawn of a correlation between a quinquelobate ligamentary field and a quinquelobate axial canal, and a pentagonal outline of a columnal. The strengthening of a ligamentary connection, directed into the angles of columnals, compensates for the higher tension, resulting from the bending of the stem towards the angles of the columnals.

Development of the ligamentary field lobes from the axial canal sides (*Angulata* type) results, in the process of morphogenesis, in the formation (appearance) of columnals with a pentagonal outline, the outer angles of which do not coincide with the axial canal angles (Text-fig. 11, 1; Text-fig. 7; IX—X).

In monolithic columnals, the most common type of the ligamentary field modifications consists of a gradual increase in its area, accompanied by a slight deepening. The axial canal constricts to the minimum ("point") dimensions, and costae are pushed towards the peripheral edge of columnals. Simultaneously with a decrease in the length of costae, their width and height are, as a rule, increased (Text-fig. 10a). The outline of columnals is closely correlated to a change in the ligamentary field dimensions. If the ligamentary field is not broad, irrespective of its shape, when the axial canal is comparatively narrow, the columnals, as a rule, have a rounded outline. Here, a phenomenon is observed, which is similar to that, when columnals with a narrow axial canal, irrespective of its outline, have round shaped edges. When the ligamentary field of a rounded outline is increased, a rounded outline of columnals is also retained. In this case, if stems have an equal tilt in all directions, the divergence angle of columnals is constant, and, thus, the ligamentary connective commissure tension also remains constant. A gradual broadening of the ligamentary field, accompanied by its deepening, can be observed in many species of Paleozoic crinoid stems. This adaptive trend is especially characteristic of Middle and Late Paleozoic crinoids. Eventually, the ligamentary field covers almost the entire articular surface of the columnals (Text-fig. 7; XVII—XVIII).

A further strengthening of a ligamentary connection (ligamentary attachment) of columnals in the trend under discussion results in the generation of morphofunctional types of stems, characterized by a granulose shagreen ligamentary field surface (Text-fig. 7; XV—XVI). Similarly to the previous case, this change in the structure of a ligamentary field is connected with its gradual broadening and the decrease of the axial canal dimensions to "point" ones, and also with the gradual pushing-out of costae towards the peripheral edge up to their complete reduction. The constriction of the axial canal cavity to such minimum dimensions show that it ceases playing any significant

role for enclosing the axial connective commissure. SHAGREEN ("shagreen tubercles") first appears near the axial canal walls, in the centre of the articular surface. Further, it covers the entire ligamentary field area. The appearance of shagreen tubercles favoured an increase of the overall attachment area of ligamentary muscle connection. This might certainly be regarded as a progressive adaptation of stems developing towards flexibility and mobility. Possibly, the appearance of tubercles points not only to an increase of the attachment area of connective ligaments, but also to their qualitative change. Certain adaptive trends of crinoids with a shagreen ligamentary field are known from the Silurian and Devonian, but this feature of the stem structure is particularly pronounced in Late Paleozoic crinoids. A common evolutionary trend of stems, connected with the development of a shagreen surface of the ligamentary field, finally, results in free mobile or swimming stem-bearing forms.



Text-fig. 11. Morphogenesis of crinoid stems of the Angulata (I) and Strialata (II) type.

A fundamentally new evolutionary trend of the ligamentary field is illustrated by specific morphofunctional types, to which stems of planktonic crinoids, *Scyphocrinites* (Text-fig. 7; XI—XII) belong. Their columnals have a deep ligamentary field. Simple coarse radial costae are found on the articular surface. *Scyphocrinites* stems served as a link between the cup and pneumatophorous chambered lobolites. Thus, becomes clear the role of deep ligamentary fields in columnals, which formed a large cavity for a great mass of a ligamentary connective commissure subject to great tensile stresses. Coarse costae on the articular surface, probably, counteracted intensive torsional stresses. A disturb-

ance of the normal relations of the stem with the cup and arms, and the loss of a supporting function, in this case, leads to a disturbance of the regular disposition of plates in the cup.

Another evolutionary trend is illustrated by peculiar morphofunctional types of crinoid stems with a divided articulation, known from the Ordovician and Early Silurian (*Divisicrinus*, *Sibiricrinus* etc.). The main element in the articulation of columnals of this type is a ligamentary field with the surface, subdivided by coarse radial costae into several sectors. The functional significance of these coarse costae is, apparently, the same as that of costae in the ligamentary field of *Scyphocrinitidae*.

Characteristic evolutionary trends of a ligamentary connection of a columnal are also illustrated by *Hexacrinites* and *Platycrinites* morphofunctional stem types (Text-fig. 7; XIII—XIV). A gradual evolution of the ligamentary field, covering the articular surface, and its deepening result in the formation of a narrow circular ridge (papilla) in the central part of the articular surface, with the help of which the ligament becomes separated from the axial canal cavity. The term "perilumen" was proposed for it (MOORE, JEFFORDS & MILLER 1968). The formation of a ligamentary field, not connected with the axial canal cavity, is commonly accompanied by reduction of costae on the articular surface. The axial canal cavity in this case is constricted to the minimum dimensions ("point"). The function of binding columnals is accomplished by an elastic connective tie, which filled in depressions in the ligamentary field. A large, deep ligamentary field is frequently ornamented by radial costae, or shagreen tubercles, which is indicative of a large attachment area of the ligamentary connective tissue and its great mass. This points to a high mobility degree of such stems, whereas stable round and the derivative ellipsoidal shapes of columnals, point to an even amplitude of their tilt in all directions. The morphofunctional type of stems under discussion, which we termed mamillial (STUKALINA 1979 a), is found only in single Ordovician and Silurian genera (*Altimarginalicrinus*, *Scalaricrinus*); however, it is widespread in many adaptive trends among Devonian and, especially, Late Paleozoic crinoids (*Hexacrinites*, *Ctenocrinus*, *Lampterocrinus*, *Gilbertocrinus*, *Laudonomphalus*, *Kojvicrinus*, *Pinegicrinus*, etc.). In *Platycrinites* (synarthrial) morphofunctional types of stems, as well as in mamillial types, the axial canal cavity is isolated from that of the ligamentary field by a ridge. There, it is not a circular ridge, but it is strongly elongated lengthwise, due to which, the articular surface is subdivided into two equal parts. The ligamentary field is subdivided by the ridge into two symmetrical depressions, the axial canal retains its "point" dimensions, and costae on the articular surface are almost entirely reduced. The formation of a longitudinal ridge limits a uniform divergence of columnals with the tilting of the stem. Their tilt along the ridge, i.e. along the long axis of a columnal, creates a very small divergence effect of columnals, whereas the tilt angle of the stem turns out to be low. The longer the ridge, the smaller the divergence angle of columnals. Conversely, the tilt of columnals along a short axis, i.e. from a longitudinal ridge should give a large divergence angle of columnals. The shorter the axis, the larger tilt angle the columnal should have. Thus, each columnal has the greatest freedom of movement in the direction of a short axis; and the smallest one, in the direction of a long axis. Thus, it becomes clear that the more the columnal is elongated along the long axis, which is connected with its acquiring an ellipsoidal outline, the more mobile it is. Columnals of the type described in a stem are commonly turned relative to each other in a horizontal plane. A screw-like distribution of columnals allows an equal tilt of the stems in all directions. A highly advanced synarthrodial morphofunctional articulation type of stems is characteristic of the Ordovician genus *Ristnacrinus*, many Devonian and, especially, Carboniferous and Permian crinoids (*Platyplateum*, *Platycrinites*, *Eucladocrinites*, etc.) (MOORE & JEFFORDS 1968, Pls. 3—6). The formation of a longitudinal ridge in the synarthrodial type of articulation should, naturally, be connected with further development of a circular ridge in the mamillial type of articulation. A successive evolution of morphofunctional types of *Hexacrinites* and *Platycrinites* stems might point to their possible genetic links. It is also of interest that between *Hexacrinites* and *Platycrinites* phylogenetic relations are also assumed to exist as regards the structure of calices (YAKOVLEV 1946; MOORE & LAUDON 1943).

The above morphogenesis pattern is based on the analysis of fossil fragments of Paleozoic crinoid stems.

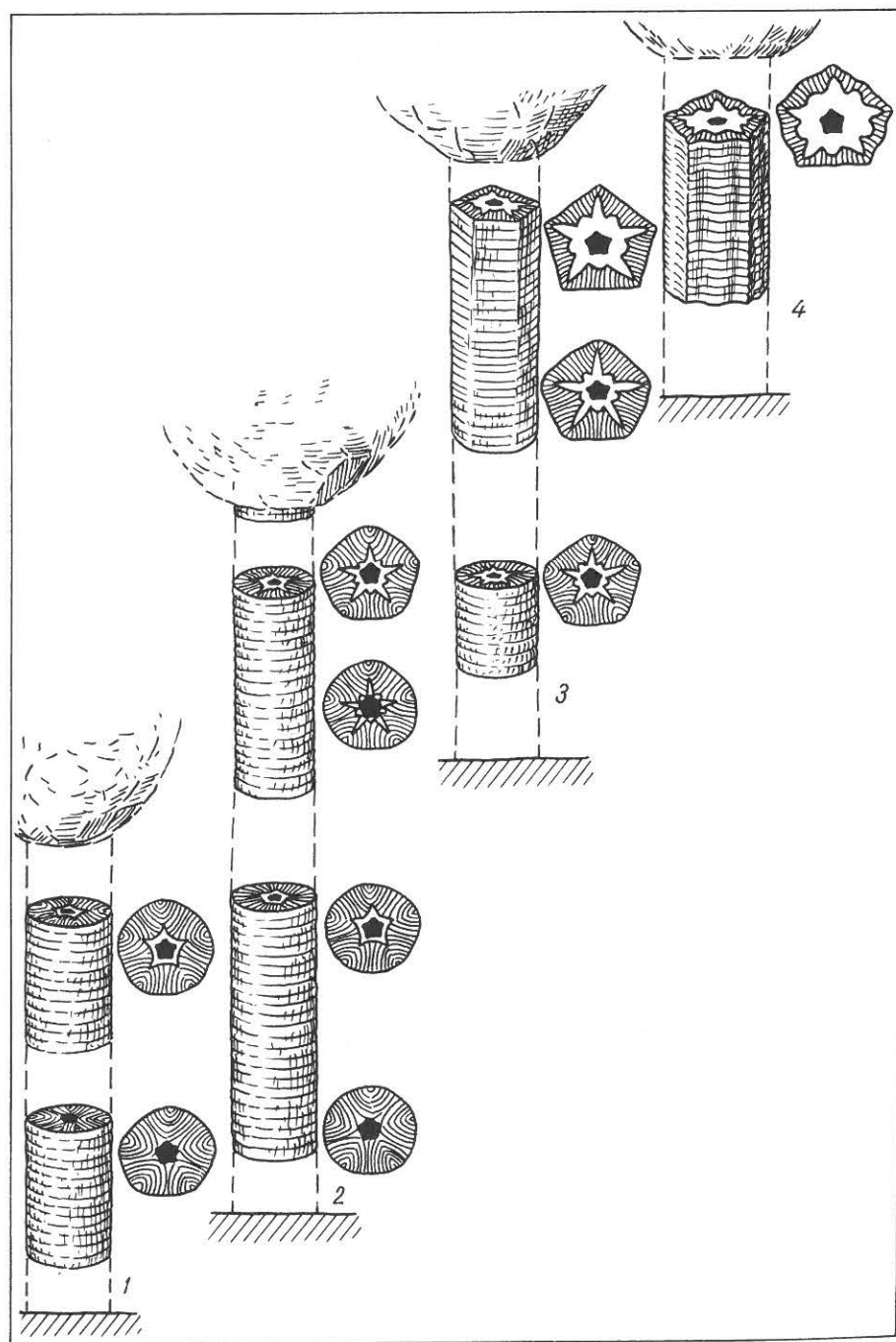
Summing up the foregoing, it might be stated that in most cases, the general evolutionary trend of crinoid stems finally results in the appearance of specialized morphofunctional types, a further evolution of which may lead to stemless fixed or freely mobile forms.

As is known, stem-bearing crinoid forms are again widespread in Mesozoic; their phylogenetic links with the Paleozoic predecessors are in many respects vague.

Probably, many of them may turn out to be secondary stem-bearing descendants of Upper Paleozoic stemless ancestors. In this case, it might be assumed that the ontogeny of recent crinoids (particularly, *Antedon*) accounts only for the Mesozoic and Cenozoic stages of crinoid evolution.

Ontogeny

BATHER (1898, 1900) and JAEKEL (1894, 1918), and later EHRENBURG (1922 etc.) paid attention to gradual changes in the structure of stems. It was noted that the lower distal part of the stem retains features of the oldest organization.

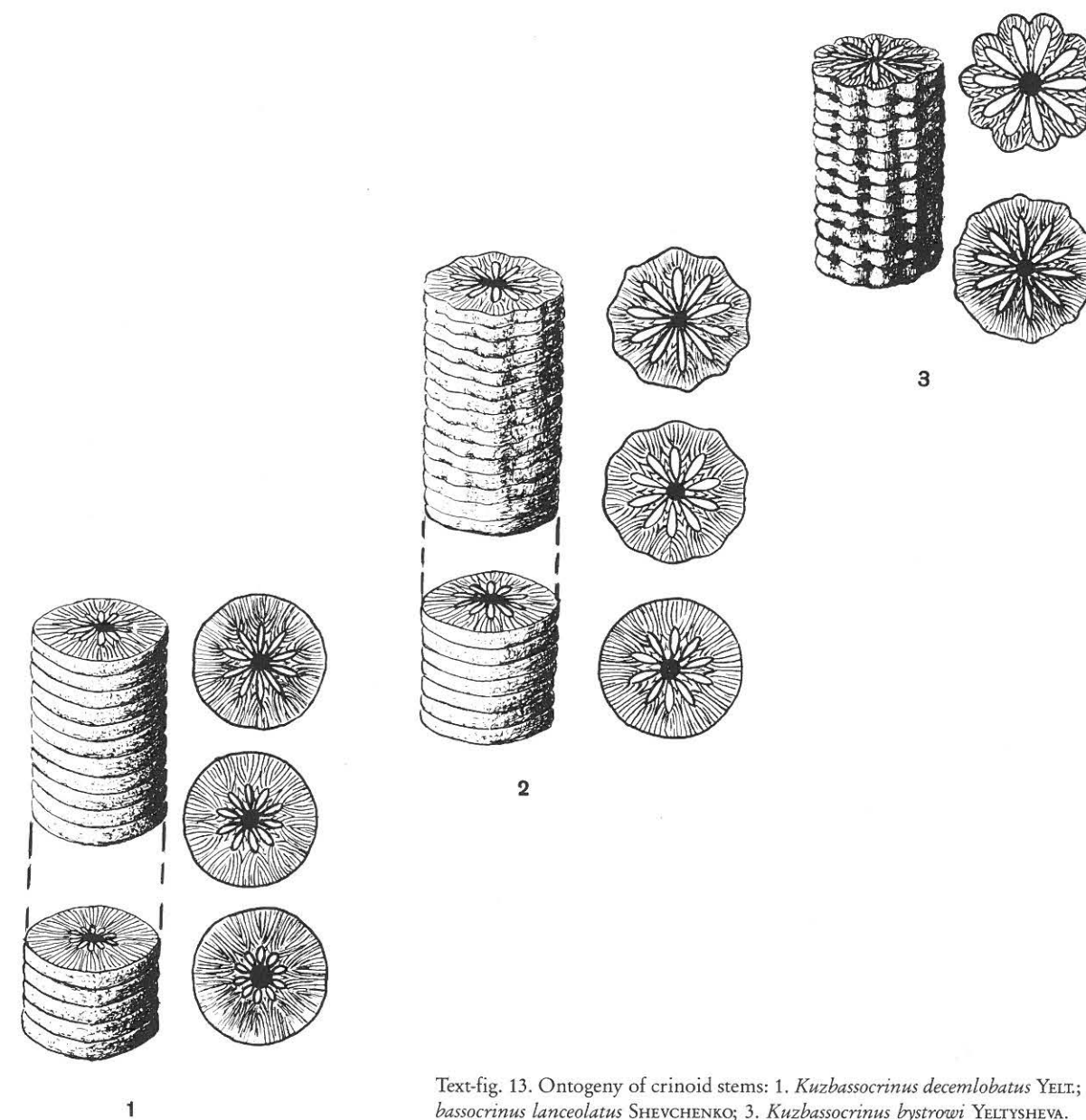


Text-fig. 12. Ontogeny of crinoid stems: 1. *Pennatocrinus subpennatus* (YELTSYSHEVA); 2. *Decacrinus ovalis* STUKALINA; 3. *Decacrinus pennatus* YELTSYSHEVA; 4. *Decacrinus ornatus* STUKALINA (after STUKALINA 1968).

Their observations were concerned with changes in the pentamerous structure of columnals. The ontogenetic succession of the appearance of these features is illustrated by the known reconstruction of *Dictenocrinus decadactylus* by BATHER. In the lower part of this crinoid stem, columnals are made up of steplike pentameres. This is clearly traced along a zigzag-shaped suture line on the lateral surface. Higher, the pentameres gradually acquire a horizontal disposition, forming vertical rows with even suture lines along the stem axis. In the proximal part of a stem, columnals are made up of pentameres, arranged in strict horizontal rows. Suture lines between them are weak. This points to a gradual fusion of pentameres into monolithic columnals which make up the proximal part of a stem.

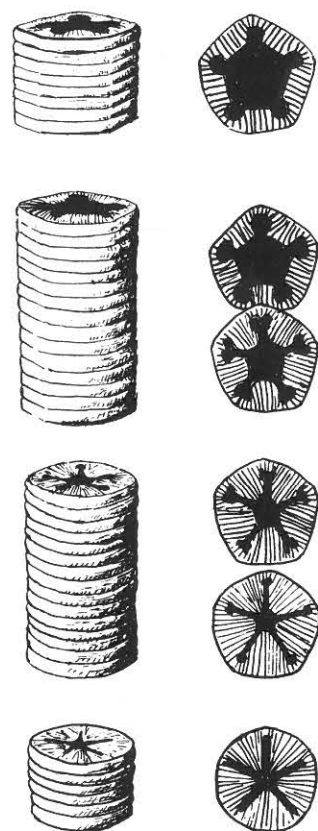
The stem succession of changes in the pentamerous structure of stems might be observed in *Euspirocrinus spiralis* ANG., *Streptocrinus crotalurus* ANG., *Mariocrinus pachydactylus* HALL, *Glyptocrinus plumosus* HALL; according to UBAGHS, it is illustrated by *Obiocrinus*, *Calceocrinus*, *Barycrinus*, *Anomalocrinus*, *Thenarocrinus*, *Mastigocrinus*, *Ottawacrinus* (UBAGHS 1953).

This obvious ontogenetic succession refers to the postembryonal evolution of crinoids. Thus, it might be regarded as the final stages of ontogeny, connected with the individual growth of animals from young to adult forms.



Text-fig. 13. Ontogeny of crinoid stems: 1. *Kuzbassocrinus decemlobatus* YELT; 2. *Kuzbassocrinus lanceolatus* SHEVCHENKO; 3. *Kuzbassocrinus bystrowi* YELTSYSHEVA.

The ontogenetic succession of appearance of features within one stem, recorded by BATHER and other workers, proves to be not a unique one. Depending on the adaptive trend, a similar succession of changes might apply to the ligamentary field, ribbing, correlation of the dimensions of columnals and other features, which reflect changes and improving functions of the stem movements (its capacity to bend) (STUKALINA 1965). The oldest features are recorded in distal columnals. Their preservation in this part of the stem is, probably, favoured by the functional role of its holdfast as the least mobile part. Old features are also frequently observed in the youngest columnals (internodals and infranodals), appearing in the case of new formations due to intercalation. Later, these features are quickly "muffled" by specialized species features. Later species features are formed in the most advanced proximal columnals by extensions (anabolism).



Text-fig. 14. Ontogeny of *Bystrowicrinus bilobatus* (YELTYISHEVA) (after STUKALINA 1982).

Thus, further developing BATHER's assumption concerning possible ontogenetic studies based on stems, we might draw the following conclusion: an object for the study of postembryonal stages of ontogenetic evolution might be pentamerous forms and stems which have lost traces of a pentamerous structure, i. e. forms in which stages of a pentamerous structure are missing from individual evolution. It is noteworthy that certain changes in the morphological features of stems, manifested during various ontogenetic stages, are similar to the general pattern of morphogenesis (STUKALINA 1968 a). This circumstance, as well as morphogenesis, gives us a good possibility of establishing certain phylogenetic relations between comparatively low taxonomic units of families, genera, and species.

On the face of it, all discussions concerning a possibility of ontogenetic studies based on stems might prove pointless. In practice, a scientist frequently has to do with small stem fragments, or their dissociated columnals. Nevertheless, ontogenetic studies might be quite real. Collecting numerous columnals at one locality, one might easily assign them to different morphofunctional types and arrange them in a morphological series with successively differing morphological characters.

In crinoids with a narrow axial canal and connective ligaments, the most developed morphofunctional types of columnals characterize the proximal part of a stem (Text-fig. 12, 13). Unlikely, in species, which have stems with a

broad axial canal, the proximal part of a stem is usually represented by the most primitive morphofunctional types of columnals (Text-fig. 14). They characterize the differentiation of the stem and calyx cavities which is not distinct enough.

Thus, the determination of morphological changes in the succession of columnals is established, primarily, closely connected with an evaluation of the functional significance of their morphological characters. The absence of the morphofunctional analysis of the columnals under consideration might lead to erroneous conclusions about the direction of morphological changes, or turn this task into an unsolvable dilemma.

In the process of studying old crinoid stems, similar reconstructions, based on the morphofunctional analysis, were accomplished by the author for species of the following genera: *Mediocrinus*, *Syndetocrinus*, *Ramulicrinus*, *Chingizocrinus*, *Ramosocrinus*, *Catagraphiocrinus*, *Baltocrinus*, *Webericrinus*, *Particrinus*, *Bystrowicrinus*, *Fascicrinus*, *Sigillatocrinus*, *Anthinocrinus*, *Bazaricrinus*, *Florincrinus*, *Pennatocrinus*, *Podolocrinus*, *Decacrinus*, *Tastjicrinus*, *Kuzbassocrinus*, etc. (STUKALINA 1977, 1979 a, b, c, 1980, etc.).

In the present paper, the author illustrates the use of ontogenetic studies exemplified by establishing relations between the genera *Pennatocrinus* and *Decacrinus* (Text-fig. 12). The characteristic structural feature of the stems of the genera under discussion is the articular surface of the columnals. In their centre, there is the hole of the axial canal, which is commonly narrow and has a pentagonal cross section. The depression in the articular surface is covered by a ligamentary field, subdivided into five (*Pennatocrinus*) and ten (*Decacrinus*) lobes. The lobes served as the attachment place for elastic soft connective ligaments, which brought about the extension of the columnals. A "rigid" union of the columnals was realized by a system of radial and pinnate short costae located along the margin of the columnals. Morphological characters of *Pennatocrinus* and *Decacrinus* display a directed change with time, viz. the rosette of the ligamentary field gradually increases in size and covers the whole articular surface of the columnals; the axial canal is constricted to the minimum dimensions, costae become larger, more pronounced and are pushed towards the peripheral edge of the columnals; the outline of the columnals changes, as well as the lateral surface relief. The most significant, decisive role is played by morphogenesis of the structural features of the ligamentary field (change of its dimensions and shape, shape of lobes, character of their subdivision) (Text-fig. 15). It is noteworthy that such regular morphogenetic changes of the stems with a decempartite ligamentary field are also recorded in species of Early Devonian genera *Podolocrinus*, *Tastjicrinus*, *Aulnocrinus*, *Kuzbassocrinus* (STUKALINA 1977).

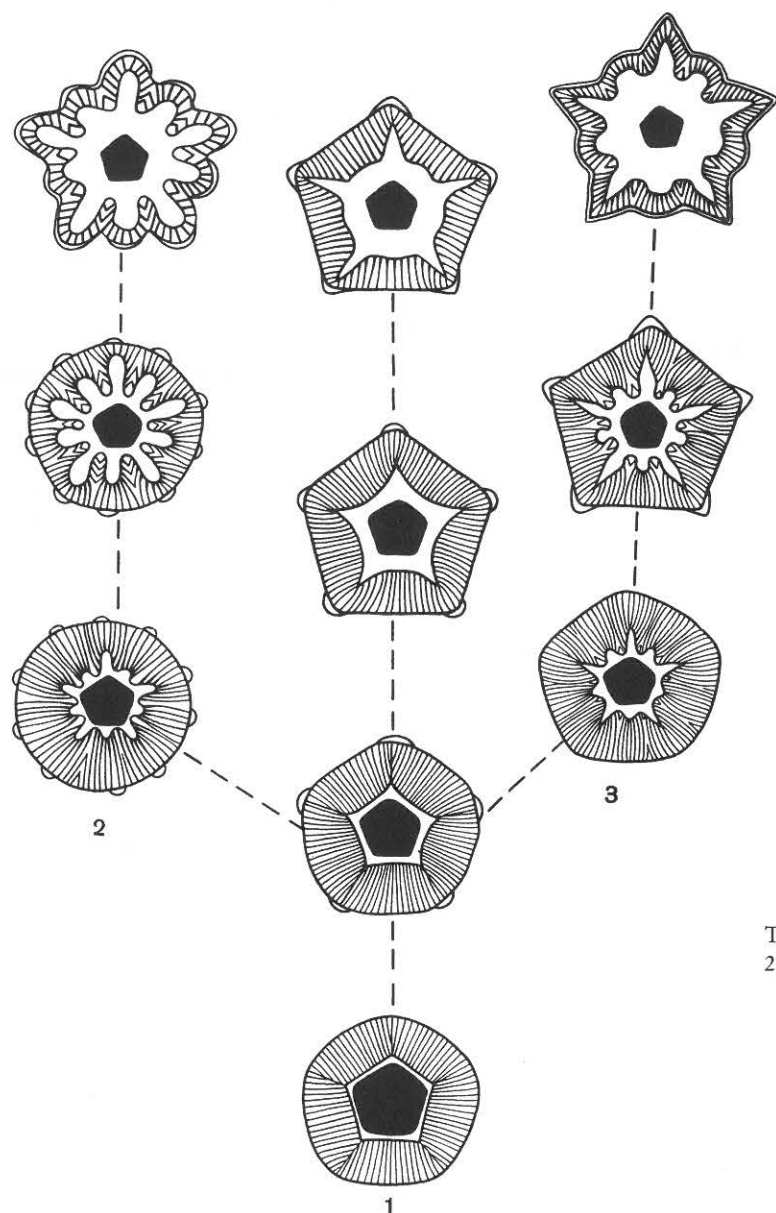
When estimating ontogenetic changes of morphological characters of *Pennatocrinus* and *Decacrinus* stems, use was made of representative samples, numbering several hundreds of dissociated columnals, stem ossicles and their impressions, from which moulds were cast. Serial collections of the material studied were taken by the author from the Upper Silurian and Lower Devonian sections of Central Kazakhstan (Northern Balkhash area and southern Karaganda area) (STUKALINA 1975). The stratigraphic interval investigated comprises the Tokrau, Ainasuj, Kokbaital, Balkhash and Sardzhal horizons (equivalents of Pridolian, Gedinnian and Siegenian).

In the course of the analysis, it was taken into account that the proximal part of the stems reconstructed, as the most mobile one, is characterized by columnals with the most developed lobate ligamentary field.

Pennatocrinus stems (*P. subpennatus* (YELT)) display the following ontogenetic succession of morphological characters of the columnals viz. distal columnals of an early stage have a narrow pentagonal axial canal; the ligamentary field is lacking. In proximal columnals, around the axial canal, there is a thin rim of the ligamentary field, its outline repeating that of the axial canal. Similarly in the structural features of the articular surface the proximal columnals of *Pennatocrinus* and distal columnals of *Decacrinus* display the same succession of characters. In distal *Decacrinus* columnals of an earlier stage, a ligamentary field is almost lacking. At the next stage, it represents a narrow rim around the axial canal, repeating its outline. The proximal *Decacrinus* columnals are more developed: their axial canal is smaller, the angles of the ligamentary field form narrow acute lobes, between which five additional semicircular lobes are later developed. Thus, when individual successions of morphological changes in *Pennatocrinus* and *Decacrinus* stems are compared, certain successive links in their evolution are revealed. This becomes most distinct when distal columnals of one genus are compared with proximal columnals of another one. This allows assuming close, if not direct genetic links between *Pennatocrinus* and *Decacrinus* genera, of which the former one is an ancestral form.

The oldest representatives of *Decacrinus* genus — *D. ovalis* (STUK.) retain all the major structural features of *Pennatocrinus* (*P. subpennatus*) stems in their distal part. Their earliest (distal) columnals have no ligamentary field; in later distal columnals, a simple ligamentary field is developed, forming a narrow rim around the axial canal. Prox-

imal columnals of *D. ovalis* have a weakly developed decempartite ligamentary field. The structure of proximal columnals of *D. ovalis* is repeated in distal columnals of *Decacrinus pennatus* YELT. Proximal columnals of *D. pennatus*, in contrast to those having a lower position in the stem, are characterized by a well-developed decempartite ligamentary field. Only the proximal columnals of *Decacrinus ornatus* STUK. are known. They differ from the proximal columnals of *D. pennatus* by a more developed decempartite ligamentary field, which covers almost the entire articular surface.



Text-fig. 15. Morphogenesis of crinoid stems: 1. *Pennatocrinus*; 2. *Podolocrinus*; 3. *Decacrinus* (after STUKALINA 1977).

Thus, tracing the relations of species within the genera *Pennatocrinus* and *Decacrinus*, the following series might be established: *P. subpennatus* — *D. ovalis* — *D. pennatus* — *D. ornatus*. This phylogenetic continuous series of species served as a basis for zonal subdivision of Lower Devonian deposits on the USSR territory (STUKALINA 1981, 1982 a, 1985).

Using the basic principles of morphogenesis and ontogeny, worked out by the author, YELTYSHEVA & SIZOVA (1971) analyzed ontogenetic changes in the stems of the following species: *Porcunicrinus octonarius* YELT. (Late Ordovician of Estonia), *Hexacrinites quadriformis* SIZOVA (Devonian of Central Kazakhstan), and *Decacrinus pennatus* YELT. (Early

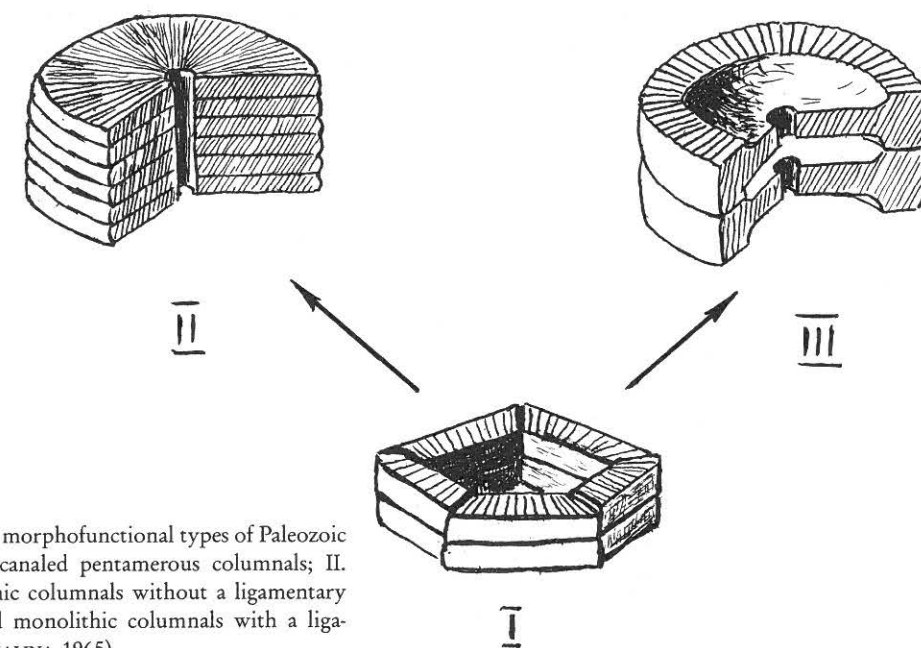
Devonian of Central Kazakhstan). These studies once again emphasized the possibility and necessity of using ontogenetic studies when analyzing crinoid skeletal formations represented by stem ossicles.

