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Morphogenesis and Evolution of Crinoids and Other Pelmatozoan Echinoderms in the Early Paleozoic

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Abstract—The morphogenesis and homologies of the major skeletal structures of crinoids and similar Early Paleozoic echinoderms are analyzed on the basis of comparative morphological analysis. The study of symmetry and asymmetry in the structure and morphogenesis of pelmatozoan echinoderms increases the understanding of the mechanism and sequence of the early development of different types of symmetry in evolution. It is shown that the appearance and diversification of crinoids in the Ordovician played a major role in the Ordovician evolutionary radiation of the marine biota, which resulted in the appearance of many classes of marine animals that have survived until the present day. The development of the morphological organization of higher taxa of echinoderms is discussed, and evolutionary trends, from the formation of the archetype to the development of more specialized structures, are revealed. The study is based on extensive material, particularly from the Ordovician of the Baltic region.

Key words: crinoids, pelmatozoan echinoderms, Early Paleozoic, comparative morphology, evolutionary patterns.

INTRODUCTION

Studying the emergence and early evolution of the morphological organization of higher taxa is one of the most important and interesting tasks of the modern science of evolutionary morphology. This task is approached from different sides by neontologists and paleontologists, studying quite diverse groups and aspects of the problem. However, most researchers use the cladistic method, interpreting an organism as a set of characters and studying the possible order of their appearance in specific organisms. This method has produced important and interesting results, especially in the study of lower taxa. However, using this approach does not cover the formation of archetypes. The present study attempts to bridge this gap by studying the evolution of taxa from the point of view of the formation of their body plans.

Echinoderms are one of the most suitable fossil groups for studying the origin and early evolution of the organization of higher taxa, since they have a diverse skeletal morphology that clearly reflects the structure of the soft body and long, well-recorded geochronological range (the entire Phanerozoic). Among Echinodermata, the subphylum of pelmatozoan echinoderms, with its largest class Crinoidea, is of particular interest.

The origin of the crinoid body plan is, at present, the subject of intense debate. Some researchers believe that crinoids evolved independently of the other pelmatozoan echinoderms, which had brachioles, and, based on this, recognize crinoids as a separate subphylum. Others suggest that the morphological organization of crinoids evolved from that of the geochronologically older class Eocrinoidea.

The solution of this problem is one of the most important tasks in the study of the evolution of marine biota, because the appearance of crinoids in the Ordovician was one of the major factors that sharply changed the composition of marine substrates. The resulting wide distribution of hardgrounds in the Ordovician caused those rapid changes in the entire marine biota that are referred to as the Ordovician radiation. As a result, the Cambrian evolutionary fauna was replaced by the Paleozoic fauna, which included most classes that have survived to the present day. This problem is of international interest. For instance, a special IGCP international project is devoted to the major events of the Ordovician biodiversification.

Pelmatozoan echinoderms, including crinoids, were the major group that revolutionized the development of the entire marine benthic community in the Ordovician. Therefore, this study was primarily focused on the origin and early evolution of the morphological organization of the higher echinoderm taxa. For this, it was necessary to reveal the patterns and trends in the early evolution of echinoderms and, first of all, the origin and development of the crinoid archetype.

Crinoids are one of the most interesting classes of echinoderms both from the point of view of morphology and for addressing general problems of evolution, classification, and morphogenesis that can be resolved based on representatives of this class. The first crinoids, not taking into account the bizarre *Echmatocrinus*, are known from the Lower Ordovician. However, recent crinoids are also widespread. Therefore, in studying the earliest representatives, data on the soft body, ontogeny, and functional morphology of extant forms can be used. The origin of crinoids is closely connected with the problem of the origin of the entire phylum Echinodermata and more so with that of the origin of the many ancient groups closely related to crinoids. This has required study outside the framework of the class Crinoidea to analyze the origin and early evolution of crinoids. Echinoderms have a high and diverse symmetry. Therefore, in order to study the morphology of echinoderms, it was necessary to discuss the manifestations of symmetry and its violations, enantiomorphism in different structures, and how it was influenced by the primary left-sided organization of echinoderms. When it was possible, the symmetry of morphogenetic processes leading to the symmetry of the resulting morphotypes was revealed, and, based on this, possible homologies of structures were determined.

It was shown that the wide distribution of crinoids in the Ordovician played a major role in the development of the Ordovician radiation of marine biota, which determined the appearance of many classes of marine animals that have survived until the present day. Therefore, the appearance of crinoids and closely related classes of echinoderms in the Ordovician indicated more general patterns in the formation of higher taxa of marine benthic animals.

The tasks of the present study were formulated as follows: (1) substantiation of the homologies between the major structures of pelmatozoan echinoderms, primarily crinoids, on the basis of the analysis of the morphogenetic mechanism of the rearrangement of the body plans in the higher taxa of Pelmatozoa and of the formation of the crinoid archetype; (2) reconstruction of the symmetry of morphogenetic processes occurring at the time of appearance and development of pelmatozoan echinoderms and analysis of its effect on the symmetry of the resulting morphotypes; and (3) investigation of the role of the interactions between the morphogenetic processes and environmental factors in the early evolution of the organization of the higher taxa of echinoderms.

This study is composed of three closely connected parts. The first part discusses the homologies of the major structures of the skeleton of crinoids and other pelmatozoans, because the homologies of many structures cannot be adequately analyzed without considering them outside the class Crinoidea and without referring to the entire phylum Echinodermata. The data obtained support the subphylum Pelmatozoa, as opposed to Edrioblastoidea and Edrioasteroidea. The second part discusses, based on the specific features of the morphogenesis of crinoids, symmetry and asymmetry in the entire phylum Echinodermata, including their origin, early evolution, and development. The third part considers the appearance of the higher taxa of echinoderms and the Ordovician evolutionary radiation, when most echinoderm classes emerged, including all of those that have survived.

This study is based on extensive material, primarily on a large collection of echinoderms from the Ordovician of the Baltic region, collected by myself and my colleagues in the course of special fieldwork. In addition, I used the collection of Ordovician echinoderms collected by R.F. Hecker and donated to him by other researchers. I made extensive use of the echinoderm collections from the Cambrian of Yakutia, the Ordovician of the United States, the Silurian and Devonian of Podolia, Baltic region, the Urals, and the Tian Shan. I also studied many collections in the museums of St. Petersburg, the United States, and Australia. A large part of the material studied was described and published. A smaller part of the material used in this study has never previously been published.

PART 1. COMPARATIVE MORPHOLOGY AND HOMOLOGY OF MAJOR SKELETAL STRUCTURES IN CRINOIDS AND SIMILAR EARLY PALEOZOIC ECHINODERMS

Of all pelmatozoan echinoderms, crinoids have the stablest body plan throughout their long history, but, at the same time, are very variable in morphological detail. They are very diverse taxonomically and have the largest geochronological range. These factors combine to make them the most important class of pelmatozoan echinoderms, with which all other classes have to be compared.

My concept of pelmatozoan echinoderms comprises those echinoderms that were previously recognized by Sprinkle (1973a) in the subphyla Blastozoa and Crinozoa. In their taxonomic composition, pelmatozoan echinoderms coincide with the subphylum Crinozoa in the sense of Ubaghs (1978). At present, the subphylum Pelmatozoa includes the following classes: Crinoidea, Eocrinoidea, Rhombifera, Diploporita, Paracrinoidea, Parablastoidea, Coronata, and Blastoidea. These taxa show quite a high diversity of skeletal structure. However, this study will be concerned only with ancient and primitive structures, connected with the early stages of the evolution of pelmatozoan echinoderms. Primarily, this study will focus on the establishment of the crinoid body plan, which first appeared in the Ordovician and has remained until the present day. Therefore, this study uses predominantly material on crinoids and eocrinoids and only to a small extent on other classes. The comparison shows that many crinoid structures were first formed in eocrinoids, while the crinoid body plan could have evolved from that of eocrinoids. To support this hypothesis, the following problems concerning the structure of all major skeletal elements occurring in crinoids are to be discussed:

(1) Homologies of the thecal plates in crinoids;

(2) The anal plates in pelmatozoan echinoderms; the position of the anus and its displacement;

(3) The morphogenesis of the stem in eocrinoids and crinoids, its origin, early evolution, and function. The stem in other echinoderms. Homology of the stem in different echinoderm groups, and its comparison with the tail in Chordata;

(4) The origin of arms in Crinoidea, and their possible evolution from brachioles.

Because of their strong morphogenetic interdependence, the above problems cannot be assessed separately. The establishment of homology of the thecal plates of crinoids depends on the homology of other structures (arms, stem, and anal series) in all stemmed echinoderms and should be based on the general plan of their morphogenesis and its possibilities for evolutionary change. This gives insight into the problem of the origin of crinoids and, thus, into the substantiation of their classification. Thus, the solution of one problem of the homology of thecal plates involves a broad range of interrelated problems, which are to be discussed below.

Therefore, the review of knowledge concerning the homology of the thecal plates in crinoids is followed by the study of homology and origin of most major structures in the skeleton of pelmatozoan echinoderms.

SECTION 1. HOMOLOGY OF CIRCLETS AND THECAL PLATES IN CRINOIDS AND SIMILAR PELMATOZOAN GROUPS

The theca in crinoids is the main receptacle for the internal organs. It is usually supported by a stem, elevating it above the sea floor, but it is itself a support for the food-gathering apparatus, i.e., arms (Fig. 1). The theca is usually clearly subdivided into the aboral part (cup) and the oral part (tegmen). Free arms, supported by so-called radials, extend at the boundary between these two parts. In the simplest case, a circlet of basal plates lies below the radials. In so-called dicyclic forms, an infrabasal circlet is located below the basal circlet (Fig. 2). In monocyclic forms, the infrabasal circlet is absent, while the stem extends directly from the basal circlet. The orals are the main plates of the tegmen, which occur between the ambulacra and form a circlet surrounding and covering the mouth. The plates of the underlying circlet usually alternate with the plates of the overlying circlet, like bricks in a wall, so that the middle of each plate occurs on the extension of the seam between the overlying and underlying plates. Usually, the so-called anal plates occur in the anal interray, in the radial circlet. These anal plates violate the pentaradiate symmetry and support the anal structures. The theca of crinoids can also contain other plates, which considerably increase its size. This is especially characteristic of the subclass Camerata, but also occurs in other crinoids. In most cases, the origin of these additional plates is clear; most often, they are brachial or interbrachial plates included in the theca. They are clearly secondary in relation to the primary dicyclic or monocyclic cup. Their origin and the way in which they are included in the theca are of limited interest, connected with features of one or another group of crinoids. Therefore, they will not be considered here. However, the cup of crinoids also contains other plates, of unknown origin and homology, which may reflect the origin of crinoids in general. For instance, these may be superradials of many disparids or the so-called lintel circlet of some of the earliest crinoids. These structures will be discussed in greater detail.

DIFFERENT CONCEPTS OF HOMOLOGY OF CIRCLETS

Until recently, almost all specialists on crinoids, beginning with Wachsmuth and Springer (1880, 1885, 1897), believed that the radial, basal, and infrabasal circlets are homologous in all crinoids (Moore and Laudon, 1943; Ubaghs, 1953, 1978; Moore, 1962; Arendt and Hecker, 1964; Yakovlev, 1964; Moore *et al.*, 1973). Based on Wachsmuth and Springer's rule (1885), reduction of some circlets was suggested for some crinoids (so-called pseudomonocyclic forms). However, Moore (1955) suggested that among camerate crinoids the radial and basal plates might not be homologous. However, the homology of radial, basal, and infrabasal plates in eocrinoids was widely accepted. These assumptions of homology were based on the ontogeny of modern crinoids. All modern crinoids are, at least at early ontogenetic stages of skeletal development, dicyclic, i.e., all of them have infrabasal and basal circlets. Slightly later in ontogeny, the radial circlet appears (Rasmussen, 1978a, 1978b). However, at the later stages, the infrabasal circlet can disappear; it is either reduced or fuses with the basal circlet. The crinoid cup, in this case, becomes pseudomonocyclic. Since of the three circlets of the cup, the infrabasal circlet is the one to disappear, a conclusion can be drawn that in all monocyclic crinoids the infrabasal circlet is absent. This assumption was supported by the fact that, in many fossil dicyclic crinoids (e.g., in Flexibilia), the infrabasal circlet was reduced to a very small size and could even be confined to the stem facet, i.e., it was completely hidden under the stem. It was, therefore, natural to assume that the infrabasal circlet was reduced in the first place and that this process gave rise to the monocyclic crinoids. Such assumptions were virtually universally accepted until recently, when new hypotheses emerged. As a result, widely accepted concepts of homology of the plates of the crinoid cup were considerably changed (Simms, 1993, 1994; Ausich, 1996, 1997). The present study proposes a new, considerably different, homology of the plates and circlets of the cup that is based on their evolutionary morphogenesis. However, before the new views on the homology of the thecal circlets are proposed, previous concepts are discussed. The traditional concepts are quite simple, and briefly outlined above. According to these concepts, the disappearance or appearance of the infrabasal circlet represented major processes in the evolutionary divergence of monocyclic and dicyclic groups of crinoids. This suggests that, in evolutionary morphogenesis, the infrabasal circlet was the least important, that it was the last to appear, and therefore was the first to disappear. Indeed, the functional role of the infrabasal circlet in the cup is not great, because it occupies only a small part of the entire area of the skeleton and is reduced in

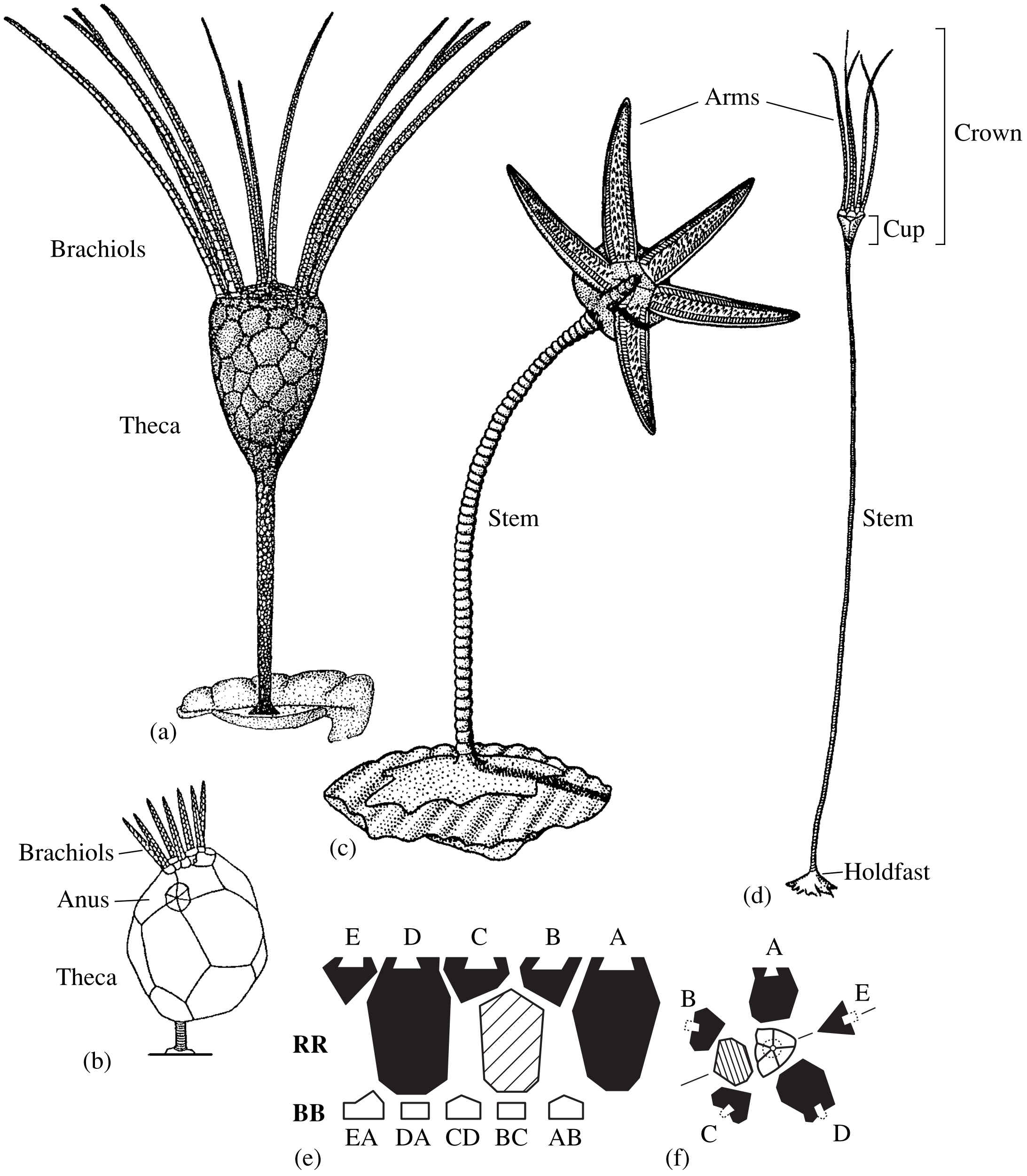


Fig. 1. Arrangement of major skeletal parts in crinoids and eocrinoids and two schemes showing the arrangement of plates in the cup. (a, b) eocrinoids: (a) *Gogia* from the Middle Cambrian of Utah, the United States; (b) reconstruction of *Cryptocrinites* sp. from the Middle Ordovician of the Leningrad Region; (c–f) crinoids (c) reconstruction of *Parapisocrinus* sp.; (d–f) reconstruction of *Pisocrinus* sp. and arrangement of plates in the cup of this genus: (e) lateral view; (f) bottom view. Modified figures are after: (a) Parsley, 1997, reconstruction Sumrall; (b) Rozhnov, 1994; (c–f) Rozhnov, 1981. The radials are black, the basals are white, the inferradial is hatched. The rays (A, B, C, D, E), interrays (AB, BC, CD, DE, EA), and corresponding structures here and below are designated according to Carpenter's system.

many taxa. According to Wachsmuth and Springer (1885), when the infrabasal circlet is completely reduced, the proportions of the angles of the axial canal in the stem, sutures between the pentameres of the stem, and some other structures of the stem and the proximal circlet of the cup are changed. The proportions of these structures were studied in great detail by Warn (1975) and Stukalina (1966, 1986), who suggested a convenient form of these proportions (Fig. 3). A complete reduction of the infrabasal circlet in primarily dicyclic forms is extremely rare and does not mean that it was absent during all of the ontogenetic stages. Therefore, although its morphological role in the cup is small, the role of the infrabasal circlet as a structure organizing the arrangement of other plates in the cup and its general architecture may be quite large. This is the probable reason for its presence in all dicyclic forms, at least at one of the ontogenetic stages. This fact has not received enough attention, although it may be very important for homologization of the thecal circlets. The basal circlet in monocyclic forms develops in exactly the same way. The latter will be discussed below, following a review of the recently published work of M. Simms and W. Ausich.

Simms (1993, 1994) proposed a new, more complex, interpretation of the homology of the thecal plates in the class Crinoidea, based on other principles. He indicated that the use of the terms "dicyclic" and "monocyclic" is outdated, because it suggests, without any further evidence, that the uppermost circlet is homologous in all crinoids. He disagreed with this assumption to suggest that the cups be called dicyclic or tricyclic, terms which do not carry any assumption of the homology of the circlets. He indicated that the traditional point of view, according to which the radial and basal circlets in tricyclic Cladida and diplobatrid Camerata are homologous (one to the upper, and the other to the lower, circlets of dicyclic disparids, hybocrinids, and monobatrid camerates), suggests a considerable difference in the position of the anal series of plates of the major crinoid taxa. This assumption casts doubts on the homology of the anal plates in the class Crinoidea. Ubaghs (1978) previously discussed and outlined these doubts. For instance, in cladids (tricyclic crinoids), the so-called anal X is in the "radial" circlet, while in many disparids (dicyclic forms), it lies above the upper circlet and is joined with one or two of its plates. Simms suggests, based on the principle of parsimony (the most economical path of evolution), that the anal series is homologous in all crinoids, whereas its differing position in relation to the circlets of the thecal plates depends on the presence or absence of one or another circlet in the theca. Therefore, if, for instance, in nature, the uppermost circlet of any crinoid is shown to be homologous to the basal circlet of another crinoid, which is possible in cases where the primary so-called radial circlet disappears, then, based on the position of the arms, all other homologization would be incorrect. However, this statement is not always accurate, because for such an incorrect homologization to be possible, the circlet lying beneath the disappeared radial circlet should have turned to 36°. Otherwise each arm would extend from two plates, rather than from one. For instance, in the genus *Tetragonocrinus* (Fig. 4) from the Lower Ordovician of the Leningrad Region, each of the three arms is supported by at least three plates of the cup, which, in this case, quite reasonably, are considered to be basal (Arendt, 1987; Rozhnov, 1988). The radial circlet in *Tetragonocrinus* was either reduced, or grew outside the cup, and morphologically represents the first brachials.

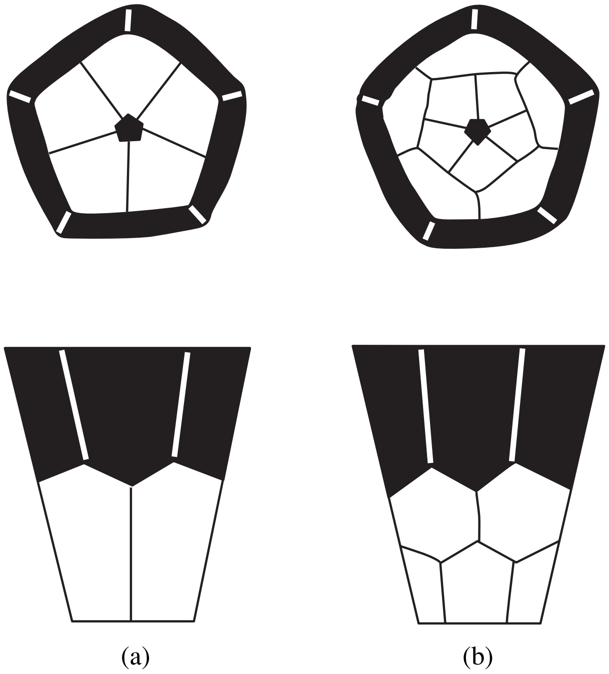


Fig. 2. Schemes showing the structure of (a) monocyclic and (b) dicyclic cups, and positions of the circlets according to Wachsmuth and Springer's rule. The radials (PR) and lumen (opening for the axial canal) are black, the basals (BB) and infrabasals (IBB) are white.

Simms suggests the use of a system of coordinates connected with the point of origin of the arms relative to the stem for the homologization of circlets. The orientation of stem pentameres, the angles of the axial canal, and some other characters should also be taken into account. To create a special system of coordinates and (using the principal of parsimony) to establish the homology of crinoid plates, it is necessary to extend the study beyond the limitations of the morphology of this class, suggest new hypotheses of its origin, and substantiate theories of the evolution of its morphogenesis. Only on this basis can one talk about the real homology of the plates. Using this approach, Ausich was able to make considerable progress.

Ausich (1996, 1997, 1998a) proposed a somewhat different theory of homology of the circlets in crinoids to that of Simms, based on the following assumptions: (1) The ancestral crinoids had a cup composed of four circlets, radial, basal, infrabasal, and proximal (which he called the lintel circlet). Among crinoids, the lintel circlet is best expressed in the Lower Ordovician *Aethocrinus moorei* Ubaghs, which, as he suggests, should be treated as a separate subclass Aethocrinea (Ausich, 1998a). (2) Like Simms, Ausich suggests that any circlet could be reduced in the phylogeny of crinoids. (3) In ontogeny, the relative orientation of plates in the circlets was determined at the time of the

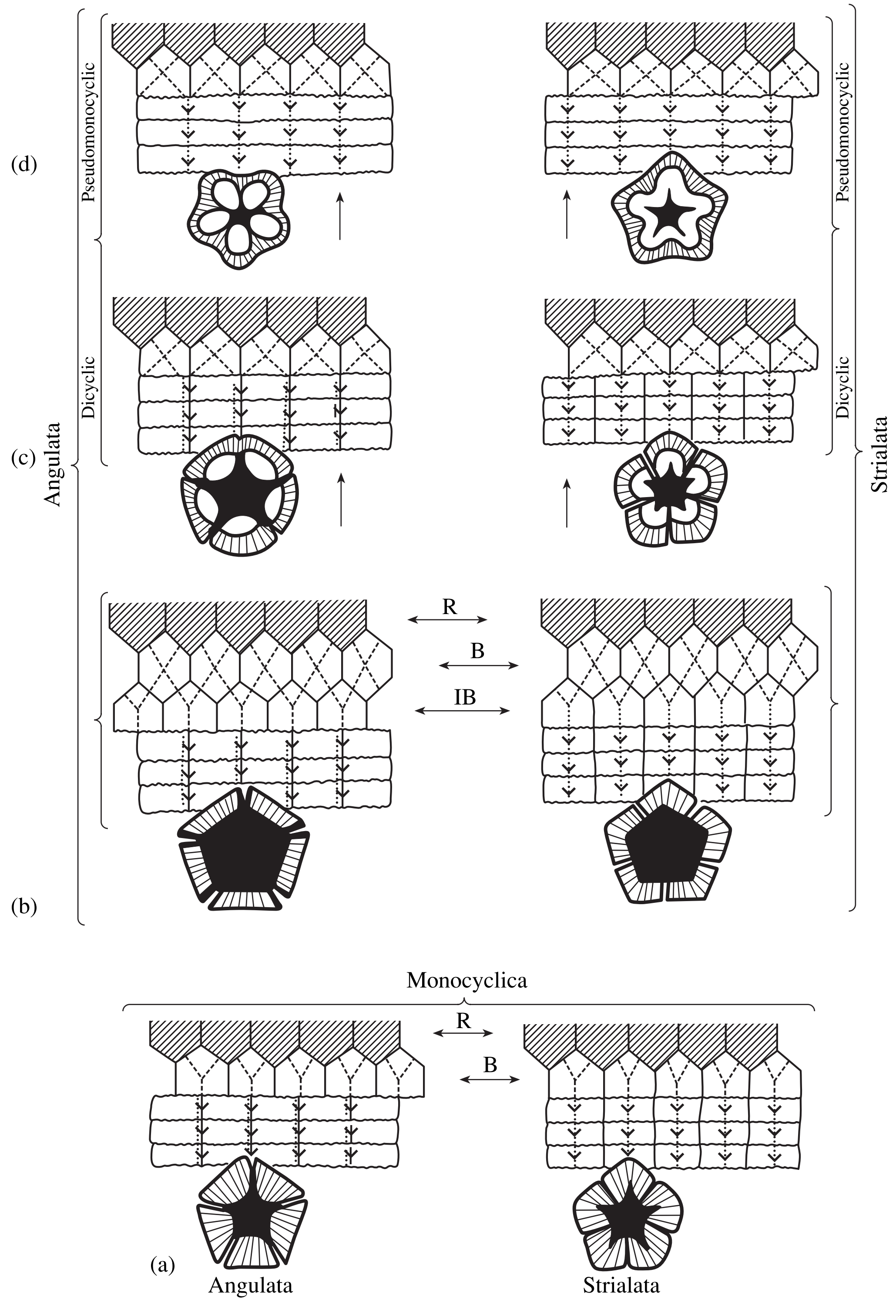


Fig. 3. Arrangement of the morphological elements of the angulate (left) and strialate (right) types of the stem and cup in (a) monocyclic, (b) dicyclic, and (c–d) pseudomonocyclic crinoids. Dashed lines show the positions of nervous cords after Bather's (1900) reconstruction. Cusps show the positions of the corners of the axial canal in the stem. Radials are shown by diagonal hatching, the axial canal of the stem is black, (R) radials, (B) basals, (IB) infrabasals (after Stukalina, 1986).

first development of the sutures between the plates of the cup; this time corresponds to the late cystoid and early pentacrinoid stage in the development of modern comatulids. Before the sutures in the cup are formed, the plates in the neighboring circlets are positioned to alternate at 36°, and after this the position of the pri-

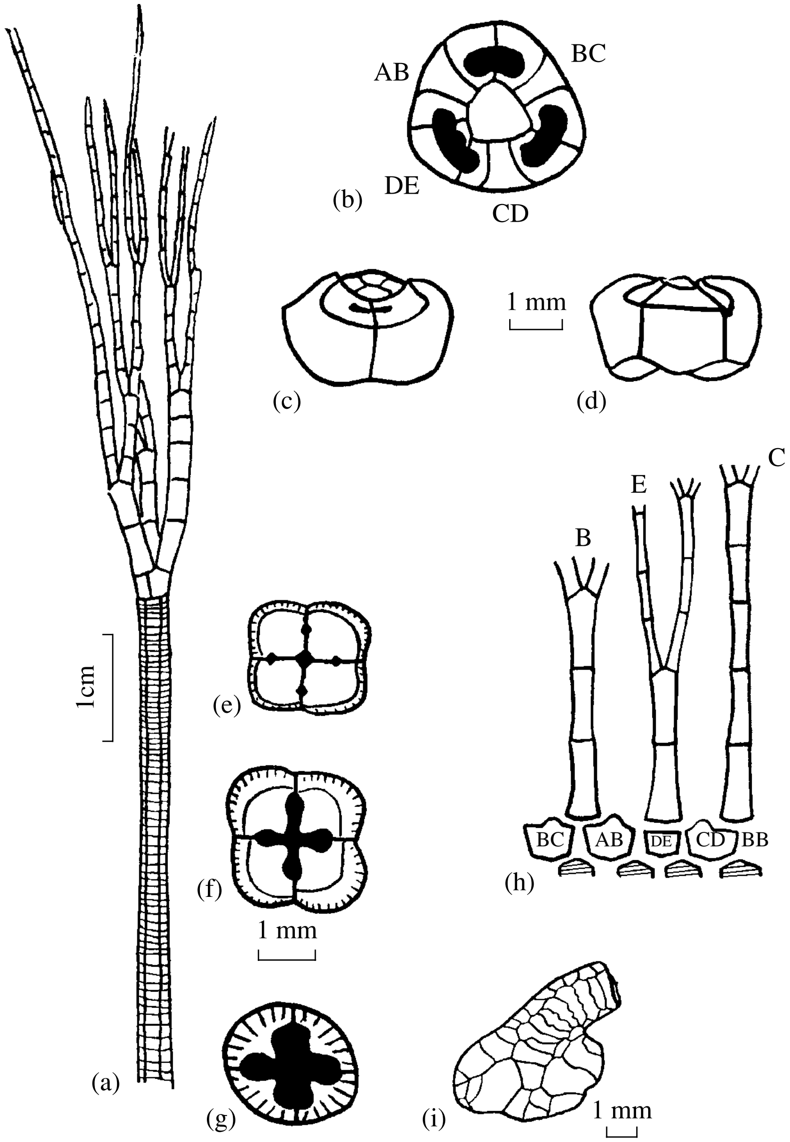


Fig. 4. Morphology of the genus *Tetragonocrinus* from the lower part of the Middle Ordovician (Upper Arenig, Volkhovian) of the Leningrad Region. The cup is composed of one circlet of basal plates. (a) General view of the crown with a fragment of the stem, (b, c, d) cup: (b) upper view, (c) lateral view, B ray, (d) lateral view, interray DE, (e, f, g) structure of columnals in different regions of the stem, (h) arrangement of the plates of the cup, arms, and stem. Articular facets and the axial canal are black; (i) holdfast (after Rozhnov, 1988).

mary plates is fixed. (4) The ratio of the angles between the axial canal of the stem and the position of the plates of the lowermost circlet of the cup is only defined by which plates were present at the base of the cup at the time of differentiation of the axial canal of the stem and chambered organ, while the entoneural system is expanding.

NEW HYPOTHESIS OF CIRCLET HOMOLOGY

A new approach to the problem of circlet homology is discussed below. At first, it seems impossible to establish the homology of plates within the class studied, because a system expanding beyond the limits of the taxon under study is needed to establish the homology of structures of this taxon. In this situation, the homology of plates should be based on supposed morphological transformations that occurred at the time of the origin of the class Crinoidea. In addition, it may be assumed that any circlet could have been reduced. Indeed, it was possible. However, in this case, the probability of the reduction of circlets would be different and would depend on the morphogenesis of the theca in general. For instance, according to Mennert's rule, structures that appear in ontogeny last usually disappear first. This, in turn, may depend on historical morphogenesis. Therefore, before any circlet homology is proposed, a model of the thecal morphogenesis should be introduced, both in evolutionary and ontogenetic

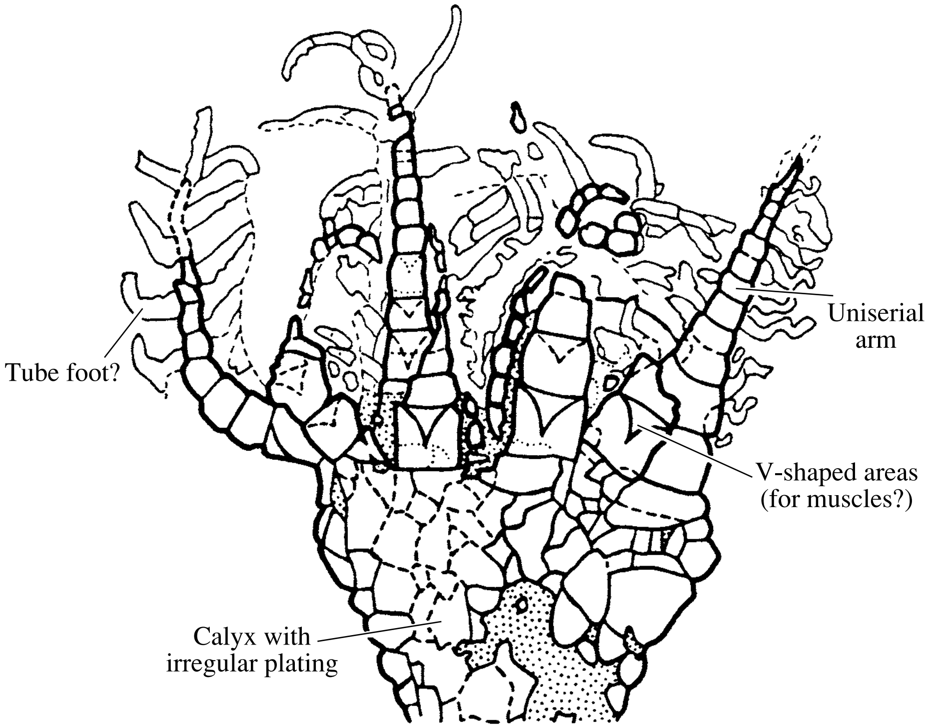


Fig. 5. Morphology of the genus *Echmatocrinus* (Middle Cambrian of Canada) (after Sprinkle, 1973).

perspectives. Such a model will be proposed and discussed below, based on several general assumptions and facts.

HISTORICAL MORPHOGENESIS OF THE THECA OF PELMATOZOAN ECHINODERMS

First of all, the possible ancestors of crinoids are to be discussed. All classes of Echinoderms, including crinoids, have a feature in common, i.e., their roots and ancestral classes are unknown, while the intermediate forms between the classes are absent in the fossil record (Rozhnov, 1995, 1996, 1997, 1998). Instead of crinoids, other stemmed echinoderms (eocrinoids) lived in the Cambrian. Eocrinoids are distinguished from crinoids primarily by their food-gathering appendages. In crinoids, these are intrathecal appendages (arms), while in eocrinoids these are extrathecal appendages (brachioles). At present, after the study of Sprinkle (1973a), an opinion that the arms and brachioles appeared independently is firmly established. Based on this, the classes of Echinodermata possessing brachioles are recognized as the subphylum Blastozoa, while crinoids (virtually the only class with arms) are recognized as the subphylum Crinozoa. It is believed that these two subphyla were separated at least in the Early Cambrian, i.e., when they acquired a skeleton. However, apart from the Middle Cambrian genus *Echmatocrinus* from the famous Burgess Shale, no certain representatives of Crinozoa are known from the Cambrian. The genus *Echmatocrinus* (Fig. 5) differs strikingly from typical crinoids. Hence, it cannot be considered to be ancestral to crinoids, and its systematic position among stemmed echinoderms is not clear. More so, its assignment to Echinodermata is doubtful (Conway Morris, 1993; Ausich and Babcock, 1996).

It is evident that the theca of crinoids, which is formed by a small number of plates that are compactly arranged in three or four circlets (including the oral circlet) and are well adjusted to each other, could not have evolved directly from any structure of soft-bodied animals. The theca certainly has a history of gradual development and early evolution. At the same time, the crinoid theca (and crinoids) appeared suddenly in the fossil record; the theca was still absent in the Late Cambrian, but was already present in the Early Ordovician. This may suggest that the theca of crinoids was produced by the reorganization of the theca of eocrinoids, which were widely distributed in the Cambrian. A sudden appearance of the crinoid theca suggests that it was produced by paedomorphic changes of the ancestral multiplated eocrinoid theca. Ausich (1997, 1999) suggested that it evolved from a tetracyclic cup similar to that of the rhombiferous cystoid *Scoliocystis* (Fig. 6), which he considered to be the most probable ancestor of crinoids. However, rhombiferous cystoids do not occur in the Cambrian and, more likely, represent specialized descendants of eocrinoids. There is no need to suggest that the immediate ancestors of crinoids had four circlets in their cup. Otherwise, the current problem would be transformed into a problem of the sudden

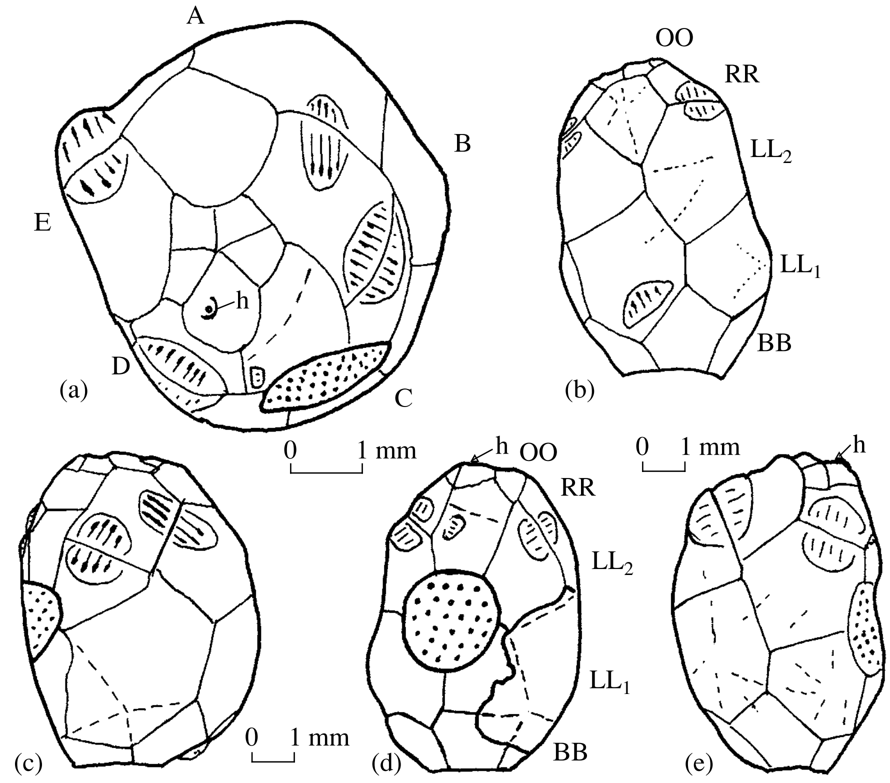


Fig. 6. Structure of the theca of holotype (PIN no. 2/1004) in *Scoliocystis thersites* Jaekel (Rhombifera): (a) upper view; (b) lateral view, ray A; (c) lateral view, ray C; (d) lateral view, interray CD; and (e) lateral view, ray E. (BB) basal circlet, (LL_1) lower lateral circlet, (LL_2) upper lateral circlet, (RR) radial circlet, (OO) oral circlet, and (h) hydropore.

appearance of a cup with four circlets in evolution. It is sufficient to suggest that eocrinoids with polycyclic cups were ancestors of crinoids. It is not necessary to suggest that the entire ancestral theca was arranged in clear circlets. Recently, Sprinkle and Guensburg (1997) suggested that crinoids and eocrinoids evolved synchronously from Edrioasteroidea. Brachioles evolved from the biserial covering plates of the ambulacra of Edrioasteroidea, while their arms evolved from the uniserial plates covering the bottom of the ambulacra, when the plates extended outside the ambulacral area. The possibility of such an extension, and even of the branching of the ambulacra, is supported by the structure of a new genus of Edrioasteroidea from the Middle Cambrian of Iran (Rozhnov and Guensburg, in prep.). However, there is no evidence that the aboral skeleton of the brachioles and arms evolved from the series of the ambulacral plates. If this hypothesis is accepted, too many questions emerge that have no answers. Even Sprinkle and Guensburg, who accept this concept, suggest that the typical biserial or tricyclic crinoid theca evolved from the polycyclic theca by paedomorphosis at the beginning of the Ordovician. This opinion they based on a large crinoid (not yet described) from the Lower Ordovician of North America, which is one of the earliest of the true crinoids. It has well developed arms, but has a theca composed of many plates, which are not yet arranged in circlets. Certainly, this crinoid may be ancestral to all or many groups of post-Cambrian crinoids. However, this requires more evidence and demands that the probable phylogeny of each crinoid subclass be considered. Generally, this find only indicates possible combinations of typically crinoid characters (well developed arms) and eocrinoid characters (theca composed of many plates poorly arranged in circlets). To study the problem of the origin of the monocyclic and dicyclic crinoid theca, the ontogenetic development of the multiplated theca is more important. This is discussed in greater detail below, under an assumption that the crinoid theca could have evolved from a multiplated theca of the eocrinoid type. Because the structure of such a theca and its development are closely connected with the appearance of the skeleton in Echinodermata in general (including its appearance in evolution), this problem must also be discussed.

The first eocrinoids had a theca composed of poorly arranged plates. The theca gradually transited into the peduncle (holdfast in the sense of Sprinkle, 1973a) without a distinct margin. In two genera, *Lepidocystis* and *Kinzercystis*, from the Lower Cambrian of North America (Pennsylvania), the aboral part of the theca and the peduncle are built of imbricating plates (Sprinkle, 1973a). This can indicate their possible origin from the Edrioasteroidea or, more precisely, the combination

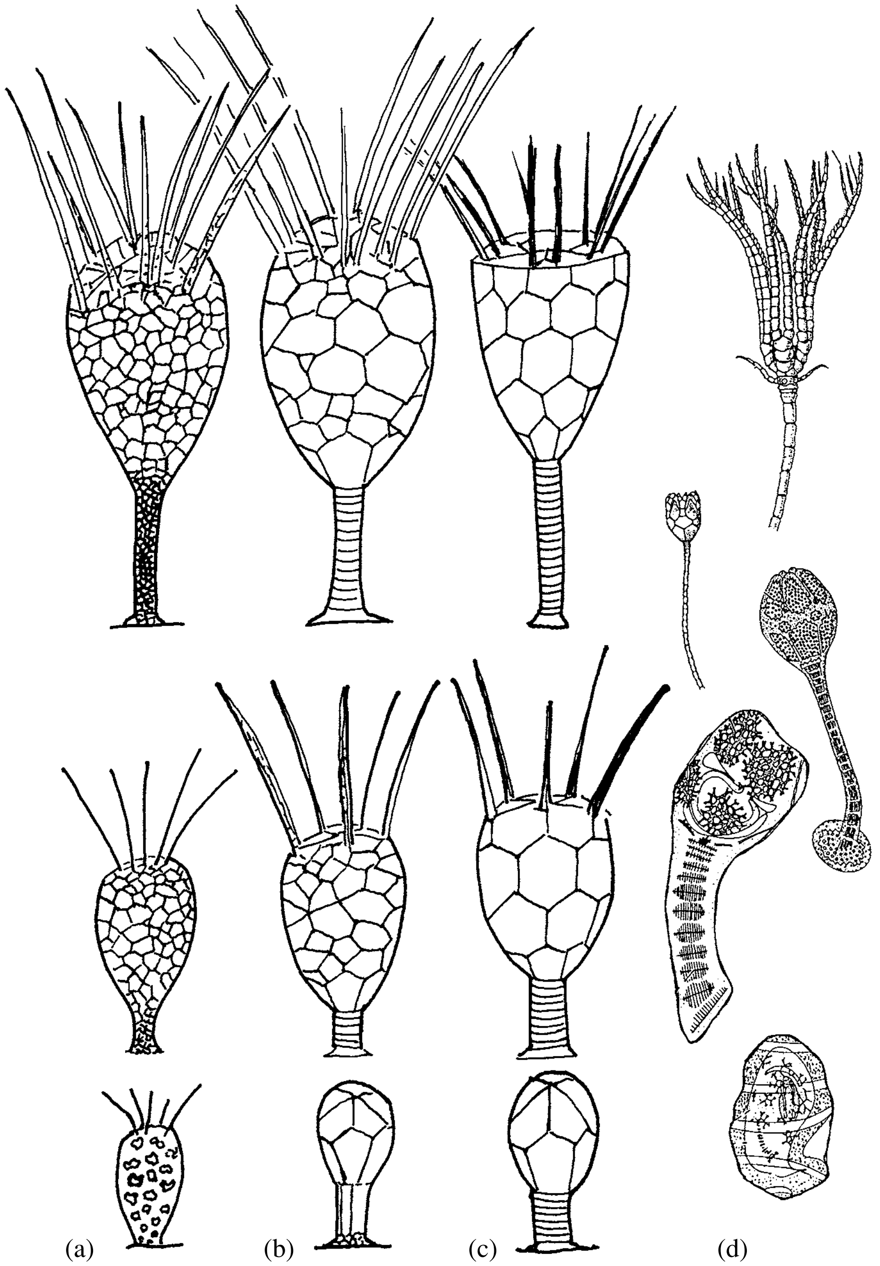


Fig. 7. (a–c) Supposed evolution of ontogeny of the eocrinoid skeleton and (d) development of the skeleton in extant crinoids.

of eocrinoid and edrioasteroid characters at time when they evolved from a common ancestral group. In the majority of other genera, the theca is tessellate, i.e., it is composed of plates contacting each other. Representatives of the genus *Gogia* (Fig. 1a) could be an example of such structure. The majority of plates, especially in the middle part of the theca, in many crinoids are arranged irregularly, without distinct arrangement into circlets. However, already in the earliest eocrinoids, pentaradiate symmetry is seen in the arrangement of food-gathering grooves extending from the mouth. Their symmetrical arrangement apparently determined the five-rayed arrangement of the mouth plates surrounding the ambulacra in places where they extend from the mouth. I suggest that these plates are homologous to the orals of the later eocrinoids and crinoids. The pentaradiate arrangement of the orals is the first display of pentamery in the skeleton of the eocrinoid theca. Other plates appeared in various places in the growing theca and poorly-separated peduncle without any distinct pattern (Fig. 7). It is probable that the ontogeny of the skeleton of such eocrinoids was relatively simple. At the later stages of ontogeny when the soft body already became sac-shaped and possessed a peduncle, incipient thecal plates began to appear more or less synchronously in different places. They rapidly

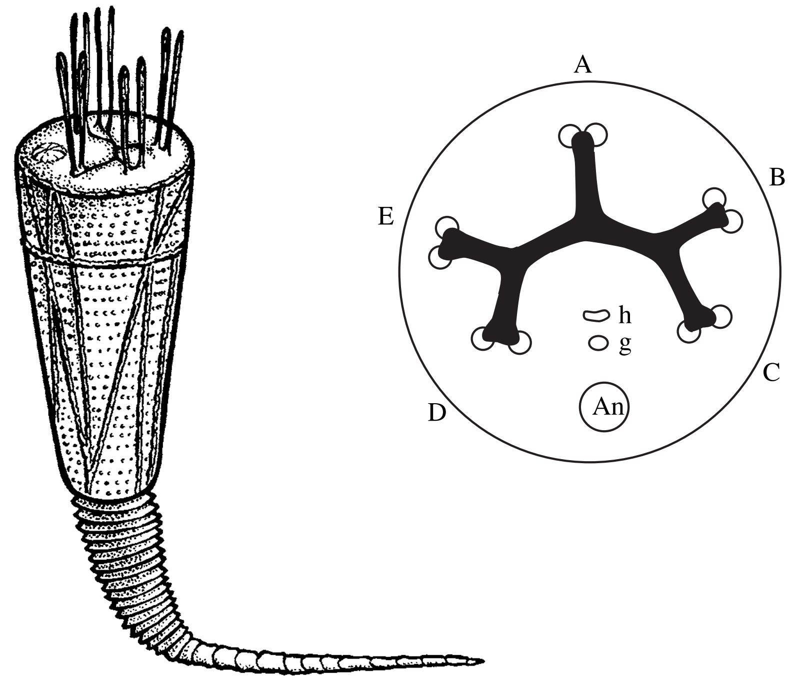


Fig. 8. Reconstruction of the eocrinoid *Ridersia* (left) and location of ambulacra, hydropore (h), gonopore (g), and anus (An) on the oral surface (right) (Middle Cambrian of Australia).

enlarged and soon became fused to form a skeletal capsule, i.e., a theca with a peduncle. All plates were arranged asymmetrically and irregularly. Only the plates surrounding the mouth showed an organizing effect produced by the ambulacra. These plates were arranged according to the 2–1–2 model. The 2–1–2 model of the arrangement of the ambulacra means that each pair of ambulacra (B and C, D and E) appeared by the branching of the single ambulacrum, whereas the ambulacrum A, occurring opposite to the hydropore, was unpaired and atomous. In the opinion of the majority of researchers, such a structure indicated the emergence of pentaradiate symmetry from the initial triradiate symmetry. This is discussed in detail in the chapter on symmetry.

After the appearance of the true stem, followed by the separation of the theca, a circlet composed of five, four, or three plates appeared at its base (Fig. 7b). In eocrinoids, this circlet is usually referred to as basal. Its possible homology to the circlets of crinoids will be discussed below. Numerous irregularly arranged plates are located between the oral and basal circlets, which appeared phylogenetically later. In my opinion, this separation of the symmetrical oral and basal circlets by the zone of irregularly arranged plates is a direct indication of the ontogenetic sequence in the development of the thecal skeleton.

Compared to the ancestral theca, the development of the skeleton was displaced to the earlier ontogenetic stages, while the number of plates appearing more or less simultaneously at the beginning of the formation of the skeleton, decreased. In general, such a development of the skeleton has been retained by modern crinoids. Evidently, the pentamerous arrangement of the orals should have determined the symmetrical arrangement of the basals, which appear simultaneously with the orals or immediately after. At first, they could have been arranged irregularly, but later they were arranged in pentaradiate circlets, while the number of circlets in adults could be quite large (reaching seven or eight).

When the majority of circlets were reduced in phylogeny, a type of theca similar to that of crinoids could have been formed. However, the theca of crinoids has another feature; it is distinctly subdivided into oral and aboral parts. Similar subdivision, although less sharp, also occurs in some eocrinoids. Initially, this subdivision could have been determined by ecology. When eocrinoids mainly used the gravitational flow of food particles, all ambulacra were confined to the upper part of the theca, above the ambitus (the widest part of the theca). In a globe-shaped theca, there is no sharp shoulder between its sides, while the border between the oral and aboral parts of the theca lacking ambulacra is not very distinct. In a conical theca, which gave an opportunity for a higher elevation of the food-gathering apparatus above the bottom, and with a flattened upper part of the theca, the border between the dorsal and ventral parts became very distinct in some crinoids, for instance, in the Cambrian *Ridersia* from Australia (Jell *et al.*, 1985) (Fig. 8).

The above facts suggest a model for the development of the crinoid theca (Fig. 9). The juvenile theca in the ancestral eocrinoids was more or less conical, and was subdivided into oral and aboral zones. The oral zone at this ontogenetic stage was formed by the oral circlet only, while the aboral part was formed by two or

Table 1. New terminology of circlets based on their homology and its approximate correspondence to traditional terminology

Terminology of circlets based on homology	Traditional terminology of circlets	
polycyclic theca	monocyclic theca	dicyclic theca
Brachial		
Upper lateral		Radial
Lower lateral	Radial	Basal
Basal	Basal	Infrabasal
Lintel		

three circlets of plates, the lowest of which was basal. Plates in the neighboring circlets were arranged interradially, since they were initially formed as plates which surrounded the proximal parts of the ambulacra extending from the mouth. The plates of the circlet surrounding the oral plates were arranged radially. If the first brachioles appeared at this stage, they should have appeared first at the border between the oral and aboral parts of the theca and should have been supported by these radially arranged plates. Assuming that such a juvenile crinoid will retain its structure in the adult stages as a result of paedomorphosis, the resulting theca may be considered to be part of a typical crinoid body plan. The ambulacrum approaching the brachiole discontinues its branching and changes its growth direction. The brachiole is transformed into an arm. The derivation of the arms from the brachiole-possessing ambulacra will be discussed in detail in another section. Below, a possible pattern of such a scenario for the appearance of the crinoid theca and the implications for its homologies are discussed.

In contrast to Ausich, I suggest that the cup ancestral to the crinoid cup could have had more than four circlets. This can be assumed based on the fact that the thecal plates of the earliest pelmatozoan echinoderms began organizing in circlets when they were involved in the pentaradiate symmetry, which at first embraced only the ambulacral and food-gathering systems. The optimal shape for each of the plates regularly covering a theca is a regular hexagon. In such a plate the width equals the height. Therefore, when the pentaradiate symmetry was spread over the entire theca, the number of circlets present in the globe shaped theca and arranged in parallel to the so-called equator should have been equal to the number of meridionally orientated rows of plates, i.e., to the number of rays (five). Because the anal interray is usually additionally widened, while the theca itself is extended in height, the number of circlets in the theca can exceed five. This is, for instance, observed in cryptocrinid eocrinoids. However, for the crinoid type of the plate arrangement to occur, not only the number of circlets is important, but more so, the sequence of the appearance of circlets in the ontogeny of the initial theca.

As mentioned above, Ausich (1996, 1997) suggested that the monocyclic and dicyclic cups evolved from the initial tetracyclic cup as a result of reduction of one or two circlets. He emphasized that any of the circlets could have become reduced. Indeed, theoretically, any circlet could disappear, but the probability of this disappearance is different in each case. According to Mennert's rule, the structures that disappear first are more likely to be those that appeared last in the ontogeny. Therefore, the probability of different homologies of circlets in monocyclic and dicyclic crinoids is different. The data on the ontogeny of Paleozoic and modern crinoids clearly show that the basal (or infrabasal) and oral circlets appear first in ontogeny, while the radial circlet is the last to appear. As was shown above, the structure of some eocrinoids with well-developed basal and oral circlets and plates irregularly spaced between them suggests that the basal and oral circlets (i.e., proximal and distal circlets) do appear first in ontogeny. Therefore, these two circlets should usually be reduced last. The next circlet in crinoids appears between the oral plates and the basal circlet. This is indicated by the fact that the zone of the appearance of new plates is situated in this particular place. This is also seen in the structure of many eocrinoids (in the corners between the large plates, there are smaller plates that appear later). If the reduction produced by paedomorphosis reached the most proximal circlet, a monocyclic cup is produced. In this cup, the circlet that appeared third later became radial because it supported the developing arms.

The place of emergence of the fourth circlet in the eocrinoid ontogeny is not particularly evident, because of insufficient data. It could equally have appeared immediately above the basal circlet or below the oral circlet. Depending on this, in dicyclic crinoids, it could become either basal or radial. This is why it is homologous to either of the circlets in the monocyclic cups. Its homologies are still unclear, if one considers exclusively the morphology of eocrinoids, a group as yet insufficiently studied in this respect. However, judging from the skeletal ontogeny of the dicyclic crinoids (primarily Paleozoic), the place of its emergence seems more certain. It appeared immediately above the initial basal circlet, which in dicyclic crinoids is commonly referred to as infrabasal.

Based on the above data on the morphogenesis of the Early Paleozoic pelmatozoan echinoderms, the term *primary theca* is introduced here to designate the theca appearing at the time of differentiation of the stem, but before the appearance of the arms. In crinoids with a limited number of plates in the cup inherited from the primary theca, the theca could grow by inclusion of the proximal pentameres of both the stem and brachials. The latter process was far more common.

TERMINOLOGY OF CIRCLETS

To avoid any terminological confusion before further discussion, the terminology of the circlets should be clarified. Traditional designations of circlets, as

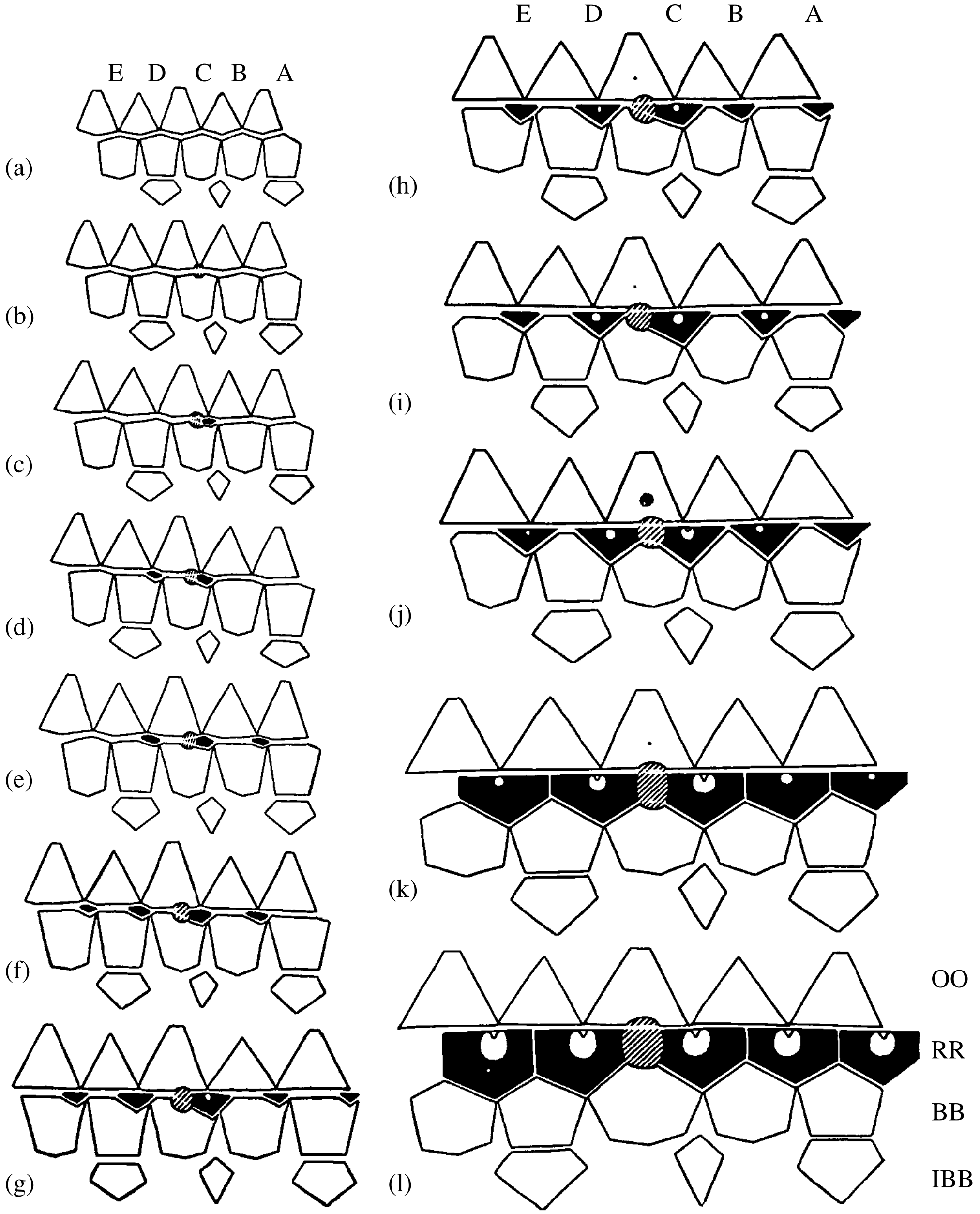


Fig. 9. Ontogeny of the skeleton of the theca (a–l) in the Permian cladid crinoid *Cranocrinus praestans* Arendt (after Arendt, 1970). Radials (except articular facets) are black. The hydropore is shown by a dot. Periproct is shown by diagonal hatching. (OO) orals, (RR) radials, (BB) basals, and (IBB) infrabasals.

shown above, do not always indicate actual homology. For instance, the basal circlet of monocyclic forms, in my opinion, is homologous to the infrabasal circlet, rather than to the basal circlet of the dicyclic forms. Therefore, based on homology, new designations for the circlets should have been introduced, as by Simms and Ausich. However, this would have caused greater confusion, because the old terminology is well established and needs to be referred to. Therefore, I will continue using the traditional terminology but purely in a morphological, descriptive way and will indicate, wherever necessary, which group is being discussed. At the same time, a new terminology, universal for pelmatozoan echinoderms, will be introduced. This new terminology is based on the homology of circlets and indicates their actual or supposed order of appearance in ontogeny (Table 1).

The proximal circlet in the crinoid cup, traditionally referred to as basal in monocyclic forms and as infrabasal in dicyclic forms, will be referred to here as basal in both cases. The circlet located between the proximal circlet, referred to as basal here, and the distal circlet will be designated lateral in dicyclic forms. The cup may include several lateral circlets, e.g., in some

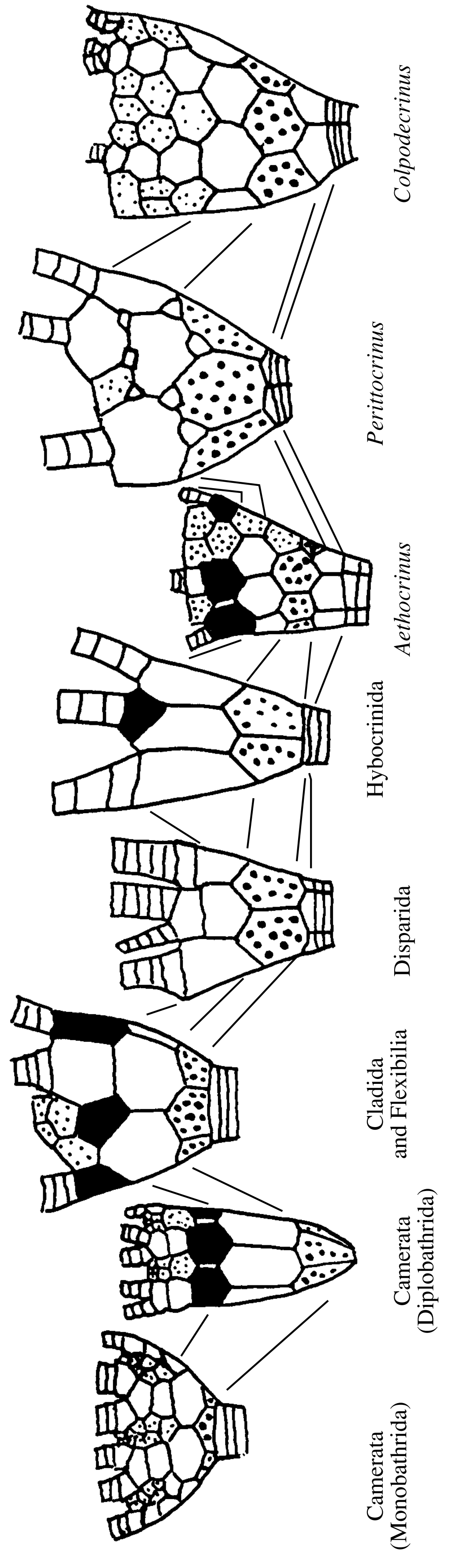


Fig. 10. Homologies of the circlets in crinoid cups. Radials of dicyclic forms are black; homologs of the distal circlet of the so-called primary cup (basals and infrabasals of dicyclic cups) are dotted, anals and interbrachials are filled with small dots, other plates are white; (Lint) lintel circlet (or proximal columnal of the stem subdivided into pentameres), (sR) superradial of disparids.

Rhombifera and Diploporita. The lowermost, in this case, will be called the first circlet; the one above, the second; and so on. The term *radial circlet*, in the framework of this terminology, based on the circlet homology of pelmatozoan echinoderms, is totally rejected. Ausich proposed the name *lintel circlet* for the rarely occurring fourth circlet, which lies below the basal circlet in the cup of some crinoids. This name is retained here, although, as will be shown below, the lintel circlet is not a genuine cup circlet and, more likely, represents a proximal columnal. In addition, brachials can also be parts of the cup that forms circlets. Such circlets will be referred to as brachial circlets. However, as mentioned above, this terminology is necessary only for discussions of homology and for comparisons of higher taxonomic groups. Therefore, it will be used only in specific cases. In all other cases, a traditional terminology of circlets will be used.

The basal circlet in dicyclic forms appears in crinoid ontogeny between the infrabasal and radial circlets and develops earlier than the radial circlet. This is clearly observed in the structure of many crinoids, e.g., in *Cranocrinus* and other hypocrinid crinoids (Fig. 9), the ontogeny of which was studied in detail by Arendt (1970). From this a conclusion can be drawn that, in the polycyclic ancestors of crinoids, it appeared directly above the infrabasal circlet (which was the most proximal).

HOMOLOGIES OF CIRCLETS

Homologies of the Infrabasal, Basal, and Radial Circlets

The following homology of circlets in the crinoid cup can be drawn from the above discussion of the thecal morphology of pelmatozoan echinoderms (crinoids in particular) (Fig. 10, Tables 2, 3). The proximal circlet is homologous in all crinoids; i.e., in traditional terminology the so-called infrabasal circlet of dicyclic crinoids is homologous to the basal circlet of monocyclic crinoids. In contrast to the traditional interpretation, the radials are not homologous in dicyclic and monocyclic crinoids. The radials in monocyclic forms are homologous to the so-called basal circlet of the dicyclic forms (lateral circlet in terminology based on homology). The homologies of the radial circlet of dicyclic crinoids are absent in monocyclic crinoids. The only exception is some hybocrinids (discussed below).

Before the table of homologies in crinoids is introduced, the homologies of the so-called lintel circlet (terminology of Ausich) and superradials, present in some crinoids, should be discussed.

Homologies of the Lintel Circlet

According to Ausich, the lintel circlet is the proximal circlet of the cup of the probable ancestor of crinoids, which, in his opinion, had four circlets. Among known fossils, the lintel circlet is best repre-

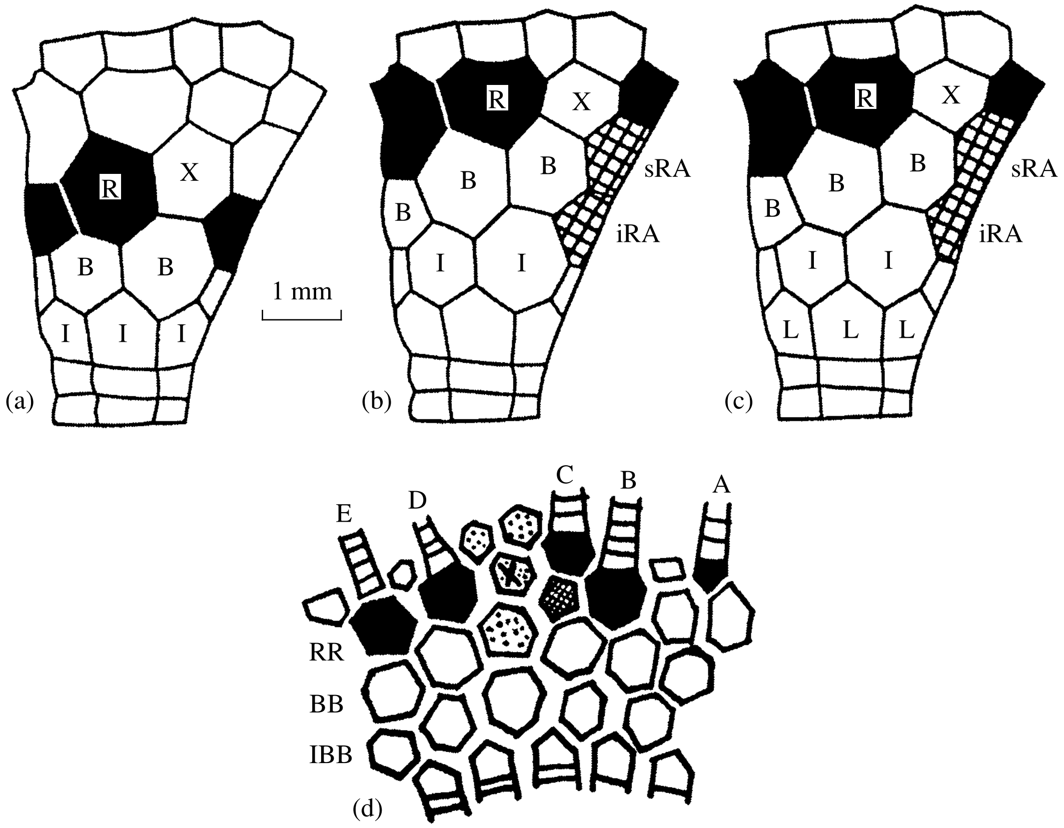


Fig. 11. Homology of the plates of the genus *Aethocrinus* after different authors: (a) Ubaghs, 1969; (b) Philip and Strimple, 1971; (c) Ausich, 1996; (d) Rozhnov, 1988. (L) plates of the lintel circlet, (I) plates of the infrabasal circlet (IBB), (B) plates of the basal circlet (BB), (R) plates of the radial circlet (RR), (X) anal plate, (sRA) superradial, (iRA) inferradial; radials are black, anals are dotted, radianals are covered by double hatching.

sented in the Lower Ordovician genus *Aethocrinus*. The structure of the cup of this genus is interpreted differently by different researchers (Fig. 11). The debate is mostly concerned with the position of the border between the cup and the stem, and between the cup and the arms. Ubaghs (1969), who was the first to describe this genus, believed that the border between the stem and the cup lies between the proximal (not tapered) columnal and the base of the first tapered plates, which he considered to be infrabasal. Correspondingly, the first brachials in the cup were interradial. This interpretation appeared doubtful. Therefore, another interpretation was proposed later. The infrabasal circlet of Ubaghs was excluded from the cup and considered to belong to the stem (Philip and Strimple, 1971; Rozhnov, 1988; etc.). In this case, the cup was typically dicyclic. Ausich (1996, 1997, 1998a, 1998b, 1999) proposed that the cup of *Aethocrinus* be considered tetracyclic, and designated the proximal circlet as the lintel. In all other respects, he interpreted the structure of the cup above the lintel circlet in a similar way to Philip and Strimple. Therefore, judging from the above concept of the origin of the crinoid theca, it is necessary to indicate the homologies of the lintel circlet. Should it be really considered to be the circlet of the cup or the proximal columnal?

Judging from the size of the plates and their shape, the lintel circlet certainly belongs to the theca. However, judging from the coincidence of the borders between the plates and those between the pentameres of the stem, it can be considered to belong to the stem. However, this is likely to be an approach characteristic of functional morphology; thus, it does not indicate any homologies. Indeed, this genus, like some other crinoids, primarily disparids, does not have a sharp border between the cavity of the cup and the axial canal of the stem; i.e., the cavity of the theca gradually transits into the cavity of the axial canal (Fig. 12a). In the majority of crinoids this transition is sharp; i.e., the axial canal begins on the flattened bottom of the cavity of the cup by a clearly outlined opening (Fig. 12b). Modern crinoids have a five-chambered organ located near this opening of the canal and strands extending from this organ into the axial canal. The proximal border of the cup could have been determined from the position of the five-chambered organ, but it is not possible in fossils similar to *Aethocrinus*. Therefore, to understand the origin of the lintel circlet, the junction of the stem with the cup in *Aethocrinus* should be com-

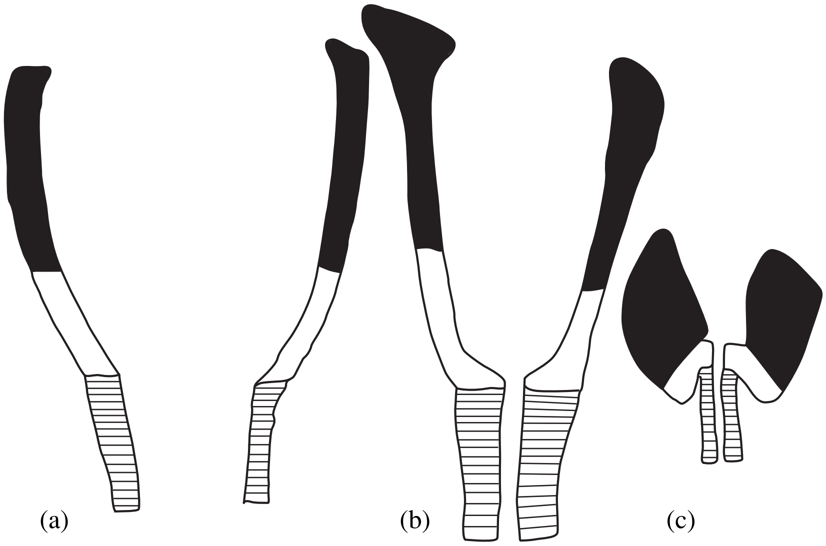


Fig. 12. Relationships between the thecal and stem cavities in some crinoids: (a) the cavity of the theca gradually merges into the cavity of the stem (*Grammocrinus* Eichwald); (b) the cavity of the cup is distinctly delineated from the cavity of the stem (*Pisocrinus* De Koninck); (c) the cavity of the theca is distinctly delineated from the cavity of the stem, the proximal part of which is embraced by the radials (*Parapisocrinus* Mu).

pared to that in other crinoids (those in which the thecal cavity gradually merges into the axial canal of the stem and also those with a sharp border between these two skeletal cavities).

From the functional point of view, the junction between the theca and the stem should be strong. In most crinoids, a special stem facet occurs at the base of the cup, to which the proximal columnal is attached by its wide attachment surface. Sometimes, to achieve even more strength, the stem facet is deepened, and the proximal columnal is embraced by the wall at the base of the cup (Fig. 12c) (e.g., in the genus *Parapisocrinus*) (Rozhnov, 1981). In taxa with a wide axial canal and thin stem and cup walls, the increased strength of the junction between the stem and the theca may be achieved only because of the angularity of the border. This is facilitated by the alternating sutures between the plates at the base of the cup and the sutures between the pentameres of the stem. Therefore, the proximal ends of the pentameres of the proximal columnal are tapered and enter along the sutures between the plates of the base of the cup. Such a structure is observed in many primitive disparids, e.g., in the genus *Virucrinus* from the Middle Ordovician of Estonia (Rozhnov, 1990a). The proximal columnal of the stem with tapered pentameres is interpreted by all researchers as a columnal rather than a circlet of the cup (Fig. 13). This is indicated by its initial structure and size, which are similar to those of other columnals, and also by the variable tapering. It seems probable that the proximal columnal is homologous to the lintel circlet of *Aethocrinus*, from which it is morphologically distinguished only by its smaller height. Therefore, although morphologically and functionally the lintel circlet belongs to the cup, morphogenetically, it is a proximal columnal composed of five parts. Indeed, the proxistele with a wide axial canal, which gradually merges into the cavity of the cup, could contain some organs that in other crinoids occurred entirely within the cavity of the cup. For instance, in early crinoids, such organs may have included the gonad. The lintel circlet, from this point of view, represented a proxistele. A gradual transition of the cavity of the cup to the cavity of the stem indicates one of two primary morphogenetic mechanisms enabling the appearance of the stem in the ancestral eocrinoids; the transformation of the primary peduncle (holdfast), which is discussed in detail in the section on the origin of the stem.

Homologies of the Superradial Plates in Disparids

Another important problem concerning the homology of the circlets in the theca is related to the so-called superradials present in Disparida, some Cladida, and Flexibilia. Their origin is a very important problem for understanding the homologies of the circlets. The superradials occur as continuations of the inferradials in one or several interrays. Their number and position are important diagnostic characteristics of disparids (Ubaghs, 1953; Moore, 1952). Usually, the superradials were considered to be parts of the radial circlet, but their origin remained uncertain. Theoretically, they may represent either the remains of an ancestral circlet, or brachials included in the cup. The study of Sevastopulo and Lane (1988) on the ontogeny and phylogeny of disparid inadunates, in which, for the first time, the ontogeny of *Homocrinus* is described, is very important for understanding the appearance of the superradials (Fig. 14). Based on these data, Ausich (1997) suggested

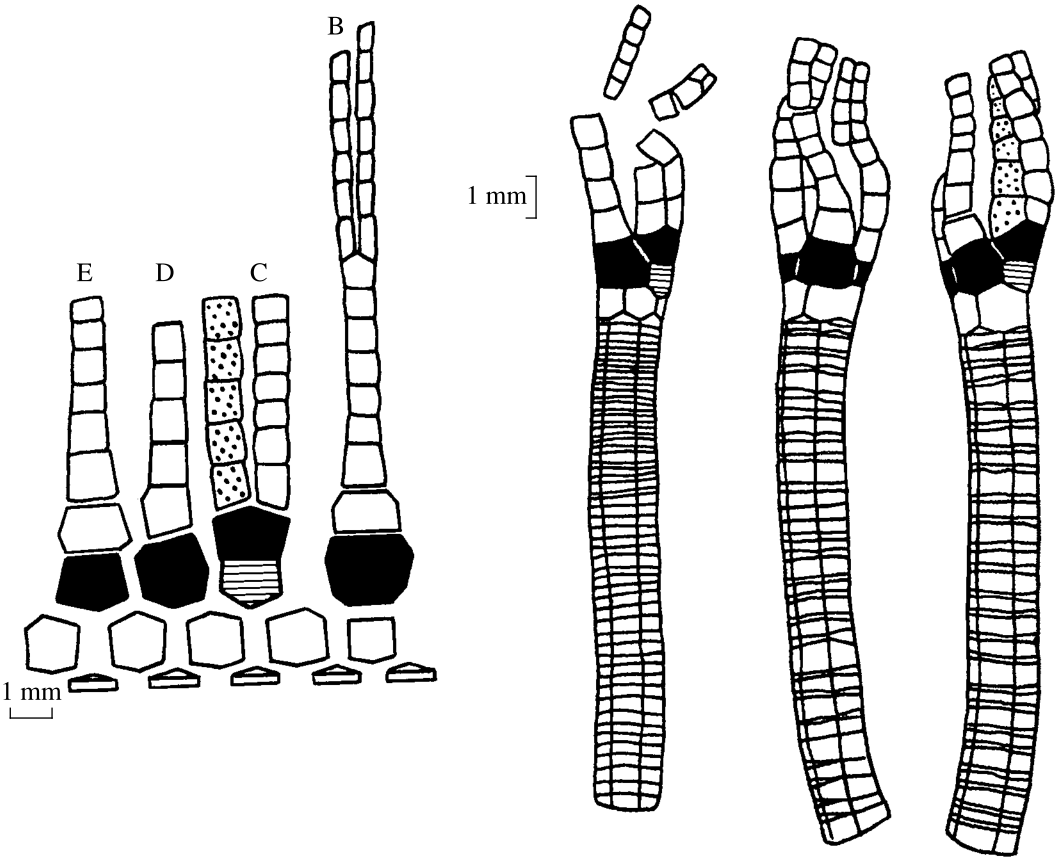


Fig. 13. Morphology of the genus *Virucrinus* (disparid crinoid) from the Middle Ordovician (Keila Horizon of Estonia). The proximal circlet of the stem is composed of pentameres. The tapering proximal ends of the proximal circlet alternate with the basals of the cup. Because the border between the cavity of the cup and the axial plate of the stem is indistinct, this proximal circlet can also be considered to be the lintel circlet incorporated into the cup (after Rozhnov, 1990). Radials are black, the lower radial is horizontally hatched, the plates of the anal tube are dotted.

an unusual homology of the thecal plates in disparids with compound radials and substantiated it as follows.

At the earliest known ontogenetic stages, the cup of representatives of the genus *Homocrinus*, according to Ausich's interpretation, has three circlets of plates. A circlet composed of five so-called radials of different size in the radial position occurred between the five plates of the so-called basal circlet and the five plates of the oral circlet. Three radial plates were large and directly contacted the oral circlet. Two other plates of this circlet were small and did not contact the oral plates. If the structure of the juveniles is compared to that of the adults, the large radials correspond to large unpaired radials (A and D), while the small radials correspond to the inferradials of the paired radials (B, C, and E). At the later ontogenetic stages, one more (although interrupted) circlet appears in the cup. These are so-called superradials B, C, and E. According to Ausich, these three superradials compose a separate circlet, because, in ontogeny, they appear after the two circlets lying below. Ausich considered this uppermost circlet to be homologous to the true radial circlet of other crinoids, because it is the uppermost in the cup and is positioned radially. Also, its plates lie at the base of the arms and, in ontogeny, appear in the A–E–B sequence, which is typical of radials. The middle circlet combining the inferradials B, C, and E, and the simple A and D radials, he considered to be homologous to the so-called infrabasal circlet of other crinoids, since they lie lower than the radials and are positioned radially. Ausich suggested that the circlet of the cup of disparid inadunates, corresponding to the so-called basal circlet of dicyclic cladid inadunates, was reduced, whereas the lowermost circlet of disparids (basal in traditional terminology) is homologous to the lintel circlet, well-developed in *Aethocrinus*. Thus, in this interpretation of the homology, the arms were attached to the three plates of the radial circlet and two plates of the so-called infrabasal circlet.

