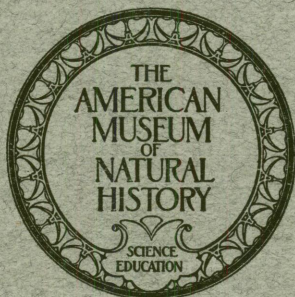


BULLETIN
OF
THE AMERICAN MUSEUM
OF NATURAL HISTORY

VOLUME LIX, 1929-1933



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Article I.—PELMATOZOAN ROOT-FORMS (FIXATION)

BY KURT EHRENBERG¹

42 TEXT FIGURES

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I. INTRODUCTION

During the last century, *Pelmatozoa* have been studied very carefully by many excellent workers. From the time of J. S. Miller, whose well-known "Natural History of Crinoidea or Lily-shaped Animals" (1821) marks the beginning of the epoch, until today, many short papers and numerous larger publications have informed us about pelmatozoan structure, systematic order, etc. Nevertheless, not all parts of the skeleton have been studied in like manner. As in vertebrate palæontology, which holds the skull as the object of greatest interest, so among the *Pelmatozoa* the crown or theca has been most carefully studied. Reasons for this are apparent, for the skull and the theca have a greater systematic value, they are better preserved in rocks, and they have, because of the organs located in them, a relatively dominant position compared with the other body divisions.

Among crinoids the arrangement of plates of the calyx wall, the structure of the anal region, tegmen, and arms, and the branching and mode of union between the joints of the arms, are of the greatest value for systematic arrangement and for morphological and phylogenetical researches; the shape of the theca and its parts is the key to many biological problems. Also among other *Pelmatozoa* the conditions are rather similar. Such facts have been established by the work of Bather, Springer, Jaekel, Wanner, and others who have dealt with the subject in recent years.

Granting the great importance of the theca, however, does not mean that the other parts can be omitted either in systematic and phylogenetic or in morphologic and biologic studies. For biological, and subsequently for some phylogenetical researches, the stem and root should be considered. It should be remembered that the characteristic crinoid, the typical pelmatozoan structure, is to be understood as an expression of the sessile mode of life whereby the stem and the root represent the organs which connect and fix the body to the substratum. These organs are to be given consideration in dealing with the problem of sessility as a whole as well as with the adaptations to different kinds of sessility in the various families, genera, and species. The important part these organs play concerning the biological investigation of *Pelmatozoa* did not remain unrecognized, for in recent years authorities have studied the subject. It can scarcely be denied, however, that our present knowledge about stems and roots, their special functions, and the biological meaning of their various modifications, needs to be increased.

With this object in view, I used the opportunity offered by an invitation of the International Education Board of New York to visit the museums of the United States for the purpose of studying some of the beautiful collections of Pelmatozoa at Washington, Albany, New Haven, and New York.¹ Some of the results of these studies are given in this paper. Although the problems cited are not fully exhausted, due in part to the condition and small quantity of material and to the limited extent of the author's studies and experiences, it is hoped that they may be of use for the better understanding of the lowermost section of the pelmatozoan skeleton.

II. GENERAL REMARKS ON ROOTS

With the intention of discussing different root-forms, their structures and functions, it may be advisable to make some general comment about roots. What is a root? That question may be thought unnecessary and singular, but it is, nevertheless, worthy of attention.

The term "root" has been employed in a sense more functional than morphological. Wachsmuth and Springer² said in 1897 that the "cirri of the distal end are the radicular cirri and form the root." From this, and other statements, it is fairly clear that they consider the root only as the distal stem-portion, including the appendages, in so far as it serves for fixation.

In this regard, Jaekel,³ who perhaps dealt most intensively with the problem of stem and root, seems to believe similarly, as far as one may judge from his remarks in 1899 and 1918. Bather⁴ says, in enumerating the parts of a crinoid body: "A normal crinoid consists of a 'crown,' . . . a 'stem' which is fixed to the sea-floor or to some solid body by a 'root' (radix)"; later,⁵ when describing these parts, he does not mention the root as a special organ but speaks only of the attachment by the distal end of the stem. And from opinions expressed by other investigators, similar views are recognized concerning pelmatozoan roots.

From the foregoing statement it seems fairly clear that the term

¹In this regard the writer is especially indebted to the late Dr. F. Springer, to Dr. R. S. Bassler, Dr. E. O. Ulrich, Dr. E. Kirk, and Dr. A. H. Clark of the United States National Museum, Washington; to the late Dr. John M. Clarke, to Dr. Ruedemann, and Winifred Goldring of the New York State Museum, Albany; to Professor R. S. Lull, C. Schuchert, C. O. Dunbar, of the Peabody Museum, Yale University, New Haven, Connecticut, and to the late Dr. E. O. Hovey, to Dr. C. A. Reeds, and to Mr. E. J. Foyle of the American Museum of Natural History, New York. To Dr. Reeds and the authorities of the last-named museum, the author is further indebted for the editing and publication of this paper.

²Wachsmuth and Springer, 1897, "North American Crinoidea Camerata." *Memoirs Museum of Comparative Zoology of Harvard College*, Cambridge, Mass., XX, p. 32.

³Jaekel, O., 1899, "Stammesgesch. d. Pelmatozoen," I, Berlin; also "Phylogenie und System d. Pelmatozoen." *Pal. Z.*, Berlin, III, p. 5, 1918.

⁴Bather, F. A., 1900, "Echinoderma" (Lankester, *Treatise on Zoology*, III), p. 99.

⁵*Loc. cit.*, p. 106.

"root" has been applied chiefly in a functional sense. It need not be emphasized that the determination of Wachsmuth and Springer, just noted, does not suffice to characterize the root as a special organ. In any genus, like *Rhizocrinus*,¹ in which the fixation is usually effected by radicular cirri or rootlets, the body section, functioning as a root, is not essentially different or marked off from the immediately following stem-portion. Under such conditions there seems to be no reason for considering the root a special organ. In dealing, however, with so-called "encrusting roots" like *Torynocrinus*,² or disciform "roots" like *Aspidocrinus*, in which the structure appears to be separated from the stem, one is justified in asking if it could not be a special organ, and if such structures are homologous to the aforementioned one.

Under normal conditions fixation takes place in the distal end of the stem. But is the distal end always the same?

In a special paper written in 1922,³ the author discussed more fully certain cases in the pelmatozoan group where sessility or fixation has not been maintained throughout life and the specimen became free by solution from the distal end of the stem. Either the same individual⁴ or its descendants, having the greater part of the stem preserved, became fixed again by means of what has become the distal end of the stem. Such secondary fixation may have been effected by a structure quite similar to the primary root, or by some peculiar modification such as a loop or manifold coiling. In both cases the question arises: is the term "root" to be used if fixation takes place, not by the original distal end but by a distal end formed only from the loss of the original? Indeed, one might ask: are the cirri of *Antedon* and its allies (which serve for fixation temporarily) or the broadened bases of the Holopidæ to be considered under the term "root" in the aforementioned sense?

To these questions, and many others which might be asked, it is difficult to give satisfactory answers. However, the writer will attempt to discuss the subject as fully as space permits.

III. DIFFERENT TYPES OF ROOTS

In discussing these problems, it seems most practical to examine the different types of fixation, or the roots found among living and extinct Pelmatozoa.

¹See page 6.

²Compare figure 39.

³Ehrenberg, K., 1922, "Ueber eingerollte Pelmatozoenstiele und ihre Beziehungen zur Sessilität," *Acta Zoologica*, III, Stockholm. See also "Bau und Lebensweise von *Herpetocrinus*," *Fal. Z.*, V., 1922 (older bibliography on the subject included in both papers).

⁴The fact that the distal end of the stem is not always the same in young and in adult has been mentioned by Wachsmuth and Springer, *loc cit.*, p. 50.

Pelmatozoan roots, using the term in the broadest sense, can be grouped in two types. From a chiefly phylogenetic point the most primitive type, named "Hohlwurzel"¹ or "Wurzelblase" (root-cyst), which consists of a pavement of irregular, polygonal plates inclosing a rather large cavity, is in contrast to the normal or compact root, the "Normalwurzel"² or "Kompaktwurzel," which possesses a relatively small lumen and a solid and more regular structure. On the other hand, roots may be distinguished with respect to their general shape, special structure, and functions.

1. RHIZOCRINUS-LIKE ROOTS

In considering the different kinds of roots, chiefly from the last-mentioned points, one may first note the type from which the term "root" is derived. In this type the so-called root shows a form comparable to the undermost body sections of trees or other plants. Such a root-type is represented by the living genera *Rhizocrinus* and *Bathycrinus*. The name of the former indicates that the distal end of the stem resembles what is usually called a "root" (Fig. 1) which is characterized by one or two main trunks and several branching appendages.

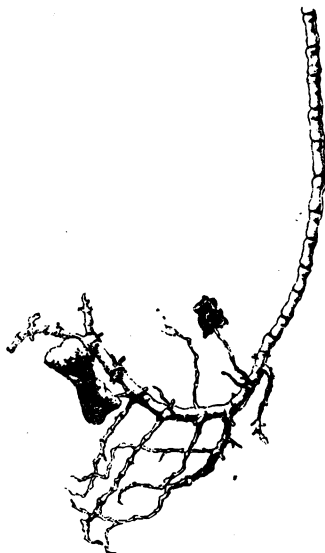


Fig. 1. Root of *Rhizocrinus lofotensis* Sars. After Carpenter, 1884. About $\frac{3}{4}$.

In a morphological examination of roots of this type, it may be noted that the stem continues into the root without interruption or marked change in the shape of the joints. Indeed, the latter are scarcely altered as the distal stem-portion progresses toward the true root-region; and as far as the stem and its direct downward prolongation are considered, a line of differentiation is scarcely detectable.³ Sometimes the main trunk of the root may bifurcate or may break into several branches; the rootlets may or may not branch again into smaller appendages.

¹Jaekel, O., 1904, "Ueber sogenannte Lobolithen," *Mai-Prot. Deutsche geol. Ges.*, LVI, p. 60, and 1918, p. 15.

²This classification, of course, may not be without exception, as many types of roots are of an intermediate character.

³This is especially true when the distal stem-joints are of a uniform and more or less primitive type. When the stem-joints are highly modified, some change in form may be recognized, although this change is neither abrupt nor very distinct as is apparent in *Rhizocrinus* with its dice-box-shaped distal stem-joints.

Besides the main root, its direct prolongation and the rootlets, there often occur what have been called radicular cirri. These are typical cirri springing off from stem-joints or the joints of the main roots (root-trunks); and the only difference between these and other cirri is that the radicular ones take part in the fixation and form therewith a constituent part of the root. As already indicated, such radicular cirri occur together with rootlets, or either may occur alone. According to Carpenter,¹ one of these modifications may be more or less characteristic within a species or genus (e.g., *Bathycrinus*), or all three may exist in the same species.

The variation made obvious by comparing figures 1 and 2 leads to observations from a biological point of view, for if variation within one species is not restricted to the lesser details but touches the whole shape of a body section, biological reasons have proved to be responsible in the majority of cases. Sometimes, of course, inner factors seem to cause such variability, as in the case of degeneration. On the other hand, degeneration itself may be the result of the environmental conditions, and thus biological reasons may be effective, as has been shown recently by Abel² in a paper on that subject.

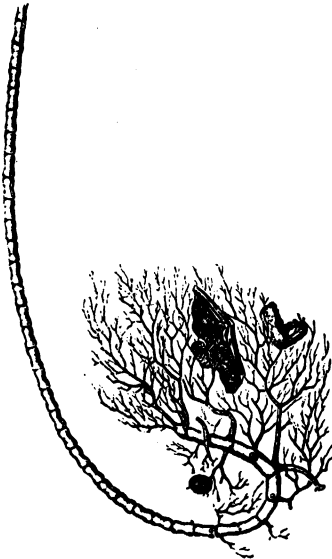


Fig. 2. Root of *Rhizocrinus lofotensis* Sars. Copied from Bather, 1900. About $\frac{3}{4}$.

Searching for the reason for root-variability, it is wise to consider first the function of this part of the crinoid. Pelmatozoan roots, like plant roots, may have several functions or uses. In the plant kingdom, roots gather food, sometimes serve as granaries, and usually fix the specimen to the ground. Although pelmatozoan roots cannot be compared directly to plant roots, still some similarity

exists, especially in the matter of fixation, in so far as only typical roots are considered.

The reason for root-variability lies in the nature of the two factors of fixation: the organ for fixation, which is the root, and the substratum to which it is attached. Also other sessile creatures such as many oysters,

¹Carpenter, P. H., 1884, Challenger Report, Zool., XI (*Crinoidea*, I).

²Abel, O., 1923, "Gedanken über die Ursachen der Degeneration," etc., Pal. Hung., I, Budapest.

corals and sponges show great variety in the general form of the section of the body which is in direct contact with the substratum. In some cases degeneration or some other factors may be responsible, as in some parasites, but in general the reason for such variability can be sought chiefly in the substratum. Of course, a root like that of *Rhizocrinus* is not directly comparable to an oyster shell. It is perhaps more comparable to a plant-root, and I am inclined to suppose also that a growing pelmatozoan root of this type reacts on stimuli coming from the substratum. Direct comparison with plant-roots seems impossible, for, in the latter, chemical stimuli connected with the nutrition-function play an important part.¹ In consideration of mechanical factors, however, such comparison may be admitted, and it seems quite conceivable that relatively slight differences in condition of the substratum may influence the form of *Rhizocrinus*-like roots to a recognizable degree.²

Besides these mechanical reactions, about which our present knowledge is not extensive, chemical reactions are traceable, although they are not comparable to those among plants. This is shown by the encrusting tips of rootlets and radicular cirri (Fig. 3). By the so-called encrusting, free ends of root constituents take hold on little stones or other firm objects which they meet as they grow on the muddy bottom. Sometimes finger-like processes are produced by secondary secretion of calcareous matter. At times they become so firmly cemented to this object that it is often impossible to separate them without destruction.

Fixation by roots of the aforementioned type is of course possible only in a substratum somewhat weaker than the calcareous matter composing these roots. In accordance with this is the statement of Wachsmuth and Springer in 1897 and of Bather in 1900 that such roots are found on crinoids that live in muddy ground. Therefore, whenever fossil crinoids with a *Rhizocrinus*-like root occur in a sediment which formed a rather solid bottom, it may

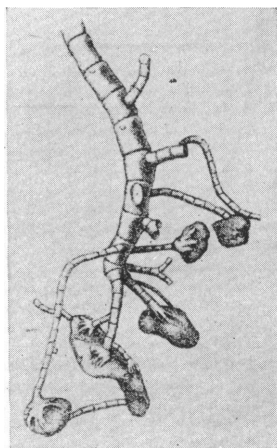


Fig. 3 Root of *Rhizocrinus rawsoni* Pourtales. After Carpenter, 1884. About $1\frac{1}{2}$.

¹Compare Kerner, A. v., 1887, *Pflanzenleben*, I, Leipzig, pp. 730-34.

²Intentionally only slight differences in substratum are mentioned. The reactions on larger ones will be discussed later.

be maintained that these crinoids were brought from some other place. This, then, is an allochthon occurrence.¹

2. MODIFICATIONS OF RHIZOCRINUS-LIKE ROOTS

a. Creeping-Root-trunks

In *Rhizocrinus* the root usually shows a vertical orientation, that is, the main trunk joins the substratum in a vertical position. In other cases, however, the root approaches a more horizontal orientation, an upper and a lower half of the main-root-joints being distinguishable. In the latter case the finer branches do not spring off all around the main root, but only, or mainly, from its under half, as in some of the creeping-root-trunks of trees and plants.

This occurrence is to be observed in some of the isolated roots in the Springer collection (Figs. 4a and 4b).² In figure 4a may be observed the "ramus ascendens" to the stem, bearing in its middle part what seems to

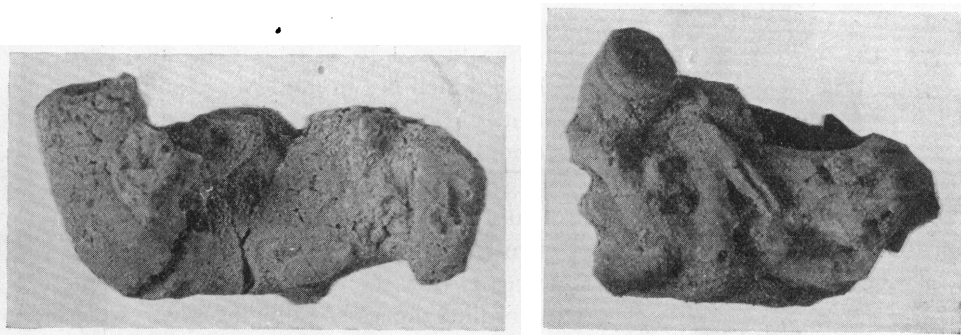


Fig. 4a, b. Creeping-root-trunks. From the Lower Burlington, Burlington, Iowa, specimens in the Springer Collection of the U. S. National Museum. About $\frac{1}{4}$.

be a process, but which really is a number of proximal joints of a heavy cirrus. A similar process is also visible below. The fragment above the horizontal root-section may be a foreign stem, a fragment not belonging to the root-trunk, but cemented to it only by secondary deposition of

¹Compare Ehrenberg, K., 1924, "Über das Vorkommen von Fossilresten, ein Beitrag zur paläobiologischen Terminologie," *Naturwissenschaften*, 12, Jahrg. XXIX, pp. 593-96. I refer now to the combination of terms "synchron-allochthones" or "heterochron-allochthones Vorkommen" respectively, instead of the combination of terms "Vorkommen auf sekundärer Lagerstätte" and "isochrone" or "heterochrone Umlagerung." This I shall discuss further in an article, "Erhaltungszustand und Vorkommen der Fossilreste und die Methoden ihrer Erforschung," which will be published in the "Handbuch der biologischen Arbeitmethoden," Berlin and Vienna.