Not long ago the possibility of using changes in the morphological characters of the stems in ontogenetic studies of Paleozoic crinoids was convincingly illustrated by MOORE, JEFFORDS & MILLER (1968) for Pennsylvanian crinoid columnals and pluricolumnals and by WARN & STRIMPLE (1977) for inadunate crinoids, *Cincinnaticrinus varibrachialis* from the Ordovician of North America. BROWER (1973, 1974 a, b) placed particular emphasis on individual growth features of the stems from young to adult forms in chambered crinoids in general, and carried out interesting studies of *Xenocrinus*. GLUCHOWSKI (1984) described ontogenetic changes in *Mediocrinus microgrumosus* YU. DUBATOLOVA stems.

Taxonomic evaluation of the morphological characters of stems

A specific use of morphofunctional analysis, illustrated by discussion of the most characteristic major morphofunctional types of stems, and the pattern of their formation and evolution, is closely connected with a taxonomic evaluation of the morphological characters of stems and determining the subordination of characters.

Among all morphological characters of crinoid stems, the most important from viewpoint of systematics are, probably, those dealing with the articular surface.



Text-fig. 16. Three major morphofunctional types of Paleozoic crinoid stems: I. broad-canaled pentamerous columnals; II. narrow-canaled monolithic columnals without a ligamentary field; III. narrow-canaled monolithic columnals with a ligamentary field (after STUKALINA 1965).

Among all the morphofunctional types of crinoid stems known, three major types can be distinguished, which correspond to the three major adaptive evolutionary trends (Text-fig. 16). The first type comprises stems which are composed of columnals with a broad pentagonal axial canal; the second one, stems, made up of columnals with a narrow axial canal without ligamentary fields; the third one, stems with a narrow axial canal and well-developed ligamentary fields.

In most primitive morphofunctional types, characterized by a pentamerous structure and a broad axial canal cavity (first type), the most significant feature is the axial canal structure (its dimensions, shape, character of subdivision). Structural features of the canal reflect the character and type of the axial connective commissure, the most important element of columnal articulation at an early evolutionary stage of stem-bearing crinoids. Relative to the axial canal, features, which characterize a regular arrangement of pentameres in a stem, should have a subordinate significance.

A certain trend towards changes in the disposition of pentameres, viz. from stepped to horizontal rows, is eventually typical of all crinoids with a pentamerous structure. The same holds true for the character of ribbing on the articular surface and outlines of columnals.

With the increase of the articular surface at the expense of the gradual constriction of the axial canal, all the diverse outlines and shapes of the axial canal are gradually reduced to a point. The axial canal constriction is associated with weakening of the axial connective commissure up to its complete reduction and the transfer of its function to ligamentary connective commissure (or muscles) developed in the articular surface (third type). The main taxonomic significance is that of the ligamentary field morphology (its dimensions, shape, character of subdivision, degree of deepening, granulation, structure or ridges) and proportions of the ligamentary field diameter and the columnal diameters.

In morphofunctional types of stems, illustrating a gradual axial canal constriction with a ligament-free attachment of columnals being retained (second type), the major taxonomic characters are the ribbing of the articular surface and the ratio of the height and diameter of columnals.

Therefore, two main conclusions can be drawn: 1) the taxonomic value of morphological features of stems does not remain constant at different stages of crinoid evolution; and 2) the same morphological features of stems, depending on the evolutionary trend of crinoids, can have different taxonomic significance.

The above morphofunctional types can have parallel evolution in different phylogenetic branches. Thus, features which characterize them, should be regarded as features of relatively low taxonomic rank, conventionally not going beyond the scope of families.

Generally, of the above characters, a higher taxonomic significance should be given to those which account for an adaptive evolutionary trend. A lower taxonomic rank should be assigned to those features which characterize the evolutionary level of this adaptive trend.

Relative to these characters, features of a higher taxonomic rank are morphological elements, referring to types of a pentamerous structure of columnals. The Angulata type is characterized by sutures running from the axial canal angles. In the Strialata type, interpentamerous sutures diverge from the axial canal sides (STUKALINA 1967). With the loss of sutures joining segments, types of the former pentamerous structure of columnals are traceable from the disposition of the ligamentary field lobes relative to the axial canal angles (see Text-fig. 11). This allows the tracing of phylogenetic links from primitive pentamerous stems to advanced forms, represented by monolithic columnals. Thus, an opportunity arises of distinguishing quite a number of morphofunctional types of stems with a parallel evolution.

The great significance of this feature is not limited by the classification of dissociated stem ossicles. It could also be used in a general classification of crinoids.

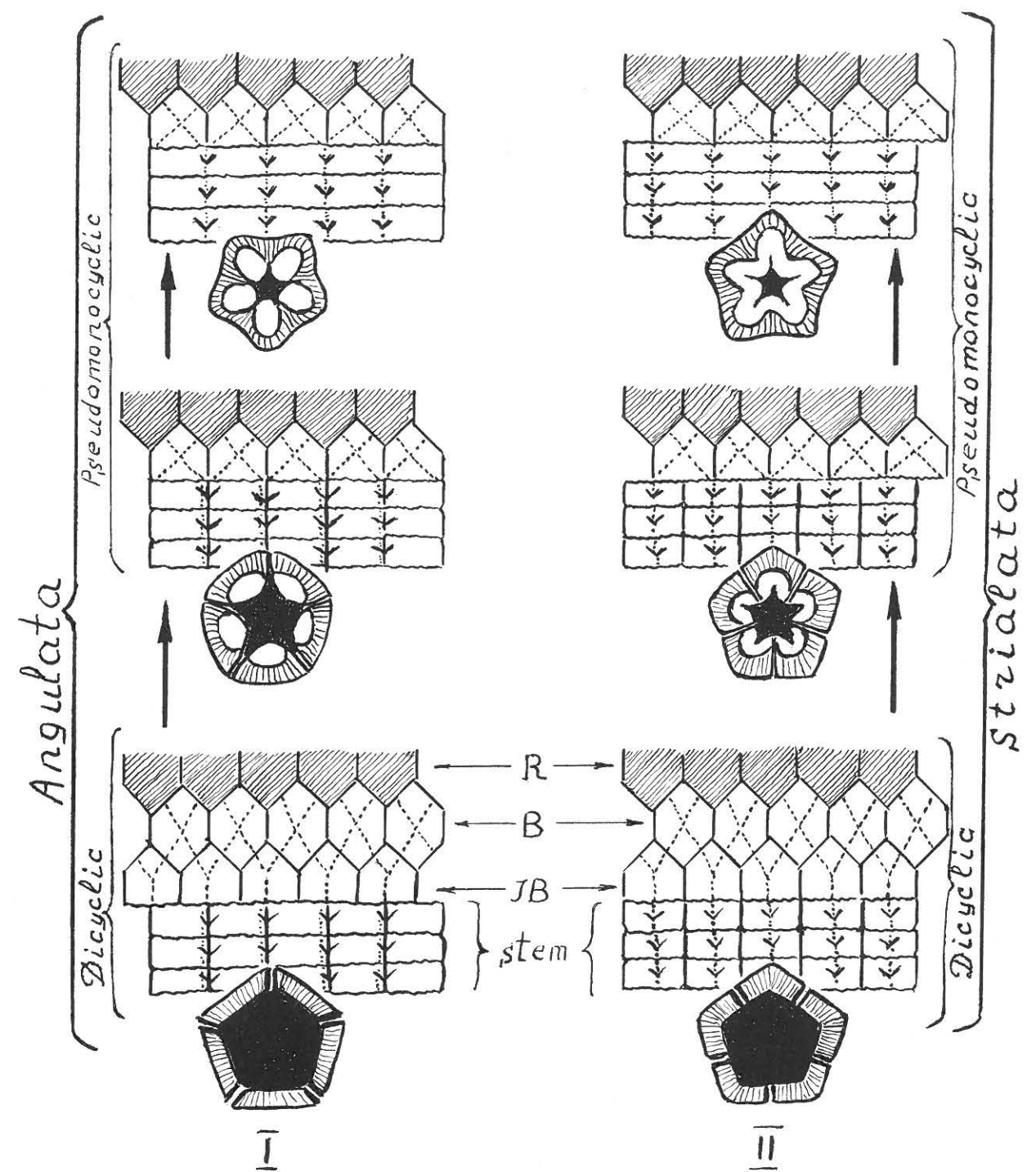
After two different types of a pentamerous structure of stems are established, it becomes quite obvious that the well-known WACHSMUTH & SPRINGER's "law" can hold true only for crinoids with the Angulata-type stem structure. In crinoids which have stems of a Strialata-type, sutures of columnal segments are not alternated with sutures of the calyx basal plates, but coincide with them. Axial canal angles lie between segment sutures. This is well illustrated by UBAGHS (1969, 1972) in the description of *Aethocrinus moorei* UBAGHS, i.e. species with a Strialata-type stem.

Thus, there is a possibility of distinguishing two taxonomic categories based on the stem structure (Angulata and Strialata) among dicyclic (and, probably, also among monocyclic) crinoids.

In those cases where pentamerous columnals become monolithic and sutures disappear in the process of morphogenesis, the type of a former pentamerous structure, as was already mentioned, is established from the disposition of the ligamentary field lobes relative to the axial canal angles (Text-fig. 11). This makes it possible to establish the same taxonomic categories among crinoids with a pseudomonocyclic structure of the cup. If this is so, the rank of the feature of a type pentamerous structure of crinoid stems appears to be higher than that of a dicyclic and pseudomonocyclic structure of the cup base.

Apparently, only this feature allows the most reliable classification of crinoids into two systematic categories of a high rank. One of them comprises monocyclic proper crinoids. The other one, dicyclic and pseudomonocyclic crinoids.

The feature of the disposition of the axial canal angles of the stem relative to the dorsal plates of the cup has a higher taxonomic rank. Thus, it might be taken as a rule that the disposition of angles of the stem canals in dicyclic crinoids of Angulata and Strialata types and the derivative pseudomonocyclic crinoids always corresponds to the posi-

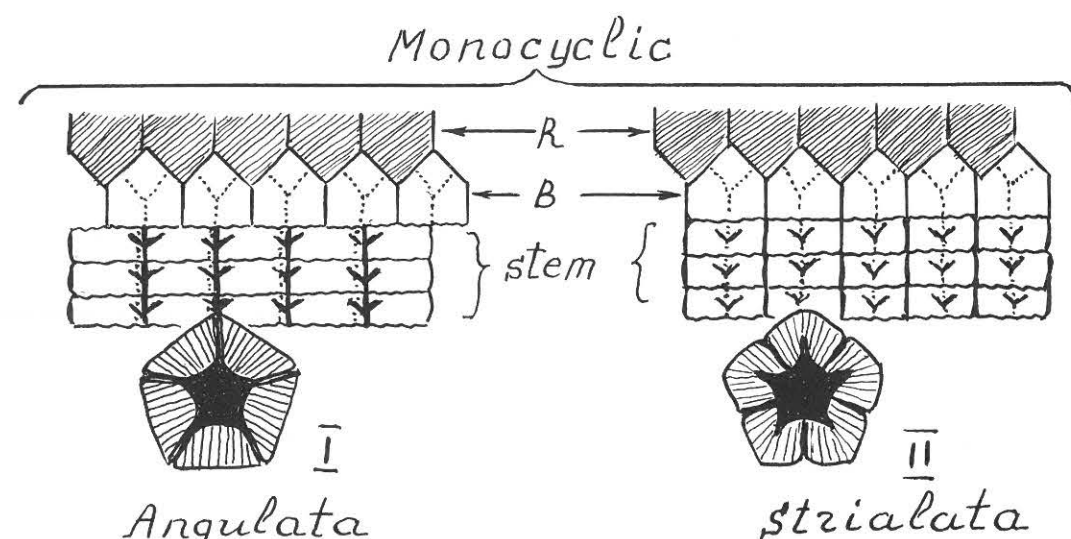


Text-fig. 17. A basic scheme of morphogenesis of dicyclic crinoids: I. dicyclic crinoids with stems of Angulata type; II. dicyclic crinoids with stems of Strialata type; RR, radials; BB, basals; IBB, infrabasals; and ... (dotted line) — axial cords (the location of axial cords in cups is given after BATHER's (1900) reconstruction); ♣ ("ticks"), position of the axial canal angles in a stem.

tion of the radial cup plates (Text-fig. 17). As to monocyclic crinoids proper, in them the stem canal angles display an interradial disposition (Text-fig. 18).

This conclusion casts doubt on WARNA's "rule" (1973) about the origin of monocyclic crinoids from dicyclic crinoids of Strialata type (i.e. from pseudodicyclic crinoids in WARNA's terminology).

The constancy (stability) and, thus, the high taxonomic significance of this feature is, apparently, due to the fact that the axial canal angles determine the position of the axial cords in the stem and are strictly correlated to the distribution of the axial cords in a cup.



Text-fig. 18. Correlation scheme of morphological elements of stem and cup in monocyclic crinoids: I. monocyclic crinoids with stems of Angulata type; II. monocyclic crinoids with stems of Strialata type a possible version; RR, radials; BB, basals; ... (dotted line) — axial cords (the location of axial cords in cups is given after BATHER's (1900) reconstruction); ♯ ("ticks") position of the axial canal angles in a stem.

Classification of the Ordovician, Silurian and Lower Devonian crinoids based on the stems

The main aim of the classification proposed was establishing of genetic links between crinoids. It is based on analysis of the functional significance of morphological characters of the stem structure at different stages of crinoid evolution in Early and Middle Paleozoic.

The classification proposed is an illustration of applying the method of studying crinoid stems on the basis of their morphofunctional analysis. This classification presupposes distinguishing subordinate systematic units, including categories of groups, orders, families, genera and species (STUKALINA 1966, 1968, etc.). The relations between genera and families of crinoids are most clear in this classification, the stems of which display distinct features of a pentamerous structure. Their morphogenetic relations are based on a gradual evolution of a ligament-free and ligamentary attachment of the columnals. This, primarily, shows up in the structure of the axial canal and the ligamentary field. Less clear are genetic links between forms with a narrow canal, lacking features of a pentamerous structure and having different types of a ligament-free and ligamentary attachment of the columnals. There, in the families distinguished, in the present state of knowledge, morphologically similar morphofunctional types of different genesis may be combined.

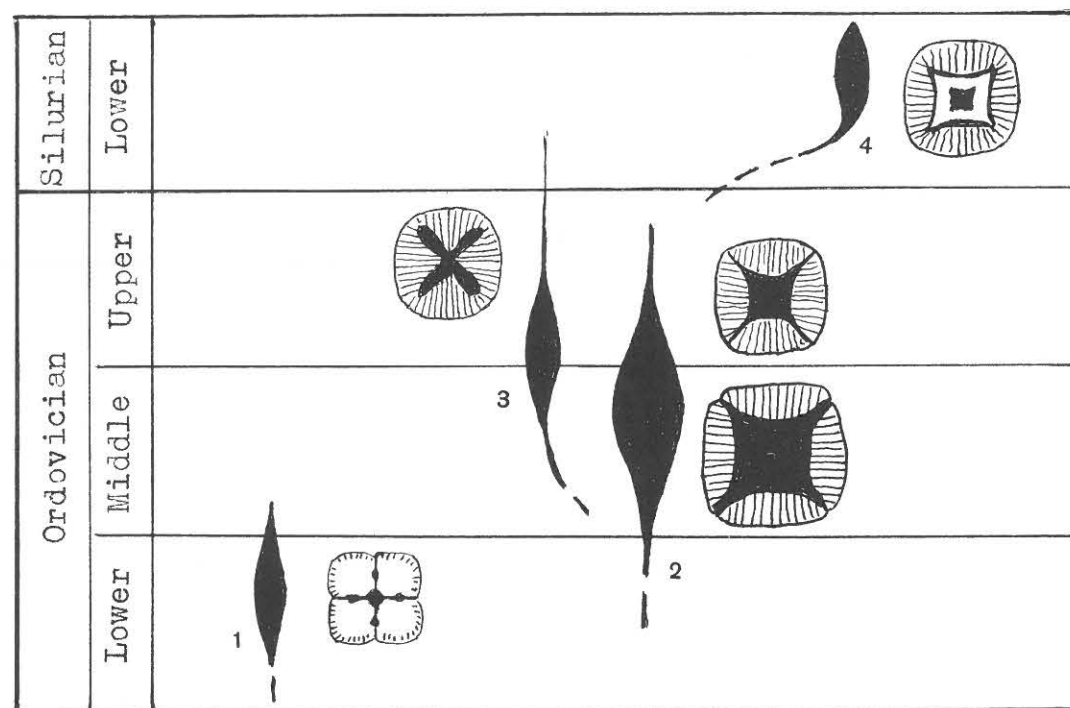
Among crinoids known from the Ordovician, Silurian, and Lower Devonian of the USSR, by now over five hundred species names correspond to the criterion of validity (Internat. Code Zool. Nomencl., 1964 (Russ. transl. 1966). In the classification proposed, most of the species are assigned to 161 genera, 65 families, and three groups, viz. Quadrilaterata, Pentamerata, and Asegmentata. Pentamerata group comprises two orders, Angulata and Strialata.

The classification scheme adopted can be represented as follows:

- Group Quadrilaterata STUKALINA 1966
 - Family Tetragnocrinidae STUKALINA 1980
 - Family Dwortsowaecrinidae STUKALINA 1980
 - Family Berelicerinidae STUKALINA 1980
 - Family Tetraptocrinidae Y. DUBATOLOVA 1971
- Group Pentamerata STUKALINA 1966
 - Order Angulata STUKALINA 1967
 - Family Apertocrinidae STUKALINA 1968
 - Family Compositocrinidae STUKALINA 1979
 - Family Webercrinidae STUKALINA 1979
 - Family Egiarowicrinidae STUKALINA 1982
 - Family Bystrowicrinidae YELTSHEWA & STUKALINA 1963
 - Family Flexicrinidae STUKALINA 1980
 - Family Dulanocrinidae STUKALINA 1980
 - Family Klunnikowicrinidae STUKALINA 1982
 - Family Artificiosocrinidae STUKALINA 1982
 - Family Ramosocrinidae STUKALINA 1979
 - Family Muschketowicrinidae STUKALINA 1982
 - Family Mediocrinidae STUKALINA 1982
 - Family Parvicrinidae STUKALINA 1979
 - Family Lunaricrinidae STUKALINA 1980
 - Family Stellaricrinidae STUKALINA 1982
 - Family Selenjachicrinidae STUKALINA 1982
 - Family Fascicrinidae STUKALINA 1980
 - Family Fibracrinidae STUKALINA 1980
 - Family Particrinidae STUKALINA 1968
 - Family Pulchelicrinidae STUKALINA 1982
 - Family Sellicrinidae STUKALINA 1980
 - Family Lunulacrinidae STUKALINA 1982
 - Family Mirabilicrinidae STUKALINA 1979
 - Family Malovicrinidae STUKALINA 1968
 - Family Catagraphiocrinidae STUKALINA 1968
 - Family Baltocrinidae STUKALINA 1979
 - Family Babanicrinidae STUKALINA 1969
 - Family Caragachicrinidae STUKALINA 1980
 - Family Sigillatocrinidae STUKALINA 1980
 - Family Lobocrinidae STUKALINA 1982
 - Family Angusticrinidae STUKALINA 1980
 - Family Lobatocrinidae STUKALINA, fam. nov. (in litt.)
 - Family Uzenicrinidae STUKALINA 1982
 - Family Bazaricrinidae STUKALINA 1982
 - Family Anthinocrinidae SHEWTCHEIKO 1966
 - Family Facetocrinidae STUKALINA 1968
 - Genus incertae familia
 - Genus Chingizocrinus STUKALINA 1982
 - Genus Clavaticrinus POLOZHICHINA 1980
 - Genus Crotalocrinites AUSTIN & AUSTIN 1842 (sensu lato)
 - Genus Divisicrinus STUKALINA 1980
 - Genus Rugulosocrinus STUKALINA 1979
 - Genus Rookuelacrinus STUKALINA 1979
 - Genus Glyptocrinus HALL 1847 (sensu lato)
 - Genus Granulosocrinus STUKALINA 1985
 - Genus Jruccrinus STUKALINA 1982
 - Genus Kaplunaecrinus STUKALINA 1977
 - Genus Pentatlobatocrinus STUKALINA 1978
 - Genus Schizocrinus HALL 1847 (sensu lato)
 - Genus Syndetocrinus KIRK 1933 (sensu lato)
 - Genus Tolenicrinus STUKALINA 1975

- Order Strialata STUKALINA 1967
 - Family Dentifercrinidae STUKALINA 1978
 - Family Algasocrinidae STUKALINA 1982
 - Family Comptocrinidae STUKALINA 1979
 - Family Kitabicrinidae STUKALINA 1978
 - Family Pennatocrinidae STUKALINA 1975
 - Family Podolocrinidae STUKALINA 1977
 - Family Decacrinidae YELTSHEWA 1957 (sensu str.)
 - Family Rosulicrinidae STUKALINA 1980
 - Genus incertae familia
 - Genus Sartanicrinus STUKALINA 1985
 - Genus Zervaschanocrinus SHEWTCHEIKO 1966
 - Genus Raricrinus POLOZHICHINA 1980
 - Incerti ordinis
 - Family Altimarginalicrinidae STUKALINA 1979
 - Family Apporetocrinidae Y. DUBATOLOVA 1971
 - Family Asperocrinidae STUKALINA 1975
 - Family Crossotocrinidae Y. DUBATOLOVA 1971
 - Family Haplotetocrinidae Y. DUBATOLOVA 1971
 - Family Kstutocrinidae SHEWTCHEIKO 1966
 - Family Kuzbassocrinidae STUKALINA 1975
 - Family Multifidocrinidae STUKALINA 1980
 - Family Nirundacrinidae STUKALINA 1979
 - Family Salaiocrinidae Y. DUBATOLOVA 1971
 - Family Schyschatocrinidae Y. DUBATOLOVA 1971
 - Family Sibiricrinidae STUKALINA 1980
 - Family Stenocrinidae Y. DUBATOLOVA 1971
 - Family Tasujicrinidae STUKALINA 1977
 - Genus incertae familia
 - Genus Acanthocrinus ROEMER 1850 (sensu lato)
 - Genus Agathocrinus SHEWTCHEIKO 1967 (sensu lato)
 - Genus Amurocrinus Y. DUBATOLOVA 1971
 - Genus Costatocrinus STUKALINA 1975
 - Genus Cuboideocrinus STUKALINA 1980
 - Genus Dastaricrinus STUKALINA 1985
 - Genus Desmidocrinus ANGELIN 1878 (sensu lato)
 - Genus Dolatocrinus LYON 1857 (sensu lato)
 - Genus Fascicularicrinus STUKALINA 1982
 - Genus Ferulacrinus STUKALINA 1978
 - Genus Hexacrinites AUSTIN & AUSTIN 1843 (sensu lato)
 - Genus Scalaricrinus STUKALINA 1982
 - Genus Medinecrinus STUKALINA 1965
 - Genus Ordinaricrinus STUKALINA 1980
 - Genus Pandocrinus STUKALINA 1965
 - Genus Parabexacrinus SHEWTCHEIKO 1967 (sensu lato)
 - Genus Pestericrinus STUKALINA in RZONSNITSKAJA 1968
 - Genus Platycrinites MILLER 1821 (sensu lato)
 - Genus Ristnacrinus ÖPIK 1934 (sensu lato)
 - Genus Vallaticrinus STUKALINA 1980
- Group Asegmentata
 - Incerti ordinis
 - Family Peribolocrinidae Y. DUBATOLOVA 1971
 - Genus incertae familia
 - Genus Tantalocrinus STUKALINA 1975

A tetracatinal symmetry is recorded in stems of relatively rare groups of crinoids determined on the basis of general systematics. Thus, columnals with a quadrangular and tetralobate axial canal are recorded in a number of inadunate crinoids. Among them are the Early Ordovician genus *Ramseycrinus* and the Devonian genera *Ancyrocrinus*, *Arachmocrinus*, *Gasterocoma*, *Myrtillocrinus*, *Mictocrinus*, *Schultzicrinus*, and *Nanocrinus*, *Lecythocrinus*, *Corymocrinus*, and *Cupressocrinites*. It is noteworthy that in the scheme of inadunate crinoids (MOORE & LAUDON 1943; UBAGHS 1953), these genera either belong to old phylogenetic branches, or, as Gastecomidae, display a close affinity with old primitive crinoids. Among camerate crinoids, tetragonal columnals are described in Late Ordovician *Xenocrinus*, *Compsocrinus* and *Colpodecrinus*. It should be noted that a distinct pentacatinal symmetry is recorded in the structure of the axial canal of *Xenocrinus* stems.



Text-fig. 21. Phylogenetic relations of Tetragonocrinidae (1), Dwortsowaecrinidae (2, 3) and Bereljicrinidae (4) families.

The Quadrilaterata group comprises six families. The existence of the oldest family, Tetragonocrinidae, is associated with the close of the Early Ordovician (Volkhov time on the East European Platform). The Tetragonocrinidae stand well apart. Though they belong to the oldest crinoids known in the Ordovician, their stems belong to a highly developed morphofunctional type. In their axial canal, a very narrow central stock is distinguished and four narrow peripheral canals. YU. ARENDT (1985) assigns the family Tetragonocrinidae to monocyclic inadunates. Widespread in the Middle and Late Ordovician of Kazakhstan and Central Asia are representatives of another family, Dwortsowaecrinidae. From the historical viewpoint, they illustrate well gradual morphogenetic changes, connected with a gradual consolidation of columnals and constriction of the axial canal cavity due to 1) a simple reduction of dimensions and preservation of the initial shape (*Dwortsowaecrinus* and *Porkunicrinus*), 2) formation of differentiated lobes with a subsequent separation of independent peripheral canals (*Tatjanicrinus*). The consolidation of tetramerous columnals, accompanied by constriction of the axial canal, generation and development of the ligamentary field, is illustrated in the Early Silurian by the Bereljicrinidae family (Text-fig. 21). Probably, it is genetically related to the family Dwortsowaecrinidae. It occurs in the Early Silurian (Wenlockian) of the Altai.

Standing apart from the Ordovician and Early Silurian Quadrilaterata are Early Devonian families Tetraptocrinidae and Trilobocrinidae. Both families were established by YU. DUBATOLOVA (1971). Consolidated Tetraptocrinidae and Trilobocrinidae columnals are assigned to broad-canaled forms. Their morphogenetic modifications are also associated with a gradual constriction of the axial canal cavity, accompanied by the generation of differentiated

lobes. Representatives of Tetraptocrinidae and Trilobocrinidae are widespread in the Lower Devonian carbonate facies of Salair, Eastern slope of the Urals and South Tien Shan (Zeravshan Ridge).

A pentacatinal symmetry in crinoid stems, belonging to Pentamerata group, shows up in the same way, as in Quadrilaterata, in the structure of the axial canal, ligamentary field, disposition of costae on the articular surface, frequently, in the shape of columnals, and in the distribution pattern of sculptural formations on the lateral surface of columnals; in pentamerous forms, in the presence of five pentameres on columnals. Besides, we might also assign to Pentamerata group those stems which have lost features of a pentacatinal symmetry in their structure; however, their other characteristics point to a genetic link with stems, in which a pentacatinal symmetry is rather distinct. Pentamerata group, probably, comprises the vast majority of the known inadunates and camerates, determined on the basis of a general systematics.

The Pentamerata group is subdivided into two orders, viz. Angulata and Strialata.

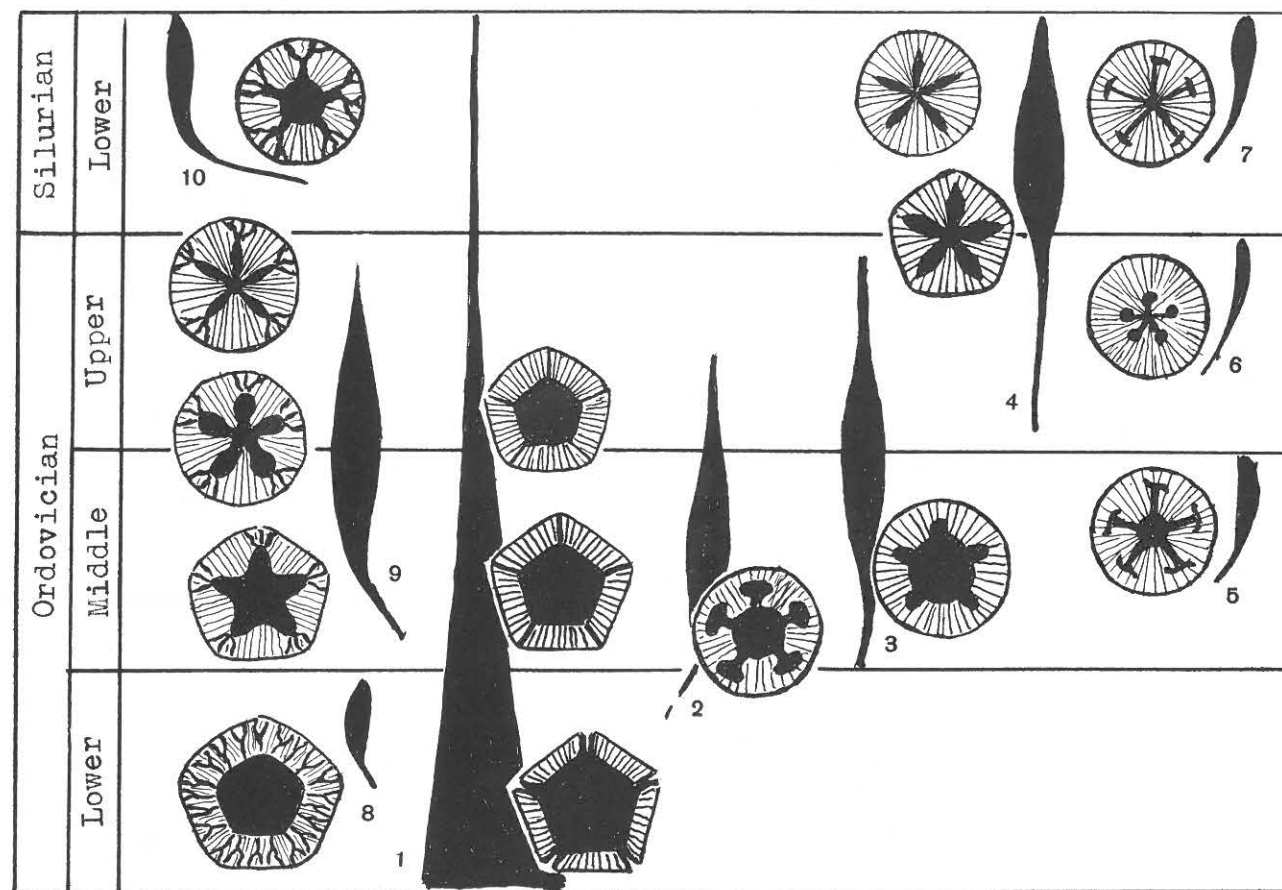
In pentamerous forms of the order Angulata, interpentamerous suture lines run from the axial canal angles to the angles of columnals. The ligamentary field of Angulata stems is developed within pentameres in direction away from the axial canal walls. The outer face of each pentamere acquires an outline, repeating that of the ligamentary field. The direction of the axial canal angles in Angulata stems does not coincide with that of the ligamentary field angles and the outline of the columnals. Thus, the position of the axial canal in Angulata representatives relative to the outlines of the ligamentary field and columnals seems to be "overturned". In stems, which have lost visible pentamerous features, but have retained them for a long time in the inner structure of columnals, the pattern of the ligamentary field evolution allows one to distinguish easily representatives of the Angulata group. The order Strialata comprises crinoids, the stems of which also have a pentamerous structure. Interpentamerous suture lines in crinoids of the order Strialata are perpendicular to the axial canal sides and the sides of columnals. The ligamentary field of these stems is developed from the axial canal angles. The position of the axial canal in representatives of this order relative to the outlines of the ligamentary field and columnals is "normal", i.e. the direction of the axial canal angles coincides with that of the ligamentary field angles.

Establishing relations between families and genera within the orders Angulata and Strialata is based on the analysis of morphogenetic modifications of the stems, traced in a gradual consolidation of pentamerous columnals, a gradual constriction of the axial canal, appearance and development of the ligamentary field. Major stages in their evolution are determined by the presence or absence of features of a pentamerous structure of stems.