This is a logical and innovative interpretation of the homologies, although somewhat contradictory. For instance, it is well known that in ontogeny the plates can migrate from rays into interrays and vice versa (Arendt, 1970). However, the hypothesis that the superradial plates compose a separate, although incomplete, circlet homologous to one of the complete circlets of

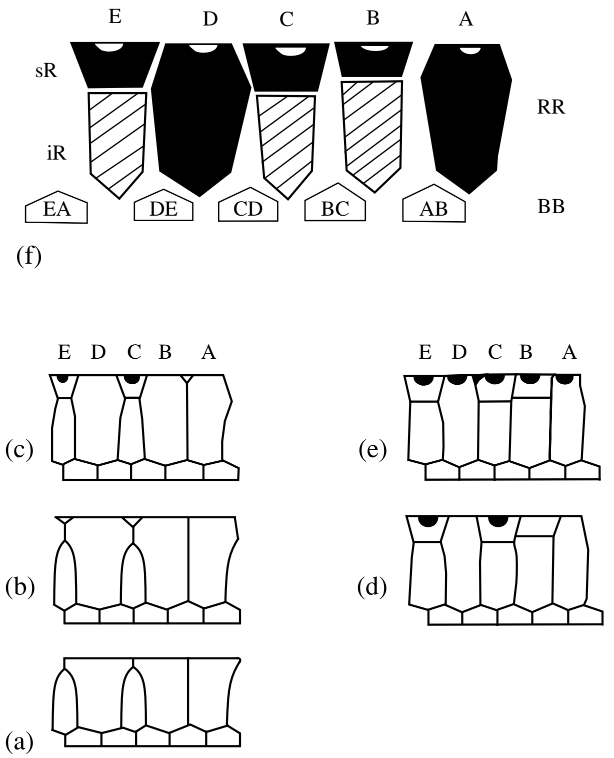


Fig. 14. Genus *Homocrinus*: (f) composition and relationships between the plates in the cup of the adult (a–e) ontogeny of the skeleton of the cup (after Lane and Sevastopulo, 1982).

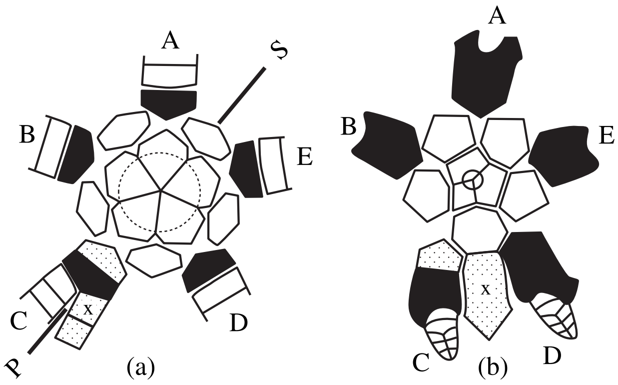


Fig. 15. Crinoids with paired radials in the C radius: (a) cladid crinoids (genus *Merocrinus*); (b) flexible crinoids (genus *Mysticocrinus*). Radials are black, the lower C radial is hatched, anals are dotted (after Moore *et al.*, 1978a, 1978b).

other crinoids needs to be carefully checked. Below, an attempt is made to check this hypothesis in the framework of the above-proposed model of the evolution of the crinoid theca from the polycyclic eocrinoid theca. According to this model, the orals and basals had to be the first plates to appear, while the laterals should have been the second, and radials should have been the third. Hence, they had to be reduced in reverse sequence. The plates of the oral circlet were initially placed interradially and did not change their position, since their arrangement is rigidly connected with the position of the radial ambulacral canals and the hydropore. Therefore, the radial and interradial position of the other plates, at all ontogenetic stages, can be conveniently estimated from their relationship to the orals. The basals were initially positioned radially. When the next, lateral, circlet appeared between the oral and basal, they had to migrate into the interradial position. When another circlet appeared, this time between the lateral and oral, the basal circlet had to return to the radial position, while the lateral circlet had to migrate to the interradial position, because the plates below the oral circlet always appear in a position alternating with that of the orals.

Based on this sequence and Ausich's hypothesis that the superradial plates represent a morphogenetically independent circlet, the following homology of the disparid circlets can be proposed:

(1) The basal circlet of the monocyclic cup is homologous to the infrabasal circlet of the dicyclic cup.

(2) The circlet composed by so-called large simple radials and inferradials is homologous to the basal circlet of the dicyclic crinoids, and the radial circlet of the monocyclic crinoids.

(3) An incomplete (interrupted) circlet of so-called superradials is homologous to the radial circlet of the dicyclic crinoids.

Thus, Ausich's hypothesis of the independence of the circlet composed of so-called superradials can be applied to the approach proposed in this study, although it leads to different homologies of the disparid circlets. The incompleteness of this circlet may be explained by the paedomorphic development of the A and D plates, which corresponds to the sequence of their appearance in ontogeny. However, it is not clear why, in the previous circlets, the plates in the A and D rays developed faster than others, while the circlet in general did not change its radial position when the next circlet appeared. However, these difficulties can be explained, although not very convincingly, by different heterochronies. A more serious complication emerges when the structure of the C ray in disparids, cladids (monocyclic and dicyclic inadunates), and Flexibilia is compared.

This is the following difficulty in the interpretation of the superradial plates as the remains of the radial circlet. Many disparids have superradials in two (Cincinnaticrinacea) or in one (Iocrinacea) ray rather than in three. The disparids with a single superradial always occurring in the C ray appeared in the fossil record before the others and were among the first crinoids (Lower Ordovician). Indeed, even in this case, the single C superradial may be interpreted as the remains of a pentamerous circlet. However, exactly the same structure of ray C, when two plates occurred one above another in the cup, can be observed in some cladids (*Merocrinus*) and Flexibilia (*Mysticocrinus*) (Fig. 15).

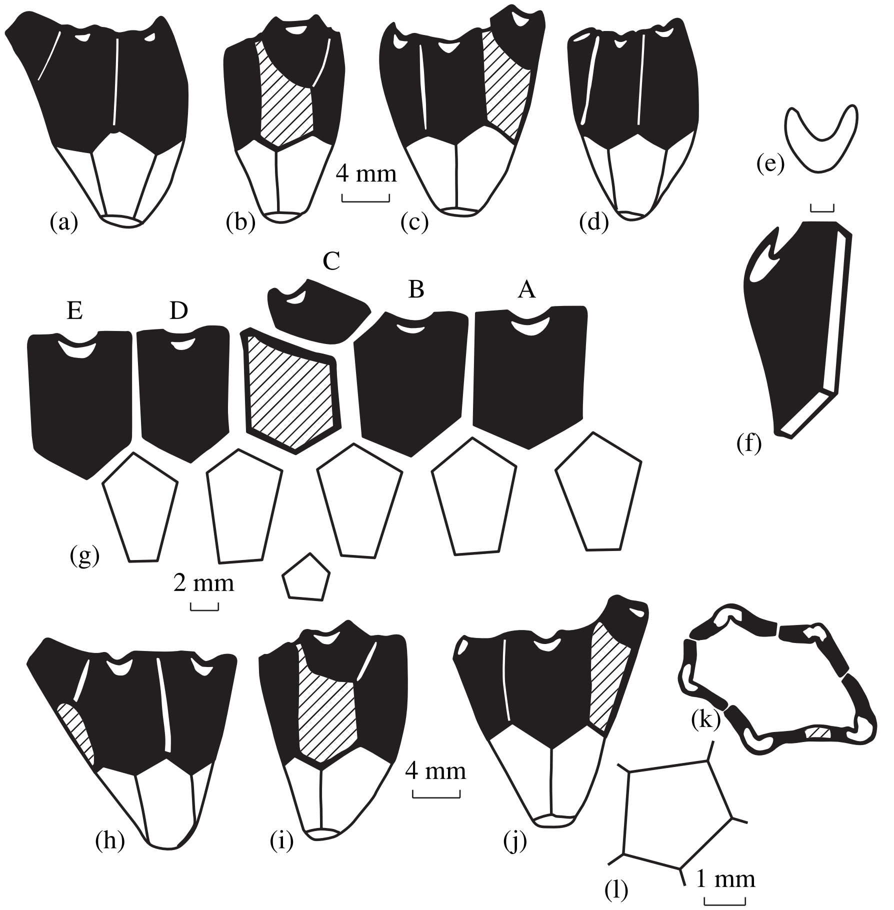


Fig. 16. Morphology of the cup of the hybocrinid crinoid *Hoplocrinus usvensis* Rozhnov from the Ordovician of the Urals: (a–d, h–j) lateral view of the cup: (a) AB interray, (b) C ray, (c) D ray, (d) EA interray, (h) B ray, (i) C ray, (j) D ray, (k) upper view of the cup, (e) shape of the articular facet, (f) radial plate, (g) arrangement of plates in the cup, (l) shape of the centrodorsal (reduced stem composed of several fused columnals). Radials are black, the inferradial is diagonally hatched.

For such a structure to appear in dicyclic forms, a mechanism of the emergence of paired radials similar to that in monocyclic forms, but based on the reduction of another circlet, has to be assumed. However, such a coincidence seems unlikely, especially in some cases, for instance in *Merocrinus* the superradial seems to be more connected in its origin to the brachials. A similar genetic connection of the C superradial to the brachial plates can be observed among monocyclic inadunates (disparids) in the superfamily Iocrinacea. In this case, the inclusion of the first brachial in the cup seems more likely. Functionally, it can be explained by the necessity of an ontogenetically earlier development of the anal tube, which is known to embrace the left branch of arm C. Morphogenetically, this could be produced by the faster maturing of the C radial to provide the possibility of the extension of the first brachial. As was noted above, in the ontogeny of many crinoids all structures, including the radial, appear earlier in the C ray than in other rays. Thus, when the first brachial appeared above the C radial, the remaining plates continued growing, the cup increased in size, and the first brachial in the C ray increased within it. A morphological lineage can be found among iocrinids which displays this mechanism of the development of the C superradial. Assuming that the C superradial in iocrinids (and hence in all other disparids) is brachial in its origin, then in all other rays the superradial is also most likely to have developed from brachials. This is supported by the fact that in the C, B, and E rays, in which the presence of the superradials is typical, the structures usually develop faster than in the two others.

Therefore, it is suggested that the superradials of disparids represent the first brachials, included in the cup and morphologically imitating an incomplete circlet, rather than the remains of a circlet, which was originally present in the ancestral cup. From this point of view, the ontogeny of the cup in *Homocrinus* is complex and indicates a stage in the phylogeny of disparids when the superradials became more morphogenetically connected with the development of the cup rather than with the arms. This is especially clearly seen when the morphology of the lower and superradials in disparids is compared to that in hybocrinids.

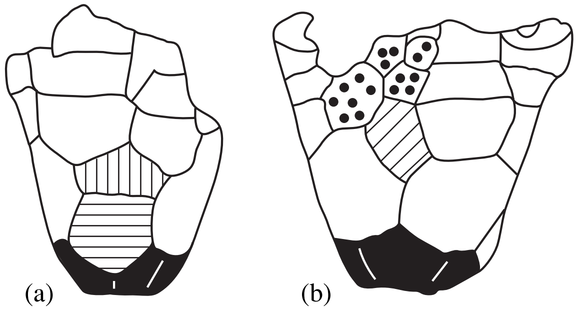


Fig. 17. Paired basal in an aberrant specimen of the cladid crinoid *Moskovicrinus multiplex* (Trd) from the Myachkovian, Middle Carboniferous, from the quarry near the village of Myachkovo, Moscow Region: (a) lateral view of the cup, AB interray with a paired basal; (b) lateral view of the cup, the anal ray has a typical structure. The AB inferradial is horizontally dashed, AB superradial is vertically hatched. The radianal is diagonally hatched, plates of the anal area are dotted.

Homologies of the C Superradial in Hybocrinids

In contrast to disparids, in some hybocrinids, the C superradial is more likely to represent the remains of the primary radial circlet. It is more likely to have evolved by the reduction of the plates of this circlet into four rays out of five. This opinion supports the structure and position of the plates in the genus *Hoplocrinus* from the Ordovician of the Baltic region and the Urals (Männil, 1959; Rozhnov, 1985a, 1985b). This genus has a superradial in the C ray, which is morphologically considerably different from that of Inadunata and Flexibilia (Fig. 16). First, it is noticeably raised above the level of other radials; second, it lies not immediately above the inferradial, as in disparids, but displaced clockwise to it (in contrast to cladids, in which this plate is displaced counterclockwise). The distal part of the inferradial is narrowed. The narrow part reaches the border of the cup and contacts the tegmen, although not from the side of the CD interray, where it could be used to support the anal cone, but from the side of the BC interray, where the expansion of the space between the facets from which the arms extended is functionally unexplained and, therefore, indicates a historical morphogenesis only. It seems evident that this structure indicates that the origin of the C superradial in *Hoplocrinus* was not connected with the inclusion of brachials in the cup, but more likely was connected to the ancestral third circlet, from which only one plate remained in the C ray. Thus, in this genus, the arms in the four rays A, B, D, and E extend from the lateral circlet, while in the C ray they extend from the primary radial circlet. This apparently was also happening in other hybocrinid genera with a similar composition of plates in the cup. Such an interpretation of plate homologies in hybocrinids explains many features of their morphology, which cannot be explained if they are interpreted as in disparids. This hypothesis of the origin of the superradial is also supported by the interesting aberrant specimen of *Hoplocrinus* sp. from the Middle Ordovician of the Leningrad Region, in which the superradial is absent, while one of the radials has two facets.

Homologies of the C Radial and the Radianal Plates in Cladida and Flexibilia

The acceptance of the homologies of the superradials in disparids suggests the acceptance of certain homologies for the C radial and for the radianal plate in cladids and flexibles (Fig. 10). This follows from the homology of the superradial in disparids to the C radial in cladids, and the C inferradial in disparids to the radianal of cladids. This homology is based on the similar structure of the C ray in some cladids (*Merocrinus*), Flexibilia (*Mysticocrinus*), and disparids, i.e., immediately below the C radial, possessing the articular facet, there is another radially positioned plate (in other words, the lower and superradials are observed in the C ray) (Fig. 15). In most Cladida and Flexibilia, the inferradial is displaced toward the CD interray and is called the radianal, because it supports a series of anal plates (Fig. 17b). However, the origin of the radianal plate is positively established based on the morphology of cladids and flexibles, because all stages of its migration from the inferradial position in the C ray to the interradial position in the CD interray are known (Philip, 1964, 1965). Hence, Ausich's hypothesis of the homology of the superradial circlet in disparids to the radial circlet in cladids and the inferradial circlet (together with unseparated radials) to the infrabasal circlet of cladids leads to a serious contradiction. This contradiction can be resolved, if a different homology is suggested; that the superradials of disparids are the brachials included in the cup, while the inferradials and unseparated radials are homologous to the radials of the A, B, C, and D rays and the radianal of cladids. Hence, the C radial of cladids is homologous to the superradial of disparids and is the first brachial plate included in the cup. However, there is an opinion based on the ontogeny of modern crinoids that the radials represent only the base of the brachial series of plates, i.e., the first brachials included in the cup. Apparently, in some modern crinoids and in many early disparids, the radials and brachials could be combined morphogenetically, because in some disparids, the distal border of the cup is difficult to define, because it is not clear where the border is between the radials and the arms (Fig. 13). However, such morphogenetic combination of arms and radials seems secondary, although it could have appeared quite easily as a result of some paedomorphic processes.

In addition, it is worth mentioning that the presence of the lower and superradials in the C ray, although it could be achieved by different means (e.g., compare the structure of disparids and hybocrinids), indicates features of the development of the anal area inherited from ancestral eocrinoids. This conclusion is supported by the characteristic subdivision of the plate of the lateral circlet in the C ray into upper and lower parts, e.g., in

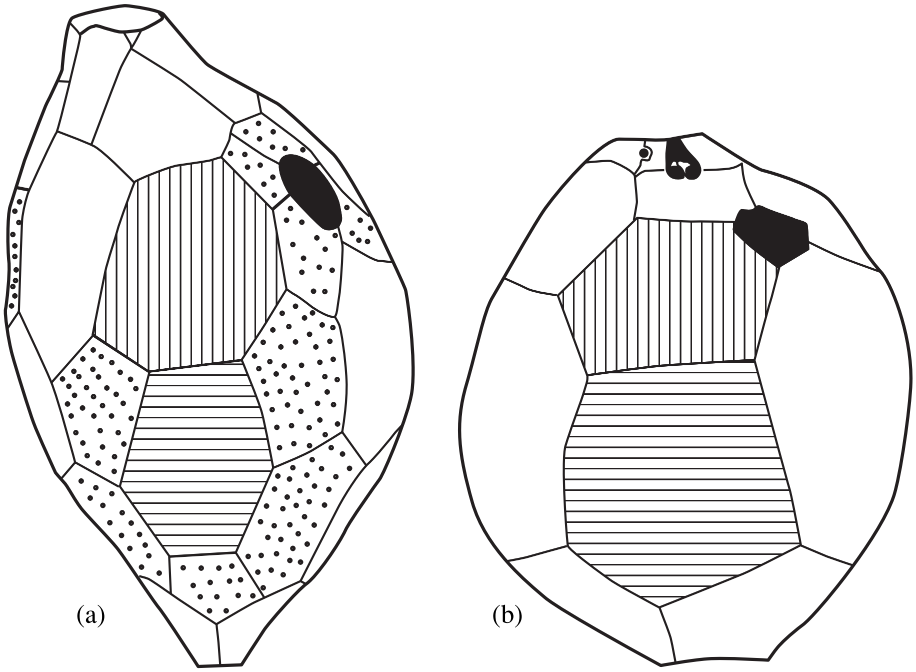


Fig. 18. Superlateral (vertical hatching) and inferlateral (horizontal hatching) in the C ray in the C ray in the paracrinoid *Springerocystis longicollis* Bassler and eocrinoid *Cryptocrinites* sp.

Cryptocrinites (Fig. 18). This primary subdivision was related both to the faster development of structures in this ray in eocrinoids and to the close connection of its development with the growth of the rectum. However, for a more positive judgment of this process in eocrinoids, the data available at present are insufficient.

Thus, the suggested homologies of the thecal circlets in crinoids and their comparison to the previous schemes of homologies are summarized in Tables 2 and 3 and are shown in Fig. 10.

Special Cases of Circlet Homology

The above-proposed homology of circlets is based on the order of appearance of circlets in ontogeny. The first circlets to appear were infrabasal and oral, followed by basal, and eventually by the radial circlet. This order of appearance was present in the dicyclic forms. In monocyclic forms, the basal circlet was embraced by the ambulacral radial canals. Its plates were morphogenetically connected to the food grooves to form a united structure. Above these plates, the appearance of other plates in the cup followed a different sequence, i.e., radial series of plates, usually separated by interradial series, appeared in the neighboring circlets instead of alternating plates. The appearance of the superradial model of cup growth is certainly connected to the appearance of arms, when this model was included within the cup in circumstances when the radial ambulacral tentacles had not grown ontogeneti-

Table 2. Terminology of the circlets of the aboral cup based on homology and the names of the plates in the circlets in traditional terminology in major groups of Crinoidea

Terminology of circlets based on homology	Plates composing the circlets (in traditional terminology)					
	Disparida	Hybocrinida	Cladida Flexibilia Articulata	*Aethocrinus*	Camerata monocyclic	Camerata dicyclic
Brachial	Superradials	Absent	Radial C (superradial C)	Absent	Brachial	Brachial
Lateral upper	Absent	Superradial	Radials (except C) and radianal	Radials	Absent	Radials
Lateral lower	Radials and inferradials	Radials and an inferradial	Basal	Basal	Radials	Basal
Basal	Basal	Basal	Infrabasal	Infrabasal	Basal	Infrabasal
Lintel	Proximal columnal	Absent	Absent	Lintel	Absent	Absent

Table 3. Homology of circlets of the crinoid cup interpreted by different researchers

Homology of circlets interpreted by different researchers (terminology of circlets is traditional)																
proposed here						Ausich, 1997				Simms, 1994						
designations based on circlet homology	traditional designations															
Polycyclic cup	*Aethocrinus*	Cladida Flexibilia Articulata	Camerata (Monobathrida)	Disparida	Hybocrinida (Hoplocrinus)	*Aethocrinus*	Cladida Flexibilia Articulata	Camerata (Monobathrida)	Disparida	Cladida	Disparida	Hybocrinida	Camerata (Diplobathrida)	Camerata (Glyptocrinina)	Camerata (Periechocrinacea)	Camerata (Xenocrinacea)
Br1		sR	–	sRR												
LL_2	RR	RR			sR	RR	RR	RR	sRR	RR	BB	sR	RR	BB	RR	RR
LL_1	BB	BB	RR	RR+iR	RR+iR	BB	BB	BB		BB	IBB	RR+iR	BB	IBB	IBB	BB
BB	IBB	IBB	BB	BB	BB	IBB	IBB	–	RR+iRR	IBB	–	BB	IBB	–	–	–
Lint	Lint		–	SC	–	Lint	–	–	Lint	–	–	–	–	–	–	–

Note: Explanations: (RR) radial circlet; (BB) basal circlet; (IBB) infrabasal circlet; (sRR) radial circlet composed of a single superradial C (radial C); (Brl) circlet composed of the first brachials included in the cup; (R+iP) circlet composed of radials and inferradials; (RR+iRR) infrabasal circlet composed of simple plates and inferradials; (Lint) lintel circlet; (SC) columnal.

cally to the base of the free arms. This morphogenetically interesting process is especially characteristic of Camerata and is very diverse in this group.

However, an increase in the size of the cup could also occur in other ways. For instance, in a very interesting family of camerate crinoids, Acrocrinidae, which was recently extensively studied by Arendt (1995) based on material from the Carboniferous of the Moscow Basin, new plates, often arranged in circlets, were also formed after the appearance of the radials. In the genera of this family, a distinct growth zone appeared between the basal and radial plates. This zone, in which new plates appeared, sometimes existed throughout the lifetime of an individual (Fig. 19). This zone of cup growth replaced the superradial growth zone characteristic of many other Camerata.

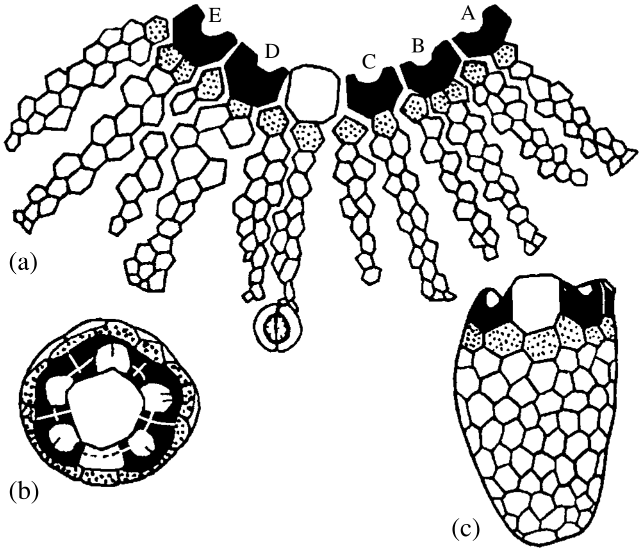


Fig. 19. Composition and arrangement of cup plates in the acrocrinid *Erlangeracrocrinus elongatus* Arendt (camerate crinoid) from the Middle Carboniferous of the Moscow Region (after Arendt, 1995): (a) arrangement of plates in the cup, (b) upper view of the cup, (c) lateral view of the cup, anal interray. Radials are black, the distal plates of the intercalary zone are dotted.

Another pattern of inclusion of brachials in the cup and their fusion with the radials is known in the camerate family Parahexacrinaceae, described from the Lower Devonian of the Zeravshan Range (Shevchenko, 1967). However, this example will be discussed in a later section on the morphogenesis of arms. In the same section, the appearance of additional radials in some Pisocrinacea (disparid inadunates) will be considered.

ACCESSORY PLATES OF PERITTOCRINIDS, THEIR ARRANGEMENT, CONNECTION WITH RESPIRATORY STRUCTURES, PROBABLE ORIGIN, AND HOMOLOGIES

MORPHOLOGY AND POSITION OF ACCESSORY PLATES

The so-called accessory plates of perittocrinids are of particular interest, because perittocrinids are among the earliest crinoids, and the arrangement and homologies of their plates may be important for the understanding of the origin of crinoids in general (Fig. 22). Two systems of accessory plates of perittocrinids (or two interrupted circlets, if they are considered from the

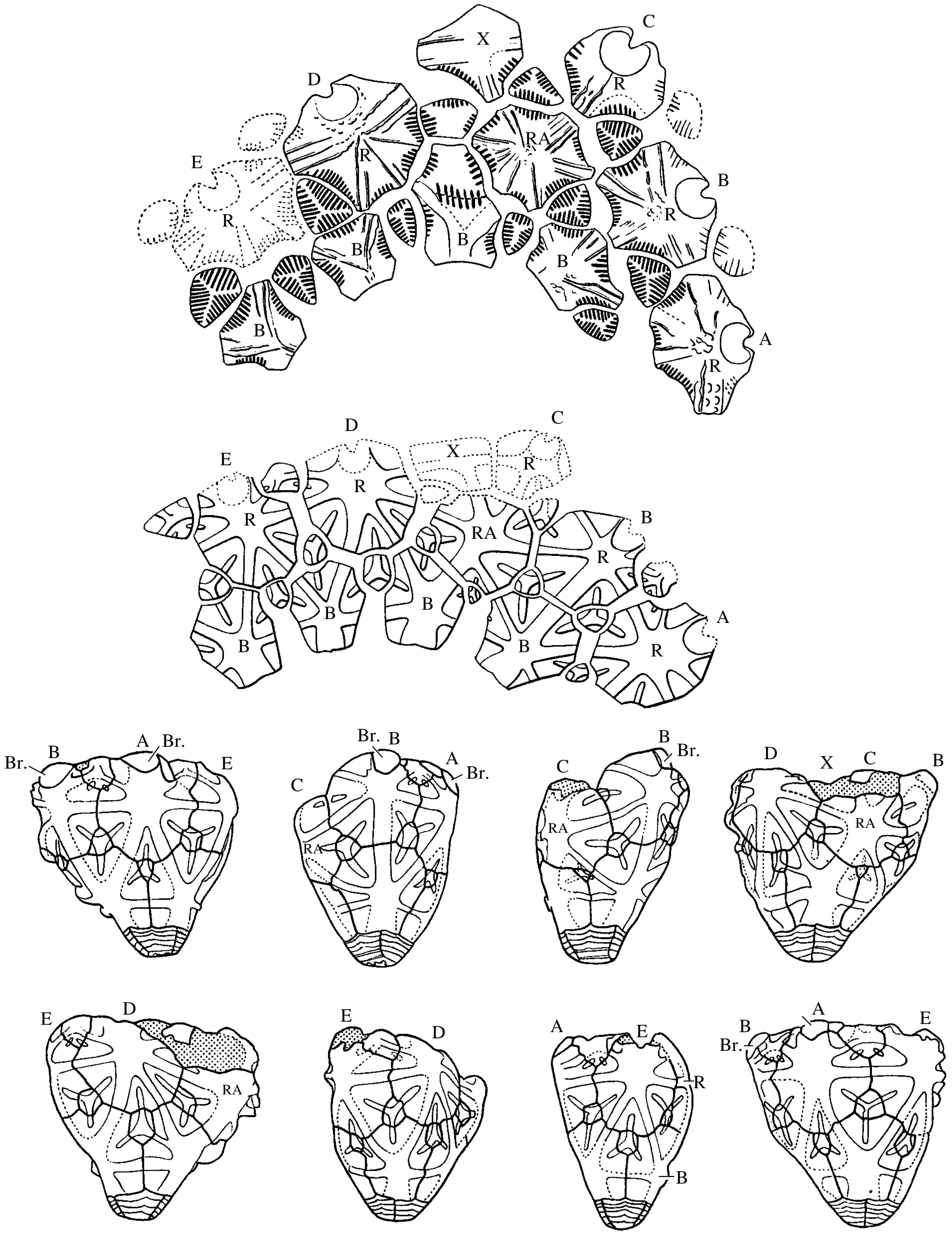


Fig. 20. Composition and arrangement of the thecal plates in perittocrinids (after Ubaghs, 1971). (a) *Perittocrinus radiatus* Beyrich, (b–j) *Tetracionocrinus transitor* (Jaekel).

point of view of organization in circlets) are situated between the distal parts of the basal plates and between the proximal parts of the radial plates. Until now, they have been only known from two cups from the Ordovician of the Leningrad Region. They were first described, briefly, by Jaekel (1918) and later (in greater detail) by Ubaghs (1971), when he prepared material for publication in *Treatise*…. Based on the second specimen, Ubaghs established a new genus, *Tetracionocrinus*. However, based on new data and judging from the variability of plates, indicating different ontogenetic stages, the difference between these two genera appears to represent different ontogenetic stages of the same or closely related species.

The largest known number of accessory plates is 14, but reconstruction of the complete cup shows that it consisted of at least 16 accessory plates (Ubaghs, 1971, text-fig. 1b). Four accessory plates occurred between the distal parts of the basal plates (both known perittocrinid cups have four basal plates), immediately below the radials. Five accessory plates occurred between the B radial and the C superradial, between the C superradial and the anal plate, and between the anal plate and the D radial. The latter accessory plate lies directly on another accessory plate. Therefore, they can be considered to be a superradial and inferradial, as in the C ray. However, they were apparently separated from one another by the connecting projections of the neighboring radials: the C inferradial and the D radial. This can be concluded from the structure of a smaller cup described by Ubaghs (1971, text-fig. 1c) as *Tetracionocrinus transitor.* In my opinion, further studies and new material may show that this species is in fact a juvenile of *Perittocrinus radiatus.* Thus, the radial circlet of perittocrinids may be interrupted by accessory plates in the CD interray in adults or more advanced forms or may be complete in younger individuals or more primitive forms. Another two plates are known between the distal parts of the A and B radials and the C superradial. It is quite possible that similar accessory plates were also present between the distal parts of other radials and on the margins of the anal plate in its distal part, bordering with the respective radials. The correspondence of these distal accessory plates to the orals is not known, because the oral side of the cups is not preserved. Judging from the shapes of isolated radial and basal plates, in some other, as yet undescribed, perittocrinid species, the number of accessory plates could be even fewer.

HOMOLOGY OF THE ACCESSORY PLATES, IN THE OPINION OF O. JAEKEL AND G. UBAGHS

The problem of the homology of the accessory plates was discussed by Jaekel (1902, 1918) and Ubaghs (1971). Jaekel suggested that these plates have different origins. He suggested that the accessory plates of perittocrinids lying between the basal plates are homologous to the radials of Camerata (in Jaekel's terminology the radials of Camerata are called Costalia 1). The radials of perittocrinids he associated with the higher-lying plates of Camerata (Costalia 2), bearing arms (Jaekel, 1902, p. 1094). Thus, in modern terminology, he considered the radials of Inadunata to be homologous to the first fixed primibrachials of Camerata. The remaining accessory plates occurring in the corners between the large plates, Jaekel considered to be homologous to the interradials of Camerata. In addition, he suggested that the so-called pectinirhombs are growth zones, the centers of which were the centers of the formation of new plates.

Ubaghs (1971) justifiably noted that different origins can hardly be surmised for these groups of accessory plates, because all of them are of similar size and position relative to the large plates and have folds forming a specific structure, apparently with a respiratory function. In addition, he noted that there is no evidence against the homology of the radials of inadunates to the radials of Camerata and that *Perittocrinus* gave rise to Camerata. Ubaghs also noted that, theoretically, there are two possibilities: (1) accessory plates are inherited or (2) they represent morphological innovations. The choice in this case is difficult, because ancestors are not known for either perittocrinids or inadunates. Nevertheless, Ubaghs presented arguments for and against both hypotheses.

If the accessory plates are inherited from the ancestors of perittocrinids, they should be homologous and correspond to those plates of the theca of primitive inadunates that were not well organized in circlets, were variable in number, and were situated in the middle part of the theca (Ubaghs, 1969, p. 22). However, all plates of the primitive thecae, including those irregularly spaced or poorly organized, perform predominantly the mechanical function of strengthening the theca and supporting the food-gathering apparatus. The accessory plates in perittocrinids are completely different. All of them are located in so-called dead corners and have no influence on the strength of the theca, although they support and protect specific structures, which are commonly believed to be responsible for respiration. Therefore, before possible morphogenetic processes of the formation of the accessory plates in perittocrinids are considered, the structure and possible functions of the porous structures of the theca of pelmatozoan echinoderms must be discussed.

SYSTEM OF PORES AND FOLDS OF THE THINNER STEREOM IN PELMATOZOAN ECHINODERMS, AND THEIR POSSIBLE FUNCTIONS

Many Cambrian echinoderms have pores that usually occur on the sutures between the plates (Figs. 21, 92). These are so-called sutural pores. Usually, the structure of pores is very complex. They may be covered by a thin stereom; and sometimes they are connected by a system of folds. In this case, they are referred to as epispires. Such pore structure is especially characteristic of the Cambrian eocrinoids. In Rhombifera, which first appeared in the Ordovician, a simple pore structure was transformed into a complex and diverse structure of rhombic pores. In Diploporita, which appeared at the same time, the pores acquired a specific structure and are referred to as diplopores. In crinoids pores occur relatively rarely and are found only in some early genera (e.g., *Porocrinus*) and, sometimes, in the Late Paleozoic crinoids, in which they occur at the point of fusion of several sutures between the plates. In perittocrinids, thin zones of the stereom on the folds at the contacts between the plates of the cup can be considered to be pores, especially as these places often show openings in the skeletal tissue.

Usually, all these structures are believed to have a respiratory function, because the intensity of exchange between the coelomic cavity and the seawater was considerably higher than elsewhere, due to the sharp increase in the contact surface area between the two media and because of the highly increased penetrability of the stereom (which was thinner in these places). Indeed, respiration in these places could be to some extent increased, and these pores could play some role in respiration. However, it was unlikely to have been their main function. The intensity of respiration is known to indicate the intensity of an animal's metabolism. When the body size is the same, the intensity of metabolism is proportional to the amount of oxygen consumed. However, the intensity of metabolism is to the same extent proportional to the energy received, i.e., to the amount of food consumed. Hence, the rate of metabolism can be judged by morphological criteria, i.e., with all other characters equal, the more developed the food-gathering system, the more intense is the metabolism. Consequently, the more developed the food-gathering system, the more developed the respiratory structures should be. However, the actual pattern is the opposite. When the crinoid body plan, with its powerful food-gathering system, including long, branching arms with a wide food groove, appeared, all pore structures rapidly disappeared. Supposedly, they became redundant. It may be suggested that the arms of crinoids began to play a role in respiration and, therefore, the pore system became redundant. This may be partly true, especially because the food-gathering apparatus of many crinoids occurs approximately one meter above the sea floor, whereas the brachioles of eocrinoids were not elevated more than 10 centimeters. The bottom layers of the seawater are known to have a low oxygen content, but at the same time they are enriched in dissolved organic matter. I am inclined to think that feeding on dissolved organic matter was the main function of the pore structures of the theca of primitive pelmatozoan echinoderms. Only this assumption can adequately explain the huge difference between the very weak food-gathering apparatus and the powerful pore system, which densely covers the entire theca, as in, for example, the rhombiferous genus *Echinosphaerites*, the diploporite genus *Sphaeronites*, or the eocrinoid genus *Simonkovicrinus* (Fig. 21). This is supported by the fact that modern echinoderms, like other invertebrates, can absorb dissolved nutrients (amino acids and carbohydrates) from the seawater (Bynion, 1972; West *et al.*, 1977; Meyer, 1982). For instance, West (1978) showed that the arms and cirri of the modern comatulid crinoid *Leptometra phalangium* can absorb dissolved amino acid and glucose. He also suggested that the animal could obtain food from the bottom water layer, where the concentration of dissolved nutrients was high. The absorption of nutrients directly from the seawater could be the main feeding strategy in juvenile crinoids with undeveloped arms (Lane and Breimer, 1974). The above data suggest that the main function of the pore structures of the earliest primitive echinoderms was feeding (absorption of dissolved nutrients and even bacteria), while the respiratory function was only accessory.

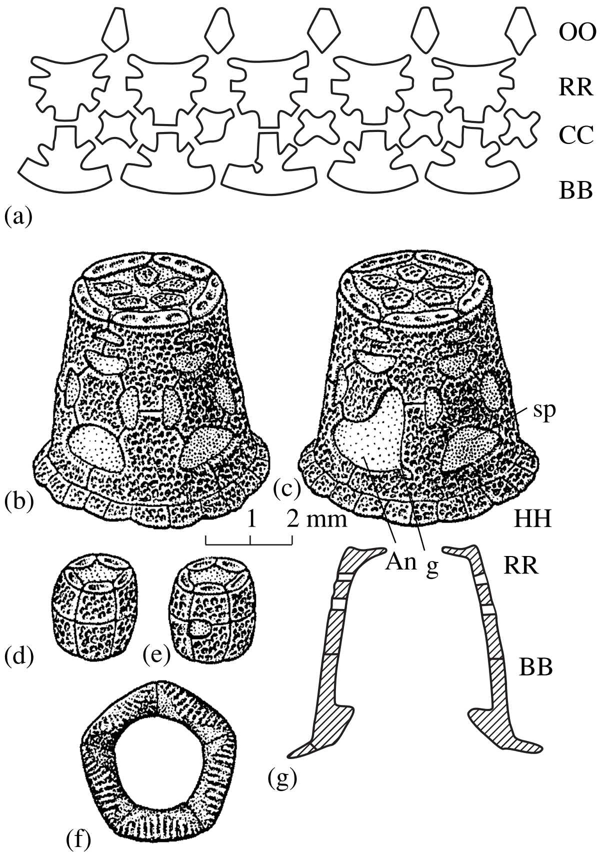


Fig. 21. Reconstruction of the eocrinoid *Simonkovicrinus reticulatus* Rozhnov showing (e) very large sutural pores, (An) anus, and (g) gonopore placed low (after Rozhnov, 1991).

The folds on the theca of perittocrinids, like the accessory plates, occurred mainly at the fusion of three sutures between the main plates, which are referred to as dead corners from the mechanical point of view. They represent systems of folds located on the adjacent margins of the main and accessory plates. The number of folds increases toward the margins of the plates, because of the appearance of smaller folds, while the thickness of the stereom rapidly decreases until openings appear at the point of contact between the folds on the neighboring plates. This suggests that the intensity of the exchange between the coelomic cavities and the seawater in these places was considerably higher than in the other zones, because of the sharp increase in the surface area of the contact zone between these two media and due to the markedly increased penetrability of the stereom, which was thinner in these areas. Usually these structures are referred to as respiratory, but in fact they could be more universal because they could also perform ion exchange and feed on dissolved organic matter, even bacteria, as shown above. The problem of correspondence of these three functions in perittocrinids does not seem simple. In Eocrinoidea, Rhombifera, and Diploporita, all of which have these structures, the respiratory function could dominate only occasionally, because they had a poorly developed ambulacral system, which would have been responsible for respiration. However, perittocrinids had relatively well-developed arms and, hence, radial ambulacral canals. The walls of these canals had a large surface area contacting the external medium, the blood system, and the system of the coelomic lacunas. Hence, they were capable of providing a sufficient rate of respiration (as suggested for the majority of crinoids). Under normal conditions, perittocrinids could apparently provide themselves with food using only their arms, but when the supply of relatively large particles was small, they could use the fold structures of the cup with a thinned stereom to absorb organic matter. Occasionally this feeding strategy became dominant.

FOLDS OF THE THINNED STEREOM OF PERITTOCRINIDS AND THEIR PROBABLE HOMOLOGIES WITH THE EPISPIRES OF EOCRINOIDEA, THE PORES OF CRINOIDEA, THE DIPLOPORES OF DIPLOPORITA, AND THE PORE RHOMBS OF RHOMBIFERA

Systems of folds on the plates of cups in perittocrinids are different in *Perittocrinus* and *Tetracionocrinus*. Therefore, these systems should first be described in both genera separately, and then compared.

In *Perittocrinus radiatus*, a system of large solitary folds is present only on the main plates. Between these main folds, secondary folds are formed. These folds are arranged in groups on the main and accessory plates and are perpendicular to the sutures between the plates. Each fold of the second order on the main plate is joined to the corresponding fold on the accessory plate, without changing its direction. Each group of folds occupies an area that is rhomboid in outline. Each of these rhomboid figures is subdivided diagonally by the suture, between the main and accessory plates. The longest fold of the second order runs along another diagonal of this folded rhomb (pectinirhomb), which is perpendicular to the suture between the main and the accessory plates. To the left and right of this fold, the folds of the second order are gradually shortened as their distance from the central fold increases, and they become closer to the corners of the accessory plates, thus forming a rhomb shape. On the main plates, the folded rhombs are bordered by the folds of the first order, but do not extend as far, and are separated from them by a small, depressed area. On the accessory plates, the rhombs are delineated by narrow, even space-lacking folds. Each accessory plate possesses three halves of a rhomb (three folded triangles). Therefore, the space separating them represents three depressions extending from the corners of the accessory plate and joined in its center. Thus, each group of folds of the second order forming rhomboid structures is well separated from the others.

In *Tetracionocrinus*, the system of folds of the first order is very similar to that in *Perittocrinus radiatus*, although Ubaghs (1971, p. 322) suggested that the true folds exist only in the former genus, while in the latter they are in fact ridges, because they are not reflected on the inner side. The morphology of some plates and its ontogenetic changes in *Perittocrinus radiatus* show that this difference is not significant and is less pronounced in juveniles. In large plates, the folds of the first order are true folds only near the very edge of the plates, while in the remaining parts they are merely ridges, because they are not pronounced on the inner side. In small plates, they appear to be genuine folds but occupy a much larger proportion of the plate. In addition, in the main plates of the juveniles of this species, there is no fundamental difference in morphology between the folds of the first and second orders (they differ only in size and location). Unfortunately, it is not known whether the ends of the folds in juveniles were joined in the centers of the accessory plates, as in *Tetracionocrinus*, or whether they did not reach the centers, being separated by a small space, as in adults of *Perittocrinus radiatus.* Nevertheless, it is very probable, judging from the morphology of the plates of the juveniles of this species, that the median folds of the second order were joined in the middle of the accessory plates. In any case, this could depend on the time of the appearance of the accessory plates. When they appeared earlier than the first folds of the second order on the main plates, the resulting folds were joined in the centers of these plates. When the accessory plates appeared later than the appearance of these folds, they shifted aside the folds joined in the dead corners. As a result, the centers of the accessory plates did not have folds. Consequently, *Tetracionocrinus transitor* may be a juvenile specimen of *Perittocrinus radiatus*, or a closely related species rather than a separate genus.

The folded structures in both perittocrinid genera are apparently homologous to each other and only partly homologous to the pore structures of the theca in eocrinoids in diploporite and rhombiferous cystoids and in some crinoids, because in my view they have the same morphogenetic basis for potential development and functioning of the somatocoels. Some researchers connect the existence of the specific coelom in the skel-

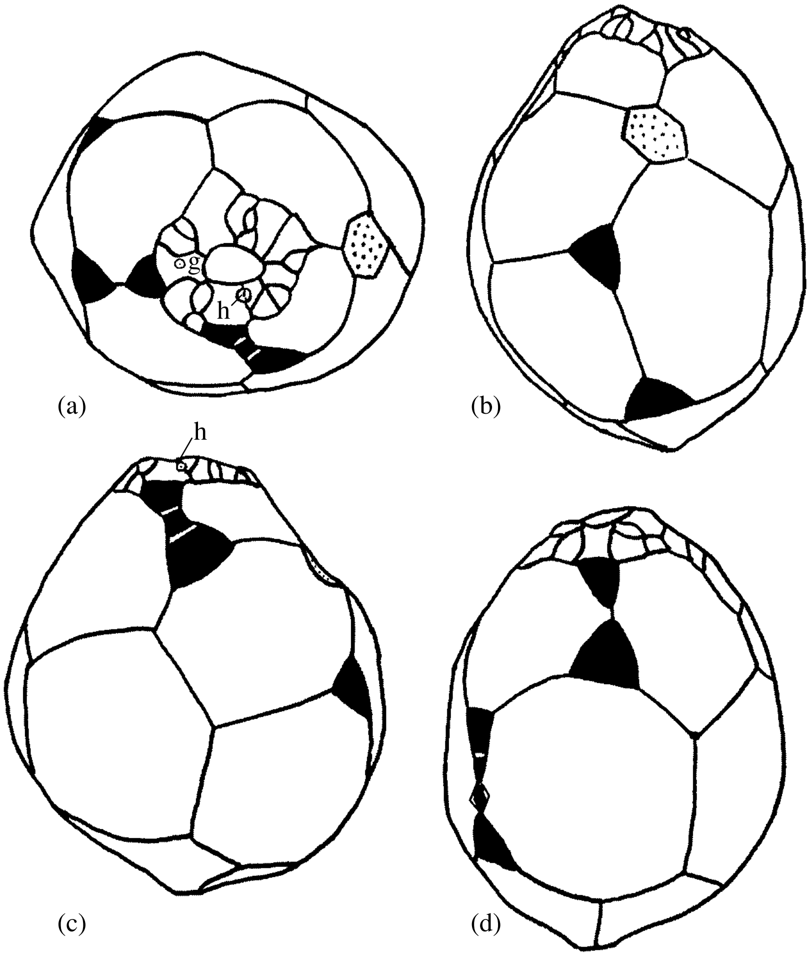


Fig. 22. Aberrant specimen of the eocrinoid *Cryptocrinites* sp. with accessory plates. (a) Upper view; (b) lateral view, interray BC; (c) lateral view, interray CD; (d) lateral view, interray DE; accessory plates are black, anus is dotted; (h) hydropole; and (g) gonopore.

eton of pelmatozoan echinoderms with the respiratory structures. For instance, Paul (1967, pp. 231, 243–247) noted that the system of pectinirhombs of the rhombiferous cystoids could have been connected by an inner system of canals with the water-vascular (ambulacral) system. Sprinkle (1973a, p. 35) suggested that epispires and similar structures known in several groups of primitive echinoderms might represent "the earliest type of water-vascular system, which had already developed in the Precambrian echinoderms." This opinion is closely connected with his hypothesis substantiated in the same study that the blastozoan echinoderms did not have ambulacral radial canals extending outside the cup. It is suggested here that the folded structures of the cup of perittocrinids, as in other crinoids in which they occur, and the systems of pores in other pelmatozoan echinoderms were connected with the specialized peripheral zones of the right and left somatocoels occupying most of the cup rather than with a specific coelom. This assumption is supported by the regular arrangement of the folded structures on the cup surface in *Perittocrinus* and of the pores in many other pelmatozoan echinoderms. In addition, perittocrinids had typical arms, containing radial ambulacral canals. Therefore, it is difficult to suggest the presence of another type of ambulacral canal within the cup.

Morphologically, pore and fold structures appeared to a large extent independently in the skeleton of the major groups of pelmatozoan echinoderms. Nevertheless, the appearance of complex pore structures occurred gradually rather than instantly. Therefore, a morphological succession can be reconstructed from known structures. The primitive epispires expressed as sutural pores (pores on the sutures between the plates) were certainly the first to appear. The irregular arrangement of these pores on the sutures apparently weakened the structure of the cup. Therefore, they were subsequently positioned at the meeting points of the three sutures of the neighboring plates, i.e., in the so-called dead corners. This arrangement did not greatly affect the strength of the theca. In addition, the pores could have been covered by a thin layer of stereom, much

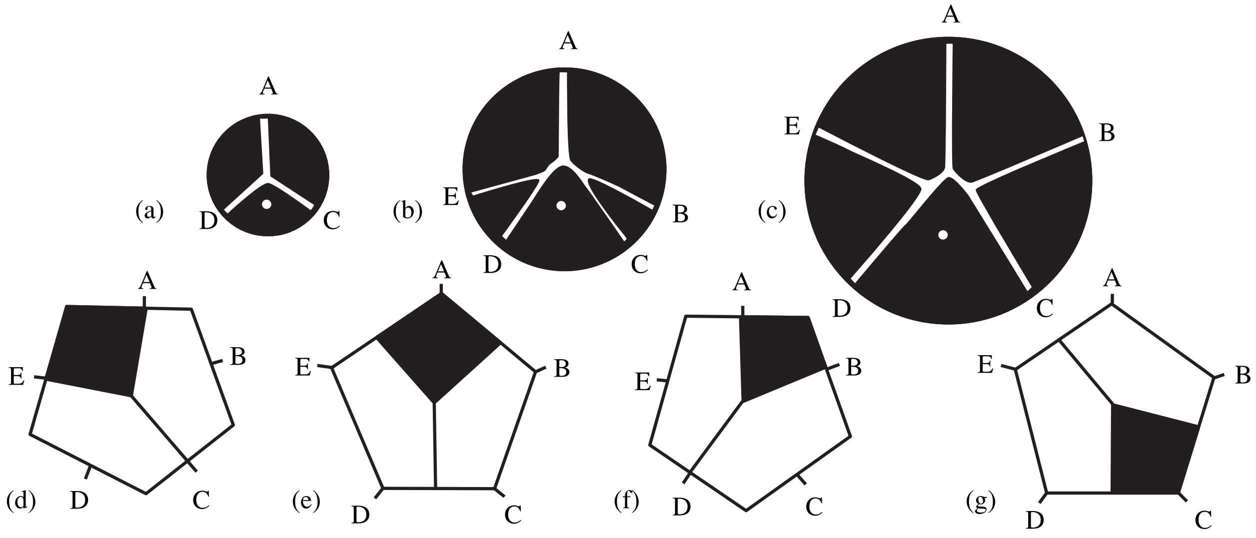


Fig. 23. Structure and possible stages of development of the oral circlet in (a–c) crinoids and position of the small plate in the tripartite proximal circlet in (d) some paracrinoids and eocrinoid *Cryptocrinites*, (e) some crinoids, (f) blastoids, and (g) Flexibilia. Although unpaired small plates of the proximal circlet of adults occupy different positions in relation to the ambulacra, their origin in ontogeny could be similar, and could correspond to the primary triradiate symmetry of the ambulacra.

thinner than in the adjacent zones. This could hardly disturb the performance of their functions, because the stereom was microporous. However, this might have improved the system of connection between the plates. To improve the above functions, the surface area of the contact between these structures and the water outside should have increased. This was achieved by the development of the folds on the involved skeletal parts of the theca. Since the respiratory structures were originally connected to the sutures between the plates, the appearance of the new plates led to an increase in their number. In perittocrinids, these two processes were combined; accessory plates appeared in the dead corners, and folding increased in the sutures between them. Possibly, the accessory plates in perittocrinids were originally separated from the corresponding parts (distal or proximal) of the main plates, because in the earlier representatives of the genus *Perittocrinus* (in which folds are very strongly developed) the accessory plates are small and poorly developed compared to the stratigraphically younger *Perittocrinus radiatus.* However, insufficient material on perittocrinids and closely related groups does not allow a positive conclusion. It seems possible that the accessory plates are the remains of two accessory circlets, which in the ancestral polycyclic forms occurred between the basal and radial circlets. Such structures could very possibly have developed as a result of heterochronies. However, in this case the radial circlet of perittocrinids is not homologous to the radial circlet even of the dicyclic forms and represents a separate circlet (third lateral in the above-proposed homology-based terminology). In this terminology, the radial circlet of dicyclic forms is called the second lateral, whereas in monocyclic forms it is called the first lateral (see Table 2). However, this seems unlikely.

It is more likely that the accessory plates in *Perittocrinus* represent a specific system of plates, an innovation developed to increase the size of the theca through the appearance of the accessory plates at the late ontogenetic stages. This system apparently appeared in the same way as the above-mentioned acrocrinids. This, in my opinion, precluded their further development into a separate circlet in descendants. A similar arrangement of the accessory plates is known in the aberrant specimen of the eocrinoid *Cryptocrinites*, described by Yakovlev (1918) from the Ordovician of the Leningrad Region (Fig. 22).

HOMOLOGIES OF PLATES IN THE CIRCLETS OF CRINOIDS

FIVE-PIECE, FOUR-PIECE, AND THREE-PIECE PROXIMAL CIRCLETS OF PELMATOZOAN ECHINODERMS

Comparing the pentamerous circlets, in most cases the homologies of the plates in these circlets are established based on the rays, or interrays, in which these plates occur, but what should be done in the case of four-piece, or three-piece circlets (Figs. 20, 23)? How can plates in these circlets be homologized with the plates of the five-piece circlet? In this case, the establishment of these homologies becomes more complex, because we must reveal the morphogenetic process that resulted in the disappearance or underdevelopment of a certain plate. This is difficult to do because of insufficient data on the morphogenesis of fossil crinoids. Nevertheless, the morphogenetic concept of the development of circlets in crinoids proposed here allows some insight into it.

In discussing the development of the superradials in disparids, a certain sequence of the appearance of the radials and related structures in the ontogeny of crinoids was noted (Moore, 1940; Wright, 1941; Moore and Evers, 1942; Koenig, 1965; Arendt, 1970; Brower, 1978; Lane, 1978; Lane and Sevastopulo, 1982, 1985; Sevastopulo and Lane, 1988). A similar sequence was recorded in eocrinoids (Rozhnov, 1994). In the discussion below on the origin of pentamery in echinoderms it is shown that this sequence indicates a morphogenetic mechanism for the appearance of five-rayed symmetry via a stage of three-rayed symmetry. According to the suggested model of evolution of the crinoid theca from the eocrinoid theca, specific features of the development of pentamery should have been reflected in the morphology of the radial circlet, but primarily in the morphology of the oral and basal circlets. In the oral circlet, this feature has been long recognized by many researchers. It is the presence of the diad and triad among the five oral plates, indicating the position of the food grooves extending from the mouth, following the model 2–1–2 (in the A ray the groove is unpaired, while in the remaining rays, the grooves in pairs extend from a single branch). Morphologically, three oral plates (triad) are larger than the others and contact one another by their distal ends in the middle of the oral area. Two other plates (diad) are somewhat smaller, and their distal ends do not reach the center of the oral area (Fig. 23). Generally, the arrangement of the food grooves following the model 2–1–2 reflects the evolution of pentaradiate symmetry from triradiate symmetry. This will be discussed in detail in the section on symmetry. In my opinion, the primarily tripartite basal, or infrabasal, circlet, known both in crinoids and eocrinoids, also indicates the process of development of pentaradiate symmetry. Below, an attempt is made to test it by showing a possible morphogenetic mechanism of the development of the tripartite proximal circlet. This will allow a possible homology of plates in the three-piece or four-piece basal circlet. This is discussed in detail below.

HOMOLOGIES OF THE UNPAIRED PLATE IN THE THREE-PIECE CIRCLET OF PELMATOZOAN ECHINODERMS

Some higher taxa have a proximal circlet (basal, or infrabasal) formed by only three plates. Two of these plates are large (paired), while one (unpaired) is small, half the size of the large plate (Fig. 23). Correspondingly, each large plate occupies two rays, or interrays, whereas a small plate occupies only one.

For instance, crinoids of the subclass Flexibilia have a so-called infrabasal circlet composed of three plates, one of which (unpaired) is half the size of each of the other two. In all known cases, the unpaired plate occurs on the C ray, except in some specimens of *Forbesiocrinus*, in which the unpaired plate occurs on the A ray (Moore, 1978).

Many cladid inadunates of the family Hypocrinidae also have an infrabasal circlet composed of three plates, one of which is unpaired. This small unpaired plate may occur on the A or C ray or more rarely on others (Arendt, 1970). In the Ordovician eocrinoid *Cryptocrinus*, the basal circlet is composed of two large plates and one small, unpaired plate that occurs in the EA interray (Rozhnov, 1994). *Rhipidocystis*, an eocrinoid with a flat theca, has a similar structure of basal circlet. Supposedly, its unpaired basal plate also occurred in the EA interray (Rozhnov, 1994). In Blastoidea, the basal circlet also has three plates, one of which (unpaired) usually occurs on the EA interray (Beaver, 1967). In paracrinoids, according to Sumrall (1997), the unpaired basal plate occurs on the BC interray. My data show that this unpaired basal in paracrinoids can be situated in various interrays (Fig. 24).

It is usually suggested that three plates in the proximal (so-called infrabasal) circlet appeared as a result of the fusion of four of the five primary plates. For instance, in hypocrinids, as noted by Arendt (1970, p. 63) "it was probably of little adaptive significance which plates were fused." It is not clear what adaptive significance a circlet composed of three plates could have, when the above-located circlet was composed of five plates. However, Arendt also noted that the position of the unpaired plate might be connected with the sequence of the appearance of the radial plates in ontogeny. This observation may be of key importance for the understanding of the development of tripartite circlets. However, it should be connected not just with the sequence of the appearance of the radial plates, but with deeper ontogenetic processes, when the pentaradiate symmetry of the theca is just beginning to develop, i.e., with the sequence of the ontogenetic appearance of the ambulacral canals and oral plates. It seems the only plausible explanation of the presence of three rather than five plates alternating with the five plates of the above-lying circlet, which has no apparent adaptive significance. The morphogenesis of the pentaradiate symmetry in these structures, as will be shown below, will allow recognition and explanation of the pattern in the position of the unpaired plate.

According to many researchers, the usual model of the appearance of pentaradiate symmetry in the phylogeny of crinoids and many other echinoderms is described by the formula 2–1–2. This formula indicates the unpaired appearance of the ambulacrum A in ontogeny and a paired connection of the remaining four ambulacra. Usually, this connection is expressed by the fact that each pair of the B and C, D and E ambulacra is formed by the branching of a single short groove extending from the mouth. Often, grooves in these pairs are not equal (one is formed by branching from another). In the ontogeny of the ambulacral system, this morphogenetic inequality of the ambulacra should apparently be expressed by a certain sequence of appearance of the ambulacral canals. This sequence is reflected in the observed sequence of the appearance of the radials and the facets on them which are used for the arms' attachment. In addition, as noted above, the inequality of the ambulacra is reflected in the position of

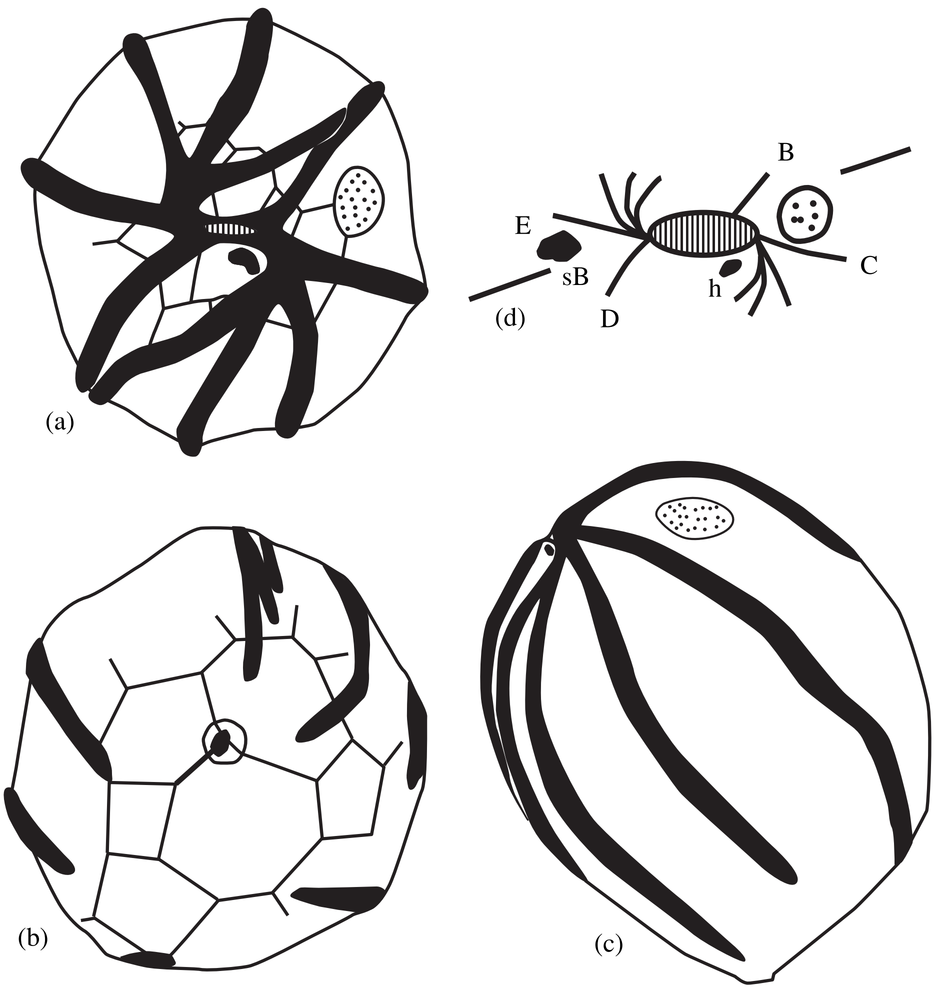


Fig. 24. Position of the major structure of the theca in paracrinoids *Malocystes murchisoni* E. Billings. CMS-P50436. Ambulacra are black, anus is dotted, mouth is shown by vertical hatching, (sB) small basal, and (h) hydropore.

the orals. Three of them, the AB, CD, and EA orals, are larger than two others (BC and DE), and contact each other by their distal ends in the center, above the mouth, whereas the ends of the two other plates do not reach the center and, thus, remain separated. Certainly, this arrangement of the orals indicates the primary sequence of their appearance in the ontogeny of their ancestors, based on the 2–1–2 model of the appearance of the food gathering grooves. This hypothesis agrees with the fact that the oral on the CD interray in some crinoids may be paired, consisting of right and left independent plates. Apparently, the latter is caused by the presence of the hydropore in the middle of this interray, and a stone canal extending from it.

The distal (oral) and proximal (basal or infrabasal) circlets are the first to develop in the ontogeny of the crinoid theca. It is these two circlets, appearing at the early stages, that determine the subsequent structure of the entire theca. Therefore, the development of these circlets at the early stages should be more or less rigidly correlated. If the AB, CD, and EA orals appeared first in ontogeny, then the first plates to appear in the basal circlet should be positioned radially and correspond to the first incipient radial ambulacral canals A; B, or C; D, or E. Which of the paired incipient ambulacral canals appears earlier is important for the primary position of the orals, basals, and infrabasals (closely connected to the orals in the early ontogeny) hence defining the direction of the branching of the canal.

It is important that the arrangement of plates in the proximal circlet, if it appeared relatively early in ontogeny, should reflect the triradiate symmetry, in which the A ray will potentially correspond to only one ambulacrum, and each of the two others to the two ambulacra appearing somewhat later. Therefore, the proportion of the size of the skeleton-secreting zones, and their separation in the basal circlet at this ontogenetic stage, can indicate the proportions of the appearing ambulacra. If such proportions are fixed in the ontogeny of the basal circlet when its morphogenetic correlations with the oral circlet are weakened in its further development, then the adults should have a characteristic ratio of basal plates, i.e., two large (paired) and one smaller (unpaired) basal plate.

However, the ray in which the unpaired basal plate will originally be located also depends on the sequence of appearance of the three original ambulacra, which could be different. Therefore, the unpaired basal plate could originally appear in the A, B, or E ray. Generally, though not invariably, the ambulacrum on the A ray appeared last in ontogeny, judging from the appearance of the radials and radial facets in fossils. This could also determine the frequency of the appearance of the unpaired plate on a given ray. In addition, the sequence of the appearance of the ambulacra in ontogeny determined the position of the basal and infrabasal plates indirectly, through the position of the oral plates. Therefore, if, for instance, the unpaired A ambulacrum determined the position of the unpaired plate in the basal circlet, it should have originally appeared not on the A ray, i.e., to the left of the corresponding unpaired oral plate, but on the B ray, to the right of this oral plate. This is connected with the original left-handed development of echinoderms, related to the disappearance of the right protocoel and mesocoel and the resulting tendency for morphogenetic processes to occur in the clockwise direction (i.e., from left to right). The influence of the original left-handed development on the morphogenesis of structures in echinoderms is discussed in the chapter on symmetry.

In addition, in ontogeny, after the appearance of the basal circlet, the infrabasal circlet rotated in relation to the oral circlet for half of the radius, i.e., 36°. This was necessary to preserve the alternating arrangement of plates in the neighboring circlets (like in a brick wall), and should have determined the position of the unpaired basal plate in the adults. Assuming this, in the adult dicyclic forms, the unpaired plate should have been shifted clockwise for one radius, and in the monocyclic it should have been displaced into the neighboring interray. According to the proposed model of morphogenesis of plates and circlets, a permanent position of the unpaired infrabasal plate in the C ray in Flexibilia represents an archaic characteristic reflecting the original development of pentaradiate symmetry through triradiate symmetry and the primary morphogenetic influence of the unpaired A ambulacrum through the orals, to the position of the unpaired plate in the basal circlet. According to this hypothesis, the original formation of the unpaired infrabasal plate in the ontogeny of Flexibilia occurred in the B ray.

For comparison, the position of the unpaired basal plate in Blastoidea, based on the above assumption, was originally the same as in Flexibilia, i.e., on the B ray. Indeed, in adults, this plate is usually located on the AB interray. Because it is situated in the basal circlet, after the appearance of the radial circlet, it should have been displaced by a half-radius in a clockwise direction. Therefore, it would have originally appeared in the B ray. In the polycyclic eocrinoid *Cryptocrinites*, a small, unpaired basal plate occurred in the EA interray. Perhaps, the incipient plate was displaced clockwise from its original position on the B ray in the ancestral polycyclic forms. However, this seems unlikely, because assuming this, the plate would have inscribed too a large circle. Apparently, in this case, the morphogenesis occurred somewhat differently. For instance, the displacement of circlets clockwise could have finished at earlier ontogenetic stages, because the appearance of the new circlets (third or fourth) in these forms apparently occurred without a displacement, with the latest plates already appearing in new positions. Because of this, the alternation of the plates in the new circlets was irregular. Therefore, the position of the unpaired basal plate is difficult to establish in these taxa due to insufficient data. The study of Paracrinoidea may help to resolve this problem.

How can the proposed model be tested? Unfortunately, in most cases, including the Flexibilia (which have the most characteristic structure of the basal circlet) it is not possible to see it directly because their early ontogeny remains poorly known. However, in the Early Permian hypocrinid (Cladida, Inadunata) *Cranocrinus praestans* Arendt, the ontogenetic changes of the theca, thoroughly described by Arendt, support the proposed model (Fig. 9). In this species, the unpaired infrabasal plate occurs in the C ray. As noted above, the radial or interradial position of structures in the ontogeny should be determined in relation to the radial ambulacral canals and hydropore, the positions of which are well defined even before the appearance of the radial plates in the structure of the oral circlet. The ontogenetic changes described by Arendt (1970) show a rotation of the infrabasal and basal circlets clockwise in relation to the oral circlet, after the radial circlet appeared. As a result, the unpaired infrabasal plate is displaced from the BC interray to the C ray together with the already formed basal circlet. Extrapolating this tendency toward a clockwise displacement, it is possible to suggest that before the appearance of the basal circlet, the unpaired infrabasal plate occurred in the B ray. This supports the possibility of such a displacement in Flexibilia. In contrast to Flexibilia, which show a stable archaic position of the basal plate, in hypocrinids, the unpaired basal plate could have originally occurred in other rays, usually in the E ray. This could have resulted from the increased diversity in the sequence of the appearance of the radial plates and, hence, radial ambulacral canals.

HOMOLOGIES OF PLATES IN THE FOUR-PART CIRCLET

This model can also be tested on the four-part basal and infrabasal circlets of the Ordovician genera *Perittocrinus* and *Colpodecrinus* (Fig. 20). Supposedly, the missing fifth plate in these genera corresponds to the unpaired plate of Flexibilia, because this structure of the proximal circlet in this group appears to be deep-rooted and connected with the morphogenetic mechanism of the appearance of the pentaradiate symmetry. The four-rayed stem in these genera supports this suggestion. In *Colpodecrinus*, the AB, or BC basal plate is absent in the basal circlet. This results from the fact that only one basal plate occurs radially, directly below the B ray, and has a single tapering. However, judging from the fact that the displacement of the plates in crinoids usually occurs clockwise, it is most likely that it is the BC plate, which is absent in the basal circlet. In any case, it can be positively stated that this genus did not have the B plate in the lintel circlet or a corresponding pentamere in the stem. This structure can, with a certain degree of confidence, be explained by the appearance of the basal circlet in this taxon at a stage of ontogeny when four ambulacra were already formed, while the development of the fifth ambulacrum was arrested. This, through the morphogenesis of the orals, was transmitted onto the basal circlet. Here, the correspondence to the original location of the unpaired plate of Flexibilia and Blastoidea in the C ray is observed. The lintel circlet, like the stem, received its four-part structure through the morphogenetic influence of the basal circlet. This suggests that the development of the pentaradiate symmetry of the food-gathering system directly influenced the morphology of the oral circlet in crinoids and, through this circlet, the morphology of the basal circlet in those forms retaining archaic features in the thecal morphology. However, in many crinoids, the secondary changes in the morphology of the most proximal circlet was affected by many other factors, primarily by the morphogenesis of the circlet lying immediately above (basal or radial). One of the most interesting cases is described in the section on asymmetry, where the influence of the original asymmetry on the frequency of the appearance of the left- and right-sided forms in echinoderm structures is discussed.

HOMOLOGY OF THE THECAL CIRCLET AS A MORPHOGENETIC PROBLEM

It was shown in this chapter that interpretation of the homology of the circlets and plates in the theca of crinoids should primarily be based on the morphogenesis of structures rather than just on their morphology, which can be similar in distant forms but very different in closely related forms. This approach allows the following major conclusions on the origin and homology of circlets and plates of the crinoid theca:

(1) Dicyclic and monocyclic crinoid cups appeared as a result of paedomorphosis of the original polycyclic forms.

(2) The basal circlet of monocyclic crinoids is homologous to the infrabasal circlet of dicyclic crinoids.

(3) The basal circlet of dicyclic forms is homologous to the radial circlet of monocyclic crinoids.

(4) The radial circlet of dicyclic forms is homologous to the third (counting from the proximal end) circlet of polycyclic forms and is not homologous to the radial circlet of monocyclic forms.

(5) The lintel circlet, present in some crinoids and occurring below the basal circlet in monocyclic forms and below the infrabasal circlet of dicyclic forms resulted from the inclusion of the proximal columnal that was subdivided into pentameres in the cup.

(6) The superradials of disparids resulted from the inclusion of the first brachials in the cup. Their development in some (rather than in all) rays was determined by a clearly seen sequence of the ontogenetic development of the radials.

(7) The superradial in the C ray of the genera *Hoplocrinus, Hybocrinus*, and other hybocrinids represents the remains of the reduced radial circlet, which is homologous to the radial circlet of dicyclic crinoids. This plate is not homologous to the upper C radial of disparids.

(8) Accessory plates of perittocrinids represent a morphological innovation connected to the appearance of accessory fold structures with a thinned stereom. Through these fold structures (and the pore structures of other pelmatozoan echinoderms), feeding on bacteria and dissolved organic matter was performed. The respiratory function was only secondary. These structures are connected with somatocoels and in this sense homologous, although many of them appeared independently. They did not have a direct connection with the ambulacral system.

(9) The consistent structure of the basal or infrabasal circlet in many groups of crinoids, eocrinoids, and paracrinoids was composed of three plates, one of which was small and unpaired, is determined by the sequence of the development of pentaradiate symmetry of the ambulacral system from the primary triradiate symmetry. The appearance of the unpaired plate in ontogeny originally corresponded to the unpaired A ambulacrum and occurred in the B ray. The further displacement of this plate in ontogeny occurred clockwise and resulted from the morphogenesis of the dicyclic or monocyclic cup.

SECTION 2. ORIGIN AND HOMOLOGIES OF THE ANAL STRUCTURES IN THE SKELETON OF PELMATOZOAN ECHINODERMS

The anal structures in the skeleton of pelmatozoan echinoderms represent an expansion in the theca of the animal, resulting from the position of the rectum, or anal exit, which is typically formed or surrounded by special plates. The anal structures can also extend outside the theca in the form of an anal tube, or a large anal sac, performing some additional functions connected with respiration, feeding, and reproduction. The anal structures are most diverse and best-studied in crinoids. Features of their structure are used in the systematics and taxonomy of many taxa in this class, although the homologies of some plates are debatable. Therefore, it is necessary to study the evolutionary morphogenesis of these structures and to discuss their origin in order to substantiate convincingly the concepts of homology. In eocrinoids, the anal structures are less clearly expressed. They are more uniform and are studied much more poorly than in crinoids. Therefore, the anal structures are discussed below in greater detail in crinoids, while the data on their organization in other classes of pelmatozoan echinoderms will be used only for discussing their homologies and origin.

ANAL STRUCTURES IN THE SKELETON OF CRINOIDEA

Among Paleozoic crinoids, the structure of the anal area is considerably different in Camerata, on the one hand, and in Inadunata and Flexibilia on the other. In the first subclass (Camerata), the anus is located on the top of the small anal pyramid, which is only slightly elevated above the thecal surface. In this sense, the anus is very similar to the anal structure of the ancestral eocrinoids. In Inadunata and Flexibilia, the anus is usually located at the end of the large anal sac or on a long armlike process (Fig. 25). These represent recently formed structures that do not occur in other echinoderms. Among Inadunata, the diversity of extrathecal anal structures is the highest and reflects different stages of the development of these structures.

STRUCTURE AND HOMOLOGIES OF THE PLATES OF THE ANAL SERIES IN DISPARIDA

In monocyclic inadunates (Disparida), the anus is located on the end of an armlike process. Dorsally, this projection is usually almost identical to the dorsal skeleton of an arm. Functionally, the dorsal skeleton of the anal projection represents the first left branch of the dorsal skeleton of the arm in the C ray (Fig. 25d). Comparative morphology of disparids clearly shows that such an interpretation is also correct morphogenetically. Therefore, the anal projection of disparids can be interpreted as a morphogenetic combination of the rectum with the left branch of the dorsal skeleton of the arm in the C ray. This hypothesis is also supported by the fact that, in some disparids of the family Eustenocrinidae and superfamily Calceocrinaceae, the rectum completely embraces the dorsal skeleton of the arm in the C ray (Figs. 26, 81). As a result, this crinoid becomes effectively four-armed; the other structures of the arm, except the aboral skeleton, do not develop in the C ray of this crinoid.

When the low anal cone of eocrinoids is compared to the long anal tube of disparids, it becomes clear that the rectum and its primary skeleton are not capable, on their own, of metameric growth. The use of the dorsal skeleton of the arm for better support of the rectum allowed considerable elongation of the rectum, and a significant increase in the distance between the mouth and anus. However, the latter change has less functional

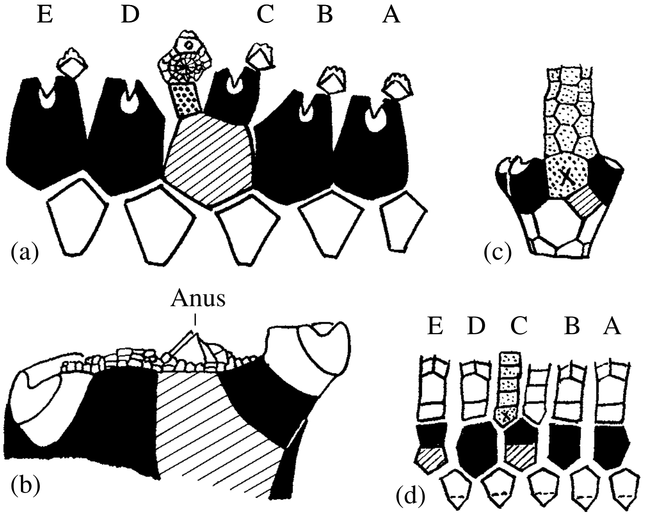


Fig. 25. Structure of the anal interray in (a, b) hybocrinids, (c) monocyclic inadunates, and (d) dicyclic inadunates: (a) arrangement of plates in the theca of *Hybocrinus nitidus* Sinclair; (b) anal interray in *Hoplocrinus estonus* Opik, specimen PIN, no. 4125/9; (c) *Botryocrinus cucurbitaceous* (Angelin), lateral view of the cup, CD interray; (d) arrangement of plates in the crown of *Columbicrinus crassus* Ulrich (after Rozhnov, 1985).

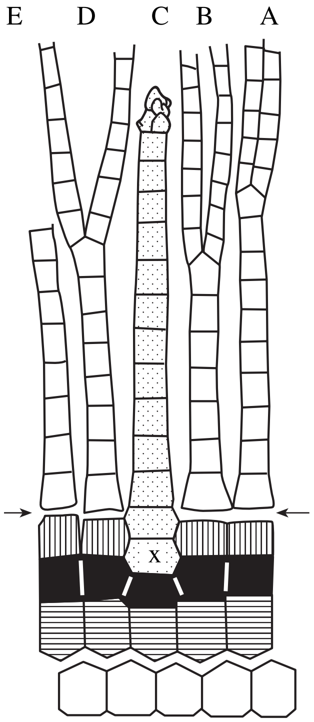


Fig. 26. Composition and relationships of the plates of the crown in the genus *Eustenocrinus* Ulrich. Aboral skeleton of the arm in the C ray is completely occupied by the rectum and transformed into the anal tube (after Moore, 1962). Inferradials are horizontally hatched, radials are black, the first brachials are vertically hatched, anals are dotted. Arrows indicate the probable border of the cup.

importance than is generally thought, because the mouth in pelmatozoan echinoderms does not catch food from the outside, but receives it through the food grooves from a wide food-gathering network of arms or brachioles. A considerable elongation of the upper part of the digestive tract, which allowed increased capacity for digestion without an increase in the size of the dorsal cup, was apparently of much greater importance. In addition, in further evolution, this allowed a considerable increase in the functional possibilities of the resulting anal sac. It played a noticeably larger role in respiration and, perhaps, in feeding on dissolved organic matter; it could also have lodged a gonad. This last assumption is very important, because it explains the large volume of the so-called anal sac in dicyclic inadunates, which later formed on this morphogenetic basis.

STRUCTURE AND HOMOLOGIES OF THE PLATES OF THE ANAL SERIES IN CLADIDA

In the crinoid subclass Cladida (primarily Dendrocrinina and Poteriocrinina), the anal structures are represented by a very large sac covered with plates, which occupies a large space above the theca, between the arms. Its surface, from the peripheral side, is composed of plates, which are morphologically similar to those of the cup, while from the inside it is often composed of lines of small plates (often star-shaped) with pores in between them. The anal opening occurs on the end of the anal sac and is covered by the plates of the anal pyramid. The anal sac of Cladida is distinguished from the anal tube of Disparida not only by its size, but also by the fact that its peripheral proximal part is included in the cup; generally, one or two plates of its base are included in the cup (Fig. 25d). One of these plates is referred to as the radianal, while the other is called the anal X. Morphological series show that the radial plate is homologous to the C superradial or to the first auxiliary plate in the C ray in disparids. The anal X is homologous to the first plate of the anal tube of disparids, i.e., to the first plate of the aboral skeleton of the first left branch of the arm in the C ray. This indicates the presence of the inferradial in the C ray in some Cladida and Flexibilia. Different variations of homologies of these plates are carefully discussed in the brief but informative studies of Philip (1964, 1965). It is noteworthy that it is not necessary to give a different name to each slightly different morphology, because they all essentially correspond to the first left branch of the aboral skeleton of the arm in the ray. Some disparids also occasionally have an anal sac (e.g., *Iocrinus*). However, in these taxa, all anal plates occur outside the cup. This may indicate the origin of cladids and disparids from polycyclic forms, through variously deep paedomorphic changes. What was the reason for the appearance of the large anal sac in inadunates, and what functions could it perform? It appears that the main reason for the appearance and subsequent increase of the anal sac was the migration of the gonad into it. This is considered in greater detail below.

POSITION OF THE GONAD IN INADUNATA

Compared to Eocrinoidea, inadunates have a relatively smaller theca. It is especially noticeable when the total size of the body, including the length of the stem and the food-gathering system, are compared. The size of the theca in inadunates, and especially in disparids, does not in most cases exceed 10% of the size of the stem and arms and is sometimes even smaller. In most eocrinoids, the size of the theca considerably exceeds the combined size of the stem and brachioles, and it is always at least 50% of the total size of the body. In mature individuals, the gonad occupies a considerable space. Crinoids do not have a gonopore in the theca (unlike eocrinoids and cystoids). Therefore, the gonad, especially considering its large size and the small size of the theca in inadunates, should have been at least partly outside the theca. In modern crinoids, the gonad develops in pinnules. In many Paleozoic inadunates, pinnules are absent. The development of the gonad in the arms should have disturbed the food-gathering function. Hence, it is reasonable to suggest that the gonad was not lodged in the arms or inside the theca. The only other possible place to house it would have been in the anal expansion in disparids, and in the anal sac in cladids. If this assumption is correct, the development of the gonad in the inadunate crinoids would have differed considerably from that in ancestral eocrinoids and modern articulated crinoids. In contrast to eocrinoids and other Blastozoan echinoderms, the gonad in crinoids developed outside the theca. However, as in these groups, the gonad in crinoids only developed in one interray (anal) and apparently, together with the stone and pore canals and a system of blood vessels, formed a complex of organs similar to that of starfish, brittle-stars, and sea urchins. In most modern crinoids (Fig. 27), a series of cells containing the primary sex cells adjoins the upper part of the Axial organ (Glandular organ) (which at the base occurs in the central cavity of the chambered organ and at the top is blindly terminated near the oral hemal ring). This series of cells continues to the genital cords of the arms (Fedotov, 1951). In contrast to a single gonad occurring in the anal interray, as in the earliest crinoids, in modern crinoids there are many genital glands. They are lodged in the pinnules and are adjoined by the genital cord extending around the esophagus and connected, in stalked forms, with the cell complex of the axial genital cord. The structure of the reproductive system in modern crinoids depends on pentaradiate symmetry. However, in many early crinoids, it was apparently not radially symmetrical, and the position of the gonad in these groups could vary considerably. In most taxa it was most likely located outside the theca, in the anal structures, whereas in some it could migrate in the opposite direction, to the stem, or even to the holdfast.