²Compare Springer's paper cited in footnote, page 12. An example of a creeping-root-trunk is furnished also by a specimen from the Burlington limestone, figured by Wachsmuth and Springer, 1897, *op. cit.*, Plate I, Fig. 1, which is supposed to belong to *Poteriocrinus*.

stereom. On the right is seen the root somewhat flattened and expanded horizontally and deformed by secondary stereom. Traces of radicular cirri are shown below. Joints of the root in the region of the curvature are wedge-shaped or cuneiform, although the photograph does not show them so clearly. Figure 4b shows generally the same features but a greater incrustation and numerous irregular radicular cirri.

From this it seems that the crinoids to which roots formed in this way belong, have the crown borne by an upright stem, and the root, more or less horizontal, cemented to the substratum. Cuneiform stem-joints in the curved region indicate that no great movement of the distal stem against the root was possible. Keeping in mind that such creeping-root-trunks mean only a modification of a *Rhizocrinus*-like root occurring on rather soft ground, it may be understood that an adaptation of that root-type for fixation to a harder substratum must be considered.



Fig. 5. A branching root, which took hold on a stem-fragment from the Lower Burlington limestone. Specimen in the Springer Collection of the U. S. National Museum. $\frac{1}{2}$.

This substratum may be the sea-bottom itself, as in the specimens shown in figures 4a and 4b, or it may be any hard object which lies in muddy or sandy sediment. Many modifications occur which demonstrate the dependence of form upon the special conditions of the substratum. Figure 5 shows a root which took hold on a stem-fragment of another crinoid. Irregular branches may try to fix themselves by flat, finger-like processes, clinging their whole length, while side by side with them other branches may try to embrace the fragment in a spider-like manner, only the end touching and being attached to the substratum. Figure 6 shows a specimen with a normal stem or root-joint above,¹ perforated by the axial canal and having a well-marked concavity towards the left and under end as seen by the observer. Just above the latter with its small groove, is a coarsely

granulated mass surrounded by a fairly smooth structure. Accurate examination shows that this smooth structure belongs to the crinoid

¹The only observable peculiarity is in the six or seven short processes which radiate from the axial canal in a manner somewhat similar to that shown in *Herpetocrinus* (*Myelodactylus*), as figured by Bather in "Crinoidea of Gotland," I, Kgl. Sv. Ak. Handl. Bd., 25, 1, 1892, Stockholm.

itself. The granulated mass represents the substratum on which the pelmatozoan took hold by growing around with two flat, curved processes originating from a root of an originally normal structure, as is indicated by the cirrus-fragment in the lower right corner.

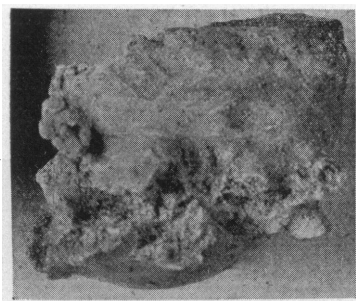


Fig. 6. A normal branching root which became highly modified by a peculiar mode of fixation, from the same horizon and locality as Fig. 4. Specimen in the Springer Collection of the U. S. National Museum.

Despite the great differences in the modifications discussed, one characteristic is common: the modification must be conceived for an adaptation to tight fixation on a rather firm substratum. Comparing these types with a *Rhizocrinus*-like root, there is no doubt that, entirely apart from the consistency of the substratum, a crinoid with a *Rhizocrinus*-like root could easily give up fixation without destroying any of its root structures, except perhaps the finest appendages. Whenever a crinoid with a *Rhizocrinus*-like root has become free in that way, either voluntarily or by storm waves, it may not have been too difficult for it to anchor again to the ground. The above modifications

offer quite different conditions in this respect. Voluntary freedom was possible only by separation somewhere along the stem, leaving the root, and forming a new attachment by a new root. These conclusions permit the opinion that the *Rhizocrinus*-like root exhibits an adaptation to fixation on soft ground and also to a living-place undisturbed by high, storm-whipped waves, although previously enumerated modifications have seemed to indicate a firm ground and moving water.¹

b. *Ancyrocrinus*

Among the other modifications of roots from the *Rhizocrinus*-type, *Ancyrocrinus* may be considered. *Ancyrocrinus bulbosus*, described by

¹Somewhat different are the conditions described by Doederlein in the case of *Metacrinus*. In this instance, many individuals seem to have formed "forests" whereby the distal stem-portions lie horizontally and were entangled by their cirri, forming a wicker-work of roots, with crowns upon the upright stem-portions (Compare Kirk, 1911, "The Structure and Relationships of Certain Eleutherozoic Pelmatozoa." Proc. U. S. Nat. Mus., XLI, p. 41). Regardless of the consistency of the bottom, however, the stems or roots took hold upon another object, that is, upon a hard substratum. Quite the same is valid for a similar occurrence described by Beringer (see page 12, footnote 2) from the Triassic pentacrinids of southern Germany. Beringer for such mode of fixation proposed a special term, "Schlingtypenheftung." We prefer, however, to make no use of this term, since such mode of fixation means not a simple type as the types distinguished within this paper, but a complex type, combined of many types discussed here under special names, as fixation by *Rhizocrinus*-like roots, by stems, by non-radicular cirri, etc.

Hall in 1862, has been discussed by many students¹ including Wachsmuth and Springer in 1897, by Bather in 1900, by Kirk in 1911, by Springer in 1917, by Goldring in 1923, and by the writer in 1922. These authors seem to agree with Hall that this peculiar modification means an adaptation for fixation, not permanently, but for a mode of life for which the writer has proposed the term "semi-sessile."² Concerning the morphology of *Ancyrocrinus*, not much more has been said than that the grapple consists of the end of the stem and the radicular cirri, both modified by the secondary deposition of stereom.³ Thereby the cirri, directed

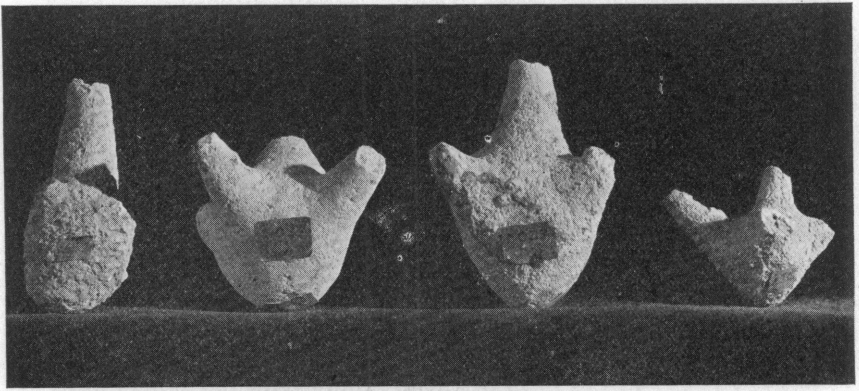


Fig. 7. *Ancyrocrinus bulbosus* Hall. Rather normal specimens from the Hamilton group, Charleston, Indiana. $\frac{1}{2}$. A. M. N. H. $\frac{5037}{2}$.

obliquely upward, stiffened, making impossible a movement of one joint against the other. The same was obviously the case with the stem or root itself which has become rounded below. Figure 7, from the Hall Collection in the American Museum of Natural History, shows such typical forms. In each case the four cirrus-like processes are observed to be

¹Hall, J., 1862, 15th Annual Report, N. Y. State Cab., pp. 117-119, Pl. I, Figs. 25-28.

Wachsmuth and Springer, *loc. cit.*, p. 50.

Bather, *loc. cit.*, pp. 134 and 177.

Kirk, E., 1911, *loc. cit.*, p. 46.

Springer, F., 1917, "On the Crinoid Genus *Scyphocrinus* and Its Bulbous Root, *Camarocrinus*," Smiths. Inst. Washington, Publ. 2440, p. 10.

Ehrenberg, K., 1922, *Acta Zoologica*, III, pp. 295 ff.

Goldring, W., 1923, "The Devonian Crinoids of the State of New York," N. Y. State Museum, Mem. XVI, Albany, pp. 456 ff., Pl. LIX, Figs. 14-16.

²Ehrenberg, K., *Acta Zoologica*, p. 297, footnote 49, where a clear definition has been given. It seems necessary to refer expressly to my previous statements, since K. C. Beringer has lately introduced the term "semi-sessile" as new, and in a different sense, although he quotes my paper. In the same paper (*Jahresh. Ver. vaterl. Naturk. Württemberg*, Jg. 82, 1926), he also mentions *Ancyrocrinus* and seems inclined to the belief that it was permanently fixed (*loc. cit.*, p. 23). As I have already elsewhere mentioned ("Die Stellung der Paläobiologie in der Biologie als Gesamtwissenschaft," *Biologica Generalis*, III, 3, 1927) the use made by man of an anchor suffices to show that Beringer's view is highly improbable. For the rest, I may refer to the following deductions.

*Compare also Springer, *loc. cit.*, 1917, Pl. v, Fig. 10.

arranged symmetrically in a verticil around the stem. Where these processes are broken away near their bases (right-hand specimen in figure 7), they are perforated by a central canal by which they may be identified as true cirri; although a little more distal (the second specimen from the left in figure 7), no traces of the cirrus canal are visible. The cirri and the stem in that region show no traces of the original segmentation in consequence of the secondary depositions of the stereom. That

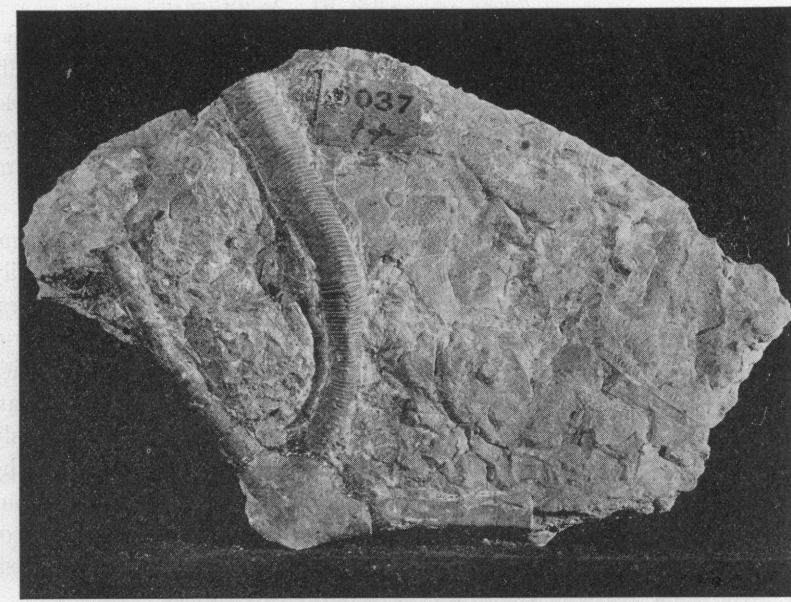


Fig. 8. A somewhat different-looking *Ancyrocrinus bulbosus* Hall, probably young with a rather long stem-portion preserved, from the Hamilton Group, Lake Erie. About $\frac{1}{2}$. A. M. N. H. $\frac{5037}{1+}$.

the latter does not extend far upward is indicated by a specimen in the collection of the New York State Museum at Albany and figures by Goldring (*loc. cit.*, Pl. LIX, Fig. 14).

Somewhat different is the view represented by another specimen in the collection of the American Museum of Natural History. Here (Fig. 8) the stem, being in the upper part quadrangular and becoming round distally as usual, shows a pronounced tapering. It is followed distad by what seems to be the root; however, no sign of transition is visible. The "root" itself appears to have been flattened. Off-springing cirri, three in number (in figure 8, only two are visible), show the single joints

fairly well, as do many of the undermost stem-joints. From the morphological under-end of the "root," the fourpartite axial canal is observable. Undoubtedly, therefore, some downward prolongation of the root must have taken place.

An indication of the nature of this prolongation is shown by another specimen recently acquired by the New York State Museum. It was described by Goldring as *Ancyrocrinus quinquepartitus* (Fig. 9). As indicated by the visible sutures, this is a very young specimen and shows below a somewhat knob-like ossicle, suturally connected with the "root." It seems possible, therefore, that the specimen in figure 8 possessed a similar structure which was lost during fossilization.

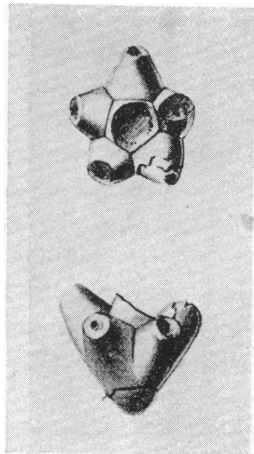


Fig. 9. *Ancyrocrinus quinquepartitus* Goldring, a young specimen showing sutures and a knob-like ossicle below. After Goldring, 1923. Above: upper view. Below: side view. $\frac{1}{4}$.

It is, of course, possible that the prolongation was of another shape (page 19), especially if the great degree of variability in the general form and detail structure among *Ancyrocrinus* forms is considered. As Kirk stated, "at times the spurs depart from the normal arrangement, where all are on the same plane, and are variously situated at different levels." This, as well as the statement that "occasionally more than four spurs are present," cannot give a correct idea of the number of diversities which may astonish the observer of figures 10 and 11.

In figure 10, long, slender forms, and short, broad ones are noted, a difference not explicable by the greater or minor deposition of secondary stereom. Many other differences are shown. In the upper row, the long, slender specimen in the left corner shows three cirri on different levels, and behind there is a fourth springing off in the level of the undermost visible cirrus. On the neighboring specimen, of much more pronounced long, slender form, three cirri, forming with a fourth one on the back a regular verticil near the upper end, are followed by one cirrus on a deeper level. The third specimen of this row has a double verticil in three sectors, while in the fourth only one cirrus is present, situated just below the two planes. The right-hand specimen shows fragments of three cirri on the foreside and two at the left. On the right is a cirrus-socket a little higher

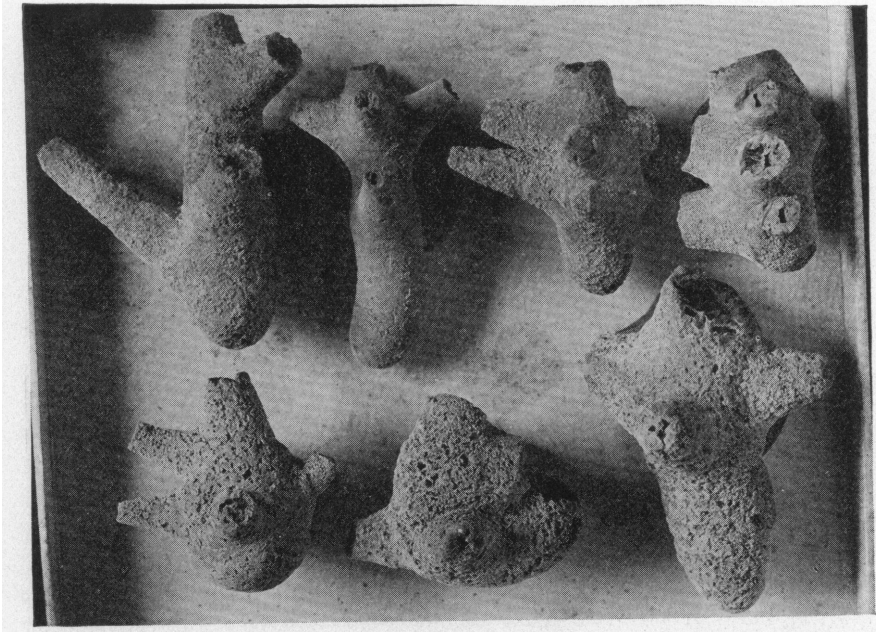


Fig. 10. Different *Ancyrocrini* from the Springer Collection of the U. S. National Museum. About $\frac{3}{8}$. Most specimens labeled: *A. spinosus*, Hamilton Group, Clark County, Indiana; the left-hand specimen from the observer, in the under row, comes from Speed Mills; in the others, the locality is not named. Both the right-hand specimens in the upper row are labeled: Upper Helderberg Group, Clark Co., Indiana. The second specimen from the left in the same row is labeled: *A. bulbosus*, Hamilton Group, Clark Co., Indiana.

than the others while the projection half-way between indicates that the cirrus has been lost and the rupture overgrown. In a similar manner, on the back side, one cirrus above is followed by two projections. In the under row the left specimen, with one normal cirlet and one upper cirrus, is similar in that regard to the second upper one with the difference that the cirlet is below and the single cirrus above. The middle specimen has two cirri below (in front and left), and two above (behind and right), with an irregular projection which probably has nothing to do with a regular cirrus. The last shows three cirri above and the one on the fore-side a bit deeper, whereby the backside cirrus is not directly opposite but somewhat nearer the left.