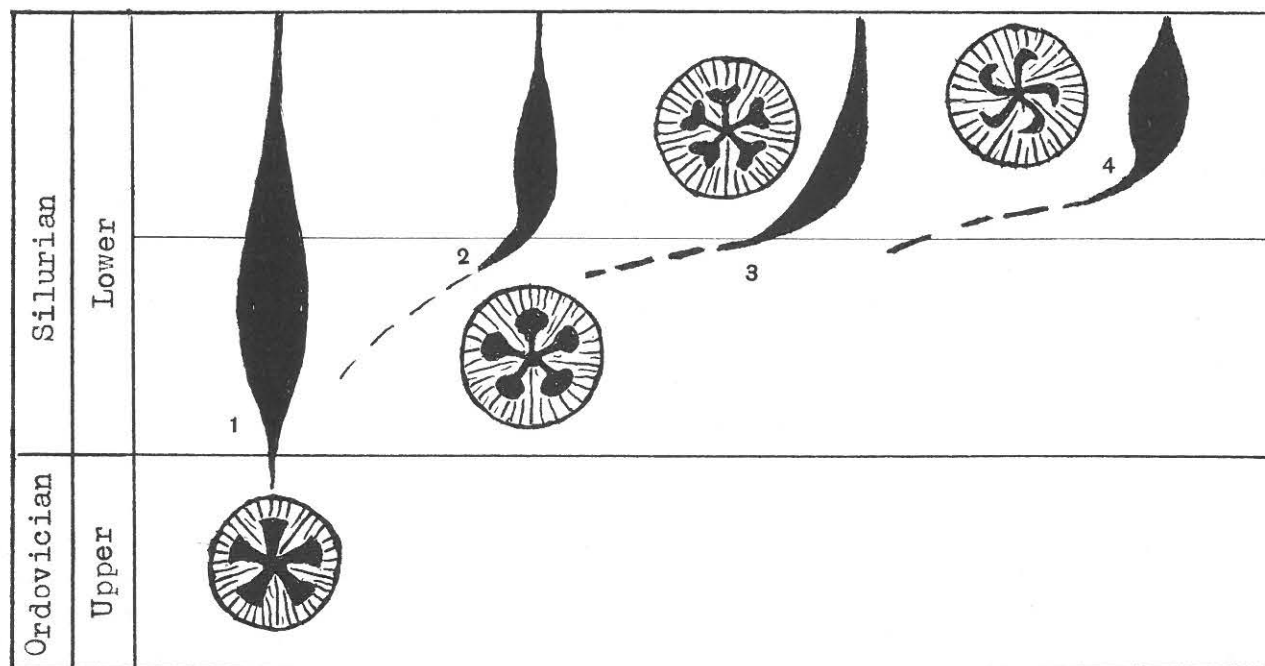
The oldest branch in the order Angulata is, probably, the family Apertocrinidae (Text-fig. 22). It is characterized by a simple structure and a certain stability of a broad axial canal, connected with stability and other features of a primitive structure of stems, viz. absence of a ligamentary field and low columnals. The evolution history of the Apertocrinidae family might be traced continuously from Early Ordovician to Late Silurian. Representatives of Apertocrinidae have an extensive geographical distribution. They are found on the territory of Kazakhstan and Central Asia, Northeast USSR, Siberia, Urals, and the East European Platform.

A gradual consolidation of pentamerous columnals and a gradual constriction of the axial canal in *Apertocrinus* morphofunctional type determines the appearance of numerous new branches, genetically related to the Apertocrinidae (Text-fig. 22). The character of modifications of the axial canal allows outlining two major trends in its evolution. The first one, with a gradual reduction of the axial canal, is characterized by formation of differentiated lobes (Text-fig. 22, 23, 24). The second trend, a more progressive one, is noted for a simple reduction of the axial canal with its basic shape being retained.

Taxa, illustrating the first evolutionary trend, are relatively few in Early and Middle Paleozoic and are commonly represented by conservative, slowly advancing branches. The oldest among them are the families Compositocrinidae and Webericrinidae. Both families are genetically related to the Apertocrinidae. Crinoid stems of these families have a very broad axial canal cavity, distinguished within which is a broad central part and short lobes, directed into angles of columnals: broad digitate (Compositocrinidae), or bulb-like trilobate (Webericrinidae). The evolutionary history of both families is connected with Middle Ordovician (mainly) and Late Ordovician. The family Compositocrinidae is found on the territory of Kazakhstan, Central Asia, and the Siberian Platform. The family Webericrinidae belongs to an endemic group among the Ordovician crinoids of Kazakhstan. The *Compositocrinus* morphofunctional type of stems among the known Middle Paleozoic crinoids are also found in the Middle Silurian of the Urals, Siberia, Kazakhstan, and Central Asia. They are assigned to the Equisarowicrinidae family. The family Equisarowicrinidae,



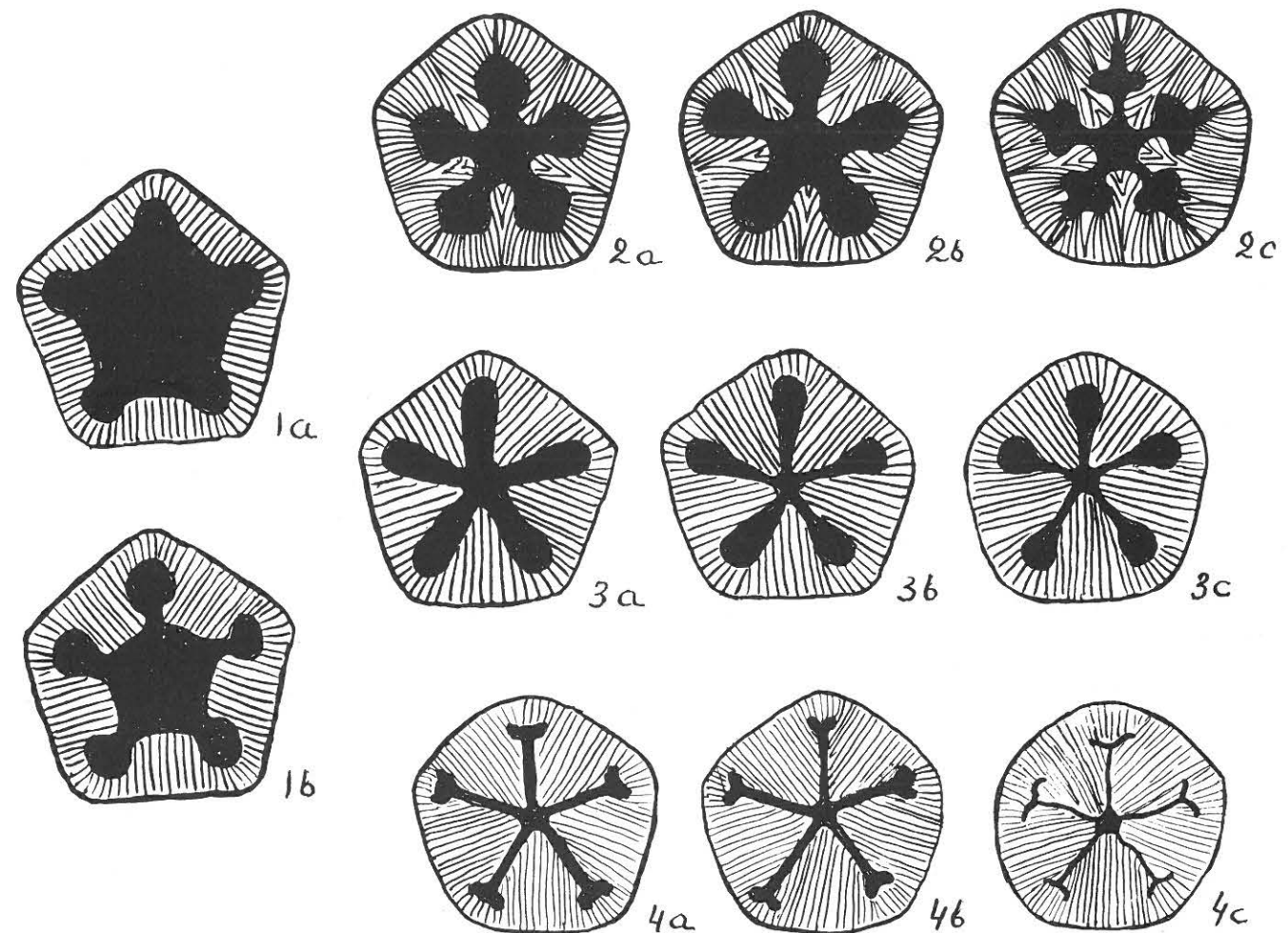
Text-fig. 22. Phylogenetic relations of Apertocrinidae (1), Webericrinidae (2), Compositocrinidae (3), Bystrowicrinidae (4), Flexicrinidae (5), Dulanocrinidae (6), Klunnikowicrinidae (7), Artificiosocrinidae (8), Ramosocrinidae (9) and Muschketovicrinidae (10) families.



Text-fig. 23. Phylogenetic relations of Bystrowicrinus (1, 2, 3) and Klunnikowicrinus (4) genera.

separated from Compositocrinidae by a considerable time interval, are also genetically related to the family Apertocrinidae.

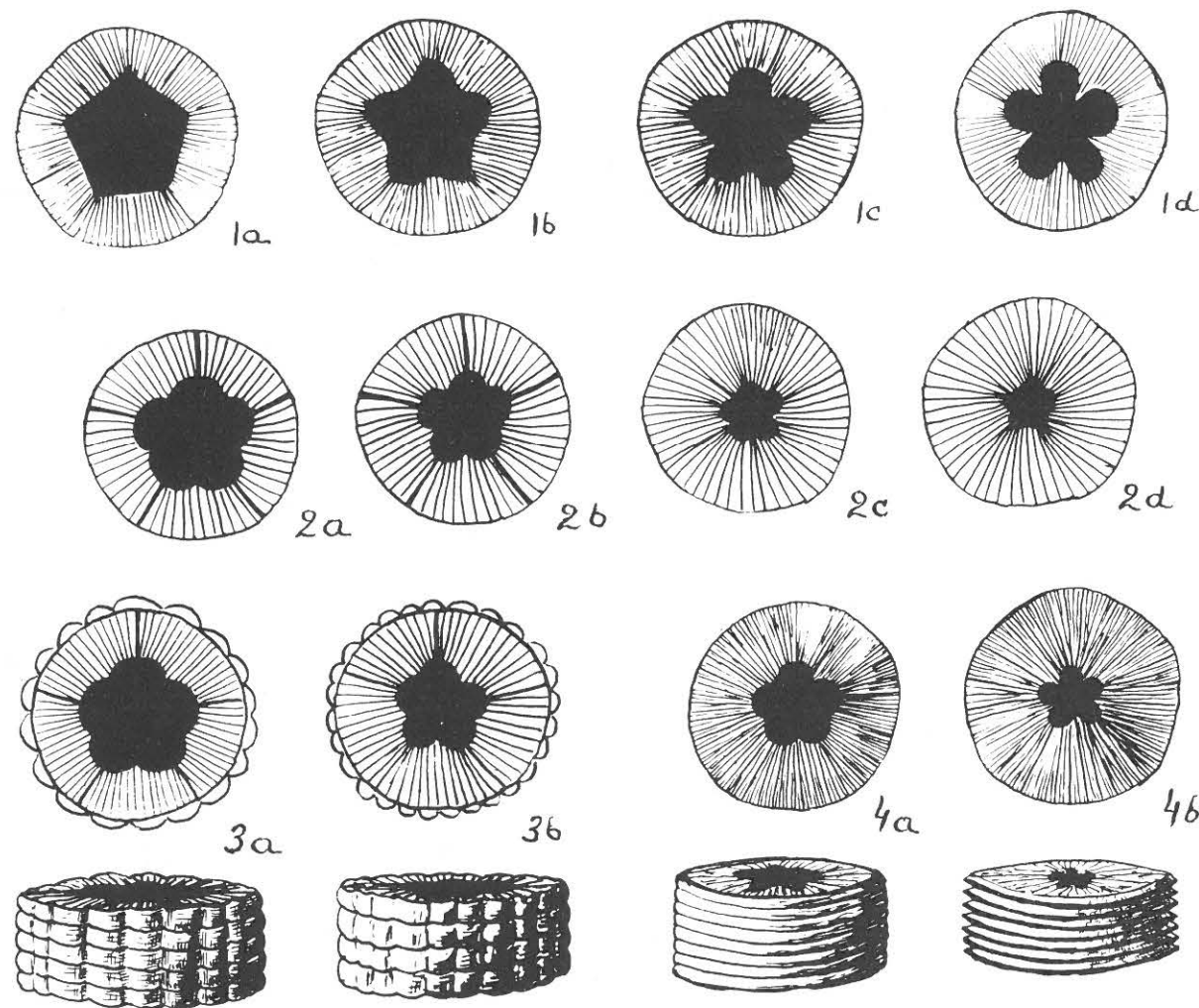
The further evolution of the axial canal of "*Compositocrinus* type" results in a marked constriction of its central stock and formation of long lobes, and forward directed angles of columnals. Lobes of the canal are first connected with its central part. Later, they lose this connection and become independent canals. Such features are typical of the family Bystrowicrinidae, which is closely related in its origin to the family Compositocrinidae (Text-fig. 22). Long lobes of the axial canal may have different dimensions and shapes. The family Bystrowicrinidae has a wide stratigraphic range and geographic distribution. Its representatives are known in the Middle Ordovician and Early Silurian of the Northeast USSR, Siberia, Urals, Kazakhstan, Central Asia, and the Arctic areas. This family culminates in Wenlock (Early Silurian).



Text-fig. 24. Morphotypes of crinoid stems: 1 a, b — *Bakanasocrinus clavatus* STUKALINA, x 8; Middle Ordovician; 2 a, b, c — *Webericrinus variabilis* STUKALINA, x 9; Middle Ordovician; 3 a, b — *Bystrowicrinus quinquelobatus* YELTYSHEVA, x 7; Lower Silurian; 4 a, b, c — *Flexicrinus flexus* STUKALINA & TUJUTJAN, x 10, Middle Ordovician.

Further evolution of the axial canal of *Bystrowicrinus* type results in the generation of specialized morphofunctional types. Their diagnostic features are curved slit-like lobes, thickened in the distal part, and a very narrow central stock (Text-fig. 24, 4). These features are taxonomic for three families, separated by large time intervals, viz. Flexicrinidae, Dulanocrinidae, and Klunnikowicrinidae. Representatives of the Flexicrinidae are known from the Middle Ordovician of Kazakhstan. The family Dulanocrinidae is widespread in the second half of the Late Ordovician in Kazakhstan. The evolutionary history of Klunnikowicrinidae is connected with Wenlock (Early Silurian) of Central Asia.

The trend towards a gradual constriction of the axial canal of *Apertocrinus* type, similar to that discussed above, can also be illustrated by the families Artificiosocrinidae, Ramosocrinidae, and Muschketowicrinidae (Text-fig. 22). These families belong to specialized groups, separated by considerable time intervals. Genetically, they are related to Apertocrinidae. These crinoid groups are characterized by the axial canal structure, also known in inadunate crinoids, Crotalocrinitidae (*Crotalocrinites*, *Syndetocrinus*) and camerate crinoids, Polypeltidae (*Tribliocrinus*). Its specific character consists of the fact that adjacent to the main stock of the axial canal is a dense network of very fine branched lateral canals, which penetrate the walls of the stems. Numerous holes of canals are seen on the lateral surface of stems. The family Artificiosocrinidae is characteristic of Early Ordovician of the East European Platform. Representatives of the Ramosocrinidae, known from the Middle and Late Ordovician of the Arctic areas, Siberia and Kazakhstan, have a wider stratigraphic range and geographic distribution. The family Muschketowicrinidae occurs within a narrow stratigraphic range, viz. in the Wenlock of Central Asia (SHEVCHENKO 1971), East European Platform, and Tuva.

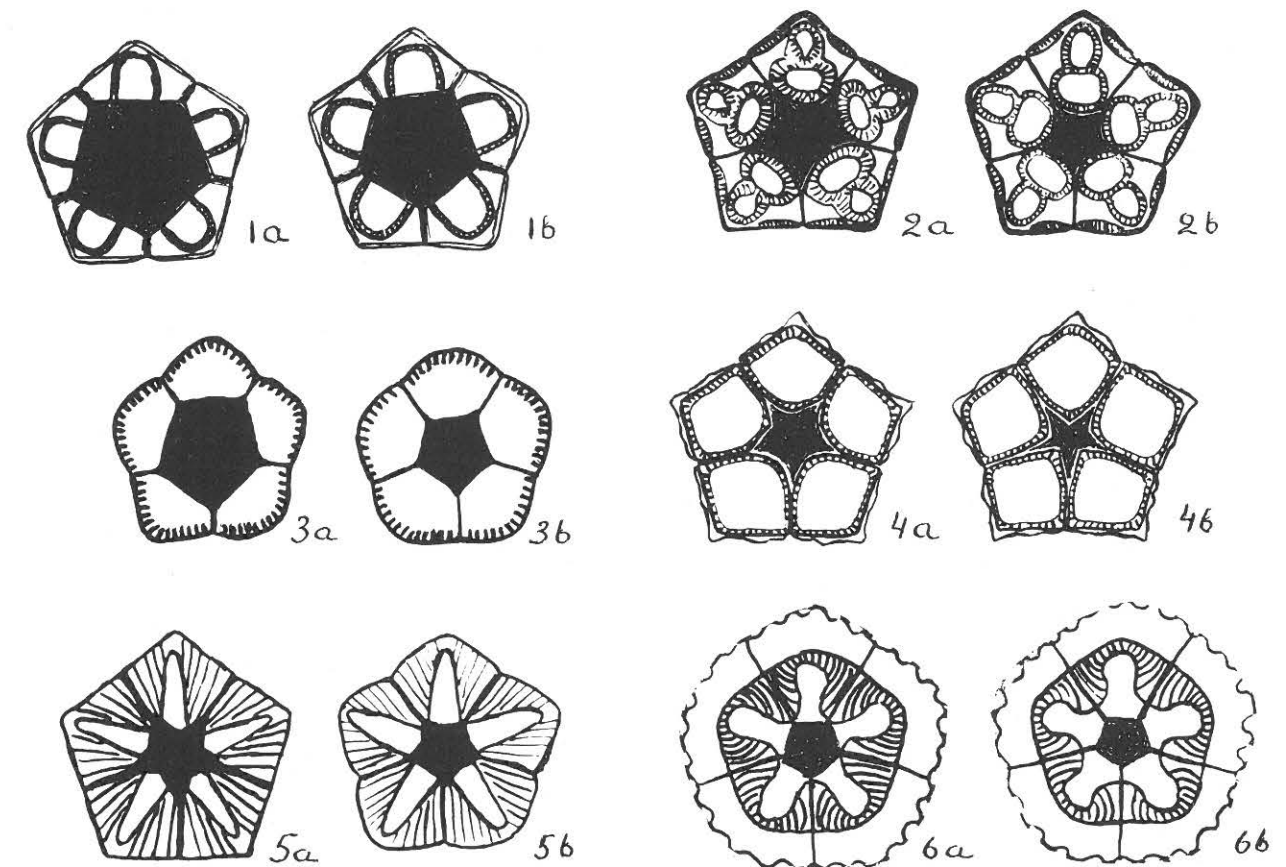


Text-fig. 25. Morphotypes of crinoid stems: 1a, b, c, d — *Crotalocrinites? borealis* YELTSHEVA, x 6, Lower Silurian; 2a, b, c, d — *Mediocrinus medius* YELTSHEVA & STUKALINA, x 6, Upper Silurian — Lower Devonian; 3a, b — *Mediocrinus rugatus* STUKALINA, x 6, Upper Silurian; 4a, b — *Pandocrinus plicatus* STUKALINA, x 7, Upper Silurian.

At the end of Early Silurian, the long-lived family Mediocrinidae is related to the Apertocrinidae family. Similar to the Apertocrinidae, the Mediocrinidae are characterized by a stable broad axial canal cavity, though their axial canal, unlike that of Apertocrinidae, has a distinct lobate shape (Text-fig. 25). The structure of lobes in the Mediocrinidae differs markedly from that of Compositocrinidae, Webericrinidae, Bystrowicrinidae, Flexicrinidae, etc. The lobes of their axial canal are weakly subdivided, low, with gentle semicircular summits. The Mediocrinidae are

found in Late Silurian (mainly) and Early Devonian of many regions, viz. Kazakhstan, Central Asia, Salair, Urals. The Mediocrinidae family may have genetic links with crinoids of Crotalocrinitidae family and *Kaplunaecrinus*. Their taxonomic character, as it is in the Artificiosocrinidae, Ramosocrinidae, and Muschketowicrinidae, is also the structure of the axial canal, which has numerous lateral branches. It is of interest that the Crotalocrinitidae frequently simultaneously display features of a distinct pentamerous structure of the Angulata-type stems. Representatives of Crotalocrinitidae throughout the USSR territory are widespread in Silurian, particularly in Wenlock and Ludlow. Crinoids of the genus *Kaplunaecrinus* are characteristic of the Early Devonian of Kazakhstan, Central Asia, and the Urals.

Genetic links with the family Mediocrinidae can also be assumed for planktonic *Scyphocrinites*. *Scyphocrinites* belong to a specialized short-lived group of crinoids, recorded in Late Silurian and the beginning of Early Devonian. Stems of *Scyphocrinites* are made up of low columnals. They have a broad quinquelobate axial canal and a deep ligamentary field. Arranged regularly throughout the ligamentary field surface are simple radial costae. Stems of planktonic *Scyphocrinites* were a link between the mobile cup and pneumatophorous chambered lobolites. On the USSR territory (Kazakhstan, Podolia, and the Urals), *Scyphocrinites* characterize the boundary between Silurian and Devonian.



Text-fig. 26. Morphotypes of crinoid stems: 1a, b — *Parvicrinus parvus* STUKALINA, x 9, Middle Ordovician; 2a, b — *Mirabilicrinus mirabilis* (YELTSHEVA), x 6, Middle Ordovician; 3a, b — *Lunaticrinus notus* STUKALINA, x 7, Upper Ordovician; 4a, b — *Morkokacrinus morkokaensis* (YELTSHEVA), x 6, Middle Ordovician; 5a, b — *Lobatocrinus angustus* STUKALINA, x 8, Upper Ordovician; 6a, b — *Sigillatocrinus sigillatus* STUKALINA, x 8, Middle Ordovician.

An essentially new type of articulation of columnals is observed within the order Angulata in the families Selenjachicrinidae, Parvicrinidae, and Lunaticrinidae (Text-fig. 26). Crinoids with a distinct pentamerous structure of stems belong to these families. They are characterized by a broad axial canal of Apertocrinus type, which allows assuming that they are related to the families Apertocrinidae. These broad-canaled forms have distinct deepening of ligamentary fields, devoid of ribbing, in the central part of the articular surface of these columnals. These families represent

discrete, short-lived endemic groups. The Selenjachicrinidae family was widespread at the beginning of Middle Ordovician. It is reported from the Selenyakh Range in the Northeast USSR. The family Parvicrinidae is found in Middle Ordovician of the Siberian Platform. The family Lunaricrinidae is characteristic of Late Ordovician of Kazakhstan.

In the assemblage of taxa, belonging to the order Angulata and illustrating a gradual constriction of the axial canal, two dominant branches are also distinguished, viz. the families Stellaricrinidae and Malovicrinidae. Crinoid stems of these families belong to broad-canaled forms, retaining a stable pentamerous structure of columnals and their ligament-free attachment. These families are widespread in the Ordovician and Early Silurian. Their representatives are found on the territory of Kazakhstan, Central Asia, Siberia, and Arctic areas. Morphofunctional types of Stellaricrinidae and Malovicrinidae stems are rather mobile as regards form-generation. Quite a number of families and genera form a genetically single assemblage with these families. Their characteristic taxonomic feature is the articulation of the columnals.

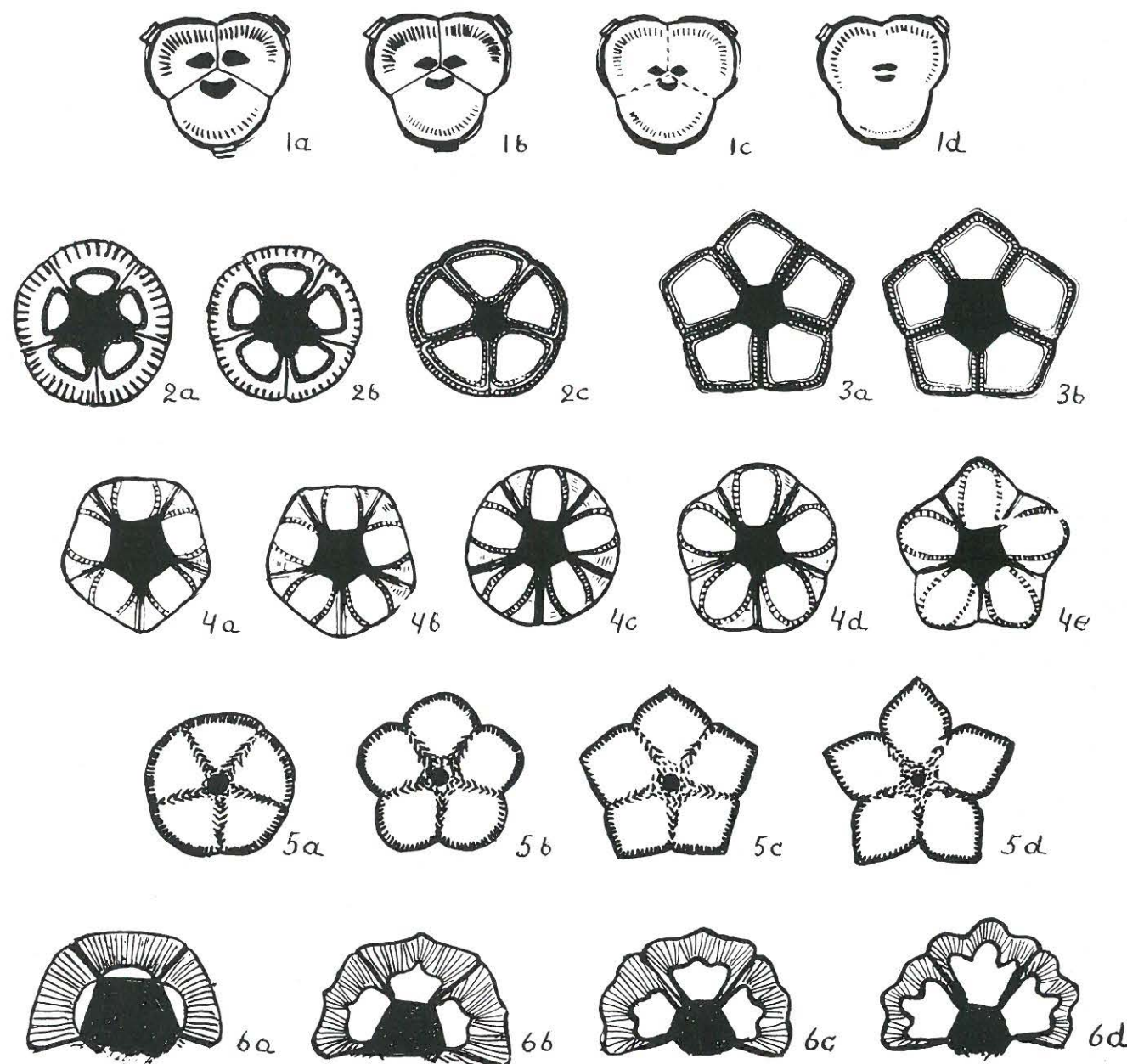
In the family Fascicrinidae which retains the initial *Stellaricrinus* type of the axial canal, fine bifurcating costae with a fan-shaped disposition participate in the articulation of columnals. In the family Fibracrinidae, which is also genetically related to the Stellaricrinidae, on the articular surface of the pentameres, there is a fine interlacing of bent and multiple bifurcating costae. Both families form isolated groupings. Representatives of the Fascicrinidae are widespread in Ordovician and Early Silurian of Kazakhstan and Central Asia. They are also known from the Late Ordovician of Siberia. The family Fibracrinidae is endemic; it is recognized in the Middle Ordovician of Kazakhstan. A taxonomic character of other families related to Stellaricrinidae (Particrinidae, Pulchelicrinidae, Lunulacrinidae, Sellicrinidae, Mirabilicrinidae), is the ligamentary articulation of the columnals. The Particrinidae, Pulchelicrinidae and Lunulacrinidae are characterized by broad ligamentary pits, covering almost the entire surface of pentameres and surrounded by continuous relief ridges. The Particrinidae family occurs in the Middle Ordovician of the Siberian Platform and Central Taimyr. The family Pulchelicrinidae, in the same stratigraphic interval, is known in the North-east USSR; the family Lunulacrinidae characterizes the first half of Late Ordovician on the East European Platform. Diagnostic features of the family Sellicrinidae are strongly dissected saddle-shaped broad lobes of the ligamentary field. This family occurs in the Middle Ordovician of Kazakhstan. Standing apart from the families under consideration is the family Mirabilicrinidae. Representatives of the Mirabilicrinidae are characterized by the "bullial" articulation type of pentameres, making up columnals, which is relatively rare in Ordovician crinoid stems. Most of the articular surface of each columnal is taken up by "bulla" (Text-fig. 3, 3; Text-fig. 26, 2), a well outlined elevated area, approaching an oval in its shape. The central part of the oval is taken by one (*Ramulicrinus*), or two ligamentary pits (*Mirabilicrinus*, *Kalgacrinus*, *Fossulacrinus*). Fine costae are arranged along the margins of the bulla and along the margin of columnals. The oldest among the *Mirabilicrinus*, *Kalgacrinus* genera occurs in the Early Ordovician of the Northeast USSR, The *Mirabilicrinus* genus belongs to the most characteristic Middle Ordovician genera in the territory of Siberia, Central Taimyr, Urals, and Kazakhstan. The *Ramulicrinus* genus is endemic, its occurrence is connected with the beginning of Late Ordovician in Eastern Kazakhstan. The genus *Fossulacrinus* characterizes the beginning of Late Ordovician on the East European Platform.

The family Malovicrinidae comprises crinoids, the stems of which retain the initial pentagonal shape of the axial canal. The ligamentary field in Malovicrinidae is either absent or is extremely weak, forming shallow depressions in the articular surface. Similarly to the Ordovician, in Early Silurian, the Malovicrinidae family is related to numerous families and genera, characterized by a well-developed ligamentary articulation of the columnals. The specialization of stems in this direction was primarily determined by the development and improvement of various types of ligamentary articulation of pentamerous narrow-canaled columnals. Let us consider some of the most characteristic adaptive trends.

The most long-term history in the Ordovician was that of the families Baltocrinidae and Babanicrinidae. The Baltocrinidae are noted for a pentapartial articulation type of columnals (Text-fig. 3, 1; Text-fig. 27) typical for the families Particrinidae and Pulchelicrinidae. The family Baltocrinidae is typical of the Middle Ordovician of the East European Platform. Representatives of Baltocrinidae are also known from Middle Ordovician of the Urals, Kazakhstan and Central Asia (South Tien Shan). Taxonomic features of the lenticular columnals of Babanicrinidae stems are deep, isolated ligamentary pits having a bulb-like or trapezoidal shape (*Babanicrinus*) with characteristic saddle-shaped summits of the ligamentary pits (*Conspectocrinus*). The Babanicrinidae are found in Middle and Late Ordovician of Kazakhstan, Central Asia, Urals and East European Platform.

Short-lived branches in the Middle Ordovician are formed by the endemic families, Caragachicrinidae, Sigillatocrinidae and Angusticrinidae. The ligamentary field of Caragachicrinidae, Sigillatocrinidae and Angusticrinidae has a lobate structure (Text-fig. 26). The Caragachicrinidae have lobes of a triangular shape with a broad base. The Sigillatocrinidae are characterized by digitate lobes, fused at the base. The Angusticrinidae have narrow slit-like lobes (Plate 5, fig. 15).

In Early Silurian, the family Malovicrinidae is related to a short-lived family Uzenicrinidae. Representatives of the Uzenicrinidae family are known in Early Silurian only from the territory of Eastern Kazakhstan. They are noted for a bulb-like shape of the ligamentary field lobes which are strongly constricted in the proximal part.



Text-fig. 27. Morphotypes of crinoid stems: 1 a, b, c, d — *Myelodactylus flexibilis* STUKALINA, x 10, Lower Silurian; 2 a, b, c — *Particrinus partitus* (YELTSYSHEVA), x 9, Middle Ordovician; 3 a, b — *Particrinus multipartites* (YELTSYSHEVA), x 6, Middle Ordovician; 4 a, b, c, d, e — *Ramulicrinus ramulus* STUKALINA, x 8, Upper Ordovician; 5 a, b, c, d — *Baltocrinus guttaeformis* (YELTSYSHEVA), x 6, Middle Ordovician; 6 a, b, c, d — *Catagraphiocrinus quindecimlobatus* YELTSYSHEVA & STUKALINA, x 6, Middle Ordovician.