I suggested this previously, when describing peculiar multiplated holdfasts from the Middle Ordovician of Estonia (Hints *et al.*, 1989). The structure of these holdfasts and the possible occurrence of the gonad in

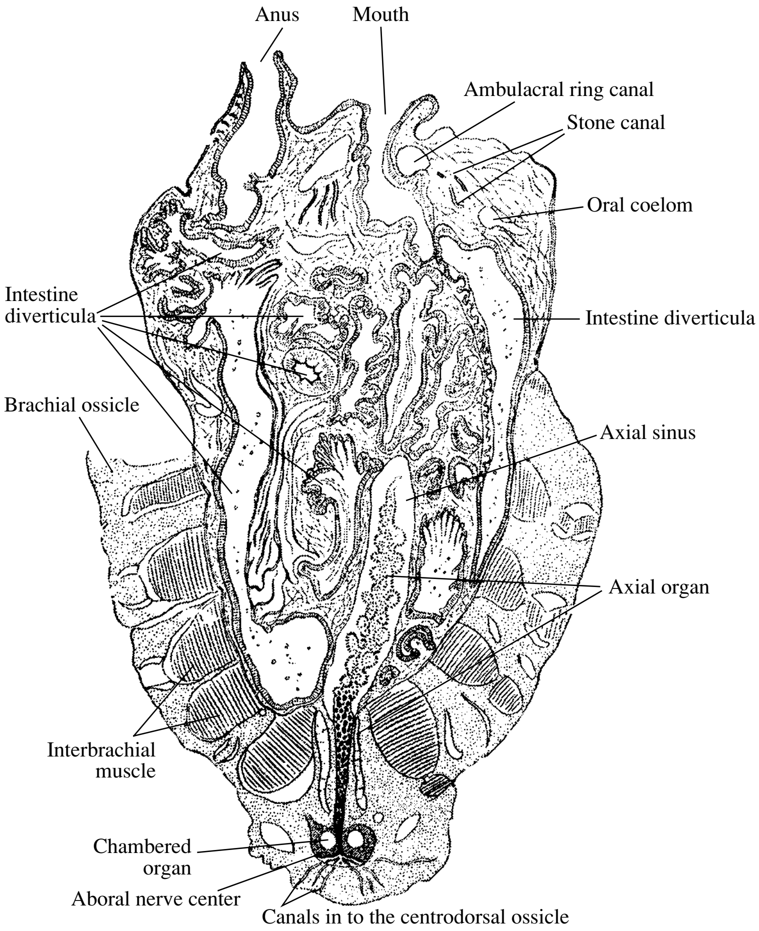


Fig. 27. Vertical section through the middle of the cup of the crinoid *Heliometra glacialis* (after Ivanov *et al.*, 1946).

them are discussed in the section on the structure of the stem. Thus, the appearance of the anal sac in crinoids could be functionally connected not only with the elongation of the digestive system, but also with the necessity for a special container for the gonad. The following morphological sequence is observed in the development of the anal area: (1) a low anal pyramid on the side of the theca in its distal (or, more rarely, proximal or middle) part (all blastozoan echinoderms and most crinoids, primarily Camerata); (2) an armlike process, elevated above the cup (most disparid crinoids); (3) an anal sac (most cladid inadunates and Flexibilia). The anal pyramid is present in all three morphological types of anal area. Its purpose is to enable active pulsation of the rectum, to inject and eject water. Apparently, in many cases, this was an important mode of respiration. From the comparative-morphological point of view, it is not just the structure of the anal pyramid, the anal sac, or the anal armlike process that is most interesting, but the arrangement and homology of the plates at the base of these structures, which mostly represent parts of the theca.

STRUCTURE OF THE ANAL AREA IN HYBOCRINIDS

The structure of the anal area in hybocrinids (like many other structures) was usually considered to be the same as in disparids, or only slightly different. Therefore, until recently, they were placed in the order Disparida within the inadunate Crinoidea (Moore *et al.*, 1978). Rozhnov (1985a, 1985b) recognized them as a separate subclass Hybocrinea (within Crinoidea). One of the arguments in favor of this proposal was the presence of the anal pyramid in *Hoplocrinus*, which I observed in this genus above the extended left part of the inferradial (Fig. 25b). It was clear from this structure that the anal plate in the cup of *Hybocrinus* is a plate of the tegmen that was included in the cup (Fig. 25a), or a new structure that filled the extension in the cup used for the rectum, and is not connected with the left posterior branch of the arm in the C ray, as in disparids. Thus, the anal structures in hybocrinids represent only slightly modified structures of ancestral eocrinoids.

ORIGIN OF THE ANAL PLATES IN THE THECA OF PELMATOZOAN ECHINODERMS

Among all pelmatozoan echinoderms, and possibly all echinoderms, the plates of the anal pyramid covering the anal opening are probably homologous, because they have a very ancient origin. All other structures evolved later. The plates covering the extension in the theca, where the rectum is located, evolved later, and in many groups could have appeared synchronously. The anal tube and the anal sac of crinoids evolved even later. To understand the homology of the plates of the anal area, their origin should be revealed. With this purpose, their structure in primitive eocrinoid taxa is discussed below, but a few words should be said beforehand about the structure and ontogeny of the digestive system of crinoids.

The intestine of crinoids, which is subdivided into the esophagus, middle intestine, and rectum, begins with the mouth opening in the middle of the oral part of the theca. Consisting of a narrow tube, it turns clockwise (seen from the oral side), descends into the wide part of the middle intestine, from which the branch of the rectum again ascends, and opens by the anal opening at the top of the anal pyramid. It is very important that the intestine is coiled clockwise, because it indicates the direction of growth in taxa with more primitive ontogeny than modern crinoids. Its primary clockwise coiling, very typical of all echinoderms, is, as shown in the section on symmetry, connected with the primary left-sided asymmetry of all echinoderms. It is noteworthy that the coiling intestine usually forms a complete circle, i.e., the anterior end is curved from the centrally positioned mouth in the CD interray and is coiled clockwise, eventually opening into the anal opening, also in the CD interray. Sometimes this circle is incomplete, and the anus occurs in the C ray, or even in the BC interray. Such deviations are apparently connected with heterochronies appearing in the process of ontogeny. Thus, the CD interray is especially important for the digestive system, because it contains both the descending branch of the digestive tract (close to the axis of the theca), and the ascending branch, running along the wall of the theca and terminating by the lateral or upper lateral anus. Hence, the anal CD interray should be wider than the other interrays. In many eocrinoids, and many camerate crinoids, the increase in the width of the interray is achieved by additional plates, or by a series of additional plates with an anal pyramid at their distal end in this interray. In some eocrinoids, cystoids, and some crinoids, the ascending branch of the rectum was very short, and the anus was located closer to the distal end of the theca (Fig. 21). In these cases, special anal plates were usually absent.

In the multiplated eocrinoids, the arrangement of the anal plates became more regular as the arrangement of the thecal plates became more regular. Their growth and arrangement were in accordance with the developing circlets of the thecal plates. No fundamental difficulties arise in homologization of the anal plates in different groups, while the interpretation of the correspondence of the anal plates in different groups depends on the homologization of the circlets in each case. However, the same applies to homologization of the anal plates of the camerate crinoids.

In disparid crinoids, all anal plates occur outside the cup, and originate from the plates of the dorsal skeleton of the left branch of the C arm in the C ray, or in some cases the entire C arm. In some disparids, for instance, in iocrinids, this homology is evident, since the anal projection branches off the C arm. The branching of the anal tube did not necessarily occur immediately above the superradial (it could also be higher). However, in the phylogeny of crinoids there is a trend towards displacement of the branching point to within the cup. As was discussed in the section on the homology of thecal circlets, this process led to appearance of the superradials, including those in other rays, which somewhat complicates the recognition of the homologies of the anal plates. For instance, in pisocrinids (disparid inadunates) the origin of the anal series of plates is slightly masked, because this series is supported by a specific expanded projection composed of the lateral parts of the C and D cup plates. However, even in this case, the homologies and origin of the anal plates are not difficult to recognize when these crinoids are compared to the ancestral homocrinids.

The situation is different with Cladida and Flexibilia. One or two anal plates (sometimes more) are included in the cup, while the remaining plates of the anal sac occur outside the cup (Fig. 25c). The problem lies in interpreting the homology of the anal plates in the cup; are they homologous to the original plates of the theca of the eocrinoid ancestors, or to the plates of the left branch of the C arm included in the cup? The answer to this question is certain. Morphological sequences, equivalent to those among disparids, convincingly show that the so-called radianal plate in this group is derived from a primary radial, usually displaced clockwise from its original position to the left. The radial plate lying above it is derived from the first brachial included in the cup, whereas the anal pate X is derived from the first plate of the left branch of the arm in the C ray, which gave rise to the anal sac after being embraced by the rectum. As shown above, the radials of monocyclic and dicyclic crinoids are not homologous. Hence, the radianal plate of cladids is not homologous to the C inferradial of disparids, as was previously assumed. However, the C radial of cladids and the C superradial of disparids are homologous, because both are derived from the first brachials (Fig. 28). Thus, the similar morphogenetic mechanism of development of the anal sac in Disparida, Cladida, and Flexibilia resulted in a similar structure of the C ray, although it was based on transformations of originally different plates.

The origin of the anal series in the camerate crinoids is different. It is not connected with the plates of the arm being included in the cup. Partly, the anal plates, at least those occurring within the primary cup, were inherited from the ancestral crinoids. Partly, they are innovations connected with the interambulacral plates, appearing when the arms are included in the theca above the primary cup.

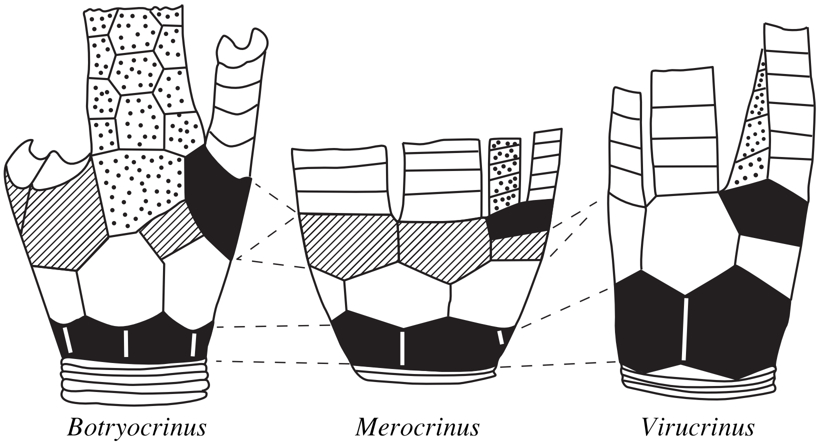


Fig. 28. Homologies of the anals in typical cladid crinoids (left), cladids with the paired radial in the C ray (center), and a disparid crinoid (right). Infrabasals of cladids, basals of disparids, radials, and superradials in the C ray are black, radials and the radianal of cladids are diagonally hatched, anals are dotted.

The anal structure is different in hybocrinids (Figs. 25a, 25b). Although the structure of the anal area and the C ray in the genus *Hybocrinus* is similar to that in inadunates, the origin of these structures was apparently different in these groups (Rozhnov, 1985a, 1985b). This is indicated by the fact that, instead of the anal sac, this genus had only the anal pyramid, which is not capable of significant distal growth. Therefore, the anal plate in this genus originated from the inclusion into the ventral part of the theca of one of the tegmen plates surrounding the anal pyramid. This hypothesis is supported by the structure of the closely related genus *Hoplocrinus* from the Ordovician of the Baltic region, which lacks the anal plate. Instead of this plate, in the anal interray, this genus has an elongated left distal part of the inferradial plate of the C ray.

To summarize the above discussion, the following conclusions on the anal structures in pelmatozoan echinoderms can be made:

(1) The anal structures in the skeleton of most pelmatozoan echinoderms are confined to the theca, and represent an expansion of one of the interrays (usually the CD interray, containing the hydropore, but sometimes the previous BC interray), covered by special plates and used to embrace the rectum. Such expansion terminates in the anal pyramid, covering the anal opening.

(2) In some crinoids (Inadunata and Flexibilia), the anal pyramid occurs at the end of a specific anal tube, or anal sac, projecting far outside the theca.

(3) The anal tube in Disparida morphogenetically originated from the aboral skeleton of the first left branch of the arm in the C ray embraced by the rectum.

(4) In some cases, the rectum may completely embrace the aboral skeleton of the arm in the C ray. In this case, the other structures in the C ray do not develop.

(5) The anal sac of Cladida represents a further development of the aboral skeleton of the left branch of the C arm, proximally included in the theca.

(6) The anal tube and anal sac of Inadunata and Flexibilia were not only used to contain the rectum, but possibly also the gonad.

(7) The anal structures in the skeleton of Inadunata, Flexibilia, and hence, Articulata, are morphological innovations, and are not homologous to the anal structures of Camerata and ancestral Eocrinoidea, or to those of Hybocrinida.

(8) The radianal plate of Cladida is homologous to the superradial of most Disparida, and originates from the first auxiliary brachial included in the cup.

(9) The anal plate X of Cladida is homologous to the first plate of the first left branch of the aboral skeleton of the C arm in Disparida.

(10) The anal structures of Hybocrinida are homologous to those of the ancestral Eocrinoidea, and probably some Camerata, but they are not homologous to the anal structures of Inadunata and Flexibilia.

SECTION 3. ORIGIN AND HOMOLOGIES OF THE STEM IN PELMATOZOAN ECHINODERMS

The stem is present in almost all pelmatozoan echinoderms (Fig. 1). In a few taxa it is reduced, and in some is completely absent. The stem is connected to the theca by its proximal end, and to the substrate by its distal end. Therefore, the distal end of the stem usually has a specific attachment structure (holdfast) that may be simple or complex. The stem is composed of metameres (columnals), with an axial canal in the center. In some eocrinoids, instead of the stem, there is a nonmetameric or weakly metameric extension, poorly separated from the theca, and possessing an attachment sole. Its skeleton is composed of more or less irregularly arranged polygonal plates, rather than separate ossicles. Sprinkle (1973a) referred to this type of stemlike projection as the holdfast, but to avoid confusion with the genuine holdfast on the distal end of the stem, it is here called the peduncle.

HOMOLOGIES OF THE METAMERIC APPENDAGES IN DEUTEROSTOMES

Before the discussion of the origin of the stem, and the explanation of various combinations of the stem and theca, possible homologies of the stem to the attachment processes, taillike appendages, and some other structures of deuterostomes are considered. Apart from the above mentioned (1) metameric stem and (2) nonmetameric peduncle, echinoderms have the following appendages and attachment structures: (3) peduncle in some starfish larvae, appearing when they settle and later disappearing; (4) attachment sole and collar in Edrioasteroidea; (5) stem in Edrioasteroblastoidea; (6) stele in Homostelea; (7) arm in Homoiostelea; (8) metameric appendage in Stylophora.

The rays of starfish, somasteroids, and brittle stars, the arms of crinoids, as well as the brachioles of cystoids and other groups, are also appendages of the body. However, these structures appear in large numbers in the ontogeny, and participate in several systems of organs of different origin. This suggests that they represent a specific form of growth of radially symmetrical echinoderms. Therefore, their homologies should be considered within the radially symmetrical echinoderms, whereas only the separate structures of these appendages may be correlated with those in other echinoderms, chordates, and hemichordates. It is unconvincing to suggest, for instance, that the ray of a brittlestar and the metameric appendage of Stylophora are homologous. Brachioles and other appendages, apart from the fixation peduncle, of starfish larvae are adaptations to the larval lifestyle, and their homologies are unclear. Among hemichordates, a useful example is the proboscis of Enteropneusta. The proboscis is derived from the protocoel, and has a single proboscis pore located on the left. Following the proboscis there is a short medium body division (mesosome), represented by the so-called collar. Pterobranchia have a posterior contractible stolon, and one of the genera (*Cephalodiscus*) has a fixation organ, apparently formed from a small depression with glandular cells on the posterior end of the larva. Among chordates, an interesting organ for this comparison is the tail, present in cephalochordates, vertebrates, and some tunicates (ascidians). It is noteworthy that the larvae of ascidians have anterior fixation papillae, which are not regarded as homologous with the preoral fixation lobe of echinoderms (Ivanova-Kazas, 1978).

What is the similarity and difference between all the above appendages of deuterostomes from the morphogenetic point of view, and with which can the stem of pelmatozoan echinoderms be compared? This comparison can be based on the coeloms constituting these structures. For instance, the tail of chordates is formed by somatocoels. However, the stem of crinoids contains a five-chambered organ connected, in its origin, with somatocoel. This suggests that these structures are homologous (Malakhov, 1977, 1982, 1989, 1996). The presence of somatocoel in the stem of crinoids is a major difference between the crinoid stem and the fixation peduncle of the larvae of some starfish, because the peduncle is formed using axocoels (Fedotov, 1923). However, there is an important similarity between the peduncle of the starfish larvae and the stem of crinoids; both have a holdfast on the end, which is, in both cases formed from the preoral lobe. Based on this fact, Ivanova-Kazas (1997) considered the view of Malakhov on the homology of the crinoid stem and the tail of chordates to be erroneous, without taking into account the participation of the somatocoel in the development of the crinoid stem. It seems that the development of the crinoid stem and the peduncle of starfish from the preoral lobe, and the attachment of echinoderm larvae by the preoral lobe, are extremely important for establishing the homologies of these structures, because they indicate deep morphophysiological correlations between many processes of development. However, it is necessary to take into account the presence of the particular coeloms in these structures. Hence, it can be concluded that the stem of pelmatozoan echinoderms evolved as a result of integration of morphogenetic potential of the somatocoels and the preoral lobe (Rozhnov, 1986, 1987a, 1990b). Another hypothesis, that echinoderms, like pterobranchiates, used a morphological innovation on the morphological posterior end of the body (so-called tail) (Malakhov, 1989) to attach to the substrate, contradicts paleontological data, because the stem, as shown below, gradually develops from the nonmetameric attached part of the body (Sprinkle, 1973a), or by polymerization of the attachment disk. Therefore, the stem of the pelmatozoan echinoderms is only partly homologous to the tail of chordates, only because it is also connected in its origin with the somatocoels. The stem is partly homologous to the attachment peduncle of some starfish larvae, because in both groups the place of fixation originated from the preoral lobes. It is noteworthy that in starfish this podium is not metameric. Perhaps it was connected with the absence of a morphogenetic link between the posterior coeloms and the holdfast. The anterior coeloms apparently had lesser potential for independent metameric growth. However, the presence of the stem in Edrioblastoidea may be connected with the metameric growth of the protocoel morphogenetically connected with the holdfast. In this case, the stems of crinoids and edrioblastoids are not homologous. This problem is discussed in greater detail below, when discussing the structure of edrioblastoids. The stele of the Homostelea (Cincta), which does not have a holdfast on its end (Ubaghs, 1967d), can be homologized with the tail of chordates. The establish-

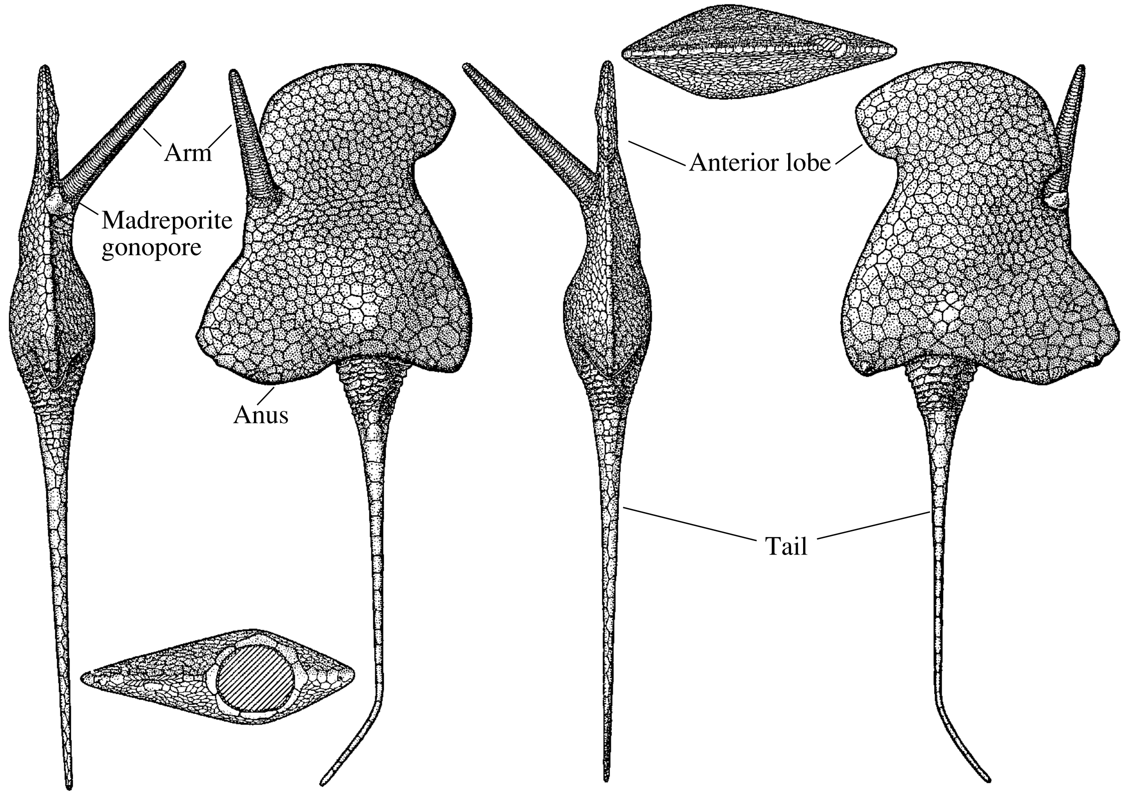


Fig. 29. Reconstruction of the skeleton of *Maennilia estonica* (Soluta) from the Middle Ordovician (Caradoc, Keila Horizon) of Estonia.

ment of Homoiostelea (Soluta) is difficult, because recently a holdfast was found in the earliest representatives of this group.

STELE AND STRUCTURE OF THE SKELETON OF HOMOIOSTELEA (SOLUTA)

The stele of Homoiostelea can be homologized with the tail of chordates, and hence, partly, with the stem of Pelmatozoa. However, for detailed consideration, the development of so-called larval and postlarval segments in the chordate body should be taken into account (Ivanov, 1944; Svetlov, 1957), whereas in echinoderms the presence of the larval segments is only apparent. The problem of the larval and postlarval segments and metamerism is discussed in detail below, when the symmetry in echinoderms is discussed. The accepted homology of the stele of Soluta greatly depends on which concept of their origin is applied. In recent years, P. Jefferies has been working on the part of calciochordate theory dealing with the evolutionary transition from a *Cephalodiscus*-like ancestor to echinoderms and chordates. He has thoroughly studied and described the morphology of Soluta (or Homoiostelea), which is of great importance in this respect. First of all, this is a detailed description of *Dendrocystoides scoticus* from the Upper Ordovician of Girvan, i.e., the same locality that yielded *Cothurnocystis elizae*, a famous cornute stylophore species (Jefferies, 1990). Many morphological details, and a new interpretation of the animal's position in life, were based on the description of the skeleton of the genus *Maennilia*, closely associated with *Dendrocystoides* from the Middle Ordovician of Estonia (Rozhnov and Jefferies, 1996).

What are Soluta? They have a theca, a tail, a food-gathering process (arm) of typical echinoderm structure, an anus, a madreporite, and a gonopore (Fig. 29). Paleontologists generally agree on the interpretation of these body parts, although Jefferies refers to the theca as the head, which is necessary for the calciochordate theory. In addition, he discovered slit pores between the plates in some genera, which he interpreted as gill slits. The well preserved skeleton of *Maennilia estonica* does not have clearly visible pores. These pores may be present on impressions of *Dendrocystoides* from Girvan. Jefferies suggested that the preoral lobe contained the gonad. This is also possible, because of the presence of the gonopore at the base of the lobe.

The arm of Soluta represents a long process (approximately half the length of the theca) covered by four series of plates. The beginning of the arm is outlined by rigidly articulated plates. The structure and functions of the arm are discussed in detail in the chapter on the homology of the food-gathering processes in echi-

Fig. 30. The earliest solute species *Coleicarpus sprinklei* Daley, from the Middle Cambrian of Utah, has a holdfast on the end of the tail. Specimen UCGM 46438, with three adult individuals attached to a fragment of an agnostid cephalon.

noderms. Here, possible homologies of the stele are discussed in the light of new, differently interpreted data.

In a recent paper Parsley (1997) suggested Soluta as possible close relative of Eocrinoidea (Fig. 30), based on the presence of the small holdfast on the end of the stele in *Coleiacarpus* (Fig. 31), one of the earliest Soluta. The presence of this structure makes this genus similar to some species of the Cambrian eocrinoid genus *Gogia*. This hypothesis is doubtful, because of other features of Soluta and Eocrinoidea. Firstly, doubts arise because of the arms and ambulacral ring; the food-gathering apparatus of eocrinoids, with its radial and often pentaradiate symmetry, is fundamentally different from that of Soluta (which had a single arm), and could not have evolved by a simple increase in number of arms, because it is connected with a complex anatomical reconstruction of the entire body. Otherwise, some Soluta would have occasionally had at least two arms. In Soluta and Eocrinoidea, the ambulacral system was certainly different. In Soluta, it included a sac-like equivalent of the ring canal of the recent echinoderms (this is indicated by the absence of radial symmetry), and a ring-shaped, or at least horseshoe-shaped (in cases where it was interrupted) ambulacral canal in eocrinoids. Another important doubt concerns the possibility of homologization of the eocrinoid stem and the tail of Soluta, although in the earliest Soluta the tail could be fixed by a special structure to the substrate. The stem of Eocrinoidea, like the stem of Crinoidea, represents a morphological and morphogenetic combi-

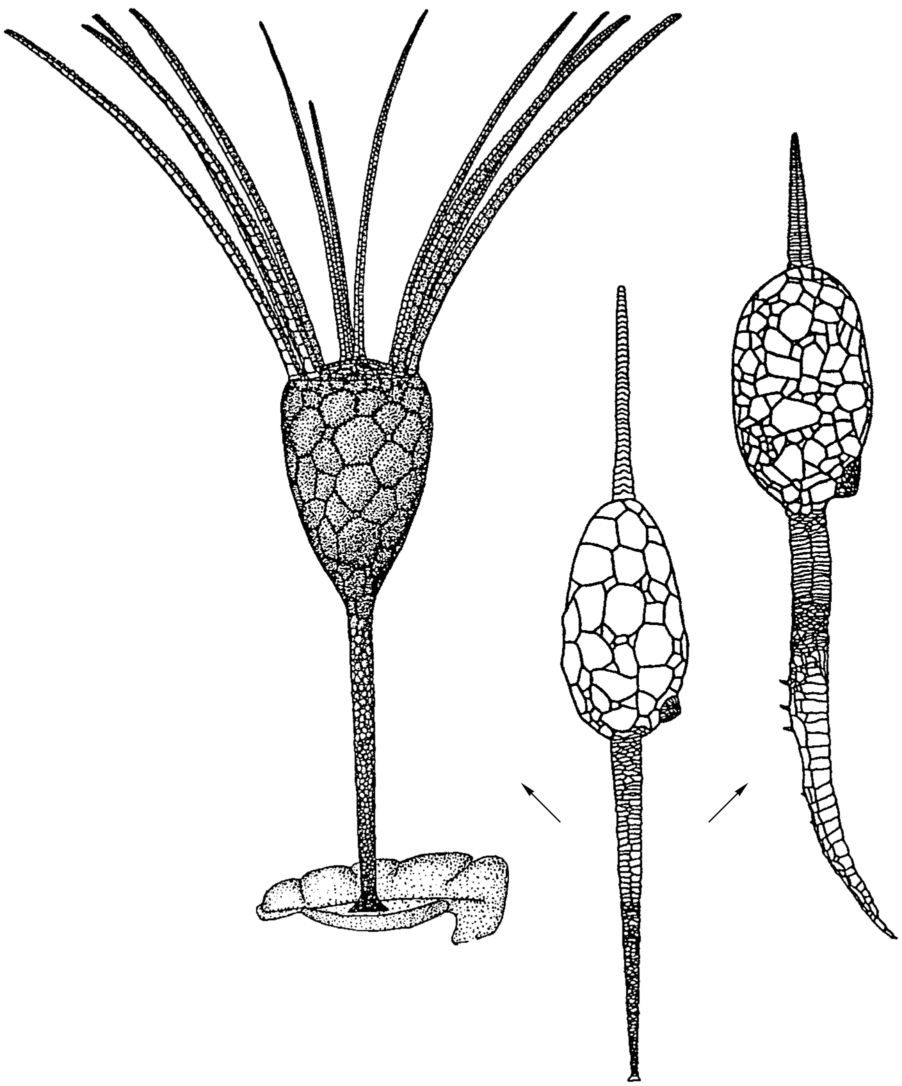


Fig. 31. Illustration of Parsley's (1971) hypothesis of close relationships of the earliest Soluta and the eocrinoid *Gogia*. The primitive solute *Coleicarpus* has a globe-shaped theca, and a holdfast on the end of the tail. Adult Soluta have no holdfast.

nation of the fixation of the preoral lobe of the larva and the projection of the somatocoel. This morphogenetic connection was established to have occurred at the time of the phylogenetic twisting of the attached ancestor of pelmatozoan echinoderms, which was close to the time of the appearance of radial symmetry in this group. Soluta, a group originally lacking radial symmetry, apparently did not have this morphogenetic, or simply morphological, combination of structures. Therefore, the stem of Eocrinoidea is only partly homologous to the tail of Soluta, because somatocoels take part in both structures. However, their holdfasts are completely nonhomologous, because in Eocrinoidea the holdfast is homologous to the preoral lobe of the echinoderm larva, and, possibly, to the preoral body division of Pterobranchia (*Cephalodiscus*), while in Soluta, this rarely occurring structure may be a morphological innovation, or may be homologous to the holdfast on the stem of *Cephalodiscus*, which is not connected to the preoral lobe of the larva. Therefore, Jefferies' opinion about the evolution of Soluta from a *Cephalodiscus*-like ancestor seems more reasonable (Jefferies, 1986, 1990, 1997; Jefferies *et al.*, 1986).

METAMERIC APPENDAGE OF STYLOPHORA

There is no agreement about the interpretation of the metameric appendage of Stylophora (Fig. 32). For instance, Jefferies (1967, 1986, 1969, 1979, 1986, 1977) interpreted this metameric process as a tail, and described these animals using chordate terminology. In his interpretation, the axial longitudinal groove on the surface of the stylocone and the ventral part of the process represents room for the notochord, covered on top by the dorsal nervous cord and the muscles lying above it. Inside, the notochord contained a blood vessel, from

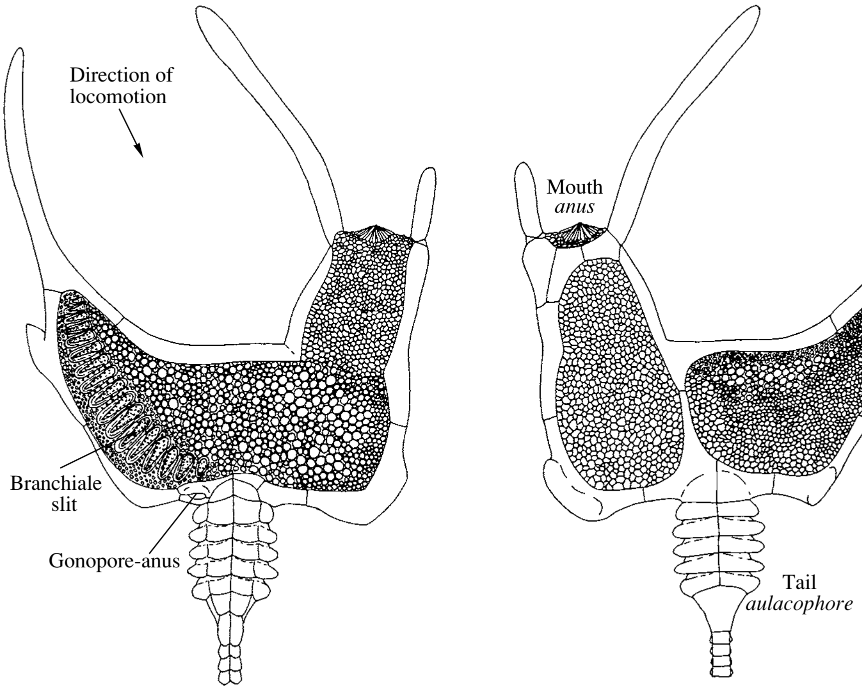


Fig. 32. Structure of the cornute *Cothurnocystis elizae* according to the calciochordate theory (regular font) and aulacophore theory (italics).

which lateral canals extended to the right and the left in each segment (indicated by the presence of transverse grooves). Based on the interpretation of the segmented division as a tail containing a notochord, the calciochordate theory suggests all other interpretations of the structure of these animals, i.e., the position of the mouth and anus, interpretation of the contour pores as gill slits, the presence of the buccal cavity and the pharynx in the head. Ubaghs (1967c, 1981) considered the segmented appendage of Stylophora to be a flexible food-gathering organ, called it the aulacophore, and compared it to the arm of ophiuroides. In his opinion, the groove inside the cavity of the aulacophore on the surface of the stylocone and the ventral plates, enclosed the radial ambulacral canal, while the transverse grooves indicate the extending ambulacral podia. Dorsal plates are homologous to the cover plates of crinoids. This echinoderm, or aulacophore, interpretation of the metameric appendage suggests the following interpretation of the remaining part of the body of stylophores. The mouth was intrathecal, connected with the food-gathering canal. The canal extended from the food groove on the stylocone, and ran through the muscles of the proximal part of the aulacophore. The anus, in the shape of the anal cone, was on the opposite side of the body (the mouth according to the calciochordate hypothesis). The opening, near the point that the aulacophore entered the theca, represented a hydropore (anus-hydropore according to Jefferies). The contour pores are interpreted as respiratory organs. But how did they perform this function? Apparently, through the gill slits. The class Stylophora includes two subclasses, Cornuta with a completely asymmetrical body, and Mitrata with a more or less bilaterally symmetrical body (Ubaghs, 1967c). It is noteworthy that asymmetrical Cornuta appeared in the fossil record considerably earlier than the bilaterally symmetrical Mitrata. The morphology of the theca in these two subclasses is very different, but the structure of the complex metameric process extending from the theca is similar in the subclasses, and based on these shared features, they are united in the same class.

The morphology of Cornuta and Mitrata and its evolution, including the transition to true Chordata, is the major and fundamental part of calciochordate theory. The evolutionary history of this group is described by Jefferies in detail, but it is based on the hypothesis that the metameric process is a tail, which is possible, but not certain. If this assumption is not correct, the entire interpretation of the morphology of Stylophora and the calciochordate theory will collapse. Thus, at present, the homology of the metameric process of Stylophora is not certain, because its interpretation remains ambiguous.

THE STEM OF EDRIOBLASTOIDEA AND COLLAR OF EDRIOASTEROIDEA

The morphology of the small Early Paleozoic group of so-called Edrioblastoidea, members of which have a well-developed stem (Figs. 33a, 33b, 33f), is particularly interesting for studying the homologies of the

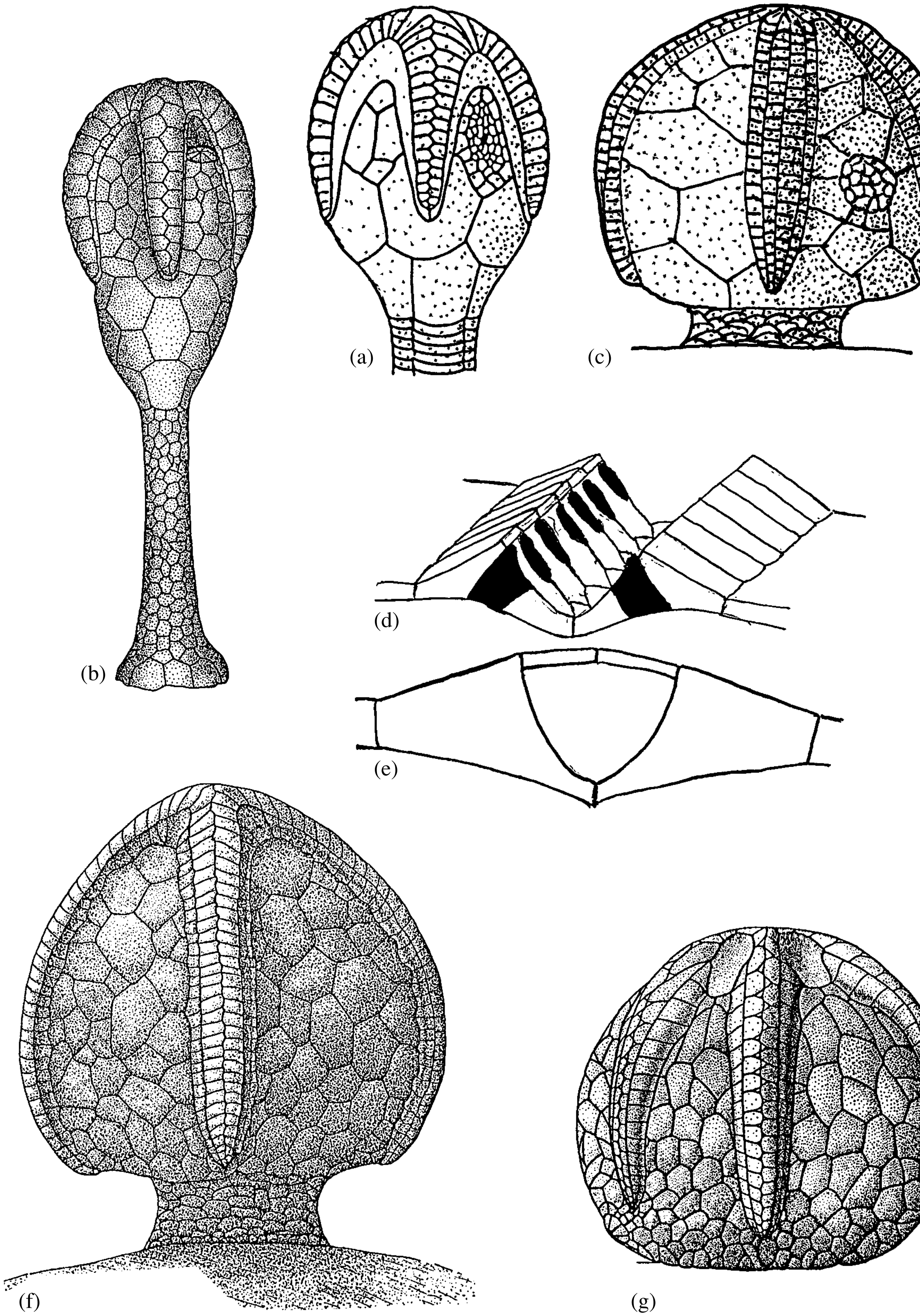


Fig. 33. Representatives of (a, b) Edrioblastoidea and (c–g) similar Edrioasteroidea: (a) *Astrocystites*, (b) *Cambroblastus* (after Smith and Jell, 1990); (c–e) new genus of Edrioasteroidea from the lower part of the Upper Arenig, (Volkhovian) of the Leningrad Region: (c) general view, reconstruction, (d) scheme of the structure of the ambulacrum (cover plates are removed, pores are black); (e) cross section through the ambulacrum; (f) *Paredriophus* (after Guensburg and Sprinkle, 1994); (g) *Totioglobus* (after Bell and Sprinkle, 1978).

stem of pelmatozoan echinoderms. The morphology of some Edrioasteroidea that have a special structure elevating the theca over the substrate (collar) (Figs. 33c, 33d, 33e) is also important in this respect. But, are these structures homologous to the stem of Pelmatozoa? The answer to this question is very important for understanding the origin of both pelmatozoan and eleutherozoan echinoderms.

Edrioblastoidea is a small group of sessile Cambrian and Ordovician echinoderms which shares common features with both Edrioasteroidea and Blastoidea (Fig. 33a, 33b, 33f). This uncertainty allowed Fay (1962, 1967a) to assign the single then-known edrioblastoid genus *Astrocystites* to a separate class. Later, after more new edrioblastoids, *Cambroblastus* Smith et Jell, 1990 and *Lampteroblastus* Guensburg et Sprinkle, 1994, had been found, and new morphological data on edrioblastoids had been obtained, this group was considered to be closely related to the Ordovician family Cyathocystidae.

At the very end of the last century, Whiteaves (1897) described *Astrocystites ottawaensis*, the first known representative of Edrioblastoidea. Three specimens of this species were found in the Trenton Limestone (Middle Ordovician, Caradoc) of Ottawa (Canada). Bather (1914) interpreted this species as a member of Edrioblastoidea. Hudson (1927) assigned the genus to Blastoidea, whereas Fay (1962, 1967a) assigned it to a separate class. It is interesting that despite the rarity of well-preserved specimens of *Astrocystites*, there are indications that some beds in the Trenton Limestone are almost completely composed of isolated plates belonging to this genus (Spencer, 1938). The second edrioblastoid genus, *Cambroblastus*, was described from the Franconian (middle part of the Upper Cambrian) of Queensland by Smith and Jell (1990). These authors did not recognize the independent status of the class Edrioblastoidea, and treated this group as the order Edrioblastoida Fay (1962) within the class Edrioasteroidea. Recently, Guensburg and Sprinkle (1994) described a third genus, *Lampteroblastus*, assigned to the family (Astrocystitidae Bassler, 1935). This family, together with another unusual family (Cyathocystidae Bather, 1899), they assigned to the suborder (Edrioblastoidina Fay, 1962), within one of the four edrioasteroid orders (Edrioblastoidina Fay, 1962) that they recognized.

The edrioblastoid body was distinctly subdivided into two parts, stem and theca. Brachioles, or other similar skeleton-like processes belonging to the food-gathering system, were absent. The structure of the distal part of the body and the holdfast are known only in *Cambroblastus*. The stem of *Cambroblastus* widens slightly distally, and rapidly merges into a small conical holdfast composed of relatively large polygonal plates. The theca has both edrioasteroid and pelmatozoan (blastoid) features. Therefore, in the description of the theca, edrioasteroid and blastoid terminology is used. However, the resemblance of these terminologies does not necessarily indicate a homology of corresponding structures.

In *Astrocystites*, the theca is blastoid-shaped, up to 40 mm long and 30 mm high. The average size is somewhat smaller, up to 25 mm wide and 23 mm high. The theca has well-developed pentaradiate symmetry, due to the alternation of the five deeply distally descending ambulacra, and five interambulacral zones, and also due to the presence of five pentamerous circlets in the proximal part of the theca. Apart from the oral, *Astrocystites* has two complete, uninterrupted circlets, in which the plates of the neighboring radii contact each other. These are the basal circlet, composed of five plates, and the radial circlet, also of five plates with deep incisions for the entry of the ambulacra. This genus has five deltoid plates, which form arches surrounding the upper part of the interambulacra, and cover half of the bottom of each of the two neighboring ambulacra. Five almost triangular oral plates, meeting by their ends on the top of the theca in the center of the peristomial region, occur distally from the deltoid plates, in the interambulacra.

The ambulacra are long, descending to a distance of approximately one third of the theca, reaching the suture between the basal plates. The radial plate underlies the majority of the adoral half of the ambulacrum. The ends of the ambulacra adjoining the basal plates are (at least occasionally) curved clockwise (D ray), or counter-clockwise (E ray) (in oral view) (Mintz, 1970). The ambulacra are noticeably elevated above the thecal surface. The central part of the bottom of each ambulacrum is occupied by the ambulacral groove, U-shaped in cross section, with a noticeable straight suture running along the median line of the groove and separating the so-called wings of the two neighboring deltoid plates. A single row of elongated pores occurs on the elevated lateral margins of each ambulacrum. The stem is known only in its proximal part. Its diameter at the point of union with the theca is about one-third of the maximum width of the theca. The diameter rapidly narrows distally. The proximal part of the stem is composed of five low five-piece columnals, which are not distinctly outlined. The borders between the pentameres of the stem occur on the extension of the sutures between the basal sutures. The genus *Lampteroblastus* Guensburg et Sprinkle, 1994 comes from the Lower Ordovician of North America (Fillmore Formation; Trilobite Zone G-2, Middle Ibexian (base of the Arenig); Western Utah, USA). A single species of this genus is represented by the incompletely preserved holotype. The theca is strongly elongated, almost cylindrical distally and conical proximally. Its height is about 16 mm; the maximum width is 9 mm. The ambulacra are straight and short, rapidly tapering and curved sharply downwards near the apex. Their arrangement is described by the 2–1–2 formula. The cover plates are raised high, and are alternate with the sutures (a suture is located opposite the middle of the plate). The oral cover plates are not differentiated. Five interradially placed cover plates meet on the top of the theca above the mouth. The ambulacral groove was apparently deep and V-shaped in cross section. Plates covering the bottom of the ambulacra are not known. The interambulacra each contain one large deltoid triangular plate. Six circlets of plates occur proximally on the deltoid plates and ambulacra. Each of these circlets was apparently composed of five plates. Wide, rounded ridges, especially strongly developed in the middle part of the theca, run along their external surface. The plates of the basal circlet and of the one lying above it were the largest. They contacted one another by their lateral margins, i.e., these circlets were complete (uninterrupted). The radial plates were small, did not contact each other, and only marginally contacted the ends of the ambulacra. The stem is only known proximally. It is narrow and rapidly narrowing, composed of the wedge-plates forming coarse chevrons. The hydropore and periproct are not known.

The third known edrioblastoid genus, *Cambroblastus* Smith and Jell, 1990, comes from the middle part of the Upper Cambrian (Franconian) of Australia (Western Queensland). A single species of this genus, *C. enubilatus* Smith and Jell, 1990, is represented by two specimens, of which the holotype is well preserved. The theca is elongated, blastoid-shaped, small, 10–11 mm high and 6–7 mm wide. The thecal surface is smooth. The ambulacra are straight, long, extending from the top of the theca following the 2–1–2 pattern, and reach a distance of approximately half the height of the theca. The ambulacral groove is U-shaped in cross section. Its bottom is covered by biserially arranged plates. The sutural pores between the plates are not found. The cover plates are high, and form an arch above the ambulacral groove. Five large cover plates, one in each radius, meeting in the center, occur above the mouth. The periproct occurs near the top of the theca. It is composed of small, wedge-shaped plates. The lower part of the theca is cup-shaped, and was composed of at least three circlets of plates. The basal circlet was composed of five plates contacting one another by their lateral sides. A small radial plate with a small incision lies below the end of each ambulacrum.

The radial plates did not contact each other by their lateral margins. Their circlet was interrupted. The borders of the plates between the basal and radial circlets are not clearly seen because of poor preservation, hence, it is difficult to see whether or not the plates are arranged in regular circlets. The stem is cylindrical, narrowing in the middle, and widening toward the base. Apparently, it was composed of very small, polygonal plates. Near the base of the stem, these plates are larger and more clearly polygonal. The stem terminates with the holdfast, which is composed of relatively large polygonal plates. However, the complete structure and size of the holdfast are unknown.

Thus, all three genera, presently assigned to the Edrioblastoidea, are quite similar, sharing many important characters, and are readily distinguishable from other similar taxa. A combination of characteristics allowing their assignment to the same group includes:

(1) A body subdivided into a theca and stem;

(2) Ambulacra that are intrathecal, not branching, and represent independent structures within the theca;

(3) Processes connected with the ambulacra (brachioles, or arms) are absent;

(4) The theca is tessellate, built by contacting plates, which are more or less arranged in circlets.

Other characteristics are not uniform in all representatives.

A comparison of Edrioblastoidea and Edrioasteroidea shows that they comprise a single group, because the structure of the oral part of the theca may be very similar. The similar structure of the ambulacra and their growth pattern is an important feature, which unites Edrioblastoidea and Edrioasteroidea; this is different in Pelmatozoa. The ambulacra in Edrioblastoidea are petaloid. They grow strictly meridionally, and were variably elevated above the level of the interambulacral part of the theca. The aboral ends of the interambulacra do not extend outside the theca, and are terminated by the incisions of the oral plates. This indicates their specific growth pattern equivalent, for instance, to the growth of the ambulacrum in echinoids. The radial plates of Edrioblastoidea are in this respect equivalent to the ocular plates of echinoids. The plates covering the bottom of the ambulacral canals are biserial, and have pores on the sutures. Pores are found in three genera. The pores are thought to be connected with the ambulacral tube feet. Supposedly, the tube feet extended outside, into the ambulacral groove through these pores in cases when the radial canal was inside the theca, or it is possible that the tube feet were connected through these pores to the ampullae in cases when the radial canal ran outside, on the bottom of the ambulacral groove. The absence of pores in *Cambroblastus* can possibly be explained by poor preservation (Smith and Jell, 1990), but it could be due to the small size of the individuals in this genus. The latter explanation is more likely, because the sutures between the cover plates are clearly visible. If this explanation is correct, then it confirms the external position of the radial canal in Edrioblastoidea.

In addition, recently transitional forms were discovered between the typical Edrioasteroidea and Edrioblastoidea. For instance, a new genus from the Lower Ordovician of the Leningrad Region has a typical edrioblastoid theca, but instead of a stem it has a collar, typical of Edrioasteroidea (Figs. 33c–33e). This indicates the presence of a morphological sequence reflecting the apparent evolution of the stem in Edrioblastoidea: a collar composed of imbricating plates—a stem composed of tessellate plates—a stem composed of series of pentameres (Fig. 34). This morphological sequence differs noticeably from the similar morphological sequence reflecting the evolution of the stem in

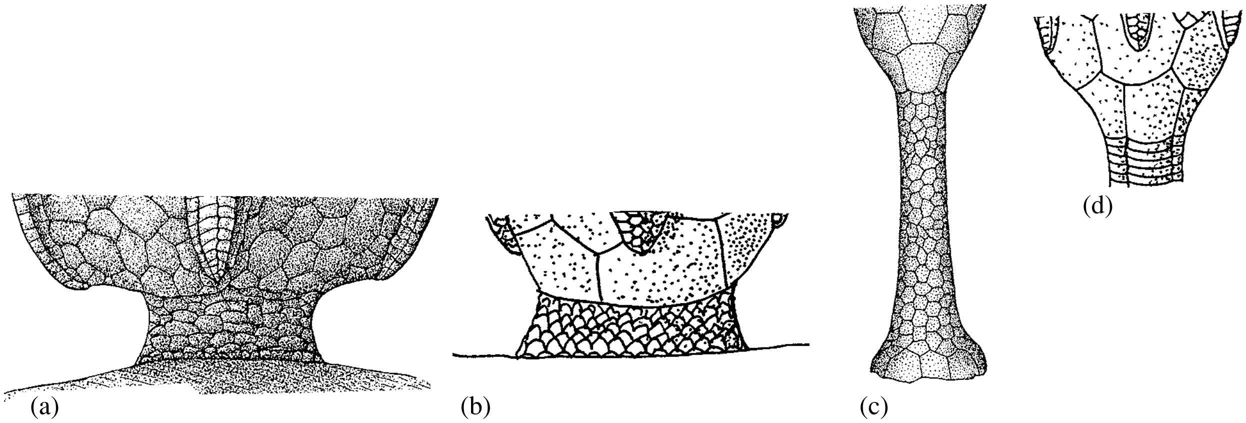


Fig. 34. Scheme showing the morphogenesis of the stem in Edrioblastoidea: (a) indistinctly delineated collar formed by imbricate plates (*Paredriophus*); (b) distinctly delineated collar formed by imbricate plates (new genus from the Ordovician of the Leningrad Region); (c) stem composed of numerous tessellate plates (*Cambroblastus*); (d) stem of indistinctly outlined pentamerous columnals (*Astrocystites*).

eocrinoids and crinoids in its incompleteness, and in its limited morphological potential (restrained evolution). Can this stem be homologized with the pelmatozoan stem? No confident answer is possible at present. However, I am inclined to think that it is impossible for the following reasons: The stem of pelmatozoan echinoderms morphogenetically represents a combination of the preoral lobe with attachment sole, the surface of which is used for the fixation of the larvae, and somatocoels. This allows the metameric stem to grow in length virtually unrestricted. The problem with homology to the stem of Edrioblastoidea, is that it is not clear which coeloms took part in the development of the edrioblastoid stem, the anterior (as in the larvae of some starfish), or the posterior (as in Pelmatozoa) (Fig. 35).

In some recent starfish (e.g., in *Asterias rubens*), the larva, at the end of the Pelagic Stage, develops a small peduncle, formed, as in crinoids, from the preoral lobe. In starfish, this attached peduncle stem is curved later in ontogeny, so that the oral side of the developing starfish faces the substrate, while the aboral disc faces upwards (Ivanova-Kazas, 1978). This suggests the hypothesis that free-living taxa evolved from sessile, stalked echinoderms (Bather, 1900; Heider, 1912). However, this hypothesis is beset with major difficulties, because the cavity of the stem of the starfish larva is formed by the somatocoel (Fig. 35). Hence, in this case only the fixation structures of the preoral lobe are homologous. Which cavity was located in the stem of Edrioblastoidea? Could it be a cavity of the protocoel, at least at early ontogenetic stages, as in starfish? This hypothesis allows a new evaluation of the old theory of the origin of starfish and other free-living echinoderms. Smith and Jell, when homologizing the edrioblastoid stem with the elongated theca of Edrioasteroidea *Cyathocystis* and *Pyrgocystis*, make an erroneous assumption or simplification, because a stem can be called a stem only when it is separated from a theca. In the above two genera, there is no such separation. This can also indicate that Edrioasteroidea did not have close morphogenetic relationships between the somatocoels and preoral lobe of their larva; otherwise such a separation would have appeared.

INNER ORGANS CONNECTED WITH THE STEM

Above, general data on the stem homology in pelmatozoan echinoderms are discussed, but details allowing recognition of the origin and early evolution of the stem are of primary interest.

The rich fossil material of pelmatozoan echinoderms gives important insights into the external side of this process, but data on the soft body of recent crinoids are necessary to understand the internal side of this process. The skeleton of the crinoid stem contains an axial canal, extending from the cavity of the cup and reaching the holdfast. The cavity of this axial canal can be very narrow, but can occupy a considerable part of the stem. Recent crinoids have a five-chambered organ inside the axial canal. This organ is formed by a system of cavities formed by coeloms. It is represented by five narrow canals, separated by interradial septa, and arranged around the central cavity. According to Fedotov (1951), five canals lie in the axial part of the cup cavity, and are well separated from the general body cavity, although embryologically they represent a product of the right posterior (or abactinal) coelom. On the abactinal side of the cup, these canals are inflated to form the chambered organ, which is surrounded by the central part of the ectoneural system (Fig. 27). The chambered organ continues along the axis of the stem, secondarily expanding in the zones possessing cirri, and secondarily giving rise to the vessels in the cirri. The central cavity of the chambered organ, which is part of the axial zone of the general body cavity, continues at the top into the cup and contains the so-called

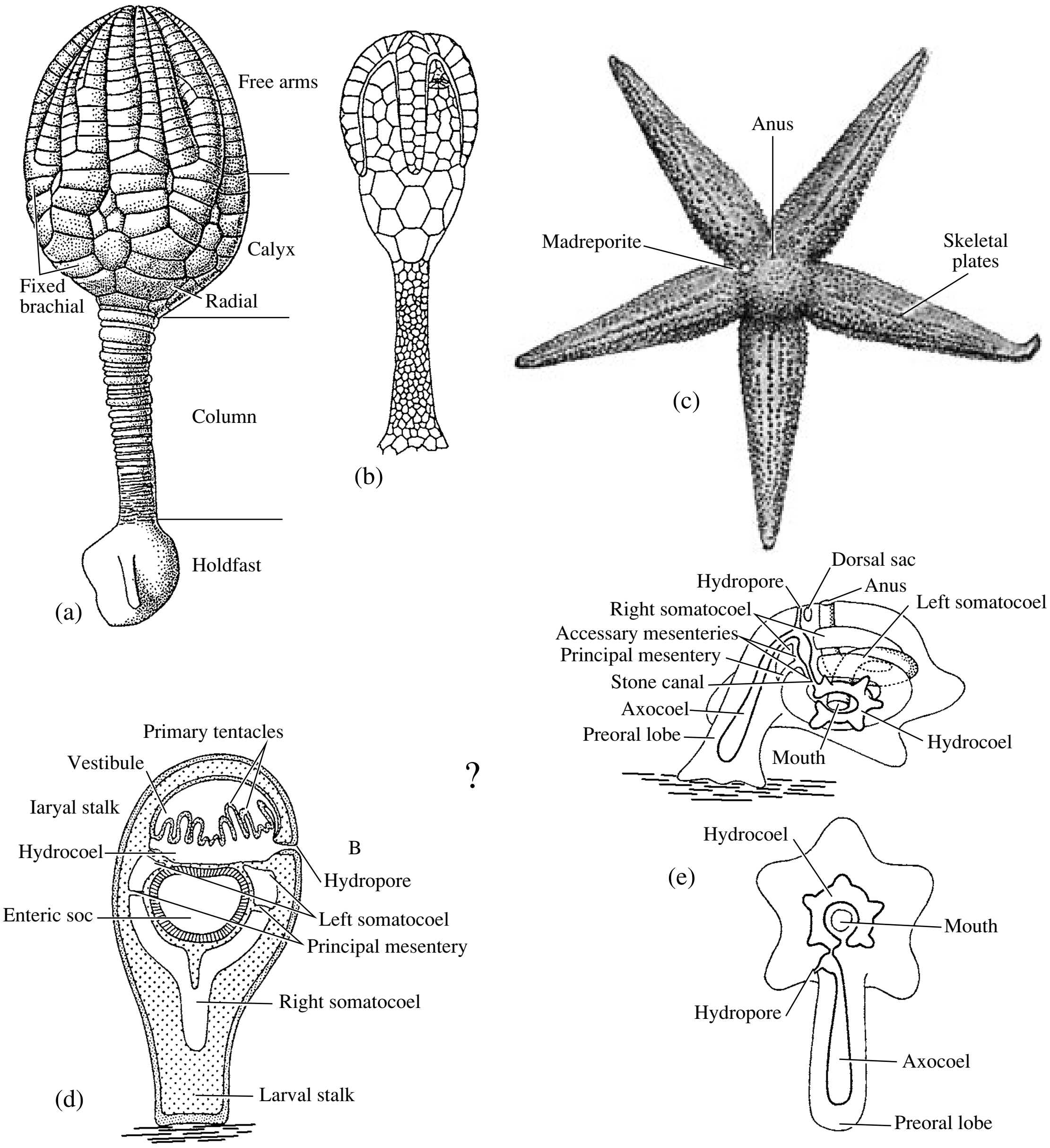


Fig. 35. Scheme showing the structure of the (a–c) skeleton of the adult individuals and (d–e) soft body of the larva of crinoids, starfish, and edrioblastoids. The stem of edrioblastoids can be homologous to the larval stem of starfish.

axial cord (Fig. 27). In stemmed forms, the central cavity of the chambered organ is blind-ended on the top. The axial cord, or glandular organ, is blind-ended on the top near the oral blood ring. In the upper part, the axial cord is adjoined by a complex of cells containing the primary sex cells and continuing into the genital cords in the arms. Thus, in recent crinoids, the five-chambered organ occurring in the stem is connected by the axial cord with the complex of sex cells, from which cords extend into the arms. However, embryological data show that in ontogeny, crinoids had a primary incipient genital structure developing from the axial cord, lying in the anal interray and disappearing before the end of the pentacrinoid stage. Based on this, embryologists suggest that the ancestors of crinoids had only one genital gland lying in the anal interray (Ivanova-Kazas, 1978). This agrees with paleontological data, which indicates that eocrinoids and cystoids had a special gonopore in the theca to excrete sex products, while in crinoids the gonopore was absent, because the sex products were excreted through the arms. This problem is discussed in the section on anal structures. Another aspect of this problem is discussed here, i.e., the position of the primary gonad in eocrinoids and the possibility of its existence in the earliest crinoids. In recent crinoids, the gonads are located in the arms and pinnules. Sex products are excreted through the disrupted body wall or through special ducts. It is certain that in

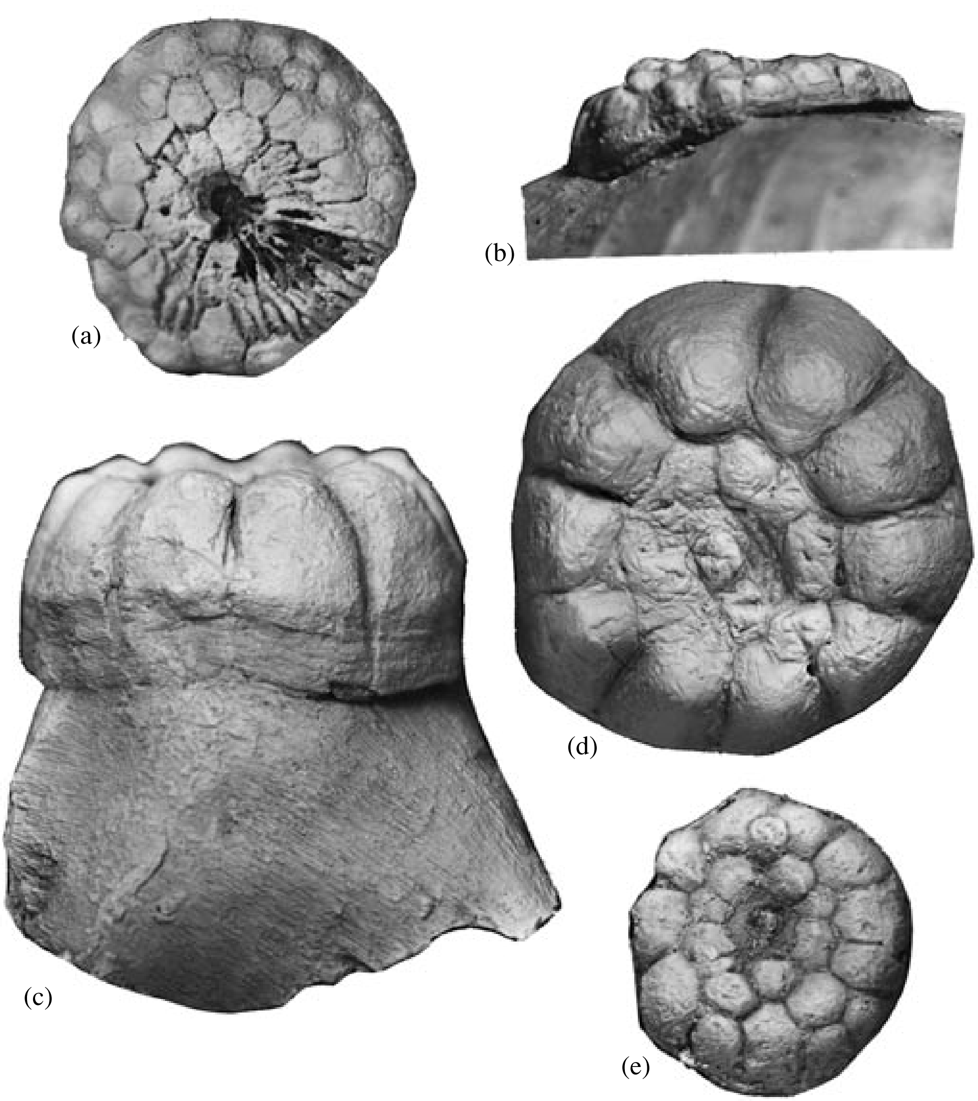


Fig. 36. Multiplated holdfast of crinoids from the Ordovician (Caradoc, Keila Horizon) of Estonia (after Hints *et al.*, 1989). (a) Ec 1924 upper view; (b) PIN4125/368, lateral view; (c, d) Ec 1924; (c) lateral view; (d) upper view; and (e) Ec 1923 upper view.

some early crinoids, gonads could have occurred inside the cup, at least in those taxa with weakly developed arms, and more so in armless taxa. Within the cup, the gonads could have occurred both in its distal part, around the esophagus, and apparently in the proximal part of the cup in early crinoids. The latter suggestion is supported by the place of the development of the genital stolon, and its close connection with the development of the axial cord and five-chambered organ. Furthermore, it seems that the primary function of the genital cord was to transport sex products from the primary gonad, which occurred in the proximal part of the theca in the ancestors of crinoids, in the gonopore or to the arms in the earliest crinoids. This is indicated by the migration of the sex cell in the ontogeny of recent crinoids, from the primary incipient genital structure (in the mesentery between the oral and aboral coeloms), into the genital stolon of the five-chambered organ (Ivanov, 1937). Therefore, it is possible to suggest that those crinoids, in which the cup cavity passed into the wide axial canal of the proximal part of the stem without any sharp border, the gonad could be partly located in the axial canal of the stem. This was functionally important for crinoids with a small cup cavity. Furthermore, Hints *et al.* (1989) suggested that in some Ordovician crinoids the gonad could also occur in the specialized multiplated holdfast, which has a relatively large cavity. The structure of these holdfasts is very complex (Fig. 36) compared to those in other taxa. An arch of polygonal plates arranged in concentric circles occurs above a single plate, directly attached to the substrate. A large cavity, divided by septa of different orders, occurred between the arch and the basal plate. A crater-like depression occurred in the center of the holdfast. The pentamerous stem extended upward from this depression. The axial canal of the stem merged into the inner cavity of the holdfast. Warn and Strimple (1977), based on the joint occurrence of similar holdfasts and known cups, showed that they belong to the closest representatives of Cincinnaticrinacea and homocrinids. Later, Brower and Veinus (1978) concluded that they may belong to other groups of crinoids. A sharp difference between the size of the cavity of the wide holdfast, and the diameter of the stem extending from it (hence the small space inside the theca) requires an explanation. One of the more probable explanations is that the gonad was located in the holdfast. Migration of the sex cells at one of the ontogenetic stages in recent crinoids into the genital stolon of the five-chambered organ (Ivanov, 1937) makes this assumption convincing. It is possible that in eocrinoids with an peduncle, rather than a stem, the gonad could be located in the wide proximal part of this peduncle. The fact that the gonopore in some eocrinoids could be located in the lower part of the theca (Fig. 21) (e.g., in *Simoncovicrinus* from the Lower Ordovician of the Leningrad Region) (Rozhnov, 1991) makes this hypothesis even more credible. From this point of view, it is useful to discuss the development of the peduncle, and its evolutionary transition into the true stem, which occurred synchronously in a few groups of Eocrinoidea. This will be discussed elsewhere in the paper, while the pentaradiate symmetry in the skeleton of the stem, and its correspondence with the pentaradiate symmetry of the theca and the five-chambered organ, are discussed below.

RADIAL SYMMETRY OF THE STEM

In many of the earliest crinoids, the cross-section of the axial canal of the stem is pentagonal, five-lobed. It is natural to suggest that the canals of the five-chambered organ penetrating the stem were in the corners, or in the lobes of the axial canal, i.e., were orientated in the same way as these structures in relation to the radial canals of the ambulacral system. In addition, they should correspond to the orientation of cirri (when they are present on the stem), because the branches of the canals of the five-chambered organ enter the cirri. The stem of many of the ancient crinoids was formed by a series of pentameres, rather than by entire ossicles, i.e., each columnal was composed of five sectors (pentameres) separated by sutures (Fig. 3). According to Stukalina (1986) it is possible to establish the former position of the pentameres from the structure of the ligament field, when the sutures between them are lost in the course of evolution. The corners of the axial canal of the stem could coincide or not with the sutures between the pentameres. Stukalina (1966, 1986) called the first type of the arrangement angulate (sutural lines extend from the corners of the axial canal), and the second, strialate (sutural lines are perpendicular to the walls of the axial canal). Therefore, instead of Wachsmuth and Springer's rule describing the arrangement of the plates of the theca and the stem, discussed above, all possible variants are observed, i.e., a simple combination of characters. The above rule only reflects the most common variants. Stukalina (1986) recognized six combinations of the number and arrangement of the circlets, sutural lines of the pentameres, and arrangement of the axial canals. She recognized two major groups of variants of these combinations, angulate and strialate (Fig. 3). In the angulate group, the corners of the axial canal of the stem coincides with the sutures between the pentameres, while in the strialate group the corners alternate with the sutures. Two variants were known for the dicyclic forms: (1) in the case of the angulate structure the pentameres of the stem alternate with the infrabasal plates, while in the case of the strialate structure these pentameres lie on their continuation. According to Stukalina, in both cases, the corners of the axial canal of the stem alternate with the sutures between the infrabasal plates, and occur on the same line with the sutures between the basal plates. Thus, in dicyclic forms, the corners of the axial canal are always radial. In monocyclic forms the infrabasal circlet is absent, while the corners of the axial canal of the stem alternate with the stem between the basal plates, i.e., positioned interradially. In addition, there are also pseudomonocyclic forms, which have only basal plates below the radial plates, but with the corners of the axial canal occurring on the continuation of the sutures of the basal circlet and positioned radially. In this case the pentameres of the stem alternate with the basal plates (strialate type) or are arranged in the same line (angulate type). Similarly, pseudodicyclic forms can be recognized with angulate and strialate types.

The articulation between the stem and the cup is still poorly studied in many crinoids, hence, the actual diversity may be revealed only by further studies. However, Stukalina (1986) showed that the strialate type of plate arrangement was widespread in the Early and Middle Paleozoic, although the number of families and genera of this type is considerably smaller than are those of the angulate type. Judging from Ubaghs's descriptions (1969, 1978), the Early Ordovician *Aethocrinus moorei* Ubaghs had a strialate type of plate arrangement. Judging from the articulation between the axial canal and the cup in *Hybocrinus* and *Hoplocrinus*, the corners of the axial canal in hybocrinids are positioned radially, and hence, the cup is pseudomonocyclic, although it is not clear whether it is angulate, or strialate. In disparids, only the angulate type of the stem is known so far. However, recently among them, a different, previously unknown, type of structure of the base of the cup and stem was observed. It was most clearly seen in *Virucrinus* Rozhnov (Fig. 13), but it also occurs in some other genera (Rozhnov, 1990a). In this genus, pentameres of the most proximal columnal are somewhat larger than other pentameres, and have pointed proximal ends entering the sutures between the basal plates, and alternating with the basal plates. These pentameres are very similar to the infrabasal plates,

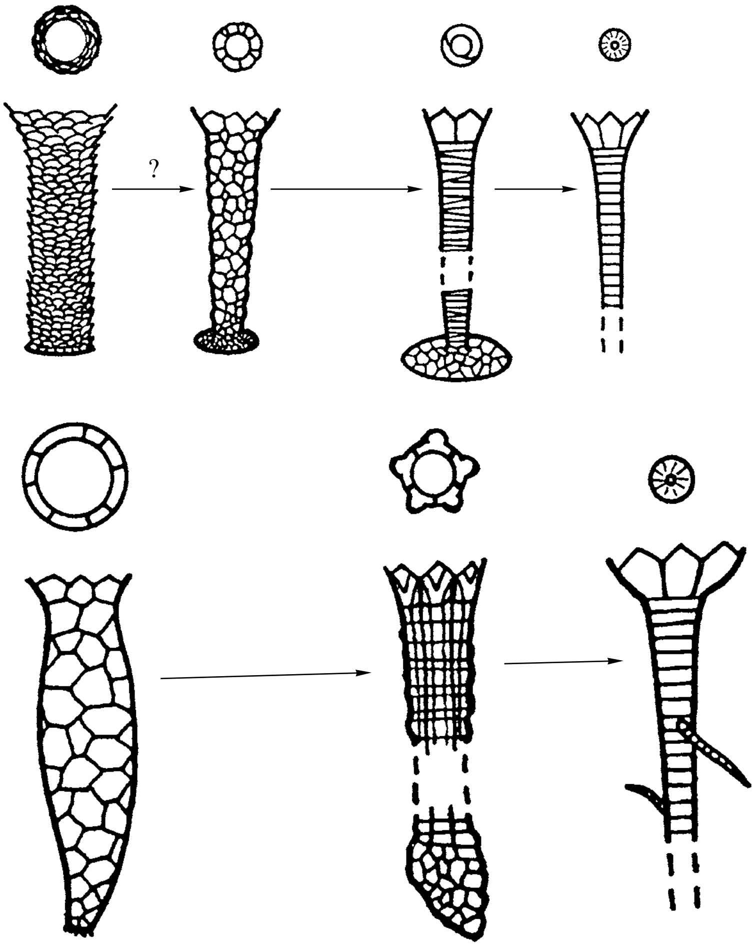


Fig. 37. Scheme showing the morphogenesis of the stem in eocrinoids (top) and in crinoids (bottom) (after Sprinkle, 1973).

especially because the border between the cup and the stem is quite uncertain, since the cup has no special skeletal bottom. The stem is angulate, because the corners of the axial canal coincide with the borders between the pentameres of the stem, including those between the most proximal pentameres resembling the infrabasal plates, which are positioned radially. If this so-called circlet is considered to be part of the stem, the cup is typically monocyclic. If it is considered to be an infrabasal circlet in the cup, the cup is pseudodicyclic. The study of the neural cords may be very important for understanding the diversity of types of dicyclic and monocyclic forms. The supposed arrangement of these cords is shown in Stukalina's scheme. However, their actual position is poorly known.

ORIGIN OF THE STEM

THE EVOLUTIONARY TRANSITION FROM THE PEDUNCLE TO THE STEM IN EOCRINOIDS AND CRINOIDS

The above discussion allows the conclusion to be drawn that, in many early crinoids, the orientation of the corners of the axial canals (and, correspondingly, the canals of the five-chambered organ), was formed independently of the orientation of the pentameres. What could determine their orientation? To answer this question it is necessary to address the model of the evolutionary transition from the peduncle to the true stem (Figs. 37). Morphological series of this transition are revealed in eocrinoids, and, according to Sprinkle (1973a), in crinoids. Among crinoids, he suggests the following morphological series: peduncle (holdfast) formed by imbricate plates in *Lepidocystis*, the peduncle composed of tessellate uneven, irregularly arranged plates in *Gogia*, the peduncle of crescent-shaped plates in *Acadocrinus*, and the stem composed of low columnals in *Eustypocystis* (Fig. 37). Sprinkle suggested some phylogenetic implications regarding this series, but this is very doubtful. In his opinion, the transition from the peduncle to the stem in the evolution of eocrinoids occurred around the Middle–Upper Cambrian boundary. The suggested morpho–phylogenetic lineage for crinoids, in his interpretation, is as follows: peduncle composed of irregularly arranged tessellate plates of different sizes in *Echmatocrinus*, to the stem with the distal end of the above type, and with a more

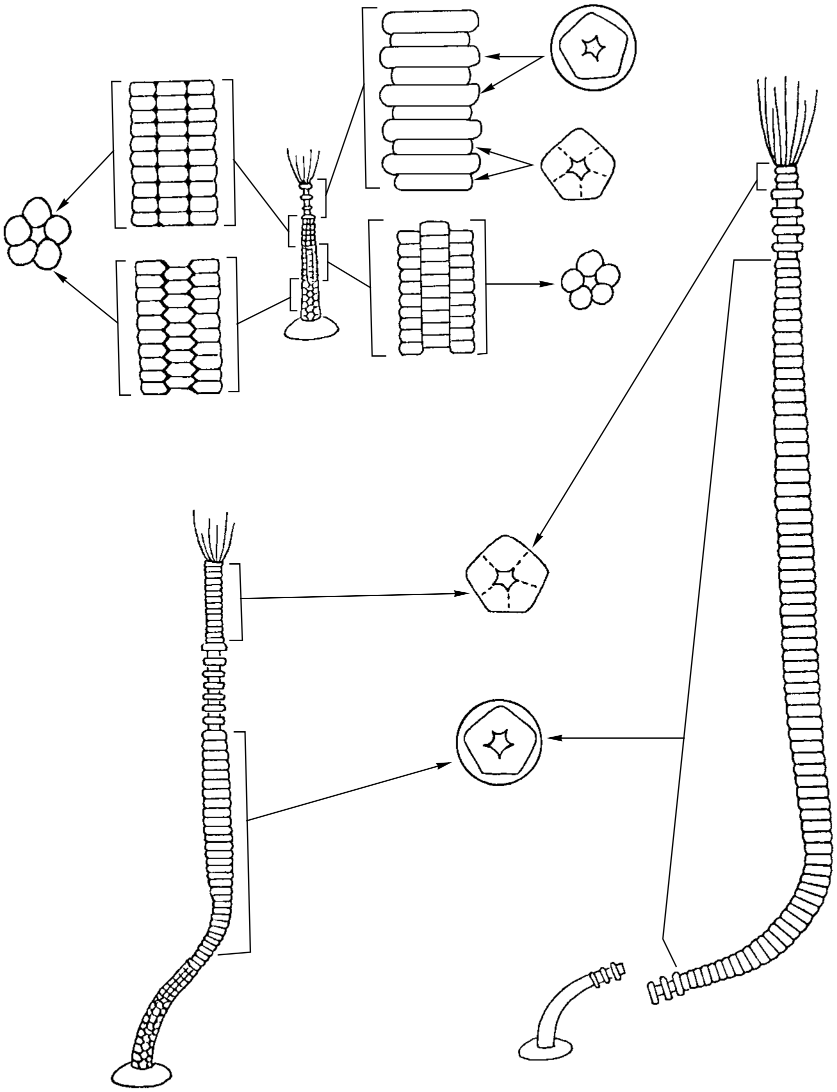


Fig. 38. Morphology of the stem of the disparid crinoid *Cincinnaticrinus variabrachiatus* suggesting possible ontogenetic and evolutionary changes in the pentamerous stem of crinoids (after Warn and Strimple, 1977).

typical proximal end in *Aethocrinus*, to the stem of all later crinoids (Fig. 37). This morphological series is difficult to interpret phylogenetically, because the assignment of *Echmatocrinus* to crinoids, and more so the possibility that this genus is an ancestor of crinoids, is presently much debated. The above morphological lineages are discussed below in the light of new data.

The main morphological difference between the peduncle and the stem, is the ability of the stem for unlimited metameric growth. Each columnal represents a separate metamere. The elongation of the stem occurred by the addition of new metameres (a process characteristic of many animal groups), rather than by general growth of a single structure. Metameric growth is similar to regeneration. The transition to metameric growth in the peduncle could occur by different means. One of them corresponds with the above morphological series. The plates covering the peduncle gradually became more regularly arranged, and transform into semicircular and circular structures with a large inner cavity. Apparently, eocrinoids, like recent crinoids, had processes (or one process) of the right somatocoel, although, in contrast to crinoids, these extremities were not structured as a five-chambered organ. This is indicated by the absence of structures with pentaradiate symmetry in the peduncle and stem of Eocrinoidea. It is possible that in some Ordovician eocrinoids (such as *Rhipidocystis*) the chambered organ had acquired a triradiate structure, which was ancestral to the pentaradiate structure. This is indicated by the three-lobed axial canal of the stem found in some species of this genus (but see Rozhnov, 1989). The proximal part of the stem could also contain some other organs, e.g., gonads. As a result, the peduncle became pseudometameric, not because of metameric growth, but because of its function, primarily, increased flexibility. Since the main functional significance of the appearance of this pseudometamerism was in the increased flexibility of the stem, the plates were rearranged into circular series. Along the stem, the plates were also arranged in vertical columns rather than in alternating horizontal rows (brick wall). The latter arrangement is characteristic of the theca, where the rigidity of the external capsule was necessary. However, the arrangement of the plates in vertical columns is more characteristic of the early evolution of the stem in crinoids (Fig. 38). The appearance of such a pseudometameric peduncle-stem and other skeletal elements in ontogeny could have been gradually displaced to the earlier growth stages, because the size of eocrinoids could rapidly increase in the evolution. Based on this, the true metameric growth of the peduncle-stem could have evolved from the appearance of new columnals in the developing growth zones. Such growth zones appeared first of all on the border between the proximal expanded part of the stem (proxistele) and middle part (mesistele), the longest in the stem. The proxistele was a gradual transition to the theca and apparently contained some internal organs, thus saving space inside the theca. The mesistele was used for the elongation of the stem and, hence, increased elevation above the sea bottom. At the same time, the stem became more separated from the theca. In primitive eocrinoids, the theca, at least in the lower part, and the peduncle were covered by almost identical, small, polygonal plates forming a skeleton, which was reasonably flexible and rigid and functioned to support and protect the body. However, as the body (theca and stem) grew, the rigidity of the theca became of primary importance, while flexibility was the main trend in the development of the stem. Consequently, the plates in the stem were arranged in vertical columns and circular series, whereas the plates in the theca formed circlets arranged in a brick-wall pattern. This process will be discussed in detail below, when analyzing the development of the stem and cup in crinoids. The next section describes another mechanism of the appearance of metameric growth in the stem that is based on morphogenetic interactions between the stem and holdfast.

DEVELOPMENT OF THE STEM BY POLYMERIZATION OF THE HOLDFAST

Well-developed columnals with a very narrow axial canal have been recorded from such ancient strata as the very base of the Middle Cambrian in association with holdfasts that are shaped like a small monolithic attachment disk (Figs. 39, 40). The axial canal in these columnals and in the holdfast is very small; therefore, it is difficult to imagine the gradual development of these columnals (taking into account their very early geochronological age) as a result of the fusion of the plates surrounding the soft body of the peduncle. A more realistic mechanism of their evolution can be described as follows.

After the settling of the larva and its attachment to a substrate, the holdfast (small attachment sole) could rapidly be transformed into a single monolithic plate, since its functioning did not require a large inner cavity to enclose the soft body and also did not require great flexibility. The small size of the holdfast facilitated the development of its monolithic structure. As a result, a peduncle covered with irregularly arranged small plates, and with a large cavity inside, rested on this monolithic attachment disk. If the more successful survival of such eocrinoids required a higher elevation of the crown above the sea bottom, this could be achieved by polymerization (metamerization in terms of symmetry) of the attachment disk. A new disk was formed above the primary disk. In contrast to the primary disk, the distal and proximal parts of this new disk were similar in shape and size; morphologically, it was a columnal. New columnals (attachment disks) increased in number to elevate the peduncle and theca above the sea bottom. The growth zone, in this case of metamerism, was primarily located immediately above the attachment disk. This was the simplest and fastest means of transition to metameric growth of the stem-like structure. Its disadvantage was the very narrow axial canal, which precluded further elongation of the stem. For Cambrian eocrinoids, however, the long stem was not very important, because it could not be fixed by the small and primitive holdfast. In later crinoids, the diameter of this canal could slightly increase, which is observed in their Ordovician representatives. The hypothesis of the appearance of the stem by polymerization of the holdfast (attachment disk) is supported, for instance, by holdfast-shaped columnals of eocrinoids from the Middle Cambrian of Iran (Fig. 40).

Both of these patterns of the metameric growth could have been combined. The result of such combination is apparently observed in the stem structure of many Cystoidea. An example of this structure is observed in *Echinoencrinites* as a combination of the relatively long flexible near-theca part of the stem with specialized circular columnals and a wide inner cavity with the long distal part composed of barrel-shaped columnals with a narrow axial canal (Fig. 41).