In figure 11, the first two specimens are remarkable because they are so distinctly curved. The first form, flattened toward right and behind, has only two cirri, invisible in the figure, while the second one has six, two

invisible ones being situated above and below the middle cirrus. Two following specimens characterize another type with two of the four cirri closer together. The fifth specimen shows three cirri, and on the back side one above and one below. In the under row the left-hand specimen with rather normal cirrus arrangement seems remarkable, in that its fourpartite axial canal indicates a downward prolongation which must have been similar to that found in *Ancyrocrinus quinquepartitus* (see page 14). The three remaining forms belong to another group, in which

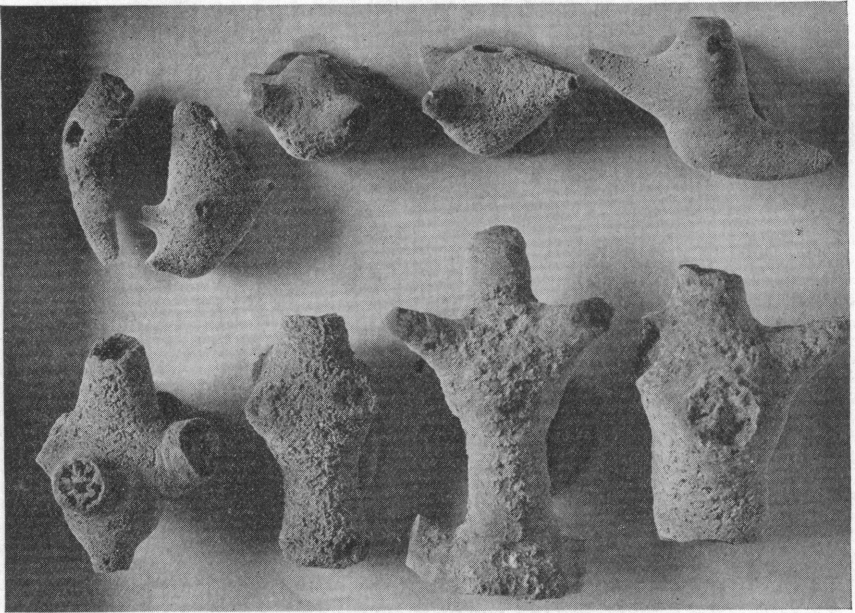


Fig. 11. Different *Ancyrocrini* (*A. spinosus*) from the Springer Collection of the U. S. National Museum. About $\frac{1}{8}$ ". In the upper row, all the specimens, except the left one, and in the under row the two right ones were labeled: Hamilton Group, Speed Mills, Clark Co., Indiana. In the under row the left specimen was labeled: Upper Helderberg, Clark Co., Indiana; the two remaining specimens were not labeled, but probably belong to the same occurrence.

the under end is somewhat flattened and truncated, suggesting that it rested on a rather solid surface. Certain differences in cirri are evident among these three specimens. The left specimen has two circlets; the four upper cirri are of normal diameter, while the lower ones, just at the base, must have been much smaller. The middle one, which bears a label with the remark, "fixed," shows only four cirri, two upper and two

lower, and the last specimen exhibits four cirri, situated in the upper region, with three on nearly the same level.

The above facts, observable on the specimens just described, offer some problems. It may be noted, first, that all the figured specimens, except that in figure 9, which comes from the Oriskany sandstone of New York, seem to belong to the Hamilton Group. Besides figure 8, and Goldring's figure 14 of Pl. LIX, all are in a silicified condition. The specimens of figure 7 were collected at Charlestown, Indiana, and those in figures 10 and 11 are mostly labeled Clark County, Indiana. There is little doubt that the four unlabeled specimens are from the same locality. Since all varieties occur in a small area, if not in a single locality, specific discriminations must be of problematic value, with separation possible only from the points of view of stratigraphic and geographic distribution.

In this respect it may be emphasized that the repeatedly mentioned variability of the *Ancyrocrinus* species clearly indicates that form and detail structure have not become fixed hereditarily.

Considering *Ancyrocrinus* in a morphological and biological sense, and omitting what we know of it from previous authors, it is apparent that the term *Ancyrocrinus* refers to some part of the echinoderm skeleton, that it is in the pelmatozoan class, and is recognized as a stem. Anticipating that the anchors may represent only a lower and not an upper stem region (as is indicated in figure 8 with the remarkable stem-portion above the anchor), the pelmatozoan group to which *Ancyrocrinus* belongs must be noted. Excluding the stemless *Thecoidea* (*Edrioasteroidea*), there remain crinoids, cystoids (including blastoids) and carpoids. Because the anchors themselves are not certain criteria, the final decision must be based upon the normal stem-joints. These are in accord with what is known of crinoid columnals, but do they not agree with columnals of other groups? Beneath "styloid" or "styloconus,"¹ the carpoids show columnals of an entirely different structure. But also, undivided, cylindrical stem-joints appear (e.g., *Cothurnocystis*),² which seem to be not unlike those found among crinoids. Concerning cystoids and blastoids it must be remembered that, as Jaekel³ states, stems in blastoids are composed of normal discoid ossicles. Special attention may be called to *Lepadocrinus*, in which the distal stem region is composed of apparently discoid columnals which are overgrown with secondary stereom deposited in the adult stage in a manner similar to that found in *Ancyrocrinus* (compare pages 29 ff., Figs. 21 and 22). It must be remembered, however,

¹Jaekel, O., *loc. cit.*, 1918, p. 115.

²Bather, F. A., 1925, "*Cothurnocystis*: a Study in Adaptation," *Pal. Z.*, VII, 1, p. 3.

³Jaekel, O., 1918, *loc. cit.*, p. 103.

that the knowledge of stem and stem-joints among the non-crinoid pelmatozoa has remained comparatively fragmentary.¹ Since so little is known of stem-joints, the question concerning the classification of *Ancyrocrinus* appears perhaps not so unjustified as at first sight. To my knowledge, however, true cirri have not been observed in specimens other than those of the crinoid group, and inasmuch as true cirri are present in *Ancyrocrinus*, this form may be considered a crinoid until similar structures are found in cystoids, blastoids, or carpoids.

But let us return to the question as to which stem-region is represented by the anchor. Since our previous discussion (page 17) leaves the upper stem-region out of consideration, we have to decide between the middle and the under stem-region, the latter of which coincides with the root-region in the broadest sense. In a purely physiological sense the great majority of *Ancyrocrini* doubtless represent the distal end. But if we remember that in some cases a downward prolongation below the anchor is clearly indicated, and if we further realize that the rounding-off below, so well seen in many specimens, was possible only after loosing the fixation, we may become inclined to regard *Ancyrocrinus* not as the morphological (primary) distal end (root), but rather as belonging to the so-called middle stem-region. On the other hand, in most palæozoic crinoids, cirri are rather restricted to the lowest portion of the column² and specimens of *Ancyrocrinus* show hardly any traces of cirri or cirrus-sockets above the anchor.³ Therefore, we may refer the anchor to the lowest or root-portion, in the broadest sense. That, of course, is quite in contrast to the previous impression. In that regard a decision may be reached by critical examination of the downward prolongations already mentioned. Thereby it is found that they possess a structure more like that of the cirrus type than of the stem. From this, as well as from the observation of the specimens with the truncated ends shown in figure 11, I am inclined to suppose that the anchor represents a true root-portion; or, in other words, that separation from the surface took place by breaking loose, not above but within the primary root.⁴

Because *Ancyrocrinus* is not normally sessile, it is necessary to discuss the method and origin of its special adaptation. For that purpose we may again consider the specimen in figure 8. This specimen, with its

¹Jaekel's statement of 1899 seems valid some twenty-five years later.

²Compare Wachsmuth and Springer, *loc. cit.*, p. 41.

³The only exception known to me is one specimen figured by Goldring (*loc. cit.*, Pl. LIX, Fig. 14) in which one place of cirrus insertion is to be seen in the uppermost part of the preserved stem portion.

⁴In accordance with this belief the comparison with *Pentacrinus* (*Annacrinus*) *wyville-thomsoni* (Wachsmuth and Springer, *loc. cit.*, p. 50) seems justified only in so far as the creation of a secondary organ for anchoring is concerned.

long, slender cirri and its small anchor center, seems entirely different from the others. Let it be assumed that the downward prolongation was not in the form of a knob-like ossicle but was similar in shape to a cirrus as in the upper left specimen in figure 11. Under such an assumption the specimen in figure 8 would not be greatly different from a normal branching root, and fixation must have occurred in a similar manner. The downward prolongation, here destroyed in fossilization, may have been cast off and stereom deposited secondarily, thereby rounding off the "root" and overcrusting the cirri and undermost stem-joints. This process, if continued, would doubtless produce such a specimen as that shown in figure 7. It may be assumed, therefore, that the specimen in figure 8 represents a young individual, a normal ontogenetic stage, and that *Ancyrocrinus*, or rather the forms to which the *Ancyrocrinus* "root" belonged, were fixed, when young, by a normal root. These became free by breaking within the primary root, and the remaining portions were modified by secondary depositions of stereom into a sort of grapnel, which perhaps may have functioned "as a drag or ballast" (Kirk, *loc. cit.*, p. 46) but more probably served as an anchor whenever the animals, according to their semi-sessile habits, wanted rest. Such fixation, however, would have been rather unsteady and possible only on a loose mud or sand-bottom surface, in rather quiet water.

This development of *Ancyrocrinus* is in many respects hypothetical. In forms such as Goldring's *Ancyrocrinus quinquepartitus*, it is apparent that the stage represented in the specimen in figure 8 may not have been run through in the ontogeny. Perhaps the larval stage was followed directly by the formation of a knob-like ossicle, and figure 8 means only an exceptional case. Perhaps this ontogenetic development had not yet become fixed, with a stage like figure 8 occurring at times but not always. To decide that question seems almost impossible.¹ But, whatever the exact development may have been, we are entitled, in my belief, to suppose that the phylogenetic course led from a normal *Rhizocrinus*-like root to the true *Ancyrocrinus*-structure. In this, evolution has not achieved its aim. Forms with truncated bases² are to be understood only as attempts to regain tighter hold on a rather solid surface. Finally, the fact that no crown has been found in connection with the anchor indicates a further change during later life in which the so-called anchor was cast off. Thereby we get the impression that the anchor cannot have

¹Regarding the great variability among adult forms, the writer is inclined to suppose that the latter was the case.

²That these truncated bases are secondary structures independent from the primary distal ends hardly needs to be discussed.

been a good adaptation and that this method of partly regaining the freedom lost by the early ancestors did not succeed.¹

c.—*Camarocrinus*

Lobolithus, or *Camarocrinus*, which departs from a normal root-type even more than *Ancyrocrinus*, was recently discovered to be really the root of *Scyphocrinus*. This curious form has been carefully studied by Schuchert² and Springer.³ Although the structure of *Camarocrinus*, its history, mode of occurrence, origin and biology have been discussed, the assumptions are not entirely satisfactory. Because I have dealt with this in another paper,⁴ few details are given here.

According to Schuchert and Springer, these bulbs consist of the following structures (Fig. 12a): (1) a horizontally branching root; (2) sac-

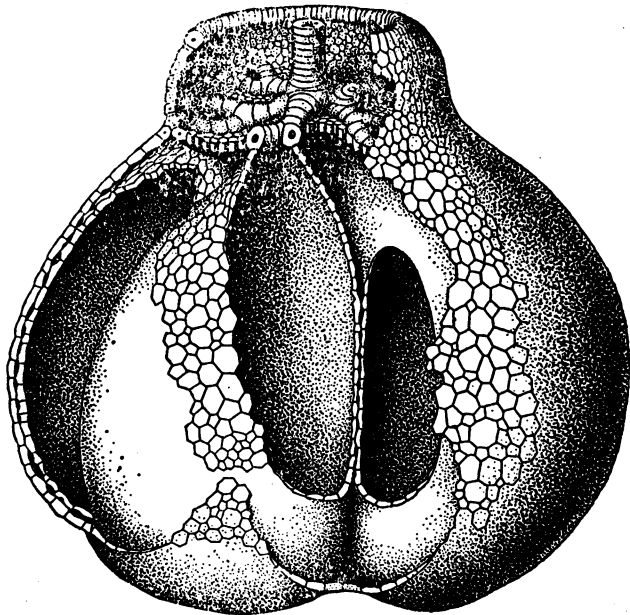


Fig. 12a. Restoration of a "*Camarocrinus*" root of *Scyphocrinns*, after Springer, 1917. $\frac{1}{1}$.

¹Compare Ehrenberg, K., 1922, *loc. cit.*

²Schuchert, C., 1904, "On Siluric and Devonian Cystidea and *Camarocrinus*," *Smiths. Inst. Misc. Coll. (Quart. Issue)* XLVII, Pt. 2, Washington, D. C.

³Springer, F., 1917, "On the Crinoid Genus *Scyphocrinus* and Its Bulbous Root, *Camarocrinus*," *Smith. Inst., Publ.* 2440, Washington, D. C.

Both papers contain additional bibliography.

⁴Ehrenberg, K., "Zur Frage der biologischen Deutung der ('*Camarocrinus*-' Wurzeln (Lobolithen) von *Scyphocrinus*," *Pal. Z.* VIII, 1, 1926. To the bibliography cited therein may be added, F. A. Bather, 1919, *Geol. Mag.*, Dec. VI, Vol. V, No. 9, pages 276-277, with which paper I have not been previously acquainted.

like, single-walled chambers (which are closed except for one opening above and extend downward from each peripheral bifurcation of rootlets, so that the walls of the single chambers lie to some extent close together and leave in the center a polygonal space which Schuchert terms the "medio-basal" chamber); (3) the collar which surrounds the area occu-

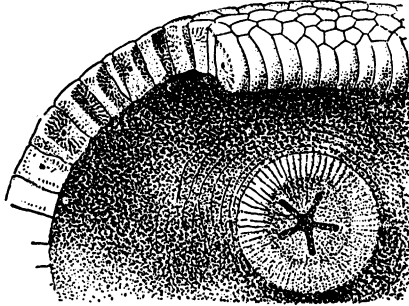


Fig. 12b. Part of a "*Camarocrinus*" root of *Scyphocrinus*, seen from above, after Springer, 1917. $\frac{1}{2}$. Compare page 24, footnote 2.

piated by the roots and the sac openings between the peripheral dichotoms; (4) a horizontal pavement between the root-members; and (5) a wall enclosing all the sacs and constituting the outer wall of the bulb. All the structures mentioned under 2-5 seem to be composed of irregular plates.

Springer states that the sacs or sac-walls are derived from the pairs of peripheral rootlets. Each pair divides into numerous ramifications which are connected, by growth of undifferentiated plates, to form a pair of curved extensions, which by the meeting and fusion of their edges make a circlet of four or more ovoid sacs. The collar, the pavement and the outer wall were produced from the principal root members "by continuous multiplication in different directions."¹ The appearance of radiating striæ and of a rather central perforation on the surface of the polygonal plates of the collar was considered by Springer to be additional proof that these plates were highly modified root-elements.

As Springer pointed out,² the very young stem terminated in a tapering portion. From the latter, which was rather horizontally situated, the upper stem rose obliquely as figure 13a shows, representing a stage in which the one-sided root-branching has already begun. Consequently

¹Springer, *op. cit.*, p. 15.

²Springer, *op. cit.*, pp. 16 ff.

(Fig. 13b-d) the primary distal end becomes more reduced, while the stem reaches an almost vertical position.¹

If this were the course of development it would be remarkable because of the conclusion thereby permitted concerning the mode of life of young forms.² In the author's opinion it would further point to an ancestor with some sort of creeping-root-trunk.

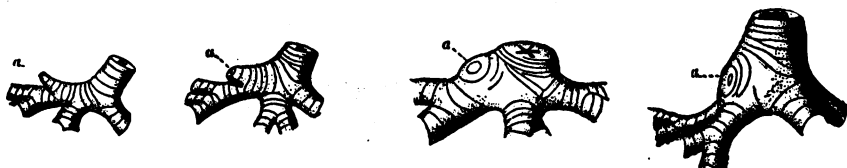


Fig. 13. Four successive stages of growth of the original root-region of *Scyphocrinus* (bulbs omitted), after Springer, 1917. $\frac{5}{8}$. a = primary terminal root.

Having shown that these bulbs must be regarded, according to Schuchert and Springer, as highly modified branching roots,³ probably from a type spreading mainly in a horizontal direction, their biological meaning may be discussed. Apart from the views that these unique bulbs represent sea urchins or cystid thecae, views which need no discussion,⁴ they have been regarded as "brood-pouches" or receptacles of the genital organs, as merely enlarged roots and as floats and cysts caused by parasites. What Haeckel⁵ and others mean by "brood-pouches" is not entirely clear.

Jaekel evidently has deduced, from his⁶ view that the primitive Hohlwurzel originally lodged the genital organs, the idea that in *Camarocrinus* this primary function of the root has been retained with modifi-

¹This development did not always occur equally, for the writer observed young specimens which were more advanced than older ones. This is a phenomenon known to anyone who has studied the ontogeny of any animal in a large series of specimens, and it therefore does not touch the correctness of Springer's opinion. It may be noted that a stage comparable to that shown in figure 13b has been observed by the author on a "*Lobolithus*" from the upper Silurian of Karlstein, Bohemia (now in the Palaeontological and Palaeobiological Institute of the University of Vienna). The process marked by "a" in figure 13 looks like a boring and shows a wider inner lumen and not a small canal as suggested by Springer's figures. It is possible that the wide lumen was caused afterwards during fossilization, although no traces of rupture are visible, for the borders of this process are rather smooth.

²In regard to the assumed young roots lodged on mature bulbs (Springer, *loc. cit.*, pp. 18-19), I cannot agree, for it has not been sufficiently proven that these are young *Camarocrini*.

³Sardeson in the *Journal of Geology*, XVI, No. 3, 1908, pp. 239-254, tries to derive *Camarocrinus* from a discoid root like *Lichenocrinus* (compare page 49), although Schuchert, whom he also quotes, has shown that the starting point of *Camarocrinus* must have been a branching root and that *Lichenocrinus* has no direct relation to *Camarocrinus*. Because Schuchert's investigations have been confirmed by Springer, Sardeson's view may be definitely abandoned.

⁴It may be noted that Deecke (*Neues Jahrbuch für Mineralogie, etc.*, 1915, Bd. II, p. 17) thinks that *Camarocrinus* also could be *Pharetrones*. But the typical echinoderm structure of the skeletal elements excludes such a suggestion.

⁵Compare Schuchert, *op. cit.*, pp. 256-259.

⁶Jaekel, O., 1904, "Ueber sogenannte Lobolithen," *Mai-Prot. Deutsch. geol. Ges.*, Bd. LVI, pp. 59-63, and 1918, *op. cit.*, p. 18.

cation in form and structure. But this view must raise the objection that *Camarocrinus* cannot be directly derived from such a "Hohlwurzel," and hence its ancestral root-type could not have lodged the genital organs, just as it does not for example in the root of *Rhizocrinus*. For this reason, Jaekel's idea loses much of its probability.¹

Springer's view (*op. cit.*, pp. 9 ff) is scarcely more satisfying. Referring here also for more detailed discussion to the paper cited, it may be stated briefly that these bulbs mean such a unique and peculiar modification that they cannot have "served merely as enlarged roots." They must have had a special meaning.