Morphofunctional types of stems under consideration, genetically related to the Malovicrinidae, display distinct features of a pentamerous structure. Their loss is accompanied by a gradual constriction of the axial canal cavity. However, the ligamentary field retains the pattern of its evolution. It covers the articular surface from the axial canal walls towards the peripheral margin of columnals, forming characteristic lobes. The character and evolutionary trend of the ligamentary field favours determination and the establishment of links between quite a number of branches, genetically related to the initial morphofunctional type of crinoids of the family Malovicrinidae. This refers primarily to the families Bazaricrinidae, Anthinocrinidae, and Facetocrinidae, which have extremely diverse forms in Silurian and Devonian. Among the oldest forms, the evolution history of which goes back to the Early Silurian, are the families Bazaricrinidae and Facetocrinidae (Text-fig. 28). A distinctive feature of the Bazaricrinidae are narrow digitate lobes of the ligamentary field. A diagnostic feature of the Facetocrinidae family is a ligamentary field, not differentiated into lobes, developing from the axial canal walls and having a stellate outline in plan. The shape of the ligamentary field rosette both in Bazaricrinidae, and in Facetocrinidae is remarkably stable throughout Silurian and Early Devonian, as well as a pentagonal outline of the columnals proper. The first representatives of the family Anthinocrinidae are known from Late Silurian (*Anthinocrinus*); in Early Devonian, it is represented by several genera, the most characteristic of which are *Florincrinus*, *Kotanocrinus*, *Uruschicrinus*. A taxonomic character of the family Anthinocrinidae is the rosette structure in the lobate ligamentary field. Broad lobes of the ligamentary field of the Anthinocrinidae with semicircular summits display a trend towards fusion in the central part of the articular surface, and the ligamentary field rosette is gradually broadened to cover almost the entire articular surface. The axial canal is constricted to the minimum dimensions, costae become large and are pushed off to the margin of columnals. The columnals acquire a stable round shape. This general morphogenesis pattern of the Anthinocrinidae stems can be further used for working-out the classification of the Anthinocrinidae. Representatives of the Bazaricrinidae are mainly characteristic of the Silurian of Kazakhstan, Siberian Platform, Tuva, and Central Asia. Species and genera of the families Facetocrinidae and Anthinocrinidae, beginning with the Late Silurian, are widespread in Kazakhstan, Central Asia, Podolia, Salair, Urals, and Arctic areas.

In the order Strialata, the main old branch of the Apertocrinidae type is also distinguished. It has a long history and is noted for the relatively simple structure of the stems. This branch among Strialata is illustrated by the family Dentiferocrinidae. The stems of the Dentiferocrinidae have distinct features of a pentamerous structure, a stable and very broad axial canal and a symplexial articulation of the columnals. The evolutionary history of the Dentiferocrinidae is traced continuously in the Middle and Late Ordovician, as well as the Early Silurian of Siberia, Kazakhstan, Central Asia, Urals, Arctic areas, and East European Platform.

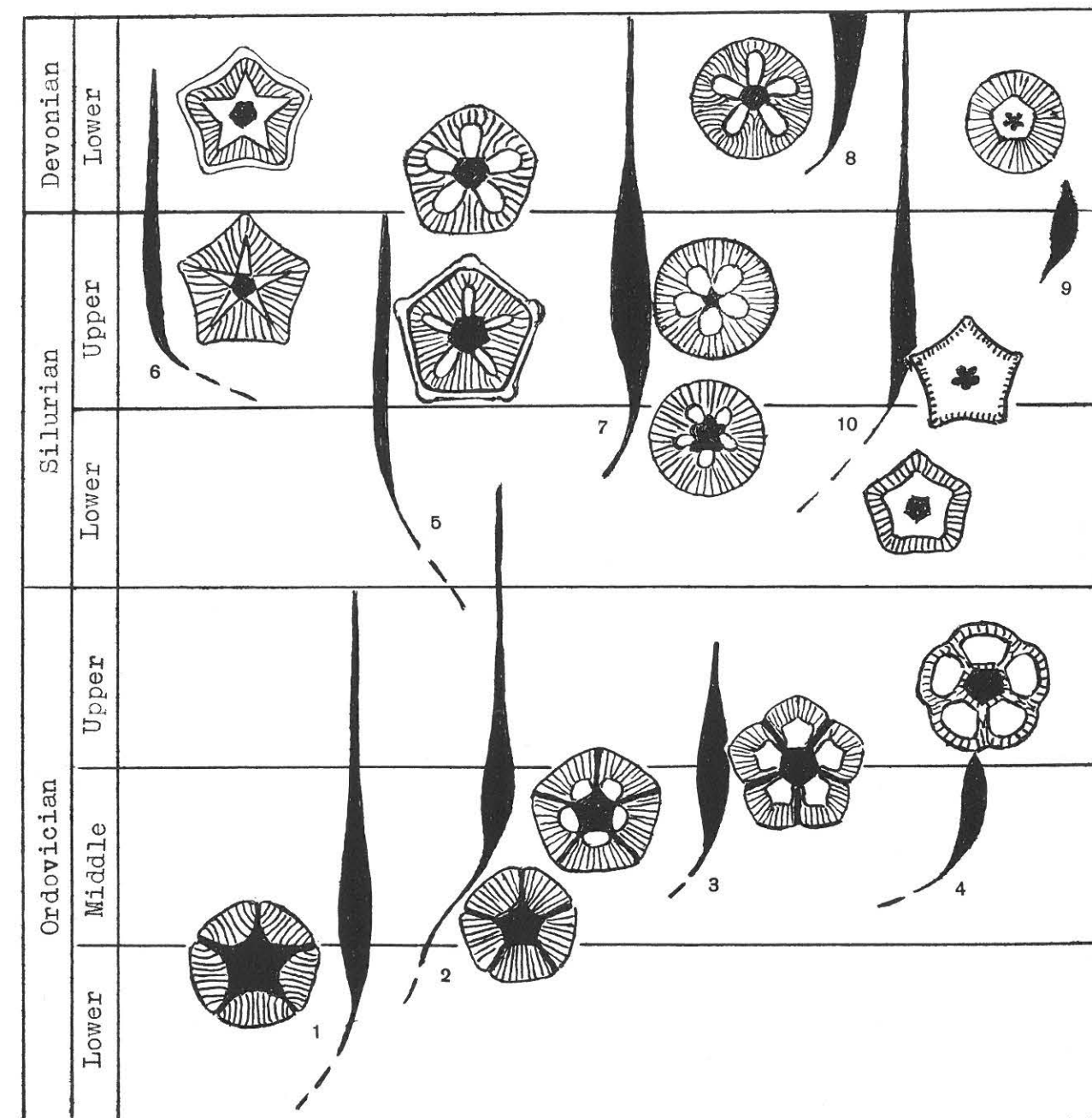
In the number of families and genera the order Strialata is much inferior to the order Angulata. Nevertheless, among Strialata crinoids, distinct evolutionary trends can also be traced. They are connected with a gradual consolidation of columnals, constriction of the axial canal cavity and the regular development of the ligamentary field. Thus, one of the characteristic evolutionary trends of Strialata crinoid stems is illustrated by the Algasocrinidae family. Similar morphofunctional types of stems in the order Angulata are recorded among representatives of the Compositocrinidae and Webericrinidae families. The Algasocrinidae family comprises crinoids, the stems of which have a clear pentamerous structure. In their axial canal, there is a very broad major stock, pentagonal in section, and long lobes with constricted proximal parts and markedly widened distal parts. The columnals of Algasocrinidae have a symplexial articulation. Algasocrinidae occur in the Middle Ordovician of Kazakhstan.

Another evolutionary trend of crinoid stems with a pentamerous structure in the order Strialata can be traced in a number of phylogenetic branches. In the Ordovician and Early Silurian, these are the families Rosulicrinidae, Comptocrinidae, and Kitabicrinidae. In Late Silurian and Early Devonian, they are illustrated by the families Penatocrinidae, Podoliocrinidae, Decacrinidae, and the genera *Raricrinus* and *Zeravschanocrinus*.

The family Rosulicrinidae comprises crinoids, in which the distinctive feature of the stems is the structure of a quinquelobate axial canal and a quinquelobate ligamentary field. Among crinoids of the order Angulata, such a morphofunctional type of stems is unknown. The Rosulicrinidae family is endemic (STUKALINA 1980). It occurs in the beginning of Late Ordovician in Kazakhstan.

The Ordovician family Comptocrinidae displays pronounced features of the order Strialata. It is characterized by a stellate ligamentary field and coarse relief costae of different thickness and height, forming a pinnate framing of the ligamentary field lobes. This family stands well apart from other forms. Representatives of the Comptocrinidae are characteristic of Middle Ordovician of the Siberian Platform and Central Taimyr.

In Early Silurian, the family Dentiferocrinidae is genetically related to the family Kitabicrinidae. A diagnostic feature of Kitabicrinidae is the structure of the stellate ligamentary field, the long lobes of which have a characteristic shape of an isosceles triangle with a broad base. Similar to Comptocrinidae, the family Kitabicrinidae is endemic. It occurs in the Early Silurian (Llandovery) of the South Tien Shan.



Text-fig. 28. Phylogenetic relations of the Stellaricrinidae (1), Malovicrinidae (2), Lunaricrinidae (3), Particrinidae (4), Bazaricrinidae (5), Forinosocrinidae (6), Anthinocrinidae (7, 8) and Facetocrinidae (9, 10).

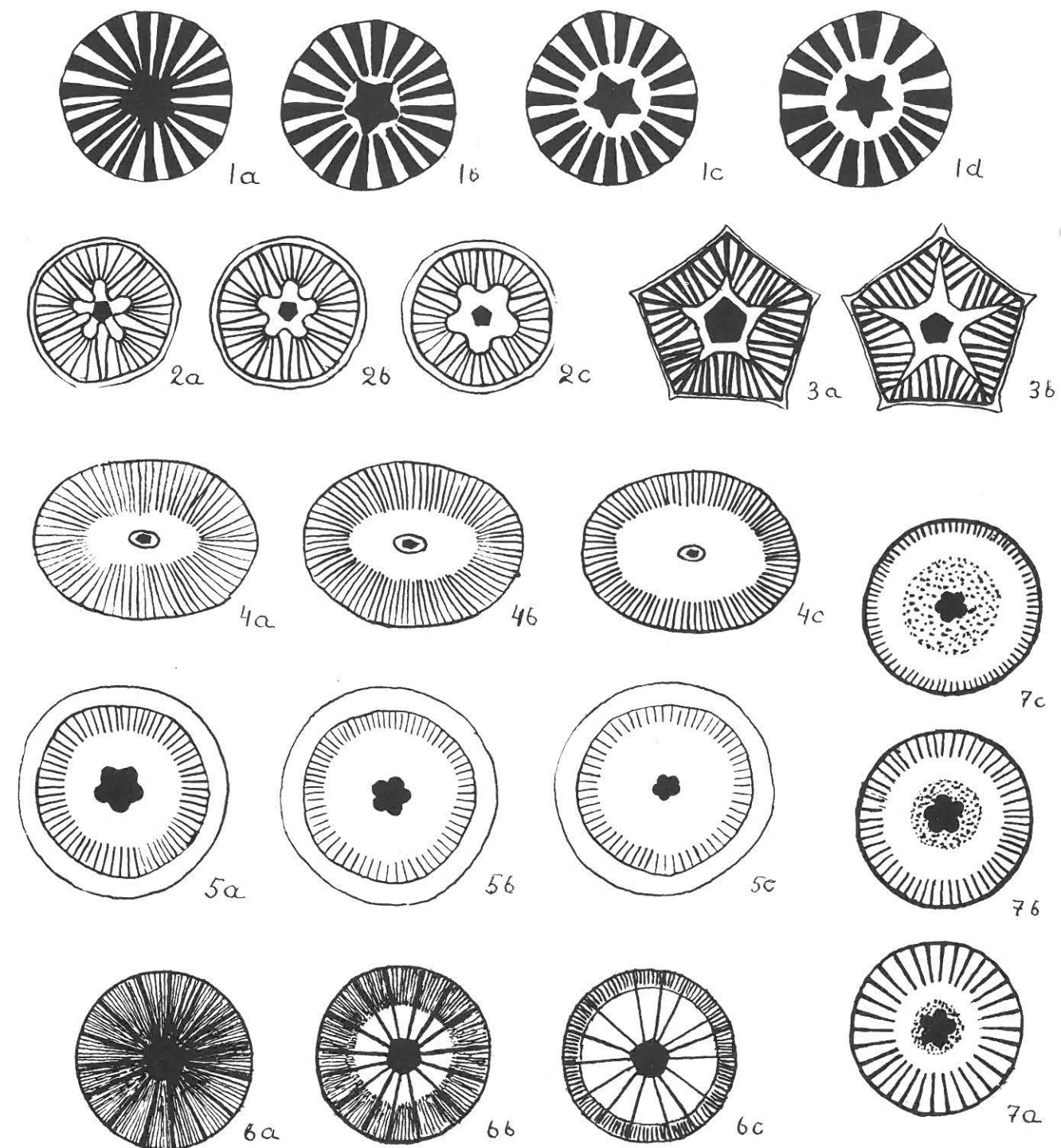
A characteristic structural feature of crinoid stems of the Pennatocrinidae, Podoliocrinidae and Decacrinidae families is the articular surface of the columnals. In their centre, there is the narrow hole of the axial canal with a pentagonal section. The depression of the articular surface is taken up by the ligamentary field, subdivided into ten lobes. A rigid articulation was realized by a system of radial and pinnate crenulae and short crenulae, arranged along the margin of the columnals. The morphological features of the Pennatocrinidae, Podoliocrinidae and Decacrinidae change with time: the ligamentary field rosette is gradually increased in size to cover the entire articular surface of columnals; the axial canal is constricted to the minimum dimensions; costae become larger, more distinct and are pushed off to the peripheral margin of the columnals. Proceeding from the morphogenesis scheme of stems of the Decacrinidae and Podoliocrinidae types, it might be assumed that there are certain phylogenetic links between these stems and those of the Pennatocrinidae type, regarding the Pennatocrinidae as the initial type. Thus, in Early Devonian, there are three synchronous trends of crinoid evolution. One of them illustrates the slowly advancing Pennatocrinidae family which occurs in Late Silurian and the beginning of Early Devonian in Kazakhstan and Podolia. Another evolutionary trend is illustrated by the family Podoliocrinidae, which is found in the Early Devonian of Kazakhstan, Podolia, and Central Asia. The third evolutionary trend is represented by the family Decacrinidae. Representatives of the Decacrinidae are widespread in Early Devonian of Kazakhstan, Gorny Altai, Far East, and North America (MOORE & JEFFORDS 1968).

In the order Strialata, widespread in Early Devonian, are morphofunctional types of stems, a diagnostic feature of which is the structure of the quinquelobate ligamentary field. Among them are *Zeravschanocrinus* and *Raricrinus*, which differ markedly from other forms. *Zeravschanocrinus* was described by SHEVCHENKO (1966). Its taxonomic features are as follows: a strongly dissected rosette of the quinquelobate ligamentary field with five narrow, long, almost slit-like lobes, developing from the axial canal angles. The genus *Raricrinus* was established by A. I. POLOZHIKHINA (1980). Its main taxonomic character is also the structure of the ligamentary field rosette. As distinct from the *Zeravschanocrinus*, in *Raricrinus* the ligamentary field lobes are short, bulb-like, markedly constricted at the base. Both genera in the Early Devonian form short-lived branches. The *Zeravschanocrinus* genus is characteristic of Early Devonian of Central Asia, Urals, and Arctic areas. *Raricrinus* genus occurs in Early Devonian of Kazakhstan and Far East.

The Pentamerata group, besides families and genera, clearly belonging to orders Angulata and Strialata, also comprises crinoid families and genera, which lack features of these orders. Stems of crinoids, belonging to these genera and families, do not have a pentamerous structure. Their columnals are monolithic, have a narrow axial canal with distinct features of a pentacatal symmetry. Phylogenetic links of these families and genera are not confirmed. In the present state of knowledge, they probably comprise morphologically similar forms, which are developing simultaneously in different phylogenetic branches. One of the major evolutionary trends consists in the gradual evolution and complication of a ligament-free junction of the columnals. Another one is characterized by a rapid progressive change of the ligamentary junction of columnals. The first evolutionary trend might be illustrated by the following families and genera: Crossotocrinidae, Haplotetocrinidae, Salairocrinidae. *Clavaticrinus* (= *Pentapetalocrinus*), *Sibiricrinus*, Multifidocrinidae, *Ferulacrinus*, *Fasciculacrinus*, *Medinecrinus*, *Costatocrinus*. The families Crossotocrinidae and Haplotetocrinidae are similar to the family Mediocrinidae in their structure of the axial canal of stems. Both families were distinguished by YU. DUBATOLOVA (1971). They are found in the Lower Devonian of Salair and Gorny Altai. The evolution of the *Mediocrinus*-type axial canal, connected with its gradual constriction, is illustrated by the family Salairicrinidae and the genus *Clavaticrinus*. The family Salairicrinidae has a wide stratigraphic range and geographic distribution. It is known from Early and Middle Devonian of Salair, Central Asia, Urals, and Northeast. Crinoids of the genus *Clavaticrinus* are similar to Angulata crinoids of the Equisarowicrinidae. They are reported from the Lower Devonian of the Northeast Balkhash are (POLOZHIKHINA 1980) and were described by YU. A. DUBATOLOVA (1980) from the Lower Devonian of Rudny Altai.

The family Sibiricrinidae comprises crinoids with a divided articulation type of stems, rather rarely found in the Early and Middle Paleozoic. This articulation type of columnals was described in the Ordovician genus *Divisicrinus* and the Silurian genus *Sibiricrinus*. The family Sibiricrinidae is characteristic of Early Silurian and, mainly, the Wenlockian time of Siberia, Kazakhstan, Tuva, and Podolia. Structural features of the axial canal of the Sibiricrinidae stems allow assuming its genetic links with the family Malovicrinidae of the order Angulata.

A highly developed and specialized morphofunctional type of crinoid stems in Early Paleozoic is illustrated by crinoids of the family Multifidocrinidae and the genera *Ferulacrinus* and *Fascicularicrinus*. Monolithic elliptical and

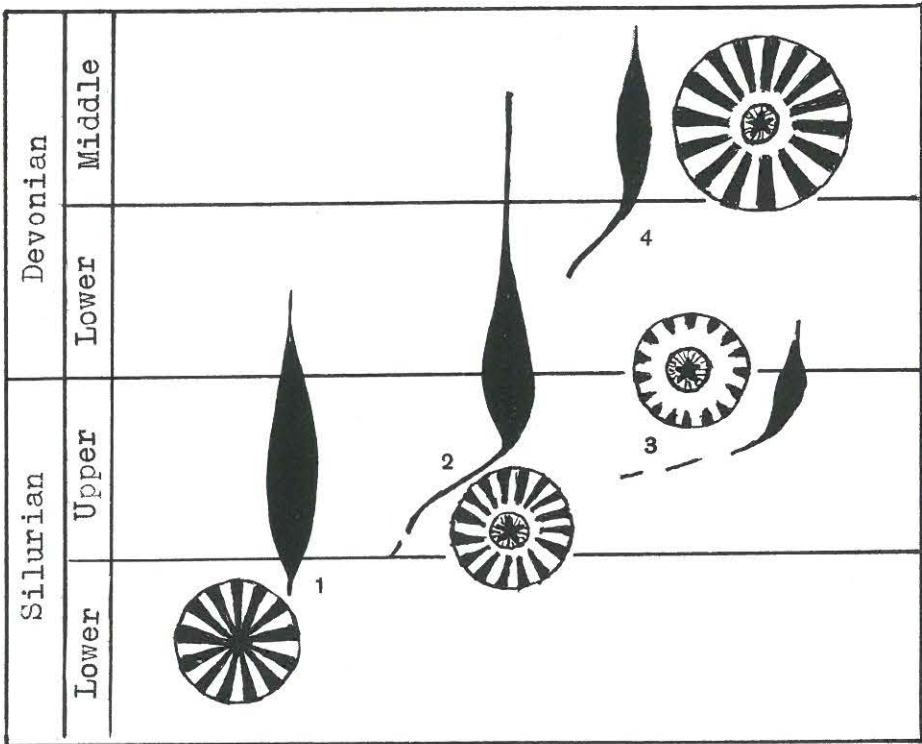


Text-fig. 29. Morphotypes of crinoid stems: 1 a, b, c, d — *Costatocrinus clamosus* STUKALINA, x 10, Lower Silurian; 2 a, b, c — *Anthinocrinus podolicus* YELTYSHEVA, x 10, Upper Silurian; 3 a, b — *Comptocrinus comptus* (YELTYSHEVA), x 7, Middle Ordovician; 4 a, b, c — *Hexacrinites ? humilicarinatus* YELTYSHEVA, x 5, Lower Devonian; 5 a, b, c — *Tolenicrinus clarus* STUKALINA, x 10, Lower Silurian; 6 a, b, c — *Sibiricrinus disjunctus* STUKALINA, x 6, Lower Silurian; 7 a, b, c — *Tjulkulicrinus tjulkulensis* STUKALINA, x 10, Lower Silurian.

round columnals of *Multifidocrinus*, *Ferulacrinus* and *Fascicularicrinus* stems, lacking features of a pentamerous structure, have an almost point axial canal. The type of ribbing on their articular surface is characterized by the grouping of costae into paired bundles. Costae in bundles, arranged along the long axis of columnals are always larger and show more relief than those forming bundles along the short axis of columnals. Morphofunctional types of crinoid stems of *Ristnacrinus*, *Platycrinites*, *Eucladocrinus* etc. have a certain analogy with the forms described. *Ferulacrinus* was described from Middle Ordovician of the South Tien Shan; *Fascicularicrinus*, from the Lower Silurian (Llandovery) of the Siberian Platform.

Crinoids of the genus *Costatocrinus*, widespread in Late Silurian and the beginning of Early Devonian in Kazakhstan, Central Asia, Urals, and Podolia, are characterized by a system of a few large relief costae, widened abruptly or bifurcating near the edge of the columnals (*Costatocrinus*). High columnals of the *Costatocrinus* have a lenticular or barrel-like shape. The evolutionary trend of mobility and flexibility in columnals of the morphofunctional type under consideration results in the formation of a ligamentary field depression in the central part of the articular surface (*Kstutocrinus*, *Nimiocrinus*).

One of the evolutionary trends of a ligament-free junction, accompanied by a gradual constriction of the axial canal, can be illustrated by the crinoids of the genus *Medinecrinus*. The evolution of *Medinecrinus* is slow and displays no outbreaks in form-generation. Representatives of *Medinecrinus* are well known in Silurian and, particularly, Early Devonian; they are ubiquitously widespread in the Middle Paleozoic.



Text-fig. 30. Phylogenetic relations of *Costatocrinus* (1), *Asperocrinus* (2, 3), and *Nimiocrinus* (4).

Tolenicrinus is, probably, genetically related to *Mediocrinus*. Similar to *Mediocrinus*, *Tolenicrinus* belongs to a group of crinoids, which is widespread in the Middle Paleozoic and has a low evolution rate. Representatives of the genus *Tolenicrinus* illustrate an evolutionary trend of the ligamentary junction of the columnals in the case of a rather narrow axial canal and, practically, only slightly changing height of the columnals. The development of a ligamentary attachment and the associated broadening of the ligamentary field along the articular surface of the columnals result in a gradual reduction of costae through their displacement to the peripheral part of the articular surface up to a complete disappearance. The final stage of the stem evolution in this direction is marked by the appearance of swimming stemless forms.

Stratigraphic distribution of characteristic species		ZONAL SUBDIVISION ON CRINOIDS	
Silurian	Upper	Paradecacrinus orientalis	Facetocrinus pentagonus
	Lower	Decacrinus decemcrassus	Florocrinus proteus
		Decacrinus roseliformis	Kuzbassocrinus bimidigitatus
		Decacrinus ornatus	Asperocrinus giganteus
Devonian	Lower	Decacrinus pennatus	Hexacrinites tuberosus
		Decacrinus ovalis	Hexacrinites humilicarinatus
		Podolocrinus nikirovae	Hexacrinites subbiconcavus
		Scyphocrinites -Pennatocrinus subpennatus	Hexacrinites inflatus
			Asperocrinus echinatus
			Kaplunacrinus rimosus
			Kaplunacrinus kaplunae
			Kuzbassocrinus subtilis
			Florocrinus floreus
			Tastjicrinus paucicostatus
			Kuzbassocrinus bystrowi
			Tastjicrinus tastjiensis
			Facetocrinus stellatus
			Facetocrinus ajinasuensis
			Gregariocrinus forus
			Decacrinus pennatus
			Decacrinus ornatus
			Decacrinus pennatus
			Decacrinus ovalis
			Podolocrinus nikirovae
			Scyphocrinites -Pennatocrinus subpennatus

Text-fig. 31. Scheme of zonal division of Lower Devonian in the USSR based on crinoids.

One of the manifestation forms of the high mobility of columnals is the mamillial articulation type. A distinctive feature of this type is the central circular ridge (perilumen), which is framing the axial canal hole in the form of a papilla. The mamillial articulation type is common among Middle and, particularly, Late Paleozoic crinoids. It is described in a number of camerate crinoids, viz. *Hexacrinites*, *Ctenocrinus*, *Dichocrinus*, *Gilbertocrinus*, *Arthroacantha*, as well as *Cyclocaudex*, *Laudonamphalus*, *Florycyclus*, *Cyclocrista*, *Pinegicrinus*, *Kojvicrinus*, etc. In the Ordovician and Early Silurian, where forms with distinct features of a pentamerous structure of the stems are dominant among crinoids, the mamillial articulation type is quite rare. Among Ordovician crinoids of Siberia and Taimyr, it is described in the genus *Altimarginalicrinus*; in Early Silurian, in the genus *Scalaricrinus*, occurring on the Siberian Platform. In Lower Devonian, crinoids with a mamillial articulation type of columnals are widespread. One of them belongs to the family Asperocrinidae. For other forms, the generic name *Hexacrinites* is traditionally used. The Asperocrinidae are widespread in the Lower Devonian of Kazakhstan and Northern France. Stems of *Hexacrinites*? (s.l.) crinoids were described from Lower and Middle Devonian of the Arctic areas, Urals, Central Asia, Armenia, Kazakhstan, Podolia, Salair, Gorny Altai.

Further evolution and improvement of the mamillial morphofunctional type results in the appearance and development of the longitudinal transverse ridge (fulcral ridge) on the articular surface. The axial canal retains its point dimensions, and the costae on the articular surface are almost entirely reduced. The articulation of the columnals in crinoid stems of such types is known from literature under the name of synanthry (MOORE & JEFFORDS 1968). It is common in Late Paleozoic crinoids and is most typical in camerate crinoids of the genus *Platycrinites*. Among Early Paleozoic crinoids, such types of articulation are recorded in *Ristnacrinus*, established by ÖRIK from the Late Ordovician of Estonia.

One of the characteristic evolutionary trends of Early and Middle Paleozoic crinoids, associated with the improvement of the ligamentary junction of the columnals, is illustrated in Early Silurian by the genus *Dastaricrinus*; in Early Devonian by the families Kuzbassocrinidae and Tastjicrinidae. Their taxonomic character is the structure of a decem-partite ligamentary field. In the Kuzbassocrinidae, the ligamentary field lobes are markedly differentiated both in the proximal, and distal parts. The *Tastjicrinus* and *Dastaricrinus* have lobes, which are commonly fused in the proximal part and differentiated in the distal direction. In the evolution of the ligamentary field of *Kuzbassocrinus* and *Tastjicrinus* the initial type is unknown. Therefore, phylogenetic links between the families Kuzbassocrinidae and Tastjicrinidae, which are synchronous in Early Devonian, are unknown. Representatives of the *Kuzbassocrinus* are typical for the Lower Devonian of Central Asia, Salair, Urals, Gorny Altai, and the Far East. In the Tastjicrinidae family the type genus *Tastjicrinus* is endemic. It occurs in the Lower Devonian of Kazakhstan; another genus, *Gurjevskocrinus* was described from the Lower Devonian of Salair; *Aulnocrinus* is characteristic of the Lower Devonian of Kazakhstan (POLOSHIKHINA 1980) and the Armorican Massif in Northern France and Spain (LE MENN 1970).

The third group, the Asegmentata, comprises crinoids, marked by features of a high organization. Their columnals are monolithic plates, which have lost all features of a pentamerous structure. Both columnals proper, and their axial canal and the ligamentary field have a stable round or elliptical outline. By its genesis, the group is, most likely, related to the Pentamerata and is a later phylogenetic branch as compared to it. Crinoids of the subclass Flexibilia, probably, belong to Asegmentata. As compared to the Pentamerata and Quadrilaterata, the Asegmentata group is not abundant in Early and Middle Paleozoic. To this group we assign the family Peribolocrinidae, distinguished by YU. DUBATOLOVA (1971) and occurring in the Lower Devonian of Salair, as well as the genus *Tantalocrinus* genus, found in the Early Devonian of Kazakhstan and the genus *Simplocrinus*, characteristic of the Ordovician on the East European Platform (GINDA 1985). The same group also comprises several species of crinoid stems with a round outline of the axial canal, the systematic position of which is not clear (incertae sedis). They are found in the Ordovician of Estonia and Podolia, Silurian and Early Devonian of Podolia, South Tien Shan, Central Taimyr, Salair, Estonia, and the Siberian Platform.

Conclusion

The use of the method of morphofunctional analysis in the studies of dissociated crinoid fragments, represented by stems, makes it possible to work out their classification based on a phylogenetic principle.

In working-out the crinoid systematics based on stem fragments, a major role is played by the analysis of variance, namely: in the evolution and determination of an intraspecific variability, in the elaboration of a system of diagnostic features of species, and studies on crinoid ontogeny on the basis of stems.

Further thorough studies of crinoid stem morphology, including their microstructure will, probably, allow the introduction of certain corrections in relations between taxa, established on the basis of the calyx (and crown) structure.

Common methods of studies and crinoid systematics principles, irrespective of what elements they are represented by in the fossil state, makes it possible to eliminate parataxonomy in their classification and to give a more complete evolutionary pattern of the group in general. This, in its turn, opens up good prospects for a more complete use of crinoids in stratigraphy as a faunal group.

The significance of using stem fragments in the studies of Paleozoic crinoids is largely determined by the fact that owing to the study of these fossils, it is possible even now to trace major evolutionary features of this group in the Ordovician, Silurian and Lower Devonian of the USSR and to establish successive stages of its evolution in time, and the space distribution pattern. Biostratigraphic analysis of taxa, distinguished on the basis of phylogenetic principles, allows the use of these widespread skeletal ossicles not only in regional stratigraphy. They can also be used in broad regional intercontinental correlations and for solving problems on a general scale, down to distinguishing zonal units which are based on a phylogenetic succession of species. This can be illustrated by the author's studies (STUKALINA 1981), dealing with zonal subdivision of the Lower Devonian on the basis of materials from different regions of the USSR.

In the scheme given here (Text-fig. 31), a zonal subdivision of this stratigraphic interval is based on a number of species of the following families: Pennatocrinidae, Podolocrinidae, Decacrinidae, Tastjicrinidae, Kuzbassocrinidae, Anthinocrinidae, Facetocrinidae. These families reflect characteristic evolutionary trends of Devonian crinoids. The zonal scale adopted is based on a phylogenetic succession of species in the *Pennatocrinus-Decacrinus* genera, which is established by studies on morphogenetic modifications and stem ontogeny.

Studies on facies associations and space distribution of crinoid skeletal ossicles open up good prospects for their use in paleoecological and paleogeographical investigations.