The flexibility of the stem in eocrinoids was, in some cases, achieved by the imbricate (tiled) arrangement of plates, e.g., in lepidocystids. This was a primitive pattern, which was not widespread. At least, it has not been recorded in crinoids. It seems likely that it indicates the possibility that Eocrinoidea and Edrioasteroidea may have characteristics in common as a result of their origin from a common ancestor. Many early crinoids show a pentamerous stem structure, in which each columnal is composed of five sectors separated by sutures. Along the stem, the pentameres are arranged in vertical series. This provides flexibility of the stem and is enabled by the well-developed pentaradiate symme-

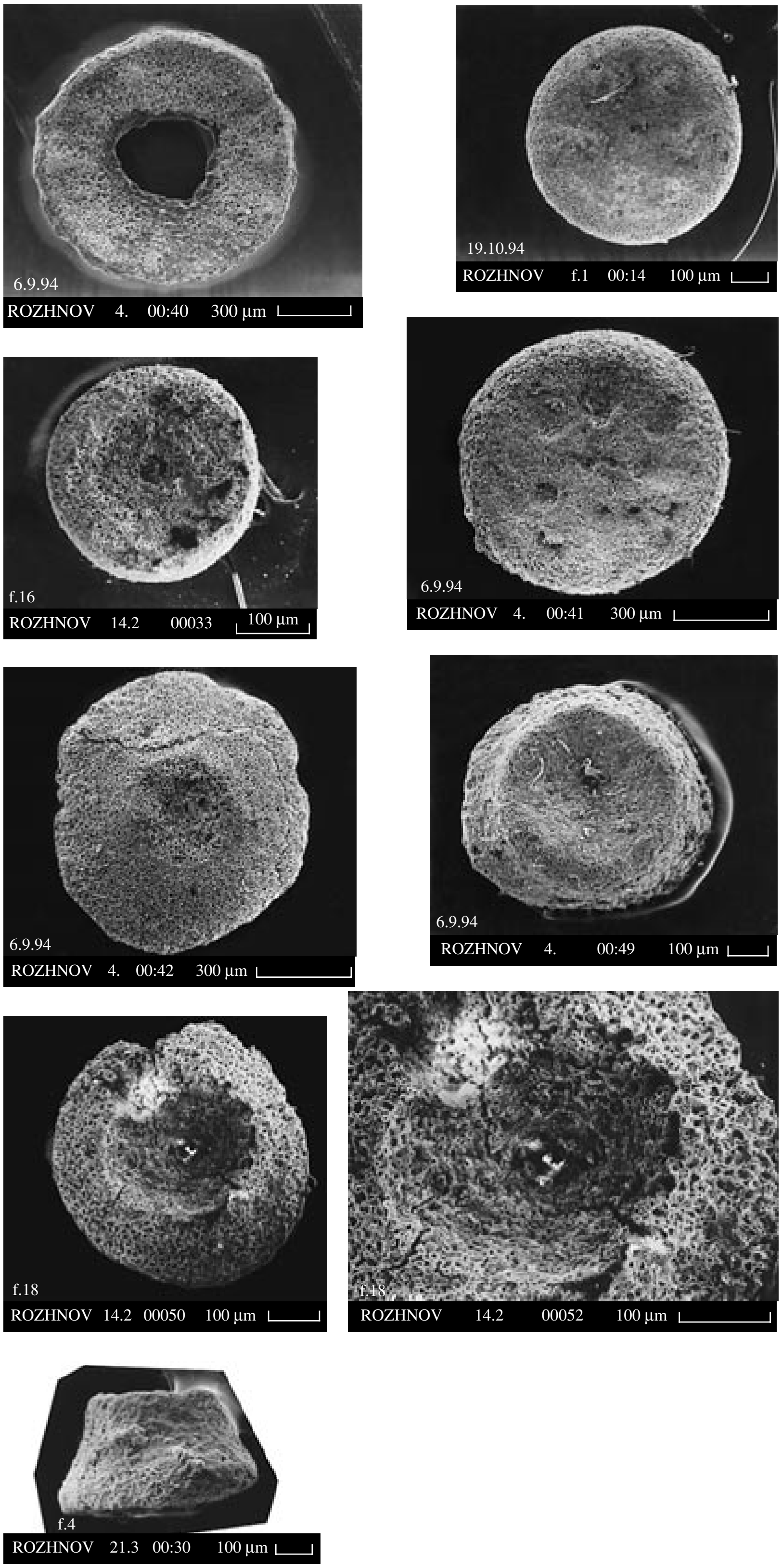


Fig. 39. Columnals and holdfast (?) from the Middle Cambrian of Australia.

Fig. 40. Columnals from the Middle Cambrian of Iran which are shaped like a holdfast.

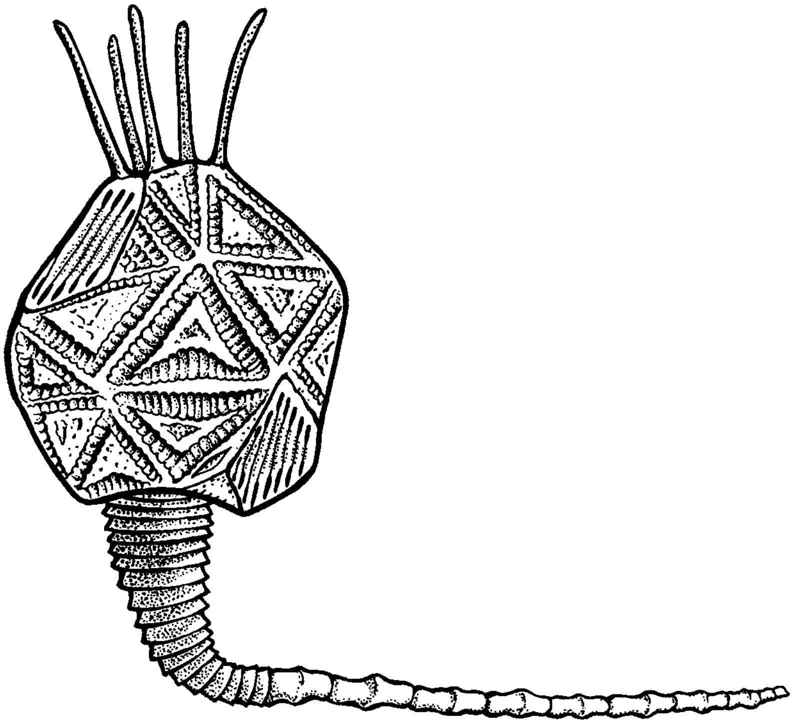


Fig. 41. General view of the *Echinoencrinites angulosus* Pander (Rhombifera) from the Ordovician of the Leningrad Region (reconstruction, ×6).

try in crinoids, which occurs in almost all of the skeletal structures. As noted above, the pentaradiate symmetry of the axial canal does not always coincide with the position of the pentameres. In some cases, the corners of the axial canal coincide with the sutures between the pentameres. In other cases, they alternate with them. Since the axial canal is essentially a cast of the five-chambered organ, it is possible to suggest, based on the above data, that the pentamery of the five-chambered organ and the pentameres of the stem were formed nonsynchronously and to some extent independently. A possible model of the development of the pentaradiate symmetry in pelmatozoan echinoderms is briefly discussed below and, in greater detail, in the chapter on symmetry. Originally, the pentaradiate symmetry only involved the food grooves approaching the mouth. This immediately defined the pentaradiate arrangement of plates surrounding these grooves. Here, the reasons for the appearance of pentamery and many of its details (e.g., its superimposition on the triradiate symmetry and some others) are not discussed, because this chapter deals with the mechanism of its distribution onto other body parts. To understand this, a possible ontogeny of the skeleton at the earliest stages of its appearance in pelmatozoan echinoderms (apparently, in Eocrinoidea) and the further evolution of the ontogeny of the skeleton should be considered. In the previous section, the development of the theca is discussed from this point of view. The development of the stem is discussed below, with a brief summary of the conclusions on the development of the theca.

DIFFERENTIATION OF THE SKELETON OF THE THECA AND STEM

It seems that an originally saclike body attached by a short and narrow peduncle to the substrate could have been the prototype of all eocrinoids. It was covered by calcite plates during one of the latest ontogenetic stages. Most likely, small and chaotically spaced calcite spicules appeared at the same time in many places, as observed during the formation of the skeleton in recent echinoderms (in which, however, the spicules are spaced by no means chaotically). Later, these spicules fused into small, polygonal plates, which varied in size and more or less chaotically covered the entire body. The size of the first eocrinoids was very small (a few millimeters). This is indicated by finds of small plates of eocrinoids from the Lower Cambrian and the basal Middle Cambrian that allow approximate reconstructions of some representatives of Eocrinoidea (Rozhnov *et al.*, 1992). As the size of the entire body increased, the number and size of the plates also increased. At some point, the optimal size of the theca, a particular proportion between the size of the plates and their number, was established. The appearance of the skeleton was shifted to the earlier ontogenetic stages. The differentiation of the plates of the theca and peduncle occurred, because of different functional requirements of the skeletons of these body parts. The theca became more rigid, there were fewer plates covering it, and they were articulated more rigidly compared to the ancestral forms. The plates of the theca were grouped in circular and semicircular structures. Five oral plates were grouped around the mouth to form the first circlet of the theca.

As the body size increased in different eocrinoid lineages, the appearance of the skeleton was shifted to earlier ontogenetic stages. Such displacement of the appearance of new characteristics deeper into ontogeny is generally characteristic of the evolution of ontogeny (Shishkin, 1981, 1987, 1988). In eocrinoids, it was facilitated by the trend in the evolution of their skeleton toward a larger role in their organization and more close correlation with the morphogenesis of other structures. Since the beginning of the development of the skeleton was shifted to earlier stages, when the juvenile animal was very small, the number of plates originally developing in the ontogeny of the theca decreased, and, being influenced by the symmetry of the ambulacra, the plates began to be arranged in variously organized circlets (Fig. 7). Although the differentiation of the skeleton of the theca and peduncle at this stage was more noticeable, it was not very distinct, because the thecal plates approximating the stem were originally very similar to the stem plates near the theca, whereas no distinct border existed in the thecal skeleton. Because of the small size of the theca at early stages of ontogeny, the number of originally developing plates was low. In some forms, only two circlets developed originally, the oral and the proximal (situated near the stem), which formed a more or less compact capsule, equivalent to the theca of recent crinoids at the so-called cystoid stage of their ontogeny. The symmetry of the oral circlet was spread onto the symmetry of the proximal circlet. The latter had five plates. As a result, the border between the theca and the stem became distinct.

The ontogeny of a hypothetical eocrinoid with a stem well delineated from the theca (e.g., *Ridersia* from the Cambrian of Australia) is described below. This stem was composed of two parts. The distal part consisted of barrel-shaped columnals with a narrow axial canal, while the proximal part consisted of low-cylindrical columnals with a relatively wide axial canal. The theca consisted of many circlets of plates. The supposed ontogeny includes a few key features. The distal part of the stem (dististele) developed in ontogeny as a few, low, almost circular plates with a narrow axial canal above the holdfast. The proximal part of the stem (proxistele) developed as sickle-shaped plates surrounding the extension of the right somatocoel (chambered organ). At later ontogenetic stages, the low cylindrical columnals of the dististele increased in number and grew in height. The sickle-shaped plates of the proxistele were transformed into numerous low-cylindrical columnals with a wide axial canal. Two circlets of plates developed originally in the theca: the oral circlet with interradially positioned plates and proximal, basal circlet with radially positioned plates. Later, plates of new circlets emerged between these two circlets. The new plates alternated with the plates of the earlier circlets, thus forcing the basal circlet and, subsequently, the new circlets to turn clockwise through 36°. The pentaradiate symmetry of the theca did not spread to the round stem.

Supposedly, the crinoids evolved from eocrinoids with the above-described ontogeny of the skeleton as a result of heterochrony, primarily paedomorphosis. The possible mechanism of transition from the eocrinoid to the crinoid body plan in relation to the stem and, partly, to the theca is discussed below (the development of the radials is discussed elsewhere in the paper, as well as other details of the early development of structures in crinoids). In many Early Paleozoic crinoids, the pentaradiate symmetry more or less involved the stem. Most important is the position of the pentameres and the corners of the axial canal, because other features of the pentamery of the stem are secondary. The possible model of the evolution of the theca and stem in primitive monocyclic crinoids (e.g., disparid inadunates) from eocrinoids is discussed below. The cup in disparids is monocyclic, i.e., apart from the radial circlet, the theca contains only two circlets, basal and oral. Without taking into account the radial plates, the hypothetical juvenile stage of the crinoid ancestor can be described as follows: the theca consisted of two circlets, oral and basal, whereas the incipient stem was composed of sickle-shaped plates irregularly arranged around the chambered organ. The columnals of the dististele were absent. At the next stage of ontogeny of this hypothetical ancestor, the pentaradiate symmetry of the theca spread onto the stem, i.e., the sickle-shaped plates were arranged in five vertical columns, while the chambered organ became five-chambered (acquired pentamery). The series of the resulting pentameres of the future stem (including the most proximal and all other pentameres) alternated the basal plates. This was necessary for firm articulation between the stem and the cup. Thus, at this stage of ontogeny, the oral plates were arranged interradially, the basal plates were arranged radially, and the pentameres of the stem were positioned interradially. The pentamery of the emerged five-chambered organ in most cases was superimposed on the symmetry of the stem in such a way that the position of the cords coincided with the borders between the columns of pentameres. Apparently, this was a sufficiently robust construction. However, as mentioned above, the arrangement could be different because of the relatively independent development of the pentamery in the stem and the five-chambered organ. When the next circlet appeared between the basal and oral circlets (this new circlet could develop into a radial circlet where it was morphogenetically correlated with the development of the radial ambulacral canals [this is discussed in another chapter]), the basal circlet was displaced into the interradial position, while the pentameres of the stem were placed radially. If the circlet appearing between the basal and oral circlets later became radial, i.e., gave rise to the arms, the resulting organization of the stem and theca would be typical for most monocyclic forms.

However, this new circlet was not necessarily connected directly to the arms. In cases where it was not, the cup became dicyclic. Later, one more circlet that was positioned radially and gave rise to the arms appeared in such a cup. Two circlets lying below and the pentameres of the stem were displaced around the axis of the theca through another 36°. As a result, the basal circlet of the theca was once again positioned radially, while the pentameres of the stem were placed interradially. This situation completely agrees with Wachsmuth and Springer's rule.

Can the fossil data support the rotation of circlets around their axes in ontogeny? Indeed, they can. Firstly, we can directly observe the displacement of the circlets in the ontogeny of the cladid crinoid *Cranocrinus* described by Arendt (1970). Secondly, the inner surface of the plates of the basal circlet of the disparid crinoid *Grammocrinus* from the Lower Ordovician of the Leningrad Region shows oblique ridges, which apparently reflect the arrangement of the cords of the neural system. This oblique appearance of the ridges also indicates the ontogenetic rotation of the plates of the basal circlet from the radial into the interradial position.

The homologies of the circlets, including those in unusual polycyclic forms, were discussed in detail above, in the chapter on thecal morphology. The possible evolution of the accessory (third or fourth) circlet in the cup from the proximal columnal is discussed in the same chapter. The possibility of the appearance of an accessory circlet by the inclusion of the proximal pentameres in the cup is quite large. The above-mentioned Middle Ordovician disparid crinoid *Virucrinus* provides an example of proximal row of the pentameres that is morphologically very similar to a circlet of the theca. The inner cavity of the cup gradually merges into the axial canal of the stem, because a skeletal boundary between these body parts is absent. Therefore, it is possible to suggest that part of the internal organs that usually occur within the cup in these forms could actually be partially inside the cavity of the stem. Theoretically, in the process of evolution, the border of the cup could develop beneath the proximal pentameres of the stem. In this case, other pentameres of the stem were arranged in one line with the plates of the distal circlet of the cup. This increases the possible diversity of the thecal structure, but apparently occurs quite rarely. Nevertheless, the proximal circlet of the unusual Early Ordovician crinoid *Aethocrinus moorei*, referred to as infrabasal by Ubaghs (1969; Moore *et al.*, 1978) and as lintel by Ausich (1997), could have evolved in this particular way.

HOMOLOGIES OF THE STEM IN DIFFERENT GROUPS OF PELMATOZOAN ECHINODERMS

This chapter discusses homologies of the stem in different groups of pelmatozoan echinoderms. As noted above, the stem in eocrinoids can morphogenetically be of two types, which can be combined in a functionally entire stem. The first type evolved as a result of the polymerization of the holdfast (attachment disk). Stems of this type have columnals that are circular in cross section and originally possessed a very narrow axial canal. The second type was formed as a result of the arrangement and subsequent fusion of small polygonal plates surrounding the chambered organ (extension of the right somatocoel into the stem). Stems of this type have columnals with a wide axial canal. When both these types are present in the same stem, the columnals of the first type form the distal part, whereas the columnals of the second type form the proximal part. Many cystoids (*Echinoencrinites*) and some eocrinoids (*Ridersia* from Australia) have such a compound stem. Which parts of the stem are present in crinoids? In the majority of disparids, for instance, the stem is certainly homologous to the second morphogenetic stem type of crinoids. This is indicated by the mechanism of its formation, reflected in the structure of many known stems. The stem of most camerates could have evolved from the first morphogenetic type of eocrinoids. This hypothesis is supported by the fact that the stem in camerates does not have primary subdivision into pentameres. The more or less wide axial canal (and its five-rayed structure) could evolve secondarily. The latter suggestion is supported by an expansion of the axial canal and by the development of the triradiate symmetry of the canal in the Ordovician eocrinoid *Rhipidocystis*, which clearly has a stem of the first morphogenetic type. Perhaps, both these types could be combined in a single stem, e.g., in cladids. However, the development of the stem from this point of view remains poorly studied.

The study of the origin and development of the stem in pelmatozoan echinoderms and its comparison with metameric appendages of other echinoderms and deuterostomes allows the following conclusions:

(1) The stem of pelmatozoan echinoderms appeared as a result of the morphogenetic and functional connection of the somatocoel and the fixation preoral lobe of the larva followed by metamerization of the resulting structure (peduncle).

(2) The metamerization of the stem and its transformation into the true stem could occur in two ways: (a) by budding of new segments from the original stumplike attachment disk (holdfast) (the zone of appearance of new columnals was in the distal part of the stem, between the holdfast and stem) and (b) by gradual arrangement of the plates covering the peduncle and their transformation into pentamerous columnals and, later, into monolithic columnals. The growth zone in this case was located between the proxistele and dististele and, later, along the entire mesistele. Both these mechanisms could occur even in the same individual.

(3) The stem of crinoids is partly homologous to the stem of Soluta and the tail of Chordata, because both originated from the somatocoels. The presence of the morphogenetic connection of the somatocoels and the preoral lobe of the larva in crinoids makes this homology incomplete.

(4) The holdfast of the earliest Soluta is not homologous to the holdfast of pelmatozoan echinoderms but is similar to the holdfast on the tail of *Cephalodiscus*.

(5) The homology of the stem of pelmatozoan echinoderms and the metameric process of Stylophora is at present not certain.

(6) The stems of crinoids and edrioblastoids are apparently non-homologous, because the stem in edrioblastoids, as in starfish, supposedly originated from the anterior coeloms. The stem of Edrioblastoidea and the collar of Edrioasteroidea are homologous.

(7) The articulation of the stem and cup in crinoids was diverse and included all possible variants. The type of articulation was determined by the time of the emergence of the five-chambered organ in the ontogeny and by particular features of the morphogenesis of the theca. The so-called law of Wachsmuth and Springer describes only the most common variants of articulation of the cup and the stem.

SECTION 4. ORIGIN AND HOMOLOGIES OF THE ARMS IN CRINOIDS

The presence of arms in crinoids is one of the major characters distinguishing them from most other classes of Echinodermata. Based on this feature, crinoids are regarded as a separate subphylum, Crinozoa, whereas almost all of the other stalked echinoderms (pelmatozoan echinoderms) are assigned to the subphylum Blastozoa, members of which have brachioles rather than arms (Sprinkle, 1973a). Hence, the origin of arms and their morphogenetic relationships with brachioles is one of the most important problems in the systematics, origin, and evolution of crinoids and all other echinoderms possessing food-gathering processes.

Disparid and, especially, hybocrinid crinoids, which have the most primitive arms, were among the first to appear in the fossil record. Therefore, these groups are of particular value in addressing the problem of the origin of arms in crinoids. However, this problem cannot be resolved without studying it beyond the limits of the class Crinoidea and analyzing the food-gathering extremities in other classes that could be the rootstock of the arms in Crinoidea or could have developed synchronously with them. Therefore, the arms should be first compared with the brachioles and then with the arm of Soluta (primitive echinoderms lacking pentaradiate symmetry). It is also essential to discuss the structure of *Echmatocrinus*, the only Cambrian pelmatozoan echinoderm known to have arms. Although the species of this genus recovered from the famous Middle Cambrian Burgess Shale possess arms, they are in many ways very different from all other crinoids. During the comparison between the arms of crinoids and the food-gathering extremities of other classes, primary importance will be given to the morphogenetic potential of these structures rather than formal correspondence of characters. Only this approach can reveal the phylogenetic relationships of different groups, in particular their morphological transitions.

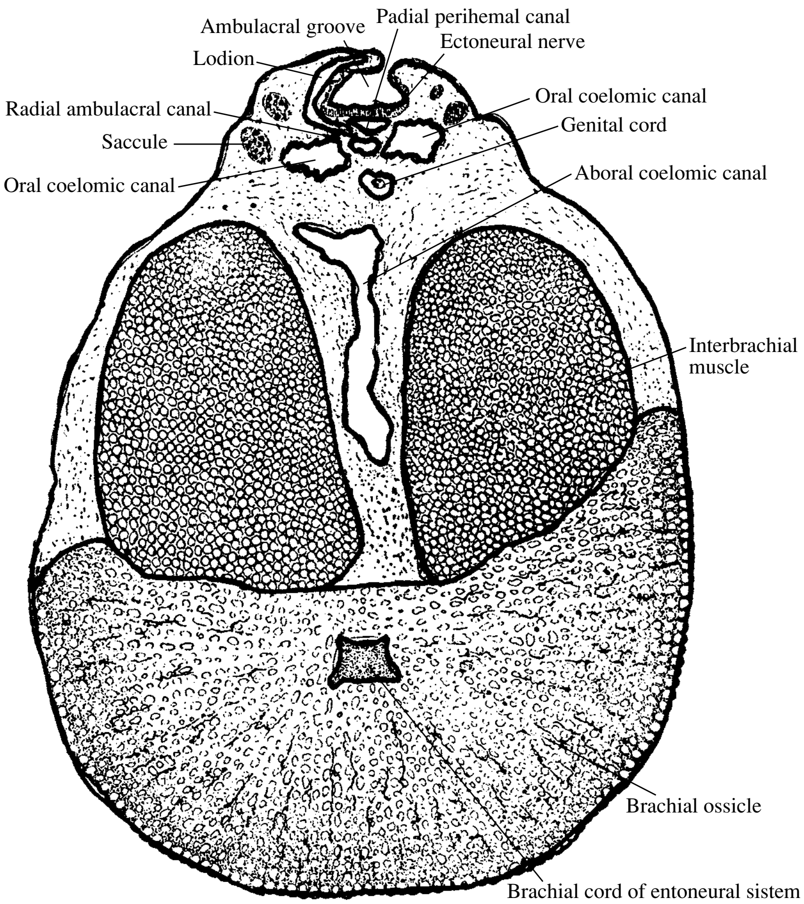


Fig. 42. Cross section through the arm of the extant crinoid *Heliometra gracialis* (after Ivanov *et al.*, 1946).

ARMS OF CRINOIDS

GENERAL DESCRIPTION

The arms of crinoids are relatively large, metameric, endothecal extensions, mainly serving to gather food particles. They are called endothecal (Ubaghs, 1967), because they develop as evaginations of the thecal wall, into which many systems of internal organs are extended (Fig. 42). The arms have a supporting skeleton built of specific series of calcite ossicles called brachials. The brachials are connected by ligaments, and in many crinoids, especially those of advanced taxa, they also have muscular articulations. In modern crinoids, muscles and ligaments are on opposite sides of the transverse fulcral ridge, and induce antagonizing differential movements of the arms and pinnules. There are three ways of identifying the presence of the muscular articulation in fossil crinoids: (1) by general morphology of the articular facet; (2) by microstructure of the stereom; and (3) by taphonomic features (Ausich and Baumiller, 1933). The presence of a distinct ridge and well-developed depression on the articular facet is thought to indicate the position of muscular articulation. At the points of ligament articulation, the stereom is gallery-structured, with pores for ligament fibers, while at the points of muscular articulation, the stereom is labyrinth-structured without special pores. The taphonomic method is based on the differing rates of disarticulation of skeletons with muscular and ligament articulations. Each method has some limitation. Nevertheless, at present it is established that muscular articulations appeared in advanced pinnulate cladids in the Early Devonian. This was one of the most important events in the history of Crinoidea, because later representatives of this lineage gave rise to the Meso–Cenozoic subclass of articulate crinoids, in which the muscular articulations in the arms are perfectly developed (Ausich and Baumiller, 1993; Simms and Sevastopulo, 1993). Some authors also note the presence of muscular articulations in other Paleozoic crinoids, including calceocrinids (Ringueberg, 1889; Springer, 1926), some other disparids (Van Sant, 1964), possibly *Pisocrinus* (Ausich, 1977), and Flexibilia (Van Sant, 1964). However, these data require reexamination with new evidence.

Usually, brachials are arranged in one row. This is their primary arrangement, because it is recorded only in the earliest crinoids. Arms structured in this way are referred to as uniserial. In some later crinoids, the arms can be biserial. In these cases, brachials in the arms occur in two parallel rows, which are displaced in rela-

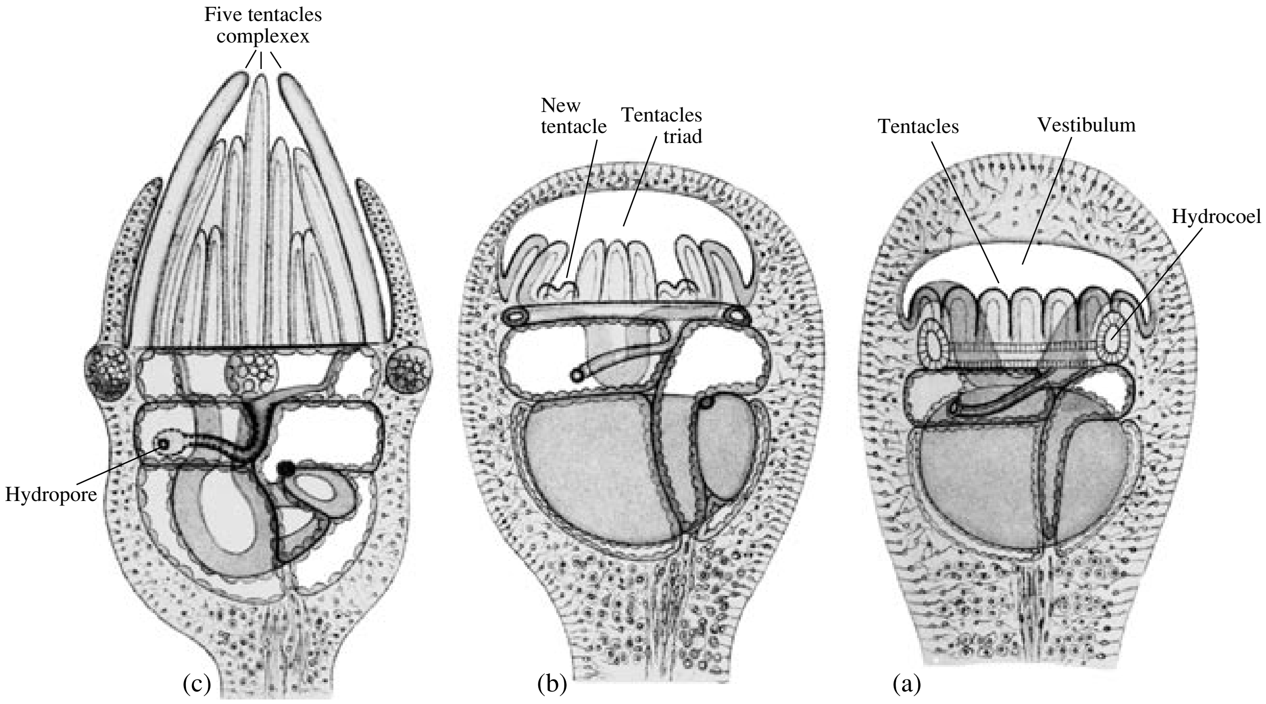


Fig. 43. Stages of development of the radial ambulacral canals in the ontogeny of the crinoid *Antedon*. At the first stage (a) three hollow tentacles extending from the ambulacral ring originate in each ray. Then (b) the incipient tentacle appears at the sides of each triad, and eventually (c) five tentacles grow in each ray. Later, four tentacles in each ray become reduced, while a single middle tentacle remains to develop into the radial ambulacral canal of the adult animal (after Barrois, 1888).

tion to each other for approximately half of the height of a brachial. The transition from the uniserial to biserial arms can be traced in many forms and is secondary in this respect. This process is thought to be connected with the necessity of increasing the number of pinnules on the arms. Pinnules are uniserial extensions occurring in many crinoids. One pinnule extends from each brachial. The arms are attached to special radial plates included in the cup. Usually, only one arm is attached to one radial, but sometimes much more. Primitive arms are usually straight and unbranched. However, in many forms, they can branch in many different ways (Broadhead, 1988).

In modern crinoids, each arm is composed of several independent, although strongly connected, parts of different system of organs (Fig. 42). In addition to the skeletal system, the arms include parts of the muscular, three neural, blood, and reproductive systems (the latter is represented by genital cords, from which genital glands are formed in the pinnules). There are also ambulacral vessels with extending ambulacral tentacles and a food groove, lined by the ciliated epithelium. In addition, each arm is penetrated by three canal-like coelomic cavities, i.e., the unpaired aboral sinus of the coelom and the paired oral sinuses of the coelom (aboral and subtentacular canals). Thus, the arms in modern crinoids are complex structures composed of the derivatives of the middle left coelom (hydrocoel) and of the posterior coeloms (somatocoels), both oral and aboral. The arms of early crinoids apparently had a similar structure. This is indicated by the fact that the earliest crinoids had all the characters characteristic of modern crinoids, although not as perfectly developed and often occurring separately rather than all together. Nevertheless, in many cases, some systems (e.g., the reproductive system) and muscular articulations in the brachials could often be absent in the arms of early crinoids.

Morphogenetically, arms represent extensions of the animal's body supported by special skeletal plates, with which the ambulacral system (originally independent) is connected at a certain stage. After the oral and aboral somatocoels extend into the arms, other systems are formed. Based on various descriptions of the ontogeny of modern crinoids, the following pattern of arm ontogeny can be revealed (Ivanov, 1937; Ivanova-Kazas, 1978). After the larva is settled, and the vestibule marking the future mouth is shifted to the top (previously on the posterior end of the larva), the bottom of the vestibule evaginates due to the development of the lobes of the hydrocoel. Each of these lobes is divided into three diverticula. As a result, five groups, of three tentacles each, appear within the vestibule, with the medium tentacle being in the radial position. After this, one more tentacle appears on the side of each group of tentacles, thus resulting in five groups of five tentacles (Fig. 43). After the development of the oral lobes possessing oral plates and the rupture of the roof of the vestibule between the oral plates, all tentacles open to the outside. After this stage, the arms begin to form. At first five radials, supporting a series of brachials, appear between the oral and basal plates. Later, five radial evaginations develop on the edges of the cup. At the same time, in each group of five tentacles of the ambulacral system, four are reduced, while the middle tentacle, occurring in the radial position, remains. Each of the remaining tentacles is connected to the radial evaginations on the edges of the cup and transforms into a radial ambulacral canal. In addition, the continuations of the oral and aboral coeloms (subtentacular and aboral canals) extend into the arms. Summarizing the above data, it is possible to say that the arms of crinoids are distal outgrowths of the body that grow metamerically and in which the right and left posterior coeloms (somatocoels), their derivatives, and the derivatives of the left intermediate coeloms (hydrocoel) are functionally combined to form a single structure.

Indeed, the structure and development of arms in the ontogeny of early crinoids were in many details different from those found in their modern counterparts. For instance, the radial trunk of the ectoneural system was not lodged in the special canal of the skeleton but ran along the bottom of the food groove. It is certain that the completely developed arms were formed as outgrowths of the body, which is indicated by their consistent distal position in the cup. It is also certain that they were connected with the ambulacral system. Other systems of organs may or may not have been equally well-developed. However, the reproductive system in the arms could have been absent, being more closely connected with the proximal part of the cup and with the stem. The main evidence supporting this hypothesis is the absence of pinnules in many early crinoids, whereas in modern crinoids, reproductive products are formed in the pinnules. Permanent development and maturing of the reproductive products in the simple, unbranched arms of many disparids and hybocrinids lacking pinnules could disturb food-gathering. Hence, it is unlikely that the maturing of the oocytes could have taken place in the arms. Although the consistent absence of the gonopore in all crinoids indicates that the reproductive products were periodically excreted through the arms or through the anus, the oocytes could have matured in the cup or even the stem or the holdfast, which in some crinoids had a relatively large cavity, e.g., in the artificial genus *Lichenocrinus* (Fig. 36), established based on the holdfast (Hints *et al.*, 1989). This hypothesis of possible various places where oocytes could have matured, from the lowermost part of the body (holdfast) to the uppermost end (pinnules), is based on the fact that the development of the reproductive products in crinoids is connected with the so-called axial genital cord. The axial cord extends along the axis of the cup and in the central part of the chambered organ inside the stem canal. At the top, it is blind-ended close to the oral blood ring. The complex of cells containing the primary sex cells is adjoined in modern crinoids to the upper part of the axial cord.

In modern crinoids, the arms are very important for respiration. Because of the large surface area, the blood and coelomic systems easily perform gas exchange and provide oxygen to all parts of the body. In most early crinoids, the arms must also have functioned in this way. However, in some early taxa, the respiratory function of the arms was apparently supplemented by gas exchange through the body wall, at points where it was thinner, and through pores that were present in some Paleozoic crinoids. The Lower and Middle Ordovician perittocrinids from the Leningrad Region are a good example (Fig. 20). The plates of the cup in this small crinoid family have a system of folds. In the periphery of the plates, these folds are quite thin, and it is possible that some species had pores where the folds of the neighboring plates were connected. These pores were similar, and possibly homologous, to the epispires of eocrinoids. These folds and pores appear to have considerably increased the intensity of gas exchange, because their presence increased the surface area of the contact between the body and the surrounding water. The thinner skeleton along the periphery of the plates facilitated the absorption of dissolved organic matter. However, the main function of these structures, as was discussed in a previous section, was to supplement food intake by feeding on dissolved organic matter and bacteria, as in some modern echinoderms. Probably, this supplementary feeding was necessary when the supply of the usual food, caught by the arms, was insufficient.

SOME FEATURES OF MORPHOGENESIS OF THE ARM SKELETON

Correlation of the Growth of the Skeleton of the Arms, the Ambulacral Radial Canals, and the Food Grooves

The ontogeny of the arms in modern crinoids, discussed above, suggests that the arm represents a complex and highly coordinated system of organs, which appear in ontogeny independently from one another. After their incorporation, the degree of their functional and morphogenetic coordination immediately becomes very high. For instance, in modern crinoids, the growth of the skeleton of the arm, food groove, and ambulacral radial canal are very strongly coordinated. However, this was not always the case in the evolution of Crinoidea. In particular, the lack of coordination of the growth of the skeleton of the arm and the food groove, on the one hand, and the radial ambulacral canal, on the other, is observed in hybocrinids (Fig. 44). In the Middle Ordovician North American genus *Hybocystites*, the skeleton of the arms in three rays is quite short, composed of six or seven ossicles, while it is completely absent in two other rays (Sprinkle and Moore, 1978; Rozhnov, 1985a, 1985b). The food grooves in three rays extend from the mouth to the bases of the arms, run along their oral side, and reach the tops of the arms. Usually, they do not terminate here, as in other crinoids, but continue onto the aboral side of the arms,

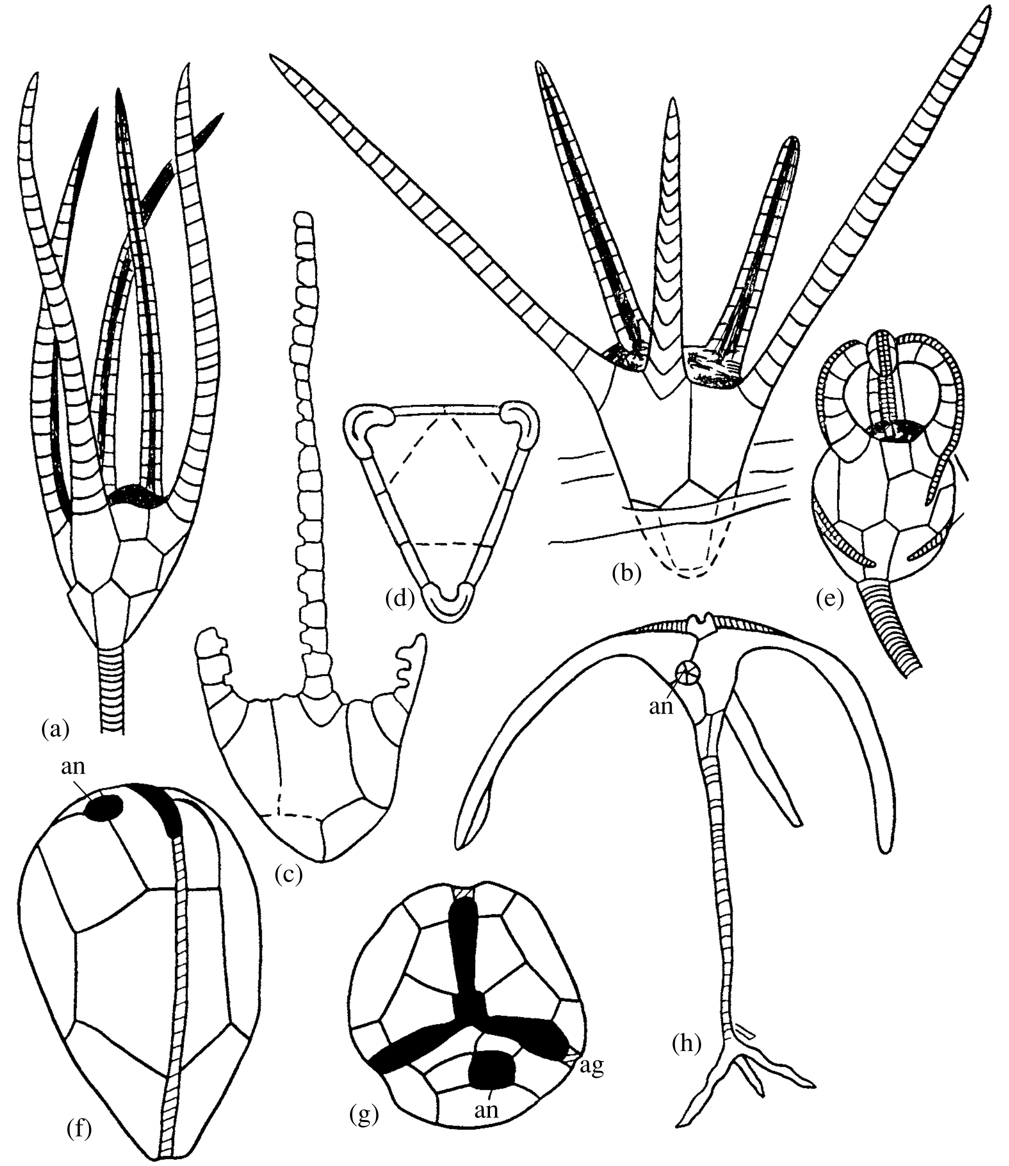


Fig. 44. Representatives of hybocrinids: (a) *Hybocrinus conicus* Washsmuth et Springer; (b) *Hoplocrinus usvensis* Rozhnov; (c–d) *Baerocrinus ungerni* Volborth; (e) *Hybocystites eldonensis* (Parks); (f–g) *Tripatocrinus pustulatus* Sprinkle; (h) *Cornucrinus longicornis* Regnell (after Rozhnov, 1985); an—anus, ag—ambulacral groove.

descend to the base, and extend to the dorsal cup, where they soon terminate. In two other rays, the dorsal (supporting) skeleton of the arms is completely absent, and the ambulacral grooves (= food groove + radial ambulacral canal) immediately descend along the dorsal cup and, sometimes, even continue onto the stem. Thus, in this case, a very high degree of independence in the development of the ambulacral groove with the cover plates (ventral skeleton of the arm) and that of the dorsal skeleton of the arm is observed. This may suggest evolutionarily independent origins of these structures in the arms, a hypothesis which will be discussed below. Among hybocrinids, there are representatives with completely developed arms (*Hybocrinus* and *Hoplocrinus*) and those without a special dorsal skeleton. In the latter case, the dorsal cup (e.g., in *Tripatocrinus*) functions as a supporting structure. Sometimes, this dorsal cup has special nonmetameric extensions (outgrown plates as in *Cornucrinus*) (Regnell, 1948; Sprinkle, 1973b; Rozhnov, 1985a, 1985b).

In many Inadunata and Flexibilia, the relatively independent development of the dorsal skeleton of the arms and of the ambulacral grooves is indicated by the entanglement of the first left branch of the dorsal skeleton of the C arm by the rectum or even by the entanglement of the entire C arm. This process is discussed in detail in the section on the anal structures of crinoids.

Thus, a certain degree of independence in the development of the dorsal skeleton of the arms and of the ambulacral groove is apparent. Nevertheless, the growth of the dorsal skeleton of the arms strongly depends on the development of the ambulacral groove, since this skeleton had only a supporting function and, apparently, appeared secondarily in relation to the ambulacral groove. The ambulacral groove is a combination of the food groove and the radial ambulacral canal. Apparently, in many cases, the radial ambulacral canal induces (using the technical embryological terminology) growth of the supporting skeleton. This may explain many features of growth and branching of the arms, the position of the pinnules, and, especially, the relationships between the arms and the radials.

The problem of the morphogenetic relationships between the arms and the radials is very important, not only in the systematics of many crinoid groups of various ranks, especially disparids, but also for the problem of the origin of arms in general. Embryologists who studied the ontogeny of modern crinoids considered the radials to be the first plates of the brachial series, essentially the first plates of the arms, which are distinguished from the other brachial plates only by their position in the cup. Indeed, the radials begin to develop later than other plates in the cup and almost simultaneously with several proximal brachials. In addition, the radials and brachials at this growth stage are similar in their width and shape, both being somewhat distant from other plates. Nevertheless, this view simplifies the actual situation. Firstly, the essential difference between the radials and brachials is not only in the position in relation to the cup, but also in the relationship with the ambulacral groove (in ontogeny, it is connected to the arm above the radial). Secondly, morphology and the scattered data on the ontogeny of Paleozoic crinoids suggest a more complex pattern. Fossil data are considered below. First of all, in many of the earliest Ordovician crinoids, the facets for the arm attachment on the radials are considerably narrower than the distal edge of the radials. Such facets are characteristic of hybocrinids, perittocrinids, many iocrinids, and many other crinoids. This indicates that the arms and radials were already somewhat independent at the earliest stages of the evolution of Crinoidea. A few existing data on the ontogeny of Paleozoic crinoids show that the radial plates, although they develop later than other plates of the cup (orals, basals, and infrabasals), still develop considerably earlier than the brachials. Their point of origin is rigidly connected to the points of origin of the lobes of the developing hydrocoel. This conclusion can be drawn based on the data from the classic monograph of Arendt (1970) on hypocrinids. In this monograph, Arendt described in great detail ontogenetic changes in the theca of several genera and, especially extensively, in *Cranocrinus praestans* (Fig. 9). In this species, at the earliest stages studied, the basals and orals alternate, unlike in the adults. Hence, some of these are (at this stage) in the radial position, and some others, in the interradial. The actual position in relation to the lobes of the hydrocoel (future radial canals) in the fossils can be only determined by the position of the hydropore, which is always in the interradial position. Arendt managed to trace the position of the hydropore at the early stages of the development of the theca of *Cranocrinus praestans.* The hydropore was in the center of one of the orals. Hence, the orals at this stage are in the interradial position, while the basals are in the radial position. Based on the data of Arendt, it is evident that all radials originate on the rays, on the borders between the orals, rather than in the interrays, as was suggested by Arendt. Consequently, the basals are later displaced in the interradial position, in contrast to the orals and connected radials. For the same reason, the position of a single radial in *Monobrachiocrinus oviformis* should also be considered radial rather than interradial. Therefore, it is difficult to agree with Arendt's hypothesis that the original position of the radials was interradial. The problem of the original arrangement of the plates is extensively discussed in the section on the structure of the theca. The important observation of Arendt that the arms on the radials are "formed in the same succession in which the radials were formed" (Arendt, 1970, p. 84) is noteworthy.

The above discussion suggests that, although the radials of crinoids were originally mostly thecal plates rather than brachials included in the cup (this follows, for instance, from the proportion between the size of the radials and arms in primitive crinoids), in later crinoids the morphogenesis of the radials was closely correlated with the morphogenesis of the arms.

Multiple Arms in the Same Ray

In some cases, the proportion between the numbers of radials and arms is unusual. The arms and radials in so-called multifaceted crinoids (i.e., those with several arms on one facet) are particularly different (Fig. 45). The morphogenetic mechanism of the appearance of several arms on one radial is different in different groups, but in each it indicates the defining role of the ambulacral radial canals in the development of the arms. All of the various mechanisms, especially those that are characteristic of disparids, are discussed below.

(1) Genus Anamesocrinus Goldring, 1923 from the monotypic family of disparid inadunates (Middle Devonian of North America). Each radial in this genus bears five similar small, narrow arms. This suggests a direct correlation with the development of the radial ambulacral canals in modern crinoids. As noted above, three incipient radial ambulacral canals appear simultaneously in each ray at one of the ontogenetic stages (Fig. 43). Slightly later, two more canals appear in each ray, thus resulting in five canals. However, four of these very soon disappear, and only the middle incipient canal remains. It is possible to assume that, in some cases, supplementary canals did not disappear as a result of heterochrony but continued into the adult

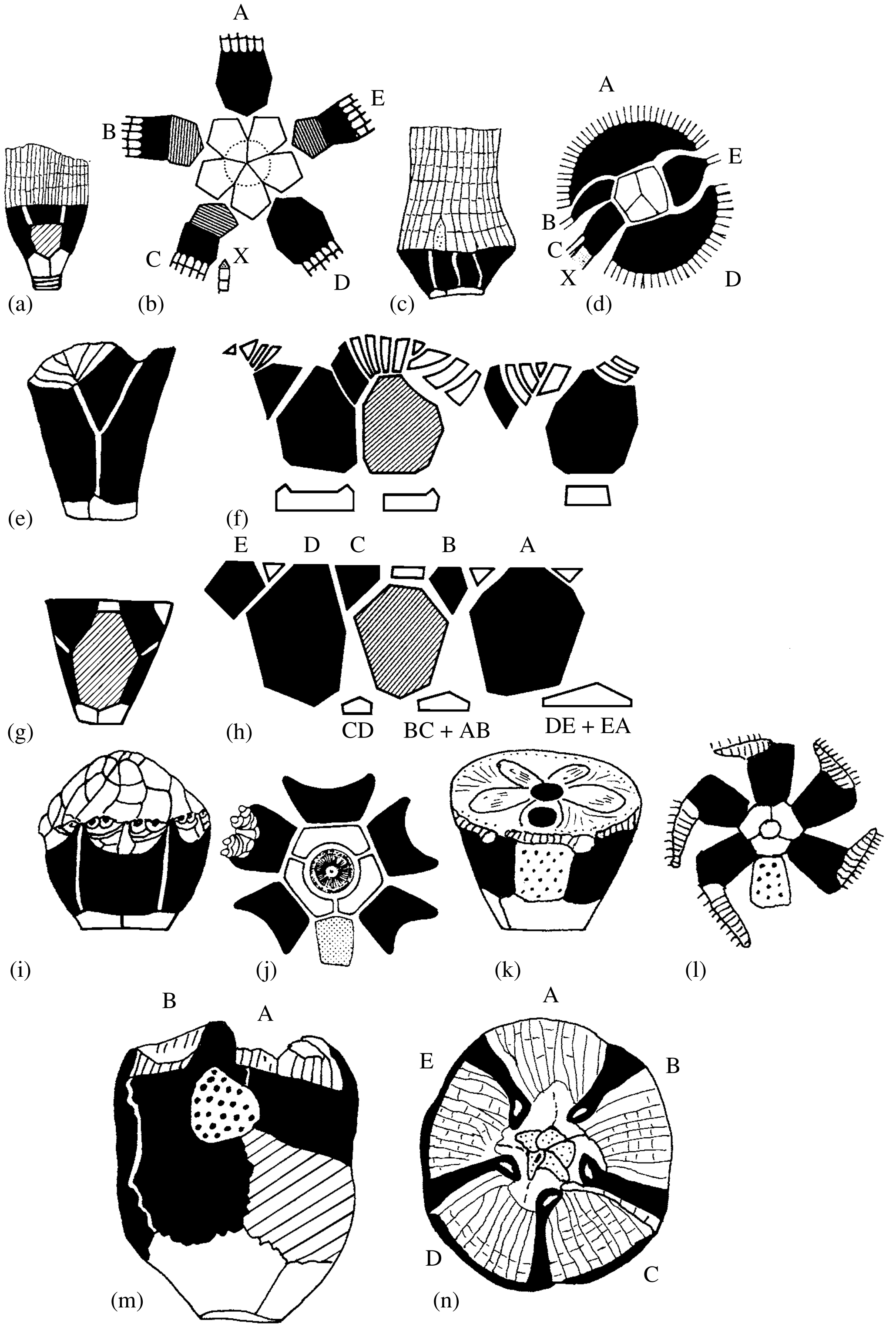


Fig. 45. Crinoids with multiple arms: (a, b) *Anamesocrinus*, (c, d) *Catillocrinus*, (e, f) *Jaekelicrinus*, (g, h) *Calycanthocrinus*, (i, j) *Agathocrinus*, (k, l) *Agostocrinus*, (m, n) *Acolocrinus*. Radials are black, inferradials are hatched, anals and orals are dotted.

stage. In such cases, each of these induces the development of a separate arm. Thus, five arms appear in each ray of the adult animal. Here, this particular mechanism of development of many arms is suggested for *Anamesocrinus*. The existence of five incipient radial canals in each ray, at one of the ontogenetic stages of modern crinoids, is discussed in the chapter on the appearance and development of symmetry in pelmatozoan echinoderms.

(2) Multifaceted radials in the superfamily Allagecrinaceae. The radials in this superfamily apparently appear in the same way as in *Anamesocrinus*. Indeed, arms in anamesocrinids and allagecrinaceans are unbranching. Hence, the ambulacral canal in these taxa does not have the potential to branch. Therefore, in allagecrinaceans, as in the above example, the process of heterochrony is suggested. This process supposedly produced the incipient ambulacral canals, which, as in modern crinoids, existed at the early ontogenetic stages and continued into the adult stage. In contrast to *Anamesocrinus*, the process of heterochrony not only revealed multiple incipient ambulacral canals, but also the sequence of the appearance of some structures of antimeres in ontogeny. As a result, multiple arms only appeared, at least in especially large numbers, in the A and D radials. The first facets for the arm attachment on these two plates (A and D) appeared later in ontogeny, after the facets of three other plates (B, C, and E). Such a sequence of facet appearance is known for several allagecrinacean species (Moore, 1940; Wright, 1941; Moore and Ewers, 1942; Strimple and Koenig, 1956; Burdick and Strimple, 1982; Lane and Sevastopulo, 1982, 1985) and in the genus *Homocrinus* from the ancestral superfamily Homocrinaceae (Sevastoplulo and Lane, 1988). Apparently, the incipient radial ambulacral canals on the ambulacral ring appeared in the same sequence. The incipient B, C, and E canals appeared earlier than two others (A and D) and completed the cycle resulting in the complete, or incomplete, reduction of the additional canals. Therefore, only one arm, or slightly more, appeared in the B, C, and E rays (the latter when not all of the additional incipient canals had yet been reduced). In this case, the number of additional arms on these plates was also low. There were even fewer arms on the plates, which appeared later in ontogeny. A large number of arms (much more than five) on each plate in many allagecrinaceans is explained by the additional polymerization (inertia of development) of the ambulacral canals at later ontogenetic stages. Thus, the development of the radial plates and arms in these genera are processes considerably separated from one another. However, in many cases their relationships were more complicated (see the example below).

(3) Multiarmed Pisocrinacea (genera Calycanthocrinus and Jaekelicrinus). Pisocrinacea, which are known from the beginning of the Silurian, had unbranching arms. In contrast to anamesocrinids and allagecrinaceans, the appearance of the additional arms in this group was connected with the appearance of accessory radials, each possessing (like main radials) a simple, unbranching arm. In the Late Devonian, another genus, with more numerous accessory plates possessing arms, appeared within the Pisocrinacea. Below, an attempt is made to explain the origin of these accessory plates from the point of view of the potential of morphogenesis of crinoids. First of all, in *Calycanthocrinus*, the accessory plates are morphologically closely connected with the small upper radials (so much that they seem to be separated parts of them). In *Jaekelicrinus bashkiricus*, some plates (there are very few) seem to originate from the large D radial, while *Jaekelicrinus yakovlevi* has several more plates connected with the large A radial (Yakovlev, 1947; Rozhnov, 1981). Thus, pisocrinids show a pattern seemingly opposite to that observed in allagecrinaceans (i.e., the largest number of accessory plates is observed in the rays on which the facets on the main plates appeared first in ontogeny). These are the B, C, and E rays. (In allagecrinaceans, the largest number of accessory facets develop in the A and D rays.) However, in Pisocrinacea, in addition to the accessory plates, there are also corresponding accessory plates, so that each plate bears only one facet. The main plates, which especially produce many accessory plates, appear last in ontogeny. This was established for the genus *Homocrinus* and extrapolated to the Pisocrinida by Sevastopulo and Lane (1988). These small radial plates, which are the last main plates to appear in ontogeny, originate from the upper radial plates. In Pisocrinacea, they are very strongly separated from the lower radial plates, so that they, first morphologically, and later also morphogenetically, represent an almost independent circlet. The following pattern is observed in this case; the first radial facets appear on those main radials that appeared last in ontogeny. The appearance of the accessory plates bearing facets requires the appearance of the accessory radial ambulacral canals. These additional canals may appear as a result of the branching of the initial radial canal. This feature enables the branching of arms in crinoids. However, in Pisocrinacea, the arms are almost always unbranching, and hence, the canals in this group are unlikely to branch. Therefore, it must be suggested that in the ontogeny of Pisocrinacea many incipient radial canals begin to develop at the very beginning of the development of the ambulacral system, as in modern crinoids and, supposedly, in Anamesocrinacea and Allagecrinacea. However, in modern crinoids, four out of five incipient canals are reduced, and only one remains in adults. In anamesocrinaceans, all five canals remain. In allagecrinaceans, the incipient canals did not appear synchronously in different rays. Those canals that appeared later discontinued their development simultaneously with the other canals, so that the accessory radial canals did not have time to become reduced. In addition, the canals acquired the ability to polymerize, so that their number could be much greater than five. This explains the uneven distribution of the facets in the rays of allagecrinaceans. Pisocrinacea had different types of heterochrony, resulting in the uneven distribution of the facets (and plates). The incipient radial ambulacral canals that appeared first reached the stage of five tentacles. After that, they did not disappear and grew to form multiple adult radial canals, which enabled the development of accessory arms. In contrast to allagecrinaceans, pisocrinaceans had not only the accessory facets, but also accessory plates within the cup. This may be explained by the fact that the upper radials in Pisocrinacea represented, morphogenetically, an almost independent circlet. In the incompletely formed dorsal cup, the additional radial canals approaching the points of development of the upper radial canals on the unoccupied space immediately induced new accessory plates. The problem of the morphogenetic relationships of the upper radials and arms is important for the systematics of disparids and for understanding the origin of the radianal plate and will be extensively discussed in the next section. Two cases, when the accessory arms extending from one plate appear as a result of transformation of branching arms are discussed below. Superficially, the result is the same, but the morphogenetic mechanism used is completely different.

(4) Multiarmed Agostocrinus Kesling et Paul, 1971. This genus comes from the Lower Ordovician of North America. It is placed in *Treatise…* among allagecrinaceans, because it has several arms on each radial (Moore *et al.*, 1978). However, the origin of these arms is slightly different from that in allagecrinaceans. Arms with numerous branches on the right side lay on their left side on the surface of the radial. As a result, small offshoots of the main branch were directed upward and resembled multiple arms.

(5) Multiarmed representatives of the family Parahexacrinidae Shevchenko, 1967 (Camerata). These species from the Lower Devonian of the Tian Shan represent another example of the process resulting in the extension of several arms from a single radial. The distinct morphological and phylogenetic lineage *Agathocrinus–Amonohexacrinus–Parahexacrinus* shows that this process is based on the spatial approximation of the auxiliary ossicles of several orders to each other and to the radial plate and on their subsequent fusion in a single plate.

Thus, the above discussion of the structure and morphology of the arms suggests the following conclusions:

(1) Among the system of organs forming the arm, the ambulacral groove could develop independently from the dorsal skeleton of the arm in primitive forms but could also grow in coordination with the dorsal skeleton (in most crinoids).

(2) The plates of the dorsal skeleton of the arms (brachials) could be both markedly different from the radials in their morphogenesis (forms with narrow radial facets and those with multiple arms on one radial) and morphogenetically similar to the radials (many forms with wide radial facets). In the latter case, the presence of several radials in one vertical row in the cup is particularly interesting. It will be discussed separately because of its particular importance for the systematics of inadunates (especially disparids).

FREE ARMS AND PAIRED RADIALS

Many disparids have two radials in a single vertical row in some rays of the cup. For instance, in the genus *Homocrinus*, as in all homocrinids, one large plate is in the A and D rays, while two plates, the upper plate and the lower (larger) plate, are in the three remaining rays (B, C, and E). In this genus, the facets for arm attachment are considerably narrower than the radials and, thus, the dorsal cup is distinctly delineated from the arms. In this case, it is easy to imagine that the radial ambulacral canal extending from the ring canal was connected to the dorsal arm at the level of the radial facets. Therefore, there is a clear morphogenetic distinction between the radials and the brachials. In the former, the radial ambulacral canal is absent, while, in the latter, the brachials serve as its receptacle and support. Why do some rays have one radial, while others have two? It is possible that the superradials are in fact brachials that were included in the dorsal cup. Another opinion, once widely accepted, is that the ancestors of disparids originally had two plates in all rays, and that these plates supposedly had a tendency to fuse. This view is not sufficiently substantiated and contradicts the structure of the earliest crinoids and the ontogeny of the species of the genus *Homocrinus* (Fig. 14). According to Sevastopulo and Lane (1988), the superradials appear after the lower and simple plates are formed. Hence, they developed later in evolutionary terms, supposedly as a result of the inclusion of the first brachials in the cup. Hypothetically, this process of inclusion could have proceeded in the following way.

Many groups of crinoids and other pelmatozoan echinoderms are known to have a certain ontogenetic sequence of development of many structures in the rays. For instance, in the B, C, and E rays, these structures are formed earlier and develop faster than in the A and D rays. This applies not only to the radial facets, based on which the sequence of the development of structures in the pentameres is normally interpreted, but also to the radials themselves (Arendt, 1970; Sevastopulo and Lane, 1988). Therefore, it is suggested that the singular radials and inferradials in *Homocrinus* or in its closest ancestor were formed in a sequence characteristic of most crinoids and at least some of the other pelmatozoan echinoderms (C, B or E, D, A). If the hypothesis that the superradials were originally the first brachials is correct, it is clear why they are formed later in the ontogeny of *Homocrinus* (after the primary radials in all five rays) (Fig. 14). The development of these primary radials apparently began in the same sequence as the facets and, hence, the radial ambulacral canals. Therefore, it is possible to suggest that in the ancestors of *Homocrinus* the arms and the first brachials appeared and began to develop at a certain ontogenetic stage within three rays, while, in the two other rays, the radials were still growing. As a result of heterochrony, the fusion of the radial ambulacral canals with the arms was shifted to slightly later stages, when the radials and basals completed the formation of a dorsal cup, while internal organs began to be lodged inside the protective skeletal capsule. Because the first brachials, although not yet connected with the ambulacral radial canals, appeared in three rays by the time of the formation of the skeletal capsule and the D and A radials, these first radials were also included in the dorsal cup, which, after this, acquired typical homocrinid features. In the genus *Homocrinus*, and again due to heterochrony, the brachials were included in the cup slightly later than the formation of the skeletal capsule was completed, but before the beginning of the development of the facets for the arm attachment. Because of this, it was possible to observe the process of their inclusion in the cup, which could be preserved as a fossil only after the consolidation of the plates. Therefore, the absence of the cups at these ontogenetic stages, even when a special search is undertaken, probably suggests that the first brachials appeared in the developing cup before the plates were associated in a single skeletal capsule. Judging from the morphology of other representatives of Homocrinidae and some related groups, the latter process was more widespread. The structure of the skeleton of *Virucrinus kegelensis* from the Middle Ordovician (Caradoc) of northern Estonia (Rozhnov, 1990) may be given as an example. This species has five basal plates, but only four radials and arms (Fig. 13). Apparently, the radial and the arm in the A ray are absent because, in this ray, structures usually appear last and disappear first. The characteristic feature of this crinoid is the absence of a distinct border in the skeleton between the dorsal cup and arms. The superradials and first brachials are morphologically very similar, like the facets between the inferradials and superradials, on the one hand, and superradials and arms, on the other hand. The superradials and inferradials in the C ray are well developed. A single large radial occurs in the D ray, while the superradial is virtually absent, because it is almost entirely located outside the dorsal cup and morphologically represents the first brachial. The A ray is completely atrophied. In two other rays, E and B, the first brachials can be located either almost completely outside the cup, if one judges from the degree of consolidation of the plates into a single cup, or completely within the cup. Thus, this feature may be highly variable between individuals. In the latter case, the first brachial plates, almost entirely fixed in the cup, are in fact the first superradials. This testifies to the homology of the superradials and the first brachials.

The primary radials (simple radials and inferradials) have a specific origin that was discussed in the section on homologies and morphogenesis of the thecal plates. It is noteworthy that in some cases the radials could be atrophied. In this case, the free arms extended directly from the basal plates, as in *Tetragonocrinus* from the Lower Ordovician of the Leningrad Region (Fig. 4) (Arendt, 1985; Rozhnov, 1988).

Among camerates, the inclusion of the brachials in the cup is very common and had particular patterns. However, the discussion of these patterns is beyond the scope of the problem considered here.

ARMS OF *ECHMATOCRINUS* AND THE EARLIEST REMAINS OF ARMS

Sprinkle (1973a) described the genus *Echmatocrinus*, which he tentatively assigned to the class Crinoidea based on several specimens from the famous Canadian locality the Burgess Shale (Fig. 5). Later, Sprinkle and Moore (1978) assigned this genus to a separate subclass within the Crinoidea. This is the only crinoid presently known from the Cambrian. Along with the general appearance, the following not unclear features allowed the assignment of this genus to primitive crinoids: a (1) cone-shaped cup composed of numerous, irregularly arranged plates; (2) at least eight uniserial arms possessing soft tentacles, interpreted as ambulacral tube feet; and (3) a holdfast composed of numerous irregularly arranged plates. This diagnosis (like the general appearance of the animal) reflected the uncertainty of the crinoid morphology of this genus. On the one hand, it is a crinoid, judging from the uniserial arms, and on the other, it is not a crinoid, judging from the structure of the cup. Additionally, the ambulacral tube feet are too large compared to their typical size. The same applies to the stereom structure of the plates: it is present, but the pores are an order of magnitude larger than in a typical stereom (the primary matrix of the plates has not been preserved). These facts cast doubt on the echinoderm nature of the genus *Echmatocrinus* and suggest another interpretation of this fossil, e.g., as an octocoral (Ausich and Babcock, 1996; Conway Morris, 1993). As a result of this uncertainty, this genus is presently difficult to use for phylogenetic reconstructions. If it is proved to be an echinoderm, it should be considered to be closer to eocrinoids, in which the food processes resembled arms. The remaining features more closely resemble eocrinoids than crinoids. Uniserial brachioles are rare in eocrinoids, but do occasionally occur. It is possible that some later rhipidocystids had uniserial brachioles. However, the uniserial structure of the brachioles previously suggested for the genus *Neorhipidocystis* was incorrect (more precisely, incomplete). At least in the type species, the right and left ossicles in the brachioles did not alternate, but were positioned strictly symmetrically to form a single ossicle with a hardly noticeable longitudinal suture (Rozhnov, 1997). In addition, material from the Middle Cambrian of Australia, given to me after maceration by P. Jell, contained ossicles of biserial brachioles and those of uniserial "arms." It is not clear whether or not these were true arms, because the arrangement and shape of the characteristic longitudinal canals on the bottoms of the brachioles and "arms" are very similar (Figs. 46, 47). This may suggest a close morphogenetic similarity of these food processes.

Before the morphogenesis of the arms is compared to that of similar food-gathering systems of other echinoderms (which is necessary for understanding the origin of arms), the following conclusions need to be briefly outlined:

(1) An arm is a complex system of organs, which have different origin.

(2) An arm, as an entire organ, developed gradually, as different incipient organs became united at the early stages of the evolution of Crinoidea.

(3) The dorsal skeleton of the arm and ambulacral groove have an independent origin; therefore, in some cases, they can develop independently of one another.

(4) The primary radials evolved independently from the dorsal skeleton of the arms; however, in evolution they can become morphogenetically close to the arms.

(5) The superradials of many Inadunata and Flexibilia are originally the first brachials included in the dorsal cup.

ARMS OF CRINOIDEA AND THE ARM OF SOLUTA

Theoretically, the arms of crinoids could appear both as a result of the transformation of brachioles and independently, using morphogenetic possibilities of the ancestral forms, which had had pentaradiate symmetry. Therefore, it is appropriate to compare the arms of crinoids with the arm of Soluta, the Early Paleozoic echinoderms which originally did not have pentaradiate symmetry, in an attempt to see what appeared earlier in crinoids, arms or pentaradiate symmetry?

It is convenient to use the well-studied *Dendrocystoides scoticus* from the famous starfish-containing locality near Girvan in Scotland (Upper Ordovician, Ashgill) and *Maennilia estonica* Rozhnov and Jefferies, 1996 (Figs. 29, 48) from the locality near the village of Vaasalemma in northern Estonia (Middle Ordovician, Caradoc) as examples for discussion of the morphology of the arm in Soluta. The morphology of the Soluta species from Scotland is taken from the detailed description by Jefferies (1990), and that of the Estonian taxon is based on material published by Rozhnov and Jefferies (1996).

The data on both species perfectly supplement each other, because the Scottish species was preserved as casts of the external and internal surfaces, whereas the Estonian species was preserved as a complete skeleton. The body of Soluta consists of a large theca (or head in Jefferies's terminology) with one or several lobes in the anterior part and a long complexly structured tail. A relatively long and strong arm extends from the anterior lateral part of the theca. The food groove extends from the arm toward the intrathecal mouth. The anal opening is located at the same side of the theca, but posteriorly. Without discussing the details of comparative anatomical interpretations of different parts of the body of Soluta, it should be said that these animals combine features of both chordates (e.g., tail) and echinoderms (e.g., calcite stereom skeleton composed of monocrystalline plates). The echinoderm features include the presence of an arm with a definite ambulacral system. The structure of the arm is discussed in greater detail below.

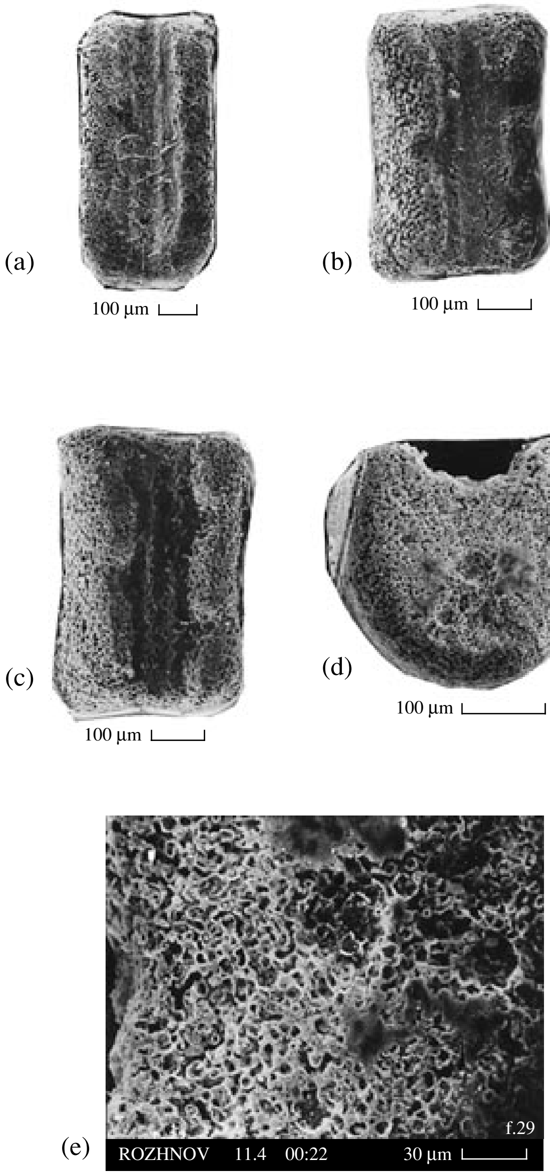


Fig. 46. Ossicles of the uniserial brachials from the lower part of the Middle Cambrian of Australia: inner view, articular surface, enlarged part of the same articular surface with the orifice of the central canal.

The arm of Soluta represents a long (approximately a half-length of the theca) process covered by four rows of plates (Figs. 29, 48–50). The beginning of the arm is contoured by special plates, rigidly connected to each other. Above, there is a zone of small, more or less flexibly connected plates. This zone, near the base of the arm, apparently enabled movement of the arm. The main part of the arm, gradually tapering distally, is above this zone. This main part of the arm is composed of four rows of plates, two of which consist of more or less imbricating plates forming the bottom of a relatively large food groove. Two other rows represent cover plates, the pointed ends of which entered the

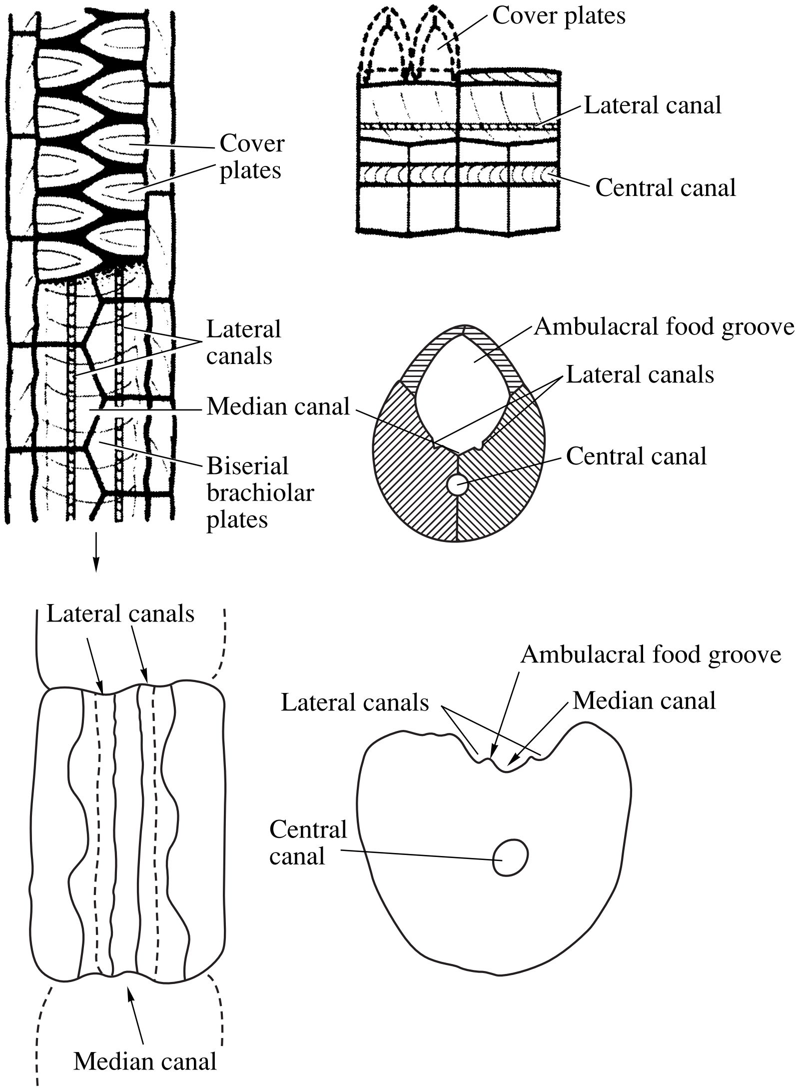


Fig. 47. Structure of the biserial brachiole in *Gogia longidactylus* from the Middle Cambrian of Nevada, USA (after Sprinkle, 1973, modified) and structure of the uniserial brachiole of the eocrinoid from the lower part of the Middle Cambrian of Australia.

spaces between the neighboring plates of these two rows. The imbricate articulation between the plates covering the bottom of the ambulacral groove allowed the arm to bend. The articulation of the cover plates in the two other rows, typical of the cover plates of many other echinoderms, allowed them to open. The plates of the neighboring rows, covering the bottom of the groove, were not positioned opposite each other but were slightly displaced, so that the sutures between the neighboring plates of the same row occurred opposite the middle of the plates of the other row. This biserial arrangement of these plates is very similar to that in brachioles of blastozoan echinoderms. In contrast to brachioles, the arm in Soluta, as in crinoids, represents an endothecal rather than epithecal structure, because the evagination of the thecal cavity certainly merged into the cavity of the arm. This is indicated not only by the character of articulation of the arm and the body and a relatively large cavity of the food groove at the base of the arm in Soluta, but also by the clear presence of a peculiar ambulacral system in the arm. The most striking indication of the presence of the ambulacral system of Soluta is the consistent presence of a particular perforated plate between the plates surrounding the base of the arm. Numerous small pores on this plate, e.g., in *Maennilia estonica*, are convincingly interpreted as multiple hydropores or madreporite, while a single large pore is interpreted as a gonopore (Figs. 49c, 49d). The ambulacral system in Soluta was most probably different from that in radially symmetrical echinoderms. Probably, instead of the ambulacral ring, they had a special saclike ambulacral cavity. A stone canal extending from one side of this cavity was terminated by the hydropore or madreporite, while a single radial ambulacral canal extended from another side of the ambulacral cavity. The structure of this radial canal and

Fig. 48. General view of the specimen of *Maennillia estonica* (Soluta) from the Middle Ordovician (Caradoc, Keila Horizon) of Estonia.

the tentacles (tube feet) extending from it surprisingly resembles that of modern crinoids, e.g., in *Antedon*, judging from the imprints of the radial canal in *Dendrocystoides scoticus*, described by Jefferies (1990). It is convincingly shown in Jefferies's paper and supported by my own observation on his material that the terminal ambulacral canal extended from the radial canal as regularly as the cover plates of the arm. As in the modern crinoid *Antedon*, each terminal canal branching off the radial canal, judging from the impressions on the cast of the inner surface of the arm, branched into three, thus representing a triad of tentacles (tube feet) extending from a shared base. The proximal tentacle of this triad was the shortest, while the distal tentacle was the longest. The middle tentacle was of intermediate length. Each triad began at the level of one cover plate and ended at the level of the next plate, because it was directed diagonally toward the anterior. The longest distal tentacle, as in modern crinoids, was between the cover plates, while the two others (short and intermediate) were terminated by the cover plate.

In modern *Antedon*, the intermediate and short ambulacral tentacles in this triad are encountered by a fold of soft tissue containing the ambulacral (cover) plate, whereas the longest tentacle is placed between the neighboring cover plates (between the lappets containing the ambulacral plates) (Figs. 43, 44). This fold

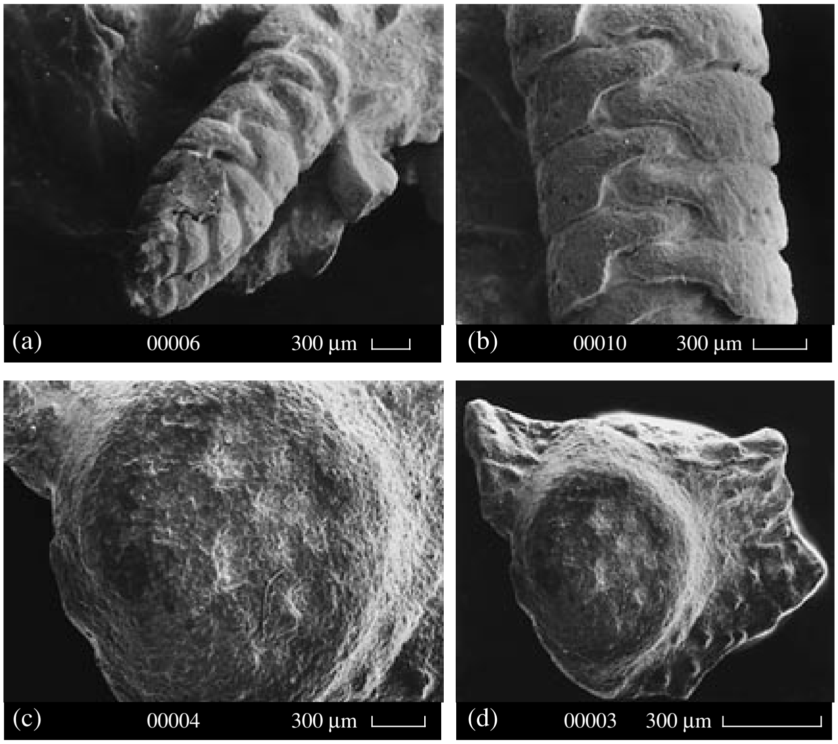


Fig. 49. Structure of the (a, b) arm and (c, d) madreporite with a gonopore of *Maennilia estonica* (Soluta) from the Middle Ordovician (Caradoc, Keila Horizon) of Estonia.

opens together with the cover plate when the corresponding tentacles expand and closes when the tentacles contract (Nichols, 1960). The musculature of these tentacles allows the longest tentacle to bend toward the ambulacral groove, the shortest tentacle to move in any direction, and the intermediate tentacle to move both toward and away from the groove. The surface of these tentacles has specific sensory papillae. Under certain circumstances, these papillae produce mucus as an adhesive for food particles. Usually, particles collected in this way first come into contact with the longest tentacle. Later, covered in mucus, they are conveyed to the medium tentacle, thence to the shortest, and eventually to the ciliated groove of the ambulacral canal, where the cilia convey the bolus of food particles, covered in mucus, into the mouth.

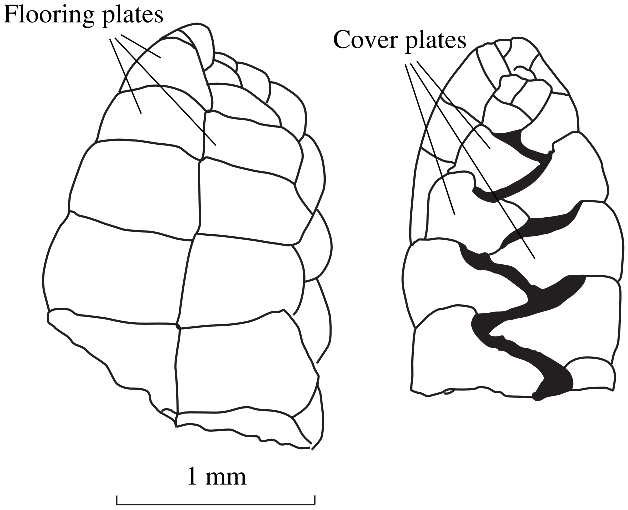


Fig. 50. Structure of the end of the arm of *Maennilia estonica* (Soluta). Middle Ordovician, Caradoc, Keila Horizon, Estonia.

A similar mechanism of food gathering and similar interactions between the ambulacral tentacles (tube feet) and cover plates is suggested for many primitive echinoderms, e.g., Edrioasteroidea (Paul and Smith, 1984). Therefore, such complete similarity between the structure of the terminal ambulacral canals in Soluta and that of extant crinoids does not seem coincidental. More likely, it reflects, according to Jefferies (1990), true homologies. Thus, although the food-gathering system of echinoderms originally did not have radial symmetry, it might have developed structures homologous to those in radially symmetrical animals. Certainly, the arms of crinoids were very different from the single arm of Soluta, because they were multiple structures capable of mutual coordination. This difference is explained by the appearance of pentaradiate symmetry, producing the interconnections between polymerized structures. However, other differences must be discussed first. Although the arm of Soluta was endothecal and had a large bulk of musculature (judging from its

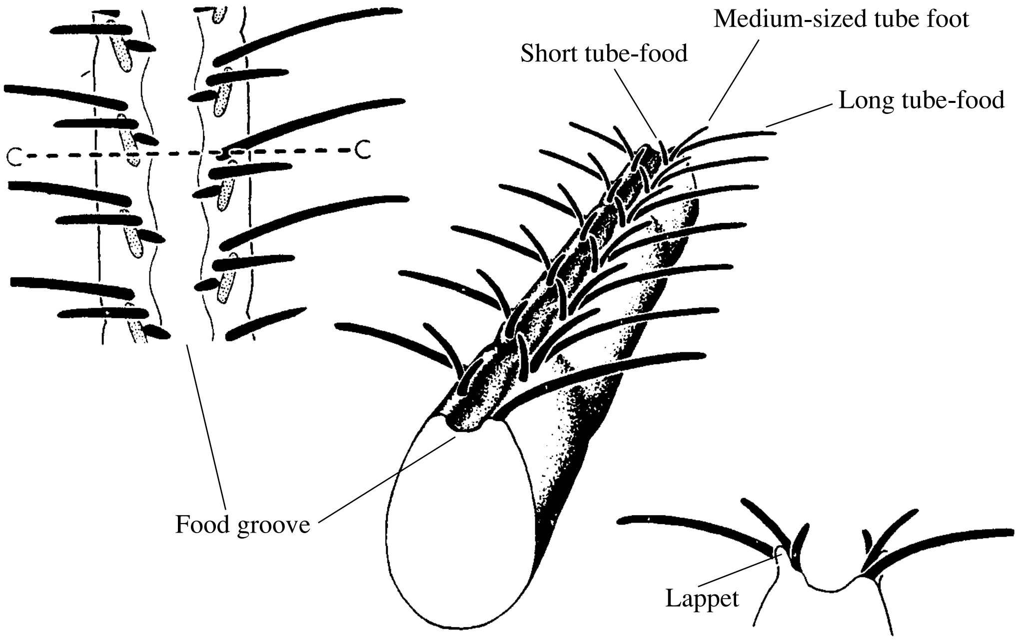


Fig. 51. Arrangement of ambulacral tentacles (tube feet) in the pinnule of a crinoid: (a) upper view, (b) lateral view, (c) cross section. Tentacles are black, the fold is dotted (after Nichols, 1960).

large cavity and the ability for free bending), its skeletal structure more closely resembles brachioles (exothecal processes of other Pelmatozoa responsible for the food-gathering function) than arms. The similarity between the arm of Soluta and brachioles is in the biserial arrangement of the plates forming the bottom of the food groove and in their incapability of branching.