The float hypothesis² is given the most discussion. The arguments advanced for it and against it are, however, somewhat disappointing. For obvious reasons it may be referred to only two principal questions. First, whether the crowns and stem show any peculiarities which point to such an uncommon mode of life. To this the answer is evidently negative. Secondly, whether the bulbs could have acted as the support of the animals floating, as generally supposed, in an inverted position, the assumption being inevitable that the chambers have been filled with a gas. The sacs, however, have large openings, and although the latter might have been closed by membranes, it is not easy to imagine how regulation of gas-pressure could have been effected. Besides, the thinness³ of the sac-walls and their partially concave curvature would scarcely enable them to endure pressure. The last view, expressed by Haeckel⁴ and then independently by Abel,⁵ suggests that the bulbs may be caused by parasites. At first sight, this hypothesis seems rather improbable. But the fact that there existed no direct communication, either between the cavities of the sacs and the stem-canal or between the so-called medio-basal chamber and the stem-canal,⁶ appears to agree fairly well with an external cause of these outgrowths. Furthermore, it hardly can be denied that such an external cause makes the trend of origin much more explicable than any of the other hypotheses where the first step of the sac-formation must always remain rather puzzling. Finally, since it is known that myzostomids sometimes cause sac-like cysts⁷ on recent

¹For more detailed discussion the author refers to the paper cited in footnote 4, page 20.

²This opinion was first expressed by Hall and then adopted by Schuchert, Sardeson, and Kirk (*op. cit.*, p. 54), while Bather (1900, *loc. cit.*) advanced this view and Barrandes' view of the cystid nature: Schuchert, 1904, *loc. cit.*, pp. 256 ff.

³Springer, *loc. cit.*, p. 7.

⁴Compare Schuchert, *op. cit.*, pp. 256-259.

⁵Abel, O., 1920, *Lehrbuch der Paläozoologie*, 1st ed., pp. 94 and 252, 2d ed., pp. 97 and 265.

⁶This fact has been already mentioned by Schuchert (*op. cit.*, p. 266), but it has not been hitherto recognized that it means a difficulty to any one of the hypotheses previously discussed.

⁷Graff, L. v., *Challenger Rept., Myzostomida*, X, 1884, XX, 1887; *Palaeontographica*, XXXI, 1885, pp. 183-192.

crinoids, without altering the normal skeleton, and that such cysts with their walls of irregular polygonal plates closely resemble singular sacs of our bulbs, the above view loses much of its strangeness. So after careful investigation, I reached the conclusion, that it is probable that the *Camarocrinus*-sacs mean nothing else than structures comparable to the so-called "Hautcysten," and may be caused by some myzostomids or a closely related form, as already suggested¹.

We turn now to the question as to how far we can speak of a modified root in the case of "*Camarocrinus*." As stated above (page 21), Springer regarded all the plates of the sac-walls, collar, etc., as highly modified root-elements. On the other hand, it is known from the "Hautcysten" of recent crinoids, that the skeletal plates in their walls originate independently from the normal skeletal elements. This means that any difficulty in our interpretation of Springer's chief argument for the derivation from the normal skeleton lies in the structure of the surfaces of the polygonal plates (page 21). It is now of importance that we note that he mentions such surface structure merely from the collar-plates.² Since only the sac-walls are comparable to the "Hautcysten," while the other structures, also after the "cyst-theory," may be modified root-elements,³ I do not see any difficulty in this regard.

In summary, then, *Camarocrinus* means a modification of a branching root (creeping-root-trunk?) on a (pathologic) parasitic foundation whereby some new elements were formed and other normal elements highly modified.⁴

3. ROOT-FUNCTIONS OF THE STEM

The modifications discussed on the foregoing pages concern typical

¹Recently Bather (Quart. Journ. Geol. Soc. London, Vol. LXXXIV, Pt. 2, 1928, p. lxxix), referring to my cited paper of 1926, expressed the opinion that "the complexity and regularity of the structure do not suggest a response to a worm nestling between the root-branches." One of these objections seems to me not justified, since in recent crinoids sacs of quite similar structure evidently are a response to a worm nestling and since also plant-cysts, caused by insects, show such regularities. (Besides, the regularity is by no means so great as may be supposed.) More difficult is the other objection concerning complexity, if Bather means, as I suppose, the great number of sacs, the outer wall, etc. In that regard the interpretation given in my paper of 1926 may be not yet entirely convincing. The possibility of it, however, must be admitted, and therefore, in this case, I think, cannot mean a real difficulty for the interpretation in general, where all other facts seem fairly well established.

²*Op. cit.*, p. 16. Compare also figure 12a and b. It may be noted that in figure 12a, copied from Springer's report, an axial canal is indicated on collar-plates and, besides that, only on one plate of the horizontal pavement and of the outer wall. Since the two last-mentioned plates are just those next to the collar, and since no such canal is indicated on any of the other plates of these categories, nor on the proper sac plates, I suppose it may have been drawn in here erroneously.

³For reasons giving more detail, see footnote 4, page 20.

⁴The frequent occurrence well shown in the slab now in the U. S. National Museum (Springer, *loc. cit.*, Pl. 1), Springer has laid to the conclusion of *Scyphocrinus* colonies. The writer has dealt in two earlier papers (Amer. Mus. Novit. No. 204, 1925; Verhdlg. Zool. bot. Ges. Wien, Vols. 74-75, 1924-25) with the problem of crinoid colonies in general and has tried to show that often what appears to be a colony may really be a postmortem assembly caused by water transportation, etc. *Scyphocrinus* in Plate 1 may suggest a true colony, and the parallel orientation of stems and crowns on this slab may have been caused by a current which destroyed the colony. It may be explained, also, as a mode of occurrence, as mere deposition by a current of parallel action which brought the remains from some other place. Springer himself must assume this at times, for some of the bulbs on the rounded side (biologically, the under one) show attached epizoa which could have settled there only after the bulbs had been washed out from the bottom.

roots (that is, sections distinguishable from the stem proper, although the border-line towards the stem often may not be exactly traceable (compare page 6). Now attention will be called to some cases where fixation is effected by the stem itself. If I speak here of "roots" (compare page 5) it is only in the sense of fixation and not in a morphological sense.

Pelmatazoan stems which end distally in some sort of loop or coil¹ are known chiefly from Palæozoic rocks. Sometimes also the crown or theca is preserved but often only the stems are found. Traces of typical roots are entirely absent. As I discussed fully in a previous paper², these coils mean an adaptation to a semi-sessile life (after the loss of the primary fixation by a normal root) in which the coiled end functioned either like the grasping tail of *Hippocampus*, or in other cases (being immovable) more probably as a drag or anchor. Such a coil appears sometimes

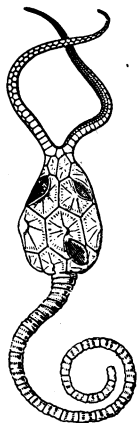


Fig. 14. *Pleurocystis filitextus*. Restoration after Bather, 1900, copied from Ehrenberg, 1922. About $\frac{1}{2}$.

to be a specific character, while at other times it seems to be only an accidental structure probably acquired after the involuntary loss of the primary fixation. However, both cases are of importance for the thorough understanding of the Pelmatazoa in regard to biology and phylogeny. They seem to be connected with the tendency to regain unlimited freedom, a tendency traceable through the whole pelmatazoan class, but never fully reaching its aim. They finally represent "fehlgeschlagene Anpassungen."

Turning now to the morphology of these coiled stems, we can easily discriminate between different groups. The simplest form has a single loop, or two or more windings, all lying in one plane, representative examples of which are *Dendrocrinus* or *Pleurocystis* (Fig. 14). In another group the enrollment did not take place within a single plane, and the "root" thus formed is cone-like or pyramidal. Examples of such "Pyramidenwurzeln" are *Thallocrinus* or *Acanthocrinus* (Fig. 15).

Somewhat different from the types just mentioned is a stem-fragment from the Chester group, Huntsville, Alabama, now in the Springer Collection of the U. S. National Museum. That specimen (Fig. 16), otherwise noteworthy by the fairly visible cirrus-sockets, shows wedge-

¹This type of coiling must not be confused with another type in which the whole stem is coiled and wound around the crown. The latter mode is omitted because it has nothing to do with fixation (compare K. Ehrenberg, 1922, see footnote 3, page 5).

²Acta Zoologica, 1922, compare footnote 3, page 5.

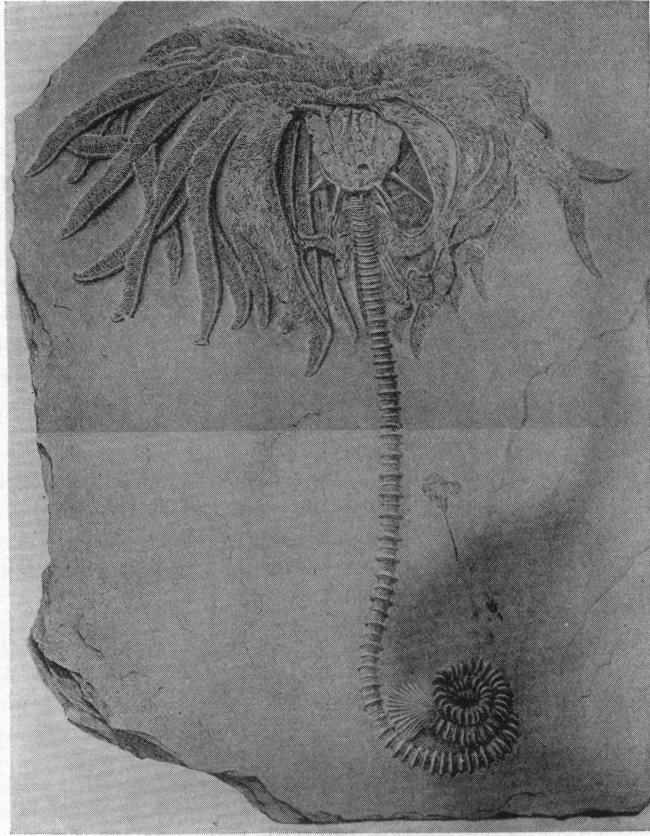


Fig. 15. *Acanthocrinus rex* Jaekel, from the Lower Devonian of Germany. After Jaekel, 1896-1897. Copied from Ehrenberg, 1922. About $\frac{1}{3}$. See page 25.

shaped joints formed in a manner that made any movement or change of the degree of coiling almost impossible. Besides that, the fact that the distal and proximal ends, where they cross, seem firmly grown, or better, welded together, clearly shows that this coiling, resulting in sessility, was continuing. The animal could become free again only by breaking loose from the attachment around what was doubtless a very small object, unless the latter had decayed.

While in the above-mentioned cases the coiling is restricted to the distal end and is rather regular, in other cases a greater portion of the stem is more or less irregularly wound around some object that will give it support. Several modifications of the normal stem-form and other

characters clearly indicate that the winding-around occurred only occasionally and endured perhaps for the remainder of the life of the animal, unless freedom was gained later on by breaking loose above the wound portion, leaving the latter either to remain in its place or to fall down. The former probably happened to a specimen of *Glyptocrinus*, described by Miller as *G. shafferi* but supposed by others to be a young *G. dyeri* (Fig. 17). "We have the tapering end¹ of this species wound around a



Fig. 16. A coiled stem-portion from the sub-Carboniferous, Chester Group, Huntsville, Alabama. Note the knob-like cirrus-sockets, especially on the right side, the wedge-shaped joints, the close union between both ends, etc. Below, a little piece has been broken away. Springer Collection, U. S. National Museum. $\frac{1}{4}$. See page 25.



Fig. 17. A distal stem-end of *Glyptocrinus shafferi* Miller (? = *G. dyeri* juv.) wound around another stem-fragment. From Ehrenberg, 1922, after Miller. About $\frac{1}{4}$.

crinoid column of a distinct species, almost as neatly as a thread can be wound upon a spool. The column gradually tapers as it coils, until it becomes so small as to be scarcely visible to the naked eye. The larger plates of the column which give it that banded appearance, or make it resemble a string of small spools, gradually diminish, and before the column terminates it becomes as smooth as a silken thread."² There is hardly anything to be added to that description. The diminishing in diameter and the flattening may be specially noted; however, it may be further remarked that among this genus such abnormal fixations by a variously coiled stem-portion seem to occur frequently. This may be in connection with the U-shaped curvature often observable in the proximal stem-region, which points to an abnormal habit, whereby one end of the "U" was occupied by the crown, while the horizontal portion lay upon the sea-bottom and the distal end was turned up and wound around branches of corals, seaweeds, or similar objects.³

¹As shown in figure 17, the winding is not restricted to what is usually called the end.

²Miller, S. A., 1880, Journ. Cincin. Soc. Nat. Hist., 3, No. 3.

³Compare Ehrenberg, K., Acta Zool., III, pp. 274 and 309.

Figure 18 also shows a stem-fragment wound around another one. Here the winding-stem forms a sort of knot, and both ends of it are turned in the same direction. In the more or less horizontal section the

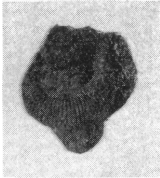


Fig. 18. Fragment of a stem wound around another stem-fragment and fixed to the latter by secondary stereom deposition. From the Waldron beds, Niagara Group, Newson, Tennessee. Specimen in the Springer Collection of the U. S. National Museum. $\frac{1}{4}$.

joints are flattened, drawn out breadthwise, and are wedge-shaped. From the stem itself, spread flat irregular processes, firmly cementing it to the straight stem. Many other examples where the same thing happened could be added. A modification of the joints, and the secondary deposition of stereom (similar to some spreading-roots discussed later on), always clearly show the firmness and durability of that connection.

Types like *Pleurocystis* and *Acanthocrinus* mean an adaptation to a secondary sessility (page 12). Such types, as represented by figures 17 and 18, can be regarded as further advanced, in so far as they mean a firmer secondary fixation which is clearly indicated by the characters mentioned above¹. On the other hand, the so-called "tapering-stems" could be taken for a stage preceding that represented by *Pleurocystis*, etc. Originating as commonly supposed, after the solution from the primary root, they probably had some prehensile power, and, since for other reasons it was not possible for the animals to maintain permanent freedom, they may have been used for occasional attachment. They may, therefore, be mentioned here under these merely physiological roots. As an example, the restoration of *Eifelocrinus* by Haarmann may be cited (Fig. 19).² A similar corkscrew twisting of the distal, tapering stem-end is shown by a specimen of *Gilbertsocrinus tuberosus* from the Crawfordsville beds; now in the American Museum of Natural History (Fig. 20)³, and many other examples could be added.

Above I have tried to show that the modifications of the stem itself can be arranged in some sort of sequence. Tapering stems represent the first stage and indicate a semi-free mode of life; the distal coiling as in *Pleurocystis*, etc., the second, semi-sessile stage⁴, and the wounded, deformed and often cemented stems the third stage or secondary sessility.

¹That the fixation also here was a secondary one is shown by the absence of any normal root.

²Haarmann, E., 1920, "Die Botryocriniden und Lophocriniden des rheinischen Unterdevons," Jahrb. preuss. geol. L. A., Bd. XLI, T. 1, H. 1, Berlin.

³In a previous paper ("The Crinoid Occurrence at Crawfordsville, Indiana," Am. Mus. Novit. No. 204, 1925), I called attention to the fact that at Crawfordsville many forms occur which have not been permanently fixed, which is one of the proofs that there has not been a true colony.

⁴Ehrenberg, K., Acta Zoologica, III, p. 297, footnote 49.

This sequence, of course, means neither an "Ahnenreihe" nor a "Stufenreihe" but only an "Anpassungsreihe" in the sense of Abel¹; in other words, these forms show only the trend of evolution and not their mutual phylogenetic interrelationships.

Another modification which is to be mentioned here is that represented by *Lepadocrinus* (*Lepocrinites*)². In this the typically cystoid-



Fig. 19. Restoration of *Eifelocrinus dohmi* Wanner, from the Devonian of Germany, in both floating and fixed condition, after Haarmann, 1920. See page 28.

theca (note the pore-rhomb on the top of figure 21) is followed by a stem-portion which is composed of rather normal ossicles and which clearly tapers distally. The tapering section, however, does not represent the end of the stem and is followed distally by a broader, apparently un-

¹Abel, O., 1912, *Grundzüge der Paläobiologie der Wirbeltiere*, Stuttgart, pp. 632 ff.

²Compare Hall, J., 1859, *Paleont. N. Y.*, III, pp. 125-128, Pl. viii, Figs. 1-23, and Conrad, 1840, *Ann. Rep. on Palæontology of New York*, p. 207, Vanuxem, 1842, *Geol. Rep. 3rd district of New York*, p. 117, Mather, *Geol. Rep. 1st district of New York*, pp. 247 and 346 (cited after Hall) and Schuchert, 1904, *op. cit.*, pp. 211-215.

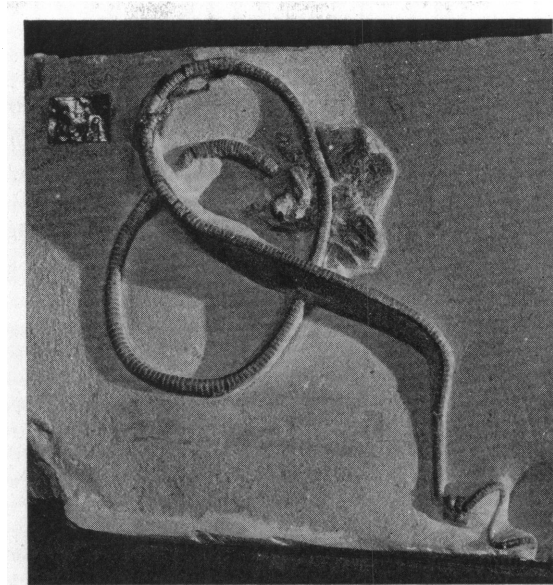


Fig. 20. Twisted and tapering stem of *Gilbertocrinus tuberosus* Lyon, from the Crawfordsville beds, Crawfordsville, Indiana. $\frac{2}{3}$. A. M. N. H. $\frac{7195}{3}$. See page 28.