References

- ANTROPOV, J. A. (1954): Ob ostatkakh *Cupressocrinus* i ikh stratigraphicheskoy znachenii v devone Volgo-Uralskoy neftjanoy oblasti [On *Cupressocrinus* remains and their stratigraphic significance in Devonian of the Volga-Urals oil field]. — Proc. Kazanian Branch Acad. Sci. USSR, (ser. geol.), 2: 12–16.
- ARENDT, YU. A. (1970): Morskie liliy gipocrinidji [Sea lilies gipocrinidae]. — Trans. Paleontol. Inst., Moscow, "Nauka", Press. 128: 1–220.
- (1985): Drevneyshie trechrukie krinoidei bez pjatiugolnoy simmetrii [Oldest triserial-armed crinoids. Without a pentacatal symmetry]. — Proc. USSR. Acad. Sci., 282, 3: 702–705.
- BATHER, F. A. (1899): A phylogenetic classification of the Pelmatozoa. — Brit. Ass. Adv. Sci., Rept., (1898): 916–923.
- (1900): The Echinodermata. The Pelmatozoa-Crinoidea. — In: LANKESTER, E. R. (ed.): Treatise on Zoology, pt. 3: 94–204, London.
- BEKLEMISHEV, W. N. (1964): Osnovy sra nitelnoy anatomii bespozvonochnykh [Fundamentals of comparative anatomy]. — Publishing House, "Nauka", Moscow, I: 428 p.
- BIESE, W. (1934): Crinoidea triadica. — In QUENSTEDT, W. (ed.): Fossilium Catalogus, I. Animalia, pt. 66: 255 p.
- BRISKEY, J. (1981): Klassifikasjon av krinoidstalker fra den overordoviciske Kalvsjøformasjonen på Hadeland. Hovedfagsoppgave i geologi (Paleontologi). — Univ. Oslo, Paleontologisk. Museum: 1–170.
- BROWER, J. C. (1973): Crinoids from the Girardeau Limestone (Ordovician). — Palaeont. Americana, 7, 46: 263–499.
- (1974a): Upper Ordovician Xenocrinoids (Crinoidea, Camerata) from Scotland. — Univ. Kansas, Paleont. Contrib. 67: 1–25.
- (1974b): Ontogeny of Camerata crinoids. — Univ. Kansas, Paleont. Contrib., 72: 1–53.
- BROWER, J. C. & VEINUS, J. (1974): Middle Ordovician crinoids from southwestern Virginia and eastern Tennessee. — Bull. Amer. Paleont., 66: 283: 125 p.

- CHAUVEL, J. & LE MENN, J. (1973): Echinodermes de l'Ordovicien supérieur de Coat-Carres, Argol (Finistère). — Soc. Geol. Mineral. Bretagne, Bull., (C), 4, 1: 39—61.
- (1979): Sur quelques échinodermes (Cystoïdes et Crinoïdes) de l'Ashgill d'Aragon. — Geobios, 12, 4: 549—587.
- CHAUVEL, J., MELENDEZ, B. & LE MENN, J. (1975): Les Echinodermes (Cystoïdes et Crinoïdes) de l'Ordovicien supérieur de Luesma (Sud de l'Aragon, Espagne). — Estud. Geol., 31: 351—364.
- DONOVAN, S. K. (1983): Tetrameric crinoid columnals from the Ordovician of Wales. — Palaeontology, 26, 4: 845—849.
- (1984a): A crinoid columnal morphospecies from the Upper Ordovician of Girvan and Kazakhstan. — Scott. Journ. Geol., 20, 2: 135—142.
- (1984b): *Ramseyocrinus* and *Ristmacrinus* from the Ordovician of Britain. — Palaeontology, 27, 3: 423—434.
- DUBATOLOVA, YU. A. (1964): Morskije lilij devona Kuzbassa [Devonian crinoids from Kuznetsk basin]. — Institute Geological and geophysic Acad. Sci. USSR, Siberian Branch, Publishing House "Nauka", Moscow: 1—154.
- (1971): Morskije lilij rannego i srednego devona Altaja i Kuzbassa [Crinoids from the Early and Middle Devonian of Altai and Kuznetsk Basin]. — Trans. Institute Geological and Geophysic Acad. Sci. USSR, Siberian Branch, Publishing House "Nauka", Moscow, 124: 1—159.
- (1976): Typ Echinodermata (Type Echinodermata). — In: DUBATOLOV, V. N. (ed.): Balkhash area — a transitional zone of Late Carboniferous biogeographical belts. — Trans. Institute Geological and Geophysic Acad. Sci. USSR, Siberian Branch, Publishing House "Nauka", Moscow, 285: 81—98.
- (1980): Echinodermata. — In: KULKOV, N. P. (ed.): Biostratigraphy of Lower and Middle Devonian of Rudny Altai. — Trans. Institute Geological and Geophysic Acad. Sci. USSR, Siberian Branch, Publishing House "Nauka", Moscow, 425: 117—147.
- EHRENBERG, K. (1922a): Bau und Lebensweise von *Herpetocrinus*. — Paläont. Z., 5: 182—208.
- (1922b): Über einige eingerollte Pelmatozoenstiele und ihre Beziehungen zur Sessilität. — Acta Zoologica, 3: 271—305.
- EICHWALD, C. E. (1856): Beitrag zur geographischen Verbreitung der fossilen Thiere Russlands. — Bull. Moscow society Naturalists, 29: 88—127.
- FEDOTOV, D. M. (1966): Evoljutsija i filogenija bespozvonochnykh zhivotnykh [Evolution and phylogeny of invertebrates]. — Publishing House "Nauka", Moscow: 1—404.
- GEIZER, H. N. & SIMON, P. R. (1976): Systematic paleontology. Class Crinoidea, subclass and order uncertain, group Cyclici MOORE and JEFFORDS, 1968. — Compass. Sigma. Gamma. Epsilon, 53, 3: 100—106.
- GINDA, V. A. (1984): Stebli novykh ordovikskikh morskikh lilij jugozapadnoy okrainy Vostochno Evropejskoy platformy [Stems of new Ordovician crinoids on the southwestern margin of the East European Platform]. — Collected papers on paleontology, Publishing House Lvov. Univ., Lvov, 21: 58—63.
- GLUCHOWSKI, E. (1980): Rozwoj ontogenetyczny *Mediocrinus microgrumosus* DUBATOLOVA ze środkowego dewonu Gor Świetokrzyskich. — Geologia, 6, 3: 19—26.
- (1981a): Paleozoic crinoid columnals and Pluricolumnals from Poland. — Zesk. nauk AGH Krakow Geol., 7, 3: 29—62.
- (1981b): Stratigraphic significance of Paleozoic crinoid columnals from Poland. — Zesk. nauk AGH Krakow Geol., 7, 2: 89—110.
- GOLDFUSS, G. A. (1862—1866): Petrefacta Germaniae, and Repertorium zu GOLDFUSS: Petrefacten Deutschlands. — Leipzig, pt. I: 234 p., pt. 2: 298 p., pt. 3: 120 p.
- HAUDE, R. (1981): Mechanik, Morphogenese und palökologische Bedeutung der "Pelmatozoen"-Stiele. — Paläont. Kurzbücher, Bd. I: Funktionsmorphologie. Paläont. Ges., München: 187—203.
- JAEL, O. (1894): Entwurf einer Morphogenie und Phylogenie der Crinoideen. — Ges. Naturf. Freunde, Sitzungsber. 4: 101—121.
- (1918): Phylogenie und System der Pelmatozoen. — Paläont. Z. (1921), 3, 1: 1—128.
- JEFFORDS, R. M. & MILLER, T. H. (1968): Ontogenetic development in late Pennsylvanian crinoid columnals and pluricolumnals. — Univ. Kans. Paleont. Contrib., Echinodermata, Art. 10, 47: 1—14.
- International Code of Zoological nomenclature adopted by the XV International Congress of Zoology. London, 1964. — transl. russ. OBRUCHEW, D. V., SVETOVIDOV, A. N. & SKAROBOGATOV, Y. J. (eds.), Publishing House "Nauka", Moscow. — Leningrad, 1966: 1—100.
- KESLING, R. V. (1963): Occurrence and variations of *Bothryocrinus thomasi* LAUDON in the Tunder bay Limestone of Michigan. — Univ. Michigan, Contrib. Museum Paleontology, 18, 15: 231—244.
- (1966): *Bothryocrinus niemani*, a new crinoid from the Middle Devonian Silica Formation of Ohio. — Univ. Michigan, Contrib. Museum Paleontology, 20, 9: 271—276.
- KONINCK, L. G. & LE HON, H. S. (1854): Recherches sur les crinoïdes du terrain carbonifère de la Belgique. — Acad. Roy. Belgique, Mem. 28, 3: 1—217.
- LANE, N. G. & MACURDA, D. B. (1975): New evidence for muscular articulations in Paleozoic crinoids. — Paleobiology, 1, 1: 59—62.
- LAUDON, L. R. (1973): Stratigraphic crinoid zonation in Iowa Mississippian rocks. — Proc. Iowa Acad. Sci., 80, 1: 25—33.
- LE MENN, J. (1970): Les Crinoïdes du Siegenien supérieur de la Rade de Brest (Finistère). — Ph. D. thesis. Univ. Rennes: 107 p.
- (1983): Les Crinoïdes du Devonien inférieur et moyen du Massif armoricain. — D. thesis. Univ. Bretagne Occidentale: 268 p.
- MACURDA, D. B. & MEYER, D. L. (1975): The microstructure of the crinoid endoskeleton. — Univ. Kansas, Paleont. Contrib., 74: 1—22.
- MILITSINA, V. S. (1973): O morskikh lilijakh iz nizhnego devona zapadnogo i vostochnogo sklonov Severnogo i Srednego Urala [On Silurian and Lower Devonian crinoids on the western and eastern slopes of the North and Mid-Urals]. — In "Fauna and biostratigraphy of Middle and Upper Paleozoic of the Urals". Trans. Sverdlovsk Inst. Mines., 43: 3—26.
- MOORE, R. C. (1939): The use of fragmentary crinoidal remains in stratigraphic paleontology. — Denison. Univ. Bull. Sci. Lab., 33: 165—250.
- (1950): Evolution of the Crinoidea in relation to major paleogeographic changes in earth history. — Internat. Geol. Congr., Rep. 18th Sess., Great Britain, 1948, pt. 12: 27—53.
- (1952): Evolution rates among crinoids. — J. Paleont. 26, 3: 338—352.
- MOORE, R. C. & JEFFORDS, R. M. (1968): Classification and nomenclature of fossil crinoids based on studies of dissociated parts of their columns. — Univ. Kansas, Paleont. Contrib., Echinodermata, Art. 9, 46: 1—86.

- MOORE, R. C., JEFFORDS, R. M. & MILLER, T. H. (1968): Morphological features of crinoid columns. — Univ. Kansas, Paleont. Contrib., Echinodermata, Art. 8, 45: 1—30.
- MOORE, R. C. & LAUDON, L. R. (1943): Evolution and classification of Paleozoic crinoids. — Geol. Soc. America, Spec. Paper, 46: 1—153.
- MOORE, R. C. & PLUMMER, F. B. (1940): Crinoids from the Upper Carboniferous and Permian strata in Texas. — Univ. Texas. Bull., 3945: 1—468.
- MOORE, R. C. & TEICHERT, C. (eds.) (1978): Treatise of Invertebrate Paleontology, Pt. T: Crinoidea. — Geol. Soc. Amer. and Univ. Kansas Press, Lawrence, Kansas.
- POLOZHICHINA, A. I. (1980): Novye devonskie i rannekamennougolnye morskije lilij Centralnogo Kazakhstana [A new Devonian and Early Carbonian crinoids from the Central Kazakhstan]. — Collected papers on new species of the ancient plants and invertebrates of the USSR, STUKALINA, G. A. (ed.), Publishing House "Nauka", Moscow, 5: 114—119.
- QUENSTEDT, F. A. (1874—76): Petrefactenkunde Deutschlands: I Abt., Bd. 4. Echinodermen (Asteriden und Encriniden). — Fres's Verlag (Leipzig): 742 p.
- ROUX, M. (1970): Introduction à l'étude des microstructures des tiges de crinoïdes. — Geobios, 3: 79—98.
- (1975): Microstructural analysis of the crinoid stem. — Univ. Kansas, Paleont. Contrib., 75: 1—7.
- SCHMIDT, W. E. (1934): Die Crinoideen des rheinischen Devons, Teil I, Die Crinoideen des Hunsrückschiefers. — Preuss. Geol. Landesanst., Abh., (n. ser.), 163: 1—149.
- (1942): Die Crinoideen des rheinischen Devons. Teil II. A. Nachtrag zu: Die Crinoideen des Hunsrückschiefers. B. Die Crinoideen des Unterdevons bis zur Cultrijugatus Zone. — Reichsstelle Bodenforsch., Abh., (n. ser.), 182 (1941): 1—253.
- SCHULTZE, L. (1867): Monographie der Echinodermen des Eifler Kalkes. — K. Akad. Wiss. Berlin, Math.-naturwiss. Kl., 26: 113—230.
- SEVASTOPULO, G. D. & KEEGAN, J. B. (1980): A technique for revealing the stereom microstructure of fossil crinoids. — Palaeontology, 23, 4: 749—756.
- SEVERTSOV, N. A. (1949): Sobranie sochineniy tom IV: Morphologicheskije zakonomernosti evoljutsii (Collected papers, tom IV: Morphological Evolution pattern). — Publishing House Acad. Sci. USSR, J. Moscow - Leningrad: 1—536.
- SHEVCHENKO (SCHEWTSCHENKO), T. V. (1966): Morskije lilij iz verkhnesilurskikh i nizhnedevonskikh otlozheniy jugozapadnogo Tian Shan i ikh stratigraphicheskoe znachenie [Crinoids from the Upper Silurian and Lower Devonian deposits of south-western Tien Shan and their stratigraphical significance]. — Trans. Geol. Board Sov. Minist. Tajik S.S.R., Paleontol. Stratigr., 2: 123—171.
- (1967): Rannedevonskie morskije lilii semeystva Parahexacrinidae fam. nov. Zeraвшanskogo khrebt [Early Devonian crinoids of family Parahexacrinidae fam. nov. of the Zeraвшan Range]. — Paleontol. Moscow, 3: 76—88.
- (1971): Nizhnesilurskie morskije lilij Zeraвшano-Gissarskoy gornoy oblasti [Lower Silurian crinoids from the Zeraвшan-Gissar mining district]. — Trans. Geol. Board Sov. Minist. Tajik S.S.R., Paleont. Stratigr., 4: 3—32.
- SIEVERTS-DORECK, H. (1947): Bemerkungen über altpaläozoische Crinoideen aus Argentinien. — N. Jb. Geol., Paläont., Monatsh., 1947(4), Abt. B: 151—156.
- SIMON, R. R. & GEIZER, H. W. (1976): A pluricolumnals assemblage from the Ames Limestone in eastern Ohio. — Compass. Sigma. Gamma. Epsilon. 53, 3: 86—99.
- SPRINGER, F. (1926): American Silurian crinoids. — Smithsonian. Inst. Pub., 2871: 1—239.
- SPRINKLE, J. (1973): Morphology and evolution of blastozoan echinoderms. — Harvard Univ., Museum Comp. Zoology, Spec. Publ.: 1—283.
- STRIMPLE, H. L. (1962a): Platycrinid columnals from the Pumpkin Creek Limestone. — Oklahoma Geology Notes, 22, 1: 3—5.
- (1962b): Crinoids from the Oologah Formation (Oklahoma). — Oklahoma Geol. Survey, Circ. 60: 1—75.
- STUKALINA, G. A. (1964a): Ordovikskie, silurijskie i rannedevonskie morskije lilij Centralnogo Kazakhstana i ikh stratigraphicheskoe znachenie [Ordovician, Silurian and Early Devonian crinoids from Central Kazakhstan and their stratigraphic significance]. — Abstract of the Candidate's (Doctor) Thesis. All-Union Geol. Res. Inst. (VSEGEI), Leningrad: 1—20.
- (1964b): K metodike izucheniya i sboram iskopaemykh ostatkov stebley morskikh lilij [On the methods of research and collecting of fossil remains of crinoid stems]. — Trans. All-Union Geol. Res. Inst., Leningrad, (n. ser.), 3: 31—35.
- (1965): O taksonomicheskom znachenii stebley drevnikh morskikh lilij [On taxonomic significance of ancient crinoid stems]. — Trans. All-Union Geol. Res. Inst. Leningrad, (n. ser.), 115: 210—217.
- (1966): O printsipakh klassifikatsii stebley drevnikh morskikh lilij [On principles of classification of stems of ancient sea lilies]. — Paleont. J., Moscow, 3: 94—102. (transl. in Internat. Geol. Review, 1967, 9, 4: 549—555).
- (1967): O taksonomicheskikh priznakakh segmentirovannykh stebley morskikh lilij [On taxonomic features of pentamerid stems crinoids of pentamerid structures]. — Trans. All-Union Geol. Res. Inst., Leningrad, (n. ser.), 129: 200—206.
- (1968a): K sistematike gruppy Pentamerata (Crinoidea) [On the systematics of the Pentamerata group (Crinoidea)]. — Paleont. J., Moscow, 1: 73—82.
- (1968b): K sistematike semeystva Decacrinidae [On the systematics of the family Decacrinidae]. — Ann. All-Union Paleont. Soc., Leningrad, 18: 250—265.
- (1975): Morskije lilii [Sea lilies]. — In: MENNER, V. V. (ed.): A characteristic of the Upper Silurian and Lower Devonian fauna of Central Kazakhstan. — Moscow, "Nedra", Press.: 133—151.
- (1976): Zavisimost stratigraphicheskogo znacheniya stebley krinoidey ot raslichnykh prinzipov ikh klassifikatsii [Dependence of stratigraphic significance of crinoid stems on different principles of their classification]. — Proc. XIII and XIV sessions of the All Union Paleont. Soc., Leningrad: 179—189.
- (1977): Klassifikatsiya gruppy Decacrinidae [Classification of the group Decacrinidae]. — In: Systematics, Evolution, Biology and Distribution of recent and fossil Echinoderms. — Materials III, All Union Colloquium on Echinoderms, Leningrad: 66—69.
- (1979a): Krinoidei krivolut'skogo, mangaseyskogo, dolborskogo i khetskogo horizontov [Crinoids of the krivolutsky, mangazeisky, dolborsky and khetsky horizons]. — In: MENNER, V. V. (ed.): Ordovician Fauna of Middle Siberian. — Trans. Geol. Inst. Acad. Sci. USSR, Publishing House "Nauka", Moscow, 330: 131—158.

- STUKALINA, G. A. (1979 b): Novoe semeystvo ordovikskikh krinoidey [A New family of Ordovician Crinoids]. — Paleont. J., Moscow, 4: 89—95.
- (1979 c): Webericrinidae — novoe semeystvo ordovikskikh krinoidey [Webericrinidae — a few family of Ordovician Crinoids]. — Annual All-Union Paleont. Soc., Leningrad, 22: 158—162.
- (1980): Novjie predstaviteli kvadrilaterat iz ordovika Kazakhstana, Urala i Vostochno-Evropejskoy platformji [A new species of Quadrilaterata from Ordovician of the Kazakhstan, Urals, East Europ. platform]. — Collected articles on new species of the ancient plants and invertebrates of the USSR, G. A. STUKALINA (ed.), Publishing House “Nauka”, Moscow, 5: 88—94.
- (1981): Krinoidei v stratigraphii ordovika, silura i nizhnego devona SSSR [Crinoids in the Ordovician, Silurian and Lower Devonian stratigraphy of the USSR]. — Abstract of the Doctor's thesis. All-Union Geol. Res. Inst. (VSEGEI), Leningrad: 1—51.
- (1982 a): O zonalnom raschlenenii i korreljatsii nizhnego u srednego devona SSSR po krinoidejam [On the zonal subdivision and correlation of the Lower and Middle Devonian in the USSR based on crinoids]. — In: Biostratigraphy of Lower and Middle Devonian boundary deposits. — Proc. Field Symp. Internat. Subcomm. Devon. Stratigraphy, Samarkand, USSR (1978), Leningrad: 139—143.
- (1982 b): K sistematike paleozoyskikh krinoidey otrjadov Angulata i Strialata [On systematics of Paleozoic Crinoids of orders Angulata and Strialata]. — Ann. All-Union Paleont. Soc., Leningrad, 25: 184—196.
- (1985): Zonalnoe delenie po krinoidejam nizhnego srednego paleozoya territorii SSSR [Zonal subdivision of the Lower and Middle Paleozoic on the USSR territory]. — Collected papers on paleontology, Publishing House Lvov. Univ., 21: 50—56.
- TERMIER, H. & TERMIER, G. (1949): Hierarchie et correlations des caractères chez les Crinoides fossiles. — Serv. Carte Geol. Algerie, Bull. (ser. I, Paleont.), 10, 1: 1—90.
- & — (1950): Invertebrés de l'ère Primair. — Palaeont. Maroc., 2, 4: 1—220.
- & — (1974): Une methode nouvelle: l'utilisation des fragments d'échinodermes contenus dans les sediments devoniens et carboniferes du Maroc. — Serv. Geol. Maroc. Notes, 35, 255: 27—53.
- UBAGHS, G. (1953): Classe des Crinoides. — In: PIVETEAU, J. (ed.): Traite de paléontologie, 3: 658—773.
- (1969): *Aethocrinus moorei* UBAGHS, n. gen. n. sp. le plus ancien crinoide dicyclique connu. — Univ. Kansas, Paleont. Contrib., 38: 1—25.
- (1972): More about *Aethocrinus moorei* UBAGHS, the oldest known dicyclid crinoid. — J. Paleont., 46, 5: 773—775.
- VYALOV, O. S. (1953): O klassifikatsii stebelkov morskikh liliy [On the classification of crinoid stems]. — Trans. Lvov. Geol. Sci., (ser. geol.), 2: 30—45.
- (1977): O printsipach klassifikatsii stebly morskikh liliy [On the principals les of classification of crinoid stems]. — In: Systematics, Evolution, Biology and Distribution of recent and fossil Echinoderms. — Materials III All-Union Coll. Echinoderms, Leningrad: 15—18.
- WAAGEN, W. & JAHN, J. (1899): Système solurien du centre de la Boheme, Recherches paléontologiques. — In: BARRANDE, J.: Famille des crinoides, pt. 2: 1—215.
- WACHSMUTH, C. & SPRINGER, F. (1897): The North American Crinoidea Camerata. — Harv. Coll. Mus. Comp. Zool. Mem., 20—21: 1—897.
- WARN, J. M. (1973): Monocyclism vs. dicyclism; a primary schism in crinoid phylogeny. — Bull. Amer. Paleontol., 67, 287: 423—441.
- WARN, J. M. & STRIMPLE, J. L. (1977): The disparid inadunate superfamilies Homocrinacea and Cincinnaticrinacea (Echinodermata: Crinoidea). Ordovician-Silurian, North American. — Bull. Amer. Paleontol., 72, 296: 1—138.
- WARREN, J. S. (1962): Form classification of crinoid stems. — Abstract. Geol. Soc. Amer. Spec. Papers, 68: p. 81.
- WEBSTER, G. D. (1974): Crinoid pluricolumnal noditaxis patterns. — J. Paleont., 48, 6: 1283—1288.
- WILLINK, R. J. (1980): A new colled-stemmed Camerate crinoid from the Permian of eastern Australia. — J. Paleont., 54, 1: 15—34.
- WRIGHT, D. K. (1983): Crinoid ossicles in Upper Ordovician benthic marine assemblages from Snowdonia, North Wales. — Palaeont., 26, 3: 585—603.
- YAKOVLEV, N. N. (1946): Hexacrinide iz verkhnego silura [Hexacrinide from Upper Silurian]. — Proc. USSR Acad. Sci., 10, 2: 149—150.
- (1947 a): Izmeneniya skeletnykh chastey morskikh liliy, vsledstvie mekhanicheskikh faktorov [Skeletal ranges of the crinoids in consequence of mechanical factors]. — Proc. USSR Acad. Sci., 56, 7: 747—749.
- (1947 b): Vliyanie mekhanicheskikh usloviy na stroenie morskikh liliy [Influence of mechanical factors on the structure of the crinoids]. — Nature, 11: 41—47.
- (1949): Eshche odna kategoriya vliyany mekhanicheskikh usloviy na stroenie morskikh liliy [One more example of the influence of mechanical conditions on the structure of crinoids]. — Proc. USSR Acad. Sci., 2: 265—267.
- (1950): O tipakh skulptury chashechki morskikh liliy, ikh proiskhozhdenii i naznachenii [On the kinds of sculpture of crinoid calyses, their origin and terminology]. — Proc. USSR Acad. Sci., (n. ser.), 70: 93—96.
- YAKOVLEV, N. N. & IVANOV, A. P. (1956): Morskie lili i blastoidei kammennougolnykh i permskikh otlozheniy SSSR [Crinoids and blastoids of the Carboniferous and Permian deposits of the USSR]. — Trans. All-Union Geol. Res. Inst. (VSEGEI), Leningrad, (n. ser.), 11: 1—142.
- YELTSYSHEVA (YELTSICHEWA), R. S. (1955): Klass Crinoidea — morskie liliy [Class Crinoidea — sea lilies]. — In: NIKIFOROVA, O. I. (ed.): Field Atlas of Ordovician and Silurian Fauna of the Siberian Platform. — All-Union Geol. Res. Inst. (VSEGEI), Leningrad, 40—47.
- (1956): Stebli morskikh i ikh klassifikatsiya [Stems of crinoids and their classification]. — Bull. Leningrad Univ. (ser. Geol. Geograph.), 12, 2: 40—46.
- (1957): O novom semeystve paleozoiskikh morskikh liliy [On a new family of Paleozoic crinoids]. — Ann. All-Union Paleont. Soc., Leningrad, 16: 218—235.
- (1960): Ordovikskie i siluriyskie krinoidei Sibirskoy platformy [Ordovician and Silurian crinoids of the Siberian platform]. — Trans. All-Union Geol. Res. Inst. (VSEGEI), (n. ser.), 40, 3: 1—39.
- (1964): Stebli ordovikskikh morskikh liliy Pribaltiki (nizhny ordovik) [Stems of Ordovician sea lilies of the Baltic area (Lower Ordovician)]. — Collection papers “Problems Paleontology”, Publishing House Leningrad, Univ., 4: 59—84.
- (1975): Krinoidei poganichnykh sloew ordovika i silura Podolii [Crinoids of Ordovician/Silurian boundary beds in Podolia]. — Collection papers “Problems Paleontology”, Publishing House Leningrad, Univ., 7: 124—144.

- YELTSYSHEVA (YELTSICHEWA), R. S. (1979): Stebli paleozoiskikh morskikh liliy Pribaltiki (verkhny ordovik) [Stems of Paleozoic sea lilies of the Baltic area (Upper Ordovician)]. — Collection papers “Problems Paleontology”, Publishing House, Leningrad. Univ., 8: 94—100.
- YELTSYSHEVA, R. S. & DUBATOLOVA, YU. A. (1960): Novye vidy devonskikh krinoidey Verkhnego Amura [New species of Devonian crinoids of the upper Amur]. — In: MARKOVSKY, B. P. (ed.): Collected papers on new species of the ancient plants and invertebrates of the USSR, pt. 11: 367—372.
- YELTSYSHEVA, R. S. & POLJARNAJA, Z. A. (1975): Crinoidea (morskie liliy) [Crinoidea (sea lilies)]. — Paleontological Atlas of Carboniferous Deposits of the Urals. Trans. All-Union Petrol. Geol. Prospect. Inst. (VNIGRI), 383: 204—207.
- YELTSYSHEVA, R. S. & SIZOVA, E. N. (1971): Ontogeneticheskie izmeneniya stebly nekotorykh paleozoyskikh krinoidey (columnals — stebli morskikh liliy) [Ontogenetic modifications of the stems of some Paleozoic crinoids (columnals — stems of sea lilies)]. — Collection papers “Problems Paleontology”, Publishing House, Leningrad, Univ., 6: 33—40.
- YELTSYSHEVA, R. S. & STUKALINA, G. A. (1963): Stebli ordovikskikh i nizhnesiluriiskikh krinoidey Tsentral'nogo Taimyra, Novoy Zemli i Vaygacha [Ordovician and Lower crinoids stems from central Taimyr Novaya Zemlya and Vaygach]. — Scientific Papers of the Arctic Geology Research Institute (NJJGA), (ser. paleontol. and biostratigr.), 2: 23—62.

Explanation of Plates

Type species are stored in the Central Science-Research Geolog. Exploration Museum named after Academician F. N. CHERNYSHEV (CNIGR Museum), Leningrad

Plate 1

- Fig. 1—5. *Tetragonocrinus pygmaeus* (EICHWALD 1960).
1. Paratypoid 40/8198, x 8; side view of a stem fragment.
 2. Paratypoid 43/8198, x 7; side view of a stem fragment.
 3. Paratypoid 37/8198, x 8; articular surface of a proximal columnal.
 4. Paratypoid 41/8198, x 6; articular surface of a distal columnal.
 5. Paratypoid 39/8198, x 8; articular surface of a distal columnal.
- Northwest East European Platform, Leningrad area. Lower Ordovician, Volkhov horizon.
- Fig. 6, 7. *Dwortsowaecrinus simplex* STUKALINA 1980.
6. Holotype 5/11746, x 10; articular surface of a proximal columnal.
 7. Paratypoid 4/11746, x 5; articular surface of a proximal columnal.
- Kazakhstan, Chuili Mountains. Upper Ordovician, Dulancara horizon, Otar Sandstone.
- Fig. 8. *Dwortsowaecrinus sculptus* STUKALINA 1980.
8. Holotype 6/11746, x 4: a — articular surface of a proximal columnal, b — side view of a stem fragment from the proximal part.
- Kazakhstan, Betpak-Dala. Middle Ordovician, Sartanmanay Limestone.
- Fig. 9. *Dwortsowaecrinus nanus* STUKALINA 1985.
9. Holotype 8/11730, x 4; side view of a stem fragment from the distal part. Kazakhstan, Betpak-Dala. Middle Ordovician, Sartanmanay Limestone.
- Fig. 10. *Dwortsowaecrinus dwortsowae* STUKALINA 1967.
10. Holotype 6/9440, x 1, x 3, 5; articular surface of a proximal columnal. Kazakhstan, Chuili Mountains. Upper Ordovician. Dulancara horizon, Accol Limestone.
- Fig. 11—13. *Dwortsowaecrinus quadrihamatus* (YELTSYSHEVA 1963).
- 11, 12. Holotype 47/8444, x 10, x 3; stem fragment from the proximal part.
 13. Paratypoids 48/8444, x 1; accumulation of stem fragments and single columnals. Arctic area, Novaya Zemlya Island. Upper Ordovician.
- Fig. 14, 15. *Dwortsowaecrinus korjickensis* STUKALINA 1980.
- 14 a, b. Holotype 2/11746, x 2; columnal from the proximal part.
 - 15 a, b. Paratypoid 3/11746, x 3; columnal from the distal part.
- Kazakhstan, Chingiz Range, Koryk River. Middle Ordovician. Algabaz Limestone.
- Fig. 16. *Tatjanicrinus kozhimensis* STUKALINA 1980.
16. Holotype 8/11746, x 7; articular surface of a proximal columnal.
- Subpolar Urals, Kozhim River. Middle Ordovician, Shchugor-Formation, Upper Part.
- Fig. 17. *Tatjanicrinus cruciformis* STUKALINA 1980.
17. Holotype 7/11746, x 5: a — upper articular surface of a proximal columnal, b — stem fragment from the proximal part, c — lower articular surface of proximal columnal.
- Kazakhstan, Chuili Mountains. Middle Ordovician, Anderken horizon, Anderken Limestone.

- Fig. 18. *Tatjanicrinus corruptus* STUKALINA 1980.
18. Holotype 11/11746, x 5; articular surface of a proximal columnal.
Kazakhstan, Tarbagatay Range. Lower Silurian, Llandoverly, Alpeis horizon, Lower part.
- Fig. 19. *Cupressocrinites ? ovatus* SHEVCHENKO 1959.
19. Exemplar 21/12225, x 3; articular surface of a proximal columnal.
South Tien Shan, Chodzha-Kurgan. Middle Devonian, Eifelian, Obisaphit Beds.
- Fig. 20, 21. *Cupressocrinites ? indefinitus* (J. DUBATOLOVA 1967).
20. Exemplar 22/12225, x 3; articular surface of a proximal columnal.
21. Exemplar 23/12225, x 3, articular surface of a distal columnal.
South Tien Shan, Chodzha-Kurgan. Middle Devonian, Eifelian, Obisaphit Beds.
- Fig. 22. *Cupressocrinites ? elegans* SHEVSHENKO 1959.
22. Exemplar 24/12225, x 3; articular surface of a proximal columnal.
South Tien Shan, Chodzha Kurgan. Middle Devonian, Eifelian, Obisaphit Beds.
- Fig. 23. *Xenocrinus ? quadrilobatus* STUKALINA & CHINTS 1980.
23. Holotype 9/11746, x 12; articular surface of a columnal.
Northwest East European Platform. Middle Ordovician, Oandu horizon.