The exceptions among brachioles only support the general rule. It seems that in this case an inability to branch and biserial arrangement only reflect the imperfection of metamerism in these structures. When metamerism embraces a complete structure to combine the metameric organization of substructures in a single entity, the structure becomes capable of a new, more advanced, and, at the same time, simpler type of growth, performed by repeating the same structures. This new type of growth opens new morphogenetic opportunities. This is discussed more extensively in the sections on the comparison of the crinoid arms and brachioles (and on the appearance and early evolution of the crinoid stem, where similar processes occurred from the point of view of the development of symmetry). Although all systems of organs in the arm of Soluta were metameric, the metamerism of each system developed, to a large extent, independently and was not united into a single system characteristic of the crinoid arms. The absence of general metameric growth of the arm in Soluta is clearly seen on the well-preserved end of the arm of *Maennilia estonica*, in the growth zone. This zone clearly shows the appearance of a new, small plate covering the bottom of the ambulacral groove on one side of the arm. Later, a corresponding but slightly proximally displaced plate appeared on the other side, etc. (Figs. 49, 50).

Thus, the arm of Soluta was similar to the arm of crinoids in that both had an endothecal origin and very similar structure of the radial ambulacral canal. However, it was very different in the degree of integration of metamerism and in the character of growth (biserial arrangement of the plates covering the bottom of the ambulacral groove). This allows the conclusion that the ambulacral system of echinoderms could potentially form food-gathering processes similar to arms and brachioles, before this system acquired any kind of radial symmetry, including pentamery.

ARMS OF CRINOIDS AND BRACHIOLES OF BLASTOZOAN ECHINODERMS

GENERAL CHARACTERIZATION OF BRACHIOLES

To resolve the problem of the origin of arms, it is particularly interesting to compare their features and morphogenetic potential with brachioles, specific food-gathering processes observed in most classes of pelmatozoan echinoderms. Brachioles are known only in Paleozoic echinoderms; hence, the structure of their soft bodies can only be approached indirectly. Brachioles represent straight, relatively short and thin, skeletal exothecal processes extending from those thecal plates that are approached by the end of the food groove or its branch (Fig. 52). Brachioles serve as a support for the food groove that continues on each of them. This considerably increases the total size of the food-gathering network. Brachioles are referred to as exothecal processes, because their cavity is not a direct continuation

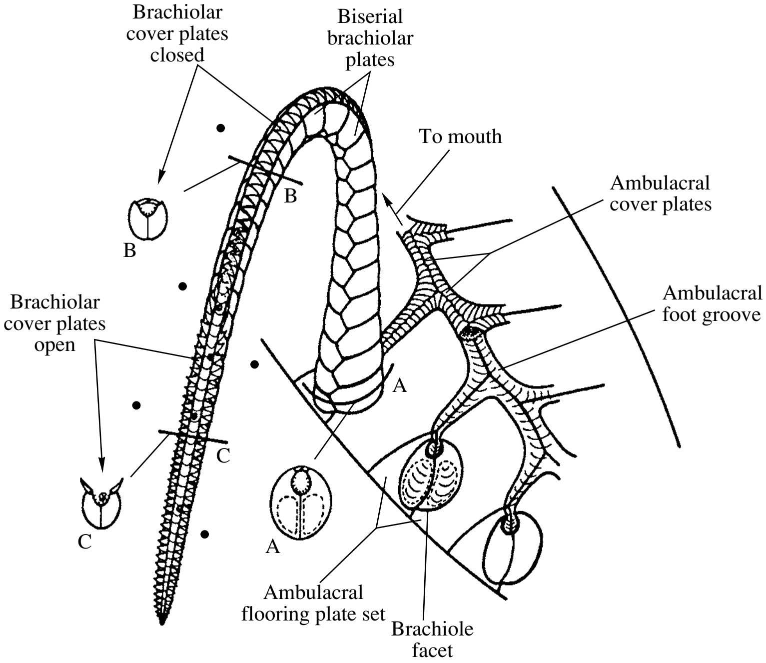


Fig. 52. Structure of the typical brachiole (after Sprinkle, 1873).

of the thecal cavity but represents only a continuation of the food groove covered by the cover plates. Brachioles are usually very simple in structure and are similar in many echinoderms, but their arrangement on the theca and relationships with the plates supporting the food groove can vary considerably.

The skeleton of the typical brachiole is usually biserial, unbranching, and lacks any, even small, skeletal processes. It is called biserial, because the plates covering the bottom of the food groove are arranged in two rows. The left row is displaced in relation to the right for half of the plate's height, so that the suture between the plates in one vertical row occurs opposite the middle of the plate of the neighboring row. Usually, the food groove is straight and runs along one side of the brachiole. Rarely, e.g., in *Gogia spiralis* from the Middle Cambrian of Utah, it is spirally coiled along the brachiole. The rows of plates composing the brachiole's skeleton are therefore also arranged spirally (Sprinkle, 1973a). The food groove is shallow and is covered by cover plates that can be considerably elevated over it to increase its size. The cover plates contact each other, but in some cases, e.g., in *Kinzercystis durhami* from the Lower Cambrian of Pennsylvania, may partially overlie each other and so have an imbricate (tiled) structure. A canal, possibly for one of the neural systems, could run inside the skeleton of the brachioles, between the rows of plates covering the bottom of the groove (brachiolar plates). The inner surface of the food groove can be even and smooth, but in some cases, e.g., in *Rhipidocysis baltica* from the Lower Ordovician of the Leningrad Region and some *Gogia* species (Cambrian), its bottom could be subdivided into three longitudinal grooves, separated by low ridges.

The structure of the zones on the thecal surface, along which the food groove extends and the brachioles are placed, may be quite different in different classes of pelmatozoan echinoderms, but their structure is particularly interesting in eocrinoids, because these were the most primitive forms preceding crinoids.

DID BRACHIOLES CONTAIN RADIAL AMBULACRAL CANALS?

Sprinkle (1973a) does not believe that brachioles contain radial ambulacral canals; he states that the main differences between brachioles and arms (hence, between Blastozoa and Crinozoa) was the presence or absence of canals. The presence of these canals in fossil crinoids is supported by comparison with extant crinoids and the character of the arm function.

As noted above, the ambulacral tube feet (tentacles) in extant crinoids perform a sensory function and produce mucus, which, acting as an adhesive, traps food particles to form a small bolus. This bolus is conveyed by the tentacles into the ciliated food groove to be further conveyed by the cilia to the mouth. Thus, the ambulacral tentacles, which are the extensions of the radial ambulacral canals, perform a food-gathering function, whereas the ciliated grooves only convey the aggregated boluses of food toward the mouth. This feeding strategy is suggested for all extinct crinoids, since all of them have a similar food-gathering system; it is difficult to imagine such a system being employed for any other food-gathering strategy.

A similar feeding strategy is suggested for some other echinoderm groups, which fed on suspended

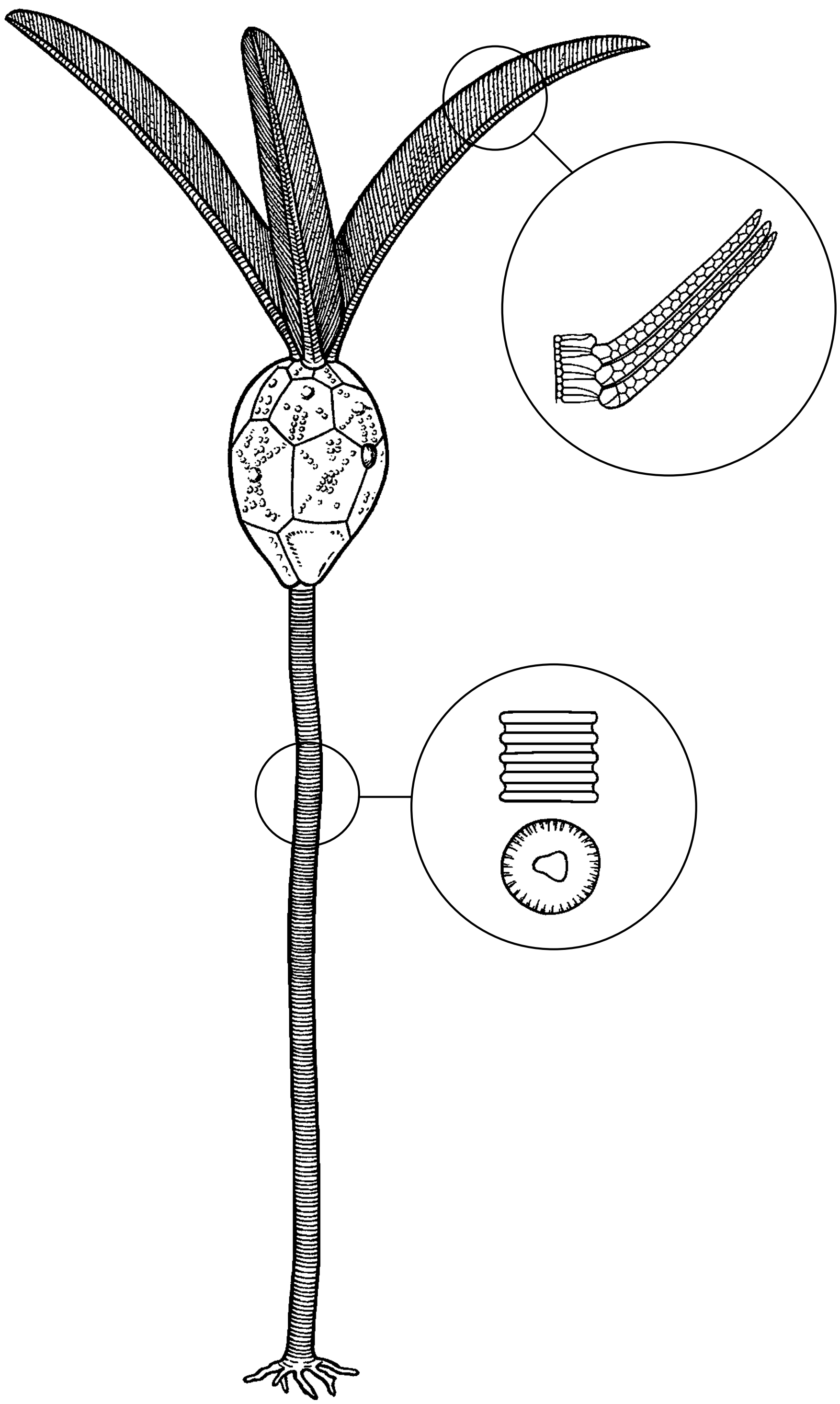


Fig. 53. Reconstruction of *Hemicosmites* sp. from the Upper Ordovician (Caradoc, Keila Horizon) of Estonia. Three biserial brachioles with numerous "pinnules," extending to the right and to the left from the main stalk of the brachioles after every two ossicles, resemble the arms of crinoids. The axial canal of the stem is three-lobed.

organic particles, e.g., for Soluta (Jefferies, 1990) and Edrioasteroidea (Paul and Smith, 1984).

In some microcrinoids, the arms are completely reduced. These animals have a different type of feeding, i.e., by absorption of dissolved nutrients from seawater. Naturally, the reduction of arms is accompanied by a reduction of the radial ambulacral canals.

Sprinkle (1973a) suggested that brachioles lacked radial ambulacral canals and, hence, lacked extending tentacles (tube feet), which they could have used to col-

Fig. 54. Biserial thick "arm" of the paracrinoid *Achradocystites* sp. with short branches. Upper Ordovician (Caradoc, Keila Horizon) of Estonia.

lect food, like crinoids. Superficially, the food-gathering system of brachioles is similar to that of crinoids. Sometimes, it is even very similar, e.g., in *Caryocrinites* and *Hemicosmites* among rhombifer cystoids (Fig. 53) and in paracrinoid *Achradocystis* (Fig. 54), so that in these cases a convergence between the brachiole-bearing ambulacra and arms may be suggested (Sprinkle, 1973a). What was the mechanism of food gathering by brachioles, if they lacked radial ambulacral canals and tube feet (tentacles)? This problem is usually overlooked. Let us discuss it here. It is accepted that brachioles were mostly used for food gathering, because the grooves placed on them eventually reached the mouth. Food particles that ended up in the groove on the brachiole could be conveyed to the mouth by cilia that apparently covered the bottom of these grooves. But, how could the food particles have come to the groove from the seawater? Assuming that they fell passively, they should have randomly fallen into the grooves, and then been conveyed to the mouth. However, the subvertical position of the food-gathering apparatus and the functioning of the plates covering the grooves (they could not open widely) contradict this assumption. The cover plates, which were not capable of opening very wide, would have obstructed the collection of a large amount of food from lateral currents. In cases of the absence of radial canals, the animal should have had a special mechanism of opening the cover plates, which in crinoids are opened by the muscles of the tentacles. Thus, the passive fall of food particles into the grooves could not have provided the animal with sufficient food.

It is possible to suggest that the cilia in the grooves created active water currents, from which the food particles were caught by the mucus produced by special glands. However, a system to concentrate the food in the groove and to remove the water (separation of the food and water flows) is absent.

This suggests that the hypothesis of the absence of the radial ambulacral canals in brachioles meets very serious difficulties when explaining the mechanism of brachiole function.

The second difficulty is related to morphogenetic problems. The ambulacral system in all extant echinoderms consists of three major parts, all of different origin. Firstly, there is the ring ambulacral canal. It surrounds the esophagus with a closed ring, although ontogenetically it develops from the small incipient hydrocoel (middle left coelom), which gradually grows in a horseshoe-shape and eventually closes. The radial canals, first appearing as lobes on the horseshoe-shaped incipient hydrocoel, extend from it. The ambulacral tentacles or more specialized genuine ambulacral tube feet develop on these canals. The origin of the third system is related to the anterior left coelom (axocoel). This system connects the hydrocoel with the surrounding water by the hydropore (or madreporite). Eocrinoids have a hydropore, so they most likely had a ring-shaped ambulacral canal as well. Was it truly a ring canal, or was it just a small spherical cavity near the esophagus, as is suggested for Soluta? If the radial canals were present, the main canal could have been circular or at least horseshoe-shaped. If not, then it could have been of any shape. However, the example of Soluta shows that the radial canal could have existed at a stage when the echinoderm did not have pentamery or an ambulacral ring. Therefore, it is difficult to imagine that Blastozoa with more or less developed pentaradiate symmetry did not have them. The hypothesis that they could have existed but were not connected with the food-gathering system seems even more unlikely. In any case, the hypothesis of the absence of the radial ambulacral canals in blastozoan echinoderms means that they are different not only from the crinozoan echinoderms, but from all other echinoderms that generally have radial canals. This hypothesis also seems unlikely to most researchers. Certainly, a secondary reduction of the radial canals in the brachioles in specialized forms, e.g., in Blastoidea, is quite possible. Thus, the hypothesis of the original absence of the radial ambulacral canals in the brachioles seems unlikely, both from functional and morphogenetic points of view.

The actual facts that enabled the hypothesis of the absence of the ambulacral canals in the brachioles are considered below. Sprinkle (1973a) believes that the strongest support of the absence of these canals in Blastozoa is the position of these canals in relation to the endoskeleton of the theca. Many extant and extinct echinoderms have the so-called closed ambulacral system. In systems of this type, the radial ambulacral canal is placed inside the theca, immediately below the skeleton. The ambulacral tube feet extending from the radial canal stretch out through the pores in the skeleton. The presence of such pores in fossil groups indicates the presence of an ambulacral system and an inner position of the radial canals. Extant and extinct crinoids have an open type of arrangement of the ambulacral radial canals. Each radial canal in these groups begins inside the theca, under its ventral skeleton. However, it soon opens outside through the opening in the radial facet and continues into the groove of the arm through its soft tissues, where the metamerically placed ambulacral tube feet extend from it. Thus, the presence of the radial canals may be indicated either by the pores for the ambulacral tube feet or by the opening through which the ambulacral canals open to the outside. Supposedly, the ambulacral canals do not run along the entire length of the food grooves but diverge at some distance from the mouth.

According to Sprinkle (1973a), in blastozoan echinoderms, i.e., those with brachioles rather than arms, neither pores for the exit of the ambulacral tentacles nor openings for the ambulacral canals are present. He observed the absence of these structures in a well-preserved specimen of the Early Cambrian eocrinoid *Kinzercystis*. This specimen shows the inner surface of the theca, near the mouth, with a single well-preserved food groove. This food groove, covered by biserially arranged plates, closely approaches the mouth pyramid, which is commonly accepted to surround the mouth. Neither a special opening for the ambulacral canal to merge into the food groove nor pores for the exit of the ambulacral tube feet are present. Furthermore, the epispires, numerous on the ventral surface, disappear near the food grooves. A similar structure, according to Sprinkle, is known in rhombifer cystoids, parablastoids, and blastoids. Blastoids are a relatively young, highly specialized group, in which, in the opinion of various researchers, the ambulacral system could be completely internal, or reduced, or entirely external, including the circumoral ambulacral ring (Sprinkle, 1973a). Therefore, the structure of blastoids does not provide very conclusive evidence in support of the absence of the ambulacral system in all echinoderms with brachioles, i.e., in all Blastozoa.

Comparisons of the possible arrangement of the radial ambulacral canals and the food grooves in primitive Blastozoa, such as Eocrinoidea, Rhombifera, and diploporite Cystoidea, with that in Crinoidea should be made carefully, because these groups differ considerably in the character of the growth of the theca. The arms in crinoids, as noted above, represent powerful outgrowths of the body. Hence, the cup, including the radials, grows partly laterally, thus forming an incomplete sphere, as in echinoids. In most Blastozoa, the growth is different. In these echinoderms, the direction of growth of the theca is such that it forms a sphere. The food grooves extending from the mouth represent the exothecal organs on the surface of the theca rather than the endothecal processes of the body. Therefore, the ambulacral radial canals (in cases where they exist) in Blastozoa with a spherical growth type of the theca, probably met with the food grooves at the exit of the food groove on the surface of the theca from under the peristome. This was unlike Crinoidea, in which the outgrowths of a different system of organs meet in one point near the radial plate to form a single powerful body process (arm). Sprinkle argued that Blastozoa did not have sufficient space near the exit of the food groove for such a conjunction. However, I am inclined to think that there was enough space. The peristome, oral plates, or the oral pyramid were considerably wider than the mouth opening. For instance, simple calculations show that the diameter of the mouth opening could be smaller than one and a half times the width of the food groove. Otherwise the length of the circumference of the mouth would not be sufficient to accommodate all five grooves approaching the mouth. However, there is no need for the diameter to be wider than two or three times the width of this groove to make the space of the mouth sufficient to receive the food simultaneously from all five grooves. This is supported by the small diameter of the mouth in extant crinoids and by observations of the well-preserved fossils. For instance, *Spheronites* sp. from the Middle Ordovician of the Baltic Basin (the well known locality of Mishina Gora in the Pskov Region) has the upper part of the esophagus preserved apparently due to calcification in the live animal. The diameter of the mouth did not exceed 0.5 mm, while the peristome was 2.5 mm in diameter. It is possible to conclude from this that the space around the mouth near the peristome was sufficient to accommodate the junction of the ambulacral canals and food grooves before their exit outside. The same applies to *Kinzercystis*, which was used as an example by Sprinkle. According to Sprinkle, the holotype of *Kinzercystis durhami* has a food groove 0.6–0.9 mm long, whereas the elongated oral pyramid is 5 × 2 mm. It is certain that in this species, as in *Spheronites* sp., the size of the oral pyramid considerably exceeded the size of the mouth opening. Hence, there was enough space under the oral pyramid for the junction of the radial canals extending from the circumoral ambulacral ring and food grooves and for their joint exit onto the surface of the theca.

These conclusions are supported by the structure of brachioles. Sprinkle, who extensively studied this structure, considered it to be proof of the absence of the ambulacral radial canals in blastozoan echinoderms. However, his evidence suggests the opposite conclusion. The structure of the brachioles of some species of the primitive Cambrian eocrinoid genus *Gogia* has been extensively described and figured by Sprinkle (1973a, pp. 26–27, text-fig. 10). He discovered three linear canals in the brachioles (Fig. 47). One of these extends within the skeleton of the brachiole along its midline, while two other canals run along the bottom of the food groove, symmetrically on the right and the left sides. Sprinkle convincingly showed that these canals could not lodge the ambulacral radial canals. The inner canal could not do it because of the absence of pores for the exits of the ambulacral radial, and the external canal, because they are paired. It is more likely, in his opinion, that the inner canal lodged the entoneural cord, whereas two other canals were perihemal or, less likely, hyponeural. It is worth mentioning in this context that I also observed canals on the bottom of the ambulacral groove in other material: in isolated ossicles of brachioles from the Middle Cambrian of Australia (Fig. 47) and brachiolophore plates of the eocrinoid *Rhipidocystis baltica*, a species with a flat theca from the Lower Ordovician of the Leningrad Region. The inner unpaired canal is absent in this species. However, the widest and well-developed third canal, restricted laterally by the walls of the neighboring canals, runs on the surface of the food groove along the axial line of the brachioles. Possibly, this canal was present in *Gogia*, but it was not so distinct. It can actually be interpreted as a placement of the radial ambulacral canal. However, in extant crinoids, the radial ambulacral canal lies in soft tissues and is, therefore, not reflected in the skeleton. Hence, it is not necessary to look for its traces on the skeleton of the brachioles in Blastozoa. Whatever way the canals in the brachioles are interpreted, whether or not they were connected with the blood or the nervous systems, it is evident that they should have been connected with the inner cavity of the theca. Therefore, there should have been a place where these canals extended from the food grooves into the theca. However, if this place did exist for the blood and nervous systems, why could it not have been used by the entering ambulacral radial canals? Thus, the structure of the brachioles in eocrinoids does not indicate that they did not have ambulacral radial canals.

In some of them, the most advanced taxa, according to Sprinkle (1973, p. 27), the width of the food grooves does not exceed 0.1 mm, which is several times less than the width of the pinnules in extant crinoids (0.25–0.5 mm). Therefore, the radial canals possibly did not fit the grooves of this size. However, firstly, this difference is not so great that it could not be compensated by a steeper arrangement of the cover plates. Secondly, such narrow grooves are known in specialized groups, in which the absence of the ambulacral canals could be connected with their specialization and be secondary. In primitive eocrinoids, such as *Gogia*, the size of the grooves was sufficient to fit the ambulacral radial canals (a view shared by Sprinkle). In many other eocrinoids, e.g., *Rhipidocystis*, they are even wider. Therefore, in most cases, especially in the most primitive Blastozoa, the structure and size of the brachioles do not contradict the possible placement of the ambulacral canals within them.

Thus, we do not have sufficient evidence that echinoderms possessing brachioles (blastozoan echinoderms) originally lacked radial ambulacral canals. Furthermore, the assumption of the absence of the radial canals and, hence, ambulacral tube feet (tentacles) in the brachioles requires special substantiation of the feeding strategy in these echinoderms, which was different from that of crinoids. A different feeding strategy is difficult to conceive, knowing the other morphological features of Blastozoa. Nobody has suggested a different strategy so far. Therefore, judging from the presence of the radial canals in all extant classes of echinoderms and their certain presence in some extinct echinoderm groups, even in groups as ancient as Soluta, which completely lacked radial symmetry, the hypothesis of the originally absent radial canals in all blastozoan echinoderms requires more evidence. As shown above, no such evidence is presently available. Therefore, it should be suggested that nonspecialized blastozoan echinoderms, such as most eocrinoids, and rhombifer and diploporite cystoids, had radial ambulacral canals. Hence, there is no evidence for the fundamental difference between the organization of the ambulacral system in Blastozoa and Crinozoa. Furthermore, there

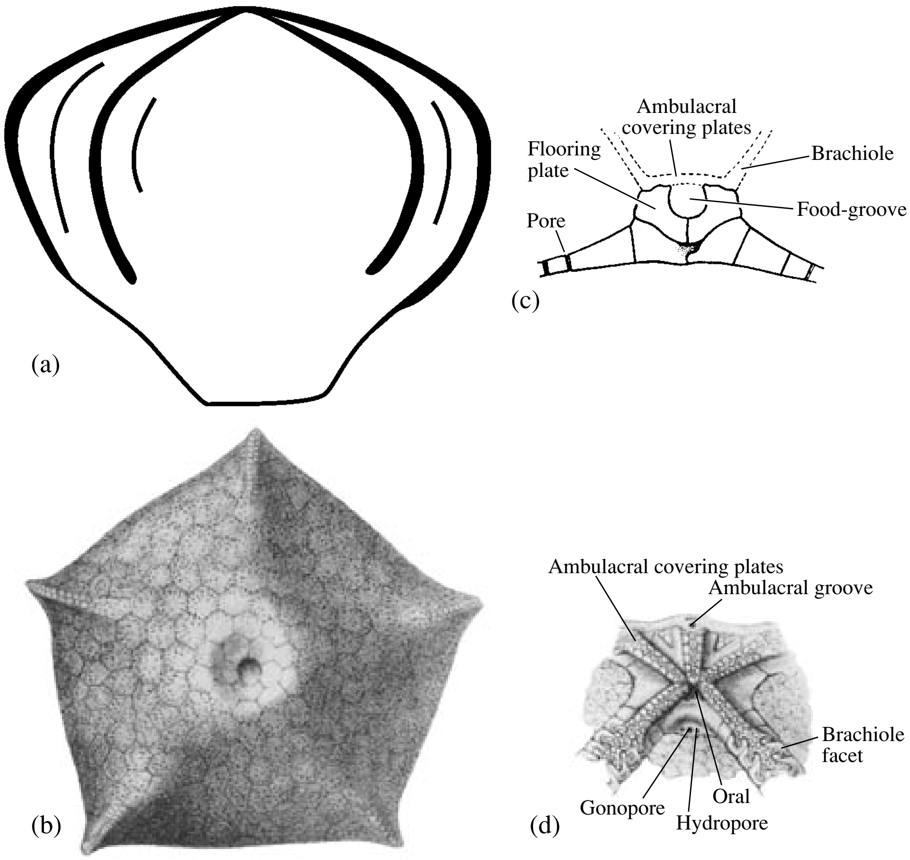


Fig. 55. Structure of *Mesocystis* (Diploporita) from the lower part of the Middle Ordovician (Upper Arenig, Volkhovian) of the Leningrad Region. (a) Lateral view, PIN no. 4125; (b) lower view; (c) cross section of ambulacrum; (d) oral pole; (b–d) after Kesling, 1967.

are data suggesting that arms repeatedly developed from brachioles. This also casts doubts on the validity of the recognition of two subphyla among the echinoderms possessing food-gathering processes.

So what is the most fundamental difference between arms and brachioles, and can arms evolve from brachioles? These questions are discussed in the next section.

POSSIBLE MODES OF EVOLUTION OF ARMS

The most important difference between arms and brachioles is not in their structure in adults (they can be very similar), but in their morphogenesis. However, it is important to discuss the differences in the morphogenesis of these food-gathering processes in association with the analysis of the morphogenesis of the theca of Blastozoa and Crinozoa, because these processes are closely connected. As shown above, there is no evidence that Blastozoan echinoderms originally lacked radial ambulacral canals. In addition, judging from the structure of some brachioles, including the earliest eocrinoids, the longitudinal groove in the brachioles certainly contained the nervous and blood systems (see above). In contrast to the arms, brachioles are usually only part of the system conveying the food to the mouth. Therefore, it is important to discuss the structure of the ambulacral groove running along the surfaces of the theca and connecting the brachioles of one ray into a network and linking this network to the mouth. For instance, the ambulacral groove extending from the surface of the theca to the mouth and running on the surface as far as the first brachiole (apparently like the brachioles themselves), housed the ambulacral, blood, and nervous systems. In early eocrinoids, this groove runs on the thecal surface over slightly modified plates, whereas in later, specialized groups of Blastozoa, these plates can form a special ambulacral area. For instance, such a well-developed ambulacral area may be observed in the Early Ordovician diploporid genus *Mesocystis* (Kesling, 1967). In this genus, the flooring plates in the ambulacral groove cross different thecal plates and are observed on the surface of the theca as an overgrown area (Fig. 55). Assuming that, in some eocrinoids, brachioles were absent, and these animals only had an ambulacral groove extending from the mouth, no fundamental difference can be found between this groove and that lacking the supporting skeleton (present in primitive crinoids and considered to be underdeveloped arms, as in some hybocrinids, e.g., *Tripatocrinus* and *Hybocystis*). Apparently, these types of grooves are not significantly different. However, when, in other hybocrinid genera, the grooves occur on the arms and grow together with the arms, the difference becomes quite prominent. Firstly, the direction of growth is changed from growth along the thecal surface restricted by the shape and size of the theca to the independent growth upward and laterally. Secondly, the growth of the groove becomes rigidly coordinated with the growth of the specific aboral skeleton. Thirdly, more systems of internal organs become connected with the ambulacral groove, e.g., the coelomic outgrowths, which are indicated by the much larger size of the ambulacral grooves in the arms compared to those on the thecal surface in fossil crinoids and by direct observation in extant species. This suggests that the ambulacral groove (and, apparently, originally the radial ambulacral canal) have a separate morphogenetic significance, since it could exist separately in extinct pelmatozoan echinoderms without a connection with either arms or brachioles. However, its connection with the specialized endothecal body outgrowths (brachioles) greatly increases the food gathering capability of an organism. Therefore, an independent ambulacral groove, not supported by the skeleton of arms or brachioles, is extremely rare among Pelmatozoa.

In this context, it is necessary to compare the ambulacra of eocrinoids and primitive crinoids with the ambulacra of Edrioasteroidea and Edrioblastoidea. What is the difference between them? Why are brachioles present in the two former classes and always absent in the third? The answer seems relatively simple. These groups have different types of thecal growth and different proportions of the growth of the theca and the ambulacra. In Edrioasteroidea and Edrioblastoidea, the ambulacra are parts of the theca. Indeed, in these groups the ambulacral and interambulacral zones of the theca, growing in coordination, can be recognized. Neither eocrinoids nor crinoids have this differentiation of the theca. The theca and ambulacra in these two groups are built separately; therefore, they can be variously combined. Therefore, even when the food groove occurs directly on the skeleton of the theca, the skeleton is just a support for it, while the ambulacrum does not take part in the structure of the theca and in the delineation of the inner organs of the theca. The growth pattern of the ambulacral radial canals in Edrioasteroidea and Edrioblastoidea did not allow them to grow outside the theca and continue on the dorsal part of the theca, when it was well formed. This generally restricted the growth of the ambulacra in Edrioasteroidea, in particular, their branching, which only rarely occurs in this group (branching of the ambulacra is known only in the Middle Ordovician genus *Thresherodiscus* from North America and in a new Middle Cambrian genus from Iran recently presented by A.Yu. Zhuravlev). It is reasonable to suggest that the total, original absence of brachioles or similar processes in Edrioasteroidea was related to this restriction.

Based on the above hypothesis, it is possible to suggest the evolutionary emergence of the brachioles. It cannot be confined to the assumption that the aboral skeleton of the brachioles evolved from the cover plates by their curving on the aboral side of the elevated ambulacrum. The problem is why, in some cases, the ambulacrum could be elevated over the theca and, in other cases, it was not rather than what the original organ from which the brachiole developed was. This can be explained by the fact that, in some cases, the ambulacral structures grew to form a part of the skeleton of the theca and, hence, the food groove could not rise above the theca. In other cases, the radial canals grew outside the theca, so that the structures directly connected with them were not part of the skeleton of the theca; hence, the ambulacrum could rise above it. It is not necessary to suggest, for such a raised ambulacrum, that its cover plates began to perform a support function and moved to the dorsal side, being transformed into the supporting skeleton. There is no morphological evidence for suggesting this. It is more reasonable to suggest that the cover plates of the food groove remained cover plates, whereas the supporting dorsal skeleton of the brachiole appeared as a morphological innovation. This hypothesis seems likely because the brachioles in echinoderms first appeared simultaneously with the skeleton or soon after. Hence, at that time, all the structures appearing in the skeleton were innovations.

More important is the problem of what the thecal and suprathecal type of growth of the ambulacral structures actually mean from the morphogenetic point of view. This problem is connected with the problem of the emergence of the ambulacral system as a whole, which is poorly represented in the fossil record. The radial ambulacral canal could, to some extent, be embedded into the skeletal tissue and could organize various parts of the skeleton of the ambulacra around itself. It is known from the development of extant echinoderms that the ambulacral system is a powerful organizer of the ontogeny. The radial canal could organize the development of the skeleton-secreting tissue both below and above itself. Apparently, it could also secondarily submerge itself inside the theca. Its growth was rigidly correlated with the rest of the skeleton of the theca. This discussion is related to the problem of the origin of the ambulacral system in echinoderms and the appearance of the radial canals in particular. This is one of the most unclear and poorly studied problems in the morphology of echinoderms. In the majority of the proposed hypotheses, the radial ambulacral canals were considered to have appeared as a result of transformations of the ancestral oral system of tentacles, into which the canals of the hydrocoel had already merged. Bather suggested that the ambulacral system developed based on the food grooves, which appeared at one of the ontogenetic stages of the ancestor of echinoderms. All these hypotheses are too general and cannot answer the question of how the radial ambulacral structure of echinoderms, including the radial ambulacral canal with the extending tentacles, the food groove covered by the ciliated epithelium, the supporting and covering skeleton, and the other systems of organs were formed. What was the original difference between the thecal and suprathecal type of growth of the ambulacra? Fossil material does not answer this question. The most general conclusions may be made based on the embryological and morphological data on modern echinoderms, assuming that the food grooves and radial ambulacral canals in the form of tentacles existed in the ancestors of echinoderms. Originally, tentacles were responsible for sensory functions, while the groove, or a furrow covered by ciliated epithelium, was responsible for food gathering. It could be different, e.g., the tentacles could be responsible for food-gathering and sensory functions, while the furrows covered by ciliated epithelium served for locomotion and respiration. Early in evolution, before echinoderms acquired a skeleton, furrows and tentacles were combined into a single structure. The morphogenetic fusion of these two structures (furrows and tentacles) could occur in two ways. In one case, when the furrows developed earlier in the ontogeny than the tentacles, the latter grew along the furrow leading to the mouth. This resulted in a thecal type of growth of the ambulacra. In the other case, in contrast, the tentacles were the first to appear in ontogeny, so that the appearing and growing furrows were superimposed on the development of tentacles. This could be the process of suprathecal growth of the ambulacra. In both cases, such a combination allowed food gathering to take place farther from the mouth. The tentacles were morphologically and physiologically well structured to form triads. As the tentacles grew, the triads polymerized. The triads extended alternatively rightward and leftward. Such alternating arrangements of triads may be explained by the subdivision of the tentacles at the point of branching into a growing part capable of further growth and a functional part bearing a working triad of tentacles. This growth pattern, apparently the earliest and least specialized, is supported by the structure of the radial ambulacral canals in modern crinoids. The lateral branches of the ambulacral canals in crinoids are regularly alternating. Each branch bears a triad of tapering tentacles, lacking ampullae. Apart from the above-described food-gathering function, they are also responsible for sensory and respiratory functions.

The primary growth type of the ambulacral radial canals may explain why the brachioles are originally biserial, with alternating rows, whereas the arms are originally uniserial. This is one of the questions that should be answered when the arms and brachioles are compared. It seems that the contrasting structure of the skeleton of the arms and brachioles is primarily explained by the difference in the degree of integration of the metameric growth of these structures, i.e., by morphogenetic, rather than functional reasons.

The plates covering the ambulacral groove of the arms and most brachioles are usually arranged biserially and alternatively. The zigzag-shaped suture between the two rows of cover plates, when the latter alternate, makes this arrangement functionally significant for the tight closure of the ambulacral groove. Any other arrangement of these plates seems less functional and more poorly adapted to opening and closing. Another explanation (which supplements rather than contradicts the previous) is in the alternating extension of the triads of the ambulacral tentacles rightward and leftward from the radial ambulacral canal. Because the cover plates are opened by the tentacles, the character of the arrangement of the triads of tentacles (tube feet) along the ambulacral groove also determines the position of the radials. As was shown above, the alternating arrangement of the triads of tentacles on the right and on the left of the radial canal is a very ancient characteristic. This branching pattern was established when the ambulacral system was just forming. Because, in the opinion of embryologists, the hydrocoel and its derivatives in extant echinoderms are very strong inductors and organizers of morphogenesis, the alternating arrangement of the tentacles (tube feet) around the radial canal could directly or indirectly affect the arrangement of the plates connected with the ambulacral canal at the time when the echinoderm skeleton was formed.

Firstly, it rigidly determined the position of the cover plates of the ambulacral grooves on the surface of the theca. The ambulacral grooves could appear phylogenetically earlier than the brachioles, which in ontogeny appeared on their ends and on the ends of their branches. Because of the functional necessity of this arrangement of the cover grooves, this feature was retained throughout all transformations of the food-gathering processes. The brachioles appeared as a result of the elevation of the end of the ambulacrum above the thecal surface. This increased the efficiency of the food-gathering system. To support the elevated end of the ambulacrum, a special aboral supporting skeleton should have appeared. It is not necessary to suggest (e.g., Paul and Smith, 1984) that the aboral skeleton of brachioles appeared from the cover plates the rows of which were bent aborally, while the cover plates of the brachioles appeared anew. There is no morphological evidence for such a hypothesis. It is more likely that the aboral skeleton was a morphological innovation. The position of the plates of the developing aboral skeleton was also determined by the growth pattern of the ambulacral radial canal with the biserial alternating arrangement of the developing triads of tentacles. Thus, when the aboral skeleton of the brachioles was developing, the constituting plates had to be originally arranged in the same way as the lateral branches of the radial canals extending toward the tentacles and as the cover plates, i.e., biserial and alternating.

The development of brachioles into arms was accompanied by the enhancement of morphogenesis, an increase in the entirety of the original food-gathering structures, and the improvement of their functioning.

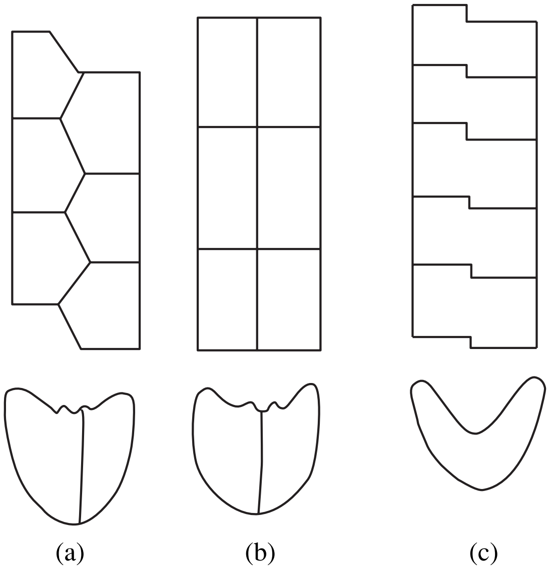


Fig. 56. Structure of the biserial brachiole in the eocrinoids (a) Rhipidocystis and (b) Neorhipidocystis, and (c) of the arm of the aberrant specimen of the hybocrinid crinoid *Hoplocrinus* sp.

Indeed, although arms and brachioles had a similar set of structures, their mutual integration throughout growth was different. This is clearly seen in fossils. First of all, the brachioles usually constitute a part of the food-gathering structures (ambulacra). Each ambulacral complex in eocrinoids and cystoids, in most cases, is spatially subdivided into the ambulacral zone extending directly along the thecal surface and the brachioles. Therefore, it would be more correct to compare an arm with a complex of brachioles combined with the interbrachiole zones of the ambulacrum rather than just a brachiole. In addition, the aboral skeleton of a brachiole is subdivided into the left and right halves, each built of a succession of structures that grow independently but in coordination with the neighboring row. It is evident that many inner structures of the soft body of brachioles have complex, variously directed correlative connections between each other and the skeleton. In the arms of crinoids, the degree of autonomy in the development of all structures is considerably lower, since they display a new, metameric growth type, which involves the entire arm rather than some parts, as occurred in the ancestral ambulacra combined with brachioles. This is indicated by the fact that an arm is a more homogenous structure, because it is not spatially subdivided into different parts between the branches or along the same arm. The proximal and distal ossicles of the same arm are always connected by a continuous chain of similar structural elements (ossicles). Each of these ossicles morphogenetically represents a metamere, while the repeated structures reflect its metameric growth. This new growth type increasingly simplifies the morphogenesis of the arm in ontogeny compared to a brachiole-bearing ambulacrum and gives considerable advantages for the development of more complex and efficient food-gathering apparatus in phylogeny. This process is well observed in fossil material both in groups with brachioles and in primitive crinoids with true arms.

Brachioles or, more precisely, brachiole-possessing ambulacra, have a tendency to improve their structure and become, eventually, real arms. For instance, Sprinkle noted a tendency of the usual ambulacra running on the thecal surface and the brachioles extending from them to transform into armlike straight ambulacra with extending pinnule-like brachioles. These armlike brachioles were observed by Sprinkle in eocrinoids (*Trachelocrinus*) and among Rhombifera in *Caryocrinites* and closely related taxa. The genus *Hemicosmites* can be added to this list (Fig. 53). In these two cases, the ambulacra independently acquired an armlike shape but retained a biserial structure of the skeleton (Sprinkle, 1975). Another type of transformation of the brachioles into armlike processes was observed by him in the North American rhipidocystids and by myself in the Baltic rhipidocystids. In this case, the biserial brachioles were transformed into cryptobiserial brachioles. The ossicles of the neighboring rows of brachioles were displaced, so that they did not alternate but occurred strictly aligned (symmetrically, opposite each other). The sutures between them became hardly noticeable and can be viewed only in polished sections under conditions of unequal shading of the neighboring skeletal elements. Among Baltic Ordovician rhipidocystids, such a condition was observed in the phylogenetic lineage *Rhipidocystis–Neorhipidocystis* (Figs. 56a, 56b). In the Middle Ordovician rhipidocystid *Petalocystites* from North America, Sprinkle observed that the change in the biserial structure of the brachioles first occurred in the proximal part and only later in the distal part (Sprinkle, 1973a).

In all the above examples, the armlike change of the brachioles or brachiole-possessing ambulacra occurred when they developed at the border between the oral and aboral parts of the theca (these parts differentiated in these genera). Evidently, the appearance of the arms is related not only to the changes in the brachioles, but also to the changes in the morphogenesis of the theca. The differentiation of the theca into oral and suboral parts led to the growth of the ambulacra at the border between these two zones and to the appearance of a new growth vector of the ambulacra, which is closely correlated with the direction of thecal growth. The details of this process are more relevant to the section on the morphology of the theca in different groups. It should only be mentioned in this context that this process was closely connected with the paedomorphic processes in the development of the theca.

One of the species of the hybocrinid genus *Hoplocrinus* from the Middle Ordovician of the Baltic Basin showed evidence of the origin of the biserial arms of crinoids from biserial brachioles. Usually, the facets of

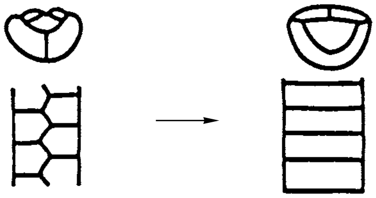
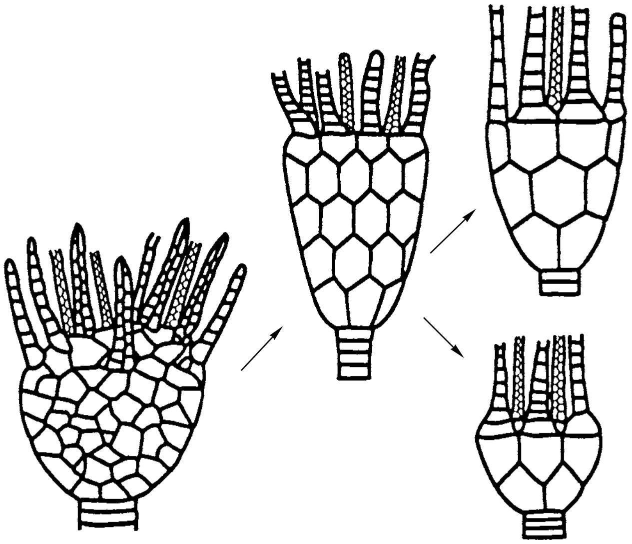
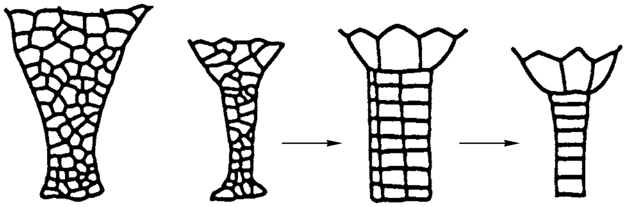
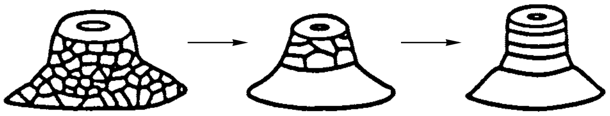
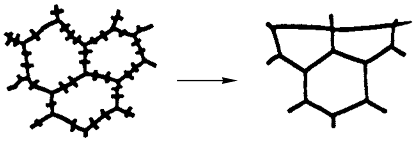
1. Transformation of biserial brachioles into uniserial arms	
2. Differentiation of the theca into the oral and aboral parts 3. Replacement of the highly varying position of numerous brachioles on the calyx by the marginal position of the arms	
4. Transformation of the aboral portion of the theca with numerous irregularly arranged plates or numerous circlets into a mono- or dicyclic calyx	
5. Transformation of the penducle first into a stem with numerous irregularly arranged plates and then into a stem composed of pentamerous and, finally, monomeric columnals	
6. Transformation of the attachment structure composed of numerous plates into that composed of a single monomeric columnal that, after the polymerization, forms the stem of several monomeric columnals	
7. Disappearance of the epispires.	

Fig. 57. Necessary changes in the structure of the skeleton in the course of the evolutionary transition from eocrinoids to crinoids.

the arms in this genus have an even and relatively smooth surface. In one specimen, the arm facet was stepped, i.e., the left and right parts of the facets were independent, separated from each other by a low but sharp vertical ledge (Fig. 56c). As a result, the left part of the facet was slightly but distinctly lower than the right. This certainly indicates that the right and left halves of the ossicle of the arm originated separately in ontogeny and grew separately for some time, resembling the development of the brachioles. Later in ontogeny, they merged into a single brachial plate. This suggests that the arms in this genus evolved from the brachioles morphologically similar to those in rhipidocystids. Apparently, this is the first direct evidence for the possible evolution of uniserial arms from biserial brachioles.

Below, the main conclusions on the origin of arms and brachioles are briefly summarized.

(1) The food-gathering processes based on the ambulacral system could appear before it acquired radial symmetry (the arm in Soluta).

(2) The brachiole-bearing ambulacra (eocrinoids) and ambulacra originally lacking brachioles (edrioasteroids) appeared as a result of the difference in the morphogenetic combination of the food grooves and radial ambulacral canals, which originally entered the tentacles surrounding the mouth (as in *Cephalodiscus*). In one case, the morphogenesis of the tentacles was dominant; hence, the appearing ambulacrum did not take part in the structure of the theca. In another case, the morphogenesis of the food groove and theca was dominant. As a result, the developed ambulacrum was included in the structure of the theca and could not rise above it to form the brachioles.

(3) The original biserial structure of the aboral skeleton of the brachioles (and that of the cover plates) resulted from the growth pattern of the ambulacral radial canals and alternatively branching lateral canals, bearing a triad of tentacles.

(4) The arms in crinoids evolved from the brachiole-bearing ambulacrum as a result of the appearance of a new growth vector. The theca was subdivided into oral and aboral parts, and the integration of different structures in the morphogenesis of the ambulacrum increased simultaneously, which led to an enhanced metameric structure. The latter is displayed by the transformation of the biserial structure of the brachioles into the uniserial structure of the arms.

(5) The arms of crinoids evolved from the brachiole-bearing ambulacra in several ways and in several lineages, based on the same morphogenetic mechanism.

CONCLUSIONS. THE DEVELOPMENT OF THE CRINOID BODY PLAN

The first part of this study discussed the major structures of pelmatozoan echinoderms, primarily the skeletal structures. Based on this, the following conclusions can be made, mostly on the development of the crinoid body plan. The crinoid body plan, similar to the morphological organization of other classes of pelmatozoan echinoderms, was formed on the basis of the morphological organization of Cambrian eocrinoids. The appearance of the arms was necessary but was not the only condition for the development of the crinoid body plan. The crinoid body plan includes the appearance of at least seven characteristics related to the skeleton (Fig. 57): (1) transformation of the biserial brachioles into uniserial arms; (2) differentiation of the theca into the cup and tegmen; (3) the replacement of varying position of the brachioles on the theca by the marginal position of the arms; (4) arrangement of the plates in the cup into two or three circlets; (5) appearance of the stem as a result of polymerization of the holdfast; (6) further development of the stem as a result of the arrangement of the original appendage; (7) disappearance of the sutural pores and epispires, and the development of a complete, nonporous cup. Each of these characteristics had already appeared in the Cambrian within Eocrinoidea, but in different combinations. Only the combination of all the above characteristics resulted in the true crinoid body plan. The characteristics were, apparently, combined due to various heterochronies.

PART 2. SYMMETRY AND ASYMMETRY IN THE MORPHOLOGY AND MORPHOGENESIS OF PELMATOZOAN ECHINODERMS

Echinoderms exhibit the highest and most diverse symmetry among all multicellular organisms. Pentaradiate symmetry is most characteristic, a symmetry that rarely occurs in other animals. Therefore, its predominance in echinoderms seems obscure, especially because its functional advantage as compared to other radial symmetries is not always apparent. Sometimes, the appearance of five-part radial symmetry is explained by its affinity to the crystallographic structure of calcite “monocrystals” from which the skeletal elements of echinoderms are built. However, this is a rather unconvincing reason for the predominance of pentaradiate symmetry, since in the majority of echinoderms it is far from being ideal, and it may be completely absent or embrace only part of the skeleton in many ancient echinoderms. Therefore, the study of the mechanism of development of pentaradiate symmetry (pentamery) in echinoderms is important for the investigation of their evolutionary morphogenesis. Echinoderms also show symmetry of another type, metamerism. It does not occur throughout the entire body, but only in parts (similar to all other symmetries). However, metamerism has not received much study despite its importance for the morphogenesis of echinoderms. Perhaps, it is closely connected with the development of pentamery. The pentaradiate symmetry is connected with five planes of symmetry. But real organisms always display irregularities in symmetry. Therefore, by neglecting some distortions and emphasizing others, we accredit different significance to each of the five possible planes of symmetry. Depending on the character of irregularity of the pentamery, these planes are displayed with different clarity. Therefore, pentamerous echinoderms have five planes of symmetry, of which one or two are particularly clearly displayed. The reasons leading to the predominance of any planes of symmetry are closely connected with the morphogenesis of echinoderms.

Where any symmetry in animals is concerned, one should always remember that there is no such thing as a perfectly symmetrical animal, and there are always irregularities in the symmetry which immediately attract one's attention. The asymmetry in echinoderms is quite pronounced and characteristic because adult nonpathological individuals of echinoderms almost always have their right protocoel and mesocoel reduced, and many other related features are also developed asymmetrically. Therefore, they can be called left-sided animals. According to Ivanova-Kazas (1978, p. 117), the reasons for the appearance of asymmetry in echinoderms is one of the hardest problems in phylogeny. Some authors explain asymmetry in echinoderms by the presence of a specific inclination to asymmetry in their organization (Grobben, 1923) or by an "idiosyncrasy" toward bilateral symmetry (MacBride, 1914). Apparently, all manifestations of symmetry and primary asymmetry are closely connected in their origin. This and possible reasons for the primary left-sided asymmetry in echinoderms will be discussed below. However, some morphological structures of echinoderms are also asymmetric and may occur both in right-sided and left-sided states. Therefore, in which cases the primary left-sided asymmetry of echinoderms affects the predominance of the right and left forms in some structures will be discussed below. Cases of deformed, crooked theca and stem in Pelmatozoa will also be considered, since they specifically elucidate the development of planes of symmetry in adult animals and their relationships with the larval plane of symmetry. These are the problems to be discussed in this chapter.

The task is facilitated because data on many types of symmetry and its distortions have already been summarized in many papers. This particularly concerns crinoids, which are of primary interest to the present study (Arendt, 1970, 1974, 1981). Thus, manifestations of symmetry will not be described only from the point of view of their diversity and bizarreness, but from the point of view of their morphogenesis, since only this approach will allow certain conclusions to be drawn about the origin of symmetry and connections between its types and manifestation in echinoderms. In fact, identical symmetrical figures, e.g., five-rayed stars, may be drawn by following different sequences of operations. The resulting figures would be different only in the history of their individual drawing patterns. How can this individual history of a structure, its "ontogeny," be revealed other than by direct observation? It can be reconstructed from incomplete specimens or from characteristic distortions in complete forms (aberrations). Therefore, this study of symmetry and morphogenesis will focus on aberrant forms of echinoderms and on the earliest preserved stages of skeletal development in fossils.

SECTION 1. SYMMETRY IN THE STRUCTURE AND MORPHOGENESIS OF PELMATOZOAN ECHINODERMS

METAMERISM

The study of the symmetry in pelmatozoan echinoderms will begin from metamerism, although usually pentamery is to be considered first. However, metamerism in echinoderms is a more ancient type of symmetry than radial symmetry, and, as is shown below, metamerism was the basis for radial symmetry.

Metamerism is the regular recurrence of identical parts along the axis, i.e., it is a translation symmetry. Because there are never two completely identical parts in an organism, one has to ignore many small differences between the metameres. Metamerism is manifested especially clearly in the structure of the stem and arms of crinoids, but it is also observed in the structure of the theca. However, it is not this metamerism that is considered here, although it shows many marked patterns important for the understanding of the morphogenesis of echinoderms and for phylogenetic reconstruction. The first to be analyzed will be the primary, the most ancient, metamerism characterizing echinoderm larvae and supposedly occurring in the ancestors of echinoderms. This metamerism is displayed by the development of the three pairs of coeloms characteristic of echinoderm larvae and the early stages of the development of other deuterostomes, including chordates and hemichordates.

When the abstract model of the translation symmetry is studied, e.g., continuous bands or tapes with a repeated pattern, the first task is to reveal the translation element, which can be found in any part of the band. When an organism is studied it is important to reveal primary segments that served as a model for the development of subsequent segments. The development of primary segments, and there are usually a few of them, differs from the model of development of subsequent segments. For instance, this is the basis for the theory of larval and postlarval metamerism in Annelida and Arthropoda, which is one of the fundamentals of the morphology of protostomes (Beklemishev, 1964). A similar theory was applied to deuterostomes (Ivanov, 1944; Svetlov, 1957). This theory did not receive further study and is poorly known. However, it may be important to the understanding of the morphogenesis of deuterostomes, including echinoderms. According to this theory, the frontal segments of the head of vertebrates and *Amphioxus*, which are homologous to the segments of the echinoderm larva (dipleurula) (Goodrich, 1913; MacBride, 1914; Fedotov, 1923), comprise the larval body of these animals, whereas the remaining part of the head, body, and tail form its postlarval body (Svetlov, 1957). This lead to a conclusion that the "primary heteronomy of the segmentation of a body is characteristic of the Chordata of Annelida as well as Arthropoda" (Svetlov, 1957, p. 3). One of the most important differences between these two parts of the body is in the direction and sequence of the growth of the segments: the caudo-rostral direction in the larval body and rostro-caudal in the postlarval direction. This phenomenon shows complete similarity to the position of the border of the opposite growth directions in protostomes between the larval and postlarval segments. The analogy is also observed in the succession of segment development. In different vertebrates, the first segments (posterior segment of the larval body and the anterior segment of the postlarval body) appear in the zone of the incipient auditory capsule. Then, the segments of the postlarval body are formed rapidly one after another, while the mandibular and premandibular segments are formed anterior to the hyoid segment. Svetlov (1957) concluded that in contrast to the various developmental patterns of the postlarval body in protostomes, the developmental patterns of the larval body in vertebrates is predictable: the segments of the dipleurula served as a substrate for the development of the olfactory and visual organs within the respective zones of the brain. The postlarval body, which appeared here as a new development, did not take part in this process. Fedotov (1923) had a similar opinion but displayed it in a slightly different aspect. He concluded that "the major feature of the coelom not only of echinoderms, Enteropneusta, and Pterobranchia, but also Chordata is that it is composed of the anterior, middle, and posterior pairs of lobes of enterocoel origin. This composition is seen at the early developmental stages of these forms and remains the clearest in adults within the Enteropneusta and Pterobranchia, whereas in Echinodermata and the majority of Chordata, the posterior pair of coelomic cavities predominates over the other two. As a result, in echinoderms, as the bilateral symmetry of the larvae is transformed into the radial symmetry of the adult animal, the right posterior larval coelom forms the aboral part, and the left coelom forms the oral part of the definitive cavity of the body, while both pairs of anterior coeloms of the unsegmented larva transform into the cavities of the system of organs to lose partly or completely (in contrast to Enteropneusta and Pterobranchia) the significance of the body cavities. In most chordates, the cavities of the two anterior pairs of the coelomic cavities … disappear. The posterior part of the coelom becomes metameric and gives rise to the definitive body cavity and, together with other parts, participates in the formation of the body of an adult animal." (p. 10).

Detailed comparison of echinoderms and chordates is beyond the scope of this study. It is important to note that metamerism in echinoderms is as complex as in chordates and has several stages of development. As in chordates, the posterior coeloms in echinoderms compose the major part of the body cavity. Do echinoderms have postlarval segments? In some groups, these are undoubtedly present. First, it is a stem in crinoids and eocrinoids. It is developed as a metameric outgrowth of the posterior right coelom and in this sense can be compared with the major body part of chordates and can be called a postlarval body. However, the fate of the larval segments in echinoderms differ strikingly from the fate of the postlarval segments in the character of its further development and in its influence on the general structure of the organism.

Thus, postlarval segments are not known in all echinoderms, but only in those having a stem or a tail (Soluta). The aulacophore of Stylophora is not considered here, because its interpretation is very debatable. The stem of crinoids, like the tail of Soluta, usually contains two parts with opposite or coinciding directions of metameric growth. In crinoids, these are proxistele and mesistele. The place of the development of new columnals (not taking intercalating columnals into account) both of the proxistele and mesistele are often in close proximity, i.e., on the boundary of these two zones. New columnals in the proxistele move toward the base of the calyx, while the columnals in the mesistele move toward the attachment structure. In contrast to the larval and postlarval segment of protostomes and chordates, the appearance and growth of new metameres occurs, although in opposite directions, toward each other. In addition, many Cystoidea have terminal growth of the columnals of the mesistele. In these cases, the direction of growth of the mesistele and proxistele is the same. As will be shown in the section dealing with the development of the stem in pelmatozoan echinoderms, this difference in the development of the columnals of the mesistele and proxistele is, in many cases, connected with the different mechanism of their origin in the phylogeny. The proxistele was historically formed as a gradual regular arrangement of the plates covering it, whereas the columnals of the mesistele, although the latter in some cases was formed in the same way, appeared as repetition or, more properly, metamerization of the attachment disc.

Usually, in crinoids, there are numerous centers of emergence of columnals and of stem growth. This facilitates rapid and more regular elongation of the stem. Numerous growth centers appear due to the regular arrangements of the places of the additional intercalary columnals. This led to the regular arrangement of the columnals of different orders, thus resulting in new more complex elements of metamerism in the stem structure, noditaxises. The element of translation in this metamerism was sometimes composed of columnals of four or five orders. The diversity of the manifestations of metamerism in the stem is easily seen from the descriptions of stem fragments in publications. This diversity is certainly very high, and although of restricted interest, is important in systematic and morphological studies of various crinoid groups (Stukalina, 1986).

Metamerism is very clearly seen in the structure of arms in crinoids and brachioles in blastozoan echinoderms. However, this type of metamerism is not complete (most organs escape it) and is less connected with the general primary metamerism of an echinoderm body. The appearance of new metameres in this case, in contrast to the stem, is always terminal. The segments of arms and those of brachioles always appear at their ends. In each of the five simple unbranching arms occurring in some crinoids, the metamerism is of a single order and occurs in all systems of organs located in the arms, including the skeleton, all three nervous systems, and the ambulacral and blood systems. In this case, the regular change in the size of the brachials, primarily their width, since their length changes only slightly, may be accounted for by a calibrating coefficient. In branched arms, the metamerism sharply increases, although in this case a calibrating coefficient can also be introduced to characterize different types of branching and even the change in branching type. The metamerism of each arm is relatively independent, although in many cases it may be very similar in all arms. In contrast to the arms, the brachioles are generally biserial, and the brachiolar plates in neighboring rows form a zigzag pattern, being displaced at a distance of a half-height one from another. Therefore, the metamerism in each row of brachiolar plates in a brachiole is considerably more complex because of the displacement of the neighboring rows. Interestingly, in the brachioles of some eocrinoids, for instance, the Ordovician *Neorhipidocystis*, the displacement of the brachiolar plates in the neighboring rows disappears and the pairs of brachiolars are fused in a single brachiolar plate with a hardly noticeable suture between them (Fig. 56). The metamerism of brachioles in this case is noticeably less complex. The metamerism of the covering plates both in arms and in brachioles is usually of a different order than the metamerism of their dorsal skeleton.

THE RELATIONSHIPS BETWEEN THE METAMERISM AND CYCLOMERY IN ECHINODERMS

The skeleton of the theca in crinoids and many blastozoan echinoderms also shows a metameric structure manifested in the successive arrangement of the rows of plates. However, in this case a different type of metamerism expressed in each circlet of thecal plates and sometimes in each columnal at early stages of their phylogeny is often overlooked. In the ontogeny of extant crinoids, the plates in the circlets of the theca first develop in a horseshoe-shaped pattern with a broad gap between the plates at the tips of the horseshoe, rather than forming a complete circle.

Developing columnals also begin to form a semicircle, which later become closed by a round plate with a canal in the middle. At this stage of the skeleton's development, each circlet of the theca displays metamerism rather than radial symmetry. Five segments of each circlet are not circled but extend to form a horseshoe shape. In extant crinoids at this stage of ontogeny, each horseshoe-shaped columnal is solid.

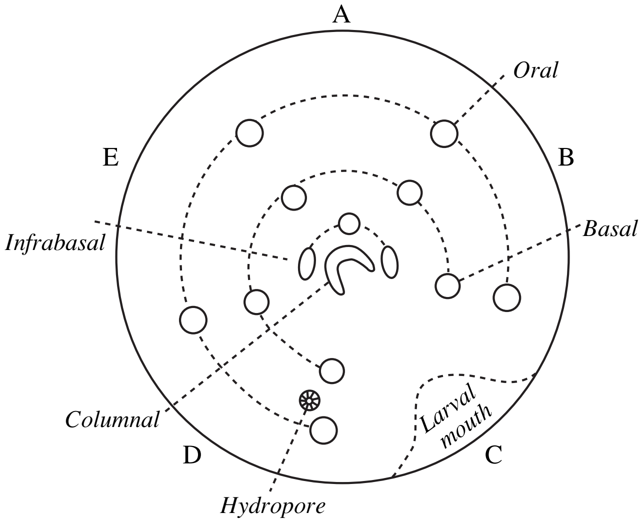


Fig. 58. Horseshoe shape of columnals and circlets in the larva of the extant crinoid (after Bury, 1888).

However, it is possible that ancient crinoids, which had a stem subdivided into pentameres, at this ontogenetic stage could have had a stem composed of five metameres arranged in a curved chain. The ontogenetic stage of the metameric rather than cyclomerous structure of the circlet plates is undoubtedly of ancient origin. This can be suggested, for instance, by the gap between the radials in calceocrinids (disparid crinoids). Theoretically, however, this could not be the original state for pelmatozoan echinoderms, because in my view explained in the chapter on the development of the theca, the skeleton in the earliest eocrinoids appeared relatively late in ontogeny and covered the entire body. In this case, how can the existence of the horseshoe-shaped stage in the development of a skeleton in extant crinoids be explained? The explanation is quite straightforward and is based on the following factors and trends: (1) the translation of the beginning of the skeletal development to the earlier ontogenetic stages; (2) distribution of five-rayed symmetry from the pentamerous arrangement of the food grooves radiating from the mouth onto the entire theca; (3) effect of the morphogenesis of the ambulacral ring canal on the development of five-rayed symmetry.

Below, the latter factor is discussed in greater detail. The water-vascular (ambulacral) system in the embryonic state of extant echinoderms functions as an inductor strongly resembling the function of the notochord in the embryonic state of chordates. The embryonic induction is the effect of one part of the embryo (inductor) on the other (recipient) resulting in a change of the morphogenesis and differentiation (Beloussov, 1993, p. 131). For instance, if in the amphibian embryo the chordomesoderm is partly transplanted to the ventral side, the ectodermal zone contacting the transplant will give rise to axial structures, including the nervous tube, somites, chord, and incipient embryonic kidneys. The ambulacral system plays a similar role in the embryonic development of echinoderms. Many systems of organs in crinoids, e.g., the ectoneural system, repeat the shape of the developing ambulacral ring, which emerges from the left mesocoel (hydrocoel).

In the ontogeny of all extant echinoderms and, apparently, of all radially symmetrical ancient echinoderms, the ambulacral ring does not appear as a completely closed ring but first has a horseshoe shape, which later closes into a ring (Fig. 58). Five lobes developing on the horseshoe later give rise to the radial ambulacral canals. Apparently, the hydrocoel, which induces the appearance of the ectoneural system and, directly or indirectly, the development of the skeletal plates, forces them to repeat the horseshoe shape of its own developmental pattern. Thus, the horseshoe shape of the developing hydrocoel is primary compared with the horseshoe shape of the arrangement of the thecal plates and other organs.

The horseshoe stage in the ontogeny of the ambulacral ring apparently reflects a phylogenetic stage of its development. This is supported by the structure of Soluta, ancient echinoderms, which primarily did not have a radial symmetry but had an armlike process and ambulacral system. Even if this group is considered a stem group of chordates (following the cladistic approach of Jefferies *et al.*, 1996 and their successors), the presence of the armlike process and the ambulacral system certainly reflects a stage of the development of these organs in echinoderms. Soluta always have a single arm and a plate near it with numerous pores. One of these pores is larger than the others and is thought to be a gonopore, whereas the others are thought to represent numerous hydropores forming a madreporite (Fig. 49). There is an evidence of the presence of the ambulacral canal and ambulacral tentacle in the armlike process (Jefferies, 1990). This is considered in detail in the chapter on the appearance of arms. Apparently, in Soluta, a group with such a body structure, the ambulacral ring is absent. Its place is occupied by a saclike hydrocoel with a single ambulacral canal extending from it into the arm. From this primary structure, especially taking into account the details of the development of the ambulacral ring in the ontogeny of echinoderms, the ambulacral ring of the emerging radially symmetrical echinoderms could develop only by the growth of this incipient structure around the esophagus and its subsequent closure.

Thus, the radial structure of the ambulacral system of echinoderms developed by the overgrowing of the primary saclike hydrocoel around the esophagus, polymerization of the extending radial canal, and the closure of the resulting metamerism into cyclomery. This is very important, because this process affects the entire morphogenesis of echinoderms and determines its features. For comparison, in corals, the radial body structure does not result from the closure of metamerism but appears in a totally different manner, through the successive division of the body cavity by emerging septa as is evident from both ontogeny and regeneration (Rozhnov, 1974). The hypothesis that the cyclomery appeared in echinoderms through the closure of metamerism allows consideration of the development of a radial symmetry characteristic of echinoderms.

RADIAL SYMMETRY OF ECHINODERMS AND DEVELOPMENT OF RADIAL SYMMETRY

The radial symmetry of echinoderms is mainly represented by five-rayed (pentaradiate) symmetry. It is not present in the entire body and is superimposed on the deep primary left-sided asymmetry of echinoderms. Eocrinoids show a morphological sequence of gradual development of the pentaradiate symmetry. Primarily, it involved only the arrangement of the food grooves near the mouth and orals around them. Later, the pentaradiate symmetry involved the basals and gradually the entire theca. Hence, the problem of the origin of pentamery in pelmatozoan echinoderms is a problem of its development in the arrangement of the food grooves and in the morphology of the ambulacral system, which is closely connected with the grooves. As mentioned above, the hydrocoel is one of the major initiators in the ontogeny of echinoderms. As it became pentaradiate, it consequently spread its direct or indirect inducing influence to the nervous and blood systems and the skeleton. The problem is how the pentaradiate symmetry of the hydrocoel is formed; did it originate independently there, or was it received from the food grooves? According to Sprinkle (1973a), brachioles and connecting food grooves of eocrinoids initially lacked radial ambulacral canals. Following this view, it becomes apparent that the arrangement of the food grooves is solely responsible for the pentaradiate symmetry of the remaining body parts, including the ambulacral system in crinoids. The symmetry of the food grooves in this case would have been optimal to cover food collection by the theca. However, the five-rayed symmetry does not necessarily follow this model, because it is not clear why it is better than, for example, the six- or seven-rayed symmetries.

The hypothesis of the initial absence of the ambulacral system in blastozoan echinoderms, including eocrinoids, is not very convincing. This problem is discussed in detail in the chapter on the origin of arms. Therefore, I suggest that the development of the five-rayed symmetry resulted from the interactions of factors determining the development of the ambulacral system and optimization of the arrangement of food grooves and was initially defined by the features of a hydrocoel and by the initial structure of the ancestor of echinoderms. Below, an attempt is made to show this and to reveal a possible mechanism of the development of the pentamery in echinoderms. In support, direct evidence from ontogeny of extant echinoderms and indirect evidence from the ontogeny of fossil echinoderms are used. The indirect data on the ontogeny of extinct

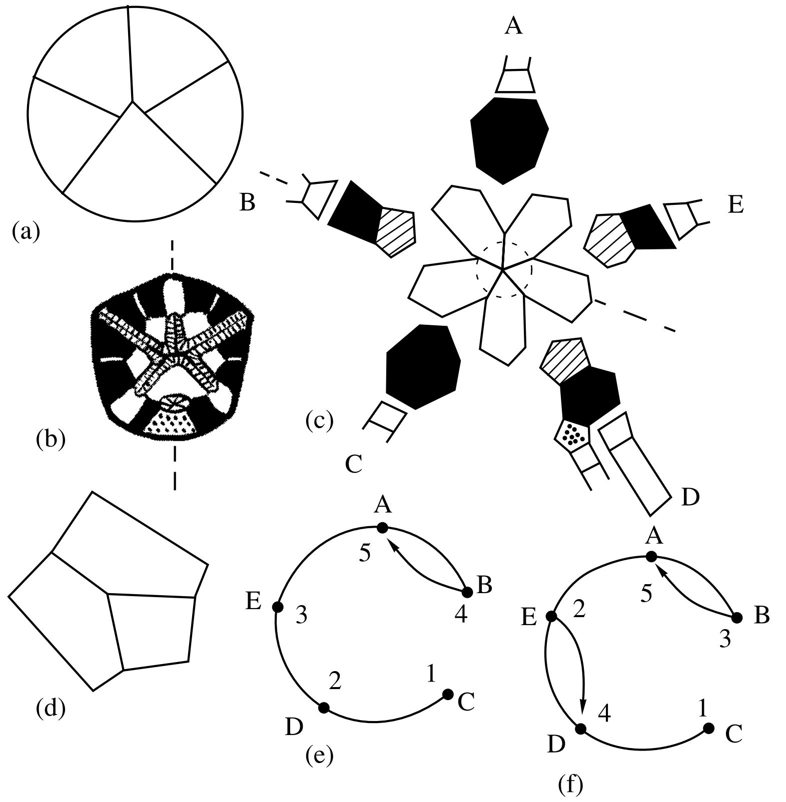


Fig. 59. Manifestation of triradiate symmetry in crinoids: (a) scheme showing the arrangement of the orals in *Pisocrinus*; (b) arrangement of food grooves and their connection with the aboral skeleton of the arms in *Hybocystites*; crinoid plane of symmetry (A-CD); (c) homocrinid plane of symmetry (E-BC) in homocrinids; (d) scheme showing the structure of the infrabasal circlet in Flexibilia; (e) sequence of development of the radials in the cladid *Cranocrinus praestans* Arendt; (f) sequence of the appearance of the radial facets of disparids. Figures indicate the sequence in which structures appeared in the rays.

echinoderms can be obtained from the analysis of the adult organisms and from aberrant individuals reflecting abnormal ontogeny. Because the hydrocoel had a strong inducing influence on the development of food grooves in the skeleton and was also closely connected with these in construction, some features of their structure and development and many aberrations certainly indicate features of the development of the ambulacral system. This is discussed in greater detail below. Five food grooves extending from the mouth reflect the pentaradiate symmetry of echinoderms. In crinoids, this spreads to the entire skeleton of the theca and often to the skeleton of the stem. Different irregularities of the pentaradiate symmetry in crinoids usually only indicate their secondary nature and the primary nature of their pentamery. In many cases, the triradiate symmetry can be seen through the pentaradiate symmetry. Based on this, the triradiate symmetry is considered to be ancestral in echinoderms (Fig. 59). The triradiate symmetry is most clearly displayed in the arrangement of food grooves: one of these, located in ray A, is always unpaired, whereas the four others are always arranged in pairs, B with C and D with E. Their paired arrangement is not only seen in their paired proximity in the vicinity of the mouth, but sometimes in the clear branching of one from another. Clearly, it indicates a primary triradiate symmetry of the ambulacral ring, since the number of feeding groups indicates the number of ambulacral canals extending from the ambulacral rings. Indeed, in the case of branching of two grooves, we observe only three grooves immediately extending from the mouth and, therefore, we can suggest with confidence that only three radial canals were extending from the ambulacral ring. Therefore, it is proposed that the extension of five radial canals directly from the ambulacral rings is phylogenetically secondary compared with three. This is supported by the fact that when five radial canals extend from the ambulacral ring and five food grooves extend from the mouth, the traces of their former, primary, triradiate structure are reflected in their size ratios and the arrangement of the orals (Fig. 59). The triradiate symmetry displayed in the arrangement of five food grooves was explained by Bather (1900) as a trace of the original succession of development of pentaradiate symmetry in crinoids. His theory has been supported by many subsequent researchers, e.g., Beklemishev (1964) and Fedotov (1951), and has been maintained virtually unchanged to the present day. Bather believed that the ancestor of crinoids had three food grooves. They were arranged on the surface of the theca in such a way that one, anterior, was directed oppositely to the anus and the hydropore, whereas the two others, right and left, were directed at an angle of 120° to the anterior groove, in a so-called crinoid plane of symmetry. Later extensions appeared in the direction of the anterior groove from each of the lateral grooves, thus increasing the coverage of the theca. In this way, another two grooves and pentaradiate symmetry appeared, which in the future determined the pentaradiate symmetry of the entire skeleton. Thus, Bather suggested that the pentaradiate symmetry of echinoderms resulted from the optimization of the number and arrangement of the food grooves on the theca, taking into account the position of the anus. This model quite adequately describes the emergence of pentaradiate symmetry; however, to understand the regularity of the changes in the pentaradiate symmetry, it is important to develop a morphogenetic model of the emergence of pentamery in echinoderms. A few questions immediately arise. Why were there three rather than five grooves originally? What is the directing groove A from the morphogenetic point of view? Possible answers are discussed below. The ambulacral system and food grooves in all extant crinoids are functionally, structurally, and morphogenetically connected to each other to such an extent that their separate existence is inconceivable. Perhaps, they could exist separately only in some very highly specialized forms. In fossil echinoderms, as indicated above and discussed in greater detail in the chapter concerning the origin of arms, this is supported by the presence of the ambulacral system in primitive asymmetric echinoderms such as Soluta. Therefore, I concluded above that three of the five segments of the ambulacral ring are primary and the other two are secondary. The secondary origin of the two segments is indicated by the fact that both these segments appeared as a result of the gradual approximation of the bifurcating point of the two ambulacral radial canals to the ambulacral ring, which ended with the radiation of all five canals directly from the ambulacral ring. Hence, the appearance of the pentaradiate symmetry in echinoderms is a product of the optimization of the number and arrangement of food grooves on the surface of the theca, taking into account the position of the anus. It was based on the previous triradiate arrangement of the food grooves and radial ambulacral canals with certain morphogenetic properties. As a result, the problem of the appearance of pentaradiate symmetry is put down to the appearance of triradiate symmetry. However, no echinoderm with a certainly primary triradiate symmetry is yet known. Helicoplacoidea may be an exception, if it is proved that their mouth was below the radiation point of the ambulacra (Derstler, 1981; Paul and Smith, 1984; Durham, 1993). In a few crinoids with more or less prominent triradiate symmetry, it is apparent that this symmetry is secondary and evolved from pentaradiate symmetry. The Ediacaran triradiate *Tribrachidium*, which is sometimes considered to be a soft-bodied Edrioasteroidea and among the earliest echinoderms, is unlikely to belong to the phylum Echinodermata (Fedonkin, 1987).

The explanation of the appearance of triradiate symmetry requires a special approach. At least three facts should be taken into consideration: (1) The ancestral structure of the ambulacral system in radially symmetrical animals should be searched for in asymmetrical echinoderms, which apparently had an ambulacral sac instead of an ambulacral canal, with a single ambulacral canal extending from the sac. (2) The ambulacral ring develops from the ambulacral sac by a horseshoe-shaped growth of the latter and its subsequent closure. (3) The initial part of the growing ring is marked by the point of extension of the stone canal. From these three facts alone it is not easy to assess which appeared first, radial symmetry or the closed ambulacral ring. Nor it is clear whether or not a stage with a horseshoe-shaped homologue of the ambulacral ring existed in the phylogeny of echinoderms. The fact that the ontogeny of the extant crinoids has a stage with a horseshoe-shaped hydrocoel with five incipient radial canals does not necessarily indicate that the same stage was present in the phylogeny. Nevertheless, some indirect data suggest that the closure of the horseshoe-shaped hydrocoel occurred after the appearance of the pentaradiate symmetry in the arrangement of the radial canals. For instance, a curved shape of the peristome in Edrioasteroidea with a well-expressed pentamery in the arrangement of the ambulacra may indicate that their hydrocoel was shaped like a horseshoe and open.

The second ambulacral groove appeared in echinoderms before they became radially symmetrical. This is indicated by the structure of the Middle Cambrian representatives of Cincta. They do not have radial symmetry and their hydrocoel was unlikely to have been ring-shaped, but an ambulacral groove extends from the right and left side of their mouth (Fig. 60). The right groove is usually considerably shorter than the left. It is possible that some Eocrinoidea with a primarily flattened theca (*Heckerites* from the Caradoc of Estonia) first had only two ambulacral canals, while the hydrocoel was not closed (Rozhnov, 1987b). However, this is nothing more than a hypothesis. However, as mentioned above, no echinoderms with only three primary ambulacral grooves are known with certainty. For instance, all known three-armed crinoids certainly evolved from five-armed ones, since they usually have traces of pentaradiate symmetry in their skeleton. It is possible that Helicoplacoidea (Fig. 60) had three ambulacra (Derstler, 1981; Paul and Smith, 1984). Durham (1993) did not support this interpretation.