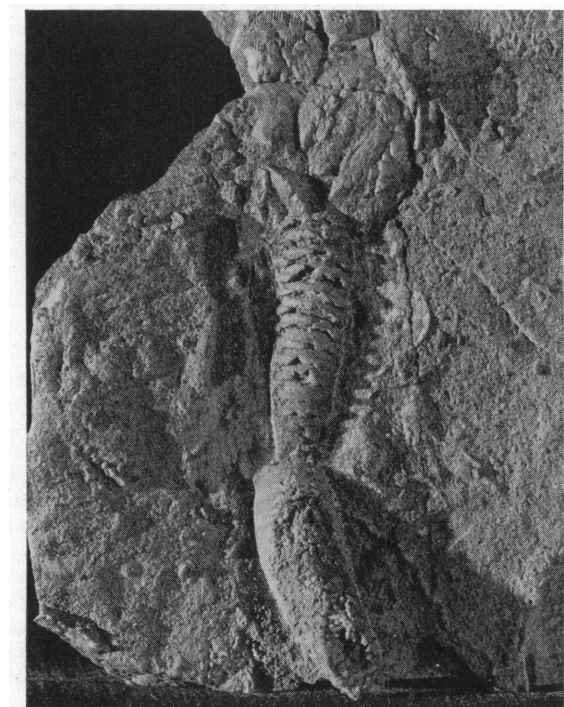


Fig. 21. *Lepidocrinus gebhardi* Conrad, from the Lower Helderberg Group, Schoharie, N. Y. Enlarged. A. M. N. H. $\frac{2285}{3}$. See page 29.

jointed, carrot-like element tapering again towards its distal end. No transition is to be remarked between this and the normal stem-part, but the distal element begins quite abruptly. The proportion of length between the theca, the normal stem and the distal portion seems to be usually about 1:1:1. However, in the Peabody Museum of Yale University, New Haven, Conn., I found a slab from the Lower Helder-

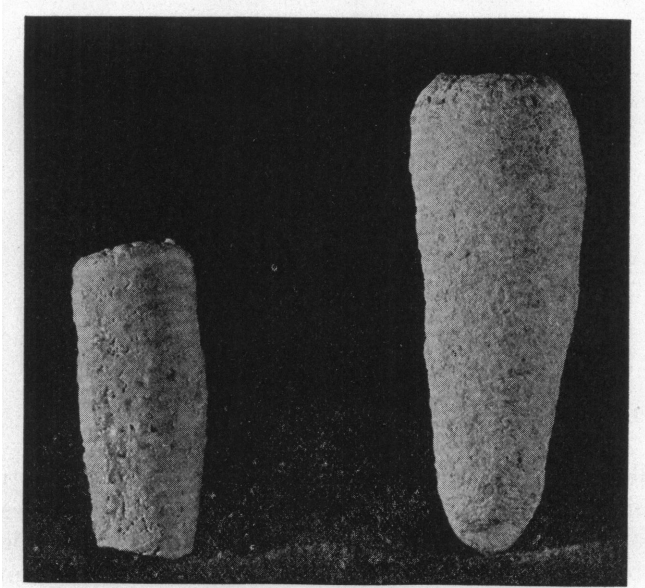


Fig. 22. A smaller (younger?) and a greater fused stem-portion of *Lepadocrinus gebhardi* Conrad, seen from the side. Locality and horizon same as Fig. 21. Enlarged. A. M. N. H. $\frac{2281}{142}$. See page 32.

berg group, Jerusalem Hill, N. Y., with several specimens, all of which possessed stems about three times as long as the theca, in which the relation between the proximal stem-portion and the distal one remained likewise 1:1. In the U. S. National Museum at Washington, isolated distal portions, from the lower Pentamerus beds, Schoharie, N. Y., are found, which were considerably longer, reaching a length of about 4 cm.

As has been already remarked by Schuchert and Kirk¹, the distal portion consists of fused columnals around which a secondary deposition of stereom took place, causing the greater breadth mentioned above. This is clearly to be seen on some smaller (= younger?) specimens, also

¹Schuchert, 1904, *loc. cit.*; Kirk, 1911, *loc. cit.*, page 17.

in the side-view (Fig. 22). The secondary stereom deposition has then not reached a high degree. The same was also the case in the left-hand specimen of Fig. 23, like the specimens of Figs. 21 and 22 of the American Museum of Natural History, where in the above view the borders between the normal joint and the secondary stereom are clearly visible.¹

Considering the morphological meaning, the resemblance to *Ancyrocrinus* (pages 11ff.) may be noted. The modification is much the same, except that in *Ancyrocrinus* the modifications concern stem or root and

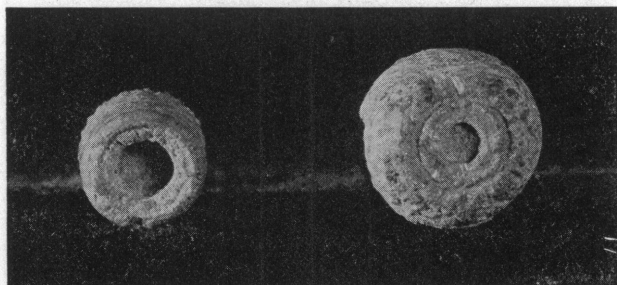


Fig. 23. The same specimen as in Fig. 22, seen from the upper end. Enlarged.

cirri, while the distal end of *Lepadocrinus* doubtless means a true stem only. Aside from that difference, the parallelism between these two is very great. In *Lepadocrinus*, also, the secondary stereom deposition seems to begin only at a certain stage of growth and to increase further on. Here, too, some forms appear less advanced than others, as is indicated by the previously mentioned forms of the Peabody Museum. In these, although the specimens seem to be wholly adult, the secondary stereom is rather thin, the segmentation not having become entirely invisible in most cases. Here, also, these ends are frequently found isolated as in *Ancyrocrinus*, and that list could be further increased.

The question is brought to attention: are the distal ends really distal stem-portions or are they homologous to the normal middle stem-portion? In Bather's² restoration of *Lepadocrinus quadrifasciatus*, the stem shows no fused columnals, and ends in a typical, sometimes encrusting (?) root. Dr. Bather informed me that this restoration is based upon actual evidence of some specimens in the British Museum, and adds that "the columnals in the distal portion of the stem of *Lepadocrinus* are

¹Sometimes the segmentation is visible also on adult specimens, but this is due to weathering (compare Hall, *loc. cit.*).

²1900, *op. cit.*, p. 61, Fig. XXX.

by no means always fused"¹. It must be admitted, however, that the stem of *L. quadrifasciatus* with its relatively high ossicles² looks somewhat different from that in *L. gebhardi*, to which our above-mentioned specimens have been referred in so far as they have been specifically determined. The peculiar fusion of stem-joints may be restricted to *L. gebhardi*, and, according to Schuchert, probably also to his *L. manlius*; or occasionally it may occur in different species. It may be that forms such as *L. quadrifasciatus* should be referred to another genus as proposed by Schuchert, and the genus *Lepadocrinus* restricted to forms with fused columnals. In every case the specimens in the British Museum indicate that the fused columnals cannot be taken for a really distal stem-portion but must be taken for a modified portion of the middle stem-region. The modified stem-region in *Lepadocrinus* is therefore not exactly homologous to that in *Ancyrocrinus*.

Besides the morphological meaning, the biological one wants further discussion. With the absence of a true root and traces of cementation in connection with the fused pieces, normal sessility has not been maintained. This fused portion, which physiologically was the distal end, could not have served for fixation on a hard bottom. The only conclusion is that it was buried, or stuck fast vertically in a soft mud from which it could be easily loosened again.³ From all this it seems highly probable that *Lepadocrini*, provided with such a fused stem-portion, maintained a semi-sessile life, wherein that portion functioned as a means of temporary fixation. Furthermore, it seems clear that this mode of life began (phylogenetically or ontogenetically) after loss of a normal root, which occurs ontogenetically only at a certain stage of growth. It may be that the fused portion also functioned as a ballast,⁴ when the animals voluntarily or involuntarily changed their abode, but this may not have been the main function. The fact that the fused portions are often found to be isolated suggests that the adaptation has not been highly advantageous and that again, later on, they were frequently cast off.

In connection with *Lepadocrinus*, another curious case may be mentioned briefly. Jäkel figured in 1918 the remains of a crinoid under the name *Drepanocrinus sessilis*. According to the merely preliminary description and to the figures, the calyx ends below in an angular, twisted, spear-like structure. After Jäkel's description we must conclude that

¹The author wishes to express here his thanks to Dr. Bather for this kind information.

²Such relatively high stem ossicles are also visible on the sketches of other specimens of *L. quadrifasciatus* kindly sent by Dr. Bather.

³Another explanation would be that the fused portion lay on the ground like the "roots" of some Carpoidea. In this case, however, the column would not be entirely round but flattened dorso-ventrally.

⁴Kirk (*loc. cit.*) seems to think this more probable than the function for temporary fixation.

the above structure represents not only the basal cup but some stem ossicles which have been entirely joined together with the adjoining calyx plates. This spear of the "sessile dwarf form" of the upper Cretaceous of Germany should have served for drilling into the marl-bottom. We may not enter here into a full discussion as to whether the latter explanation is exactly correct. For us it is of importance that the spear-like end, which somewhat resembles certain rostra of *Belemnites*, probably rested in a soft substratum and thereby also served for (temporary?) fixation.

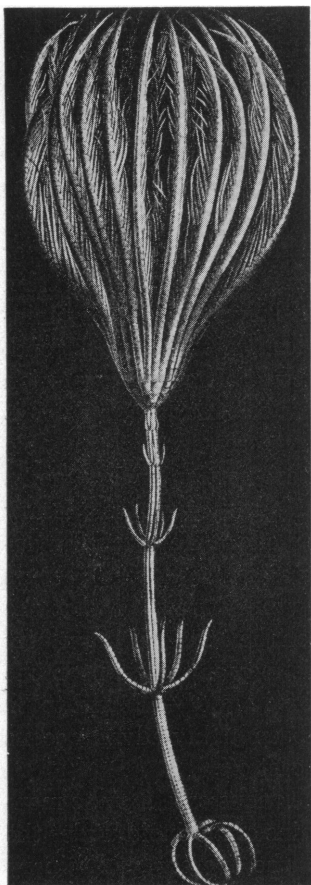


Fig. 24. *Isocrinus* (*Annacrinus*) *wyville-thomsoni* Jeffreys, after Carpenter, 1884. $\frac{1}{2}$.

4. FIXATION BY NON-RADICULAR CIRRI ("Grasping-roots")

In the aforementioned cases, fixation always has been effected either by a more or less typical root or by the stem itself. Sometimes, however (after occasional loss of the normal root or without that), fixation may be maintained also by or with the assistance of non-radicular cirri. Such fixation (occurring especially among pentacrinids) may be temporary, or permanent for at least some length of time.¹ A more advanced adaption is found in *Isocrinus* (*Annacrinus*) *wyville-thomsoni* Jeffreys whose peculiar stem-structure and probable mode of life have been discussed at some length by previous authors.² In this species the normal attachment is usually loosened by a break in the stem below a nodal joint. Consequently, the latter becomes rounded below by secondary stereom deposition, and the axial canal beneath is closed. The cirri at the whorl of that undermost nodal joint are claw-like and directed downward (Fig. 24). In this manner they function as a grasping-root for temporary attachment, not

¹Compare Carpenter, P. H., 1884, Challenger Rept. Crinoidea (Zool. XI), p. 304 and Pl. xi, and Clark, A. H., 1915, Monogr. Exist. Crin., I, Part 1 (Bull. U. S. Nat. Mus., No. 82, page 344).

²Compare Carpenter, P. H., *op. cit.*, pp. 315 ff., Kirk, E., 1911, *op. cit.*

to the bottom but to objects which can be easily clasped by such claw-like organs.

To this type of secondary fixation belong also the modifications of the recent *Antedon* and some allied forms both fossil and recent. Here (Fig. 25) the stem, and with it the primary root, have been totally lost, except the so-called centrodorsale, which consists of one or a few columnals fused together with the infrabasal-circlet. This centrodorsale usually bears cirri, arranged regularly in one row or irregularly in more rows, which chiefly serve as a means of temporary attachment, although occasionally they may be used for crawling¹ and in certain forms² perhaps for swimming.

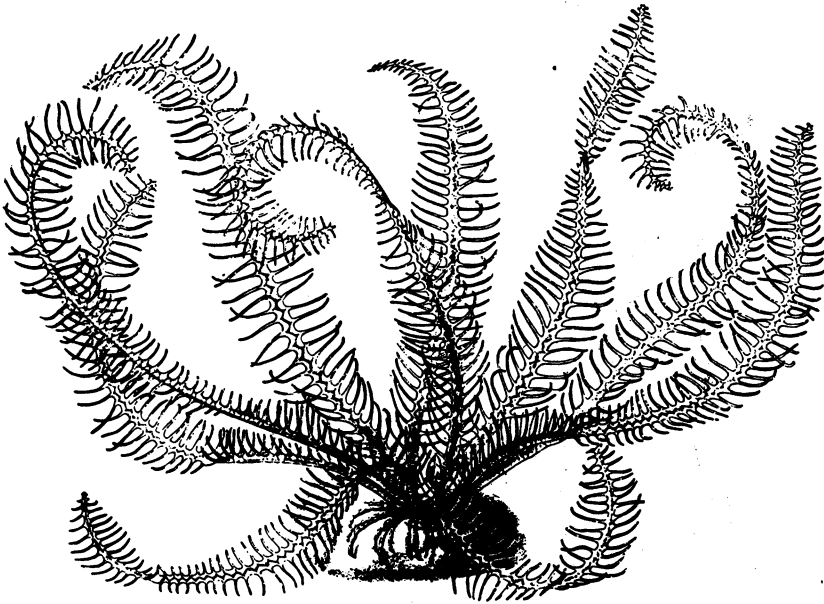


Fig. 25. *Antedon bifida*, drawn from life. After Clark, 1921.

The comatulids usually (primarily) show cirri on the proximal stem-joint, and when young, a stem of bourgeticerinoid structure. Since both characters are found together only in the young pentacrinids and, according to Jækel, in the (adult?) thiolliericrinids, these two groups must be concerned chiefly in regard to the comatulid ancestors. Possibly Jækel, who apparently is inclined to derive all comatulids from the

¹Compare Clark, A. H., 1921, Monogr. Exist. Crin., I, Pt. 2 (Bull. U. S. Nat. Mus., No. 82), pp. 593 ff.

²A functioning of this latter manner has been supposed for some Pentacrinids by Kirk (*op. cit.*, p. 40). Compare also Clark, A. H., 1915, *op. cit.* page 266.

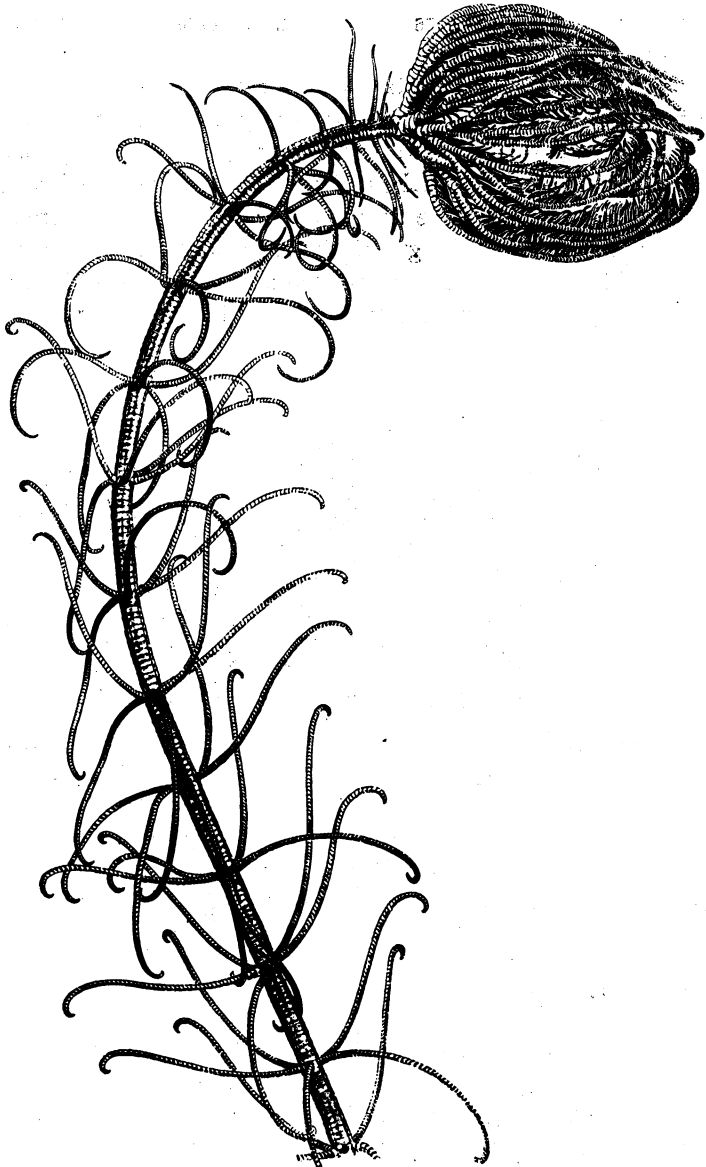


Fig. 26. *Isocrinus* (*Cenocrinus*) *asteria* Lamarck. After Carpenter, 1884. About $\frac{1}{3}$. See page 37.