Plate 2

- Fig. 1, 2. *Squameocrinus integrum* (SHEVSHENKO 1971).
1. Paratypoid 48/10447, x 7; articular surface of a proximal columnal.
2. Paratypoid 49/10447, x 7; articular surface of a proximal columnal.
South Tien Shan, Shachriomon. Lower Silurian, Minkuchar Beds.
- Fig. 3. *Squameocrinus privus* (YELTYSHEVA 1964).
3. Holotype 2/8198; x 7: a — articular surface of a proximal columnal, b — side view of a stem fragment from the proximal part. Northwest East European Platform, Estonia. Lower Ordovician, Kunda horizon.
- Fig. 4—6. *Sidericrinus depressus* STUKALINA 1968.
4. Paratypoid 3/11809, x 2.5; articular surface of a proximal columnal.
5. Paratypoid 9/11780, x 2.5; articular surface of a distal columnal.
6. Paratypoid 10/11780, x 2.5; side view of a stem fragment from the proximal part.
Kazakhstan, Betpak-Dala. Middle Ordovician, Anderken horizon.
- Fig. 7—9. *Fascicrinus fasciculus* STUKALINA 1980.
7. Paratypoid 13/11487, x 5; articular surface of a proximal columnal.
8. Paratypoid 14/11487, x 6; articular surface of a distal columnal.
9. Holotype 12/11487, x 5; articular surface of a proximal columnal.
Kazakhstan, Chuili Mountains. Middle Ordovician, Anderken horizon, Anderken Limestone.
- Fig. 10—12. *Fascicrinus concavus* STUKALINA 1980.
10. Paratypoid 17/11487, x 6; articular surface of a columnal.
11. Paratypoid 18/11487, x 6; articular surface of a proximal columnal.
12. Paratypoid 19/11487, x 5; stem fragment from the proximal part.
Kazakhstan, Chuili Mountains. Middle Ordovician, Anderken Beds, Anderken Limestone.
- Fig. 13. *Fascicrinus flabellatus* YELTYSHEVA & STUKALINA 1968.
13. Holotype 31/8443, x 6; articular surface of a proximal columnal.
Kazakhstan, Balkhash area. Middle Ordovician.
- Fig. 14—16. *Fascicrinus umbonatus* STUKALINA 1985.
14. Holotype 11/11730, x 6: a — articular surface of a proximal columnal, b — stem fragment from the proximal part.
15. Paratypoid 13/11730, x 6; stem fragment from the proximal part.
16. Paratypoid 12/11730, x 6; stem fragment from the proximal part.
Kazakhstan, Betpak-Dala. Middle Ordovician, Sartanmanay Limestone.
- Fig. 17. *Squameocrinus thunensis* STUKALINA 1979.
17. Holotype 11/11508, x 4; stem fragment from the proximal part.
Siberian Platform. Middle Ordovician, Dolbor horizon, Lower Part.
- Fig. 18. *Anderkenicrinus antiquus* STUKALINA 1985.
18. Holotype 25/11830, x 2; articular surface of a proximal columnal.
Kazakhstan, Chuili Mountains. Middle Ordovician, Anderken horizon, Anderken Limestone.
- Fig. 19. *Fibracrinus fibratus* TUJUTJAN 1970.
19. Holotype 1/10190, x 3; articular surface of a proximal columnal.
Kazakhstan, Chuili Mountains. Middle Ordovician, Anderken horizon, Anderken Limestone.

Plate 3

- Fig. 1—4. *Laticrinus incomptus* STUKALINA 1985.
1. Paratypoid 16/11730, x 3; articular surface of a proximal columnal.
2. Paratypoid 17/11730, x 6; articular surface of a distal columnal.
3. Paratypoid 19/11730, x 4; side view of a stem fragment from the proximal part.
4. Paratypoid 18/11730, x 6; side view of a stem fragment from the proximal part.
Kazakhstan, Betpak-Dala. Middle Ordovician, Anderken horizon.
- Fig. 5. *Sidericrinus* sp.
5. Exemplar 127/11809, x 4; articular surface of a columnal. Kazakhstan. Chuili Mountains. Middle Ordovician, Anderken horizon.
- Fig. 6—9. *Excisocrinus excisus* STUKALINA 1985.
6. Paratypoid 21/11730, x 5; articular surface of an internodal columnal.
7. Holotype 22/11730, x 3; articular surface of an internodal columnal.
8. Paratypoid 23/11730, x 5; side view of a fragment from the proximal part.
9. Paratypoid 24/11730, x 6; side view of a stem fragment from the proximal part.
Kazakhstan, Betpak Dala. Middle Ordovician, Sartanmanay Limestone.
- Fig. 10—14. *Malovicrinus implicatus* STUKALINA 1970.
10. Paratypoid 30/11730, x 4: a — articular surface of an internodal columnal, b — side view of a stem fragment from the proximal part.
11. Paratypoid 27/11730, x 8, side view of a stem fragment from the proximal part.
12. Paratypoid 29/11730, x 4; articular surface of an internodal columnal.
13. Paratypoid 31/11730, x 4; articular surface of an internodal columnal.
14. Paratypoid 28/11730, x 3: a — articular surface of an internodal columnal, b — side view of a stem fragment from the proximal part.
Kazakhstan, Betpak Dala. Middle Ordovician, Sartanmanay Limestone.
- Fig. 15, 16. *Malovicrinus incrustatus* STUKALINA 1985.
15. Paratypoid 33/11730, x 6; stem fragment from the upper part stems.
16. Holotype 32/11730, x 5; stem fragment from the proximal part.
Kazakhstan, Betpak Dala. Middle Ordovician, Sartanmanay Limestone.
- Fig. 17—19. *Ramosocrinus ramosus* YELTYSHEVA & STUKALINA 1963.
17. Exemplar 23/11809, x 5; articular surface of a columnals.
18. Exemplar 22/11809, x 5; articular surface of a columnals.
19. Exemplar 21/11809, x 5; articular surface of a columnals.
Kazakhstan, Chuili Mountains. Middle Ordovician, Otar Limestone.
- Fig. 20—23. *Ramosocrinus tumsjikensis* STUKALINA 1980.
20. Paratypoid 24/11809, x 4; 21. Holotype 27/11487, x 4; 22. Paratype 29/11487, x 4; 23. Paratype 30/11487, x 4: articular surface of a columnals. Kazakhstan, Chingiz Range. Upper Ordovician, Beds with *Agetolites mirabilis*.
- Fig. 24. *Artificiosocrinus artificiosus* (YELTYSHEVA 1964).
24. Holotype 8/8198, x 6; articular surface of a distal columnal.
Northwest East European Platform, Leningrad area, Lower Ordovician, Kunda horizon.

Plate 4

- Fig. 1—3. *Megalocrinus pentalobatus* STUKALINA sp. nov. (in press).
1. Paratypoid 8/12374, x 4; articular surface of a proximal columnal.
2. Holotype 92/12374, x 4; articular surface of a proximal columnal.
3. Paratypoid 12/12374, x 3; articular surface of a distal columnal.
Siberian Platform, Moyero River. Lower Silurian, Khaastyr horizon.
- Fig. 4—6. *Flexicrinus flexus* STUKALINA & TUJUTJAN 1970.
4. Paratypoid 18/11809, x 2; articular surface of a proximal columnal.
5. Paratypoid 19/11809, x 2; articular surface of a proximal columnal.
6. Holotype 5/10190, x 2; articular surface of a distal columnal.
Kazakhstan, Chingiz Range. Middle Ordovician, Koryk Limestone.
- Fig. 7, 8. *Bystrowicrinus bilobatus* (YELTYSHEVA 1960).
7. Paratypoid 40/7453, x 7; articular surface of a proximal columnal.
8. Paratypoid 12/11672, x 10; articular surface of a proximal columnal.
Siberian Platform, Lower Silurian, Khakom horizon.

- Fig. 9—14. *Bystrowicrinus quinquelobatus* (YELTYSHEVA 1955).
 9. Exemplar from the coll. 12374, x 6; articular surface of a columnal.
 10. Exemplar from the coll. 12374, x 4; articular surface of a columnal.
 11. Lectotype 19/7458, x 7; articular surface of a columnal.
 12. Exemplar 9/11672, x 10; articular surface of a columnal.
 13. Exemplar from the coll. 12374, x 5; articular surface of a columnal.
 14. Exemplar from the coll. 12374, x 6; articular surface of a columnal. Siberian Platform, Lower Silurian.
- Fig. 15, 16. *Bakanasocrinus clavatus* STUKALINA 1970.
 15. Holotype 6/10790, x 8; articular surface of a columnal. Kazakhstan, Chingiz Range, Kurbakanas River. Upper Ordovician, Beds with *Holorhynchus giganteus*.
 16. Paratypoid 14/11809, x 10, articular surface of a columnal. Kazakhstan, Chuili Mountains. Upper Ordovician, Dulancara horizon.
- Fig. 17. *Mediocrinus medius* YELTYSHEVA & STUKALINA 1965.
 17. Paratypoid 3 41/12212, x 6; articular surface of a columnal. Kazakhstan, Balkhash area. Lower Devonian.
- Fig. 18—21. *Webericrinus variabilis* STUKALINA 1979.
 18. Holotype 1/11607, x 3: a — upper articular surface of a stem fragment, b — stem fragment from the proximal part, c — lower articular surface of a stem fragment.
 19. Paratypoid 5/11607, x 3; articular surface of a distal columnal.
 20. Paratypoid 3/11607, x 3; articular surface of a columnal.
 21. Paratypoid 2/11607, x 3; articular surface of a proximal columnal. Kazakhstan, Chuili Mountains. Middle Ordovician, Anderken Limestone.
- Fig. 22. *Digiticrinus baculiformis* STUKALINA 1980.
 22. Holotype 18/11747, x 10: a — articular surface of a columnal, b — side view of a stem fragment from proximal part. Kazakhstan, Chuili Mountains. Upper Ordovician, Dulancara horizon.
- Fig. 23. *Digiticrinus bellus* STUKALINA 1980.
 23. Holotype 15/11747, x 5; articular surface of a columnal. Kazakhstan, Tarbagatay Range. Upper Ordovician, Beds with *Catenipora libera*.
- Fig. 24, 25. *Eqiasarowicrinus eqiasarowi* (YELTYSHEVA 1960).
 24. Exemplar from the coll. 12374, x 4; articular surface of a columnal.
 25. Exemplar from the coll. 12374, x 5; articular surface of a columnal. Siberian Platform. Lower Silurian, Khakom horizon.
- Fig. 26, 27. *Medinecrinus vulgaris* STUKALINA 1985.
 26. Holotype 31/12212, x 10; articular surface of a columnal.
 27. Paratypoid 33/12212, x 10; articular surface of a columnal. Kazakhstan, Balkhash area. Upper Silurian, Tokrau horizon.

Plate 5

- Fig. 1, 2. *Particrinus multipartitus* (YELTYSHEVA 1955).
 1. Lectotype 25/7453, x 5; articular surface of a nodal columnal.
 2. Paratypoid 13/11508, x 7; stem fragment from the proximal part. Siberian Platform. Middle Ordovician, Dolbor horizon, Lower Part (member IV).
- Fig. 3. *Kalgacrinus kalginensis* (YELTYSHEVA 1968).
 3. Lectotype 9/9995, x 10; articular surface of a columnal. Northeast USSR. Lower Ordovician, Tarynyurakh Formation.
- Fig. 4. *Jrucrinus antiquus* (YELTYSHEVA 1964).
 4. Holotype 7/8198, x 10; articular surface of a columnal. Northwest East European, Estonia. Lower Ordovician, Kunda horizon.
- Fig. 5, 6. *Mirabilicrinus mirabilis* (YELTYSHEVA 1955).
 5. Lectotype 7/7453, x 5; articular surface of a proximal columnal. Siberian Platform, Middle Ordovician, Mangazeja horizon.
 6. Exemplar 30/8444, x 6; articular surface of a proximal columnal. Taimyr. Middle Ordovician.
- Fig. 7—9. *Fossulacrinus fossulus* STUKALINA 1979.
 7. Paratypoid Ec 750, x 12; articular surface of a columnal.
 8. Paratypoid Ec 1774, x 12; articular surface of a columnal.
 9. Holotype Ec 1749, x 12: a — articular surface of a columnal, b — side view of a stem fragment. (Museum JG AN ESSR, Tallin). Northwest East European Platform, Estonia. Upper Ordovician, Rakvere horizon.

- Fig. 10—12. *Ramulicrinus ramulus* STUKALINA 1969.
 10. Paratypoid 1/9583, x 5; articular surface of a columnal.
 11. Paratypoid 6/9583, x 10; articular surface of a columnal.
 12. Paratypoid 4/9583, x 10; stem fragment from the proximal part. Kazakhstan, Chingiz Range, Taldyboy River. Upper Ordovician, Taldyboy Formation.
- Fig. 13. *Lunulacrinus hrustaljiensis* (YELT. & STUK. 1969).
 13. Holotype 30/8444, x 10; articular surface of a columnal. Taimyr. Upper Ordovician.
- Fig. 14. *Caragachicrinus quinquepartitus* STUKALINA 1980.
 14. Holotype 33/11487, x 4; articular surface of a columnal. Kazakhstan, Tarbagatay Range, Middle Ordovician, Karagach Formation.
- Fig. 15. *Angusticrinus excisus* STUKALINA 1980.
 15. Holotype 39/11487, x 8; articular surface of a proximal columnal. Kirgizia. Middle Ordovician, Itkebash Formation.
- Fig. 16, 17. *Kellericrinus angularis* STUKALINA 1985.
 16. Holotype 36/11730, x 6: a — articular surface of a proximal columnal, b — stem fragment from the proximal part.
 17. Paratypoid 35/11730, x 5: a — articular surface of a distal columnal, b — stem fragment from the distal part. Kazakhstan, Betpak Dala. Middle Ordovician, Sartanmanay Limestone.
- Fig. 18. *Particrinus ? grumosus* STUKALINA 1985.
 18. Holotype 38/11730, x 8: a — articular surface of a proximal columnal, b — stem fragment from the proximal part. Kazakhstan, Betpak Dala. Middle Ordovician, Sartanmanay Limestone.
- Fig. 19—24. *Particrinus partitus* (YELTYSHEVA 1960).
 19. Lectotype 48/7453, x 7; articular surface of a proximal columnal.
 20. Paratypoid 11/11508, x 10; articular surface of a proximal columnal.
 21. Paratypoid 9/11508, x 10; articular surface of a distal columnal.
 22. Paratypoid 10/11508, x 10; articular surface of a distal columnal.
 23. Paratypoid 8/11508, x 10; stem fragment from the distal part.
 24. Paratypoid 12/11508, x 10; stem fragment from the proximal part. Siberian Platform. Middle Ordovician, Mangazeja horizon.

Plate 6

- Fig. 1. *Baltocrinus lobatus* (EICHWALD 1860).
 1. Paratypoid 37/11809, x 5; articular surface of a columnal. Northwest East European Platform, Leningrad area. Middle Ordovician.
- Fig. 2. *Baltocrinus serratus* (YELTYSHEVA 1966).
 2. Paratypoid 38/11809, x 8; articular surface of a proximal columnal. Northwest East European Platform, Leningrad area. Middle Ordovician.
- Fig. 3. *Baltocrinus* sp.
 3. Exemplar 128/11809, x 8; stem fragment from the proximal part. Northwest East European Platform, Leningrad area. Middle Ordovician.
- Fig. 4—7. *Baltocrinus antiquus* (EICHWALD 1860).
 4. Exemplar Ec 1775, x 5: a — articular surface of a columnal, b — stem fragment.
 5. Exemplar Ec 1176, x 5: a — articular surface of a columnal, b — stem fragment.
 6. Exemplar Ec 1777, x 5; articular surface of a columnal. (Museum JG AN ESSR, Tallin).
 7. Exemplar 39/11809; side view of a stem fragment from the proximal part. Northwest East European Platform, Estonia (4, 5, 6) and Leningrad area (7). Middle Ordovician.
- Fig. 8—10. *Baltocrinus rostovensis* sp. nov.
 8. Paratypoid Ec 1779, x 10; fragment articular surface of a columnal.
 9. Paratypoid Ec 1780, x 10; fragment articular surface of a columnal.
 10. Holotype Ec 1778, x 10; articular surface of a columnal. (Museum JG AN ESSR). East European Platform, Yaroslavl area, Rostov. Middle Ordovician.
- Fig. 11. *Baltocrinus guttaeformis* (YELTYSHEVA 1966).
 11. Exemplar from coll. 8198, x 3; articular surface of a columnal. Northwest East European Platform, Estonia. Middle Ordovician.
- Fig. 12. *Baltocrinus brevicaisensis* (YELTYSHEVA 1966).
 12. Paratypoid 41/11809, x 4; stem fragment from the proximal part. Northwest East European Platform, Leningrad area, Khrevitsa River. Middle Ordovician.

- † Fig. 13. *Baltocrinus decorus* (KUTORGA 1846).
13. Holotype 78/3785, x 2; stem fragment from the proximal part.
Northwest East European Platform, Leningrad area, Gatchina. Middle Ordovician.
- Fig. 14, 15. *Baltocrinus gissarensis* STUKALINA, sp. nov. (in press).
14. Holotype 1/12225, x 5; articular surface of a columnal.
15. Paratypoid 2/12225, x 5; articular surface of a columnal.
South Tien Shan, Novobak. Middle Ordovician, Obikalon Beds.
- Fig. 16. *Baltocrinus kasachstanensis* STUKALINA 1979.
16. Paratypoid 1/11720, x 7; articular surface of a columnal.
Kazakhstan, Bely Cordon. Middle Ordovician, Erkebidaik horizon.

Plate 7

- Fig. 1—4. *Rugulosocrinus rugulosus* STUKALINA 1979.
1. ✓ Paratypoid Ec 1786, x 10; articular surface of a distal columnal.
2. ✓ Paratypoid Ec 1737, x 10: a — articular surface of a distal columnal, b — stem fragment from the distal part.
3. ✓ Paratypoid Ec 1739, x 10: a — articular surface of a proximal columnal, b — columnal from the proximal part.
4. ✓ Holotype Ec 1740, x 10: articular surface of a upper proximal columnal, b — columnal from the upper proximal part.
(Museum JG AN ESSR). Northwest East European Platform, Estonia. Middle Ordovician, Oandu horizon.
- † Fig. 5—12. *Rookulacrinus notabilis* STUKALINA 1979.
5. ✓ Paratypoid Ec 1747, x 10: a — articular surface of a proximal columnal, b — side view of a proximal columnal.
6. ✓ Paratypoid Ec 1746, x 10: a — articular surface of a proximal columnal, b — side view of a proximal columnal, b — side view of a distal columnal.
7. ✓ Paratypoid Ec 1745, x 10: a — articular surface of a distal columnal, b — side view of a distal columnal.
8. ✓ Paratypoid Ec 1742, x 10: a — articular surface of a distal columnal, b — side view of a distal columnal.
9. ✓ Holotype Ec 1744, x 10: a — articular surface of a proximal columnal, b — side view of a proximal columnal.
10. ✓ Paratypoid Ec 1741, x 10; articular surface of a distal columnal.
11. Paratypoid Ec 1787, x 10; articular surface of a columnal (junior form).
12. ✓ Paratypoid Ec 1743, x 10; articular surface of a columnal (junior form), (Museum JG AN ESSR, Tallin).
Northwest East European Platform, Estonia. Middle Ordovician, Oandu horizon.
- Fig. 13. *Altimarginalicrinus altimarginalis* (YELTYSHEVA 1955).
13. Paratypoid 18/11508, x 6; articular surface of a proximal columnal.
Siberian Platform, Bolshaya Nirunda River. Middle Ordovician, Mangazeja horizon.
- Fig. 14—17. *Iocrinus ? mjannili* YELTYSHEVA 1979.
14. ✓ Exemplar Ec 1773, x 10: a — articular surface of a distal columnal, b — stem fragment from the distal part.
15. ✓ Exemplar Ec 1771, x 10; articular surface of a proximal columnal.
16. ✓ Exemplar Ec 1785, x 10; stem fragment from a proximal part.
17. ✓ Exemplar Ec 1770, x 10; articular surface of a proximal columnal. (Museum JG AN ESSR, Tallin).
Northwest East European Platform, Estonia. Upper Ordovician, Pirgu horizon.
- Fig. 18. *Catagraphiocrinus accoleus* STUKALINA & TUJUTJAN 1980.
18. Holotype 31/11487, x 2; stem fragment from the proximal part.
Kazakhstan, Chuili Mountains. Upper Ordovician, Dulancara horizon, Accol Limestone.
- Fig. 19—24. *Catagraphiocrinus quindecimlobatus* (YELT. & STUK. 1963).
19. Exemplar 42/11730, x 3; articular surface of a proximal columnal.
20. Exemplar 43/11730, x 4; articular surface of a proximal columnal.
21. Exemplar 54/11730, x 3: a — articular surface of a distal columnal, b — side view of a stem fragment from the distal part.
22. Exemplar 41/11730, x 3; stem fragment from the proximal part.
23. Exemplar 40/11730, x 3; stem fragment from the proximal part.
24. Exemplar 39/11730, x 4; stem fragment from the proximal part.
Kazakhstan, Betpak Dala. Middle Ordovician, Anderken horizon.

Plate 8

- Fig. 1—7. *Ristnacrinus ? angulatus* YELTYSHEVA 1966.
1. ✓ Exemplar Ec 1759, x 8: a — upper articular surface of a columnal, b — side view columnal.
2. ✓ Exemplar Ec 1765, x 8: a — upper articular surface of a columnal, b — side view of a columnal, c — lower articular surface of a columnal.
3. ✓ Exemplar Ec 1761, x 8; articular surface of a columnal.
4. ✓ Exemplar Ec 1762, x 8: a — upper articular surface of a columnal, b — side view of a columnal.

5. ✓ Exemplar Ec 1760, x 8; articular surface of a columnal.
6. ✓ Exemplar Ec 1784, x 8; articular surface of a columnal.
7. ✓ Exemplar Ec 1764, x 8; articular surface of a columnal. (Museum JG AN ESSR, Tallin).
Northwest East European Platform, Litva. Middle Ordovician, Idavere horizon.
- Fig. 8, 9. *Babanicrinus pentaporus tuberculata* (YELTYSHEVA 1964).
8. Paratypoid 15/8198, x 10: a — articular surface of a columnal, b — side view of a columnal.
9. Holotype 19/8198, x 10; articular surface of a columnal.
Northwest East European Platform. Estonia. Lower Ordovician, Kunda horizon.
- Fig. 10. *Babanicrinus tuberosus* STUKALINA 1969.
10. Paratypoid 34/11809, x 10; articular surface of a columnal.
Kazakhstan, Chingiz Range. Upper Ordovician, Beds with Holorhynchus giganteus.
- Fig. 11, 12. *Babanicrinus kegelensis* (YELTYSHEVA 1966).
11. ✓ Exemplar Ec 1766, x 7: a — articular surface of a nodal columnal, b — side view of a stem fragment from the proximal part.
12. ✓ Exemplar Ec 1768, x 10: a — articular surface of an internodal columnal, b — side view of a stem fragment from the distal part.
(Museum IG AN ESSR). Northwest East European Platform, Estonia. Middle Ordovician, Keyla horizon.
- Fig. 13—19. *Conspectocrinus celticus* CHAUVEL & LE MENN 1973.
13. Exemplar 84/10447, x 10; articular surface of a columnal.
14. Exemplar 85/10447, x 10; articular surface of a columnal.
15. Exemplar 82/10447, x 7; articular surface of a columnal.
16. Exemplar 80/10447, x 7; articular surface of a columnal.
17. Exemplar 453/10447, x 7; articular surface of a columnal.
18. Exemplar 83/10447, x 7; articular surface of a columnal.
19. Exemplar 80/10447, x 5; base of a calyx.
South Tien Shan, Shakriomon. Middle Ordovician, Obikalon Bed.
- Fig. 20, 21. *Conspectocrinus conspectus* STUKALINA 1969.
20. Paratypoid 26/11809, x 20; articular surface of a internodal columnal.
21. Paratypoid 25/11809, x 20; articular surface of a nodal columnal.
Kazakhstan, Chuili Mountains. Upper Ordovician, Dulancara horizon, Accol Shale.

Plate 9

- Fig. 1—4. *Myelodactylus flexibilis* STUKALINA 1982.
1. Paratypoid 1/12374, x 10; side view of a stem fragment.
2. Holotype 7/11672, x 6; articular surface of a proximal columnal.
3. Paratypoid 6/12374, x 5.5; accumulation of stem fragments and single columnals.
4. Paratypoid 2/12374, x 10; side view of a stem fragment.
Siberian Platform. Lower Silurian, Khaastyr horizon.
- Fig. 5—7. *Myelodactylus rimatus* STUKALINA, sp. nov. (in press).
5. Holotype 8/12374, x 10; articular surface of a proximal columnal.
6. Paratypoid 9/12374, x 10; articular surface of a proximal columnal.
7. Paratypoid 10/12374, x 10; articular surface of a distal columnal.
Siberian Platform, Lower Silurian, Khakom horizon.
- Fig. 8, 9. *Pandocrinus pandus* STUKALINA 1965.
8. Holotype 16/8721, x 2; articular surface of a proximal columnal.
9. Paratypoid 15/8721, x 2; side view of a stem fragment.
Kazakhstan, Tarbagatay Range. Lower Devonian, Kokbaytal horizon.
- Fig. 10. *Pandocrinus plicatus* STUKALINA 1965.
10. Paratypoid 28/12212, x 5; articular surface of a columnal.
Kazakhstan, Balkhash area. Upper Silurian, Tokrau horizon.
- Fig. 11, 12. *Scyphocrinites mariannae* YAKOVLEV 1953.
11. Exemplar 32/8568, x 3; articular surface of a columnal.
12. Paratypoid 56/9986, x 3; articular surface of a columnal.
Kazakhstan, Balkhash area. Silurian/Devonian boundary beds, Ajnasu horizon, Lower part.
- Fig. 13—15. *Syndetocrinus minimus* STUKALINA 1975.
13. Paratypoid 4/12212, x 1; articular surface of a proximal columnal.
14. Paratypoid 5/12212, x 1; articular surface of a proximal columnal.
15. Paratypoid 6/12212, x 1; articular surface of a proximal columnal.
Kazakhstan, Balkhash area. Upper Silurian, Tokrau horizon.

- Fig. 16. *Crotalocrinites ? borealis* (YELTSYSHEVA 1960).
16. Paratypoid 4/7453, x 10; stem fragment from the distal part.
Siberian Platform, Moyero River. Lower Silurian, Khaastyr horizon, Upper part.

Plate 10

- Fig. 1—3. *Sibiricrinus belenae* YELTSYSHEVA 1982.
1. Exemplar 16/12374, x 6; articular surface of a columnal.
2. Exemplar 14/12374, x 6; articular surface of a columnal.
3. Exemplar 15/12374, x 4; articular surface of a columnal.
Siberian Platform. Lower Silurian, Khakom horizon.
Fig. 4, 5. *Multifidocrinus tenuicostatus* STUKALINA 1985.
4. Holotype 46/11730, x 5; articular surface of a columnal.
5. Paratypoid 47/11730, x 5; articular surface of a columnal.
Kazakhstan, Betpak Dala. Middle Ordovician. Sartanmanay Limestone.
Fig. 6, 14. *Glyptocrinus ? elegans* YELTSYSHEVA 1960.
6. Paratypoid 21/11730, x 10; articular surface of a columnal.
7. Exemplar 24/11730, x 5.5; accumulation of stem fragments and single columnals.
Siberian Platform, Moyero River. Lower Silurian, Khaastyr horizon.
Fig. 7—9. *Scalaricrinus scalariformis* (YELTSYSHEVA 1960).
7. Paratypoid 28/11730, x 10; articular surface of a columnal.
8. Paratypoid 25/11730, x 10; articular surface of a columnal.
9. Paratypoid 29/11730, x 10; side view stem fragment from the proximal part.
Siberian Platform, Omnutach River. Lower Silurian, Agidy horizon.
Fig. 10, 11. *Dastaricrinus petaloides* STUKALINA, sp. nov. (in press).
10. Paratypoid 19/11730, x 10; articular surface of an internodal columnal.
11. Holotype 20/11730, x 10; articular surface of a nodal columnal.
Siberian Platform. Omnutach River. Lower Silurian, Khakom horizon, Lower Part.
Fig. 12, 13. *Dentiferocrinus dentiferus* (YELTSYSHEVA 1955).
12. Paratypoid 34/11730, x 4; side view stem fragment from the proximal part.
13. Holotype 35/7453, x 4; side view stem fragment from the distal part.
Siberian Platform. Lower Silurian. Khaastyr horizon.

Plate 11

- Fig. 1. *Pennatocrinus praepennatus* STUKALINA 1985.
1. Paratypoid 13/12212, x 2.5; articular surface of a columnal.
Kazakhstan, Balkhash area. Upper Silurian. Tokrau horizon.
Fig. 2, 3. *Tastjicrinus paucicostatus* (YELTSYSHEVA 1957).
2. Lectotype 34/9586, x 7; articular surface of a distal columnal.
3. Paratypoid 35/9986, x 7; articular surface of a proximal columnal.
Kazakhstan, Balkhash area. Lower Devonian, Balkhash horizon.
Fig. 4—7. *Tastjicrinus tastjensis* STUKALINA 1975.
4. Paratypoid 40/9986, x 7; articular surface of a proximal columnal.
5. Paratypoid 38/9986, x 7; articular surface of a proximal columnal.
6. Holotype 39/9986, x 10; articular surface of a distal columnal.
7. Paratypoid 41/9986, x 7; articular surface of a proximal columnal.
Kazakhstan, Balkhash area. Lower Devonian, Balkhash horizon.
Fig. 8—11. *Podoliocrinus nikiforovae* YELTSYSHEVA 1957.
8. Paratypoid 32/9986, x 4; articular surface of a proximal columnal.
9. Paratypoid 22/8568, x 10; articular surface of a proximal columnal.
10. Paratypoid 33/9986, x 4; articular surface of a proximal columnal.
11. Paratypoid 22a/8568, x 4; articular surface of a proximal columnal.
Kazakhstan, Balkhash area. Lower Devonian, Balkhash horizon.
Fig. 12. *Facetocrinus pentagonus* STUKALINA 1977.
12. Holotype 7/11026, x 4; articular surface of a distal columnal.
Kazakhstan, Balkhash area. Lower Devonian, Sardzhal horizon.

- Fig. 13. *Floriacrinus florens* (YELTSYSHEVA & J. DUBATOLOVA 1967).
13. Exemplar 2/10900, x 4; articular surface of a proximal columnal.
Kazakhstan, Balkhash area. Lower Devonian, Sardzhal horizon.
Fig. 14. *Floriacrinus proteus* STUKALINA 1977.
14. Holotype 5/11026, x 5; articular surface of a proximal columnal.
Kazakhstan, Balkhash area. Lower Devonian, Sardzhal horizon.
Fig. 15—18. *Anthinocrinus radialis* STUKALINA 1975.
15. Paratypoid 15/9986, x 10; articular surface of a proximal columnal.
16. Paratypoid 14/9986, x 7; articular surface of a proximal columnal.
17. Paratypoid 13/9986, x 7; articular surface of a distal columnal.
18. Holotype 11/9986, x 7; articular surface of a distal columnal.
Kazakhstan, Balkhash area. Lower Devonian, Balkhash horizon.
Fig. 19—21. *Formosocrinus formosus* YELTSYSHEVA & SISOVA 1973.
19. Paratypoid 25/9986, x 10; articular surface of a proximal columnal.
20. Paratypoid 23/9986, x 10; articular surface of a proximal columnal.
21. Paratypoid 22/9986, x 10; articular surface of a proximal columnal.
Kazakhstan, Balkhash area. Lower Devonian, Balkhash horizon.
Fig. 22. *Formosocrinus spiculatus* POLOZHICHINA 1980.
22. Holotype VI-166/3, x 7; (Museum MGRJ, Moscow); articular surface of a columnal.
Kazakhstan, Balkhash area. Lower Devonian, Balkhash horizon.
Fig. 23, 24. *Gregariocrinus forus* (STUKALINA 1961).
23. Paratypoid 19/8721, x 3; articular surface of a distal columnal.
24. Holotype 18/8721, x 3; articular surface of a proximal columnal.
Kazakhstan, Balkhash area. Silur/Devonian boundary beds, Ajnasu horizon.
Fig. 25. *Kotanocrinus balaensis* STUKALINA 1977.
25. Holotype 6/11026, x 4; articular surface of a proximal columnals.
Kazakhstan, Balkhash area. Lower Devonian, Sardzhal horizon.
Fig. 26—28. *Facetocrinus stellatus* YELTSYSHEVA & SISOVA 1973.
26. Paratypoid 19/9986, x 10; articular surface of a proximal columnal.
27. Paratypoid 20/9986, x 10; articular surface of a proximal columnal.
28. Paratypoid 21/9980, x 10; articular surface of a proximal columnal.
Kazakhstan, Balkhash area. Lower Devonian, Balkhash horizon.
Fig. 29. *Facetocrinus quinquespinosus* (STUKALINA 1961).
29. Holotype 31/8721, x 3; articular surface of a proximal columnal.
Kazakhstan, Aksarly Range, Lower Devonian, Kokbaytal horizon.
Fig. 30—32. *Facetocrinus ajnasuensis* (STUKALINA 1961).
30. Holotype 55/9986, x 10; articular surface of a columnal.
31. Paratypoid 18/9986, x 10; articular surface of a columnal.
32. Paratypoid 19/9986, x 10; articular surface of a columnal.
Kazakhstan, Lower Devonian.
Fig. 33. *Kuzbassocrinus tuberculatus* SHEVCHENKO 1966.
33. Paratypoid 14/12225, x 5; a — articular surface of a proximal columnal, b — stem fragment from the proximal part.
South Tien Shan, Shishkat. Lower Devonian, Pandzhrut horizon.