The only result of the appearance of two ambulacral grooves was a small curvature of the hydrocoel around the esophagus, while the appearance of the third groove led to an almost complete embracing of the esophagus by the hydrocoel and was followed by its closure into a ring. This process was justified both functionally (the distribution of pressure in the water-vascular system

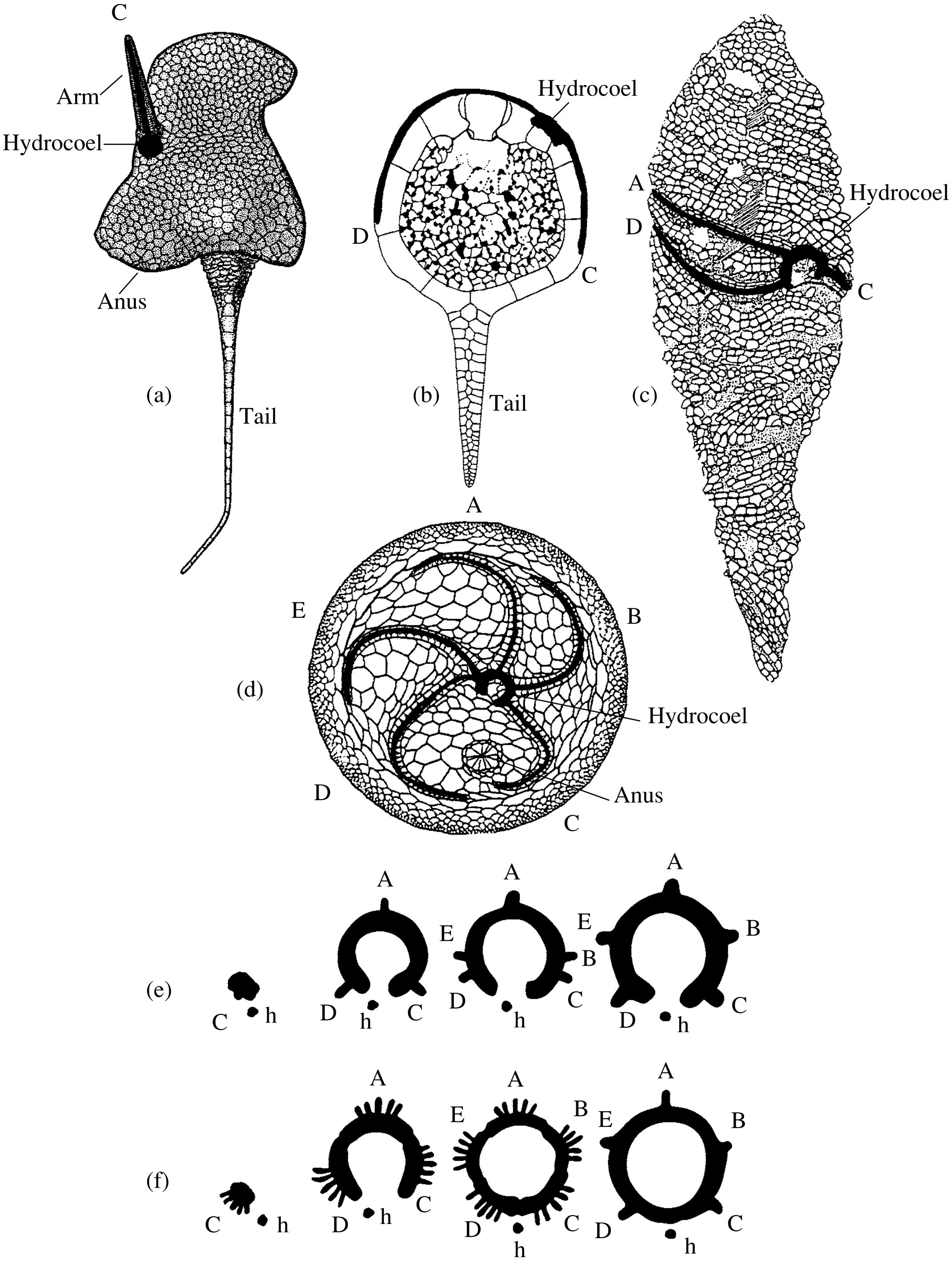


Fig. 60. Scheme showing the development of the ambulacral system in echinoderms: (a) a single radial ambulacral canal extending from a sac-like hydrocoel (Soluta); (b) two radial ambulacral canals extending from an elongated hydrocoel (Cincta); (c) three ambulacral radial canals, extending from a horseshoe-shaped hydrocoel (Helicoplacoidea); (d–e) five ambulacral radial canals, extending from the horseshoe-shaped hydrocoel in eocrinoids and edrioasteroids (supposed ontogenetic stages, the extreme right figure shows an adult); (f) five ambulacral radial canals, extending from the ambulacral ring in Crinoidea (supposed ontogenetic stages, the extreme right figure shows an adult). In crinoids, the appearance of all five incipient radial canals was shifted to the earlier stages of the development of the ambulacral system. Then the incipient structure with five tentacles was polymerized, while the hydrocoel closed to form the ambulacral ring. After that four tentacles in each ray became reduced, while the remaining one developed into the radial canal. On rare occasions all, or many, podia developed in the radial canals (multiarmed crinoids).

became more even) and morphogenetically (the curvature of the hydrocoel was completed). Thus, the hydrocoel of an echinoderm with three radial canals encircled the esophagus at least in a horseshoe-shape. However, such growth of the hydrocoel had to be connected with the changing body plan, movement of the mouth and anus, and the coiling of the intestine. Later, two of the three grooves branched, following the scheme proposed by Bather or a slightly different scheme (shown below), and the ambulacral and digestive systems became pentamerous. The pentamery later spread to other systems, including the skeleton. It is not known for certain when the closure of the hydrocoel into the ambulacral ring occurred in the phylogeny of echinoderms. However, indirect evidence, such as a curvature of the peristome with an incision toward the CD interray in some early echinoderms, may indicate that the closure of the hydrocoel occurred synchronously in different groups at the time of the emergence of new classes evolving both from Edrioasteroidea and Eocrinoidea, apparently at the end of the Cambrian–beginning of the Ordovician. This is a general scheme of the development of pentamery in echinoderms.

Many researchers suggest that the appearance of radial symmetry in echinoderms resulted from the transition to an attached life-style. The dipleurula-like nonattached ancestor of echinoderms became attached by the preoral lobe to the substrate, which resulted in the transition of the mouth and anus and the related growth and curvature of the internal organs, including the closure of the hydrocoel, which became circular. Bather (1900) suggested that the bilateral ancestor of echinoderms (Dipleurula) attached to the substrate by the right side of the anterior part of the body; hence, the atrophy of the right protocoel and mesocoel and development of other major features of echinoderms. Jefferies (1986) suggested that the bilateral common ancestor of echinoderms and chordates was similar in its body structure to the extant *Cephalodiscus* and rested on the ground by its right side, thus causing the reduction of the right coeloms. The problem of the asymmetry in Echinodermata is discussed in detail in the next section.

Summarizing the problem of the origin of pentamery in echinoderms, we can say that the closure of the left hydrocoel in a ring certainly reflects the common tendency of early echinoderms to the development of left-sided asymmetry, which is observed, for instance, in the structure of Soluta. An increase in the number of food grooves and, consequently, radial ambulacral canals up to three leads to the horseshoe-shape of the hydrocoel. A next stage in the development of the hydrocoel, its closure, is constructively stable and functionally optimal for the ambulacral system. The food-gathering systems changed accordingly and led to the appearance of two additional ambulacra (with the total number of five) by branching of from two primary ambulacra. One or two ambulacra make food-collecting possible only in the case of unidirectional currents. The increase in their number up to three, and the more so, to five makes the food-gathering system more efficient in the case of multidirectional, quickly changing currents (water turbulence in shallow waters) and allows more effective use of the gravitational flow of the food particles. However, the appearance of arms makes once again unidirectional currents favorable for food collecting. The pentamery of the ambulacral and food-gathering systems gradually spread to other systems (skeleton, nervous, and blood systems). Supposedly, this was the general sequence of the appearance of pentamery in echinoderms. The appearance of the third ambulacrum causes coiling of the hydrocoel in a horseshoe-shaped structure, closure of the ambulacral ring, and the appearance of pentamery. Therefore, pentamery was constructively predetermined and could independently develop in many groups of the very diverse phylum Echinodermata.

THE SEQUENCE OF THE APPEARANCE OF PENTAMERES IN THE ONTOGENY AND PHYLOGENY OF PELMATOZOAN ECHINODERMS

The previous chapter discusses the possibility of the process of polymerization of the hydrocoel with the extending radial canal at early stages of the echinoderm phylogeny. This process led to the appearance of the pentaradiate symmetry in the arrangement of the food grooves and resulted in the initially metameric horseshoe-shaped hydrocoel closing to form an ambulacral ring. In terms of symmetry, the emerged metamerism transformed into cyclomery. The sequence of the appearance of pentameres and the place where the hydrocoel closes in the ambulacral ring is important in characterizing pentamery because these determine the position of the planes of symmetry and manifestation of the triradiate symmetry. The sequence of appearance of the food grooves and radial ambulacral canals is seen in the arrangement of the canals and in the succession in which the facets for the arm attachment and, sometimes, brachioles and arms appear and also in the number and arrangement of the thecal plates.

Judging from the position of ambulacra and orals and from the sequence in which the arm facets and arms themselves appeared in most crinoids, the model of pentamery was as follows. Three primary grooves (A, C, and D) and two secondary (B and E) branched from the C and D grooves. This is a fundamental model for echinoderms, on which Bather's hypothesis of the origin of pentamery is based. It is often not easy to determine which of the branching grooves were primary and which were secondary, because they often diverge at the same angle from a shared short groove, whereas the sequence of appearance of facets may be different. It is possible that the branching could occur not only in the direction of the A ray, but also in the direction of the anal CD interray. The sequence of appearance of the radial facets known from fossil crinoids was reconstructed both from age variability and from an analysis of the aberrant specimens. In the latter case, Mennert's rule is used, according to which the structures that had appeared last in the ontogeny are the first to disappear. In recent crinoids, the sequence of the appearance and development of pentameres is not studied. According to Arendt (1981), whose conclusions were based on a large body of material, the radials and arms appear in the ontogeny of crinoids in the A, B, and E rays later than in C and D, whereas the reduction and atrophy of arms proceeds in the reverse order. The order of appearance of facets can change considerably, but the facet in the A ray almost always appears first, and that in the C ray appears last (Sevastopulo and Lane, 1998). In the Middle Ordovician eocrinoid *Cryptocrinites*, the sequence of the appearance of the radials (to which brachioles are attached) is established. In this genus, the radial in the A ray always appears last of all primary radials. The appearance of each next radial possessing a facet for arm attachment in the ontogeny of *Cryptocrinites*, occurs clockwise in respect to the primary radial in respect to the succession D, B, C or E, and the one in the A ray appears last (Rozhnov, 1994). This suggests that during the development of the triradiate symmetry in the phylogeny of echinoderms the radial ambulacral canal and the food groove in ray A appeared last, possibly after the branching of the other two grooves. However, the latter possibility is not very apparent, because the sequence of appearance of the two "secondary" grooves could change throughout ontogeny and could be close in time to the appearance of the corresponding primary grooves. This suggests a model of the appearance of trimery in the phylogeny of the hydrocoel (Fig. 60). A single primary radial canal of the ancestors of the radially symmetrical echinoderms corresponds to the radial canal of crinoids in the C ray. The second radial canal appears on the left (posterior to the growth direction of the hydrocoel) and is homologous to the D radial canal crinoids. The third radial canal (third metamere of the hydrocoel in terms of symmetry) is also insulated on the left of the first and occurs between the first two. When the ring ambulacral canal closes, and rays become apparent, it occurs in the A ray. The first two canals appearing earlier than the third canal more rapidly pass through their further development and are the first to branch before the A canal. This is supported by the arrangement of the food grooves in some Rhombifera. For instance, many callocystids have two pairs of symmetrically arranged ambulacra, each pair resulting from the branching of a single ambulacrum extending from the mouth. Although such a structure was secondary, resulting from the atrophy of the food groove in the A ray (this is indicated by the pentamery of the remaining thecal skeleton), it certainly reflects a constructive sequence of the development of pentaradiate symmetry. In another group of Rhombifera, specialized pleurocystids, two grooves extend from the mouth, but these are not branching. Although secondary, this structure indicates the phylogenetic sequence of the appearance of the food grooves. As a result, a stage with a pentamerous structure appeared in the ontogeny of echinoderms. It became a general organization for all pelmatozoan echinoderms and Edrioasteroidea. If this model is correct, a single ambulacral canal in Soluta extending from the ambulacral "sac" is homologous to the ambulacrum of the C ray in pelmatozoan echinoderms and to the right ambulacrum in Cincta. The left ambulacrum in Cincta is homologous to the D ambulacrum in Pelmatozoa. It is possible that helicoplacoids had three ambulacra, A, C, and D (Fig. 60).

Crinoids probably had the following stage of development in the morphogenesis of the ambulacral system. In the ontogeny of extant *Antedon*, the radial canals first appear as tentacles. The first three tentacles appear in each ray. Then, two more tentacles appear on either side. As a result, there are five tentacles in each ray at this ontogenetic stage (Fig. 43). After this, the four lateral tentacles on the sides disappear and a single tentacle remains in each ray. This tentacle gives rise to the radial ambulacral canal of the adult animal. I suggest that this is not an accidental and strange feature in the development of extant crinoids, but an indication of a phylogenetically ancient change in the development of the ambulacral ring. Perhaps, in early Paleozoic crinoids the appearance of all five incipient radial canals in the ontogeny was shifted to the earlier stage, when the incipient hydrocoel had not yet spread around the future esophagus and had not become horseshoe shaped. As it grew, the incipient radial canals gradually spread along the ambulacral ring. At some time, the incipient structure with these five incipient canals, instead of a simple growth and distribution of five primary tentacles along hydrocoel, changes to a different growth type (polymerization) to produce four additional parts with five canals each. Therefore, each ray had five incipient radial canals. Similar to extant *Antedon*, in many crinoids, the four incipient radial ambulacral canals became reduced in each ray and later did not develop at all. However, in some crinoids, especially among disparids, each of these incipient canals gave rise to a radial canal. This is how multiarmed crinoids of the family Allagecrinacea appeared. The multiarmed structure in this family indicates its specialization in the number of arms and their different size. A structure of the Middle Devonian genus *Anamesocrinus* with five identical arms in each ray (Fig. 45a) more adequately displays the suggested model of change in the morphogenesis of the ambulacral ring in the phylogeny of crinoids (Rozhnov, 1985a, 1985b).

PLANES OF SYMMETRY IN THE BODY OF PELMATOZOAN ECHINODERMS

An organism with pentaradiate symmetry may have five planes of symmetry. One or a few of these planes are especially clearly seen when the pentamery is distorted. Generally the planes of symmetry in echinoderms are marked by the position of the hydropore (madreporite); anus; mouth, if it is shifted from the center; and by various arrangements of the thecal plates or body curvature. In different echinoderm group, different planes of symmetry may prevail. The most usual plane of symmetry, which is considered the most primitive, is the so-called crinoid plane characteristic of crinoids and also occurring in many other pelmatozoan echinoderms. It extends through the A ray and CD interray. All pelmatozoan echinoderms have a hydropore or madreporite in this plane. Therefore, this plane, when considered for all echinoderms, is also called "madreporite." The position of the hydropore indicates a general organization of echinoderms formed at the time of the appearance of radially symmetrical echinoderms. Hence, its position is a starting point in the homologization of the rays and, consequently, in the comparison of the planes of symmetry. In the vast majority of crinoids and many blastozoan echinoderms, the anus is located in the same interray with the hydropore. In holothuroids, the madreporite and anus also occur in the same interray, but on opposite ends of the body. In starfishes, the anus occurs in the BC interray, adjoining the madreporite. Sea urchins have several planes of symmetry: the madreporite is located in the madreporite plane; regular sea urchins have an echinoid plane extending through the B ray and DE interray, in irregular sea urchins, the clearest plane is the Loven plane (D-AB), in which their mouth and anus are shifted. Therefore, the manifestations of the planes of symmetry in the structure of the echinoderm body can vary (Ubaghs, 1967a). Below, the origin and homology of the planes of symmetry in pelmatozoan echinoderms are discussed.

The planes of symmetry in crinoids are more clearly seen than in any other pelmatozoan echinoderms (this class will be discussed below). The madreporite plane of symmetry in this class is called *crinoid* since it is the most characteristic of this class. This plane extends through the A ray and the CD interray, where, along with the hydropore, the anus is usually located. Therefore, the CD interray is often called an anal interray. Sometimes, for instance, in some cacleocrinids and eustenocrinids (both from disparids), the anus is located in the C ray (Fig. 26). In this case, the crinoid plane is subdivided in two, a madreporite plane with a hydropore (A-CD) and another (C-EA), which is called eustenocrinid after the Ordovician genus *Eustenocrinus*. In this paper, symmetry is discussed mainly from the morphogenetic point of view to indicate how different symmetries reflect morphogenetic processes occurring throughout growth and how the symmetry of the morphogenetic process is reflected in the symmetry of the final shape of the adult organism. When the madreporite and eustenocrinid planes, of which the crinoid plane is composed, are compared from this point of view, it is clear that they differ morphogenetically. The madreporite plane reflects the initial place of the development of the hydrocoel and the development of pentamery in crinoids, since in this plane they have a "directing," unbranching food groove A. Therefore, the development of the pentamery occurred symmetrically relative to the crinoid place of symmetry. The eustenocrinid plane of symmetry, C-EA, appears because of the underdevelopment of the rectum as a result of paedomorphosis (as shown in the chapter on the development of the anals) and cessation of its development in the case when its termination (the future anus) was located in the C ray. Almost in all other crinoids, the rectum continues on making a complete circle, and the anus opens in the CD interray. Thus, the eustenocrinid plane of symmetry does not reflect the symmetry of the morphogenesis, being random and caused by procceses of a completely different character. Such a position of the anus rarely occurs in adult crinoids, but more often in blastozoan echinoderms. For instance, in the Ordovician eocrinoid *Cryptocrinites*, the anus is usually located in the B ray or, sometimes, in the BC interray. Its position is also connected with paedomorphosis (Rozhnov, 1994).

Another morphogenetically important plane of symmetry is the so-called homocrinid plane of crinoids extending through the E ray and BC interray (Fig. 1). It has this name because it is the most clearly visible in the arrangement of the paired radials in the calyx of disparid crinoids of the superfamily Homocrinacea. In these crinoids, in each of the three rays, B, C, and E, there are two radials one above another, and in two other rays there is one radial as high as two radials in the neighboring rays. Some disparids have other arrangements of radials symmetrical relative to another plane of symmetry (the so-called heterocrinid plane after the family Heterocrinidae, for which at present another, valid name Cincinnaticrinidae is used). Representatives of this family have paired radials located only in two rays, C and E. Therefore, the plane of symmetry in the calyx extends through the D ray and AB interray AB. A comparison of the development of the homocrinid and heterocrinid planes of symmetry shows that (as above) the homocrinid plane reflects the symmetry of important morphogenetic processes in the ontogeny of crinoids, whereas the appearance of the heterocrinid plane is determined by a relatively random underdevelopment of one of the rays. The fifth possible plane of symmetry should extend through the B ray and DE interray. In sea urchins, this plane is called echinoid and occurs in some regular echinoids. However, this plane only very rarely occurs in pelmatozoan echinoderms and does not have a special name. Therefore, of all five planes of symmetry occurring in pelmatozoan echinoderms, the crinoid and homocrinid planes are those which reflect the symmetry of the morphogenetic processes.

As noted above, the following morphogenetic processes in the development of crinoids and many other pelmatozoan echinoderms went through the symmetry of the crinoid plane: (1) The development of the pentaradiate symmetry from triradiate, it was this plane in which the unbranching food groove A occurred, while the two other were branching symmetrically to this

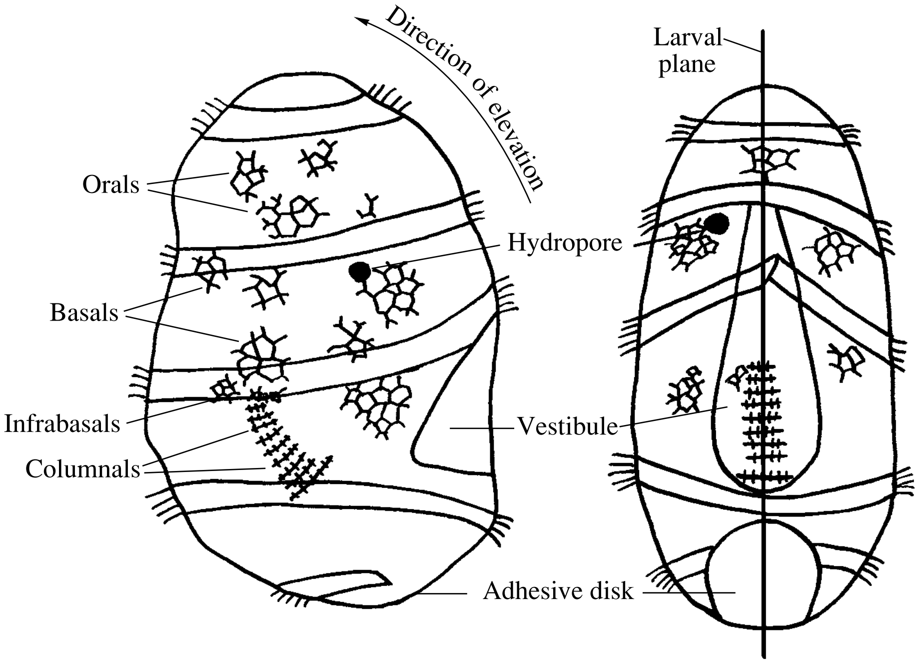


Fig. 61. Scheme showing the arrangement of the major structures and skeletal elements in relation to the larval plane of symmetry in extant crinoids.

plane. (2) The development of the incipient hydrocoel in the crinoid larvae began to the left of this plane, which is marked by the position of the hydropore. Later, the hydrocoel grew and acquired a horseshoe shape. Apparently, the opening of this horseshoe occurred in the crinoid plane, in which later the hydrocoel was closed into the ambulacral ring. The latter is not that evident, and it will be discussed below. (3) The anus in most crinoids and many other pelmatozoan echinoderms usually occurred in this plane, thus indicating a symmetrical growth of the digestive system relative to this plane. In this plane, the digestive system morphogenetically developed a complete circle, beginning with the mouth opening and terminating by the anus. Interestingly, the underdevelopment of the digestive system led to a shift of the anus to the preceding ray or interray. In the case of hyperdevelopment, the digestive system made one more or a few complete circles, and the anus was still opening in this plane. However, in that case, the anus was positioned in the center of the theca, while the mouth was shifted to the side of the theca toward ray A.

The homocrinid plane reflects other morphogenetic processes. The arrangement of the thecal plates is symmetrical to the homocrinid plane. This is a characteristic, although not general type, which will be discussed below. The curvature of the theca and stem, which is observed in pelmatozoan echinoderms in this plane, seems more important. This curvature, which is most clearly seen in the Paleozoic calceocrinids and in many Meso-Cenozoic cyrtocrinids, is connected with either paedomorphosis or hypermorphosis (discussed in another chapter) and reflects a particular process in the ontogeny of pelmatozoan echinoderms (still retained in extant crinoids): elevation, i.e., the shift of the future position of the mouth (vestibulum) from the ventral side of the larvae to the posterior ends. The mentioned shift occurs in the dorsoventral plane of doliolaria, a free-swimming crinoid larva. This allowed Lane and Webster (1967) to consider the homocrinid plane of the pentaradiate adult crinoids to be a homologue to the dorsoventral plane of symmetry in their bilateral larva (Fig. 61). But how does the plane of symmetry of the bilaterally symmetrical larva correspond to one of the planes of the radially symmetrical adult? Supposedly, it can correspond only very tentatively, as the preservation of the arrangement of a few indicative structures of the body. Other structures in adults, which are arranged around the plane of bilateral symmetry, may completely change their arrangement with respect to other structures. Therefore, an incomplete homology of the planes of symmetry is suggested. Below, this is discussed in detail in respect to the homocrinid plane.

The homocrinid plane of symmetry in crinoids extends through the E ray and BC interray. In extant crinoids, the larva at this particular stage of development has a horseshoe-shaped hydrocoel and clearly seen incipient radial canals in the form of lobes. The fate of these incipient canals may be traced, and the dorsoventral plane of the larva may be put in correspondence with either of the planes of symmetry of the adult organism. Lane and Webster (1967) attempted this and revealed that the dorsoventral plane of the crinoid larvae corresponds to the homocrinid plane of adult animals. This correspondence is indicated by the position of the hydropore, appearing already in larvae, to the left of this plane. The plane of elevation in larvae corresponds to the homocrinid plane in adults, in which the distortions of the elevation may be traced. These changes of the process of elevation in the ontogeny are responsible for the existence of large morphological distortions in the organization of many groups of pelmatozoan echinoderms and are discussed in greater detail in another chapter. It is noteworthy that in the above paper by Lane and Webster the opening in the horseshoe-shaped hydrocoel is also shown in interray BC, i.e., in their opinion, the development of the hydrocoel occurred in the homocrinid plane of symmetry. However, this hypothesis is apparently incorrect since it contradicts the studies of the ontogeny in crinoids. According to Bury (1889), who studied this problem specifically, the closure of the horseshoe-shaped hydrocoel in extant crinoids (for instance in *Antedon*) occurs in the same interray in which an onset of the stone canal and a hydropore is positioned, i.e., in the anal CD interray. The place of the close in the CD interray occurs on the side of the C ray in respect to the place of the onset of the stone canal. Bury believed that the closure of the horseshoe-shaped hydrocoel retains its primary position reflecting the evolutionary morphogenesis of the early stage of the development of the ambulacral system. To date, this view seems the most convincing, although there is no direct evidence for the maintenance of the primary position. More so, according to Bury, in other groups of extant echinoderms, the closure of the horseshoe-shaped hydrocoel occurs in other rays: in sea urchins and some holothuroids, in the AB interray; in ophiuroids and other holothuroids studied, in the BC interray; in starfish, in the DE interray. Presently, the knowledge of this problem which is important for the understanding of the historical morphogenesis of echinoderms, remains insufficient. However, it may be suggested that the position of the closure of the ambulacral ring is most likely retained in its primary position in crinoids, while in other echinoderms it was shifted due to different reasons. This problem is beyond the scope of the present study. In any case, it is important that there is only one place of closure of the ambulacral ring in all echinoderms studied. This, along with other embryological data, indicates that the ambulacral ring emerged from a single, left hydrocoel rather than was produced by the fusion of the left and right hydrocoels. From this point of view, the position of the hydropore in the crinoid larva to the left of the dorsoventral plane and the primary closure of the horseshoe-shape incipient ambulacral ring to the left of this plane, i.e., in the future interray CD of the adult radially symmetrical animal, is understandable. These features corresponds to the position of the left hydropore and morphogenesis of the left hydrocoel in the ancestors of the radially symmetrical echinoderms. This was the initial place of polymerization of the left hydrocoel with extending radial canals and this was the place where the growth of the hydrocoel was terminated after its closure. The polymerization and growth occurred around the esophagus, since the ambulacral radial canals and food grooves functionally and morphogenetically were a single unit. This first resulted in the horseshoe shape of the hydrocoel and later to its closure in the ambulacral ring. Therefore, the crinoid plane of symmetry of crinoids did not exist in their distant relatives lacking radial symmetry. Therefore, it is an innovation of the stalked echinoderms with a radial symmetry, although it marks the position of the left coelom and hydropore in these ancestors.

In contrast to the crinoid plane, the homocrinid plane partly corresponds to the dorsoventral plane of crinoid larvae and their ancestors lacking radial symmetry. In this respect, it is inherited. Morphogenetically, it corresponds to the shift of the mouth opening from the ventral side of the larva and of the hypothetical ancestor lacking radial symmetry to the posterior end of the body.

Three other planes of symmetry that occur sometimes in crinoids correspond to some distortions that occurred in the evolution of crinoids with well-developed pentaradiate symmetry. In most cases, their appearance is explained by the underdevelopment of some structures, resulting from the sequence of their emergence in ontogeny.

SECTION 2. ASYMMETRY IN THE STRUCTURE AND MORPHOGENESIS OF PELMATOZOAN ECHINODERMS

Asymmetry is defined as any departure from strict symmetry. Irregularities in bilateral symmetry are characteristic of the majority of free-living taxa (Zakharov, 1987). Echinoderms have a complex combination of metamerism and radial and bilateral symmetry. Each of these types of symmetry has characteristic irregularities, which can be combined with or causal of one another. This produces a large variety of symmetries in echinoderms. In the above section, an attempt was made to consider the symmetry of echinoderms as a result of the symmetry of morphogenetic processes. Below, the irregularities of this symmetry are discussed from the same point of view.

According to Zakharov (1987), the most widely accepted theory at present is the subdivision of all asymmetries into three major types, as suggested by Van Valen (1962). The first type includes cases when one structure is typically developed more strongly on one side than on the other. This is directed asymmetry. The second type is called antisymmetry. It is characterized by alternating stronger development of a structure on either side of the body. This corresponds with the negative connection between the sides. The third type is so-called fluctuating asymmetry. It results from the inability of organisms to develop in rigidly determined ways. In radially symmetrical echinoderms, these three type of asymmetry are morphologically developed differently compared to bilaterally symmetrical animals but are pronounced as strongly as in those (Guseva, 1968).

Directed asymmetry in echinoderms initially includes their primary left-sided aspect. Indeed, as was briefly mentioned above in the introduction to the chapter about symmetry, the structure of echinoderms is based on deep asymmetry. Primarily, this is seen in their ontogeny, i.e., in the predominant development of the left protocoel and mesocoel and the suppression of the right coeloms. This allows the assignment of echinoderms to the left-sided animals, particularly because the morphology of some other structures and the digestive system in the first place is determined by this primary left-sided arrangement. At the same time, some structures in echinoderms may have existed in right and left modifications. For instance, this includes the direction of coiling of ambulacra in Edrioasteroidea, which may be clockwise or counterclockwise, or the stems of pisocrinids, which may be left or right coiled. These manifestations of asymmetry may be referred to antisymmetry. Some manifestations of this antisymmetry may to some extent be determined by the primary left-sided arrangement of echinoderms, i.e., directed asymmetry, in other cases, the primary asymmetry of echinoderms did not affect antisymmetry. The fluctuating type of asymmetry seems more separated from the first two, both by its manifestation and the mechanism of development. The fluctuating asymmetry may, for instance, include small deviations of morphology and sculpture of the columnals from the radial symmetry. The above examples show that each of the three types of asymmetry is developed at a different ontogenetic stage, and, apparently, is of different importance in phylogeny. This is reflected by their differing taxonomic importance. The predominant development of left coeloms determines the organization of all echinoderms, and crinoids in particular. The development of the right and left forms of the basal circlet determines the structure of the taxa below or at the family level, whereas irregularities in the symmetry of sculpture in ossicles determine the structure of individuals. Therefore, the question is in which case and how much (if at all) the primary asymmetry of echinoderms affects the asymmetry of the lower levels. From this point of view, the right and left-sided structures, including directed asymmetry and antisymmetry, are discussed below. The manifestations of the fluctuating antisymmetry will be discussed separately, since they are considerably different from the above two types.

PRIMARY ASYMMETRY OF ECHINODERMS

All known echinoderms are typically left-sided animals. This is observed in the reduction of the right mesocoel (hydrocoel), the right pore of the protocoel, the right gonad, and the gonopore. Therefore, the pentaradiate symmetry characteristic of crinoids and most echinoderms does not cover the entire body, since it is superimposed onto a deep asymmetry, which is equally typical of echinoderms. In the ontogeny of modern echinoderms, this asymmetry is usually first observed in the development of the left protocoel and mesocoel. The asymmetric development of coeloms are also connected with other features, for instance, the growth of the incipient hydrocoel before it closes into the ambulacral ring clockwise and the clockwise twisting of the intestine.

The early stages in the development of coeloms, when all of them are paired, some abnormalities in their development and experiments to initiate the development of the right coeloms suggest that symmetrical, paired development was initial and characteristic for the ancestors of echinoderms. This conclusion is supported by comparison with *Cephalodiscus*, a distant relative of echinoderms. Two major questions arise when the problem of asymmetry in echinoderms is studied. First, why echinoderms have asymmetry and, second, why it is specifically left-sided asymmetry as opposed to right-sided.

Usually, the answers to these two questions are combined into one. Bather (1900) believed that the bilateral ancestor of echinoderms (dipleurula) was attached to the substrate by the right side of the anterior part of its body; hence, the atrophy of the right protocoel and mesocoel and development of other characteristic features of echinoderms. Jefferies (1986) gave a more complicated answer: a bilaterally symmetrical common ancestor of echinoderms and chordates with a body similar to modern *Cephalodiscus* rested its right side on the ground, thus giving rise led to the reduction of the right coeloms. Later, some of these animals became active swimmers and gave rise to chordates, while those passively lying on the bottom gave rise to echinoderms. The organization of both groups was based on differential development of the right and left coeloms, particularly on the reduction of the right protocoel and right mesocoel and the normal development of their left counterparts. Therefore, Jefferies (1979) combined chordates and echinoderms into a single monophyletic group, which he called Dexiothetica. This name emphasized the existence of an animal resting its right side on the bottom at early stages of the groups' development [the Greek *dexios* (right) and *theticos* (capable of lying)]. Based on this feature, Dexiothetica are opposed to Hemichordata within the Deuterostoma. In contrast, Holland (1988) tried to explain the primary left-sided asymmetry of echinoderms by the ability of the ancestors to recline on their left sides on the bottom. He suggested that the bilaterally symmetrical ancestor of echinoderms leaned the left side of its body on the bottom to collect food particles using its lower tentacles. As a result, the upper (formerly, right) tentacles disappeared and the right protocoel and mesocoel disappeared at the same time. The hypotheses of Bather, Jefferies, and Holland each in its own way explain how asymmetry could have developed in echinoderms, but

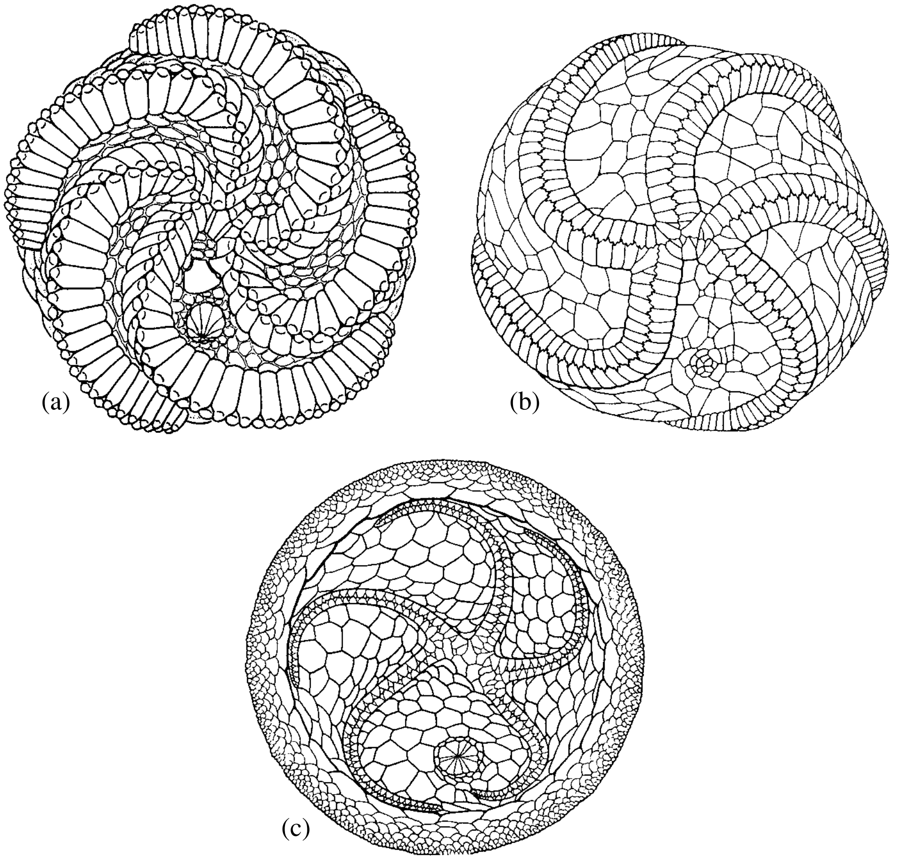


Fig. 62. Clockwise and counterclockwise curvature of the ambulacra in Edrioasteroidea: (a) *Strepaster* (all ambulacra are curved counterclockwise); (b) *Foerstediscus* (all ambulacra are curved clockwise); (c) *Isorophus* (four ambulacra are curved counterclockwise, while one ambulacrum (C) is curved clockwise (after Regnell, 1966).

they do not explain why they developed this particular asymmetry.

Indeed, they explain that the reduction of the right coeloms resulted from attaching (or reclining) the right side to (or on) the bottom. However, it is not clear why it was their right rather than leftside that the ancestors of echinoderms attached to or reclined on the bottom. And why not their ventral or dorsal sides? One possible explanation is that the predominance of right- or left-sided orientation existed in the ancestors of echinoderms long before they lay on the sea bottom. Another possible answer is that the ancestors of echinoderms were equally adapted to left- and right-sided arrangements and were lying on the ground either on the left or right side, but the left-sided forms became dominant for some reasons which are as yet unclear. If the first explanation is considered, all echinoderms should have the same type of asymmetry. In the second case, both right-sided and left-sided forms should occur among the ancient extinct echinoderms. All radially symmetrical echinoderms known to date appear to be left-sided, i.e., with well-developed left coeloms and an intestine twisted clockwise, but perhaps there are both primarily left-sided and right-sided forms among Edrioasteroidea, because many genera in this group have ambulacra curved to the right and to the left (Fig. 62). The left-coiled (counterclockwise) ambulacra are more common among Edrioasteroidea. For instance, they are characteristic of *Lebetodiscus, Lepidoconia, Streptaster, Ulrichidiscus*, and *Dinocystis*. The forms with right-coiled (clockwise) ambulacra occur more rarely. These are *Foerstediscus, Cooperidiscus*, and some species of *Edrioaster* (Regnell, 1988). Perhaps, in some cases right-coiled and left-coiled ambulacra indicate the primary clockwise and counterclockwise arrangement of echinoderms and is connected with the disappearance of right and left coeloms, respectively. However, this conclusion is contradictory to the fact that in many genera with predominant left-coiled ambulacra one (C) or, sometimes, two of them (B and C) are coiled rightward. In addition, in almost all known cases with both left- and right-coiled ambulacra, the hydropore always lies to the left of the plane of symmetry. This indicates that all Edrioasteroidea were apparently left-sided animals, while the variations in the coiling of the ambulacra just indicate the possible enantiomorphism in these structures, to varying extents independent from the primary left-sided arrangement of echinoderms.

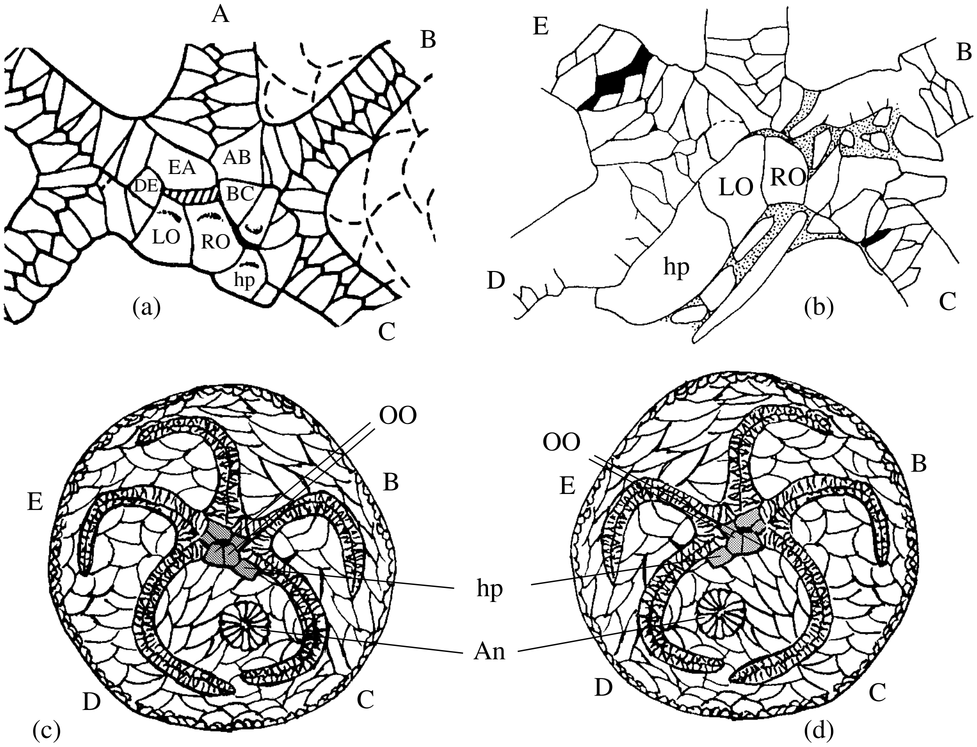


Fig. 63. Typical and mirror forms of the edrioasteroid *Krama devonica* (Bassler): (a) oral zone of the theca of a typical specimen from the Devonian of North America (after Bell, 1976); (b) oral zone of the theca of the mirror specimen from the Devonian of Spain (after Smith and Arbizu, 1987); (c, d) scheme showing the structure of the typical (left-sided) individual and mirror (right-sided) individual (after data from Bell, 1976 and Smith and Arbizu, 1987). (An) anus, (hp) hydropore plate, (o) oral, (LO) left oral in the CD interray, (RO) right oral in the CD interray.

This conclusion is supported by a single known case of a complete mirror image of a normally left-sided edrioasteroid species *Krama devonica.* The specimen was described by Smith and Arbizu (1987) from the Lower Devonian of Spain (Fig. 63). Previously, this species was known only from the Middle Devonian of North America (Bell, 1976). A single occurrence outside North America (in the Lower Devonian of Spain) was discovered to be a complete mirror image of the North American representatives. The plate with the hydropore and the opening of the hydropore in the Spanish specimen was on the left of the plane of symmetry A-CD rather than on the right as in the North American specimens and in all other known Edrioasteroidea. In addition, the ambulacrum A in the Spanish specimen is coiled clockwise, whereas in the North American specimens, it is coiled counterclockwise. The coiling of other ambulacra remained the same, to the side closest to the anal interray: B and C, clockwise; D and E, counterclockwise. Based on the mirror-image structure of the Spanish specimen (compared to the more common specimens from North America), Smith and Arbizu (1987) suggested that their specimen represented a condition in which the larval stage experienced a *situs inversus* (the larva developed right protocoel and right mesocoel instead of their left counterparts) This phenomenon is known in modern echinoderms and is described by Onshima (1921, 1922) and Ludwig (1932). *Situs inversus* is also described in carpozoan echinoderms, i.e., Ubaghs (1967) described a mirror-image specimens of the mitrate cornute *Peltocystis cornuta* from the lower Ordovician of France (Fig. 64).

Could the occurrences of right-sided echinoderms be connected with the existence of primary enantiomorphs, which appeared at the beginning of the evolution of echinoderms? A direct connection seems unlikely

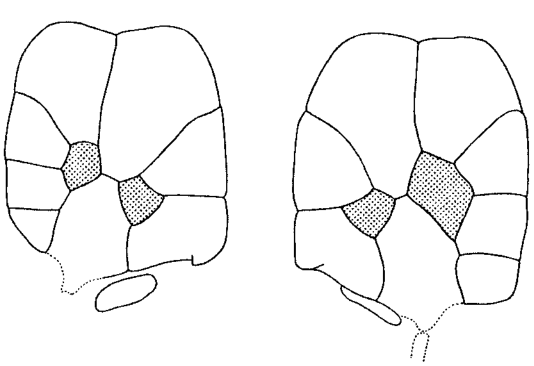


Fig. 64. Left (typical) and right (rare) forms of the mitrate *Peltocystis cornuta* Thoral from the Lower Ordovician of France (after Ubaghs, 1967).

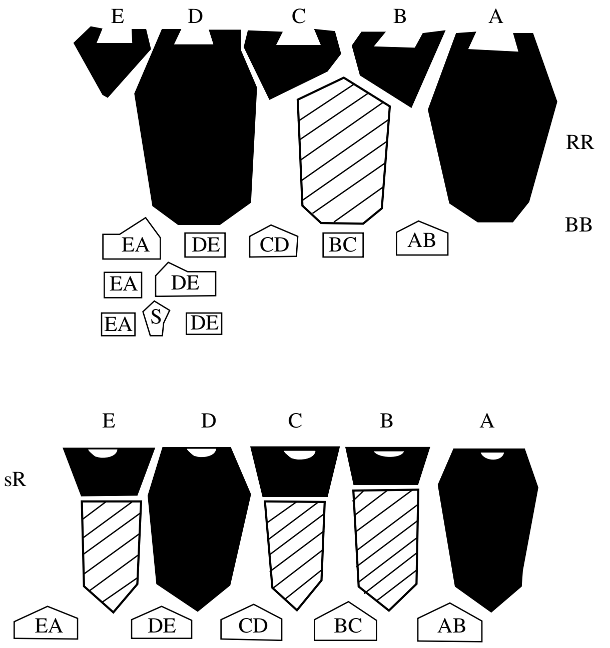


Fig. 65. Change in the composition and arrangement of plates of the cup in the course of the transition from homocrinids to pisocrinids. Radials and superradials are black. Inferradials are diagonally hatched, basals are white. 'S' indicates the sixth plate of the basal circlet, usually fused with one of the plates (DE or EA), but sometimes occurring separately.

because it is difficult to believe that, for example, the right-sided aberrations of modern sea urchins could indicate the existence of the parallel evolution of right- and left-sided forms from the emergence of the echinoderms to the present day. It seems more likely that all of the described right-sided echinoderms represent "mutations" leading to the morphologically mirror-image development. The mechanism of such mutations is poorly studied, although it apparently exists.

However, Shishkin (1988), based on the appearance of mirror variations in gastropods, disagreed with the possibility of a special mechanism leading to the appearance of mirror-image specimens. He suggested that the left- and right-handed turbospiral gastropod shells appeared as a result of originally slight deviations of the apertures of the planispiral shell from the plane of symmetry and a progressive shift of this process to earlier stages of the ontogeny. The adaptive significance of right- and left-handed deviations was different in the evolution of different phyla; hence, the frequency of one of the forms at a particular evolutionary stage of a phylum could be very low. Periodically, the adaptive roles of the two types of coiling changed, and, accordingly, the frequency of their occurrence varied against the background of the continuous parallel evolution.

In the case of enantiomorphism in echinoderms, similar processes seem very unlikely, because the parallel evolution of right-sided and left-sided forms is not reflected in the fossil record. The right-sided forms appear as rare abnormalities. Therefore, there should have been a sort of "mutation," which caused the predominant development of the right coeloms instead of their left counterparts, which would have had the same morphogenetic potential. Such forms are not uncommon among echinoderm larvae. In contrast, the adult forms with such an arrangement are extremely rare, a fact that suggest the low viability of such mutants. Nevertheless, the presence of adult mirror-image echinoderms suggests the possibility of enantiomorphism-connected rapid evolutionary transformations caused by sudden profound ontogenetic innovations. A similar mechanism is also possible in gastropods irrespective of their original mechanism of shell coiling. The ancestral planispiral shells could be originally inconspicuously right-handed or left-handed, which would determine the direction of coiling in turbospiral shells.

THE INFLUENCE OF THE ORIGINAL LEFT-SIDED ARRANGEMENT OF ECHINODERMS ON THE APPEARANCE OF RIGHT- AND LEFT-SIDED FORMS IN SOME STRUCTURES IN ECHINODERMS

The structures that may be expressed both in right- and left forms but are not connected with the above-discussed primary asymmetry occur in the organization of many echinoderm groups. However, the most clear case was observed in the basal circlet of pisocrinids (a small family of disparid inadunates) (Rozhnov, 1981).

The family Pisocrinidae Angelin, 1878 together with two others, Cicerocrinidae Jaekel, 1918 and Quiniocrinidae Rozhnov, 1981, are united in the superfamily Pisocrinacea widely occurring in the Silurian–Devonian of Europe, Asia, and Australia and in the Silurian of North America. It includes seven genera of two subfamilies and has the following characteristic features: the calyx is small or medium-sized, from conical to spherical, with a deepened or nondeepened stem facet composed of five, four (rarely), or three basals, two simple large radials (A and D), two superradials (B and C) supported by a single inferradial occupying two rays, B and C, and one small radial (E); in addition, some accessory radials may be present (Rozhnov, 1981).

Below, the structure of the calyx in the genus *Pisocrinus* de Koninck, represented by three subgenera, is considered (Fig. 65). This genus has five basals extending outside the stem facet, three large radials contacting the basal circlet, two of which (A and D) have facets for arm attachment, while one supports two symmetrically positioned superradials (B and C). Another small radial with a facet for arm attachment occurs in the E ray (Figs. 1c–1f, 65). Hence, all the plates are arranged within the homocrinid plane of symmetry. However, some small details slightly distort this bilateral symmetry. For instance, the distal process CD of the calyx from which the anal tube extends is slightly wider than others and is often shaped differently. The position of the suture between the plates in the distal extensions of

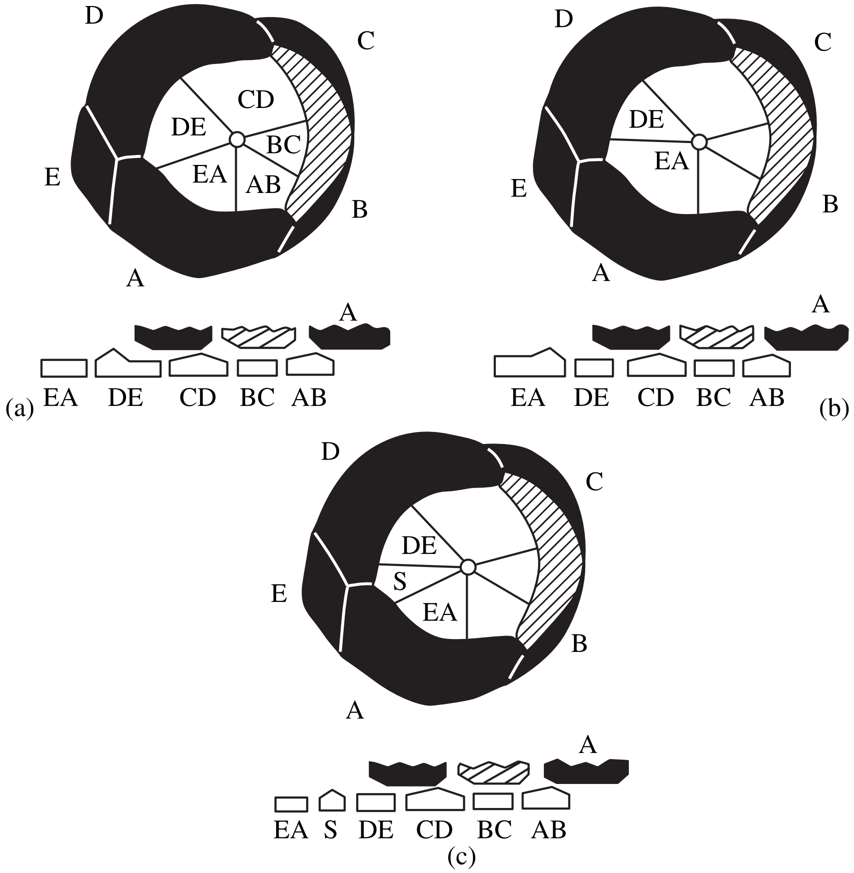


Fig. 66. Basal circlets in the genus *Pisocrinus*: (a) left, (b) right, and (c) symmetrical. Designations as in Fig. 65.

the calyx also slightly distorts the symmetry (the distal extensions of the calyx separate the articular facets in the neighboring rays). However, the structure of the basal circlet is of primary importance.

Pisocrinus have five basals differing in shape and size. Three of them taper off distally to stick along the sutures between the large radials (Fig. 65). These distally tapering portions of basals aid the rigidity of the contact between the basal and radial circlets. Because only three overlying radials contact the basal circlet, and there are only three sutures between the radials at the place of the contact, only three tapering portions of basals can occur in the basal circlet. Therefore, the five basals consists of three distally tapering basals and two basals with an even margin. The study of a large body of material, which includes different species, showed that the AB and CD basals are almost always tapering, whereas the BC basal invariably has an even margin. The two other basals have an alternating structure, either one or the other is tapering. When the DE basal is tapering, its extension occurs on its left (looking from the outside) margin, which slightly extends beyond the homocrinid plane. The neighboring EA basal is not tapering, and its right end terminates slightly before the homocrinid plane. In the alternative case, the EA basal is tapering, while the DE basal has an even distal margin without tapering. One of these types of basal circlet may be called right-sided, while another is left-sided because the structures that make them different are symmetrical in relation to the homocrinid plane of symmetry (Fig. 66). The circlet, in which the tapering occurs on the right side of the corresponding plate may be called right-sided, i.e., this is the case when the EA basal is tapering, and the neighboring DE basal has an even distal margin and is slightly narrower. The left basal circlet has an alternative arrangement. In this case, the DE basal is tapering (the tapering portion occurs on its left side), whereas the EA basal has an even distal margin and is narrower. This reference to the circlets is maintained when another, less formal approach is used. Because in the ontogeny of disparids the vestibulum defining the position of the future mouth was most likely shifted within the homocrinid E-BC plane, or this shift at least occurred in the neighboring crinoid plane (A-CD), the intersection of the homocrinid plane with the basal circlet has anterior and posterior ends. The incipient mouth opening was on or near the anterior end. In this case, this is the BC interray. If this orientation is accepted, to the right would be the circlet in which the structure is developed more strongly to the right of the homocrinid plane, i.e., when the EA basal is tapering, while DE has an even distal margin. The left basal circlet will have a tapering basal DE occurring to the left

Table 4. Frequencies of the left and right modifications of the basal circlet in *Pisocrinus*

Species	Left modifications		Right modifications	
	number of specimens	% of the total number of specimens	number of specimens	% of the total number of specimens
P. (Pisocrinus) pilula de Kon.	34	77	10	23
P. (P)trialobus R. et M.	3	100	0	0
P. (Pocillocrinus) ubaghsi Bouška	4	10	36	90
P. (Poc.) bogdani Yelt.	1	10	9	90
P. (Poc.) concinnus Rozhnov	2	30	5	70
P. (Poc.) rubeli R. et M.	24	100	0	0
P. (Granulosocrinus) globosus (Ring.)	5	85	1	15
P. (G.) gorbyi Mil.	5	100	0	0
P. (G.) jefferiesi Rozhnov	8	80	2	20
P. (G.) gemniformis Mil.	3	100	0	0
P. (G.) kurdektyrensis Rozhnov	6	75	2	25
P. (G.) lanceatus R. et M.	10	100	0	0
P. (G.) yeltyshevae Rozhnov	12	80	3	20
P. (G.) kosovensis Bouška	6	77	3	33

of the homocrinid plane with the EA basal occurring to the right of this plane. This terminology, although opposite to the formal terminology previously accepted for pisocrinids (Arendt and Rozhnov, 1979; Rozhnov *et al.*, 1989), seems more correct because it corresponds to the orientation of the axes of crinoids and their changes throughout the ontogeny.

Each specimen studied of any *Pisocrinus* species normally had either a right or left circlet in the case of the normal development of the radial circlet. However, in one case, in *Pisocrinus (Granulosocrinus) yeltyshevae* Rozhnov from the Lower Silurian of Podolia, the basal circlet was neither right nor left. It was perfectly symmetrical relative to the homocrinid plane of symmetry. The distal tapering, normally occurring either on the DE or on the EA basals, in this specimen occurred in a separate symmetrical sixth basal separating the symmetrical DE and EA basals, which were identical in shape and size and had an even, distal margin (Fig. 66c).

In the genus *Parapisocrinus*, the basal circlet also occurs in the right and left modifications, although it is not developed outside the stem facet. Similar to the genus *Pisocrinus*, the basal circlet has two basals with an even distal margin and three tapering basals wedging in along the sutures between the radials. The right and left circlets correspond completely to those in the genus *Pisocrinus*. Since the basal circlet in *Parapisocrinus* is difficult to observe without special polishing, the frequencies of the right-sided and left-sided modifications was not possible to estimate precisely. These frequencies for the *Pisocrinus* species under study are shown in Table 4.

The appearance of the right and left modifications of the basal circlet is connected to the transformations of the radial circlet during the transition from Homocrinacea to Pisocrinacea. The evolution of Pisocrinacea from Homocrinacea is unanimously accepted by all researchers studying this subject and is supported by the similar organization in these two superfamilies, some shared morphological characteristics, similar skeletal ontogeny, and successive stratigraphic ranges (Bather, 1900; Ausich, 1977; Moore *et al.*, 1978; Rozhnov, 1981; Sevastopulo and Lane, 1988). Therefore, it is certain that the pentamerous basal circlet of the earliest pisocrinids composed of basals of different size and shape evolved from the basal circlet of homocrinid composed of five identical basals.

In homocrinids, the five identical basals contacted five radials identical in the proximal part. The comparison of the skeletal morphology of the homocrinid and pisocrinid calyxes and a study of the aberrant forms (Fig. 67) showed that during the transition from the homocrinid to pisocrinid type of the calyx the C inferradial atrophied, while the B inferradial grew extensively (Fig. 65). This caused the appearance of the unpaired inferradial characteristic of pisocrinids, which occupies two rays (B and C). In addition, the E inferradial is atrophied, although it is possible that at first the E inferradial and E superradial were fused in a single plate, which was later reduced to the size of the superradial (Rozhnov, 1981). These morphological transformations are supported by the ontogenetic development of the skeleton in homocrinids and pisocrinids (Sevastopulo and Lane, 1988). As a result, five basals came into contact with three radials. This necessitated changes in the basal circlet. Although the basal circlet in crinoids appears before the radial and simultaneously to the oral circlet, the final adjustment of the circlets occurs later in ontogeny, when the calyx is more completely formed. It is apparently at this moment that the first adjustments of the size of the basals and the development of the tapering portions of basals wedging in between the radials occurred. As a result of this process, the BC basal became completely overlain five basals by the newly formed and overgrown lower redial B, which occupied two rays. Because the suture between the radials in which the tapering point of the BC basal was wedged disappeared, the tapering portion also disappeared, and the basal acquired an even distal margin. Two sutures between the radials in pisocrinids remained in the same places relative to the basal circlet as in the ancestral homocrinids. Therefore, the corresponding AB and CD basals in pisocrinids remained pointed. After the E inferradial had disappeared in the evolution of homocrinids toward pisocrinids, of the two sutures between the E radial and neighboring A and D radials, a single suture between the A and D radials persisted. Of the two tapering AE and DE basals, only one of them, C, could remain tapered. Morphogenetically, they all apparently had equal chances of becoming tapered; therefore, there should have ideally been an equal number of individuals with either plate tapering, i.e., with right and left circlets. This conclusion is supported by the fact that occasionally the region with a tapering end develops into a separate symmetrical sixth basal, while both above-mentioned basals retain an even margin. In the majority of species, however, the left modifications prevail (Table 4), except for three species in the subgenus *Pocillocrinus* in which right modifications strongly prevail. How can we explain the predominance of left modifications (in most cases) or right modifications (only in some species of a single subgenus) instead of the expected theoretically even distribution?

As mentioned above, crinoids, similar to most echinoderms, have a deep internal asymmetry, i.e., the reduction of the right protocoel and mesocoel and extensive growth of the left coeloms. This primary asymmetry has resulted in asymmetry of some subsequent morphogenetic processes, thus causing them to proceed from left to right (or clockwise). For instance, the growth of the incipient ambulacral ring and digestive system occurs in this way. In the skeletal morphogenesis this asymmetry is manifested by the direction of branching of new ambulacral grooves in the eocrinoid *Paracryptocrinites* (Fig. 68) and, sometimes, in relative displacement of circlets of the calyx in the ontogeny of some crinoids from interrays to rays (Arendt, 1970). Rozhnov (1994) described a clockwise displacement of plates in eocrinoids.

A small time lag betweeb the displacement of radials and the development of tapering zones in the basals could determine the predominance of right or left forms of the basal circlet. A real displacement of plates of the

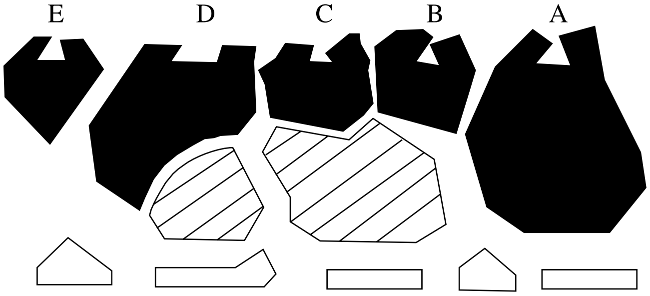


Fig. 67. Plates in the aberrant form of *Pisocrinus (Granulosocrinus) yeltyshevae* Rozhnov from the Silurian of Podolia. The presence of two inferradials indicates that pisocrinids evolved from homocrinids.

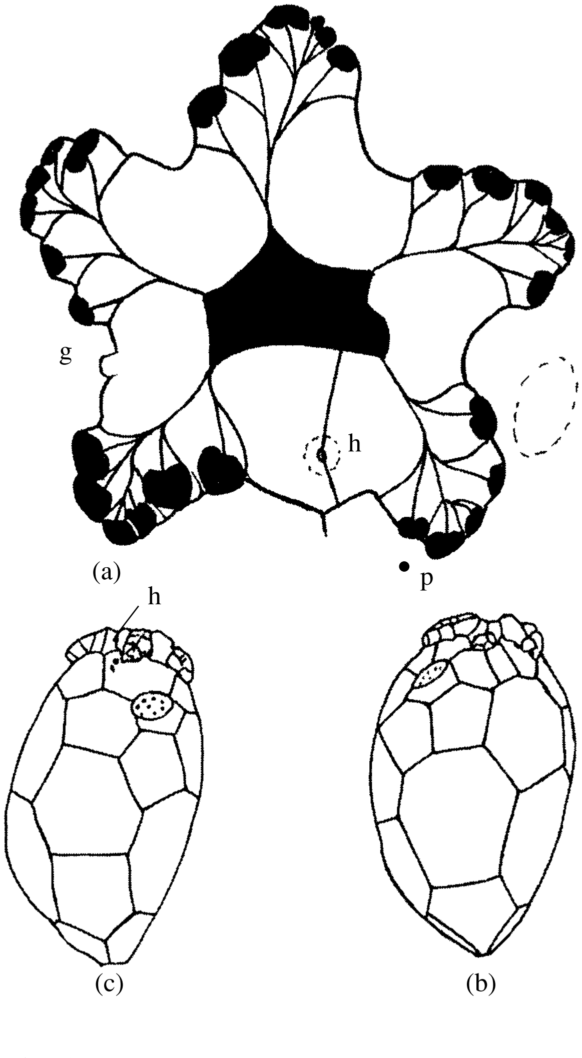


Fig. 68. Arrangement of articular facets in *Paracryptocrinites* Rozhnov et Fedorov. (a) Oral area, (b–c) lateral view of the theca: (a) AB interray, (b) C ray. Oral orifice and brachiolar facets are black. The position of the anus is shown by the dashed line. (h) Hydropore, (g) gonopore, (p) pore of the unusual function.

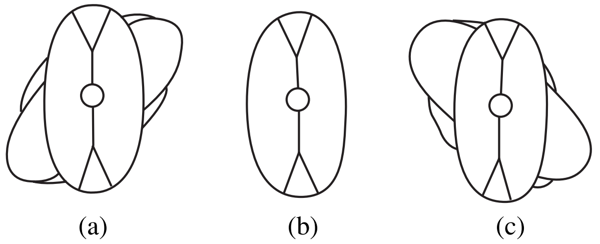


Fig. 69. Left-sided, symmetrical, and right-sided columnals of platycrinids (Crinoidea) from the Middle Carboniferous of the Moscow Basin (coll. by A.A. Erlanger).

radial circlet relative to the basals in the skeletal ontogeny is apparently indicated by the rare aberrant forms of circlets in which the basals in adults are displaced relative to the radials compared to the usual structure of the calyx. Therefore, the primary asymmetry of echinoderms (the primary left-sided arrangement) could to some extent influence the results of the later choice between the left-sided and right-sided arrangement of structures. Another possible reason for the slight displacement of radials could be connected with the sequence of their appearance in ontogeny. The radial A in crinoids is always the last to develop, whereas D generally appears noticeably earlier. A reduction or increase in the time lag between the development of the A and D radials and the resultane difference in their sizes could facilitate the appearance of tapering zones either in the DE or EA basals. In this case, the primary asymmetry of crinoids acted indirectly, because it earlier affected the development of pentamery from trimery, thus influencing the sequence of the appearance of pentameres. The delay in the displacement of the radials or the degree of differences in their growth and associated appearance of the left-sided and right-sided circlets could be determined by external conditions, e.g., small fluctuations in the water temperature. Some other so-called rendom factors could also affect this process. Hence, it is possible that in some species the left-sided arrangement could be fixed genetically.

Among crinoids, there are cases of right- and left-sided arrangement when the primary asymmetry of echinoderms did not in any way affect the distribution of the right and left modifications. For instance, it is known that the columnals of platycrinitids in the Middle Carboniferous of the Moscow Region occur in the left, right, and bilaterally symmetrical (neutral) modifications (Fig. 69). This indicates that these representatives had stems twisted both to the right and to the left. Many columnals (several hundreds) from the Novlinskaya Series of the Myachkovian (Middle Carboniferous) collected by A.A. Erlanger in a small quarry near the Domodedovo railroad station (Moscow Region) showed that the right and left columnals occur in approximately equal numbers. The sample studied apparently represents a single population, in which the number of individuals with the stem twisted to the left and to the right was the same. Hence, the primary asymmetry of echinoderms did not affect in any way the frequencies of the right and left forms.

At the same time, the stems of crinoids could be only twisted to the left. For instance, the skeletons of the Ordovician hemistreptocrinids are always twisted to the left (Fig. 70). Arendt (1976) believed that the skeleton of hemistreptocrinids is a theca of a separate echinoderm group and, based on this assumption, considered this group to be a separate class. However, I believe (Arendt and Rozhnov, 1995) that these are the remains of the stems of crinoids. In this case, it is unclear whether or not the primary left-sided arrangement of echinoderms affected the direction of twisting, or the direction was influenced by other factors.

A pentamerous basal circlet in pisocrinids was evolutionarily unstable and repeatedly gave rise to a trimerous circlet, observed in the genera *Triacrinus, Trichocrinus*, and *Regnellicrinus* and the entire family Calycanthocrinidae. A species of the genus *Parapisocrinus* (*P. malobatschatensis*) with four basals is known from the Lower Devonian of the Kuznetsk Basin. The pentamerous circlet of *Pisocrinus* finally evolved in the basal circlet consisting of three identical basals alternating, in a brick-wall pattern, with three overlying radials. The appearance of such a trimerous circlet apparently improved the construction of the calyx, made it more simple, and increased its rigidity due to fewer sutures. However, apart from this perfect arrangement, we know other types of plate arrangement in the trimerous circlet (Fig. 71). Therefore, it is interesting to find out how the primary arrangement of the pentamerous basal circlet (right or left) influenced the structure of the trimerous circlet that evolved from it.

There are differing opinions on the transition from the five to three basals in Pisocrinacea. Bather (1893) believed that basals CD and DE and basals BC and AB were fused, whereas Bouška (1956) believed that two of five original plates atrophied.

In this case, whether or not the basals were fused, or one basal grew over and took the place of the neighboring basal, is not important. Indeed, there is no difference between the situation where one basal atrophies and the neighboring basal grows over and occupies its place and the situation when two neighboring basals are joined together. The result would be exactly the same, as in both cases a larger basal takes the place of two. We can only invoke atrophy when a gradual reduction of a basal is observed in ontogeny or phylogeny, leading to its complete disappearance. If there is no gradual transition between the initial and final states in the case of the joined basals, i.e., neither of them is reduced and grows over, we should classify it as a fusion of the basals. Assuming that this is the case, the basals became fused during the transition to *Triacrinus* and *Trichocrinus* from *Pisocrinus* (Rozhnov, 1981). It is not clear which process took place during the evolution of other genera. However, as mentioned above, this has no

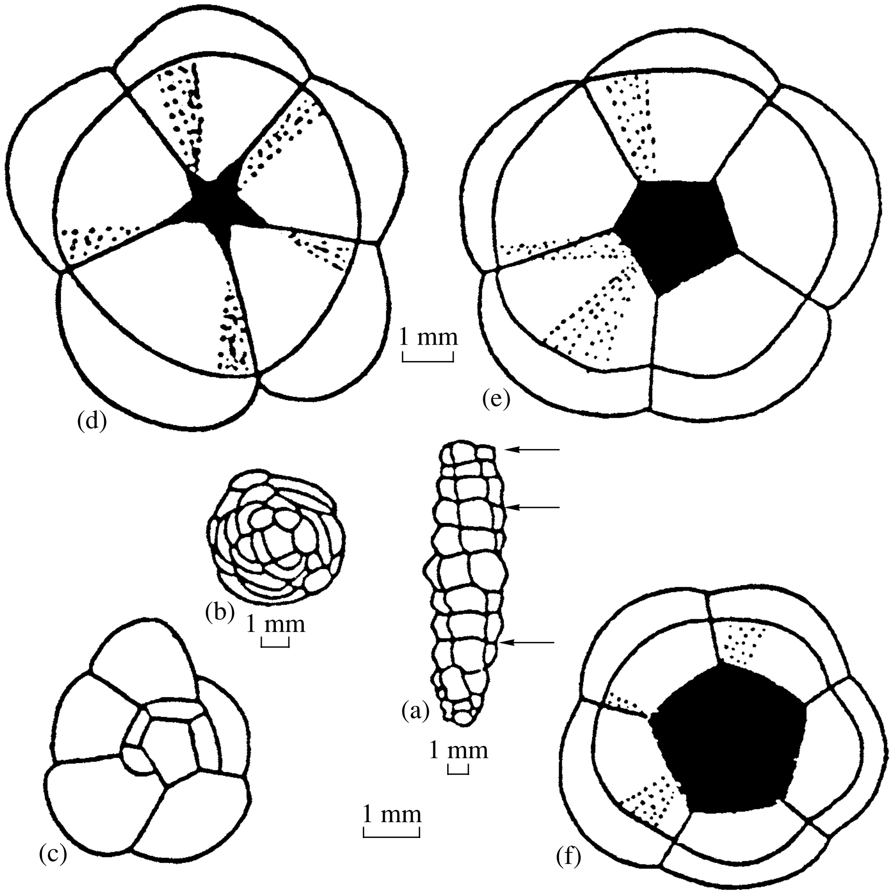


Fig. 70. Solar twisting of the stem of *Hemistreptocrinus babinensis* (Crinoidea?) Arendt et Rozhnov from the lower part of the Middle Ordovician (Upper Arenig, Volkhovian): (a) general lateral view; (b) bottom view; (c) distal end; (d–f) serial cross sections, from top to bottom. Arrows indicate the levels of the cross sections.

importance for the pattern of the final arrangement and, therefore, this process will be referred to below as fusion.

Theoretically, the trimerous basal circlet could evolve from the pentamerous circlet through any combination of fusing of the basals and from any type of original circlet, left or right. Assuming the condition of paired fusion of four basals, there are five possible transitions from five basals to three. However, because the original circlet could be either right or left, there are altogether eight possibilities (since two ways are the same in either type of a circlet). If a tapering portion of the EA or DE plate, which can also exist as a separate sixth basal, is designated as S (from Latin *sextus* [sixth]), and the fused plates are indicated by "+", then the eight means of transition will be as follows:

1. AB+BC; CD+(DE+S); EA
2. AB+BC; CD+DE; (S+EA)
3. AB+BC; CD; (DE+S+EA)
4. AB; BC+CD; (DE+S+EA)
5. EA+AB; BC+CD; (DE+S)
6. (S+EA)+AB; BC+CD; DE
7. EA+AB; BC; CD+(DE+S)
8. (S+EA)+AB; BC; CD+DE

Only one of these patterns, the fourth, results in the typical and the strongest connections of basals to radials, which interlock as in a brick wall. To achieve a similar connection using the third and fifth patterns, the following 60° turn of the radials relative to the basals and a considerable change in their shape would be necessary. The remaining five patterns could not produce an alternating construction without further reshaping of the basals. Judging from the arrangement of the tapering portions of the basals and the shape and relative size of the basals, only five patterns (first to fourth and sixth) are known in nature, the fourth pattern being the most common. Therefore, sometimes the shape and arrangement of the basals in the trimerous circlet of Pisocrinacea was determined by the left or right arrangement of the original pentamerous circlet, but it is impossible to determine which of the two enantiomorphous circlets was the original in the case of the most characteristic and common type of trimerous circlet.

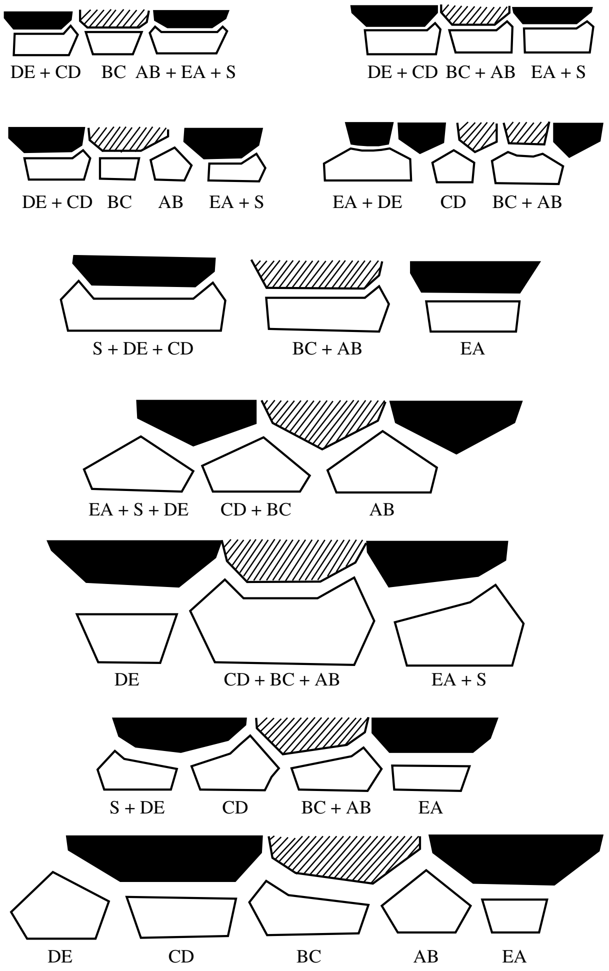


Fig. 71. Types of basal circlets composed of three and four plates in Pisocrinacea: (a, b) *Trichocrinus crepidatus* Rozhnov, Upper Silurian of the Czech Republic; (c) *Jaekelicrinus* sp.; Upper Devonian of Bashortostan; (d) *Jaekelicrinus jakovlevi* Rozhnov; both Upper Devonian of Baskkortostan; (e) *Quiniocrinus erectus* Schmidt, Middle Devonian of Germany; (f–i) *Triacrinus depressus* (J. Müller), Middle Devonian of Germany. Radials are black, the inferradial is diagonally hatched, basals are white. "S" indicates the sixth plate of the basal circlet, usually fused with one plate (DE or EA) (after Rozhnov, 1981).

Various shapes of the basals in the pentamerous basal circlet of pisocrinids and its existence in the left and right states provided a diversity of shapes in the trimerous circlet, which developed by a paired fusion of the basals. These eight possible shapes of circlet composed of three plates may be called isomers, using the terminology of stereochemistry. These shapes also include enantiomorphous pairs. However, they are not very common; a trimerous symmetrical basal circlet became dominant because of its considerable constructive advantage. The remaining types of trimerous circlets occur as more or less rare aberrations (Fig. 71).

It is also possible that three neighboring basals could join together in one. In this case, there are 16 theoretically possible patterns of reconstruction. However small the probability of these additional patterns may be, they could occur in nature. An example is one of the calyxes of *Triacrinus depressus* in which a basal occurring below the inferradial could be produced by the fusion of three basals. Therefore, a deep asymmetry which, at the beginning of echinoderm evolution was manifested by the predominant development of the left protocoel and mesocoel, at first rigidly determined the character of the newly appearing structures including a clockwise coil of the intestine, growth of the ambulacral ring, and associated direction of branching of the new ambulacral grooves, e.g., in *Cryptocrinites*. However, its influence on the right or left arrangement of smaller structures was more indirect and not always resolute. This is observed, for instance, in the basal circlet of pisocrinids. Sometimes, this influence was apparently completely absent; for instance, in the case of the direction of the twist in the stems of platycrinids from the Carboniferous of the Moscow Region. Structures, which were less determined by the effect of the primary asymmetry, widely contain parts of the original structure, which led to the existence of "isomers" and new enantiomorphous pairs among them. Among the "isomers," one shape is normally increasingly dominant, while others occur as more or less rare aberrations (e.g., in the trimerous circlet of Pisocrinacea). A predominance of one shape in this case is associated with its well pronounced constructive advantage. When there is no such clear advantage, several "isomers" may exist in more or less equal proportions. This is observed, for instance, in the trimerous infrabasal circlet of some Permian cladid inadunates of the family Hypocrinidae (Arendt, 1970; Arendt and Rozhnov, 1979).

FLUCTUATING ASYMMETRY

The fluctuating asymmetry is produced by small random changes in the process of development that are characteristic of every process of morphogenesis. Astaurov (1930, 1974) was the first to notice an independent manifestation of structures in the right and left sides of bilaterally symmetrical animals. He connected a different development of structures on the right and on the left with random fluctuations in ontogeny rather that with genetic predetermination or the influence of the environment. This effect was later named "the background noise of individual development". Since these changes can occur in the course of any process of morphogenesis, they can be observed not only in the case of bilateral symmetry but also in the case of any other type of symmetry, e.g., metamerism and radial symmetry. In the case of metamerism, each subsequent metamere may differ from the preceding metameres in some minor characteristics, which have no particular functional significance and may be a product of random disturbances. Pentameres in any pentaradiate structure of echinoderms develop a particular sequence. Small dis-

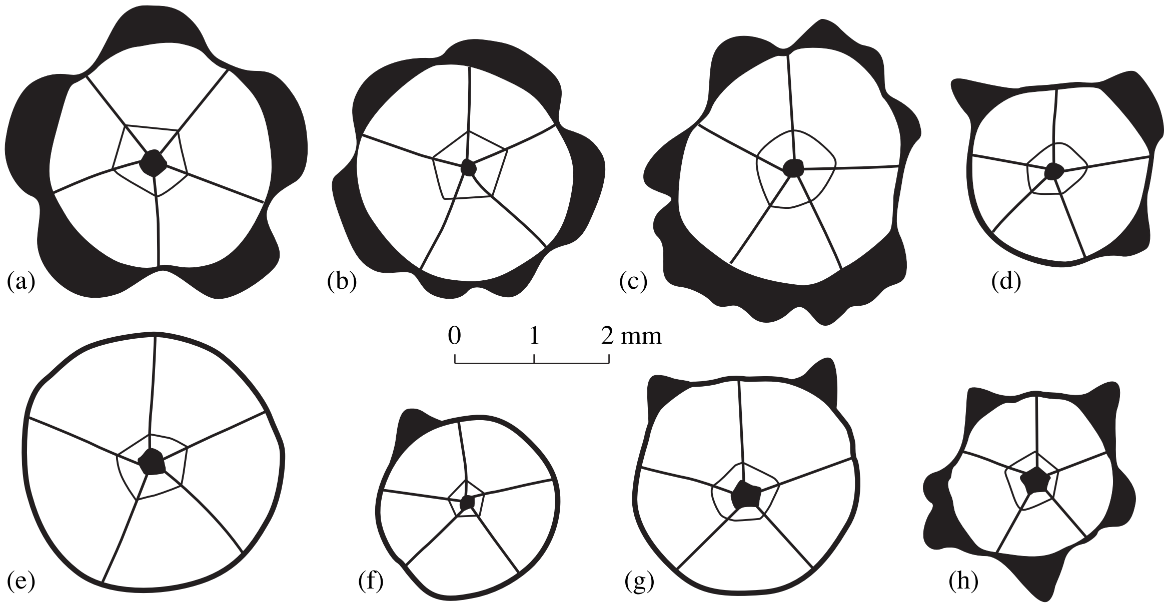


Fig. 72. Fluctuating variability of the columnals of *Pentagonocylicus monile* (Eichwald) from the Lower Ordovician of the Leningrad Region. (a) Symmetrical columnal with five lobes, specimen PIN, no. 4125/184; (b) columnal with four usual lobes and one double lobe, specimen PIN, no. 4125/174; (c) columnal with asymmetrical, partly fused lobes, specimen, PIN, no. 4125/186; (d) columnal with outgrowths in three pentameres, specimen PIN, no. 4125/185; (e) columnal without outgrowths, specimen, PIN, no. 4125/171; (f) columnal with a spinelike outgrowth in one pentamere, specimen PIN, no. 4125/191; (g) columnal with spinelike outgrowths in two pentameres, specimen PIN, no. 4125/187; (h) columnal with one spinelike outgrowths one in each of four pentameres, and with two outgrowths in the fifth pentamere, specimen, PIN, no. 4125/189. The suture between the pentameres is shown by the dashed line, the outgrowths are delineated from the main body of the columnal by the thin line.

turbances in the development of a metamere may cause asymmetry. This phenomenon is particularly noticeable in the morphology of ossicles of some crinoids. A structure of ossicles in the early Ordovician crinoid *Pentagonocyclus monile* (Eichwald, 1860) is a good example of such a phenomenon. Numerous ossicles belonging to this species are widespread in the Latorp and Volkhovian (Arenig) of the Leningrad region and Estonia. A calyx with a fragment of stem composed of these columnals has been assigned to a new genus placed in the family Iocrinidae (disparid inadunate). Each columnal is divided into five antimers. A columnal usually has “decorations” along its equator, which apparently have very little functional significance and can be regarded as “useless.” These decorations can be very different and are usually represented by spines, denticles, lobes, and entire or fringed bands. Usually, the columnals are completely radially symmetrical. However, often there is a difference in ornamentation of the antimers, e.g., a spine occurs only in one antimer, or in two or three, while in the others, any ornamentation may be absent, or an entire band is present in three antimers, while the others have lobes or denticles (Fig. 72). Thus, there is an array of diverse combinations of “decorations” of different pentamers. At least half of these irregularities may be connected with fluctuating asymmetry. In addition, columnals with small deviations from the typical ornamentation may occur. This can also be referred to as a fluctuating asymmetry, but at another morphogenetic level.

SECTION 3. THE MORPHOGENETIC BASIS FOR THE DISTORTION OF THE THECA AND STEM IN PELMATOZOAN ECHINODERMS

Echinoderms exhibit a great diversity of symmetries in their body structure. For instance, many of them have five-part symmetry accompanied by three-part symmetry, with different planes of symmetry dominating. Some parts of the body and, occasionally, the entire body show metamerism. Nevertheless, these manifestations of symmetry are always associated with a deep asymmetry in the position of coeloms and with a spiral symmetry of the digestive system. Various types of symmetry are usually explained as optimization of the construction in the process of adaptation to the environment. This is an interesting approach, but it cannot give an unambiguous answer, because there are various ways of adapting to the same environment.

Another approach primarily uses a morphogenetic basis for symmetry, i.e., a manifestation of symmetry in a structure is considered as a consequence of the symmetry of morphogenetic processes. This approach is used in the analysis of symmetry of echinoderms in the present paper, in particular for explaining various cases of distortion of the theca and the stem in pelmatozoan echinoderms. This approach requires a reconstruction of at least a few ontogenetic features in fossil echinoderms. Such a reconstruction should be based on (1) data on the ontogeny of extant taxa; (2) existing data

Fig. 73. Theca positioned at an angle to the stem in the "living fossil," Recent cyrtocrinid crinoid *Gymnocrinus recheri* Bourseau *et al.* The specimen was presented to the Paleontological Institute of the Russian Academy of Sciences by Dr. Ameziane-Cominardi.

on the ontogeny of fossil taxa; and (3) analysis of aberrant forms.