Thiolliericrinidæ¹, is right; Kirk assumes² that the comatulids are of polyphyletic origin and that a part of them comprehends descendants from the pentacrinid stock. In every case, however, it is important that among the recent Pentacrinidæ, forms exist which show how a comatulid type could have originated and could originate anew in the present or the near future. ■■■

As an example we may compare the three species *Isocrinus* (*Cenocrinus*) *asteria* (Fig. 26), *I. (Endoxocrinus) parræ* (Fig. 27), and *I. (Dip-*

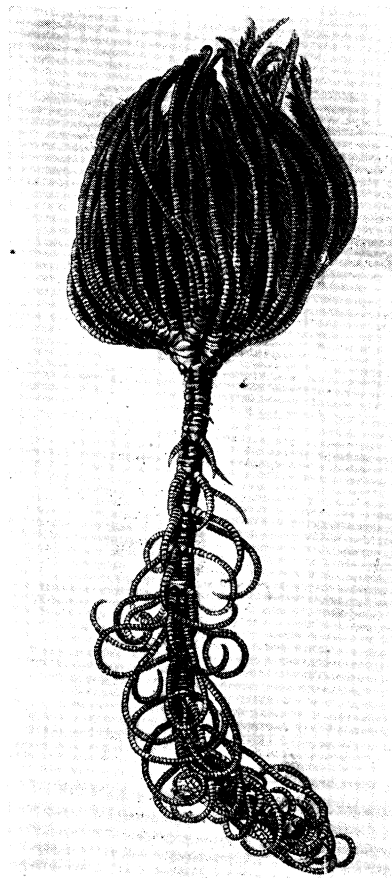


Fig. 27. *Isocrinus (Endoxocrinus) parræ* Oersted. After Carpenter, 1884. $\frac{1}{3}$.

¹1918, pp. 71 and 73.

²*Op. cit.*, pp. 67 ff.

locrinus) *maclearanus* (Fig. 28). In the first-named species, we observe a typical pentacrinid-stem of considerable length, which consists of many nodal joints and extended internodes. *I. (E.) parrae* shows a shorter stem with fewer joints at each internode. Finally, in *I. (D.) maclearanus* we find the stem short again and only one or two joints in each internode, so that the whole stem appears as rather rudimentary, and looks, with its dense trimming of cirri, like a comatulid-centrodorsale which has been drawn out somewhat lengthwise.

There can be hardly any doubt that the above species represent different steps leading from normal pentacrinids to types, where the reduced

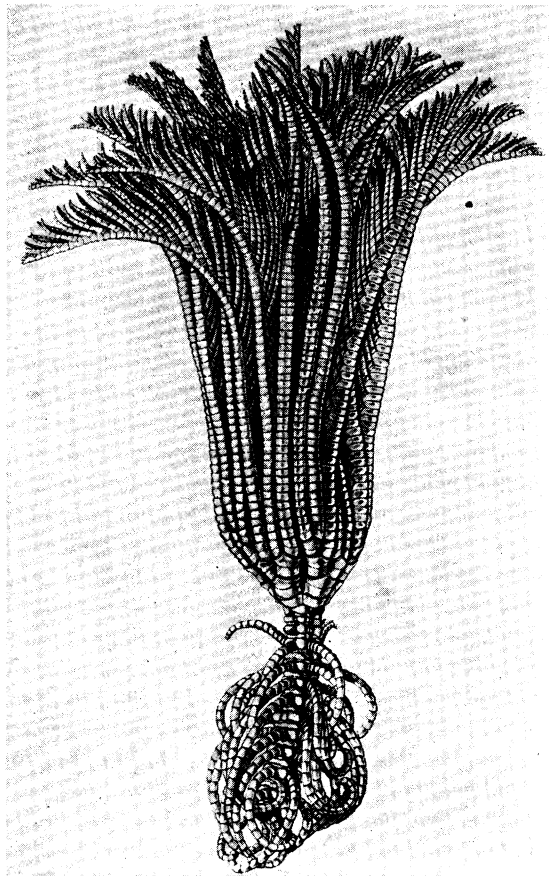


Fig. 28. *Isocrinus (Diplocrinus) maclearanus* Carpenter. After Carpenter, 1884. About $\frac{2}{3}$.

stem with its cirri indicated a comatula-like functioning at least. Besides the above series, similar ones could be added. We may not enter here into a full discussion as to whether the above series is an ancestral series (Ahnenreihe), a step-series (Stufenreihe), or only an adaptation-series (Anpassungsreihe). It seems to me to be a step-series.¹ In every case, however, it is a series comparable to that erected by Dollo among the recent marsupials. And as the conclusions, derived by Dollo on the basis of the recent forms only, have been generally accepted, it must be at least granted that the series *asteria-parraë-maclearanus* indicates a trend of the evolution within the *Isocrinus* group. Of course, here I am not able now to furnish strict proof that this trend of evolution goes farther till a true comatula-type is reached; in other words, I cannot prove now that *I. (D.) maclearanus* or its descendants must reach a comatula-stage; I cannot prove further that elsewhere a comatula-type has been reached by a *maclearanus*-like ancestor. However it seems to me that the possibility of it must be admitted in accordance with our present knowledge.

5. COMMON CHARACTERS OF ROOTS (FIXATION) DISCUSSED UNDER 1-4

In comparing the forms of roots, and the modes of fixation discussed on the preceding pages, certain features common to all may be recognized easily. In every case fixation is effected by stem-portions, by cirri, or by both. Of course the fixing stem-portions, the fixing² cirri, which mostly play a good part in the fixation, are sometimes considerably modified. They often look different from the stem-portions, which have no fixative function but only bear the crown and raise it above the ground, or from the rest of the cirri respectively. But always they are recognizable as being what they really are, true stem-portions and true cirri. Roots (fixation) of that type may be called stem-roots, and, in so far as cirri participate in the fixation, cirrus-roots.³

Besides that morphological similarity, a functional one is to be noted. In the majority of cases, and especially primarily, these stem- and cirrus-roots appear to be connected with a fixation on a loose rather than a

¹That this row cannot be an "Ahnenreihe" seems nearly certain, if Clark's new systematic arrangement, whereby these three specimens have been referred to different genera (Clark, A. H., 1923, Jour. Washington Acad. Sci., XIII, No. 1), is correct.

²Intentionally the term "radicular cirri" is avoided. For if the latter is taken physiologically, not only *e.g.*, the cirri of *Antedon* have to be subsumed under this term. We must also ask: are there cirri (except in such cases as *Herpetocrinus*, etc.) which have another function and which one? Take for instance the cirri of the middle stem-part of an *Isocrinus* (*C.*) *asteria*. Therefore the term "radicular cirri" is employable only in a morphological sense. But there similar difficulties arise from the already mentioned fact (page 5), that is, it is often hard to decide whether the distal end in a given case is the primary distal end or not. Of course, in forms like *Rhizocrinus* the decision may be easy as to what are morphologically radicular cirri but in other cases it seems hardly possible.

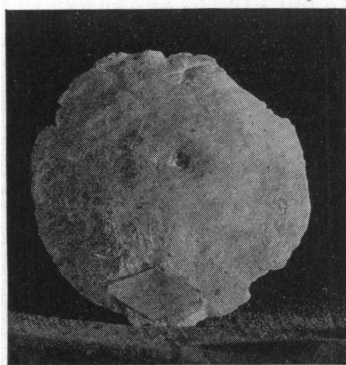
³In consequence of this statement the majority of the previously discussed cases fall in the subdivision of cirrus-roots. *Ancyrocrinus* is a stem-root and a cirrus-root. Some of the types, however, mentioned in Chapter 3 (for example, *Acanthocrinus*, *Lepadocrinus*), are only stem-roots.

firm substratum and in rather quiet water. Furthermore, they appear mostly as adaptations to an insecure fixation, sometimes even to a semi-sessile or to a semi-free mode of life, as is indicated by many of the forms previously discussed.¹

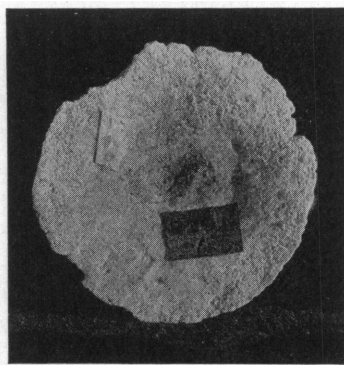
Even more attention may be called to this morphological and physiological agreement in the following discussion of forms which differ in both these directions.

6. DISCOID ROOTS

As already indicated, the term "discoid roots," a term also used by previous students, does not signify by any means a resemblance to what is commonly called a root. They rather resemble an inverted bowl-shaped body and thereby reveal a marked difference structurally and functionally from the foregoing types. However, aside from these common features, many detailed differences are to be found between the forms belonging to this group, as soon as we undertake a more intimate investigation.



29 a



29 b

Fig. 29. *Aspidocrinus scutelliformis* Hall, Lower Helderberg Group, Schoharie, N. Y.; A. M. N. H. $\frac{2291}{1\&2}$: a, seen from above; b, seen from below. $\frac{1}{4}$.

a. *Aspidocrinus*

In 1859², J. Hall founded the genus *Aspidocrinus* for some undoubtedly echinodermal remains, indicated by the cleavage-faces of broken specimens. He distinguished three species, namely *A. scutelliformis*, *A. callosus* and *A. digitatus*. To these, W. Goldring, in her "Devonian Crinoids of New York," added a fourth, *A. onondagensis*.³

A. scutelliformis (Figs. 29a and b), as already indicated by the name,

¹Here of course the pathologic *Scyphocrinus*-cysts (pages 20 ff.) must be omitted.

²Hall, J., Pal. N. Y., III, pp. 122-123, Pl. v, Figs. 13-20.

³Goldring, W., 1923, N. Y. State Museum, Mem. XVI, Albany, p. 144, Pl. LIX, Fig. 13.

resembles, in general shape, a small sea-urchin of the genus *Scutella*. A convex and a concave side are distinguishable. On the top of the former and on a corresponding place of the latter, small, partly circular deepening are to be noted. Otherwise both surfaces seem entirely without deepening or elevations and are likewise smooth except for some adhering stony particles. The specimens are frequently found free, but sometimes they appear cemented to the rock. That may be due only to fossilization. However, the fact that in such cases they have always been found to rest with the concave surface on the rock, suggests that such specimens show their normal orientation and rest on the rock to which they have been firmly attached during life. No plated structure seems to appear, although some weathered specimens of the American Museum of Natural History collection, when viewed under a magnifier, give the

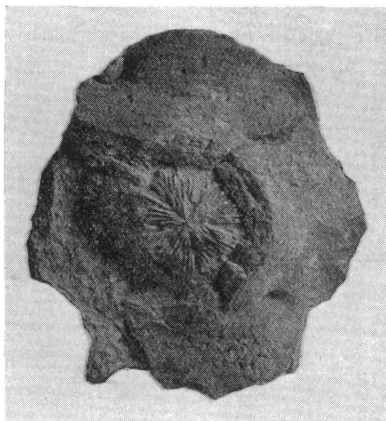


Fig. 30. *Aspidocrinus*-like discoid-root, showing lamellous structure and remnants of a polyplated integument. Trenton Limestone, Kirkfield, Ontario. Springer Collection, U. S. National Museum. About $\frac{1}{4}$.

impression that there must have been different layers, radiating lamellæ and small polygonal plates. Unfortunately, I am not able to give a more precise account on the ground of my own observation. I may, however, refer to Springer, who mentions "radiating ribs" of *Aspidocrinus*.¹ It is of further interest that some *Aspidocrinus*-like bodies, found in the Trenton limestone of Canada, clearly show on the convex side remnants of polygonal plates and interiorly radiating lamellæ (Fig. 30).²

Sometimes instead of the deepening on the convex side, a knob-like projection is found. Such was also the case in a specimen of the collection of the New York State Museum at Albany³ and there the inspection

under a magnifier proved the knob to be stem-joint remains.

The other species are similar. *A. callosus* is considerably smaller than *A. scutelliformis*, which sometimes reaches a diameter one-third

¹Compare Springer, 1917, *op. cit.*, p. 10.

²It must be mentioned that there is perhaps one difference between the specimen of Fig. 30 and *Aspidocrinus*, for in *Aspidocrinus* both the deepening seem often to have a certain connection (compare page 43); in the specimen of Fig. 30 this seems impossible if at all both such deepening had occurred before the partial destruction (compare footnote 1, page 43).

³The specimen itself was not numbered when I examined it, but it was mounted together with another one, which was labeled 408.

greater than in the specimens of figure 29. It has a side less deeply convex than the former, and the margin is divided by furrows into several lobes, or better, into "prominent rounded points or nodes, which are thickened."¹ Sometimes the furrows reach farther towards the centrum and one gets the impression of a deformation by the substratum to whose unevennesses the respective specimens must have been closely attached. *A. digitatus* is almost as large as *A. scutelliformis*. Here from near the center of the convex side, finger-like processes radiate and partly overlap one another. While all these three specimens, according to Goldring, occur together in the New Scotland limestone at Schoharie, N. Y., *A. onondagensis* comes from another horizon and locality.

What is the morphological meaning of these structures? Are they really root-like structures? While Hall suggested that *A. scutelliformis* may represent the basal cup of a crinoid, he said in regard to *A. callosus* that it resembles more a root than a crown and he believed it highly probable that *A. digitatus* was a root. Subsequently, however, it has been generally accepted that all *Aspidocrini* represent merely roots² with two exceptions. Sardeson³ thought that the *Aspidocrini* may be "columnals," and Talbot seems rather inclined to regard all *Aspidocrini* as crowns. In Talbot's "Revision of the New York Helderbergian Crinoids," she expresses her opinion as follows⁴: "These species⁵ of *Aspidocrinus* present difficulties that are as yet unsolved. Hall described the forms as bases of crinoid cups, but Wachsmuth and Springer⁶ listed them doubtfully as crinoid roots. There are two reasons, at least, for thinking that they⁷ cannot be crinoid roots or basal expansions of columns. If they are basal expansions, the concave side must be the under side and this must have rested on the mud of the seafloor. One specimen of *A. scutelliformis* in the Yale University Museum has a bryozoan attached to this concave surface, proving that this surface could not have rested on the mud. If, on the other hand, these specimens represent the base of a cup, the presence of the bryozoan might be explained by supposing that its growth took place after the upper part of the dead calyx had been broken off but while the lower part still remained attached to the column.

"Again, in undisputed examples of basal expansions, the lower or

¹Goldring, *loc. cit.*

²Compare Bather, 1900, *loc. cit.*, p. 201; Kirk, *loc. cit.*, p. 63; Springer, 1917, *loc. cit.*, p. 10, etc.

³*Op. cit.*, p. 240. From the statements on p. 200 it is not perfectly clear whether Sardeson thought of true columnals or whether he meant "part of the stem plus root" in contrast to basal cup.

⁴Talbot, M., 1905, *Am. Journ. Sci.*, XX, p. 31.

⁵*A. scutelliformis*, *callosus* and *digitatus*; *A. onondagensis* was not known at that time.

⁶Wachsmuth and Springer, 1881, "Revision of the Palæocrinoidea," (*Acad. Nat. Sci., Phila.*). Pt. II, p. 228.

⁷Under "they" according to the previous text, all *Aspidocrinus* species must be understood.

distal joints of the column enlarge and the segmentation of the column is continued into the upper part of the enlarged base. No such segments are visible in any of the specimens in question. In every good specimen, there is a clear-cut circular spot, generally dark-colored, which looks like the point of attachment of the column to the crown."

Considering Sardeson's and Talbot's statements in regard to *Aspidocrinus*, we must first emphasize the point that *Aspidocrinus* cannot be true columnals (footnote 3, page 42), for the following reason: the knob-like projection of the specimen mentioned from Albany (page 41), which undoubtedly corresponds to the circular-spot of Talbot, shows true stem-joint structure. We are, therefore, entitled to assume that the central deepening represents the place of stem-joints or stem. This evidently has been inserted¹ into the proper *Aspidocrinus*, which itself, therefore, can hardly exhibit normal columnals. On the contrary, it must be granted that just the mode of insertion seems to speak in favor of Talbot's view. For, in consequence of the above statements, the circular line in Fig. 29b could be interpreted as the boundary of the stem-plug which remained after the rest of the stem had been broken away. This stem-plug reminds one of the insertion of the stem into the cup.

Although the above part of Talbot's argument at first sight (compare page 44) seems very striking, we can not agree with her other deductions. Besides the fact that Hall by no means generally "described the forms as bases of crinoid cups," as is evident from his own statements,² it may be first noted that the cup-hypothesis seems *a priori* highly improbable for *A. callosus* and *A. digitatus* (footnote 7, page 42), since such a structure has not yet been met with among pelmatozoan cups or thecae. Furthermore, the presence of a bryozoan on the concave surface must not be of such high value in regard to the question—cup or root? Of course, by analogy, we can assume with great probability that the concave face would have been the under one in the case of a root. We can further suppose that such a root would have been more or less fixed to the substratum (compare page 41). But on the other hand, we know, through many examples, that roots of different types, which, it is probable, had been fixed (or even cemented) to the substratum (bottom, some foreign object, etc.) during life, are found isolated in the rocks, and must, therefore, have become loosened later on, before or after death.³ In such a

¹Whether the stem in all cases was going through to the under side seems doubtful. Sometimes it appears that the little hollow on the concave side was in no connection with the stem but was merely a deepening; compare footnote 2, page 41.

²Compare page 42.

³Compare for example, figures 3, 4, 30, some below-flattened *Ancyrocrini*, some *Lichenocrini* freely found in the rocks, but showing unmistakable traces of former attachment, etc.

way also the under surface of an *Aspidocrinus*-root could have been occupied by a bryozoan. We may here for example note that "*Camarocrinus*"-bulbs often show several epizoans attached (footnote 4, page 24), which, according to our previous discussions, could have settled only when the bulbs became freed or washed out from the substratum.