Plate 12

- Fig. 1, 2. *Decacrinus ovalis* STUKALINA 1968.
1. Paratypoid 307.8568, x 10; articular surface of a columnal.
2. Holotype 6/9554, x 10; articular surface of a columnal.
Kazakhstan, Balkhash area. Lower Devonian, Kokbaytal horizon.
Fig. 3—7. *Decacrinus pennatus* YELTSYSHEVA 1957.
3. Paratypoid 4/9554, x 3; articular surface of a proximal columnal.
4. Paratypoid 30/9986, x 4; articular surface of a distal columnal.
5. Paratypoid 5/9554, x 3; articular surface of a proximal columnal.
6. Paratypoid 3/9554, x 3; articular surface of a distal columnal.
7. Paratypoid 1/9554, x 3; accumulation of stem fragments and single columnals.
Kazakhstan horizon. Balkhash area. Lower Devonian, Balkhash horizon.

- Fig. 8, 10. *Decacrinus ornatus* STUKALINA 1968.
 8. Holotype 10/9554, x 10; articular surface of a distal columnal.
 9. Paratypoid 11/9554, x 5; articular surface of a proximal columnal.
 10. Paratypoid 31/9986, x 7; articular surface of a proximal columnal.
 Kazakhstan, Balkhash area. Lower Devonian, Balkhash horizon.
- Fig. 11. *Pennatocrinus subpennatus* YELT. & STUK. 1968.
 11. Paratypoid 26/9986, x 4; articular surface of a proximal columnal.
 Kazakhstan, Balkhash area. Silur/Devon boundary beds, Ajnasu horizon.
- Fig. 12. *Paradecacrinus tortuosus* STUKALINA 1977.
 12. Holotype 9/11026, x 4; articular surface of a proximal columnal.
 Far East. Lower Devonian. Bol'shenever Formation, Upper Part.
- Fig. 13. *Kuzbassocrinus minimus* STUKALINA 1977.
 13. Holotype 10/11026, x 4; articular surface of a proximal columnal.
 Far East. Lower Devonian, Bol'shenever Formation, Upper Part.
- Fig. 14, 15. *Kuzbassocrinus binidigitatus* YELTYSHEVA 1957.
 14. Paratypoid 9/10900, x 7; articular surface of a proximal columnal.
 15. Paratypoid 10/10900, x 7; articular surface of a proximal columnal.
 Far East. Lower Devonian, Bol'shenever Formation, Upper Part.

Plate 13

- Fig. 1, 2. *Acanthocrinus ? monstruosus* YELT. & STUK. 1977.
 1. Paratypoid 2/11026, x 2; articular surface of a proximal columnal.
 2. Paratypoid 3/11026, x 2; articular surface of a proximal columnal.
 Kazakhstan, Balkhash area. Lower Devonian, Sardzhal horizon.
- Fig. 3, 4. *Granulicrinus granulosus* STUKALINA 1985.
 3. Holotype 48/11730, x 4; articular surface of a proximal columnal.
 4. Paratypoid from the coll. 11730, x 4; stem fragment from the proximal part.
 Kazakhstan, Betpak Dala, Middle Ordovician, Anderken horizon.
- Fig. 5—13. *Kaplunaecrinus kaplunae* YELT. & STUK. 1977.
 5. Paratypoid 12/11026, x 2; articular surface of a proximal columnal.
 6. Paratypoid 13/11809, x 2; articular surface of a proximal columnal.
 7. Paratypoid 52/11809, x 2; articular surface of a proximal columnal.
 8. Paratypoid 13/11026, x 2; articular surface of a proximal columnal.
 9. Paratypoid 132/11809, x 2; articular surface of a distal columnal.
 10. Holotype 14/11026, x 2; articular surface of a distal columnal.
 11. Paratypoid 58/11809, x 2; articular surface of a distal columnal.
 12. Paratypoid 56/11809, x 2; articular surface of a distal columnal.
 13. Paratypoid 3/10900, x 2; articular surface of a distal columnal.
 Kazakhstan, Balkhash area. Lower Devonian, Sardzhal horizon.
- Fig. 14—16. *Cosmocrinus distinctus* STUKALINA 1977.
 14. Paratypoid 17/11026, x 5; articular surface of a proximal columnal.
 15. Paratypoid 18/11026, x 5; stem fragment from the proximal part.
 16. Holotype 15/11026, x 3; articular surface of a distal columnal.
 Kazakhstan, Chingiz Range. Middle Devonian, Besoba horizon.
- Fig. 17, 18. *Stomiocrinus rarus* SKOROPISZEVA 1969.
 17. Paratypoid 14/9707, x 3; articular surface of a proximal columnal (junior form).
 18. Paratypoid 15/9707, x 3; articular surface of a proximal columnal.
 Transbaikal area, Mergen River. Lower Permian.
- Fig. 19. *Stomiocrinus kolymensis* YELTYSHEVA 1969, in SKOROPISZEVA.
 19. Holotype 11/9707, x 2; articular surface of a proximal columnal.
 Mongolia, Barcha River. Upper Permian.
- Fig. 20. *Dolatocrinus tetragonus* SHEVSHENKO 1964.
 20. Holotype 17/12225, x 8: a — articular surface of a nodal columnal, b — side view of a nodal columnal.
 South Tien Shan, Shishkat. Lower Devonian, Pandzhrut horizon.
- Fig. 21. *Sartanicrinus sartanensis* STUKALINA 1985.
 21. Holotype 50/11730, x 3; articular surface of a proximal columnal.
 Kazakhstan, Betpak Dala. Middle Ordovician, Anderken horizon.

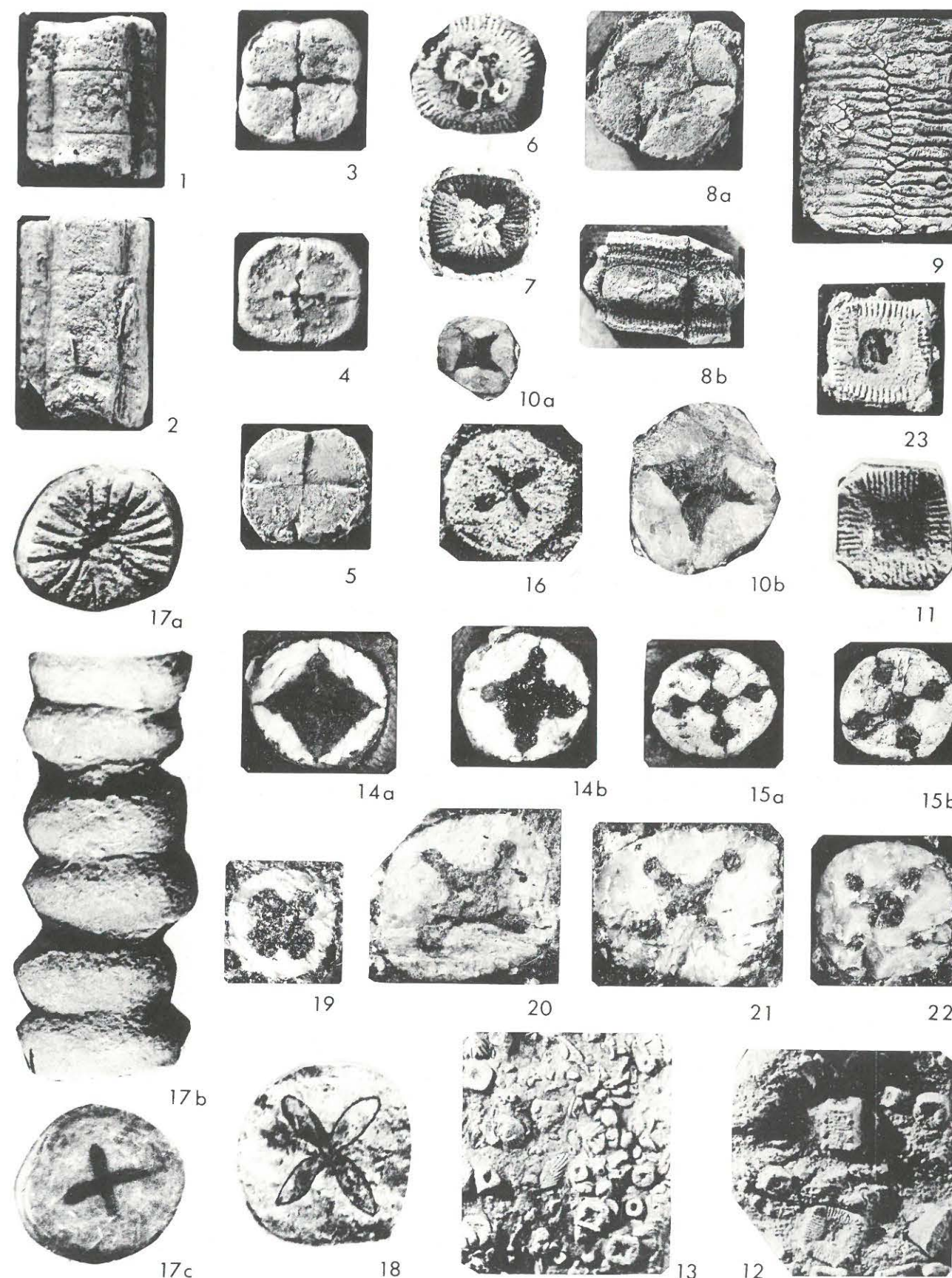
- Fig. 22, 23. *Pandocrinus fascicularis* STUKALINA 1985.
 22. Paratypoid 26/12212, x 3; articular surface of a proximal columnal.
 23. Holotype 25/12212, x 3; articular surface of a proximal columnal.
 Kazakhstan, Balkhash area. Upper Silurian, Tokrau horizon.
- Fig. 24. *Ordinacrinus ordinarius* STUKALINA 1985.
 24. Holotype 42/11747, x 5: a — stem fragment from the proximal part, b — articular surface of a proximal columnal.
 Kazakhstan, Chuili Mountains. Middle Ordovician Anderken horizon.
- Fig. 25, 26. Sp. indet.
 25. Exemplar 53/11730, x 6; stem fragment from the proximal part.
 26. Exemplar 52/11730, x 10; articular surface of a internodal columnal.
 Kazakhstan, Betpak Dala. Middle Ordovician, Anderken horizon.

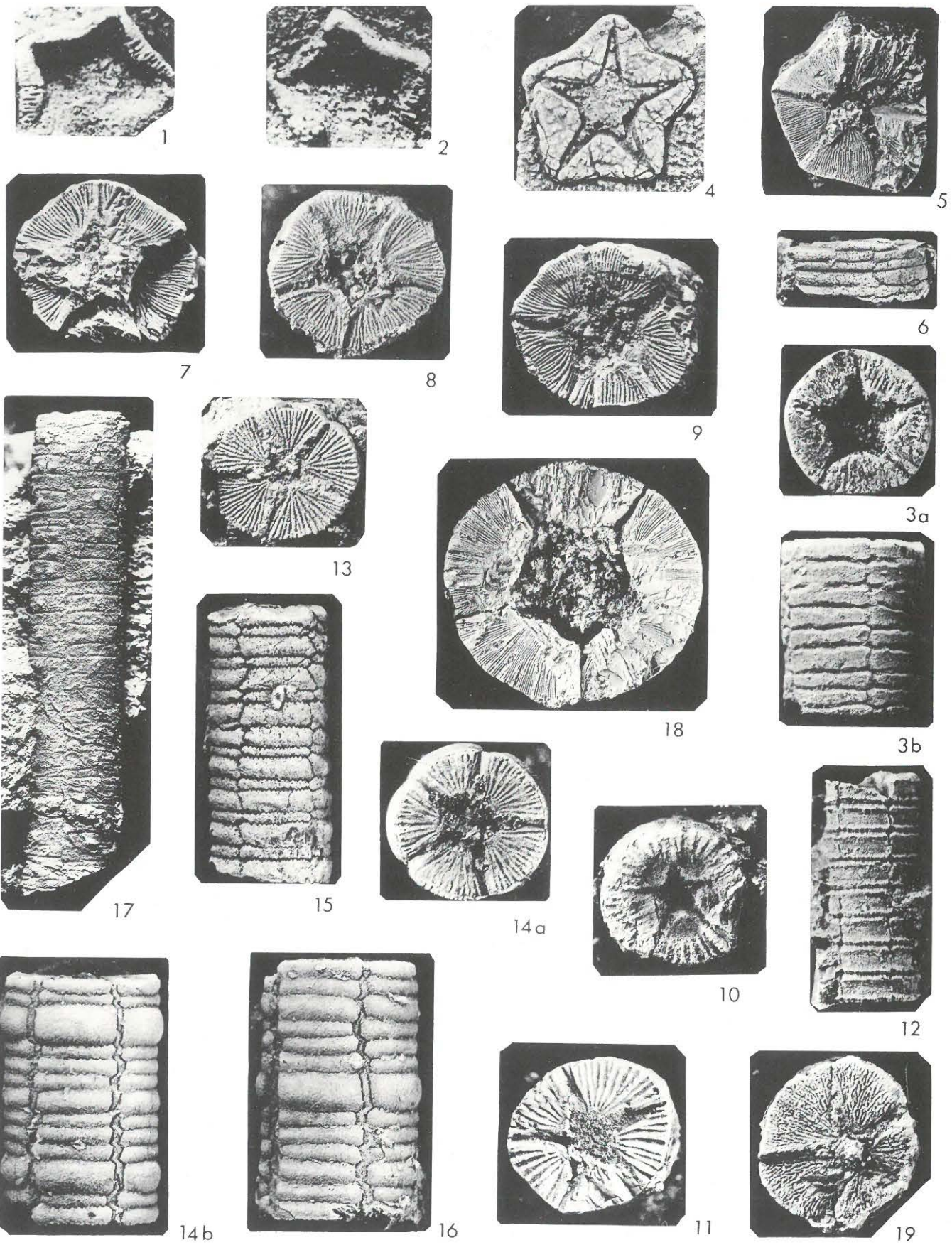
Plate 14

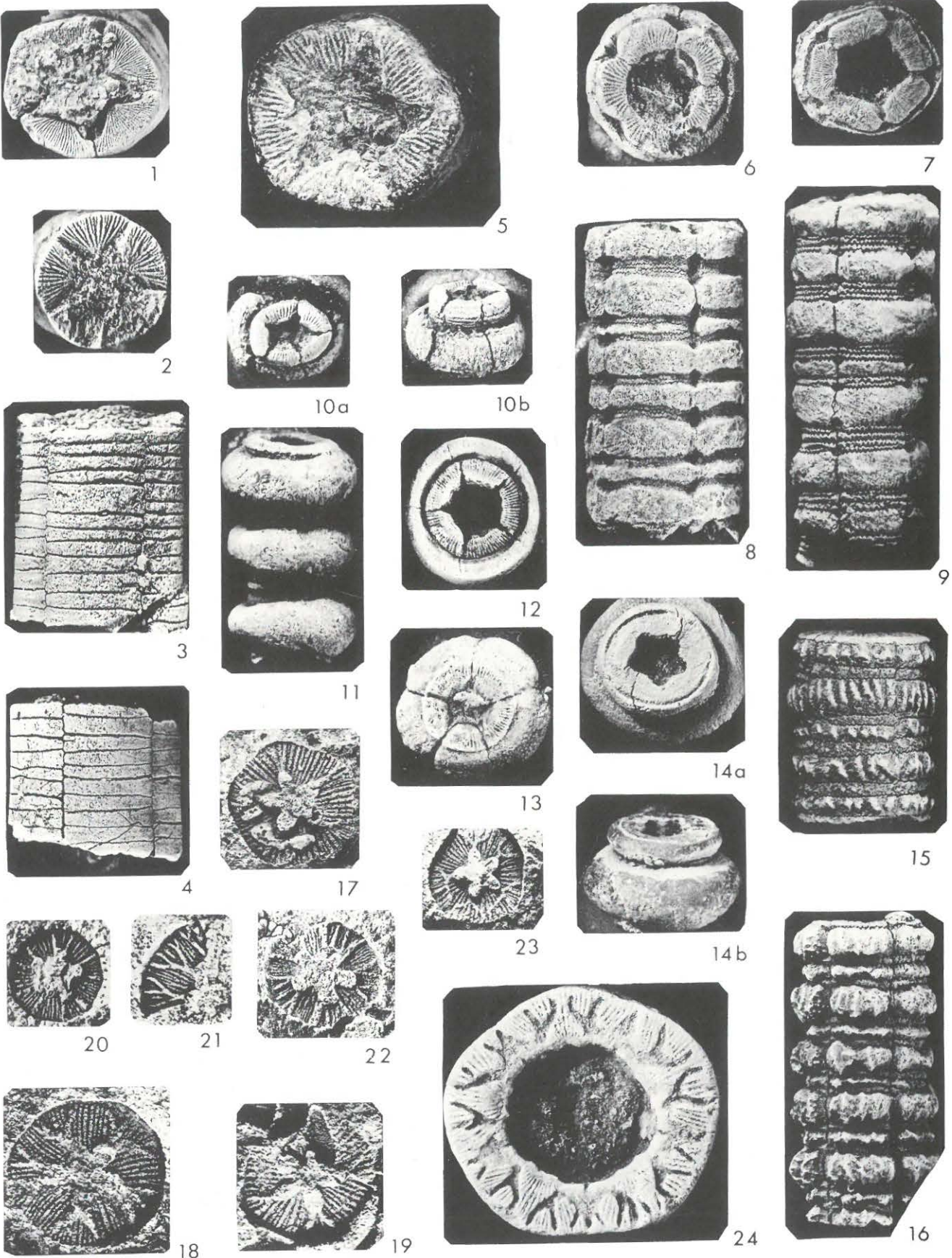
- Fig. 1—3. *Ristnacrinus marinus* ÖPIK 1934.
 1. Paratypoid Ec 1751, x 8; articular surface of a proximal columnal.
 2. Paratypoid Ec 1754, x 10; articular surface of a proximal columnal.
 3. Paratypoid Ec 1752, x 8; articular surface of a proximal columnal.
 (Museum JG AN ESSR, Tallin). Northwest East European Platform. Estonia. Middle Ordovician, Upper Part.
- Fig. 4. *Ristnacrinus tuberculatus* STUKALINA 1980.
 4. Paratypoid 7/11747, x 10; articular surface of a proximal columnal.
 Kazakhstan, Chingiz Range. Upper Ordovician.
- Fig. 5. *Ristnacrinus bifidus* STUKALINA 1980.
 5. Paratypoid 4/11747, x 10; articular surface of a proximal columnal.
 Kazakhstan, Chingiz. Upper Ordovician.
- Fig. 6, 7. *Asperocrinus ebinatus* (YELTYSHEVA 1961).
 6. Exemplar 1/10900, x 3.5; articular surface of a proximal columnal.
 7. Exemplar 46/9986, x 7; articular surface of a proximal columnal.
 Kazakhstan, Balkhash area. Lower Devonian, Kokbaytal horizon.
- Fig. 8—12. *Pinegicrinus edemskij* VANIN 1980.
 8. Paratypoid 12/11749, x 5; articular surface of a distal columnal.
 9. Paratypoid 13/11749, x 7; articular surface of a proximal columnal.
 10. Paratypoid 15/11749, x 7; articular surface of a proximal columnal.
 11. Holotype 1/11749, x 7; articular surface of a proximal columnal.
 12. Paratypoid 17/11749, x 5; stem fragment from the proximal part.
 North East European Platform. Pinega River. Upper Permian, Kazanian.
- Fig. 13—15. *Platycrinites ? texanum* MOORE & JEFFORDS 1968.
 13. Exemplar 2/11748, x 3; articular surface of a columnal.
 14. Exemplar 3/11748, x 3; articular surface of a columnal.
 15. Exemplar 1/1748, x 3; articular surface of a columnal.
 Far East, Chumavra River. Lower Carboniferous.
- Fig. 16—21. *Hexacrinites ? tuberosus* YELTYSHEVA 1961.
 16. Exemplar 84/11809, x 3; articular surface of a proximal columnal.
 17. Exemplar 82/11809, x 3; articular surface of a proximal columnal.
 18. Exemplar 79/11809, x 3; stem fragment from the distal part.
 19. Exemplar 78/11809, x 3; stem fragment from the proximal part.
 20. Exemplar 77/11809, x 3; articular surface of a distal columnal.
 21. Exemplar 90/11809, x 3; articular surface of a distal columnal.
 Kazakhstan, Chingiz Range. Middle Devonian, Besoba horizon.
- Fig. 22. *Hexacrinites ? modzalevskajae* YELTYSHEVA, 1969.
 22. Exemplar 11/10900, x 3; accumulation of stem fragments and single columnals. Far East. Lower Devonian, Imachi Formation, Lower Part.

Plate 15

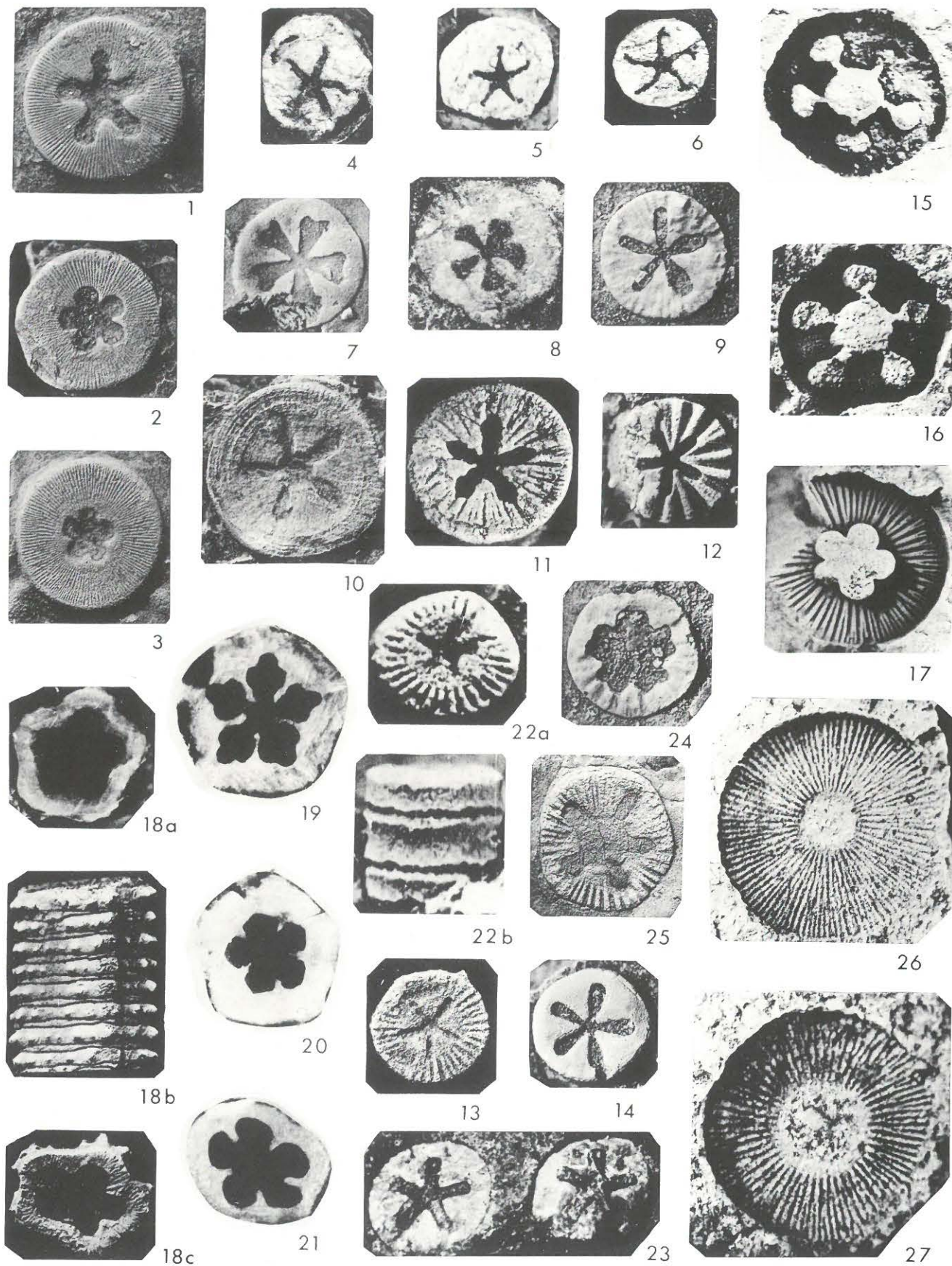
- Fig. 1, 2. *Herpetocystis ? vajgatschensis* (YELT. & STUK. 1963).
 1. Exemplar 1/11730, x 4: a — stem fragment from the proximal part, b — articular surface.
 2. Exemplar 2/11730, x 7; articular surface from the distal columnal.
 Kazakhstan, Betpak Dala. Middle Ordovician, Anderken horizon.
- Fig. 3. *Glyptostella* sp.
 3. Exemplar 129/11809, x 5; stem fragment.
 Kazakhstan, Burultas. Middle Ordovician, Anderken horizon.
- Fig. 4—6. *Clivosocystis tuberculatus* STUKALINA 1980.
 4. Paratypoid 6/11487, x 2.5; stem fragment from the proximal part.
 5. Paratypoid 7/11487, x 2.5; stem fragment from the proximal part.
 6. Holotype 5/11487, x 2.5; articular surface of a proximal columnal.
 Kazakhstan, Betpak Dala. Middle Ordovician, Anderken horizon.
- Fig. 7. *Clivosocystis clivosus* STUKALINA 1980.
 7. Holotype 3/11487, x 3; proximal part of a stem.
 Kazakhstan, Chingiz Range. Middle Ordovician, Anderken horizon.
- Fig. 8. *Flabellucystis kuusikuensis* STUKALINA 1979.
 8. Holotype Ec 1731, x 4: a — upper articular surface of a columnal, b — stem fragment from the proximal part, c — lower articular surface of a columnal. (Museum JG AN ESSR).
 Northwest East European Platform, Estonia. Middle Ordovician, Oandu horizon.
- + Fig. 9—13. *Oanducystis excisus* STUKALINA 1979.
 9. Paratypoid Ec 1782, x 5; articular surface of a columnal.
 10. Paratypoid Ec 1736, x 5; upper articular surface of a columnal.
 11. Holotype Ec 1733, x 4; lower articular surface of a columnal.
 12. Paratypoid Ec 1734, x 4; lower articular surface of a columnal.
 13. Paratypoid Ec 1732, x 5; side view of a stem fragment. (Museum JG AN ESSR, Tallin).
 Northwest East European Platform, Estonia. Middle Ordovician, Oandu horizon.
- Fig. 14, 15. *Oanducystis levis* STUKALINA 1985.
 14. Paratypoid 5/11730, x 6: a — upper articular surface of a columnal, b — lower articular surface of a columnal.
 15. Holotype 3/11730, x 6; side view of a stem fragment.
 Kazakhstan, Betpak Dala. Middle Ordovician, Sartanmanay Limestone.
- Fig. 16, 17. *Tenuicystis tenuis* STUKALINA 1985.
 16. Holotype 7/11730, x 3: a — articular surface of a distal columnal, b — stem fragment from the distal part.
 17. Paratypoid 6/11730, x 4; stem fragment from the proximal part.
 Kazakhstan, Betpak Dala, Middle Ordovician, Sartanmanay Limestone.
- Fig. 18. *Clivosocystis minusculus* STUKALINA, sp. nov. (in press).
 18. Exemplar 130/11809, x 3; accumulation of stem fragments.
 Kazakhstan, Betpak Dala. Middle Ordovician, Anderken horizon.

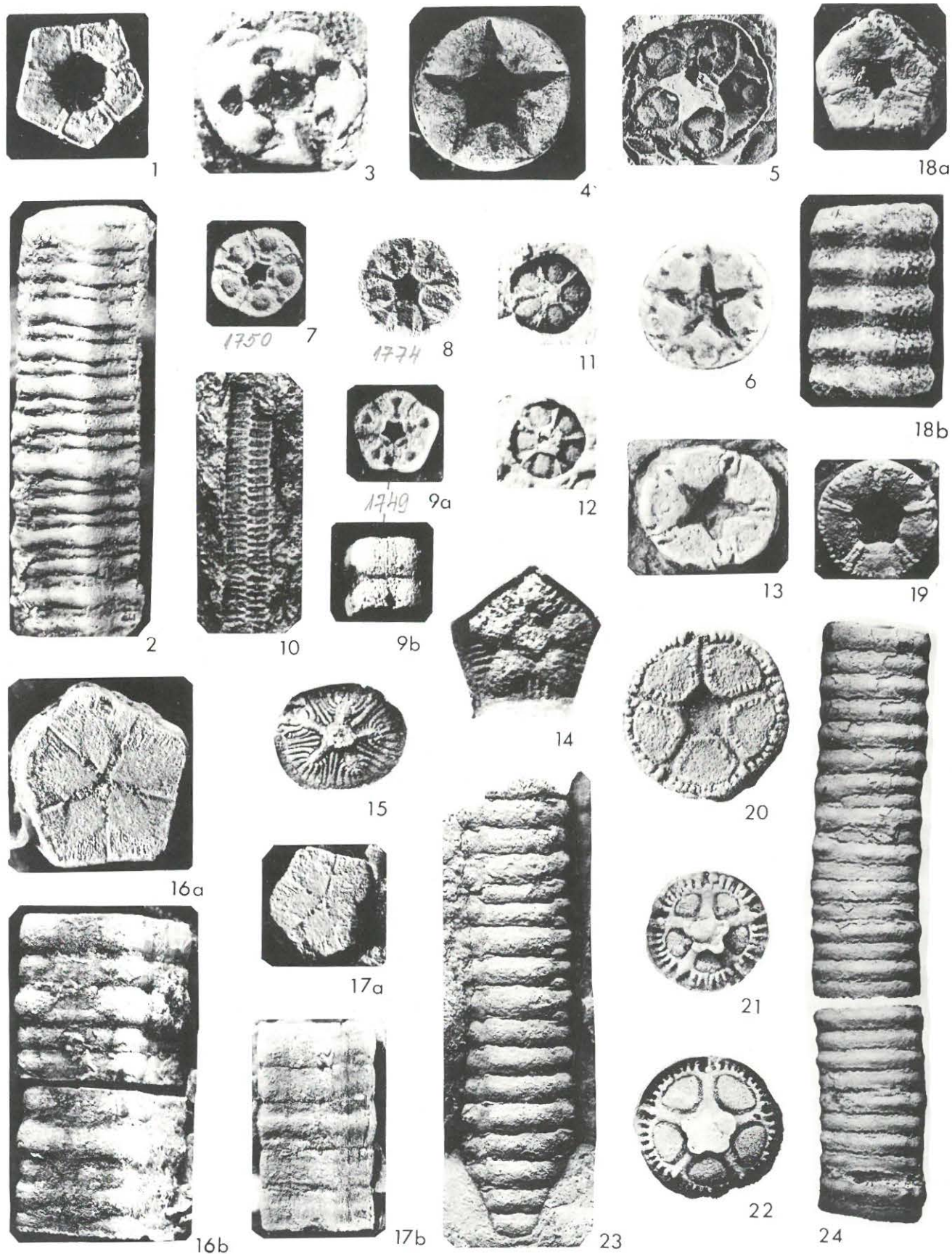






Galina A. Stukalina: Studies in Paleozoic crinoid-columnals and -stems.