The problem is to what extent can data on extant taxa be used in studying fossil representatives? For instance, which features of the ontogeny of modern crinoids (known only in several genera) can be assumed to have existed in their Ordovician ancestors? The ontogeny of an organism changes continually and could completely change over 500 million years. Furthermore, the ontogeny of organisms is strikingly equifinal, i.e., deviations throughout the ontogeny are finally compensated and the final structure remains the same. This dictates a very careful approach to the use of our knowledge of the ontogeny of extant taxa, when analyzing fossils. However, when the fossil taxa of a group are compared with the extant taxa, it is suggested that both had a similar archetype shared by all representatives of the group. Hence, the existence of a morphological archetype suggests that there is an "archetype" of morphogenesis responsible for the homologies of the adult organism. The search for the "archetype" of morphogenesis demands the use of a principle of "dynamic stability" instead of tracking examples of accurate correspondence of specific structural elements to the those in the ancestral structure. This principle explains homologies and the existence of the morphological archetype from the point of view of developmental mechanics and the hierarchy of the developmental processes in particular (Vorobyeva and Hinchliff, 1991). Using this approach, morphogenetic processes may be separated into general processes, which define the entire body plan and restrict the possibilities of its morphological transformations and secondary processes, which are superimposed onto the primary processes and which are responsible for the details of the structure against the background of the general body plan. Thus, when data on the ontogeny of extant taxa are used for morphogenetic reconstructions in fossils one should attempt to reveal hierarchies of morphogenetic processes and their interactions and to separate primary and secondary processes. A similar critical approach should be used in analyzing the ontogeny of fossil taxa.

A special method of reconstruction of morphogenetic processes and their interactions and hierarchy is based on the study of aberrant forms. Systematizing all aberrations, it is possible to reveal deviations of the respective morphogenetic processes from the usual developmental patterns, to see correlations between them, and, based on this, to work out possible and impossible definitive conditions. This approach gave the best results when analyzing the clearly outlined problem of the distortion of the stem and theca in pelmatozoan echinoderms.

DISTORTION OF THE THECA AND STEM IN CRINOIDS

Many cases of distortion of the theca and stem known in fossil and modern pelmatozoan echinoderms are not random. They occur in a certain plane of symmetry and characterize groups of different taxonomic rank. These are situations when (1) the stem and theca are curved, (2) when the axis of the theca is at an angle to the axis of the stem, and (3) when the theca is oblique (Figs. 73, 74). In all these cases, the vertical stem is associated with an inclined plane of the distal surface of the theca containing the mouth (rather than horizontal as in most erect stemmed echinoderms). Then the axis of the food-collecting appendages (arms or brachioles) would not be subvertical. It is noteworthy that crinoids and many other pelmatozoan echinoderms with a single axis of the stem and crown, which is vertical in the relaxed state, bend when feeding in a dynamic water medium in such a way that the crown is oblique and the food-collecting appendages (arms or brachioles)

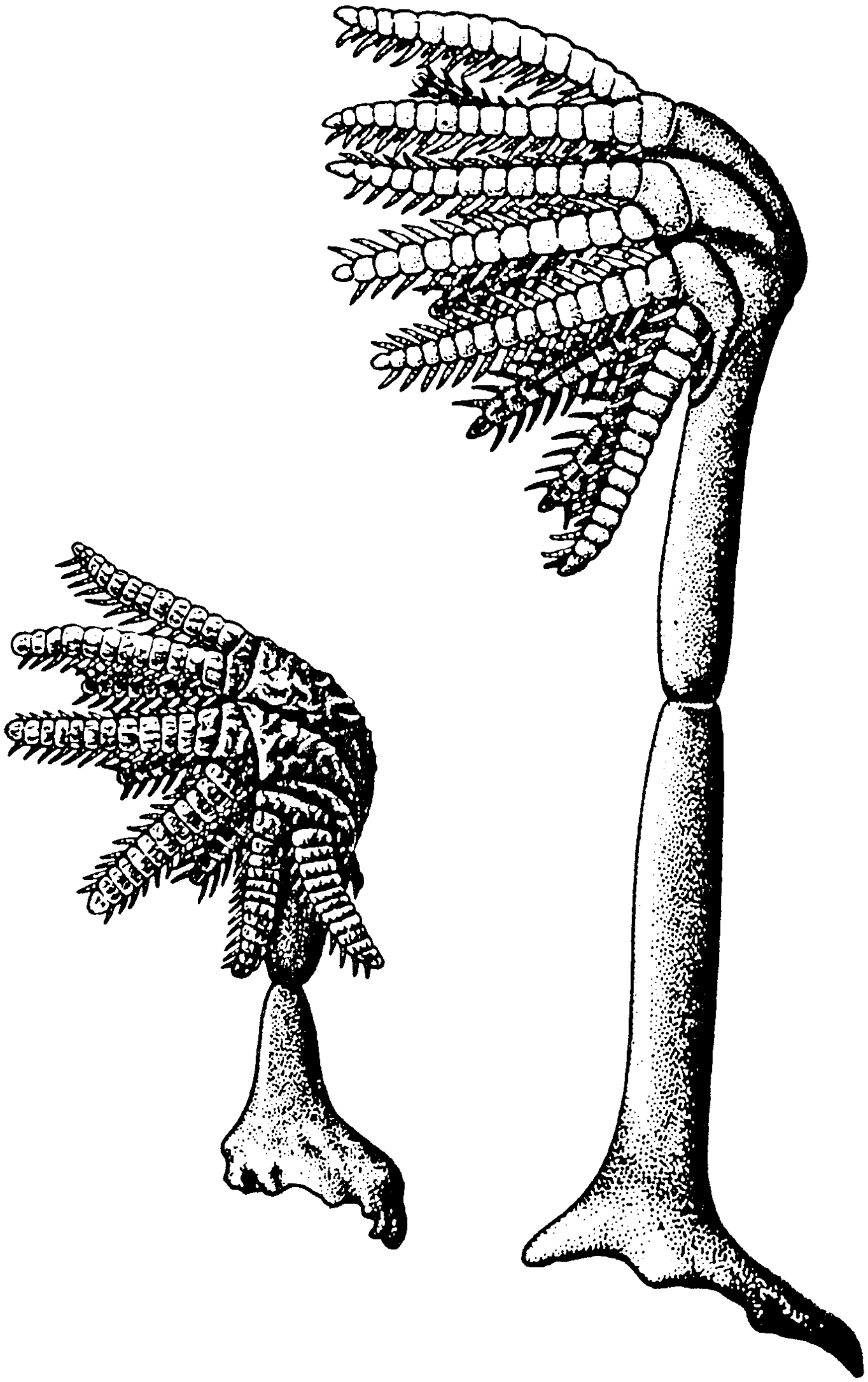


Fig. 74. Arrangement of the crown and stem in the genus *Hemicrinus* d'Orbigny, reconstructions: (a) *H. asterias* d'Orbigny; (b) *H. salgirensis* Arendt; Crimea; Lower Cretaceous, Lower Barremian (after Arendt, 1974).

extend along the current (Meyer, 1973, 1982, 1997; Meyer and Lane, 1976). In this position, turbulent currents are formed around arms (or brachioles), from which food particles settle in the food grooves, where they are covered in mucus. These small aggregations of food particles are then conveyed by ciliated epithelium toward the mouth. This is why all recorded cases of distortion of the theca and stem were thought to be connected to adaptations to currents, with a rheophilic affinity. In many cases, this is indeed so, but not always. From the morphogenetic point of view, many cases of such distortion of the stem and theca of an adult echinoderm may be related to the fundamental features of the larval development of pelmatozoan echinoderms, i.e., to the straightening or elevation of the originally curved stem and theca, a process described in the ontogeny of

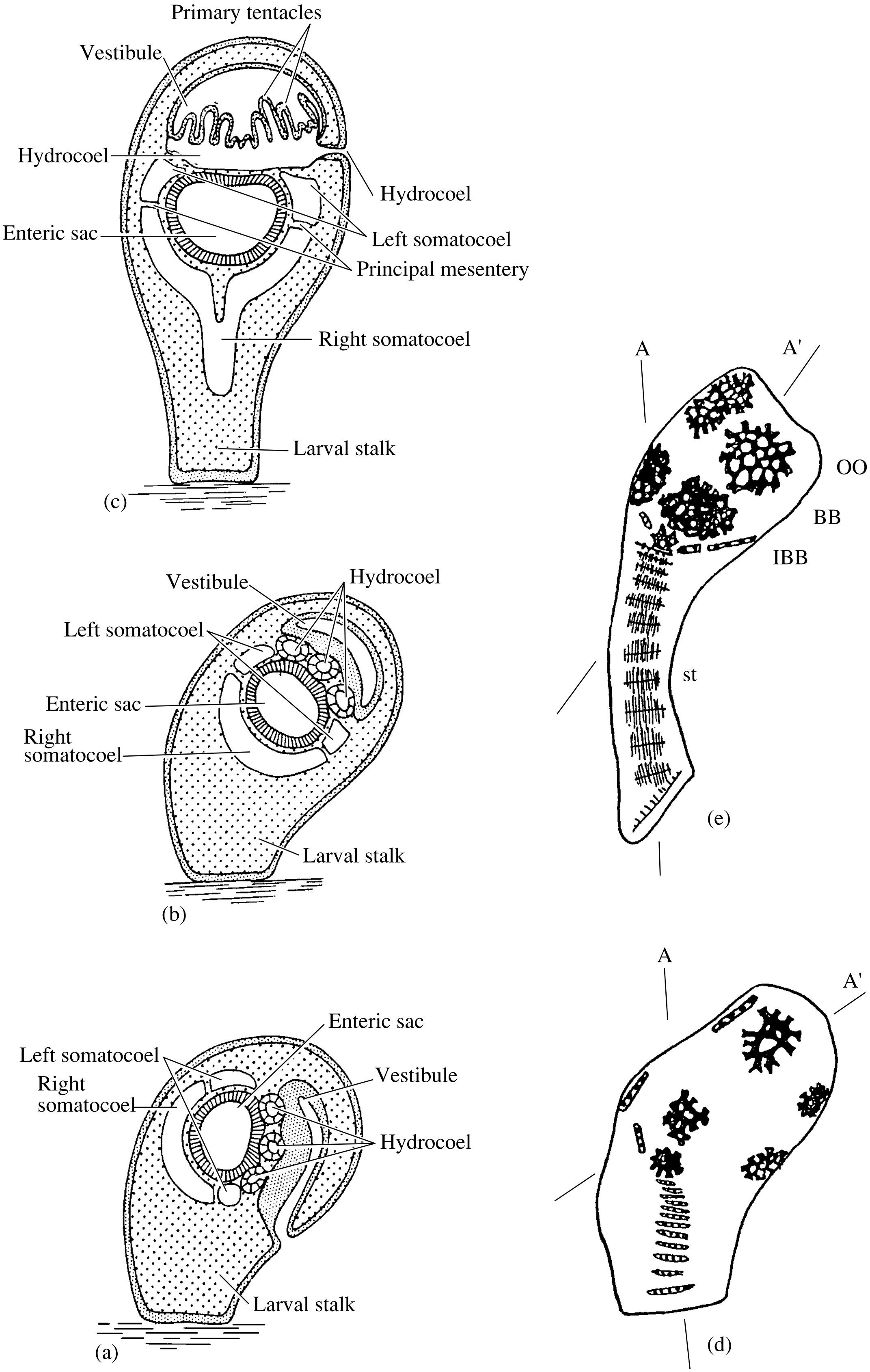


Fig. 75. Scheme illustrating the process of elevation in the ontogeny of crinoids: (a–c) scheme of the longitudinal section of the larva at the successive stages of elevation; (d–e) arrangement of the skeletal elements of the larva at different stages of elevation.

modern crinoids. This process was described in several embryological papers (Bary, 1888, 1889; Barios, 1888). Later, Heider named this process "elevation" and suggested that it was important in echinoderm phylogeny. The process of elevation is studied in detail in *Antedon rosacea* (comatulid crinoids). On the sixth day after the beginning of the development of this crinoid, incipient skeletal elements appear (Fig. 75). First these are orals, basals, and columnals. All plates of the future theca are arranged in a horseshoe widely opening to the ventral side of the larva. The incipient stem and theca extend approximately along the anterior–posterior axis of the larva, but in opposite directions, being strongly curved and lacking a common axis.

The process of elevation is a straightening of the stem and theca, which acquire a common axis (Fig. 75). In Heider's opinion, which is shared in the present paper, the elevation phylogenetically represents a shift of the mouth from the anterior end behind the attachment lobe to the posterior end of the body after the dipleurula is attached by its oral lobe and its formerly posterior end moves to the upper position. Phylogenetically, the displacement of the mouth is certainly a very early process and not only preceded pentaradiate symmetry, but radial symmetry in general. Therefore, the coincidence of the five-part symmetry of the plate arrangement in the ontogeny of modern crinoids and the process of elevation is a secondary phenomenon, which resulted from a shift in the time of initiation of plate development and their pentaradiate arrangement to earlier ontogenetic stages. Because the hydropore is already present at this stage of larval development, and five basals and five orals are arranged in a semicircle with emerging pentaradiate symmetry, interrays in which these plates should be located in adults may be determined. Bary, who described the development of *Antedon rosasea*, designated the incipient plates by indices following Carpenter's system. These classifications of the interrays are also interesting from the point of view of the relationships between the sagittal plane of symmetry of the larva, in which the elevation occurs, and the planes of symmetry of the adult pentaradiate organism. According to Bary's designations, the sagittal plane of the larva corresponds to the plane C-AE of the adult crinoid. Is this correspondence really true? Only partly. The circlets of basals and orals are opened by a wide semicircle toward the vestibulum. The hydropore occurs near one of the orals. Therefore, there appears to be no doubt of the accuracy of the designation of the incipient plates. However, the closure of this open circle can theoretically proceed in three different ways (Fig. 76): (1) due to the equal convergence of the right and left plates; (2) due to the greater displacement of the right plate; and (3) due to the greater displacement of the left plate. Depending on this, the sagittal plane of the larva may to some extent correspond to one of the following planes of symmetry of the adult animal: C-EA (1), BC-E (homocrinid), and CD-A (crinoid) planes. This correspondence may, for instance, be manifested in the case of heterochrony. If the process of elevation is halted, the body of the adult animal would remain curved (Fig. 77). This distortion was initially in the sagittal plane of symmetry. After the development of pentaradiate symmetry, this plane of curvature occurs in one of the three above planes, thus manifesting one correspondence between the sagittal plane of the larva and the plane of symmetry of the adult pentaradiate animal. Consequently, there are variations in correspondence of these planes in different pelmatozoans.

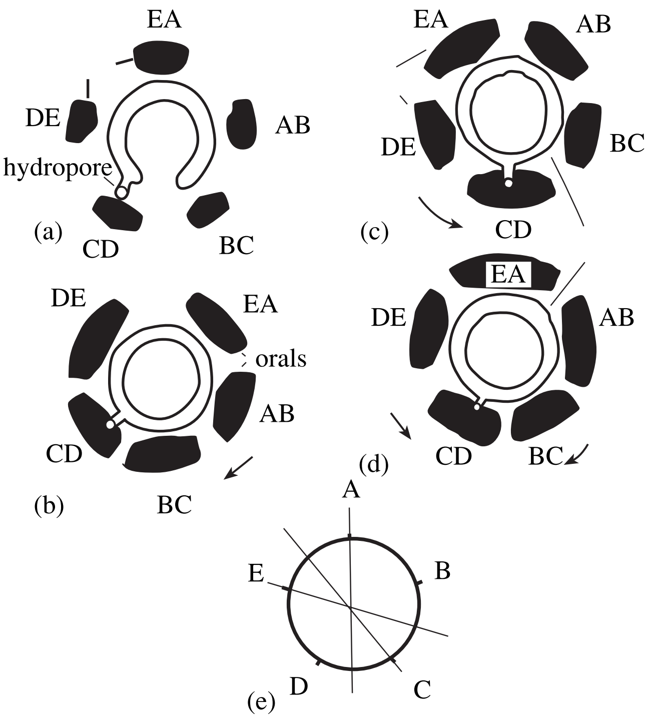


Fig. 76. (a) Arrangement of the orals around the horseshoe-shaped hydrocoel; (c–d) possible variants of the closure of the oral circlet and hydrocoel; (e) possible planes of recumbence of the theca among pelmatozoan echinoderms.

When the process of elevation is arrested, the theca will be inclined toward the C ray or toward the neighboring BC or CD rays. Depending on how rapidly it is arrested, the angle between the theca and the stem may vary. In another instance, the process of elevation is not arrested when the theca and stem are completely straightened but continues, and the theca becomes curved in the opposite direction, although in the same plane, the phenomenon is known as hypermorphosis. Apart from the very apparent results of the delay or hypermorphosis of the elevation, there may be lesser indications forming a usual array of individual variability of the deviation from the straight line. In addition, in the "feeding position," the functional curvature of the stem and theca of crinoids may occur mainly in the plane coinciding with that of the morphogenetic curvature in the development of the larva. This may result from the corresponding symmetry of the development of muscles and strands. Judging from these theoretical

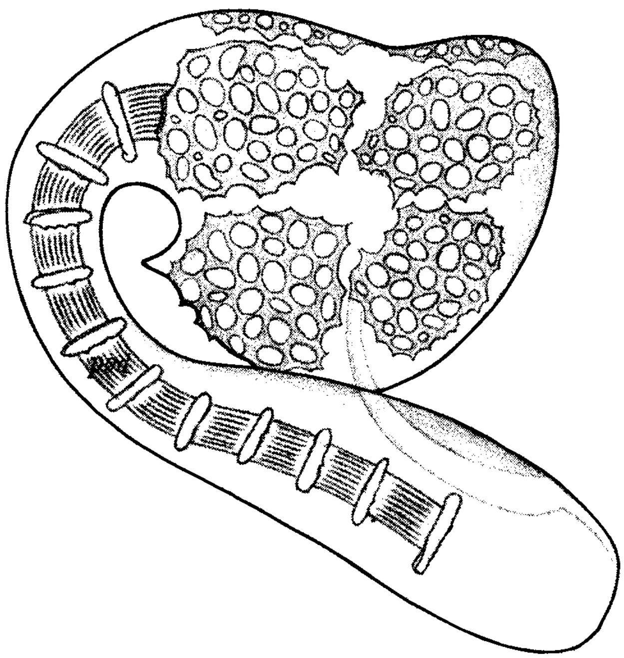


Fig. 77. Late stage of the aberrant development of Antedon (after Barrois, 1888).

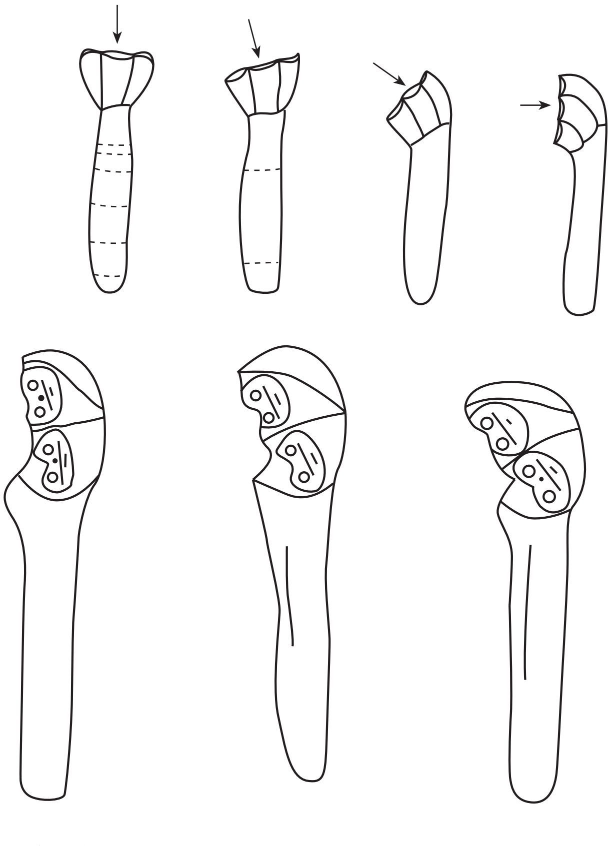


Fig. 78. Different recumbence of the cup to the stem in cyrtocrinids: *Cyrtocrinus variabilis* Arendt (upper row) and *Hemicrinus salgirensis* Arendt (lower row). Lower Cretaceous of the Crimea (after Arendt, 1974).

possibilities of the curvature of the theca and stem in adults based on the larval process of elevation known in the ontogeny of the extant crinoids and supposedly in many other stalked echinoderms, it is possible to analyze the distribution of observed cases of the body distortion in adult pelmatozoans.

Among the Articulata, the Meso-Cenozoic subclass of crinoids (these were the only pelmatozoan echinoderms at that time), the unconformity of the axes of the stem and theca is most strongly pronounced in many members of the order Cyrtocrinida (Figs. 73, 74, 78). This order is comprised of small compact crinoids with a thickened skeleton, often with strongly developed bilateral symmetry manifested by the recumbence of the calyx and the extension of the arms sideways, with a short stem lacking cirri, or without a stem. The calyx is composed either of radials only or of radials and basals. The arms are not long, each of them is usually branched once into two similar components (Arendt, 1974). Cyrtocrinida comprise two suborders, Cyrtocrinina Arendt, 1974 (stalked) and Holopodina Arendt, 1974 (nonstalked, attached to the bottom by the base of the calyx).

In the suborder Holopodina, species with an oblique calyx are considerably dominant, while in the suborder Cyrtocrinina, most members either have a single vertical axis of the stem and calyx or have these axes crossed at a slight angle. According to Arendt (1974, p. 78), in Cyrtocrinida, “a differently developed obliqueness of the distal margin of the calyx appeared as an individual variation in almost all known species. Sometimes, 50% or more of individuals showed this feature.” However, this feature is the most apparent in the family Hemicrinidae, comprising three genera. In this family, the calyx is strongly oblique, so that the arms are extended sharply sideways. Nonrecumbent representatives are extremely rare in this family. The plane of obliqueness of the calyx is named by Arendt as a tertiary plane of symmetry. He emphasized that the relationships between this plane and the secondary plane of symmetry in cyrtocrinids (a plane extending through the peristome and periproct) are completely unclear because the structures marking this plane (peristome, periproct, and related anal structures) are not preserved in fossils. Modern cyrtocrinids, so called “living fossils,” *Holopus rangi, Cyathidium foresti*, and *Gymnocrinus richeri* (Fig. 73) have not yet provided any information for the precise identification of rays. The reason is that the homology of the rays should be established on the bases of the primary position of the hydropore rather than the position of the anus (which is variable), but the identification of the position of the hydropore requires special investigations. Thus, the exact homology of the plane in which the calyx is oblique is not yet specified.

Nevertheless, it is possible to suggest the obliqueness of the calyx and the unconformity of the axes of the stem and theca is based on the ontogenetic process of elevation considered above. As a result of heterochrony, this process was halted at different stages leading to the maintenance of distortion in the adult animal. This hypothesis is well supported by the data on the variability of the structure of various representatives of Hemicrinidae published by Arendt (1974).

In *Cyrtocrinus*, the angle between the axes of the stem and calyx was usually 50°–80°; however, in rare specimens, the obliqueness was absent, and a single axis of the stem and calyx was present (Fig. 78). Radials in all species of this genus contacted each other in all the rays. In many *Hemicrinus* species, e.g., in *H. steierianus* d'Orbigny and in *H. salgirensis* Arendt, "in the case of certain obliqueness of the calyx (from 45°–60°) the stem first partly and then completely (90°) rested on the calyx in one of the interrays, moving two neighboring radials apart, which became completely separated." (Arendt, 1974). In some specimens, the stem intruded widely between the radials and contacted all plates, while in others, it only touched the opposite plates by its apex. In some specimens, these structures were completely separated, and, in marginal cases, the apex of the stem occurred completely on the ventral side of the calyx rather than being positioned laterally.

This variability may be explained by the arrest of the elevation at different stages of ontogeny. This hypothesis is supported by the separation of radials. Indeed, in the ontogeny of modern crinoids, the infrabasals, basals, and orals soon after their appearance form a semicircle opening toward ray C. Radials appear later, when all the plates form complete circlets. In the case when the process of elevation is delayed, the closure of the plates into the circlet could also be delayed. In this case, the appearing radials would form a semicircle or a horseshoe-shaped structure. This horseshoe-shaped structure would also be open toward ray C. The incipient radial C could theoretically occur either on the left of the horseshoe or on the right. Therefore, in the case of a split of the radial circlet resulting from a heterochrony, this split could separate either the B and C radials, if the incipient C plate occurred on the right side of the horseshoe, or the C and D plates, if the C incipient radial occurred on the left of the horseshoe. If no split of the circlet occurred, the plane of the obliqueness of the calyx at the time of the closure of the horseshoe extended either through the C radial, in the case when the incipient C radial occurred on the left end of the horseshoe, or through the BC ray, if the incipient of the radial was on the right side of the horseshoe (Fig. 76). Arendt (1974, text-figs. 11a–11k) showed that in the individual variability of *Cyrtocrinus variabilis* Arendt, the plane of obliqueness of the calyx extended in the proximity of the stem either through the radial, or between the radials (through the interray). Indeed, the homology of these plates remains unknown. If the above hypothesis of the possible means of appearance of the obliqueness of the cyrtocrinid calyx is correct, the plane of this obliqueness should coincide with the EA–C plane, when it lies in the proximity of the stem through the radial or coincide with one of the neighboring plates (crinoid [A–CD] or homocrinid [E–B–Q]), in the case when it occurs in the proximity of the stem between the radials. The latter two planes are especially well pronounced in the morphology of many Paleozoic crinoids. These planes are designated in accordance with their position in relation to the plane in which the primary hydropore (A–CD) occurred. The position of the anus in relation to this plane could vary slightly as is sometimes observed in some crinoids, e.g., in calceocrinids. The special study of modern cyrtocrinids, especially *Gymnocrinus*, may provide a precise identification of their rays and interrays and either support or defeat the above hypothesis of the possible appearance of the calyx's obliqueness.

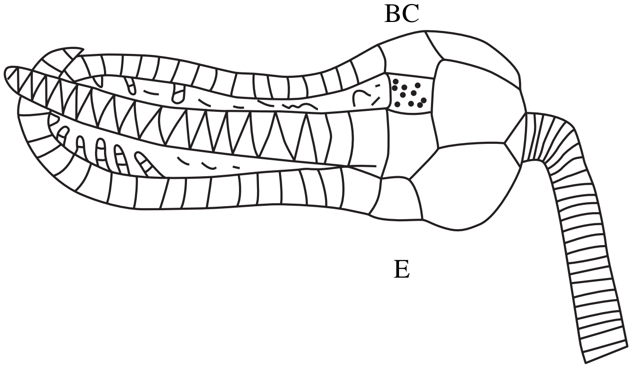


Fig. 79. Scheme showing the structure of the cladid crinoid *Jimbacrinus bostocki* Teichert from the Permian of Australia.

In many Paleozoic crinoids with an oblique calyx, the plane of obliqueness is revealed quite definitively, at least in relation to the anus. However, in most cases, the planes of the anus and hydropore in crinoids coincide. The disparity of these planes is usually readily observed, since the anus is displaced in this case to ray C and completely embraces the skeleton of the arm in ray C. Therefore, the plane of curvature in most Paleozoic crinoids is definitely homocrinid. This curvature is observed most clearly in the large family Calceocrinacae (disparid inadunates) and in the species *Jimbacrinus bostocki* Teichert, 1954 (Figs. 79, 80), belonging to the small Permian superfamily Calceospongacea (suborder Poteriocrinina of cladid inadunates). The species *Jimbacrinus bostocki*, analyzed in this study, is housed in the Department of Invertebrate Paleontology, Victoria State, Melbourne, Australia. The museum houses a large slab with an area of 0.5 m^2; this slab contains 43 crowns, most of which have stems attached (Fig. 80). The cups are large, about 30 mm in diameter, sometimes considerably larger. The height of each cup is slightly smaller than the diameter. Five infrabasals and five basals possess quite long spines. Among five radials, there is one radianal supporting a small anal sac. Arms are unbranching and pinnulate. A long and slender cylindrical stem is composed of columnals almost equal in height. The axial canal of the columnals is circular and is only one-third of the columnal's diam-

Fig. 80. Slab with well preserved specimens of *Jimbacrinus bostocki* Teichert from the Permian of Australia, ×0.3, housed in the State Museum of the State of Victoria (Melbourne, Australia).

eter. A slightly convex areola occurs around the axial canal, and the periphery possesses short ridges. Starting about 3–5 mm away from the cup base, the proximal part of the stem is composed of alternating high and low columnals. Toward the cup, their diameter decreases, and the difference between the high and low columnals increases. Approximately 1 cm from the cup base, the stem is sharply bent so that the cup's axis occurs at a considerable angle to the stem's axis. The columnals in this part are even lower, of two alternating orders, with higher columnals twice as high as the lower columnals and slightly wider. At the very base of the cup, six to eight columnals have equal height and width. This curvature in some specimens was noticed in the first description (Teichert, 1954). Teichert believed that this resulted from muscle contraction after the animal's death. In the slab studied, all specimens with preserved stems are bent in this way. Therefore, this suggests that curvature is a feature of the live animal. This is supported by more detailed observations of the curvature. It is shown that the majority of specimens in which the plane of curvature was possible to identify are bent in the homocrinid plane. Table 5 gives an idea of the orientation of the rays of the plane of stem curvature and the angle of the cup to the stem's axis.

Thus, the angle between the cup and the stem is, on average, about 70°–75° but ranges from 40° to 120°. The curvature of the stem in the homocrinid plane (E–BC) dominates (21 specimens). In the EA–C plane, the stem is curved in four specimens; and in the DE–B plane, in two. The curvature of the stem in two specimens in the AB–D plane is related to the twist of the stem upon burial; hence, these two should not be taken into account. In the remaining specimens, the plane of curvature was impossible to identify, either because of the unfavorable position of the cup on the slab, or because of a missing stem. About 20% of the specimens with a significantly curved stem in the homocrinid plane may have a curvature in the nearest (clockwise or counterclockwise) DE–B or EA–C planes, which are rotated to the half of the ray in relation to the homocrinid plane. However, there is a small possibility that this deviation may result from taphonomic reasons.

If the curvature of the stem in *Jimbacrinus bostoki* is compared to the corresponding structures in the larvae of extant crinoids prior to the elevation, it is possible to see that this curvature occurs in the same or closely located planes, but oriented in the opposite direction. Therefore, it is possible to suggest that the curvature of the adult *Jimbacrinus bostoki* appeared as a result of hypermorphosis based on the larval process of elevation, i.e., after the axes of the stem and the cup coincided, the process of elevation continued, which resulted in a new distortion of the animal, but in the opposite direction. This conclusion is supported by the fact that this distortion has a low taxonomic rank (not above species level) since the closely related species *J. (?) noetlingi* (Sieverts-Doreck, 1942) do not appear to display crookedness. Numerous species of the genus *Calceospongia* (type genus of the family) also do not show a distortion of the stem. Large morphological changes of a lower taxonomic rank, which appeared rapidly in evolution, should have had a definitive basis in the ontogeny. Only under this condition, they could appear more or less rapidly as a result of various heterochronies.

A distortion of the stem in the same homocrinid plane, as in *Jimbacrinus bostoki* but in the opposite direction, is observed in all representatives of the superfamily Calceocrinacea of disparid inadunates (Fig. 81). Despite the fact that this is the most diverse and geographically and stratigraphically widespread disparid superfamily, it is usually believed to be aberrant because of the unusual structure. The peculiarity is in that the theca and the stem have noncoinciding axes which occur at a right angle (or close to it) to each other. In contrast to *Jimbacrinus bostoki*, this distortion is connected with considerable changes in the shape of the cup and in the composition and arrangement of plates. In Calceocrinacea, the distortion of the stem in relation to the crown is certainly connected with paedomorphosis, which is indicated by the crown being inclined toward the BC interray. This is also supported by the presence of many juvenile features in the structure of adult Calceocrinacea. Because the process of elevation was present in all crinoids, it is possible that the parallel development of the calceocrinoid type of organization was present in several closely related groups of disparid crinoids.

Table 5. Orientation of the plane of stem curvature and the angle of the cup to the stem in *Jimbacrinus bostocki* on a slab from the Museum of Victoria in Melbourne, Australia

Specimen no.	Index of the plane	Angle	Specimen no.	Index of the plane	Angle
1	DE–B	75	23	E–BC	80
2	EA–C	90	24	EA–C	80
3	E–BC	80	25	E–BC	120
4	AB–D	90	26	E–BC	70
5	E–BC	90	27	E–BC	75
6	E–BC	70	28	?	?
7	DE–B	75	29	?	?
8	E–BC	60	30	EA–C	75
9	?	70	31	E–BC	70
10	E–BC	70	32	E–BC	70
11	E–BC	75	33	?	?
12	?	?	34	E–BC	
13	?	?	35	?	90
14	?	75	36	?	?
15	E–BC	40	37	E–BC	70
16	E–BC	75	38	?	?
17	?	?	39	E–BC	80
18	E–BC	45	40	E–BC	55
19	EA–C	45	41	E–BC	45
20	?	?	42	?	?
21	E–BC	75	43	?	65
22	AB–D	55			

The distortion of the axis of the stem and crown is known in hybocrinid crinoids, which were considered to be a separate subclass by Rozhnov (1985a, 1985b). These crinoids have a large or medium-sized cup compared to other crinoids. The shape of the theca is conical or rounded conical, usually symmetrical; in some genera and species, however, the cup on one side is slightly inflated, while the oral surface is more or less steeply inclined in the A–CD plane toward the A ray. This asymmetry is also seen in the displacement of the stem facet toward the A ray and in the longer CD basal compared to EA and AB. This asymmetry is a generic character of *Hybocystites* as indicated by Sprinkle and Moore (1978b, p. T572). It is present in many *Hybocrinus* species and is usual in the individual variability of some *Hoplocrinus* species. According to Sprinkle (1982), in *Hybocrinus nitidus* Sinclair, 1945 from the Bromide Formation (Caradoc), a flattened ventral part of the cup is inclined at an angle of 26° to the vertical axis of the cup, while in *H. crinerensis* Strimple et Watkins, 1949 from the same formation, it is inclined at an angle of 10° to 20° (mean 15°). The direction of the obliqueness is not indicated, but both species have a stem facet displaced toward the A ray similar to the maximum length of the CD basal, while the EA and AB basals are the shortest. Consequently, the theca in these species is curved in the plane A–CD toward the A ray. The asymmetry of the theca and the obliqueness of the ventral part of the cup in the A–CD plane toward the A ray is indicated for *Hybocrinus punctatus* (Miller et Gurley, 1895) from the Middle Ordovician of North

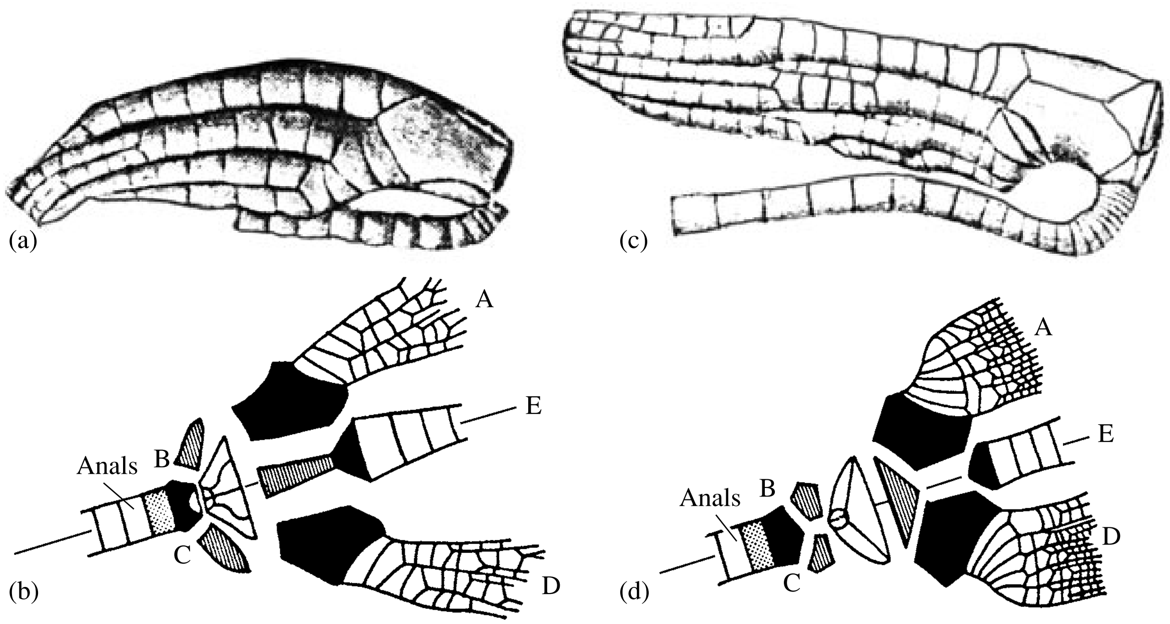


Fig. 81. Crinoids of the superfamily Calceocrinacea: (a–b) *Calceocrinus*: (a) general lateral view; (b) arrangement of the plates; (c–d) *Halysiocrinus*: (c) general lateral view, (d) arrangement of plates.

Fig. 82. General view of *Rhipidocystis baltica* from the Middle Ordovician (Arenig, Volkhovian) of the Leningrad Region.

America (Brower and Veinus, 1975). A similar distortion but with a smaller obliquity of the ventral part of the cup in relation to the vertical axis was observed in some specimens of *Hoplocrinus dipentas* (Leuchtenberg, 1843) from the Kunda and Azeri Horizons (Llanvirn) of the Leningrad Region and in *Hoplocrinus estonus* Opik, 1935 from the Idaveri Horizon of Estonia. It is suggested (Rozhnov, 1993, 1994) that this distortion in pelmatozoan echinoderms is morphogenetically connected with hypermorphosis of elevation, which occurs in the ontogeny of modern crinoids and apparently existed in the ontogeny of many pelmatozoan echinoderms. The study below attempts to reconstruct such distortion based on the elevation in two Ordovician eocrinoid genera, which were previously considered to be barely phylogenetically related.

DISTORTION OF THE THECA IN EOCRINOIDS AND PARACRINOIDS

This section attempts to display the presence of distortion of the stem and theca in the above eocrinoid genera, which could result from an elevation in ontogeny.

Rhipidocystis Jaekel, 1900 is a typical representative of the small Ordovician group of eocrinoids with a flattened theca (Figs. 82, 83). *Cryptocrinites* von Buch, 1840 is a typical representative of the group of Ordovician eocrinoids with a spheroid theca, which includes six genera of three families (Fig. 84).

Both these groups lack epispires or sutural pores, but the remaining morphological features appeared quite different. Therefore, Broadhead (1982) proposed to assign eocrinoids with a flattened theca to a separate class, whereas *Cryptocrinites* and other similar genera

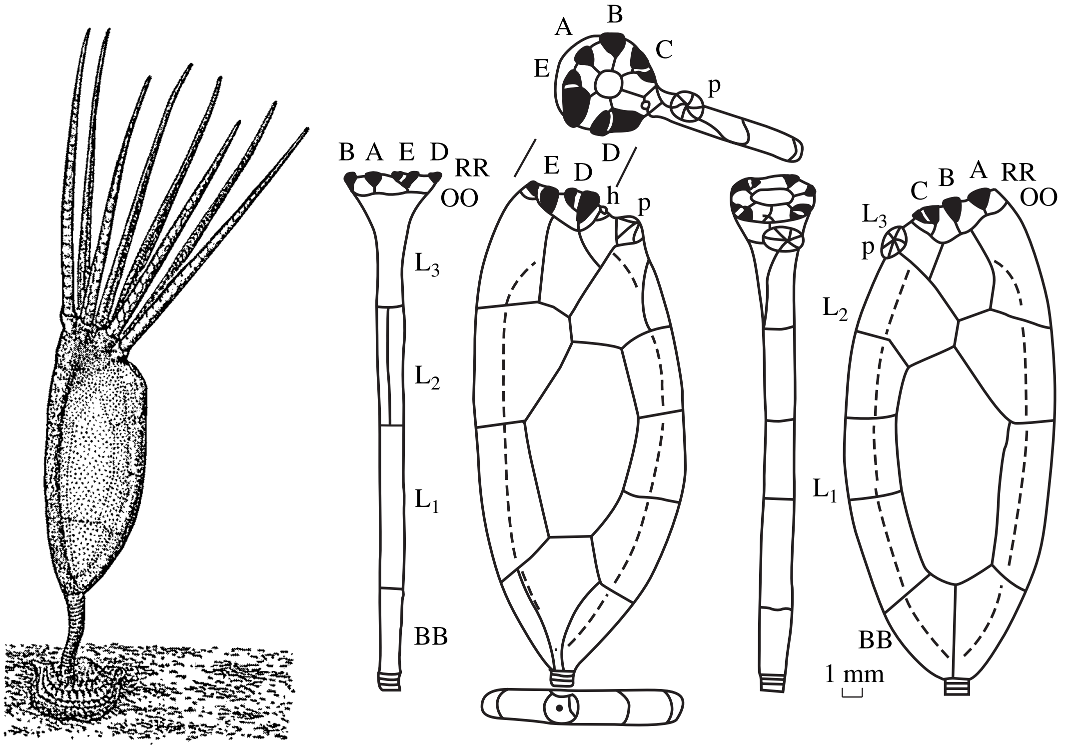


Fig. 83. Reconstruction of the life position and composition of plates of the theca in the eocrinoid *Rhipidocystis baltica* from the Middle Ordovician (Arenig, Volkhovian) of the Leningrad Region.

were tentatively assigned to the class Paracrinoidea, which shows a characteristic distortion of the theca and stem (Figs. 24, 85).

Rozhnov (1994) showed the close relationships between these two eocrinoid groups and suggested transformations, which occurred during the transition from the hypothetical ancestral form at the point of divergence of cryptocystids and rhipisocystids. Below, the transformations that are connected with the process of elevation are discussed. Rozhnov (1994) indicated that the hypothetical ancestor of *Rhipidocystis* had a spherical theca, which differed from that in *Cryptocystis* in a greater number of circlets, position of the periproct in another ray, and in the fact that the peristome was inclined in the opposite direction. From the morphogenetic point of view, the transition of the anus from the CD interray to the C or B ray (counterclockwise) is easy to explain by the delays in the development of this structure in ontogeny (paedomorphosis). The posterior intestine grows clockwise, and untimely interrupted development results in the counterclockwise shift of the anus in the adult animal, phenomenon known in calceocrinids. Distortion of the theca in *Rhypidocystis* is convincingly explained by the ontogenetic delay of elevation, the process discussed above in detail in crinoids. In *Cryptocrinites*, the peristome is inclined in the same plane as in *Rhipidocystis*, but in the opposite direction. Hence, it is possible to suggest that in this case the process of elevation did not stop when the animal became upright but continued, resulting in further distortion of the theca (hypermorphosis). Therefore, despite the fact that obliqueness of the peristome in *Cryptocrinites* and *Rhipidocystis* occurs in opposite

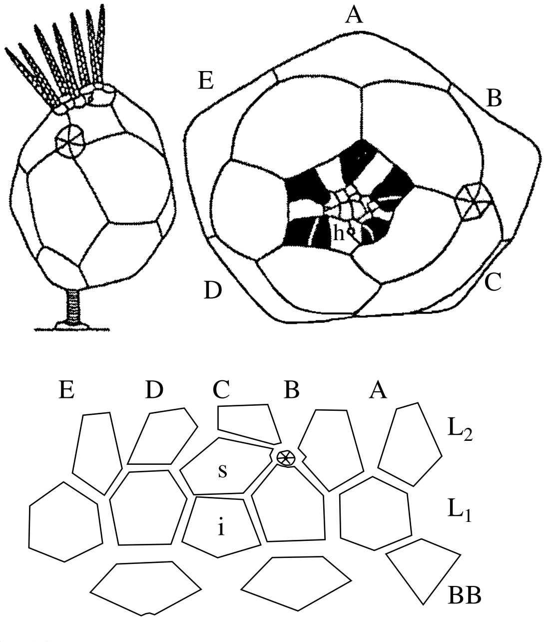


Fig. 84. Reconstruction of the life position and composition of the theca in eocrinoid *Cryptocrinites laevis* from the Middle Ordovician of the Leningrad Region.

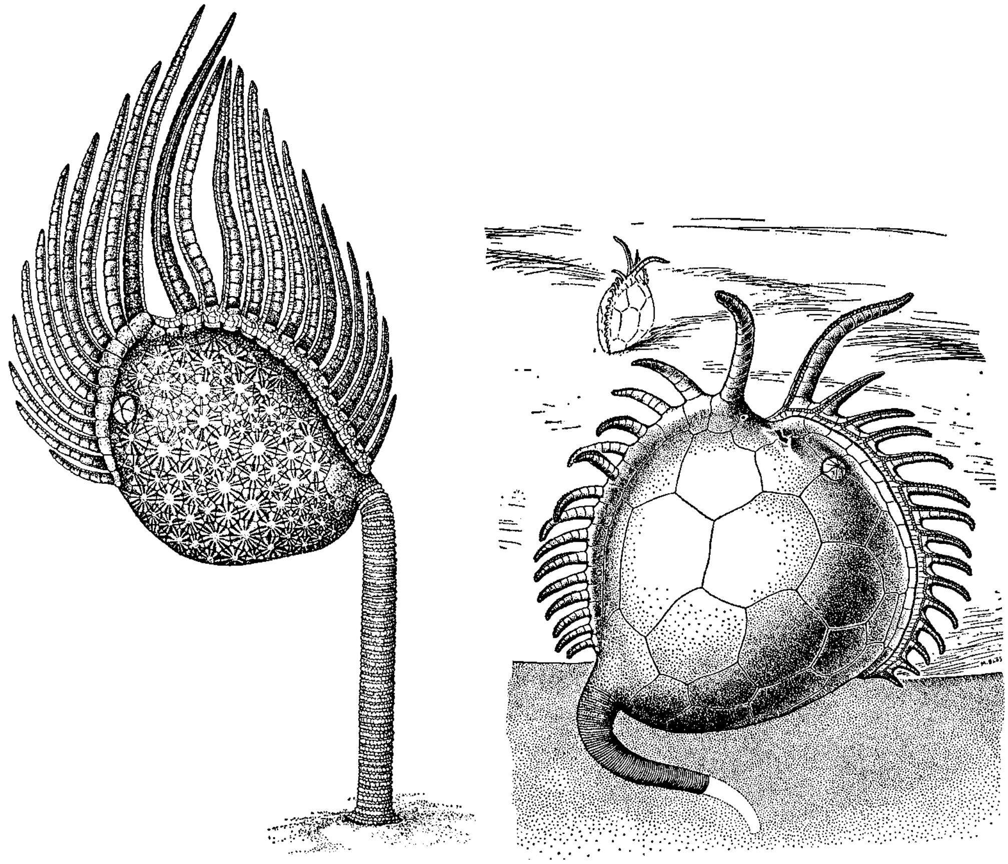


Fig. 85. Reconstruction and supposed life position of the paracrinoids *Amygdalocystites florealis* Billings (left) and *Platycystites cristatus* Bassler (right) (after Parsley and Mintz, 1975).

directions, it has the same morphological basis, i.e., elevation. In one case, this process was hyperdeveloped; and in the other, unfinished (Fig. 86).

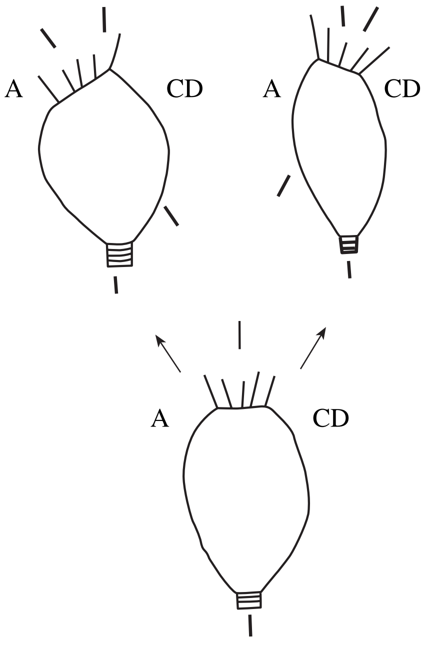


Fig. 86. Change in the direction of the curvature and recumbence of the theca in relation to the stem in the course of the evolution of *Cryptocrinites* and *Rhipidocystis* from a common ancestor (after Rozhnov, 1994).

This example shows that the ontogenetic elevation was characteristic not only of crinoids, but also occurred in the ancestral eocrinoids, and therefore, was typical of all pelmatozoan echinoderms.

The above examples of symmetry and asymmetry in the structure and morphogenesis of pelmatozoan echinoderms allows the following conclusions to be drawn:

(1) Metamerism is the major and primary type of symmetry in echinoderms. The radial symmetry of echinoderms morphogenetically represents a closed metamerism.

(2) Growth and closure of the left hydrocoel in a ring during the phylogeny indicates the general tendency of early echinoderms to develop left-sided asymmetry. The appearance of the third ambulacrum determines the coil of the hydrocoel, its closure into the ambulacral ring, and the appearance of pentamery. The pentaradiate symmetry of echinoderms is derived from triradiate symmetry.

(3) In the majority of crinoids, judging from the position of ambulacra and orals, the sequence of the

appearance of facets for arm attachment and arms themselves was the following: three primary grooves A, C, and D and two secondary grooves, B and E, branched off the grooves C and D. This pattern was followed also by many other echinoderms. However, there were other patterns, in which the branching of secondary grooves proceeded in another direction, and secondary grooves occurred in different rays.

(4) In pentaradiate pelmatozoan echinoderms, there are five possible planes of symmetry, but only two of these are morphogenetically important, crinoid (A-CD) and homocrinoid (E-BC).

(5) The primary left-sided asymmetry of echinoderms to various extent influences enantiomorphism in some structures.

(6) Many pelmatozoan echinoderms show a fluctuating asymmetry. In contrast to bilaterally symmetrical animals, radially symmetrical echinoderms display is in some pentamers in accordance with the sequence of their development.

(7) Distortion of the theca and stem occur widely in pelmatozoan echinoderms and crinoids in particular. Morphogenetically, the distortion is based on the ontogenetic process of elevation, which is well known in modern crinoids.

PART 3. ORIGIN AND DEVELOPMENT OF HIGHER TAXA OF PELMATOZOAN ECHINODERMS IN THE EARLY PALEOZOIC

In the previous chapters, the origin and development of many of the morphological structures of pelmatozoan echinoderms, including symmetry and asymmetry in the structure of their body, were discussed. The conclusion was reached that each higher taxon of echinoderm has a particular body plan, rather than being characterized by a single character acquired early in its evolution.

Indeed, some morphological structures of animals do not occur without one another. These structures in an animal form a morphogenetic entirety, a core, morphologically corresponding to a certain taxonomic rank. This indivisible entirety of characters can be called a body plan or an archetype for a taxon.

So, how did archetypes and their stable combinations of structures appear? Are there genuine phenomena in nature corresponding to these entireties, or could it be that an organism represents just a mosaic of characters randomly acquired at different stages of its evolution? There is a wide spectrum of views on this problem, from the acknowledgment of the existence of an archetype to the complete rejection of this view. Here, an attempt is made to answer this and some other important questions, using data given above on the morphology and evolution of the large phylum Echinodermata. The long evolutionary history of these animals, which is well represented in the fossil record, combined with their diverse skeletal morphology (in many details indicating the structure of the soft parts of the body), their high diversity of higher taxa, and their leading role in many marine bottom communities, make this group a particularly useful model for revealing and interpreting the origin and early evolution of higher taxa of animals.

Echinoderms are among the most unusual multicellular animals. Their anatomy is complex and controversial. The morphology of echinoderm larvae indicates their close relation to chordates, whereas adult echinoderms differ very considerably from chordates, resembling them less than many other animals. Pentaradiate symmetry, characteristic of echinoderms and generally not typical of other animals, is combined with the deep asymmetry of their body form. Echinoderms have an internal, mesodermal skeleton, which usually embraces the body of an echinoderm from outside. The skeleton is composed of separate "monocrystal" plates, which may form a rigid carapace and cover flexible processes. Each skeletal element, which appears monolithic and shows the features of a calcite monocrystal, has in fact a meshed, stereom structure and is porous. The ambulacral system, which is not observed in other animals, has a radial symmetry due to the canals radiating from a closed ring, although it is metameric and horseshoe-shaped earlier in ontogeny. These, and many other features, make echinoderms very useful in the study of a broad range of problems of morphology, morphogenesis, and ontogeny. However, this group is especially useful for studying the origin and evolution of higher taxa, since it is very diverse at higher taxonomic levels (e.g., there are over 20 known classes of echinoderms).

Of twenty classes of Echinodermata, five have survived to the Recent, while the remaining fifteen are known only from the Paleozoic (mostly from the Cambrian, Ordovician, and Silurian). Precambrian echinoderms are not known with certainty. The soft-bodied organisms that were tentatively assigned to echinoderms because of their similarity to skeletal Edrioasteroidea (Gehling, 1987; Glaessner and Wade, 1966) do not, in fact, have sufficient characteristics to assign them to echinoderms (no hydropore or anus has been reported). Classes of echinoderms are unequal in the number of representatives and time of existence. They can be subdivided into small, medium, and large (Fig. 87). Each class differs from others in a combination of characteristics, which form a distinct structural plan, rather than in a single characteristic. This set of characteristics appeared instantaneously rather than gradually. Therefore, the cladistic method cannot be used to study the phylogeny and classification of echinoderm classes. More so, cladistics does not recognize archetypes, since it considers all taxa, except for species, as artificial labels (as opposed to real objects in nature), which are used only for convenience when the diversity of the organisms is studied. Followers of strict cladistic methodology attempt to work with only the actual sets of characteristics (ideally, characteristics of

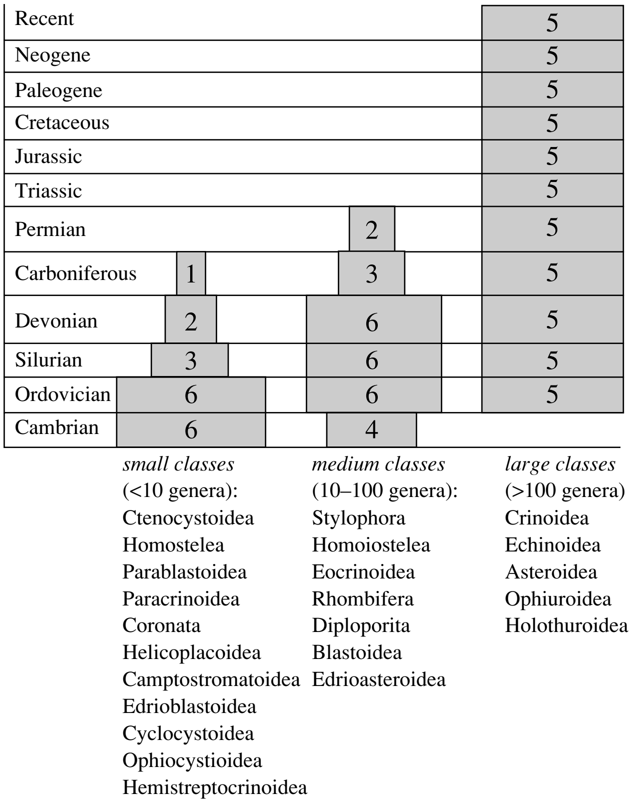


Fig. 87. Geochronological ranges of small, medium, and large classes of echinoderms.

a single individual). However, in practice they utilize a set of characteristics of a single species, or at least one genus (Sumrall, 1996).

Are there genuine body plans in nature, or are higher taxa just labels indicating sets of characters, which appeared in evolution quite randomly and gradually? This chapter will attempt to answer this question based on the example of the early evolution of higher taxa of echinoderms. First of all, the methodological aspects of this problem should be discussed.

SECTION 1. BODY PLAN, MORPHOGENESIS, AND TIME OF APPEARANCE OF HIGHER TAXA IN THE FOSSIL RECORD

From the morphological point of view, each taxon has its own body plan (archetype). This means, firstly, that any taxon differs from any other taxon of the same rank by a set of characteristics rather than by a single characteristic. Secondly, each organism has a whole hierarchy of body plans (archetypes). The body plan can be interpreted as a set of closely associated characteristics typifying a taxon. This interpretation is usually sufficient for phylogenetic and evolutionary reconstructions. However, in a deeper, morphogenetic, aspect, it is more appropriate to refer to "dynamic stability" and a hierarchy of processes of development (Hinchcliff and Vorobyeva, 1989; Vorobyeva and Hinchcliff, 1991), i.e., to the hierarchy of morphogenetic processes that lead or may lead to the appearance of morphological characteristics and their combinations. In other words, a static morphological archetype is a manifestation of the dynamic morphogenetic archetype, the archetype of specialized morphogenetic processes characterizing different levels of the animal's organization. This is especially necessary to take into account when one is dealing with fossils indicating early stages of the taxon's evolution. For instance, based on the morphology of modern classes of echinoderms, we can characterize the archetype of the Echinodermata by a combination of the three following characteristics: (1) the presence of the ambulacral system, (2) pentaradiate symmetry, and (3) a calcite skeleton composed of monocrystals. But when fossil echinoderms are taken into account, this combination will be incorrect, because they include taxa originally lacking pentaradiate symmetry and a standard ambulacral system and, sometimes, a skeleton (in cases when it is not preserved in the fossil state). However, as long as the archetype of morphogenesis is considered, everything will be in the right place. The ambulacral system will correspond to a special type of morphogenesis of coeloms, the pentaradiate symmetry to the primary asymmetry and to the process of closure of metamerism to cyclomery, whereas the calcite skeleton will correspond to a special pattern of development.

It is noteworthy that in taxa of a lower rank, the body plan is dominated by one or a few characteristics, whereas other characteristics are only slightly specific. The differences between taxa of a higher rank are sharper and more noticeable in a larger number of characteristics. That is why cladistics can adequately describe the phylogenetic relationships between species, but fails to do so for relationships between higher taxa. Supraspecific taxa, which differ in their body plans rather than in scattered characteristics, sometimes have a type of variability when the stable characteristics constituting the body plan of the taxon of a higher rank vary. This variability, which is referred to as constructive or archaic diversity, plays an important role in understanding the origin of higher taxa, especially when paleontology allows investigation of the problem over geological time.

ARCHAIC DIVERSITY AND PALEONTOLOGICAL DATA

Each individual, even a clone, is in some way unique. This diversity would have been impossible to describe, had it not been structured, especially, hierarchically. Indeed, each organism consists of superimposed systems of different levels, which develop successively or in a linear pattern in ontogeny. All these systems of characteristics build a hierarchy, which corresponds to the hierarchy of taxa considered in the framework of systematics. Some characteristics are typical of a large body of organisms, for instance a phylum. Other characteristics typify bodies of a lesser size: classes, orders, families, and genera. At each of these taxonomic levels, the definitive characteristics are usually constant and stable.

However, many groups of different ranks disturb this hierarchy. Occasionally, in a small family, variability may be observed in characteristics that are usually stable in closely related families and are characteristic of the order level (and above). Sometimes, a primitive group has a feature normally occurring in more advanced taxa. Sometimes, a small group of just a few genera has such an unusual combination of characteristics of a higher taxonomic rank, that it is regarded as a separate class. The pattern of these phenomena is usually connected with the development of the organism's structure at a certain taxonomic level. Mamkaev (1991) paid much attention to this problem. Originally, diversity` that did not fit the hierarchy was referred to as archaic. This name became popular among paleontologists. Mamkaev (1991) preferred another name, constructive diversity or original morphological diversity. By this, he emphasized that this diversity indicates features of a body plan (construction) type of organization at a particular systematic level. In his study, Mamkaev discussed methods and patterns of evolutionary morphology and formulated a rule that he observed while comparing the diversities of taxa: "The closer the taxon is to the evolutionary stage on which this functional morphological system was formed, the greater the constructive diversity of this system in this taxon" (Mamkaev, 1991, p. 50). This conclusion is based on a large body of material and is, therefore, convincing. However, many important features of the development of morphological diversity are revealed only when fossils are used (see below).

IMPORTANCE OF PALEONTOLOGICAL METHOD

Paleontological studies, although very important in broadening the known diversity of organisms, especially at the level of higher taxa, are usually based on the methods applied for studying modern organisms, which have a restricted use because of the incompleteness of fossils. However, paleontology is important as it provides the only way to observe the data obtained by evolutionary morphology in real geological time. Paleontology provides significant, interesting, and, most importantly, valid results because the incompleteness of the fossil record is not so crucial when taxa of a higher rank are considered, or when animals with a well-developed skeleton are discussed.

Only by means of paleontology can we approach the problem of how the higher taxa and corresponding morphological archetypes appeared in geological time; was it an abrupt or a gradual process?

This is a very important aspect of the theory of evolution. In fact, at present, a widespread opinion suggests that there is no significant difference between the macroevolutionary process (i.e., appearance of supraspecific taxa) and the process of microevolution (i.e., changes occurring within species). It is suggested that small changes accumulate between two divergent species, and the species diverge more and more morphologically. After some time, differences between them reach the generic level, then those of family, order, etc. The earlier the taxon appeared, and the longer the time of its existence, the higher its rank may be. At first glance, paleontological data support this rule. However, is it really true? Paleontological data applied to the problem of the origin and early evolution of higher taxa give the definitive answer that the higher taxa appear instantaneously, often simultaneously in several regions, and at the time of their appearance have a completely formed body plans.

CAUSES OF THE SEEMINGLY INSTANTANEOUS APPEARANCE OF NEW TAXA OF A HIGHER RANK

The appearance of new taxa of a higher rank is always mysterious and occurs so quickly that intermediate forms are difficult to find (Valentine, 1992). In my view, this is related both to the mechanism of the early evolution of new taxa and to our inability to recognize true intermediate forms. The appearance of taxa of a higher rank probably only occurs under certain conditions, which allow a new body plan. A new body plan is always a combination of characteristics rather than a single characteristic. Therefore, the ancestral taxon should mature, i.e., be ready to transform the body plan, and have the basis for a new combination of characteristics ready to appear. Maturity of the original taxon represents stabilization of the morphogenetic characteristics forming its body plan and a high variability of the evolutionary patterns, which take it outside the original body plan. Using such an approach, the ancestral taxon is morphogenetically and, hence, typologically of a higher rank than the descendant, since it has a larger morphogenetic and evolutionary potential. This explains the lower rank of newly appearing taxa in geological time.

To fulfill morphogenetic potential and to enable the appearance of a new body plan, a suitable environment facilitating rapid appearance, distribution, and accomplishment of morphological innovations is necessary. The appearance of such environments in geological history is usually connected with large-scale marine transgressions, when the sea flooded large areas of land, forming new, often semi-isolated, epicontinental marine basins. Occupation of large biotopes in a relatively short time could result in a fast or extremely fast increase in the number of animals and could, consequently, lead to different heterochronies in the ontogeny of many immigrants, which could be a strong morphogenetic factor at the time.

The number of heterochronies, especially instances of paedomorphosis in the ontogeny of marine animals, particularly in the process of occupation of new epicontinental seas, could sharply increase because of the arrested development of larvae, which had to travel long distances in oceanic currents. In this case, the development of a new taxon could occur particularly quickly. Literally, the larvae of the ancestral taxon, after a long journey in the ocean, could settle in a remote new region and by paedomorphosis produce a new taxon. This mechanism of appearance of new taxa was probably very common in nature, although it has not received much study. This mechanism explains the commonly observed sudden appearance of new taxa inhabiting new marine basins. This macroevolutionary mechanism is closely connected with the problem of the centers of origin and distribution of taxa, which is considered below.

CENTERS OF ORIGIN AND DISTRIBUTION OF TAXA: EVOLUTIONARY ASPECT

The problem of centers of origin and distribution of different faunal groups is an important topic of zoogeography as was indicated by Geptner (1936), who was the first to compose a general handbook on zoogeography in Russian. Geptner indicated that the data on the evolution of the animal world suggest that each animal group appeared in a certain territory, which is referred to as the center of origin of this group. Clearly, this place is, at the same time, the center of the group's distribution. However, as Geptner indicated, there is a significant difference between the centers of distribution and origin. The center of a group's origin is only its primary center of distribution, from which migration could originally begin. Groups are very often poorly represented in the place where they initially evolved from their immediate ancestor and reach their maximum diversity and number in a different place, from which they migrate widely to other regions. More so, in the region of occurrence of the ancestor, the descendant taxon is usually not found. Thus, there is a slight difference between the centers of origin and the centers of distribution; the body plan of a new group is first formed, and the combination of definitive characteristics of a new taxon is developed, in the center of origin. After migrating and finding a more favorable environment, the group develops a new body plan in the diversity of taxa of a lower rank and achieves greater abundance. Later, the group migrates widely in various directions and occupies new areas. The place where a group first reaches high abundance and diversity, which facilitates its further migration, is the center of its distribution. This center of distribution is at the same time the center of origin of the taxa of a lower rank.

Apparently, there may be several centers of distribution, e.g., primary, secondary, tertiary, etc. It is possible that a few secondary centers could occur in different places simultaneously. Centers of distributions are relatively easy to identify in the history of a group's evolution, e.g., based on its taxonomic diversity. In contrast, identification of the center of origin is not so easy. Firstly, it is assumed that there can be only one center of origin, which is a consequence of the assumption of the monophyly of taxa. For taxa of a lower rank, this is probably often true, although they did not evolve from a single pair of individuals and may have evolved from more than one population. For higher taxa it is certainly not true, because they could evolve through several parallel lineages from different taxa of a lower rank. This agrees with the concept of monophyly of Simpson (1961) who assumed that monophyly is the origin of a taxon from a single immediate ancestral taxon of the same or a lower rank through one or several lineages.

Quite often, the newly formed taxon returns from the center of distribution to the area inhabited by the ancestral taxon and displaces the latter. When the fossil record is incomplete, this complicates the history of the taxon's origin both geographically and morphogenetically. Therefore, Taylor's well-known principle of biogeography appears to be equivocal in saying that, as a result of competition, more primitive organisms and groups are displaced by younger, more advanced ones, which either immigrate or originate there. For instance, it is shown that for modern land faunas the Northern Hemisphere and, sometimes, its northern areas may be considered to be the most important center of distribution on Earth, important for the majority of groups, including those which at present only occur in the Southern Hemisphere. This suggests a northern origin for the modern fauna and the following consequence: primitive forms, members of the oldest wave of immigrants, should be displaced further to the south. The differences between the faunas of different continents should be more distinct toward the south, i.e., a divergence of faunas should be observed.

Among marine faunal groups, this pattern was established for animal assemblages inhabiting coastal and deeper-water parts of the basin. This pattern is discussed especially clearly by Sepkoski and Sheehan (1983) in their onshore-offshore theory. According to this theory, organisms migrated from shallow-water to deeper-water environments, and from the inner shelf to the outer shelf, and thence to the slope. As a result, a greater number of primitive faunal groups occurred in the deeper-water environment than of advanced groups. Sepkoski and Sheehan illustrated this theory with many examples, originally using the Early Paleozoic taxa of higher rank in the course of the Ordovician radiation.

In both of these cases (northern regions and shallow-water environment as centers of origin and distribution), it is situations with rapidly changing conditions that are most suitable for morphological and taxonomic innovations.

This problem is most interesting from the point of view of the mechanism of origin of the higher taxa of Echinodermata, especially large, medium, and small classes, in the course of the Ordovician radiation of marine biota. Preliminary data show that new taxa are formed as taxa in new geographical or ecological niches. This explains the fact that, in the case of taxa of

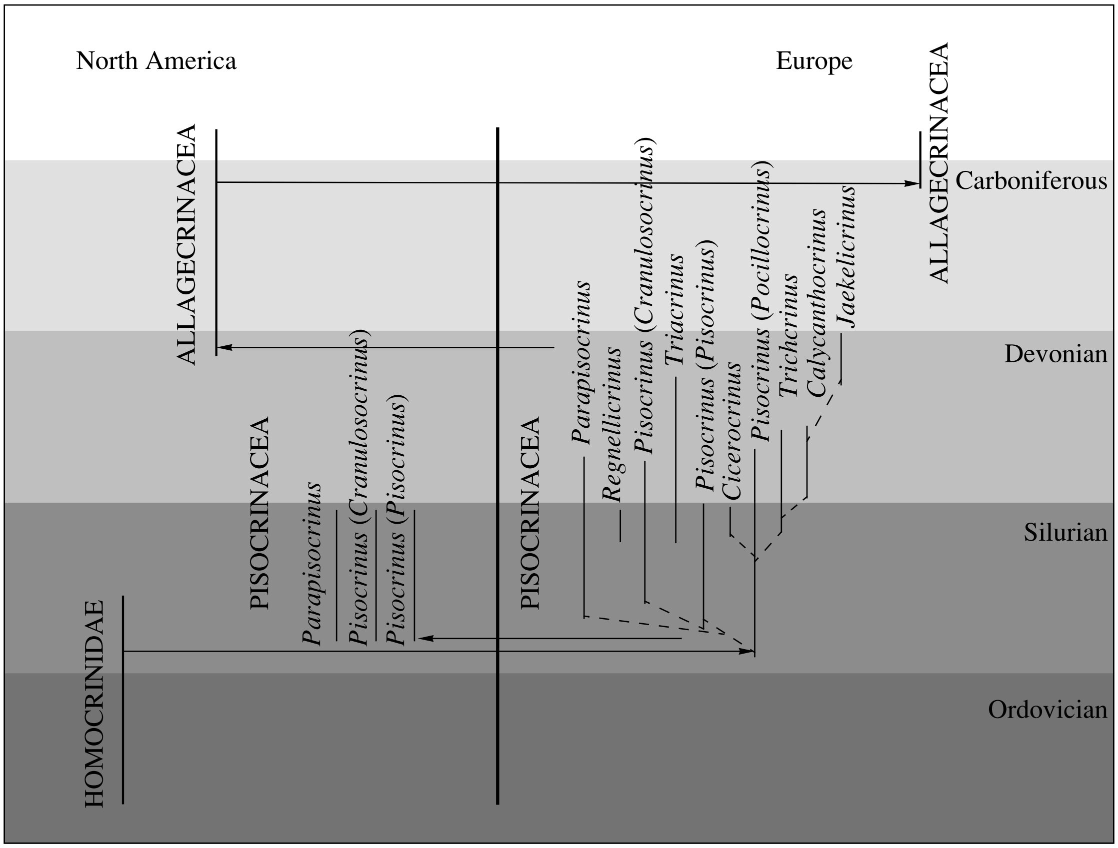


Fig. 88. Scheme showing the biogeographic and stratigraphic distribution of the ancestors and descendants of Pisocrinacea (Crinoidea, Inadunata, Disparida).

family rank, the immediate ancestor is never found together with its descendant.

It is quite difficult to show the same at class level, firstly because the echinoderm biogeography of the Lower Ordovician and Upper Cambrian is insufficiently studied, whereas the study of the morphogenetic mechanism of the origin of classes of Echinodermata has just begun. Secondly, many classes could have originated through several parallel lineages, and hence could have had several centers of origin. Therefore, is it too early to speak about the centers of origin and distribution of many classes of Echinodermata. However, there are good examples of the centers of origin and distribution of several groups of family rank among disparid crinoids. These are primarily two superfamilies, Homocrinaceae and their descendants, Pisocrinaceae.

Homocrinidae is a family of monocyclic inadunate crinoids, which appeared in the Middle Ordovician and immediately gave rise to several other families. The roots of Homocrinidae are connected with the origin of crinoids, most probably with one of the earliest groups, Iocrinidae. In contrast to their descendants, the Homocrinidae is a small group. They range only until the Middle Silurian, and are known only from North America. In the Silurian, they gave rise to Pisocrinidae. As was noted in the above analysis of symmetry, this is indicated by the comparative morphology of these groups, the ontogeny of their skeleton, and geological distribution, i.e., the latest homocrinids occurred at the same time as the earliest pisocrinids. This is one of the rare instances when all researchers unanimously agree on the relationships of large taxa. The scheme of the evolution of the pisocrinid body plan from that of homocrinids is shown in Fig. 65.

In contrast to the exclusively North American homocrinids, pisocrinids are considerably more cosmopolitan. They are well known not only in North America, but also in Eurasia and East Australia (Fig. 88). Representatives of both families are found within the same Silurian cosmopolitan province. However, homocrinids are known only from North America, while pisocrinids are also known from Eurasia and eastern Australia. Undoubtedly, Europe was the primary center of distribution of pisocrinids, particularly the Baltic Silurian Paleobasin, from where the earliest and most primitive pisocrinids and most known genera and subgenera have been recorded (Rozhnov *et al.*, 1989). In North America, beds of almost the same age as those containing the earliest European pisocrinid occurrences (Llandovery) also contain pisocrinids, although only specialized subgenera of the genus *Pisocrinus* and a specialized genus *Parapisocrinus* have been reported.

Table 6. First appearances of the classes of Echinodermata in the fossil record

Geological age	Small classes (10 genera and less)	Medium classes (10–100 genera)	Large classes (over 100 genera)
Silurian (420 Ma)		Blastoidea	
Ordovician (495 Ma)	Paracrinoidea Parablastoidea Coronata Ophiocystoidea Cyclocystoidea	Rhombifera Diploporita	Crinoidea Echinoidea Asteroidea Ophiuroidea ?Holothuroidea
Cambrian (545 Ma)	Ctenocystoidea Homostelea Helicoplacoidea	Stylophora Homoiostelea Eocrinoidea Edrioasteroidea	

Representatives of the subgenus *Pisocrinus (Pocillocrinus)*, ancestral to all pisocrinids, do not occur in North America. Thus, the most primitive pisocrinids appeared in Europe, whereas their immediate ancestors are known only from North America. This could have been considered to be a product of the incomplete fossil record, if it was not for the fact that many descendants of the ancestral subgenus *Pisocrinus (Pocillocrinus)* are known only from Eurasia and Australia (Rozhnov, 1981; Jell and Jell, 1999). Therefore, the incompleteness of the fossil record cannot be considered to be a possible reason. It could have been suggested that, at the beginning of the Silurian, homocrinids spread into Europe and rapidly became extinct after giving rise to widespread pisocrinids. However, no homocrinids have ever been found in Europe. Therefore, another hypothesis seems more plausible. The planktonic larvae of homocrinids needed too much time to spread from North America to Europe and, therefore, they could not overcome this distance at once. Arrests in their ontogeny may have helped this problem, but they were followed by the paedomorphic development of the adult organism, which produced the pisocrinid body plan. Hence, in this case the way of overcoming the problem could itself be a morphogenetic factor, while the center of origin because of this was spatially obscure. Interestingly, the characteristic morphological features of pisocrinids originally appeared in the slow-moving water of the reasonably deep marine environment rather than in the turbulent shallow waters, the place where they later became most abundant and diverse, and to which they were better adapted. The above pattern is directly opposite to the onshore-offshore theory.

The above situation, in which the geographic distributions of ancestors and descendants do not coincide, is not unique. It is typical for many taxa above the family rank. This is also shown in the subsequent history of the Pisocrinaceae. In the Late Devonian, they gave rise to the superfamily Allagecrinaceae, which became widespread in the Late Paleozoic. However, the earliest Allagecrinaceae appeared in the Upper Devonian of North America, while their immediate descendants are known only in Eurasia and Australia. Allagecrinaceae appeared in Europe only in the Carboniferous. Thus, the center of the origin of higher rank taxa is not the same as the primary center of distribution and has its own, in many ways mysterious, features.

THE TIMES OF APPEARANCE OF HIGHER TAXA IN THE GEOLOGICAL RECORD

Modern echinoderms are represented by five classes: crinoids (Crinoidea), sea urchins (Echinoidea), starfish (Asteroidea), brittle-stars (Ophiuroidea), and sea cucumbers (Holothuroidea). In addition to these five, there were at least 15 other classes in the Paleozoic. Each of these classes has a distinct body plan, although some classes are represented by only a few genera. The appearances of these classes and, correspondingly, the development of their archetypes were not scattered throughout the Phanerozoic but occurred only in the Cambrian and Ordovician (Table 6).

This timing does not seem accidental. The subsequent evolution Phanerozoic but occurred only in the Cambrian and Ordovician (Table of Echinodermata displays several important stages, each showing significant taxonomic change in various groups, in both abundance and dominance (Sepkoski, 1979, 1981, 1984). Each of these stages differs considerably from the others in many features, the most important of which is a changeable maximum taxonomic rank (Rozhnov, 1994, 1995, 1998, 2001). For instance, the Precambrian–Cambrian boundary shows the apparent first appearances of all 33 surviving phyla of multicellular animals and, possibly, of a few superphyla (Fig. 89). The first occurrence of bryozoans in the Lower Ordovician only supports the general rule, because the phylum to which bryozoans belong certainly appeared not later than the Cambrian. The Cambrian–Ordovician boundary showed the appearance of taxa not above the class or, sometimes, subphylum rank. For instance, of 20 classes of echinoderms, 12 first appeared in the Ordovician, including all five surviving at present. Not a single new class has appeared since.[1] At the Permian–Triassic boundary, the new taxa that appeared were not above subclass, and were usually orders, while at the Cretaceous–Tertiary boundary newly appearing taxa were families and superfamilies, and only rarely orders. This indicates that the marine invertebrate fauna developed to a large extent synchronously in different taxa, showing the progression from a general body plan to less important features. Studying the origin of large taxa in the geological past, we have to deal with one of the above geochronological boundaries, at which the roots of these taxa seem to be lost. Therefore, the problem of the origin of the large taxa requires a special study of the corresponding boundaries.

SECTION 2. CAMBRIAN–ORDOVICIAN LEVEL IN THE DEVELOPMENT OF ECHINODERMATA

The Cambrian–Ordovician boundary is the most interesting and favorable for such a study, because it shows the appearance of taxa of higher rank (classes), and their roots are more easily traced in the fossil record than those of the even larger taxa appearing at the Precambrian–Cambrian boundary. The Cambrian–Ordovician boundary also shows sharp changes in the environment, sedimentation, and taxonomic composition of the fauna (Rozhnov, 1994; Guensburg and Sprinkle, 1992; Sprinkle and Guensburg, 1995). Biotic and abiotic changes will be shown below to be mutually dependent, a fact that was responsible for the high rate of radiation shown by the Ordovician marine biota.

All marine invertebrates known from the Phanerozoic may be grouped into three major evolutionary faunas, dominating at different times (Sepkoski, 1979, 1981, 1984). The Cambrian evolutionary fauna appeared immediately after the Vendian and dominated until the Late Cambrian. The Paleozoic evolutionary fauna appeared between the Late Cambrian and Early Ordovician and, after that, dominated until the end of the Paleozoic. The modern evolutionary fauna gradually appeared in the Paleozoic but only became dominant after the Permian–Triassic extinction, which destroyed the major groups of the Paleozoic faunas.

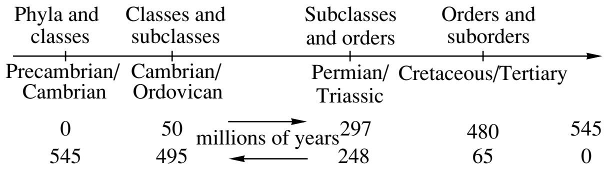


Fig. 89. Maximum taxonomic level of the evolutionary radiation of marine Metazoa in the major boundaries within the Phanerozoic.

Sprinkle (1980, 1983) showed that the fauna of Echinodermata, one of the best studied in the fossil record, passed two stages of diversification, one in the Cambrian and one in the Ordovician; this agrees well with Sepkoski's model. Sprinkle (1980, 1992) showed that the original Cambrian radiation had a peak in the Middle Cambrian, when seven or eight classes and 31 echinoderm genera existed, while in the Late Cambrian and early Ordovician, the diversity was much lower. The secondary radiation of echinoderms had a peak in the Middle Ordovician, when the number of classes reached 17, and the number of genera exceeded 210 (Sprinkle, 1980). However, Smith (1988a, 1988b, 1990), based on a cladistic analysis of the Cambrian and Early Ordovician echinoderms, showed that the original diversification of echinoderms, which began in the Early Cambrian, increased continuously, while the low diversity of echinoderms in the Late Cambrian is an artifact. Certainly, this argument can only be resolved when the Late Cambrian and Early Ordovician faunas are more completely studied. However, at present it is seen that the evolution of the marine biota was rapid, occurred in a particular way, and resulted in considerable changes in taxonomic composition. Each of these levels is characterized by its own maximum taxonomic level of radiation of marine biota (Fig. 89). The Ordovician radiation of marine biota led to the rapid replacement of the Cambrian evolutionary fauna by the Paleozoic fauna (Sepkoski, 1979, 1981, 1984). Many classes of animals characteristic of modern seas appeared as part of the Paleozoic evolutionary fauna. For instance, all five modern classes of echinoderms first appeared in the Ordovician, and their roots are lost somewhere in the Cambrian (Figs. 87, 89). At the Cambrian–Ordovician boundary, many features of the environment changed sharply, as well as sedimentation and the taxonomic composition of faunas. The interdependence of biotic and abiotic changes at the Cambrian–Ordovician boundary was responsible for the rapid radiation of marine biota in the Ordovician. Echinoderms were the group that initiated the Ordovician radiation (Rozhnov, 1994; Guensburg and Sprinkle, 1992; Sprinkle and Guensburg, 1993, 1995, etc.). Therefore, knowledge of the nature of the evolution of Early Paleozoic echinoderms is essential for understanding different aspects of Ordovician radiation.

The changes in the echinoderm environment at the Cambrian–Ordovician boundary are discussed in greater detail below.

FEEDING FEATURES OF THE EARLY PALEOZOIC ECHINODERMS AND THEIR ROLE IN BENTHIC COMMUNITIES

Ecological aspects of the early Paleozoic evolution of marine biota have attracted the attention of many researchers primarily attempting to reveal the features

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[1] Blastoidea, the first typical representatives of which are known from the Silurian, should perhaps be united in the same class with their ancestors, Ordovician coronate echinoderms. In any case, this exception just emphasizes the remarkable general rule.

of the environment and their influence on morphological and taxonomic evolution. The most complex problem of the ecological aspect of the evolution of marine biota is the identification of trophic connections, feeding chains of the fossil organisms. While this problem remains unsolved, it is impossible to reconstruct a convincing evolutionary pattern of this biota, especially in the Early Paleozoic.