Finally also the statement that "in undisputed examples of basal expansions, the lower or distal joints of the column enlarge and the segmentation of the column is continued into the upper part of the enlarged base" does not hold ground. I refer not only to what is exhibited by *Calamocrinus* (page 55), *Encrinus* (page 54), etc., but also to *Lichocrinus* and "*Camarocrinus*."

It may be said in summary that neither Sardeson's view (if he really thought of true columnals—footnote 3, page 42) seems satisfactory nor the majority of Talbot's arguments; therefore, all that remains in favor of *Aspidocrinus* being a cup is the insertion of the stem. But that argument is not convincing when more exactly considered. For if we regard the specimens of *Encrinus* later on discussed (page 54), we can hardly escape the fact that in this genus the stem is inserted, in almost exactly the same manner, into what is doubtless a discoid root. Besides that, the specimens cemented to the rock¹, in an orientation corresponding to the probable normal one of a root, may be mentioned. If they, with the cemented concave surface as suggested on page 41, represent the living condition, they cannot be basal cups. Consequently, none of the arguments of Talbot holds ground. Furthermore, since the two species *A. callosus* and *A. digitatus* nearly exclude the cup-hypothesis (page 43) and the apparent deformation of some *A. callosus* (page 42); also the whole shape, etc., in *scutelliformis* and *onondagensis* is against it¹; and since we find among the genus *Encrinus* basal expansions highly resembling a reduced *A. scutelliformis* in both outlines and stem-insertion, we reach the conclusion that all *Aspidocrini* are roots (means of fixation) and nothing else. We may further assume that the convex surface of the "root" was the upper surface (page 41), the concave face the under side, that the stem was inserted in it as in *Encrinus*, and that the remaining structure has been as previously described or suggested respectively.

Having decided that *Aspidocrini* are roots, and therefore members of the Pelmatozoan class, the question arises: to which group do they belong? Because nothing has been known concerning the crown or theca until recently, this question is answered with difficulty. Stem-fragments

¹We may specially mention the considerable amount of projecting laterally, the entire absence of any remains of arm-joints, etc.

found sticking to the root may indicate a crinoid characteristic, but this must remain a supposition. The relation of these roots to those discussed in the foregoing pages will be considered later.

We turn now to biology. As a typical *Rhizocrinus*-like root seems to be created for penetrating and thereby anchoring in a substratum of a weaker substance than the root itself, so an *Aspidocrinus*-like root is to be understood only as a means of fixation on a hard substratum, where it must have rested firmly attached or even cemented, as does a *Patella*-like gastropod or a barnacle, which it highly resembles in general outline. Such an assumption agrees very well with the fact that all *Aspidocrini*, so far as known, occur in limestone deposits, which seem to speak rather for that assumed life-condition than a shale or sandstone.

There, however, the mode of occurrence must be considered, since Hall reports¹ that specimens of *A. scutelliformis* "are extremely abundant in the upper part of the shaly limestone of the Helderberg group and sometimes form by themselves mainly, and with other fragments of crinoids, a stratum which, from the abundance of this form, was originally designated . . . as the 'scutella-limestone.' This rock is so filled with these remains that many thousands may be counted in the space of a few yards; and the other portions of the rock are made up in great measure of these broken cups² and other crinoidal remains." In other places, however, they should rarely occur. The report causes some doubt as to whether these finding-places represent also the living-places or whether we have not rather to do here with an allochthon occurrence.³ And indeed, so far as can be judged from Hall's description, it seems somewhat improbable that there have been real colonies. Rather one gets the impression that these numberless individuals have been brought together, partly broken and mingled with fragments of brachiopod shells and many other organic remains, by wave-action, and that the knob-like stem remains (page 41) were rounded into that shape during transportation.

Under such circumstances it seems doubtful that the sediment can be concerned with the living-place and fixing-condition (see above). It must be granted that the finding-place offers no hint as to an existence on a hard substratum, if there is a suspicion of allochthony. On the other hand, however, it must be granted likewise that a living-place with a hard bottom is therewith by no means excluded. Besides that, however, it may be noted that Hall's report is restricted to *A. scutelliformis*. Con-

¹*Op. cit.*, 1859.

²As already mentioned, Hall believed *A. scutelliformis* to be a cup.

³Compare footnote 1, page 9.

cerning the other forms, we are not told about a like abundance, and, although allochthony may be possible, nothing is to be seen pointing in that direction. These other species occur also exclusively in limestone (see page 45). We may further recall the specimens which probably became cemented during life (see page 41). These also are attached to limestone. Finally the apparent deformation of some *A. callosus* may be mentioned (page 42) as pointing to a hard substratum. Taking all these together, we can state that the probable allochthony of many forms makes the assumption of a hard substratum (bottom) not impossible. This opinion has been reached by analogy and by observations on some specimens.

Concerning biology, it is of further interest that no *Aspidocrinus* has ever been found in connection with stem or crown. As in similar cases, this points to a later freedom¹ of the respective animals, unless that freedom had been of long duration.

Summarizing, we may therefore assume that *Aspidocrinus* is a pelmatozoan "root" (means of fixation). The under (concave) side rested in the probably hard substratum (bottom)², the upper (convex) side bore the stem of the crinoid (?)³. The fixation may have been a rather close and fast one. Sometimes at least, the specimens were cemented apparently to the bottom, while in other cases cementation may have been loosened during fossilization, or the animals were not cemented at all. Whether the animals to which *A. scutelliformis* belonged really lived in colonies is doubtful, since the assemblages found in the rocks are apparently due to allochthony. Finally, the animals did not maintain that fixation during life, indicating that they participated in the impulse for freedom so common among Pelmatozoa.

b. *Lichenocrinus*

In different localities and horizons of the North American Ordovician and Silurian rocks, some bodies occur which were first described by Hall under the name *Lichenocrinus*. Several species have been distinguished by him and by others.⁴

¹Compare Kirk, *op. cit.*

²That the substratum has been usually the bottom itself, is indicated by the observations quoted on pages 41 and 42.

³Since we have no security about the systematic position of *Aspidocrinus*, we are of course entirely uncertain about the mutual relation or qualification of its four species.

⁴Hall, J., 1847, Pal. N. Y., I, p. 86; *ibid.*, II, p. 231; 1862, 15th Rep. N. Y. State Cab. Nat. Hist.; 1871 (1872), 24th Ann. Rep. N. Y. State Museum Nat. Hist., p. 216. Compare further Meek, F. B., 1873, Geol. Surv. Ohio, I, Palaeontology, pp. 44-52. Miller, S. A., 1879, Journ. Cincinnati Soc. Nat. Hist., *ibid.*, 1880, III, pp. 234 ff.; *ibid.*, 1881, IV, p. 317; *ibid.*, 1882, V, p. 221. Schuchert, Ch., 1900, Proc. U. S. Nat. Mus., XXII, p. 155; 1904, *op. cit.*, p. 268. Jaekel, O., 1904, *op. cit.*, p. 60. Cumings, E. R., 1908, 32nd Ann. Rep. Dept. Geol. Nat. Res. Indiana, p. 730. Slocum, A. W., and Foerste, A. F., 1919-20, Iowa Geol. Surv., XXIX, and others. (For full account for the Ordovician forms, see Bassler, R. S., 1915, U. S. Nat. Museum Bull., 92, pp. 721-722).

A *Lichenocrinus* is a more or less discoid body. The visible part in figure 31 is made up of a great number of small irregular polygonal plates, while in the center a different structure appears which may be easily recognized as a stem-fragment, especially in cases where it is of greater length. Sometimes the polygonal plates reach close to the stem, while often a deepening exists between both from which the polygonal plates seem to emerge. In regard to the stem, it may be further noted that it evidently was not composed of simple circular or quinquelobate

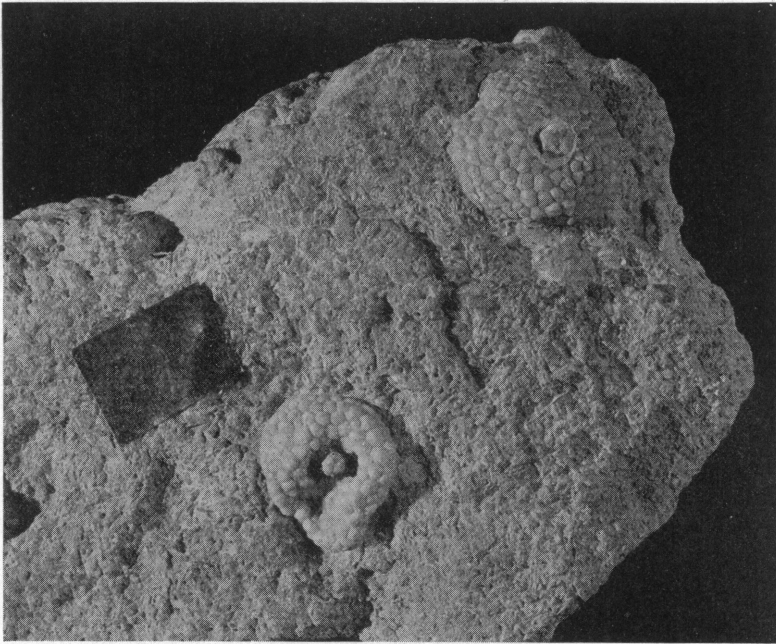


Fig. 31. *Lichenocrinus tuberculatus* Miller, Cincinnati Group, Cincinnati, Ohio.
Enlarged. A. M. N. H. $\frac{13262}{1}$.

joints, but that usually every joint consisted of five separate segments which, however, could partly coalesce. Finally, the outline of the body as seen in figure 31 is not always regular, but different irregularities seem to occur frequently.

Entirely different, however, is the specimen in figure 32, center. On the inside of a brachiopod shell a body is seen, circular in outline and evidently consisting of radiating lamellæ placed closely together. In the center these lamellæ enclose a crateriform deepening, and to the left

from the observer they appear for some extent to be overcrusted. Closer inspection, however, shows that this crust is the rest of a plated integument of the same composition as that visible in figure 31, which undoubtedly has covered the whole lamellous structure. Since in other

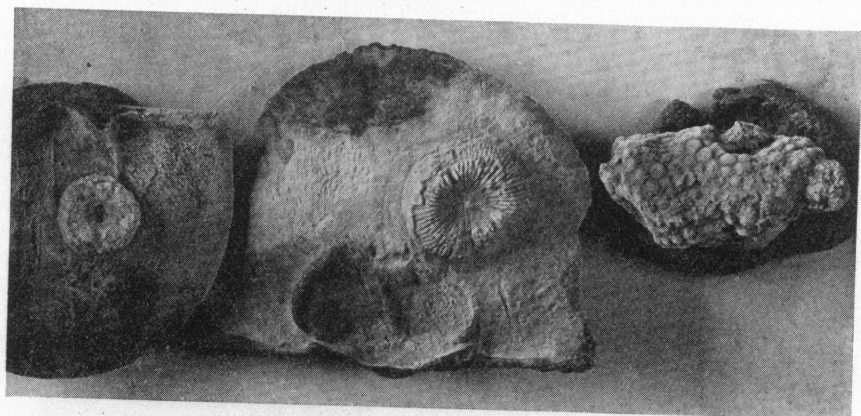


Fig. 32. Left: *Lichenocrinus* sp.; Middle: *Lichenocrinus crateriformis*, Richmond Group, Waynesville formation, base of Clarkville bed, Clinton Co., Ohio; Right: *Lichenocrinus tuberculatus* Miller, Hudson River Group, Cincinnati, Ohio; all from the Springer Collection of the U. S. National Museum. About $\frac{1}{4}$.

specimens, lamellæ are also found beneath the plated surface, we can assume a similar condition for a normal structure of *Lichenocrinus*, as was established long before.

While the one side just described is always more or less convex, the other, observable only on specimens which can be easily freed from the rock, is, as a rule, plain or a little concave; sometimes, however, it is also curved and therewith distinctly concave. The under side does not consist of a plated integument but is evidently a single apparently thin plate.¹ That basal plate has two surfaces: the outer one, usually attached, and opposite to it, an inner one. The (attached) outer surface is, as a rule, smooth, but sometimes shows projecting ribs and deepened furrows, which suggest the sculpture of some shells, to which *Lichenocrinus* is attached. The inner surface, on the contrary, shows, according to Meek (also footnote 1, page 61), radiating and bifurcating striæ, between which the lamellæ (see above) have been inserted. As Meek further reports, these striæ may be visible also from the outer (attached) side, when this

¹Compare the figures given by Meek and Cumings, *loc. cit.*

side becomes moistened and examined under a magnifier. This he mentions in connection with the thinness of that plate.

As to the morphological meaning of these bodies, different opinions have been advanced. Hall believed them to be probably crowns, and the stem he thought to be presumably a proboscis. Meek seems to have been not perfectly certain whether *Lichenocrinus* could not be some sort of crown; and Miller evidently must have been of a similar opinion, as he mentions the fact that ambulacrals, mouth, etc., are not visible. But already Hall had pointed to the possibility that *Lichenocrinus* could be a root plus a stem, and since then the latter view has been generally accepted. Yet Sardeson stated in 1908, in his repeatedly cited paper (footnote 3, page 22), that the stalk of *Lichenocrinus* "is not known to have been identified with certainty as a crinoidal structure. *Lichenocrinus*," he concluded, therefore, "can be treated only as a problematic structure," and, indeed, it must be granted that the stalk bears some unusual features. Sometimes (compare Fig. 31) the five segments which should compose one stem-joint appear somewhat irregularly arranged and suggest a rather irregularly plated structure. Furthermore, what should be the axial canal is so small that it is scarcely visible. Finally it may be added that the lamellous structure of the body itself may appear strange. But on the other hand it must be likewise granted that a stem of polygonal plates also occurs elsewhere among Pelmatozoa; that a small axial canal is a character likewise not unknown (for example, *Platycrinus*); that it would be also possible that the apparent smallness was due only to fossilization; that, wherever a longer part of this stem-like projection is observable it has entirely the appearance of a stem; and that the lamellous structure, a priori against any explanation as a crown because of the deficiency of room for the internal organs, has been also found on some *Aspidocrinus*-like bodies (Fig. 30), which can hardly represent anything else than a pelmatozoan root. Taking all this together with the fact that the structure in general allows hardly any interpretation other than that of an echinodermal remnant, we can state that, in accordance with our present knowledge, *Lichenocrinus* can mean only a pelmatozoan root or base of fixation.¹

Consequently, it needs no detailed discussion to maintain that the more or less plain surface, which is always found attached except in specimens freed from the rock, is the under one, which was attached during

¹*Lichenocrinus* has been often compared to *Camarocrinus* (p. 22, footnote 3), based upon the polyplated outside as well as upon the internal subdivision. This comparison is not valid at closer inspection. *Camarocrinus* has sacs, while *Lichenocrinus* has a basal plate with lamellae of a structure similar to some corals, as remarked by Hall. *Camarocrinus* further shows a branching root while in *Lichenocrinus* the stem is, so far as shown, undivided, making a branching root rather improbable.

life, and that the convex surface is the upper one. In regard to morphology, it may be further noted that the whole root has not been as rigid and inflexible as the lamellous structure suggests. That is proven by a specimen of *L. crateriformis* from the Hudson River Group of Richmond, Ind., now in the collection of the Peabody Museum at Yale University, where the upper surface is partly turned over to the under one, so that the whole specimen looks somewhat crippled. Here, as the specimen is free, the possibility exists that such deformation happened after death and during fossilization, when the internal lamellæ may have been destroyed. A second case is presented by a *L. tuberculatus*. This,—the right-hand specimen of figure 32,—grew around a branch-like body; thereby the upper surface became bent down at two sides, and the under one has been curved likewise. The overgrown fragment visible on the right and the undisturbed condition of the plated integument nearly excludes a deformation during fossilization. The specimen must have grown around that object and must, therefore, have been flexible. Meek observed similar cases. He believed that *Lichenocrinus* conformed during growth to the surface to which it was attached. According to him, *Lichenocrinus* was not flexible itself, but was deformed only during growth.¹ Here the irregularities mentioned on page 47 are to be remembered. If the lower specimen in figure 31 is considered, the integument seems collapsed after partial decay of the lamellæ. Perhaps also the difference in the diameter of the deepening around the stalk (page 47) is likewise to be thus explained.

One difficulty exists, however, in that regard. According to the above explanation the lamellæ would appear to have decayed before the integument. The middle specimen of figure 32, however, proves that, as must be expected, the integument, composed of a multitude of small plates, decayed before the solid lamellæ. This difficulty may perhaps be answered by the assumption that the plated integument did not rest directly upon the lamellæ during life. I do not affirm that the latter was really the case. The possibility, however, must be granted and some of the assumed post-mortem deformations, previously mentioned, might be easily explained in that way.²

Concerning biology it has been noted that *Lichenocrinus* must be regarded as a root and therefore as a means of fixation. Some adaptation to the substratum was possible, and fixation evidently took place on or

¹*Loc. cit.*, p. 49.

²Notwithstanding that there may have been a small space between the lamellæ and the integument, we cannot agree with Jaekel (1918, *op. cit.*, p. 18) who assumes also *Lichenocrinus* under the "Hohlwurzeln." The latter are morphologically different. Compare pages 66 ff.

around different substrata, such as brachiopod shells, crinoid columns and other cylindrical bodies, the sea-bottom itself and also the skeletal elements of trilobites. Therefrom we may conclude that the animals to which the *Lichenocrini* belonged were not particular in choosing their residence. About the degree of solidity of the fixation not much can be said. Fixation seems to have been rather solid. In so far, however, as a stronger cementation seems to be lacking, as free specimens are more numerous, fixation has been perhaps a little less solid than in *Aspidocrinus*.