1



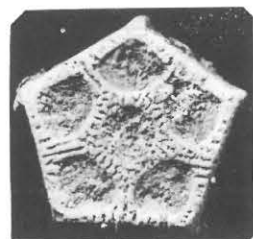
1775 4a



1779 8



11



2



4b



1776 5a



1780 9



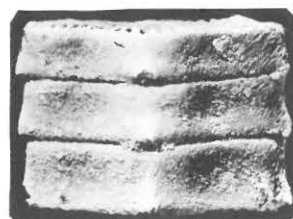
3



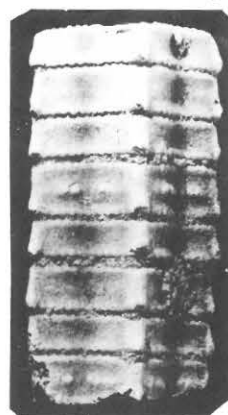
1778 10



1777 6



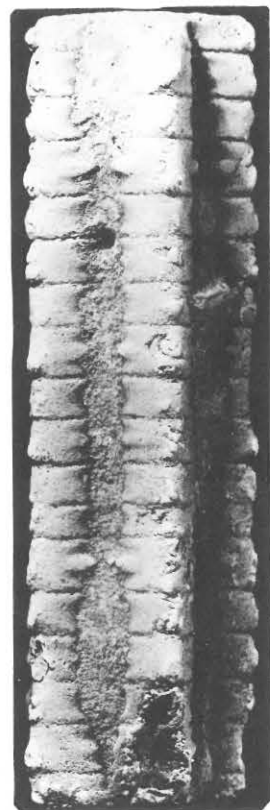
5b



7



13



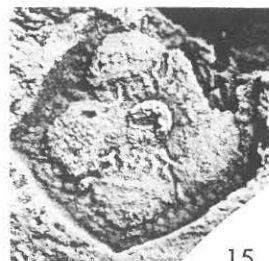
12



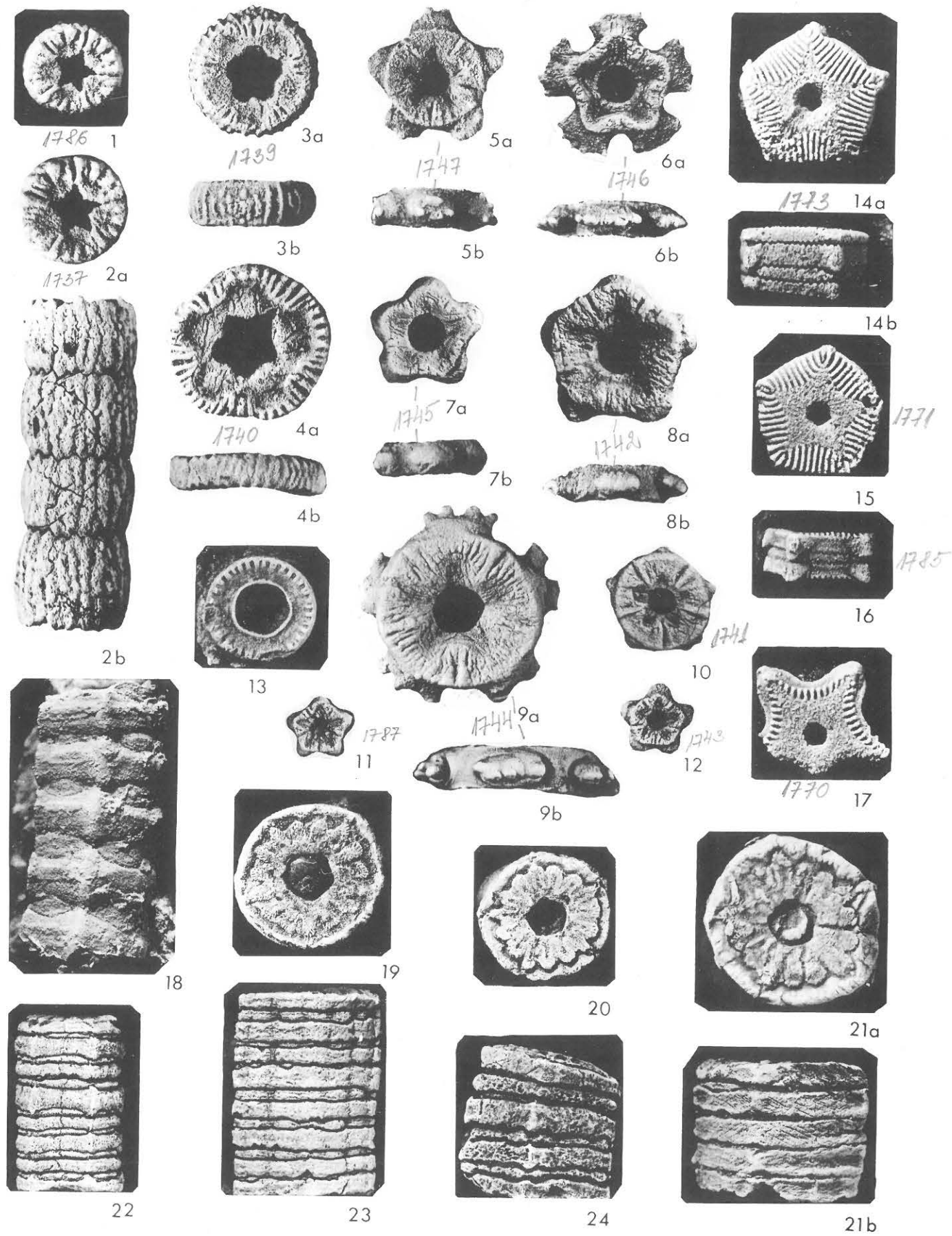
14

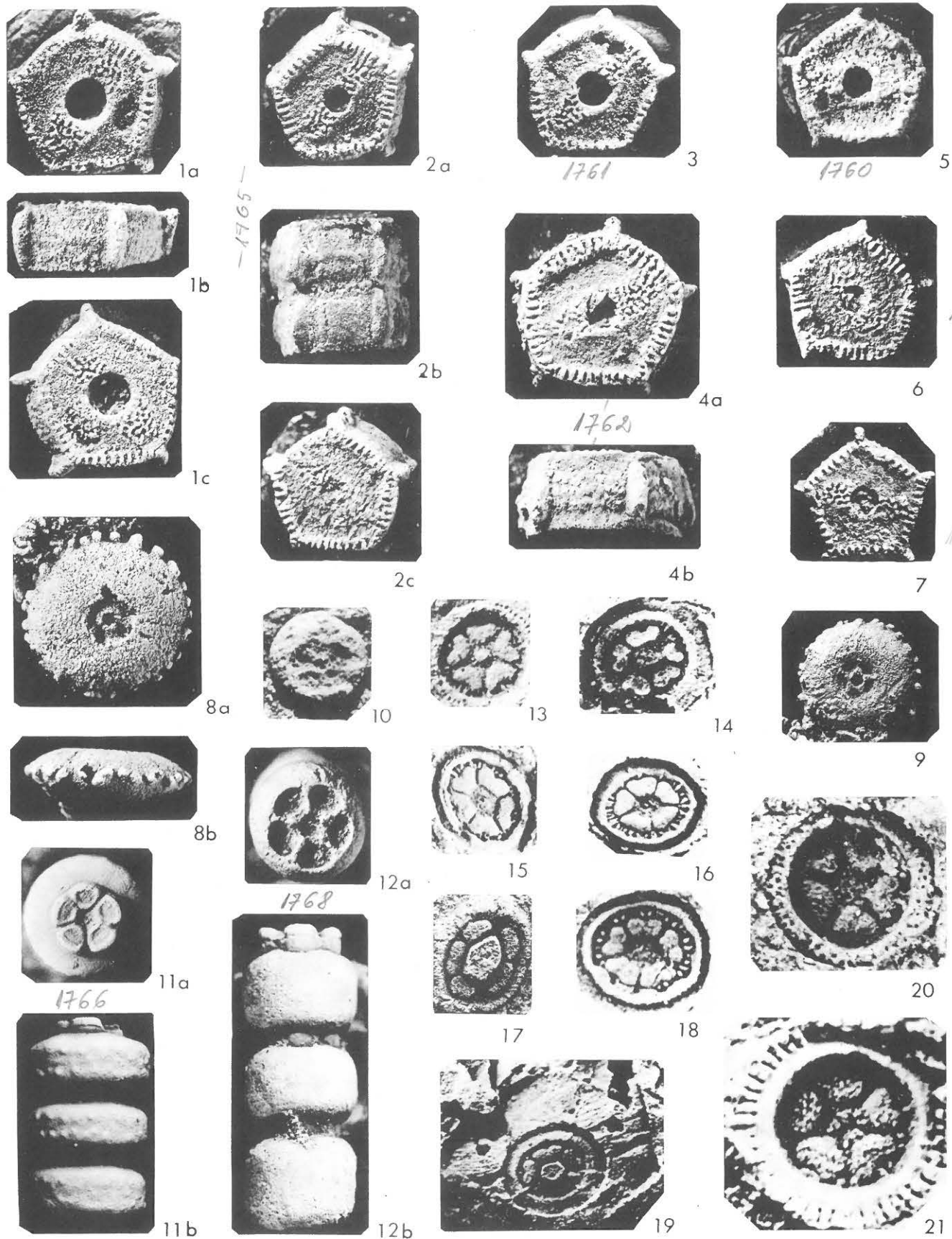


16

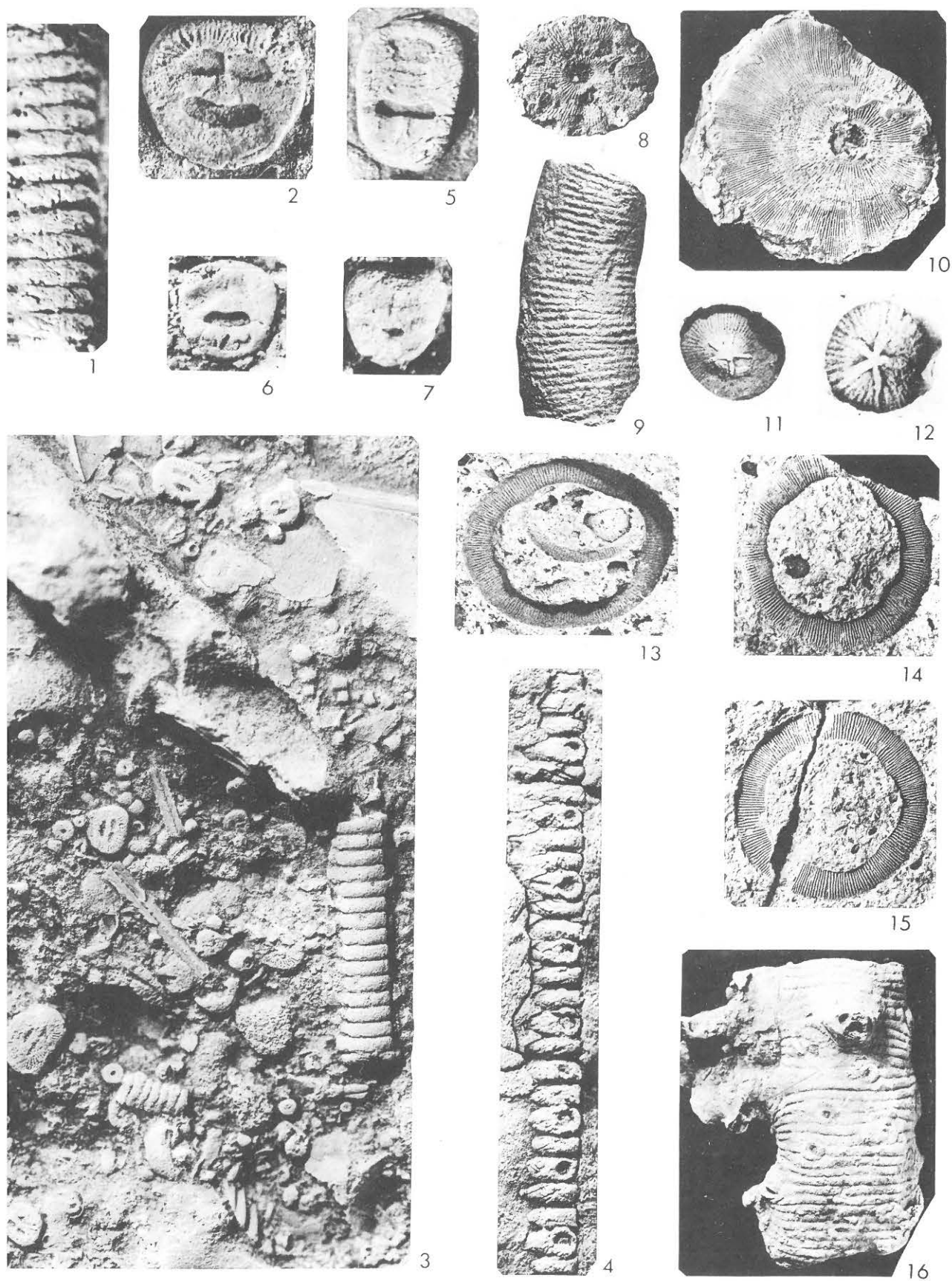


15

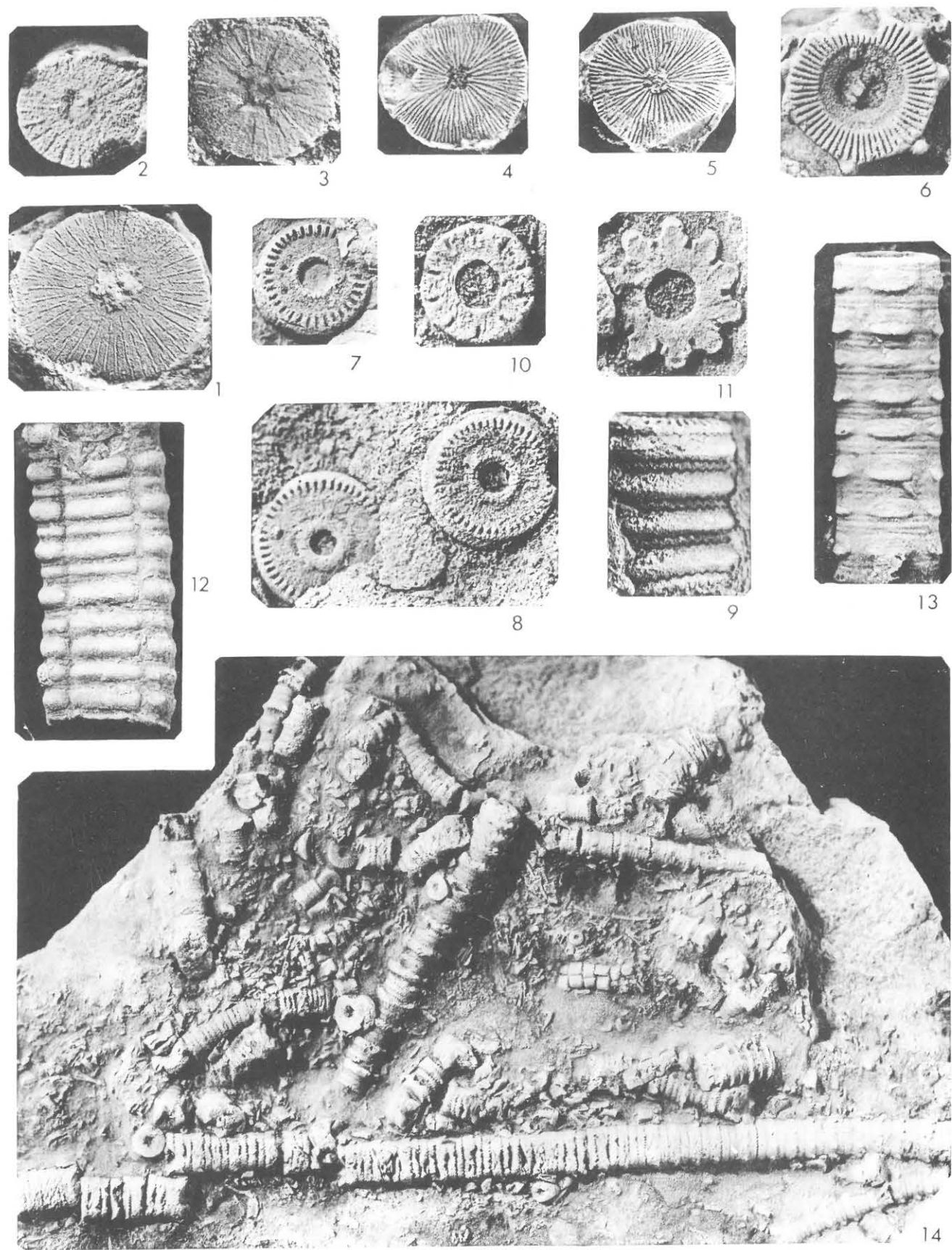




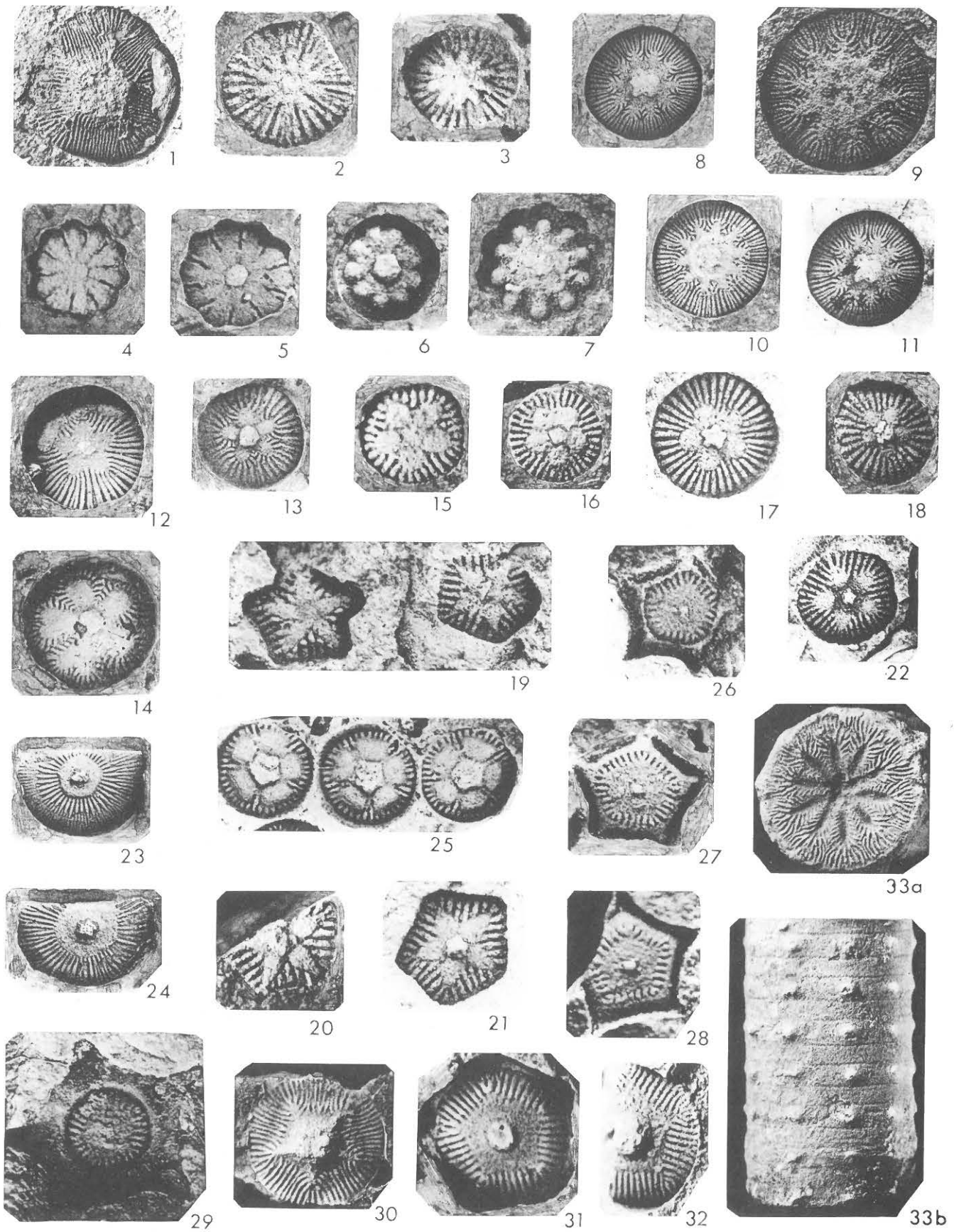
Galina A. Stukalina: Studies in Paleozoic crinoid-columns and -stems.



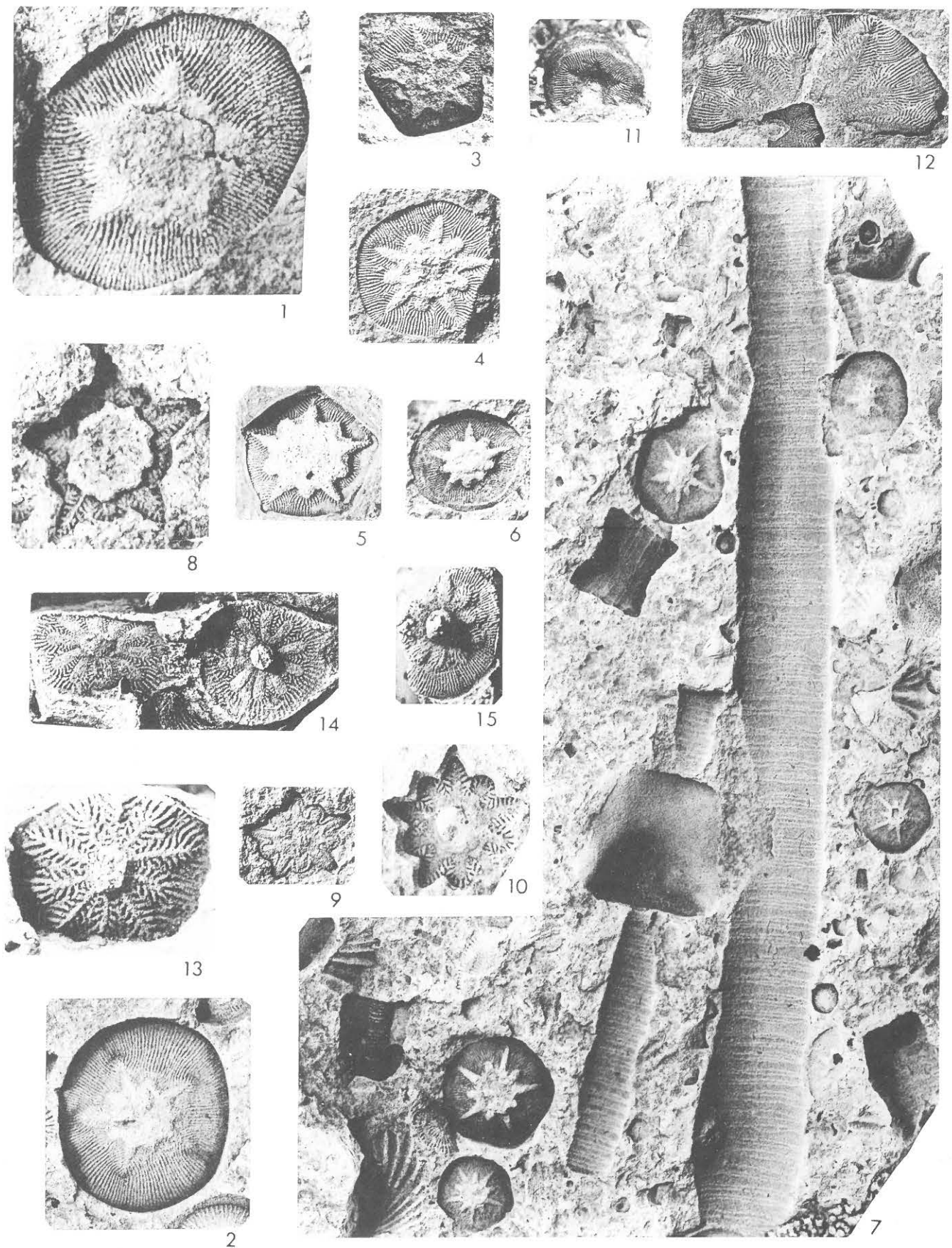
Galina A. Stukalina: Studies in Paleozoic crinoid-columnals and -stems.



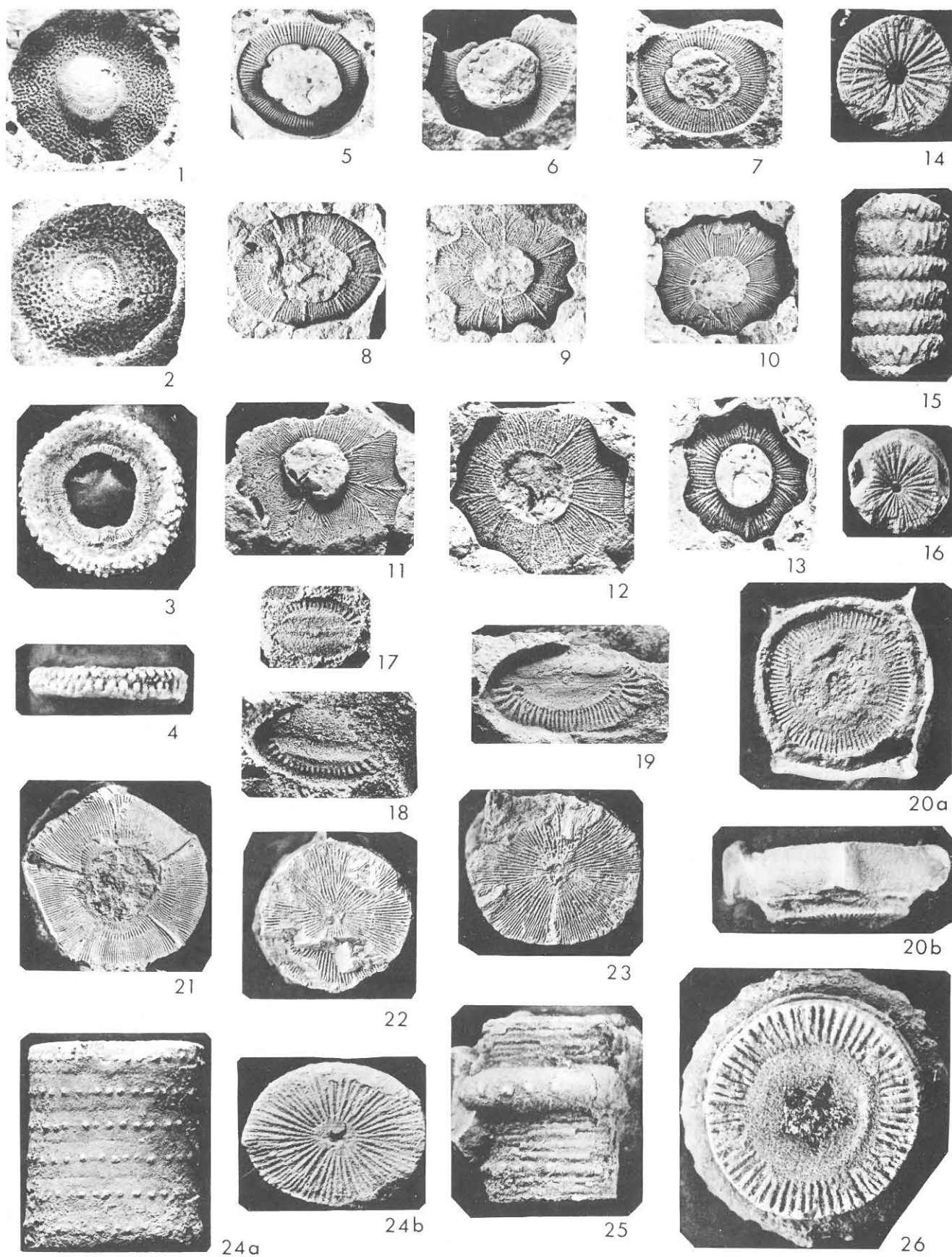
Galina A. Stukalina: Studies in Paleozoic crinoid-columns and -stems.

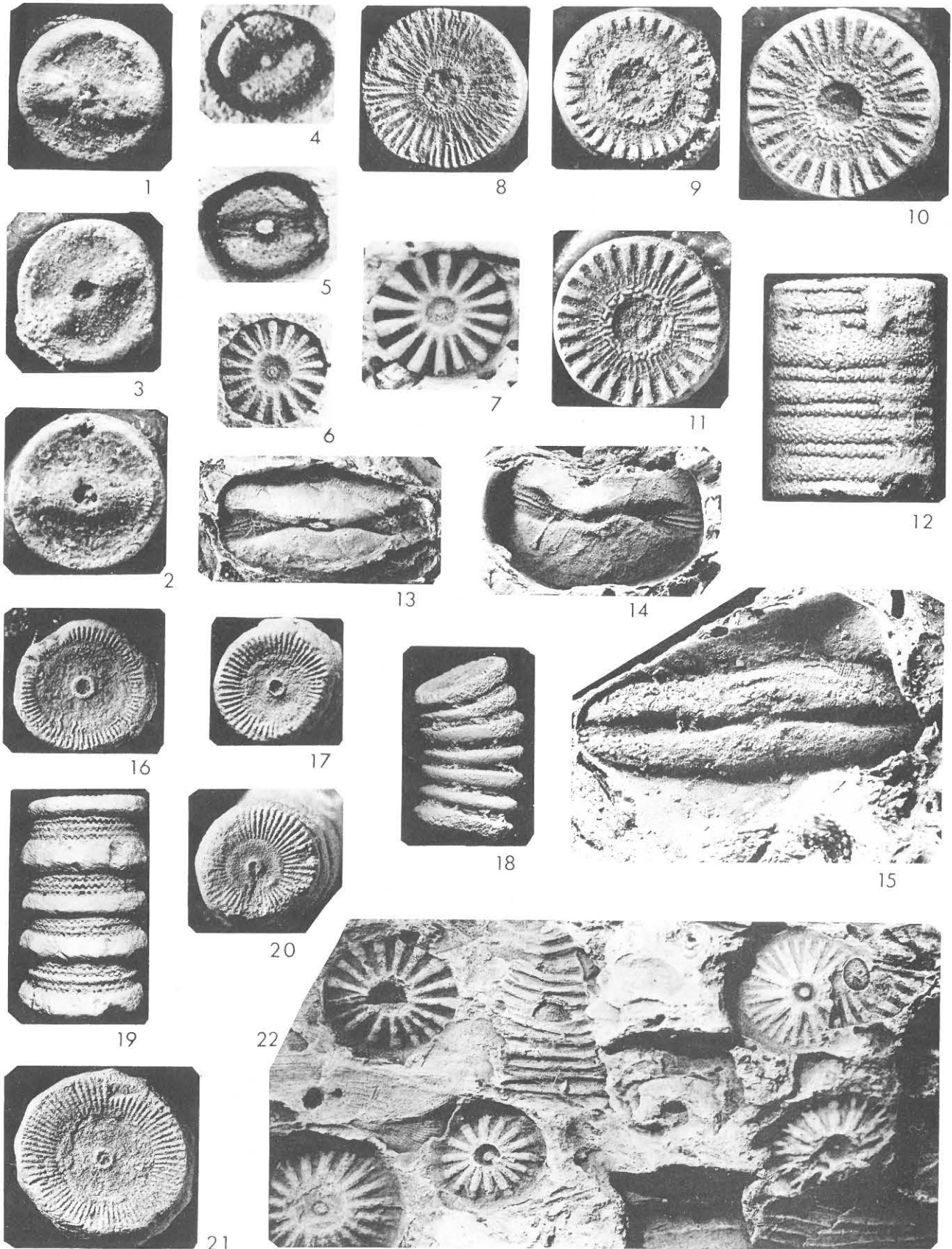


Galina A. Stukalina: Studies in Paleozoic crinoid-columns and -stems.



Galina A. Stukalina: Studies in Paleozoic crinoid-columns and -stems.





Galina A. Stukalina: Studies in Paleozoic crinoid-columns and -stems.