Echinoderms played a large role in Cambrian marine communities, and in the Ordovician, they were often a dominating group of the benthic fauna and were certainly important for the Ordovician radiation of marine invertebrates to proceed (Rozhnov, 1993, 1994, 1998; Guensburg and Sprinkle, 1992; Sprinkle and Guensburg, 1995; Wilson and Palmer, 1992). Therefore, to approach the problem of feeding in Early Paleozoic echinoderms, the question of trophic levels and feeding chains of the entire marine biota has first to be discussed.

Recent echinoderms are represented by five classes. Their role in modern benthic communities is large and diverse. In many benthic biocoenose, they are dominant groups because of their large biomass and abundance. They often form large accumulations. For instance, brittle-stars in the coral reefs of Florida are the most abundant of all macroinvertebrates (after corals) and are the usual food sources for many predators (Hendler *et al.*, 1995). In the reefs, 1 m^2 may contain up to 100 individual brittle-stars. Populations of other echinoderm classes can be as dense. Only crinoids are quite rare in modern seas.

Modern echinoderms are very diverse in their feeding habits. Many of them are passive suspension feeders, although some are active. Many are detritivores. Some are predators. Parasitism is almost absent. However, this diversity of feeding habits in echinoderms was not always the same.

Along with five classes, which survived until now, there were about 20 classes of echinoderms in the early Paleozoic. Each of these classes had its own body plan. This striking diversity of archetypes contrasted with a low diversity of feeding habits; almost all Early Paleozoic echinoderms were passive suspension feeders, and only some were supposedly detritivores. In the modern seas, the so-called eleutherozoan echinoderms (capable of moving) are dominant, whereas in the early Paleozoic biocoenoses, the majority were attached pelmatozoan echinoderms. These pelmatozoan echinoderms played possibly the most important role in the establishment of the Early Paleozoic marine biota, and their feeding habits indicate important features of the marine Early Paleozoic biocoenoses.

Before discussing this, the feeding mechanism in pelmatozoan echinoderms must be considered. This feeding mechanism apparently survived from the beginning of the evolution of this group until the present day. Many data suggest that it was probably also characteristic of the ancestors of pelmatozoan echinoderms (Rozhnov, 1998).

The feeding of most pelmatozoan echinoderms was apparently similar to that of modern crinoids because of the similar structure of the food-gathering and ambulacral systems. The feeding of extant crinoids is well studied. Below, it is described according to Meyer (1982) and Meyer and Lane (1976).

Crinoids collect food from currents, i.e., they are rheophilic animals. While feeding, the crown is recumbent along the current. Food particles are collected from the turbulent currents that are formed when the crown is positioned in this way above the food-gathering grooves on the arms. At first, food particles are held in a bolus of mucus excreted by the specific ambulacral tentacles. These tentacles are arranged along each arm in triads, periodically extending from the radial ambulacral canal. The longest tentacle in a triad grasps a mucous lump with food particles, conveys it to the middle tentacle, which transfers it to the food-gathering groove, covered by ciliate epithelium. The bolus is conveyed by cilia along the food-gathering canal to the mouth and, subsequently, reaches the digestive system. The ancient origin of this feeding pattern is supported by the structures of arms in the distant ancestors of crinoids (Soluta) (Rozhnov and Jefferies, 1996) and by the existence of triads of ambulacral tentacles along the food-gathering grooves of the arms in this group. The imprints of these triads of tentacles were found by Jefferies (1990) in the Ordovician Soluta *Dendrocystoides*.

Because the food particles grasped by the tentacles were conveyed to the food groove, their size could not exceed the width of this groove. Comparing the size of the groove in different groups, one can assess the maximum size of food particles that could be consumed by these animals. It was shown that in crinoids existing from the beginning of the Ordovician the diameter of the food groove was at least 0.25–0.5 mm, and often considerably larger. For instance, in the disparid crinoid *Sheldikhocrinus* from the Ordovician (Volkhovian, Arenig) of the Leningrad Region, the width of the food groove in the proximal part of the arms was 0.8 mm, while the cup was about 5 mm high, and in the hybocrinid crinoid *Hoplocrinus dipentas*, from slightly younger beds (Lasnamyagi, Llanvirn) of the same region, this width reached 2 mm, while the size of the theca was about 10 mm. In Cambrian eocrinoids (the only pelmatozoan echinoderms existing at that time), this diameter was considerably smaller, usually about 0.1 mm (Sprinkle, 1973). In the eocrinoid *Ridersia* from the Middle Cambrian of Australia, the width of the food groove was about 0.2 mm, while the theca was about 20 mm high. This suggests that the size of the food particles used for feeding by the Cambrian suspension-feeding echinoderms was at least three or four times smaller than the size of the particles on which crinoids fed in the Ordovician. Judging from the diameter of the food grooves, the food particles consumed by other post-Cambrian pelmatozoan echinoderms were as small as those consumed by Cambrian echinoderms. The data given below on some Middle Ordovician echinoderms of the Leningrad Region display it very clearly. In the diploporite cystoid *Spheronites*, the width of the food groove near the base of the brachioles was 0.2–0.25 mm, while the diameter of the theca was 13 mm. However, in a specimen with a theca diameter of 40 mm, this width was 0.5 mm. In the diploporite cystoid *Haplospheronis*, which was attached directly to the sea floor, the width of the food groove was 0.2–0.3 mm. In the eocrinoid *Cryptocrinites*, with a theca diameter of about 10 mm, the width of the food groove was 0.1–0.2 mm. In modern suspension-feeders, the size of the food particles usually determines the type of food. This suggests that the Ordovician crinoids had found a new food supply.

What could this new food have been, and what could have been the general food of the Early Paleozoic echinoderms? Modern crinoids mostly feed on plankton, although the proportion of organic debris in their diet is quite large. Among the planktonic organisms found in their digestive system, the most abundant are copepods, followed by dinoflagellates and diatoms. In other words, the animals studied fed on organisms from 60 μm to 2 mm in size. However, this ratio generally depends on the planktonic group of appropriate size dominating at the time. Supposedly, the earliest crinoids also mostly consumed plankton of appropriate size. On what sort of plankton could they have fed? Firstly, it could be phytoplankton. Because Ordovician crinoids inhabited shallow-water epicontinental seas, not more than a few dozen meters deep, there should have been a sufficient amount of phytoplankton in their environment. Probably, this phytoplankton was consumed by some planktonic arthropods, which could also have been fed upon by the crinoids. In addition, they could have fed on the larvae of benthic animals. It is suggested that the appearance of crinoids was connected with the adaptation by pelmatozoan echinoderms to a new source of food not available to their Cambrian ancestors, i.e., living plankton.

Indeed, the digesting of food particles by the first multicellular animals was apparently intracellular, i.e., food particles appearing in the intestine were seized and digested by special cells. In more advanced animals, the digestion occurred inside the intestinal cavity. Echinoderms have both these feeding types (Lawrence, 1982). Prosser and Brown (1962) suggested that extracellular digestion was apparently used at first to reduce large particles to a size appropriate for intracellular digestion, and only later in evolution, was intracellular digestion gradually replaced by extracellular digestion. It is possible that bacteria played an important role in this change. The first multicellular animals digested bacteria and organic matter decomposed by bacteria. Later, as a result of symbiosis with bacteria, they were able to kill and digest living organisms. Supposedly, this process of increased complexity of feeding occurred synchronously in many groups. For instance, echinoderms apparently became able to feed on living plankton at the end of the Cambrian–beginning of the Ordovician. It is suggested that this enabled the appearance of the morphological organization of crinoids.

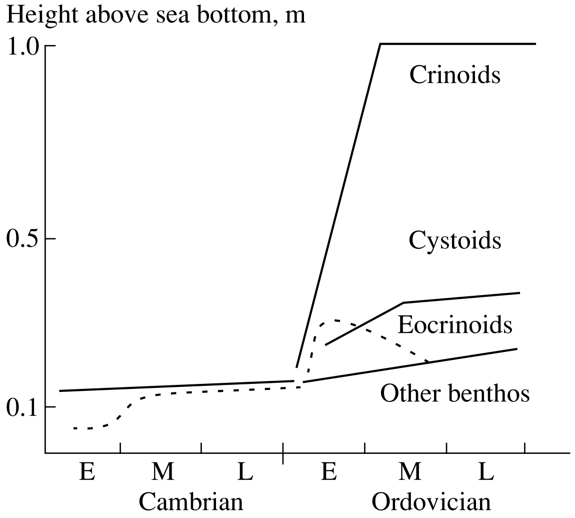

Fig. 90. Maximum height of the food-gathering system above the sea floor in some animal groups in the Cambrian and Ordovician.

This hypothesis agrees well with another change in the feeding habits of echinoderms at the Cambrian–Ordovician boundary; the higher level of the food-gathering apparatus above the sea bottom (Fig. 90). At the beginning of the Ordovician, the appearance of stemmed crinoids resulted in the appearance of tiering in the structure of the benthic community (Ausich and Bottjer, 1982; Bottjer and Ausich, 1986; Rozhnov, 1993). In the Cambrian, benthic animals were not elevated more than 10–15 cm over the bottom and often were not elevated at all. In the Ordovician and later, they were elevated over a meter and higher. The lower level in the Ordovician seas was occupied by so-called blastozoan echinoderms, which fed on small particles, while the upper level was occupied by crinoids feeding on relatively large particles. These groups did not compete for food because of the difference in the size of the food particles consumed, but they still occupied different niches. How can this fact be explained? And what changed at the Cambrian boundary? Why did some of the descendants of the Cambrian pelmatozoan echinoderms begin to seize larger particles from the higher water levels, while some retained ancestral features of feeding and were fed on small particles immediately above the bottom?

It is suggested that near the bottom the main food resource was not plankton but organic debris and bacteria inhabiting this debris. Living plankton supposedly lived mostly slightly higher up in the water. The food-gathering organs of crinoids were elevated to this level to form a new tier. In addition, it is possible that by the

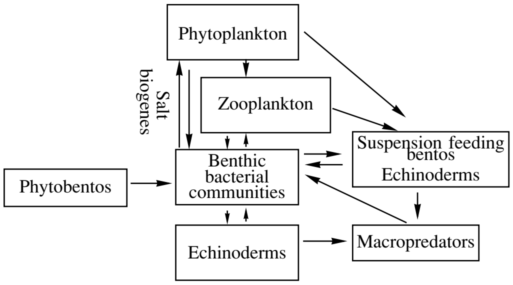

Fig. 91. Scheme showing the ecosystem of epicontinental seas in the Early Paleozoic in the position of echinoderms in this ecosystem. Arrows show the direction of flow of organic matter. The small role of macropredators is a characteristic feature of this ecosystem.

beginning of the Ordovician, zooplankton that fed on phytoplankton were rapidly radiating. Passive defense against zooplankton could result in an increase in the body size of many representatives of phytoplankton. Zooplankton cleared the water, because while seizing food particles, clay particles were filtrated and deposited with feces, as occurs in modern seas. Clearing of the water sharply increased the productivity of plankton and increased the total biomass in the seawater. This resulted in an increased influx of organic matter to the near-bottom water layer, which in turn increased the productivity of the benthos.

The bottom dwelling, benthic biota, despite the strikingly different taxonomic composition in the Cambrian and Ordovician, had an important feature in common. That was the near absence or, more precisely, insufficiency of macropredators capable of utilizing a large part of the biomass of macroinvertebrates. In modern seas, the proportion of benthos consumed by predators may be very large. For instance, according to the data published by Sorokin (1990), in modern reef biotopes with loose sediments, fish may consume up to 3% of the total benthic biomass. In the absence of predators, the mass of both living and dead benthic animals would sharply increase. Such environments apparently existed in the Early Paleozoic and were responsible for an increased amount of decomposing organic matter at the bottom of the epicontinental seas and for the diversity and abundance of bacterial communities. The sea floor was usually well aerated because the epicontinental seas, widespread in the Early Paleozoic seas, were not deep. Therefore, hypoxic conditions at the sea bottom were not common.

Some features of the hypothetical food chains in the Cambrian and Ordovician marine communities of the epicontinental seas become more understandable when they are compared to the modern reef communities, because no modern seas are adequately comparable to the ancient epicontinental seas. The modern biosystems of shelf and open ocean differ from the latter in many ways. Firstly, all Cambrian and Ordovician epicontinental seas were autotrophic ecosystems, i.e., there was apparently no significant contribution of organic matter from the land. Besides, it is important to note that the exchange rate in a medium with an impoverished content of inorganic nutrients was apparently very high because the large areas of shallow waters where mixing of the surface and bottom water layers occurs was possible. This is similar to many modern Pacific atolls. In contrast to the latter, the productivity of most epicontinental seas was much lower. Secondly, the role of bacterial communities in the circulation of organic matter in modern reefs and, apparently, in the Cambrian and Ordovician epicontinental seas was similar. In coral reefs, bacterial communities are developed on the energy basis of the mucus produced by the corals. It is well known that water drawn off from the reefs during the low tide contains organic aggregates (so-called sea snow). This aggregated organic matter is formed by bacteria from the mucus produced by the corals. The aggregated state of the majority of bacterioplankton makes it available for consumption by medium- and large-scale suspension-feeding invertebrates inhabiting reefs (Sorokin, 1990). According to Sorokin (1990, p. 102), “the filtration rate shown by fine and large-scale suspension-feeders consuming the natural bacterioplankton from the sea water was quite comparable to the filtration rate while consuming planktonic algae, which until recently were considered the major (if not the only) food resource for benthic suspension-feeders.”

Based on the comparison of the Early Paleozoic marine epicontinental assemblages with modern reef communities, we suggest that the Cambrian suspension-feeding benthos and a considerable part of the Ordovician benthos feed not on plankton but on dissociated particles of dead soft tissues of different animals and plants, organic debris, and bacterial aggregates around and near these particles (Fig. 91). The feeding of eocrinoids in the Cambrian and other blastozoan echinoderms in the Ordovician on such particles was not neccessarily performed by using brachioles (specialized food-gathering apparatus). Rather, we suggest that the feeding of Early Paleozoic echinoderms depended largely on dissolved organic matter and bacteria digested through the walls of the soft body of the animal. This feeding pattern is closely connected with the above-mentioned environmental features of the Early Paleozoic marine biota, primarily with the insufficient number of macropredators and, thus, with the strongly developed bacterial communities near the bottom. Which animals could have been macropredators in the Cambrian and Ordovician? Some arthropods could be potential predators, since they have a strong grasping apparatus. However, their number was small. Additionally, they may have been only opportunistic predators, using their strong grasping apparatus mainly to eat dead animals. In the Ordovician, some cephalopods could also be potential predators, although this is unlikely, because they have large body size, and it would have been difficult to find prey of the appropriate size. Polychaeta and some gastropods could also be potential predators, but this is almost all. The list of potential Ordovician predators published by Nevesskaya (1998) seems somewhat too large (certainly there were no predators among the starfish and bristle-stars at that time).

Nevertheless, there were predators in the Early Paleozoic, although few in number and not diverse. This is indicated, for instance, by the presence of damaged bolboporites from the Lower Ordovician of the Leningrad Region (Rozhnov and Kushlina, 2001).

In any event, the number of predators in the Cambrian and Ordovician was low and insufficient to utilize a considerable biomass. Therefore, the food chains in the Early Paleozoic bottom communities were not only considerably shorter than in similar modern communities but were different because of the large accumulation of decomposing biomass in the bottom water layers. Because of the scarcity of predators, a considerable amount of dead organisms reached the bottom; therefore, the bottom water layers in the Cambrian and Ordovician were increasingly saturated with organic matter. This high degree of saturation of the water with organic matter was apparently responsible for the characteristic features of the benthic communities in the Cambrian and Ordovician. These features affected echinoderms in the most direct and immediate way, i.e., first their feeding and subsequently the structure of their skeleton. The skeleton of the theca in different Early Paleozoic groups always has a particular system of pores (Fig. 92). In the Cambrian, these were the pores on the borders between plates, sutural pores, and epispires. In the Ordovician, these were true pore systems, represented by diplopores or various rhomboid pores. Crinoids were the sole exception, because they usually lacked pores.

It is usually thought that these pore systems were used for breathing. These areas were certainly responsible for gas exchange; it is not clear whether respiration was the main function of these pores, but this was probably not the case. Indeed, the intensity of respiration indicates the intensity of metabolism. However, the latter depends not only on the quantity of oxygen consumed but also on the quantity of food digested. Hence, the development of the respiratory systems should be proportional to the development of the food-gathering apparatus. The pore system in the theca of echinoderms is more likely inversely proportional to the development of the food gathering system. For instance, in crinoids with a much more strongly developed system of food gathering (using arms), the pore system was always more weakly developed than in other Early Paleozoic echinoderms and, more often, was completely absent. Therefore, the pore system of the Early Paleozoic echinoderms was used for feeding on dissolved organic matter and bacteria. Many recent studies have shown that in modern echinoderms feeding on the dissolved organic matter through the body wall occurs in many groups, within all five extant classes. However, such feeding only forms a significant proportion of the general diet of echinoderms under extreme conditions. Firstly, it occurs when there is no other food; secondly, when the food gathering mechanism or digestive system stops functioning properly. For instance, in bristle-stars when the disc is strongly damaged and feeding through the mouth is impossible, feeding occurs by absorbing dissolved organic matter through the body wall until the disc is completely regenerated.

A striking case of such feeding was recently discovered by Oji and Amemiya (1998) in the modern crinoid *Metacrinus*. These researchers placed an amputated fragment of a crinoid stem in a water tank. The cup, arms, and the entire digestive system were completely absent. However, this fragment of the stem fed on dissolved organic matter and survived for at least a year.

Thus, the possibility of feeding on dissolved organic matter through the body wall was experimentally discovered in modern echinoderms. Apparently, in many Early Paleozoic echinoderms, this feeding pattern was at least as important as that using ambulacral tentacles. It is probable that the pore system in the thecal skeleton was, to a large extent, used for this particular purpose.

The proportion of products supplied by the primary producers to be later digested by suspension-feeders apparently increased significantly. This led to changes in the structure and taxonomic composition of the communities of detritivores and silt-feeders, since a considerable part of the organic matter was now supplied by suspension-feeders rather than by silt-feeders. The changes in the community of detritivores and silt-feeders were facilitated by changes in the composition of the substrates over large areas at the beginning of the Ordovician, when the content of calcite debris in the soft grounds increased, and hard and semihard grounds became very widespread. The majority of the debris for hardgrounds was produced by echinoderms, trilobites, ostracodes, and brachiopods (many juvenile shells supplying large volumes of debris) and bryozoans (which produce small volumes of debris because of the monolithic skeleton). A sharp increase in the amount of calcite debris at the beginning of the Ordovician resulted in the appearance of positive feedback between the substrate and the debris-producing organisms inhabiting them. This feature of the hardgrounds, which may be referred to as self-reproduction, was the major mechanism of Ordovician evolutionary radiation.

THE MECHANISM OF ORDOVICIAN RADIATION

THE ORDOVICIAN RADIATION OF THE BENTHIC GROUPS OF FAUNA AND THE ORIGIN OF THE HARDGROUND ECOSYSTEM

The Ordovician radiation of animals, which resulted in the development of the Paleozoic type of marine fauna, did not establish any new taxa above class level, whereas the previous major radiation, at the Precambrian–Cambrian boundary, was responsible for the establishment of phyla and subphyla. The Precambrian–Cambrian is the most interesting boundary for

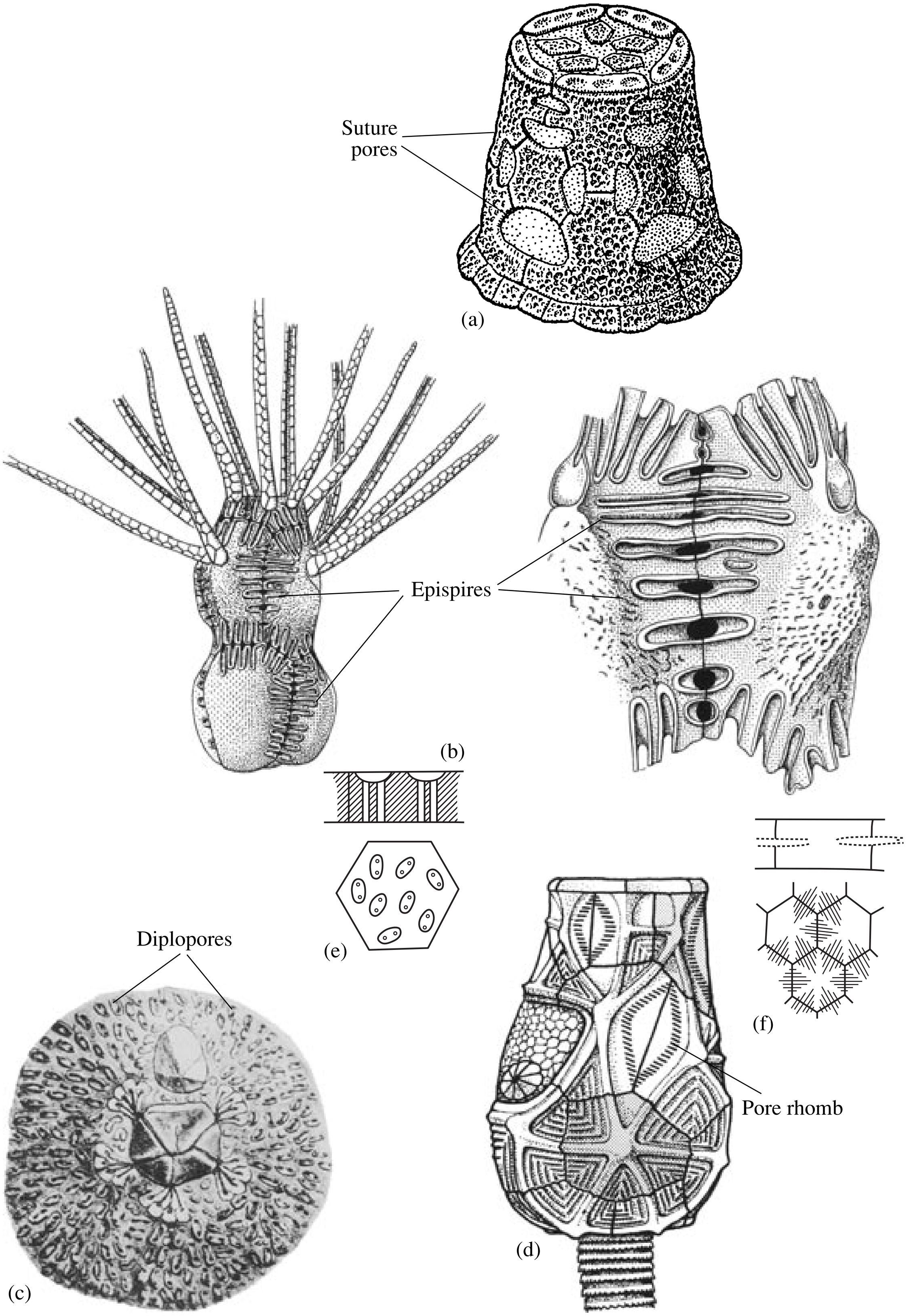

Fig. 92. Different pore system in echinoderms: (a) sutural pores in eocrinoid *Simonkovicrinus reticulatus* (lower part of the Middle Ordovician of the Leningrad Region) (after Rozhnov, 1991); (b) epispires in the eocrinoid *Lichenoides priscus* (Middle Cambrian of Bohemia) (after Ubaghs, 1967); (c) diplopores in the diploporite *Haplospheronis kiaeri* (Middle Ordovician of Norway); (d) pore rhombs in the *Homocystites anatiformis* (Rhombifera) (Middle Ordovician of North America); (e, f) generalized schemes of the section and the external surface of (e) diplopores and (f) rhombous pores [(c–e) after Kesling, 1967].

the study of the evolution of the higher taxa constituting marine biota, because it showed the greatest radiation of higher taxa in the evolution of the marine fauna. Therefore, we can compare the two consequent faunas and reveal patterns in the development and establishment of taxa of a higher rank, i.e., classes and subclasses. At the Precambrian–Cambrian boundary, the highest taxonomic level of radiation was even higher (phyla and subphyla), but it is difficult to compare the poorly preserved, soft-bodied Precambrian ancestral fauna with the Cambrian skeletal fauna.

According to Valentine's (1992) research into the macroevolution of phyla, the origin of higher taxa always remains ambiguous, irrespective of methods used (comparative embryology, comparative anatomy of adult animals, molecular biology, or paleontology). Many researchers do not treat this phenomenon as random and usually explain it assuming that many phylogenetic lineages appear suddenly. To explain high evolutionary rates at the time of origin of higher taxa, researchers either emphasize integral aspects of evolution, such as large-scale and rapid genetic changes and various heterochronies, or focus on environmental changes. In studying the Ordovician radiation, both these aspects are clearly seen, and their relationships can be revealed.

The Ordovician evolutionary radiation of the benthic fauna was affected firstly by changes in the nature of marine substrates, and secondly by those environmental factors that were typical of the entire Phanerozoic (e.g., the appearance of new epicontinental basins as a result of strong transgressions and the geographic positions of the centers of origin and centers of distribution considered above). Hardgrounds became widespread, whereas many soft grounds were enriched by debris. Below, an attempt is made to connect the radiation of the marine biota to changes in substrates and to show the mutual dependence of these processes.

Types of Hardgrounds

The fauna of hardgrounds is always very different from the fauna of soft silty substrates, both in terms of abundance and taxonomic composition. However, there are two types of hard sea floors, characterized by different hydrodynamic energy and sedimentation. Consequently, the resulting environments are also different. These are so-called rockgrounds and hardgrounds.

Rockgrounds

This type is formed during transgressions accompanied by erosion of previously accumulated deposits. They represent a high-energy environment, which to a large extent determines the adaptations of the fauna inhabiting this substrate.

The rocky sea floor has existed since the appearance of large water basins. There are areas naturally protected from wave turbulence (framework cavities, niches, and deeper areas where the bottom is hard due to its origin, i.e., submarine lava flows, fallen blocks, etc.). The rocky sea floor always constituted a small proportion of marine substrates and played a small but sometimes interesting role in the formation of marine biota.

Hardgrounds

Hardgrounds are formed as a result of synsedimentary lithification of marine sediments and are not usually associated with high levels of hydrodynamic energy. For the first time in the geological record, hardgrounds appeared in the Middle Cambrian, but from the beginning of the Ordovician, they periodically occupied large areas of the sea floor and were inhabited by an abundant and diverse benthic fauna. In some places, hardgrounds intergrade into variously soft, debris-rich substrates. This enables interactions and mixing of the faunas of hard and soft substrates.

Hardgrounds are not formed in all basins, but only in basins of specific chemical environments in so-called calcite-precipitating seas. The periodicity of the appearance of such seas, beginning from the Late Cambrian, determined the periodicity of the appearance and wide distribution of hardgrounds in geological history. For hardgrounds to appear, a certain balance between the rate of sedimentation and lithification is necessary. When sedimentation was faster than lithification, a specific kind of soft ground, with a hardened underlying layer, was formed. This provided varying degrees of semihard substrate, and the combination of these with the true hardgrounds resulted in a high diversity of benthic fauna.

Characteristics of the Early Paleozoic Sea Floor

Marine Substrates in the Cambrian

The sea floor in the Cambrian was mainly covered by soft silt sediments, with a small amount of debris. Hard bottoms occupied small areas. In the early Cambrian, these were almost entirely represented by rockgrounds. The fauna of rockgrounds is poorly known because of its poor preservation. Nevertheless, an unusual fauna was discovered in cavities that were isolated and semi-isolated from the water turbulence in the archeocyathid bioherms and reefs of western Nevada and Labrador (James *et al.*, 1977; Kobluk and James, 1979). These cavities contained algae, sponges, juvenile archaeocyathids, agglutinated foraminifers, several taxa of problematic organisms, and *Trypanites* borings. Later, a similar cryptic fauna was also discovered in the cavities of archaeocyathid reefs in many regions worldwide, including the Siberian Platform, southern Urals, Altai–Sayan Foldbelt, Mongolia, southern Australia, and Antarctica (Zhuravlev and Wood, 1995). Hardgrounds discovered in the Middle Cambrian of Green-

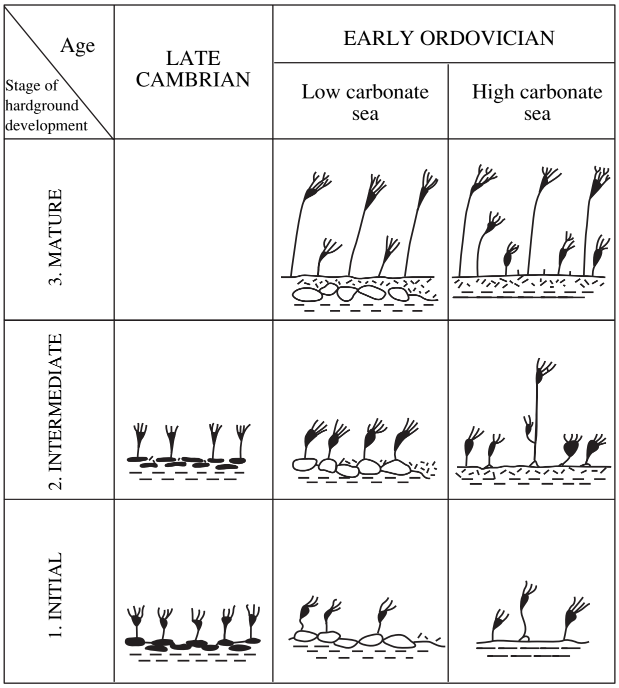

Fig. 93. Scheme showing the development of hardgrounds in the Late Cambrian and Early Ordovician.

land were formed by early diagenetic replacement of cyanobacterial mats by phosphatic minerals. Some mats show small, attached holdfasts, most likely belonging to echinoderms (Wilson and Palmer, 1992). The Upper Cambrian rocks of Nevada, Montana, and Wyoming contain eocrinoids attached to flat pebbles washed from the sediment (apparently by storms) and consolidated soon after (Brett *et al.*, 1983). Such rigid bottoms can be considered to be genuine hardgrounds, although they were somewhat different from the Ordovician hardgrounds (Rozhnov, 1994).

Thus, there are no apparent similarities between the faunas of the Cambrian rockgrounds and the first hardgrounds. The only apparent exception is *Trypanites*, the earliest borings of which were discovered in Early Cambrian cavities of archaeocyathid bioherms, i.e., on the rocky floor. The geochronologically younger *Trypanites* occur only starting from the Middle Ordovician, but on the hardgrounds, where they sometimes occupy large areas. No *Trypanites* borings have been discovered in the Middle and Upper Cambrian (Wilson and Palmer, 1992). However, the actual identity of the Lower Cambrian and Ordovician *Trypanites* borings is somewhat doubtful. Thus, the fauna of hardgrounds supposedly appeared independently from the rocky bottom fauna. Attached echinoderms were the first and rapidly became the most important components of the hardground communities.

The Late Cambrian hardgrounds were created, to a large extent, by echinoderms consolidating the cobbles on which they initially settled with debris accumulated following postmortem disarticulation of echinoderm skeletons. Calcite productivity of echinoderms in the Cambrian was low, and the calcite debris produced by them was only sufficient to fill the spaces between the cobbles. The community inhabiting such hardgrounds was not capable of increasing the area of its substrate by creating a new hardground. This and apparently the low distribution of calcite in the seas at that time were the reasons for the scarcity of hardgrounds in the Upper Cambrian.

Marine Substrates in the Ordovician

A considerable area of the Ordovician epicontinental sea floor was also covered with soft silt sediments. In contrast to the Cambrian substrates of this type, these silts typically contained large amounts of calcite debris and were often transformed into hardgrounds occupying large areas.

As in the Cambrian, Ordovician rockgrounds occupied relatively restricted areas and were scarcely populated by benthic animals (apparently, because of high water turbulence). However, a rich and diverse fauna developed in semicovered cavities of bioherms, for instance, in the cavities within the Caradoc bryozoan-algal bioherms in Estonia near the village of Vaasalemma. These cavities contained bryozoans, crinoids, cystoids, edrioasteroids, and brachiopods, often well preserved. However, this fauna was insignificant in evolutionary terms because of the limited abundance of such niches, and because they were colonized secondarily.

Ordovician hardgrounds were very widely distributed, occupied large areas, and were colonized by a characteristic and diverse fauna. This was especially typical of the Middle Ordovician. The Early Ordovician hardgrounds are considered to be transitional from the Late Cambrian hardgrounds to the Middle Ordovician and generally to the Paleozoic hardgrounds. They were similar to the Late Cambrian hardgrounds in the predominance of eocrinoids, the absence of *Trypanites* borings, and the presence of pebbled areas needed for their initiation. Similar to the Middle Ordovician hardgrounds, the Early Ordovician hardgrounds contained bryozoans. This interpretation was based on the analysis of hardgrounds in the Kanosh Shale in North America (Wilson *et al.*, 1992).

The sequence of formation of hardgrounds in the carbonate part of this section can be attributed to the following sequence of events (Fig. 93): (1) the development of carbonate nodules in the soft sediment; (2) washing of nodules and the formation of cobble lags; (3) colonization of the cobbles by echinoderms (predominantly eocrinoids); (4) accumulation of carbonate echinoderm debris; and (5) consolidation of the echinoderm debris and subsequent colonization of the resulting hardgrounds by echinoderms, bryozoans, and sponges.

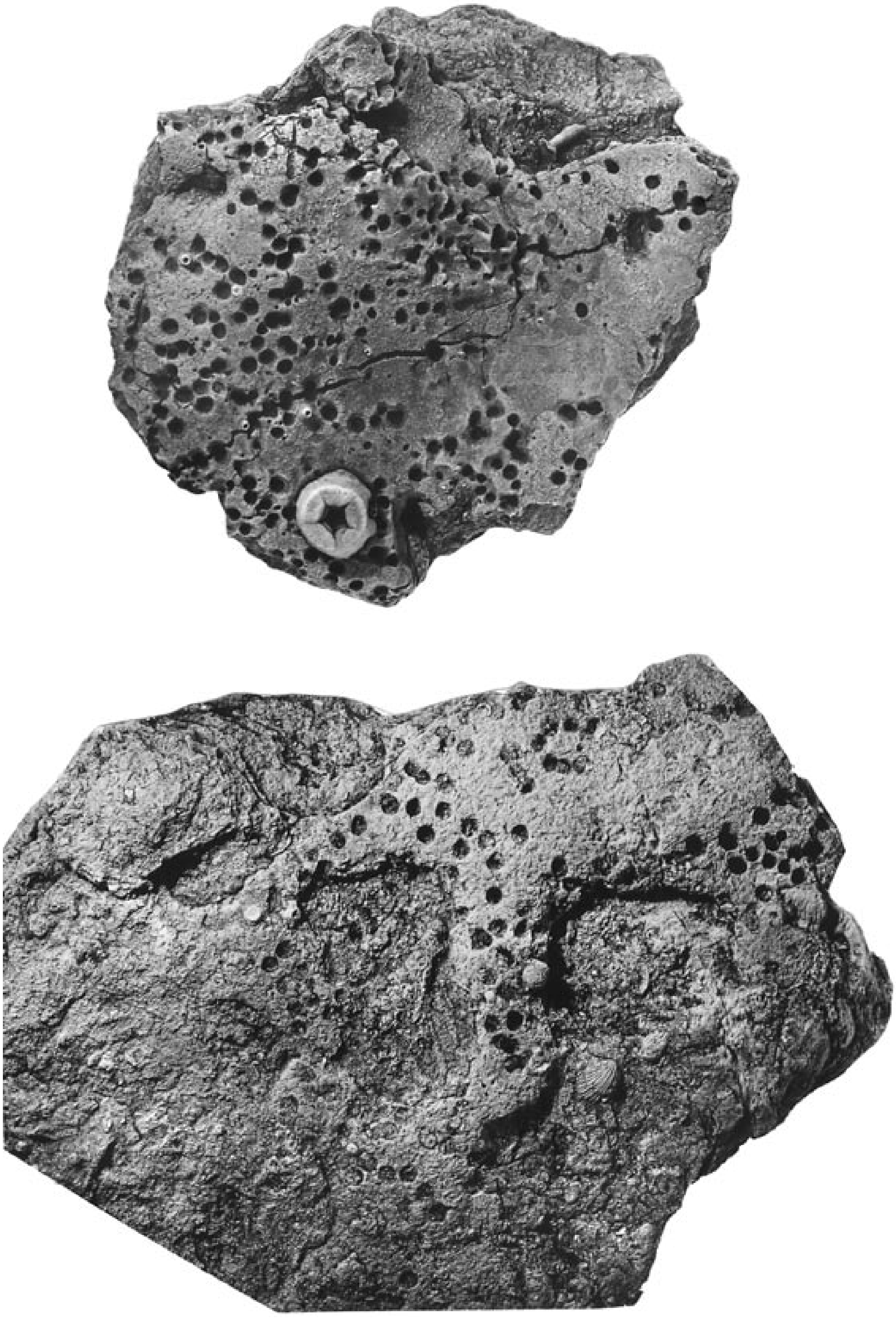

Fig. 94. Photographs showing the Middle Ordovician hardground (Volkhovian, Upper Arenig) of the Leningrad Region with *Trypanites* borings, holdfasts of crinoids and trepostomid bryozoans. The lower photograph shows the transition from the hardground to the soft substrate.

The community of the third stage of this process can be compared with the Late Cambrian community discovered on the flat cobbles sometimes cemented on the sea floor, found in the Snowy Range Formation of Montana and Wyoming (Brett *et al.*, 1983). These two communities are similar in the predominance of eocrinoids and the absence of *Trypanites* borings, which are characteristic of younger hardgrounds. However, the first instance of similarity is not very convincing, because the Early Ordovician eocrinoids are very different from the Late Cambrian ones. The Early Ordovician community was very different from that of the Late Cambrian in that it contained many bryozoans. However, the greatest difference between these hardgrounds is in the opportunities for their development. The Late Cambrian hardground community developed only on pebbles, because the debris from echinoderms and other inhabitants was enough only to consolidate some pebbles, whereas in the Kanosh Shale, the amount of debris was sufficient for hardground formation and expansion. Therefore, the equivalents of the fourth and fifth stages of the development of hardgrounds were absent in the Late Cambrian, and these stages can be considered as typically Ordovician. The accumulation of abundant debris, primarily from echinoderms, which could be quickly cemented to form hardgrounds, which rapidly expanded due to the supply of debris from other occupants, is characteristic of these stages.

The study of hardgrounds in the Early Ordovician Baltic Basin (eastern part of the Leningrad Region) has revealed further differences from Cambrian hardgrounds and allowed simulation of the process of hardground formation based on positive feedback between the development of hardgrounds and the development of benthos (primarily of echinoderms) (Rozhnov, 1994, 1995; Palmer and Rozhnov, 1995). One of these differences is the wide distribution in the Early Ordovician of *Trypanites* borings (Fig. 94), previously only recorded from Middle Cambrian rockgrounds and on Ordovician and younger hardgrounds. The second important difference is the mass supply of debris (primarily from echinoderms) by the hardground community to the environment of the sea floor. On this debris, depending on sedimentation, either new hardgrounds or soft grounds with a large amount of debris underlain by a layer of hardened ground at a certain depth developed.

Causes of Change in Marine Grounds at the Cambrian–Ordovician Boundary

The wide distribution of hardgrounds from the beginning of the Ordovician, from the point of view of abiotic factors, may be explained by changes in the chemical composition of water in many epicontinental seas. These changes were marked by a decrease in the content of dissolved magnesium ions in relation to carbon dioxide ions, which resulted in the precipitation of low-magnesium calcite instead of high-magnesium calcite and aragonite. The so-called aragonite seas were replaced by calcite seas. In the epochs of calcite seas, calcite precipitated from the water could consolidate calcite debris, widely present on the sea floor from the Ordovician. This calcite debris was the seed for the precipitation of cementing calcite. Aragonite precipitating from pore solutions in the epochs of aragonite seas could not consolidate calcite debris; thus, hardgrounds were rare.

Hardgrounds could not have developed widely in the Ordovician if it was not for the increase in the amount of calcite debris accumulating on the sea floor. The increase in the amount of debris in the Ordovician sediments was, first of all, associated with a profound change in the structure of benthic communities, especially in the carbonate-precipitating seas, where echinoderms came to play a dominant or, at least, major role. The total biomass of echinoderms sharply increased at the beginning of the Ordovician. This is supported by a major increase in the amount of echinoderm debris in post-Cambrian sediments. The supply of debris from other animals (ostracodes, brachiopods, bryozoans, and trilobites) also sharply increased. This implies that in the Ordovician the supply of calcium and its conversion by organisms increased. However, this hypothesis is difficult to test. In any case, the balance of calcium content in the seawater should have been affected as a result of the redistribution of its production between different groups of organisms (from archaeocyathids and algae to echinoderms, brachiopods, bryozoans, and mollusks).

Causes of the Increase of Calcite Production in the Ordovician

In the Ordovician, echinoderm calcite productivity increased by at least an order of magnitude compared to that in the Cambrian. This resulted from both an increase in their total number and diversity and an increased individual size. This is best displayed by the sessile pelmatozoan echinoderms. In the Cambrian, the height of eocrinoids (the main representatives of Pelmatozoa at that time) never exceeded 15 cm above the bottom, and they were typically much lower. In the Ordovician, some eocrinoids reached 25–30 cm in height, while newly appeared crinoids with a long stem could be elevated more than one meter above the sea bottom (Fig. 93) (Ausich and Bottjer, 1982; Bottjer and Ausich, 1986; Rozhnov, 1993a, 1993b). Additionally, crinoids rapidly became a dominating group among echinoderms, thus indicating that pelmatozoans were capable of consuming larger food particles. This was related to the considerable increase in the size of the food canal in crinoids compared to eocrinoids. Diverse Cystoidea, including Diploporita and Rhombifera, occasionally reached 0.5 m in height. As a result, suspension feeders exploited a part of the water column 1 m above the bottom (or even higher). This led to an increase in the number of suitable niches and in the number and biomass of echinoderms. At the same time, the body size of echinoderms sharply increased (by at least an order of magnitude).

This was connected with the replacement of small-sized groups by larger-sized groups and with a general trend toward a greater size in all echinoderm groups. This is especially noticeable when the maximum body sizes of different animals are compared.

The increase in the number and individual size of echinoderms resulted in a sharp increase in the calcite debris supply. This was facilitated by features of the echinoderm skeleton. Firstly, it was highly porous and, therefore, compared to the calcite skeleton of other animals with a similar weight, it occupied a considerably larger space. Secondly, the echinoderm skeleton was built from separate small skeletal elements, joined by organic ligament. This allowed rapid postmortem destruction of skeletons which formed numerous fragments, with accumulation of large amounts of debris on the sea floor. Calculations show that the debris resulting from the complete fragmentation of the skeleton of a crinoid one meter tall and with a stem diameter of 0.5 cm, could cover at least 0.5 m^2 of the sea floor with a layer 1 mm thick. Crinoids of this size commonly occurred in the Ordovician and often formed dense settlements. Therefore, substrates near such settlements were often made up of 50% or more echinoderm debris. Not far from these settlements, the echinoderm debris also constituted a substantial proportion of the sediment. For instance, according to Pölma (1982), in the northern structural-facies zone of the Baltic Paleobasin, the amount of echinoderm debris was usually around 25–30%, whereas near bioherms, its proportion reached 93%.

Such a change in substrates at the Cambrian–Ordovician boundary should have necessarily led to changes in composition, abundance, and structure of the entire benthos. However, another feature of echinoderm debris, i.e., the fact that each skeletal element is monocrystalline, influenced the changes on the sea floor in carbonate seas at this boundary to the largest extent. Each skeletal element is a monocrystal, and, after being buried in the sea floor, can become a seed for calcite precipitating from the sea water. In suitable conditions, abundant echinoderm debris was rapidly cemented on the sea floor to form a monolith mass. When the rate of sedimentation was equal to, or less than, the rate of cementation, substrates became rigid, and hardgrounds formed. These new hardgrounds were ideal for the settlement of stemmed echinoderms that needed rigid substrates, and they colonized them. Because of the increased tiering of echinoderms, their biomass on hardgrounds could be very large. Hardgrounds were also favorable for the settlement of many other benthic groups, such as bryozoans (which appeared in the Ordovician), ostracodes, small brachiopods, and boring organisms, among which *Trypanites* dominated.

On the sea floor, where the rate of sedimentation was higher than the rate of cementation and the debris supply was large, semihard or more or less soft substrates with a hard underlying layer slightly below the surface formed. Substrates of this type transformed, gradually and unevenly, into genuine hardgrounds and alternated with them. Therefore, the communities inhabiting them were very diverse, adjoining and penetrating each other. Thus, at the beginning of the Early Ordovician, a new community with large trophic opportunities formed in epicontinental seas, occupying large areas. The development of this community was accompanied by a fast to extremely fast growth in animal abundance, in which these animals settled in the large epicontinental seas appearing at the beginning of the Ordovician, due to the positive feedback between the substrates and the community of debris-producing organisms inhabiting them. This quality of a substrate can be described as the capability for self-reproduction.

THE CAPABILITY FOR SELF-REPRODUCTION AS A UNIQUE FEATURE OF MANY ORDOVICIAN SUBSTRATES

The capability for so-called self-reproduction was especially typical of hardgrounds (Fig. 94) but it also occurred in coarse bioclastic and clastic substrates (Fig. 95). The hardground community formed by the beginning of the Ordovician as a completely new community, was populated mainly by a new group of fauna of relatively high taxonomic order. These include, for instance, newly appearing classes of echinoderms (Crinoidea, Diploporita, and Rhombifera), the phylum Bryozoa, and many taxa of lower taxonomic rank. Thus, the formation of the first hardgrounds in geologic history and the origin of hardground communities coincide with the appearance of many new higher taxa and a sharp increase in the diversity and abundance of many marine groups. This does not seem to have been a random coincidence and, thus, demands the investigation of the relationships between the development of marine substrates and the evolution of benthic fauna. Such relationships may be seen, first of all, in the almost unique, and at least completely new for the Ordovician, ability of many marine substrates to reproduce themselves and expand.

Mechanism of Self-Reproduction

Ordovician hardgrounds were formed by the accumulation of calcite debris, supplied mainly by a benthic community inhabiting the very same substrate. In the Cambrian, for instance, the supply of debris was not sufficient for the expansion of hardgrounds. As a result, hardgrounds that could have appeared under suitable conditions could not expand and gradually declined. For comparison, Cretaceous hardgrounds were formed by debris supplied by plankton, mainly coccolithophorids, which were not directly connected with the type of sea floor. Thus, the self-reproduction of hard-

Fig. 95. The earliest root-like holdfast of crinoids from the Middle Ordovician (Upper Arenig, Volkhovian) of the Leningrad Region.

grounds is based on its capability for expansion, which depended on the community inhabiting the very same substrate. This ability is especially typical for the Ordovician, a time when hardground fauna began to develop.

Hardgrounds with Low Hydrodynamic Energy as an Ideal Settlement for Echinoderms

The feedback of Ordovician hardgrounds is connected primarily with echinoderms, for which hardgrounds with a low hydrodynamic energy are an ideal place to settle. Echinoderm larvae, especially of pelmatozoans, were planktonic and required hard surfaces on the sea floor to settle for further development. Large-shelled debris and, especially, hardgrounds are very suitable for this purpose. In addition, pelmatozoan echinoderms with high crowns, especially crinoids, needed a sufficiently strong support on the sea floor. This is resolved the most easily on hardgrounds, to which these echinoderms attach by the simplest, primitive holdfast (Fig. 94). On softer substrates, the holdfasts were considerably complicated by a ramose root system (Fig. 95). Therefore, in the Ordovician, more or less hard areas of the sea floor (such as large shells) were under suitable conditions quickly occupied by diverse attached echinoderms.

Echinoderm Debris as an Ideal Material for Hardgrounds

Echinoderm debris was an ideal material for hardgrounds in calcite seas under suitable conditions of sedimentation because of the following features: (1) the monocrystalline nature of each skeletal element, resulting in fast syntaxial growth of calcite cement precipitating from pore waters; (2) the larger volume of echinoderm debris compared to that produced by other animals of the same weight, resulting from the very porous skeleton (stereom structure); (3) the composite structure of the echinoderm skeleton, resulting in postmortem disarticulation and fragmentation into numerous ossicles even in very quiet water. Thus, hardgrounds represented an ideal place for settlement of many echinoderms, and the accumulations of their postmortem debris constituted the best material for further hardground development. The more hardgrounds expanded, the greater the number of echinoderms that settled on them, and the more material was supplied for the further expansion of hardgrounds. The positive feedback between the expansion of the area of hardgrounds and the increase of echinoderm biomass resulted in the very rapid expansion of hardgrounds over large areas and fast, to extremely fast, increases in the abundance of echinoderms and other benthic groups (Fig. 96), since it occurred in shallow-water Ordovician seas with a large supply of calcium and under suitable sedimentary conditions (when the rate of sediment accumulation is the same or lower than the rate of lithification).

The Influence of the Appearance of Self-Reproducing Hardgrounds on the Evolution of Benthic Fauna

The extremely fast growth in the number of echinoderms should have affected the rates of evolutionary transformations in this group. From the traditional point of view, the first self-reproducing hardgrounds in the Ordovician were a new, unexplored system of ecological niches, which were very favorable for the existence of many benthic groups, particularly echinoderms. The colonization of these niches should have been accompanied by specialization and universal morphogenesis of the initial fauna. Initially, the competition between the immigrants to a large extent depended on the order of arrival of individuals to occupy the niches. Therefore, natural selection favored early sexual maturity of individuals and, thus, the development of paedomorphosis, which became a strong morphogenetic mechanism at that time. This was the morphogenetic basis for the emergence of new classes. Essentially, classes of animals that are well documented in the fossil record represent strongly morphologically isolated groups, with a distinct hiatus between them, while intermediate forms are absent; the roots of the classes cannot be traced back to the Ordovician and Cambrian. Nevertheless, it is apparent that classes, for instance of Echinodermata, that first appeared in the Ordovician had evolved from unknown Cambrian skeletal echinoderms rather than from soft-bodied taxa. Therefore, since we cannot trace their direct ancestors in the fossil record at the present state of knowledge, it is possible to assume that they evolved from some Cambrian taxa at ontogenetic stages that are not preserved in the fossil record.

At present, paedomorphosis is considered to be the most efficient mechanism for acceleration of the macroevolutionary rate and for saltatory speciation (McKinney and McNamara, 1990; Smirnov, 1991). From this point of view, we return to the hypothesis of the "very promising monsters" introduced by Goldschmidt (1952). According to his hypothesis, large genetic changes leading to considerable morphological transformations of adult organisms (system mutations) may instantaneously produce new forms, which would give rise to new lineages. However, such system mutations, as was justifiably noted by the critics of this hypothesis, are usually lethal or lead to a sharp decrease in the viability of individuals, because they disrupt a genetic and morphological balance in the organism. This conflict disappears when the important role of heterochronies, primarily paedomorphosis, is accepted in large macroevolutionary transformations. Such mechanisms of evolutionary transformations require a minimum of genetic change and affect only the rate of sexual maturity, in the case of paedomorphosis, or the rate of somatic development in the case of neoteny (Smirnov, 1991). Therefore, this mechanism can result in very rapid, major changes in the morphology of adult animals and, subsequently, in the saltatory appearance of new higher taxa.

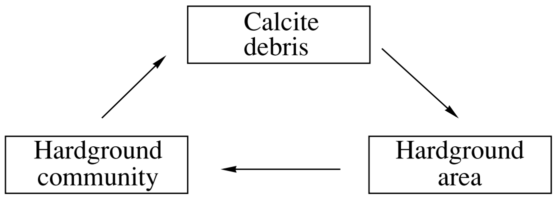

Fig. 96. Scheme showing a positive feedback between the increase in the calcite productivity of the hardground community and the increased area of the hardground.

MODEL OF THE MECHANISM OF ORDOVICIAN RADIATION

The above data suggest the following model for the mechanism of the Ordovician radiation. The mechanism of Ordovician radiation is largely based on the unique feature of many Ordovician substrates, their ability to reproduce themselves. This feature is especially clearly seen in hardgrounds, but it also occurred in coarse bioclastic-clastic carbonate substrates. Hardgrounds, or synsedimatarily lithified carbonate substrates, first appeared in the Cambrian, although they did not become widespread until the Ordovician. This was connected with changes in the seawater salinity at the end of the Cambrian–beginning of the Ordovician (the transition from so-called aragonite-precipitating to calcite-precipitating seas) and with abrupt changes in echinoderm morphology, which, from the beginning of the Ordovician, were capable of employing the basal meter of the water column, whereas their ancestors could use only basal 10–20 cm.

The Ordovician hardground was formed through the supply of calcite debris, mainly produced by organisms inhabiting the substrate itself. Pelmatozoan echinoderms were the main suppliers of calcite debris. For instance, in the Cambrian, the supply of debris from such communities was not sufficient, and the hardground that had formed under suitable conditions did not expand beyond the original size but gradually declined. In contrast, in the Cretaceous, it was formed due to the supply of debris produced by plankton, mainly coccolithophorids, organisms that were not directly connected with the nature of the sea floor. Thus, the self-reproduction of Ordovician hardgrounds was based on the possibility of expanding the hardground due to the community inhabiting it, i.e., debris supplied by echinoderm assemblages was an ideal material for the development of hardgrounds in the calcite-precipitating seas under suitable sedimentary conditions, whereas hardgrounds were ideal places for echinoderm settlements. The more hardgrounds expanded, the more echinoderms settled on them, and the more material was supplied for the expansion of these hardgrounds. The positive feedback between the expansion of hardgrounds and the increase in echinoderm biomass (Fig. 96) led to an extremely fast distribution of hardgrounds over large areas and to fast and extremely fast increases in the abundance of echinoderms and other benthic organisms in the shallow-water Ordovician seas with a large supply of calcium.

An extremely fast increase in the abundance of echinoderms led to the fast rate of evolutionary transformations in this group. Indeed, the first self-regulating hardgrounds that appeared in the Ordovician became a new, unexplored system of ecological niches, very favorable for the existence of many benthic faunal groups, particularly echinoderms. The colonization of these niches should have been accompanied by specialization and universal morphogenesis of the initial fauna. Initially, competition between the immigrants depended on the rapid occupancy of niches. Therefore, natural selection favored early sexual maturity and, thus, paedomorphosis, which became a powerful morphogenetic mechanism at that time. Thus, the explosive morphogenetic radiation at the beginning of the Ordovician is completely explained based on the above model. However, the high taxonomic rank of the characteristics involved in this morphogenetic process require further study. Possible explanations may be found by the comparison of the formation of body plans of the classes, which gave rise to new classes in the course of the Ordovician radiation (Eocrinoidea and Edrioasteroidea), and homalozoan echinoderms emerged as a result of the Cambrian radiation.

SECTION 3. DEVELOPMENT OF THE ECHINODERM BODY PLAN

PHYLOGENY OF ECHINODERMATA: A TREE OR A MEADOW?

Usually, phylogenetic schemes, such as cladograms, are represented by a tree with branching points indicating appearances (or disappearances) of diagnostic characteristics in a taxon. This type of phylogenetic reconstruction agrees with the principle of strict monophyly and successive acquisition of essential characteristics. If the principle of strict monophyly is not followed (e.g., it is accepted that a class did not necessarily evolve from a single species, genus, or even a family) and is substituted by consideration of an entire archetype (i.e., assemblages of related isolated rather than diagnostic characters), the phylogenetic reconstruction looks different (Fig. 97). This different pattern is seen especially clearly when the time of the appearance of a taxon in the geological record is taken into account (Rozhnov, 1988). From this point of view, the early evolution of the three subphyla of Echinodermata (Pelmatozoa, Eleutherozoa, and Carpozoa) in the early Paleozoic is considered below.

EVOLUTION OF PELMATOZOAN ECHINODERMS IN THE EARLY PALEOZOIC

The early evolution of the subphylum Pelmatozoa will be considered first. This subphylum includes those echinoderms that have food-gathering processes, arms or brachioles, a more or less developed pentaradiate symmetry, and, usually, a stem by which they are attached to the substrate. This subphylum includes seven or eight classes. These are Crinoidea, Rhombifera, Diploporita (Cystoidea), Blastoidea (and their ancestors Coronata), Paracrinoidea, Parablastoidea, and Eocrinoidea. Based on the structure of their food-gathering processes, these classes are at present grouped into two subphyla, Crinozoa (possessing arms) and Blastozoa (possessing brachioles). The first subphylum certainly included crinoids, while all the other classes were included in the second subphylum.

To justify the existence of the subphylum Blastozoa, Sprinkle (1973a) suggested that the radial ambulacrum of this taxon did not enter the brachioles. In his view, this is a fundamental difference between brachioles and arms. Therefore, Crinoidea, the major and, effectively, sole class of Crinozoa arose independently from Blastozoa at the beginning of the Cambrian. This conclusion was supported by the description of the Middle Cambrian *Echmatocrinus* from the famous Burgess Shale, a genus that Sprinkle (1973a) assigned to Crinoidea. However, the structure of *Echmatocrinus* differs considerably from typical crinoids, which are well represented in the Lower Ordovician. Recently, in addition, well-founded doubts were cast over the crinoid affinity of this animal (Conway Morris, 1993). For instance, Ausich and Babcock (1996) suggest that it may be an octocoral. Even if the positive echinoderm affinity of this animal is proved, it would be much closer to Eocrinoidea than to post-Cambrian crinoids. This problem is discussed in greater detail in the chapter on the morphology of pelmatozoan echinoderms. Therefore, no true representatives of Crinozoa are recorded from the Cambrian. In addition, many finds

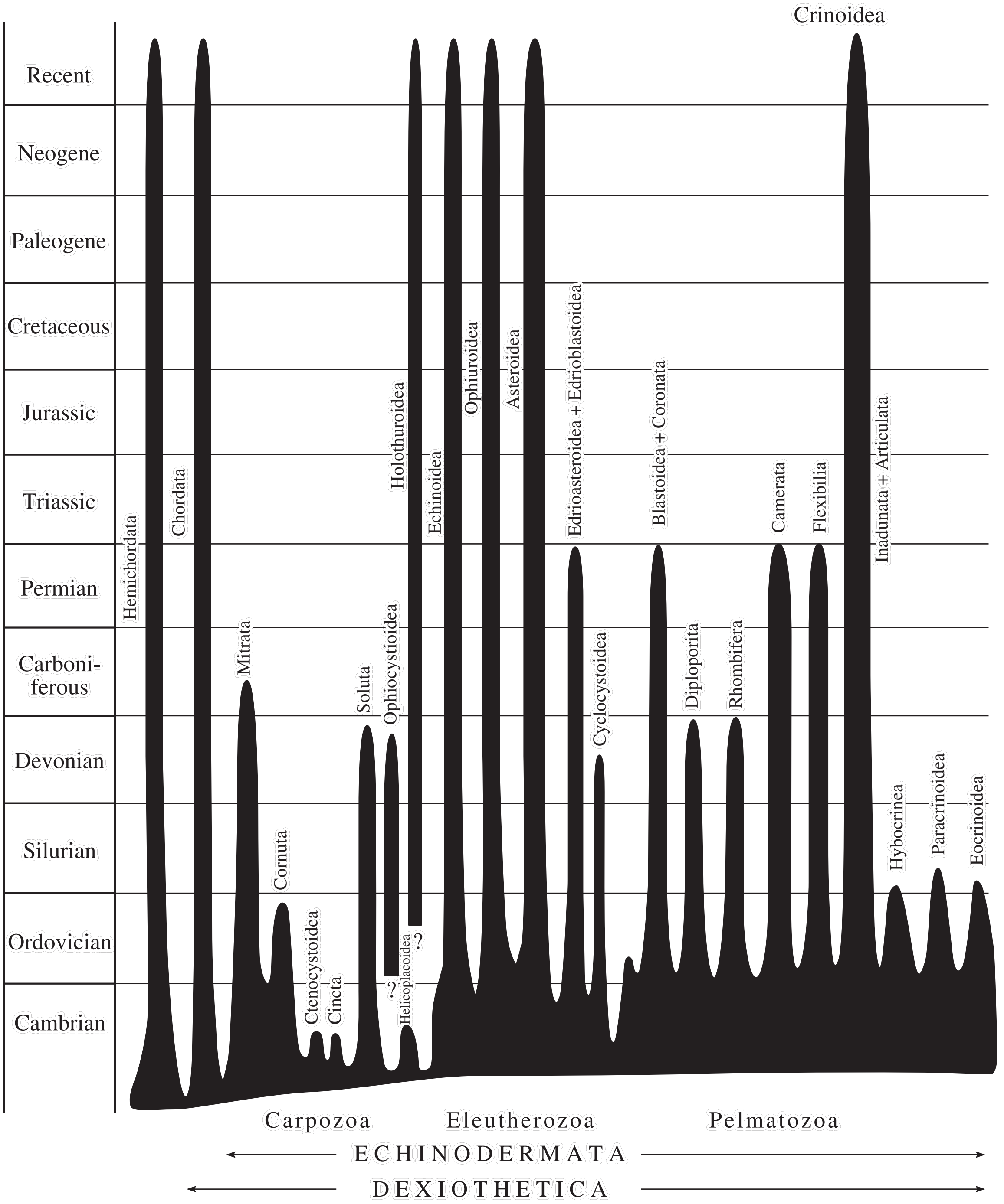

Fig. 97. Scheme of phylogenetic relationships between the major groups of echinoderms, chordates, and hemichordates. Edrioasteroidea and Eocrinoidea in the Cambrian gave rise to all post-Cambrian Eleutherozoa and Pelmatozoa and represented subphyla judging from their morphogenetic potentials.

indicate that primitive blastozoan echinoderms (class Eocrinoidea) had radial ambulacral canals, and that the arms of crinoids could have evolved from the brachiole-possessing ambulacra of eocrinoids. For instance, among members of the primitive Ordovician crinoid family Hybocrinidae, there are aberrant forms in which the uniserial arms could possibly have evolved from biserial brachioles (Fig. 56). This suggests that crinoids are more likely to have evolved from the Cambrian blastozoan echinoderms (Eocrinoidea) at the beginning of the Ordovician. Hence, the subdivision of Echinodermata with food-gathering processes into two subphyla is not convincing. Therefore, to understand the evolution of echinoderms, it is important to understand how the eocrinoid body plan could have transformed into the body plans of the derived, later classes, and, most importantly, into the crinoid body plan.

The transformation of the eocrinoid body plan to that of crinoids required, as was shown above, at least seven parallel changes of the skeletal structures rather than just the transformation of each of the brachiole-possessing ambulacra into arms (Fig. 57). It is noteworthy that the transformation of each of these structures occurred repeatedly within the Eocrinoidea. This process was reversible, i.e., new structures could return it to its previous condition in the course of evolution. This could relatively easily be achieved by various heterochronies, primarily paedomorphosis, i.e., the retention of juvenile, ancestral characters in adults. At the same time, this led to an opportunity for various combinations of characteristics, including those that later became taxonomically highly ranked. This process was responsible for the phenomenon of so-called archaic, or constructive, diversity, which was typical of primitive groups (Mamkaev, 1968, 1979, 1983, 1991). As a result, eocrinoids had almost all the characteristics that later became definitive of crinoids, although the combinations of these characteristics were often bizarre and incomplete. Some crinoid characteristics were invariably absent in these combinations. Only the combination of all seven structures resulted in the typical crinoid body plan.

According to the epigenetic theory of Schmalhausen-Waddington (see Shishkin, 1981, 1987, 1988), in the course of evolution, the early ontogenetic stages of eocrinoids should have become considerably more canalized and stabilized. When the appearance and early development of skeletal elements was shifted to these canalized stages, the development of the skeleton became more definitive and stable and clearly distinct from skeletal development in the related groups. At the final stages of development, in adults, the increased stability of ontogeny was displayed by sharply decreased fluctuations in the structure of the skeleton. At the same time, this process restricted the possibility of random combinations of characteristics at the time of heterochronies. At the beginning of the Ordovician, this, apparently, led to the subdivision of the single class Eocrinoidea into several other classes. In the Cambrian class Eocrinoidea, all major characteristics of the highest rank could form various combinations in the course of various heterochronies. From the beginning of the Ordovician, these combinations were restricted by the selection of the less highly ranked characteristics representative of the new classes. In this situation, the class Eocrinoidea represented in the Cambrian a single, undivided subphylum, while, from the Ordovician, the subphylum Pelmatozoa represented a system of classes. Each of these classes had a particular system of combined characteristics and could not enter the morphological zone of a different class. From this perspective, it is clear that the class Crinoidea, like the other classes of pelmatozoan echinoderms, evolved from Cambrian eocrinoids. However, it is not possible to determine from which particular group the crinoids had evolved, because the early stages of different eocrinoid groups could be very similar, and any of them could have given rise to the crinoid body plan. Therefore, some subclasses of crinoids could have evolved from different eocrinoid groups. Hence, they do not represent stages in the evolution of the crinoid body plan.

Thus, according to the hypothesis under discussion, classes of blastozoan and crinozoan echinoderms constitute a single subphylum, which, in the Cambrian, was represented only by eocrinoids. Eocrinoids gave rise to the entire diversity of post-Cambrian pelmatozoan echinoderms (Fig. 97).

EVOLUTION OF ELEUTHEROZOAN ECHINODERMS IN THE EARLY PALEOZOIC

The subphyla Echinozoa and Asterozoa are to be discussed in this section. Of the subclasses assigned to these subphyla, holothurians require a specific approach, because their fossil record is too poor for comparative morphological conclusions. However, for all other classes that appeared in the Ordovician, the ancestors may be only be looked for within the Cambrian Edrioasteroidea, which were as diverse as the Cambrian Eocrinoidea. Otherwise, the immediate ancestors of sea urchins and starfish should be looked for among soft-bodied animals, which are very unlikely to have been ancestors. Although this subject is poorly studied, new finds and new detailed descriptions of the morphology of Edrioasteroidea and Edrioblastoidea, which were shown to be closely connected with Edrioasteroidea, suggest interesting hypotheses. According to the recent research of Guensburg and Sprinkle (1994), Edrioblastoidea represent a small group of Edrioasteroidea with a more or less well-developed stem. It is doubtful that this stem was homologous to the stem of pelmatozoan echinoderms. Some modern starfish have a small peduncle at one of the ontogenetic stages. This peduncle is formed, as a stem in crinoids, from a preoral lobe. In starfish, the peduncle is curved later on in ontogeny, and the starfish turns, with its oral side downward. In contrast, crinoids develop a normal stem, and the oral side remains facing up. A now-abandoned hypothesis of the origin of free-living echinoderms from stemmed pelmatozoans was based on these features. This hypothesis appears to be incorrect, because only the preoral lobe was homologous in this case, whereas the cavity of the peduncle in starfish larva was formed from the axocoel, and in crinoids, it was formed from the right somatocoel (Fig. 35). Which coelomic cavity was located in the stem of Edrioblastoidea? Maybe, as in starfish, it was the axocoel cavity, at least in early ontogeny? This assumption allows a new view of the old theory of the origin of starfish and other free-living echinoderms. I am inclined to suggest that the subphyla Asterozoa and Echinozoa should be, as before, united in a single subphylum Eleutherozoa, whereas the ancestors of the respective post-Cambrian classes should be tracked back among Edrioasteroidea (Fig. 97). From this point of view, Cambrian Edrioasteroidea represent a subphylum, undivided into classes, in which different characteristics of the Ordovician classes could be variously combined.

These two echinoderm subphyla, Pelmatozoa and Eleutherozoa, which in contrast to the third subphylum, Homalozoa, did not originally have radial symmetry, included the most diverse classes as a result of Ordovician radiation. It was the pelmatozoan echinoderms that became the starting group of the Ordovician radiation according to the previously proposed model of its development (Rozhnov, 1994; Guensberg and Sprinkle, 1992; Droser, 1995; Rozhnov and Palmer, 1997; Rozhnov, 2001; Sprinkle and Guensberg, 1995). In Cambrian, each of these subphyla was not subdivided into classes, and their archaic diversity at that time gave a wide opportunity for variation and combinations of characteristics constituting body plan of Ordovician classes. The archaic diversity of the third subphylum, Carpozoa (or Homalozoa), was connected to characteristics of the higher taxonomic rank than classes (phyla and subphyla).

ARCHAIC DIVERSITY OF CARPOZOAN ECHINODERMS

Representatives of Homalozoa (or Carpozoa) did not originally have radial symmetry. They include a few very different classes, which until the present have been interpreted differently. For instance, there is an ongoing debate between the supporters of the calciochordate and aulacophore theories of organization of Stylophora, Early Paleozoic animals with a typical echinoderm skeleton, although lacking radial symmetry and apparently lacking an ambulacral system (Jefferies, 1986). A more closely related example is the organization of Soluta (Rozhnov and Jefferies, 1996). This is also a group of Early Paleozoic animals with a typical echinoderm skeleton built from monocrystalline calcite stereomic plates. They certainly had an ambulacral system, because they had a multiporous madreporite plate at the base of their only arm (Fig. 49). The structure of the arm has been studied rather thoroughly, including the plates and inner casts. Therefore, the way it functioned is very apparent, being the same as in modern crinoids. The triad of tentacles in each metamere of the arm performed different functions (Jefferies, 1990). Thus, the ambulacral system in Soluta functioned similarly to that in crinoids, but it was different morphologically, because it had, like the entire animal, neither pentaradiate nor any other radial symmetry. Therefore, the ambulacral system had a single radial canal, which is very unusual in crinoids, and, instead of the circular ambulacral ring, it apparently had a simple ambulacral sac. Soluta also had a tail, which was, as suggested by many researchers, homologous to the tail of chordates, but not homologous to the crinoid stem. Thus, these animals combined characteristics of two animal phyla, Echinodermata and Chordata. Similar situations occur in other Homalozoan groups. Whatever way their organization is interpreted, it represents combinations of characteristics of a very high rank occurring at the demarcation line separating Echinodermata and Chordata.

A DECREASE IN MINIMUM RANK OF THE NEW TAXA IN GEOLOGICAL TIME AND THE MOSAIC PATTERN OF DEVELOPMENT OF THEIR BODY PLANS

A comparison of the morphologies of the early Paleozoic echinoderms shows that the taxonomic rank of characteristics included in the archaic diversity of Carpozoa is higher than that of similar characteristics of Pelmatozoa and Eleutherozoa. This feature is certainly connected with the general pattern described above, according to which the maximum rank of newly appearing taxa decreases over geological time. For instance, no new phyla or subphyla appeared in the post-Cambrian epoch. Not one single class appeared after the Ordovician. If heterochronies are accepted as a major mechanism facilitating the appearance of new body plans of higher taxa, these phenomena can be explained by irreversible changes in ontogeny after the new taxon appears.

What can this irreversibility mean? Why can one accept the origin of echinoderms from, e.g., Ctenophora, but cannot accept that this evolution could occur repeatedly, although the supposed ancestral taxa survived until now? This question is better addressed to embryologists studying ontogenetic processes. Paleontology only records the irreversibility and unrepeatability of evolution. This fact is well represented in the fossil record of many animal groups.

For instance, Cambrian representatives of Eocrinoidea had all the morphological opportunities, which in the Ordovician were utilized, leading to the appearance of the pelmatozoan classes. In this sense, Eocrinoidea in the Cambrian were in fact a subphylum rather than a class. May one distinguish different lineages within this taxon that have led to the appearance of new classes? This seems to be an incorrect approach, because potentially any, or almost any, genus of this class could apparently have given rise to new morphological features of Ordovician classes achieved by various heterochronies. Only after the subdivision of this class-subphylum into classes does this potential disappear. Large morphological potentials displayed by Cambrian Eocrinoidea were subdivided, separated, and developed as new body plans of post-Cambrian classes. According to this, many characteristics that could be variously combined in Cambrian Eocrinoidea were in the Ordovician united in stable morphological structures, which were not capable of fundamental changes.

Thus, following the proposed hypothesis, the establishment of new taxa of Early Paleozoic echinoderms was produced by combinations of highly ranked characteristics. These combinations resulted from various

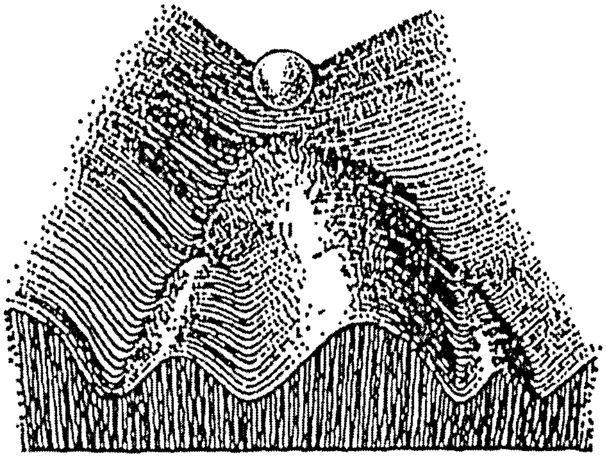

Fig. 98. Scheme of the epigenetic landscape of Waddington (after Waddington, 1957).

heterochronies, primarily paedomorphosis. Here, one has to imagine the pattern of superimpositions of ontogenetic stages in different echinoderms produced by increased body size and the subsequent reduction (subsidence) of ontogeny, when the enhanced morphogenetic processes were shortened and shifted to earlier stages. The unevenness of this subsidence led to various heterochronies. The most efficiently combined characteristics produced large new taxa, which appeared at certain boundaries in the evolution of marine biota connected with rapid environmental changes. For instance, the appearance of classes resulted from the Ordovician radiation when the Ca^{2+}/Mg^{2+} balance in the seawater changed. From the point of view of the possibility of combinations of characteristics of a high taxonomic rank, the classes of Eocrinoidea and Edrioasteroidea in the Cambrian were subphyla, whereas in the Ordovician these subphyla were subdivided into classes. Each of these classes had its own restrictions for combination of characteristics (Fig. 97). As noted above, such taxonomic differentiation in the phylogeny, similar to the so-called epigenetic landscape proposed by Waddington (1957) to illustrate the canalized nature of morphogenetic processes in the ontogeny, is conveniently displayed as an occasionally branching valley or an oblique channel (Fig. 98). A ball going down such a channel may roll from side to side because of the curvature of the bottom. This illustrates the range of variability of a taxon. When the channel branches, the ball enters a smaller channel, i.e., the range of variability becomes smaller and has a different nature. This indicates a decrease in the range of taxa that may appear after the ball entered a new channel after the branching point. Small classes especially clearly emphasize these features and do not represent intermediate groups between larger classes. In this respect, considering the level of organization, small classes appearing in the Cambrian more likely represent monotypical subphyla rather than classes. This is reflected in their archaic diversity, i.e., combinations of the characteristics of chordates and echinoderms in these taxa. Ordovician classes are true classes with a typical organization, which is reflected in the typical combinations of characteristics. Thus, the above data suggest a directed evolution of echinoderms from the establishment of the archetype and the general body plan toward the appearance of less general details, essentially based on combinations and resulting from heterochronies.

VENDIAN AND CAMBRIAN MULTICELLULAR ORGANISMS

If the data on the establishment of the higher taxa of echinoderms is extrapolated onto the earlier faunas of multicellular organisms, the Precambrian (Vendian) multicellular organisms appear to represent typical superphyla or groups of a similar rank. It is impossible to assign them to more recent phyla and classes, although some of their characteristics were already present. In this case, the synchronous appearance of the mineral skeleton immediately in many groups can be more likely explained by the closeness of the first appearances of these groups in time.

Below, is a summary of the data on the origin and early evolution of the higher taxa of pelmatozoan echinoderms in the Early Paleozoic.

First of all, all classes of blastozoan and crinozoan echinoderms represent a single subphylum represented in the Cambrian by the class Eocrinoidea, which gave rise to the entire diversity of post-Cambrian pelmatozoan echinoderms. The subphyla Asterozoa and Echinozoa should be, as before, assigned to a single subphylum Eleutherozoa, whereas the ancestors of the respective post-Cambrian classes should be looked for among Edrioasteroidea. Cambrian Eocrinoidea, like Edrioasteroidea, represent from this point of view a true subphylum, not divided into classes. In this subphylum, different characteristics typical of the Ordovician classes could be variously combined. The Ordovician radiation of marine organisms, which was responsible for the appearance of most echinoderm classes, and after which new classes never emerged, was connected to sharp changes in sea substrates at the Cambrian–Ordovician boundary and to the related changes in the abundance, composition, and structure of benthic communities. The wide distribution of hardgrounds from the beginning of the Ordovician resulted from changes in the chemical composition of the sea water in many epicontinental seas and from an increase in the calcite productivity of echinoderms compared to that in the Cambrian by at least an order of magnitude.

The ability to reproduce themselves was a unique feature of a considerable proportion of Ordovician substrates. This was based on the positive feedback between the expanding hardgrounds and calcite productivity of the animal communities inhabiting them, primarily echinoderms.

Originally, the competition between the animals immigrating to the vast regions of hardgrounds depended on the order of arrival of individuals in niches. Therefore, natural selection favored early sexual maturity; hence, the development of paedomorphosis, which became at that time a powerful morphogenetic factor. The establishment of higher taxa of Early Paleozoic echinoderms was achieved by combination of highly ranked characteristics, while the mechanism of this combination was based on heterochronies, primarily paedomorphosis.

CONCLUSIONS

The major conclusions of the study of the comparative morphology and homologies of the main skeletal structures of the pelmatozoan echinoderms, manifestations of symmetry and asymmetry in their structure and morphogenesis, primarily connected with the development of the crinoid body plan, and of the origin and early evolution of the pelmatozoan taxa in the Early Paleozoic are summarized below.

The crinoid body plan, like the morphological organization of other post-Cambrian classes of pelmatozoan echinoderms, was formed based on the morphological organization of Cambrian eocrinoids. Its development includes the appearance of at least seven characteristics directly connected with the skeleton: (1) the transition of biserial brachioles into uniserial arms; (2) subdivision of the theca into the cup and tegmen; (3) change from variously positioned brachioles on the theca to the marginal position of the arms; (4) arrangement of the plates of the cup in two or three circlets; (5) appearance of the stem, resulting from the polymerization of the holdfast; (6) development of the stem, as a result of the arrangement of the plates of the original peduncle; and (7) the disappearance of the sutural pores and epispires and development of a complete, nonporous calyx.

Each of these characteristics appeared already in the Cambrian in eocrinoids but existed in other combinations. Only the combination of all the characteristics resulted in the true crinoid body plan. The combination of these characteristics was apparently achieved through various heterochronies. Cambrian eocrinoids, like edrioasteroids, from this point of view, represent a subphylum that was not divided into classes and in which different characteristics characterizing the Ordovician classes were combined in various ways.

Metamerism is the most important and also the primary type of symmetry in echinoderms. Morphogenetically, radial symmetry in echinoderms is a closed metamerism. The pentaradiate symmetry of echinoderms constructively evolved from triradiate symmetry. Originally, echinoderms had one ambulacrum extending from the ambulacral sac. The appearance of the second ambulacrum is the first stage in the development of the horseshoe-shaped ambulacral structure from the ambulacral sac. The appearance of the third ambulacrum determined the coiling of the ambulacral sac, which as a result acquired a horseshoe shape. This allowed the appearance of triradiate, and soon after, pentaradiate symmetry, and the closure of the ambulacral horseshoe-shaped structure into a ring. The growth and closure of the left hydrocoel into a circle in phylogeny reflected a general tendency of echinoderms to develop a left-handed a symmetry. Most crinoids had the following model of pentamery. Three primary grooves, A, C, and D, and two secondary, B and E, were produced by the branching of grooves C and D. This is a basic model for many other echinoderms as well. However, there were also other models, in which the branching of the secondary grooves was on the other side, while the secondary grooves occupied different rays. In pentaradiate echinoderms, five planes of symmetry are possible, but only two of them are morphogenetically important. These are the crinoid plane (A-CD) and homocrinoid plane (E-BC).

The primary left-sided asymmetry of echinoderms, to differing extents, affected enantiomorphism in echinoderm structures. Its influence depended on the degree of direct morphogenetic connection of a fluctuating character with the morphogenesis of structures determining echinoderm organization.

Many pelmatozoan echinoderms display fluctuating asymmetry. In contrast to bilaterally symmetrical animals, in the radially symmetrical echinoderms, it is manifested in individual cyclomeres (pentameres) in correspondence with the sequence of their development.

Regular distortion of the theca and stem occur widely among crinoids and other pelmatozoan echinoderms. Morphogenetically, the distortion of the theca and stem is based on elevation, the process well known in the ontogeny of extant crinoids (migration of the incipient mouth from the ventral side of the attached larva to its upper side).

Echinoderms were the group that initiated the Ordovician radiation of the marine benthos. This radiation was connected with a coordinated change in the composition of the marine substrates and in the number, composition, and structure of benthic communities. The development, in the Ordovician, of positive feedback between the expansion of hardgrounds, and growth in the calcite productivity of the animal communities inhabiting the very same substrate, primarily echinoderms, resulted in superfast growth of the amount of benthos and rapid expansion of benthic animals over vast areas of new niches connected with hardgrounds.

Competition between the immigrants depended, to a large extent, on the order of arrival of individuals to occupy the niches. Natural selection favored early sexual maturity of individuals and, based on this, the development of paedomorphosis, which became a strong morphogenetic mechanism at that time, leading to the appearance of new archetypes. The development of archetypes was to a large extent based on heterochrony-produced combinations of various variants of structures, which appeared at the earlier stages of the evolution of the group. The data obtained indicate that the evolution of echinoderms developed from the appearance of the general body plan (archetype) to the emergence of smaller structures. This was a typical mode of development of archetypes in crinoids and other Pelmatozoa, as well as other higher taxa of marine invertebrates. The fauna of marine invertebrates also developed more or less synchronously, from the appearance of the general body plan to the evolution of smaller structures. The Precambrian–Cambrian boundary was apparently marked by the appearance of all 33 phyla of multicellular organisms that survive to the present day and, possibly, also of some superphyla. At the Cambrian–Ordovician boundary, the taxa appearing were not above class or subphylum rank.

The analysis of the material studied and the extensive literature on the Cambrian–Ordovician boundary in the development of the biosphere and the Ordovician radiation connected with this boundary allowed progress to be made toward the solution of the problem of the origin of the higher taxa of marine invertebrates. Further study of this problem requires a special parallel study of the early evolution of the higher taxa and the corresponding boundaries.

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