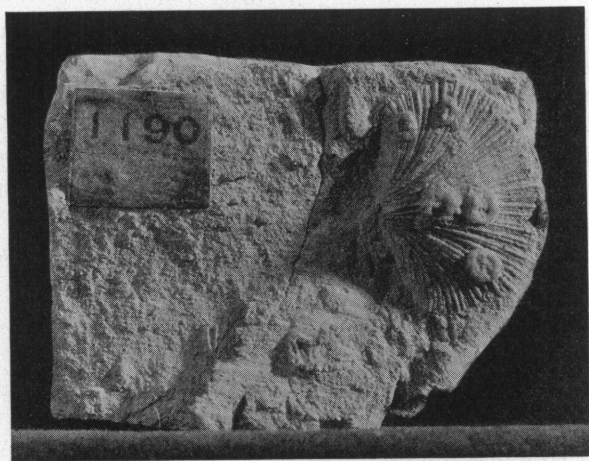


Fig. 33. Several specimens of *Lichenocrinus dyeri* (juv.) Hall, from the Hudson River Group, Cincinnati, Ohio. $\frac{1}{4}$. A. M. N. H., 1190.

Furthermore, the fact that *Lichenocrinus* is sometimes found in isolated fragments of brachiopod shells and trilobite-plates, which appear to have been fragments at the time of attachment, throws light on biology, pointing to perhaps temporary fixation, or, on the other hand, to the exclusion of violent movement of water. In that regard reference may be made again to the left-hand specimen of figure 32, situated (like the middle one of the same figure) on the inner side of the shell, for it could have settled there only after the death of the brachiopod. The outer side of the shell is entirely free of adhering stony particles. Probably, therefore, it was not cemented to the bottom and offered a very movable substratum.

Brachiopod shells seem to have been preferred in some localities. In the Hudson River Group of Cincinnati, Ohio, shells with five or six *Lichenocrini* (Fig. 33) are not rare. Sometimes such attached *Licheno*

crini are extremely small and, therefore, probably young, which points to an early attachment and to a formation of such an attachment-base early in life. In one case the author observed eight small specimens on a single shell, so close that they evidently hindered each other in growth.

While in the above examples the shells probably have been the living-place of a little colony, in the other cases the possibility of an allochthony must be admitted. In the collection of the U. S. National Museum, I have examined pieces of rock containing brachiopods with both valves usually closed; among them only bryozoa and *Lichenocrini* occurred. The latter, however, were on the bryozoa and on some intermingled fragments of *Isotelus* and seldom on the brachiopods. R. S. Bassler gave the source of the material as the base of the Waynesville formation of the Richmond Group, Ohio. The upper side of the layers seemed filled with the shells of a variety of *Zygospira recurvirostris*. It is difficult to decide whether there was a real colony or bank of brachiopods, or whether the shells have been brought together only post mortem. That the shells show no certain orientation on the material is not sufficient evidence to lead to a decision.

That occurrence, however, is of special interest. For with the remains mentioned were found crinoid crowns with stem fragments attached. These may show no direct connection with the *Lichenocrini*, but it is highly probable that they belong to them. According to Springer, who announced a description of the material, it is "a very small crinoid of the *Heterocrinus* type" whose "encrusting root" therefore should represent *Lichenocrinus*.¹ In spite of this occurrence, however, the *Lichenocrini*, so far as is known, are found usually without crowns. This indicates a change in mode of life, with freedom in a later stage. Whether reasons for this may be sought in the deficiency of space (see above) or in the unfavorable substratum (page 51) or elsewhere no decision can be made.

From the previous discussions, therefore, it is evident that *Lichenocrinus* is the discoid root of a crinoid. It consists of a basal plate with radiating lamellæ rising from the inner surface of the latter and of a plated integument. So far as can be known, the stem is inserted into it without any branching. Fixation by the basal plate was apparently rather solid and usually followed by loss of root. An adaptation of the form to the subject of attachment was evidently possible during growth. Perhaps the animals were somewhat gregarious in their habit. The systematic

¹Springer, 1917, *loc. cit.*, p. 11. E. O. Ulrich kindly informed me that he was more inclined to favor a *Homocrinus* (*Lasiocrinus*) Hall (Kirk).

value of the species now described can be criticized only in regard to the knowledge of the crowns belonging to them.

c. Other Roots Referable to this Group

Aspidocrinus and *Lichenocrinus* represent by no means all that is known of "discoïd roots." There are many more of them and we cannot pretend to give a complete list in the following pages, just as we could



Fig. 34a. *Encrinurus carnalli* Beyrich, from the Lower Muschelkalk, Trias, Germany. Specimen in the Museum at Weimar, Germany. $\frac{3}{13}$. See page 54. Photograph by W. Soergel.

not enumerate all stem- or cirrus-roots or all slight modifications of them.

When discussing *Aspidocrinus*, attention has been called among other things, to the root-type occurring in the Triassic genus *Encrinurus* (page 44). Figures 34a-c show such roots from *E. liliiformis* and *E. carnalli*.¹ A rather normal stem, consisting of round and mostly discoid columnals that become only a little or not at all enlarged in diameter distally (Fig. 34b), is inserted in a discoid root similar to the usual insertion of stem into the basal cup (Fig. 34c). The root itself highly resembles an *Aspidocrinus* in general appearance. Sometimes in the above view the outline seems a little irregular (Fig. 34c), a fact that is likewise known

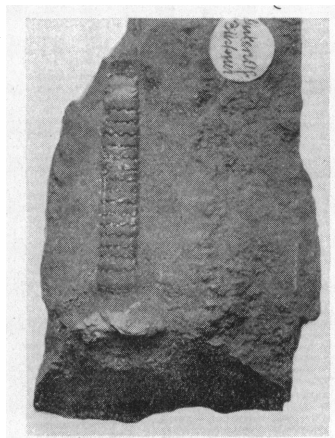


Fig. 34b. Stem-fragment and root of the same, from the Lower Muschelkalk, Trias, Gutendorf, Germany. Specimen in the Museum at Weimar, Germany. $\frac{1}{10}$. Photograph by W. Soergel.

from some *Aspidocrinus* species. So far as can be judged from figure 34b, the root was entirely massive and neither a lamellous nor a plated structure seems traceable.² Figure 34c with roots alone may represent the sea-bottom where a colony has really grown.

Nothing is visible on our figures or on the respective specimens from the under side. But, according to Quenstedt's figures and descriptions, the under-side is concave and has been attached not unlike the previously mentioned roots of this type.³ Quenstedt calls attention to some pieces which have grown on fragments of shells from the genus *Perna*. He also

¹For the photographs from which figures 34a-c have been made, the present author is indebted to Prof. Dr. W. Soergel.

²The root about the middle of figure 34a (just above "4830") looks somewhat different, especially in regard to the insertion of the stem. The specimen, however, is crushed like some others on the same slab, and the stem-fragment situated therein could hardly belong to it. I believe, therefore, it should not be given much value in this specimen, as on the under end of the same slab other roots are partly visible, exactly resembling the uncrushed specimen of figure 34b.

³Quenstedt, F. A., 1876, "Petrefaktenkunde Deutschlands," I, 4, p. 467, and tab. 107, Figs. 170, 182-184.

figures roots, one attached to another's periphery, pointing to a life in colonies like our figure 34c. Whether fixation has been maintained throughout life cannot be decided from the material the author saw, but some reasons make a permanent attachment the more probable. At any rate, the attachment was probably solid and usually took place on a rather hard substratum.¹ Finally, roots of that type seem to have been



Fig. 34c. Root-discs of *Encrinurus liliiformis* Lamarck, from the Upper Muschelkalk, Trias, Schanzengraben, Germany. Specimen in the Museum at Weimar. Photograph by W. Soergel. Reduced. See page 54.

the rule not only among the genus but also within the whole family, since Zittel, in the diagnosis of the *Encrinuridae*, states: "Stiel rund, . . . das untere Ende zu einer verdickten Scheibe ausgebreitet."²

In discussing the problem of the discoid root-forms, the descriptions and figures published by Agassiz of the aforementioned *Calamocrinus diomedæ* are of special interest.³ In only one specimen of that living

¹In a quite recent paper entitled "Ueber d. Eneriniten d. unt. Muschelkalkes von Mitteldeutschland" (Abh. preuss. geol. L. A., N. F., H. 103, Berlin, 1927), W. Biese has dealt also with these problems of root and fixation. Since his paper appeared only after the present work has been sent to print, I must restrict myself to remark that his statements seem to agree in general very well with my views, as I explained them above. (Compare also the "Diskussionsbemerkungen" to my lecture on "Festheftung und Wurzelbildung bei Pelmatozoen." Pal. Z., 10, 1, 1928, pages 51 and 52.

²v. Zittel, K. A., 1915, Grundzüge der Paläontologie, 1, 4th ed., p. 186.

³Agassiz, A., 1892, Mem. Mus. Comp. Zool. Harv. Coll., XVII, No. 2.

crinoid has the root-region been obtained. On that fragment the uppermost stem region and crown are missing; the most distal columnals show a somewhat increased diameter, which, however, diminishes again in the undermost joint. In figure 35a one gets the impression that the stem is inserted into the root in the form of a spherical articulation, while the "asymmetrical view"¹ offers a quite different aspect. Here (Fig.

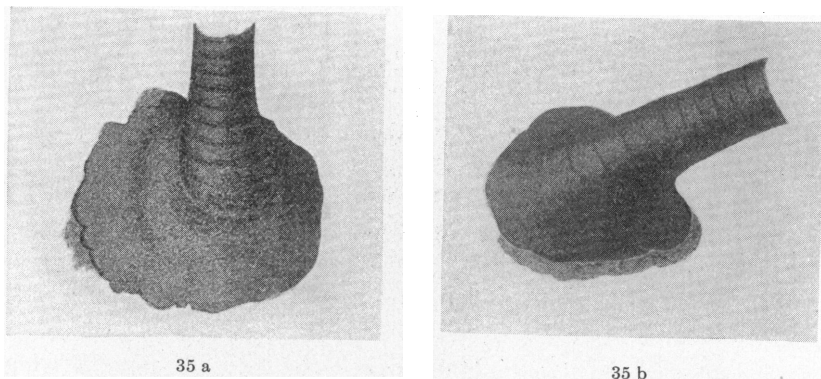


Fig. 35a and b. Two different views of the fixation of *Calamocrinus diomedæ* Agassiz. After Agassiz, 1892.

35b) the three undermost joints appear incomplete and they all seem in contact with the root, evidently in consequence of the curvature of the stem and of the attachment to an uneven surface. From the discoid root itself, which was evidently cemented to the substratum, we can say only that its upper surface seems thoroughly homogeneous, while the periphery shows an irregular outline. The under side is not visible on the figures given by Agassiz, and nothing is said about it, or about other details. On the contrary, Agassiz deals with the question of the morphology of this root. According to him,² "the root is formed by the spreading of the last joint encroaching upon a part of the last joints of the stem, thus forming a base of about three times the diameter of the stem." As the "last joints" evidently mean the three joints which are in contact with the root (see above), the "last joint" cannot mean anything else than the root itself; therefore, the above statement is to be interpreted thus: the root is formed by a modified stem-joint. Notwithstanding the fact that the description by Agassiz is insufficient for any decision, it is obvious that a fundamental question arises in regard

¹Agassiz, *op. cit.*, p. 50.

²*Op. cit.*, p. 49.

to the morphologic meaning of discoid roots in general; for we must ask whether a like explanation is applicable to other discoid root-forms as well, a question we shall return to on page 69.

Furthermore, it is worthy of note that roots of this type also seem to have occurred among the Cystoidea. Jaekel figured in 1899¹ some discoid roots, which, according to him, should probably belong to *Chirocrinus* and *Echinoencrinites*. These roots, which were placed by Jaekel in connection with stems of both a primitive and a specialized structure, are notable because of the accented thinness of their walls, which enclosed a large cavity within. The upper face is described as being "welded together" of small polygonal plates, while the under one, as far as can be judged from the figures, was interlaced by radiating lines which bifurcated peripherally. Unfortunately, nothing is said about this in the description, so that a more precise interpretation seems impossible. Also A. F. Foerste, who figures a *Comarocystites punctatus* Billings, with a root of apparently *Encrinus*-like form, gives no such details about its structure and leaves us therefore in the same condition.²

Many other such discoid roots have been discussed by Sardeson in a special paper dealing with that subject.³ Some have already been mentioned by previous authors, while others are newly described under the provisional generic name *Podolithus*. Among that genus five species are distinguished. The generic definition runs as follows:⁴ "Primitive discoid or conical crinoidal root-structures with more or less lobate margins and with a fixing plate. Region about the stem-scar not depressed. Type *Podolithus schizocrinus*. . . ." If we compare the specimens 8-26 of Sardeson's figures (Fig. 36), placed within *Podolithus*, we can hardly escape the observation that some rather different types are assembled here. Some doubt may arise whether all these forms can be comprehended under the above definition; especially when one has examined such roots more closely. He who knows how indistinct minute details usually are, will question whether in each of these forms a distinct basal plate really occurs. But at any rate the majority of these specimens are discoid roots, and they show at least partly basal plates, lamellous structures and other characters already met with among similar root-forms. Likewise some of the observations and conclusions which Sardeson mentions, the influence of the substratum, the nature of the latter, the temporary limi-

¹Jaekel, O., 1899, *op. cit.*, p. 183.

²Foerste, A. F., *Comarocystites* and *Caryocrinites*, *The Ottawa Naturalist*, XXX, 1916.

³Sardeson, F. W., *op. cit.*

⁴*Loc. cit.*, p. 242.

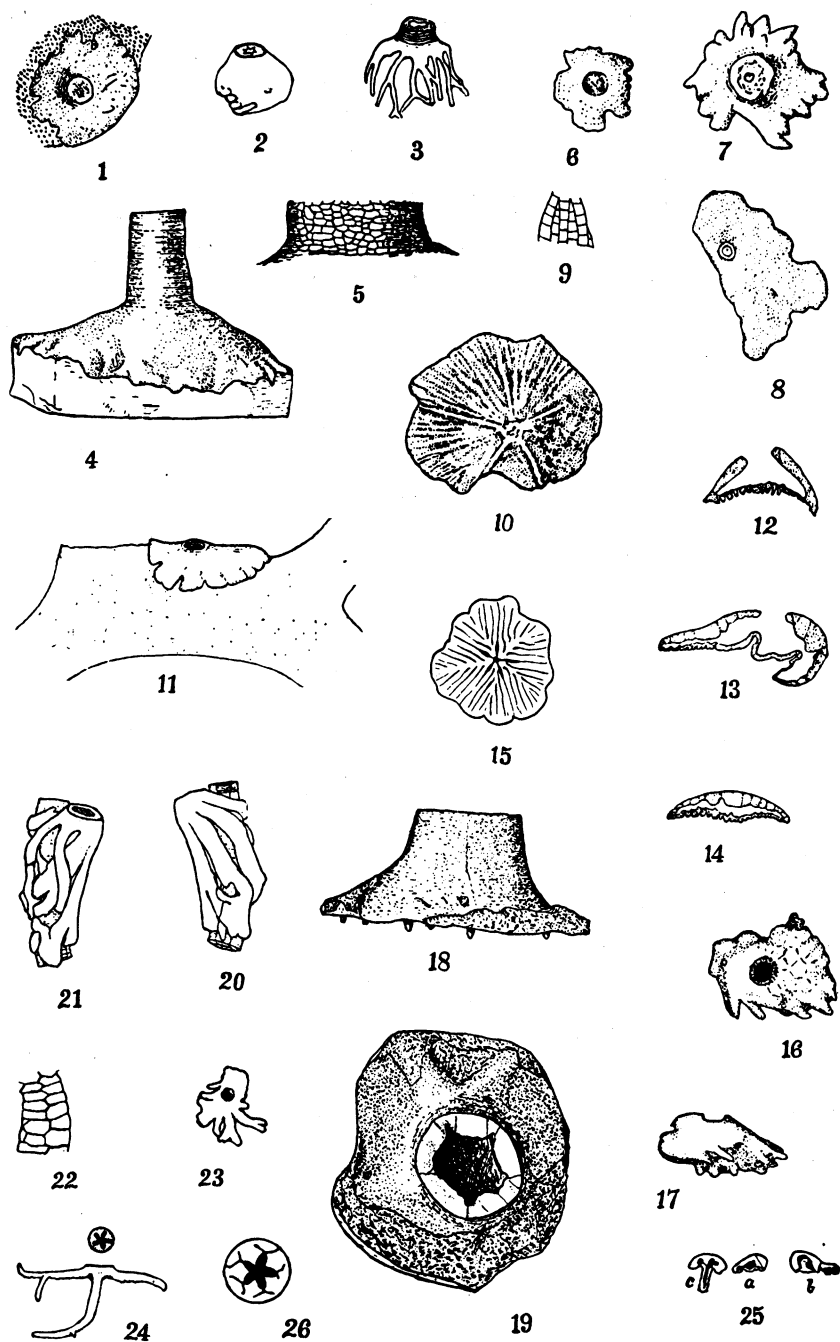


Fig. 36. Various discol roots (*Podolithus*, etc.). After Sardeson, 1908. See page 57.

tation of the fixation, etc.,¹ are entirely in conformity with those recorded from *Lichenocrinus*, *Aspidocrinus*, etc., on the foregoing pages.

Annexed to "*Podolithus*" may be mentioned a somewhat problematical structure, the *Astroporites ottawaënsis*, which curious fossil, according to Springer, was described originally by Lambe, who ranked it doubtfully with the Polyzoa (Bryozoa).² Springer himself, however, placed it at first doubtfully with the structures discussed in this paper; but later on³ he seems to have become rather convinced of its being a pelmatozoan root-part, so far as can be judged from his short note. If these *Astroporites* really represent pelmatozoan roots, as they actually appear to do, they represent only the basal plates. I had the opportunity to study such plates in the U. S. National Museum and agree almost

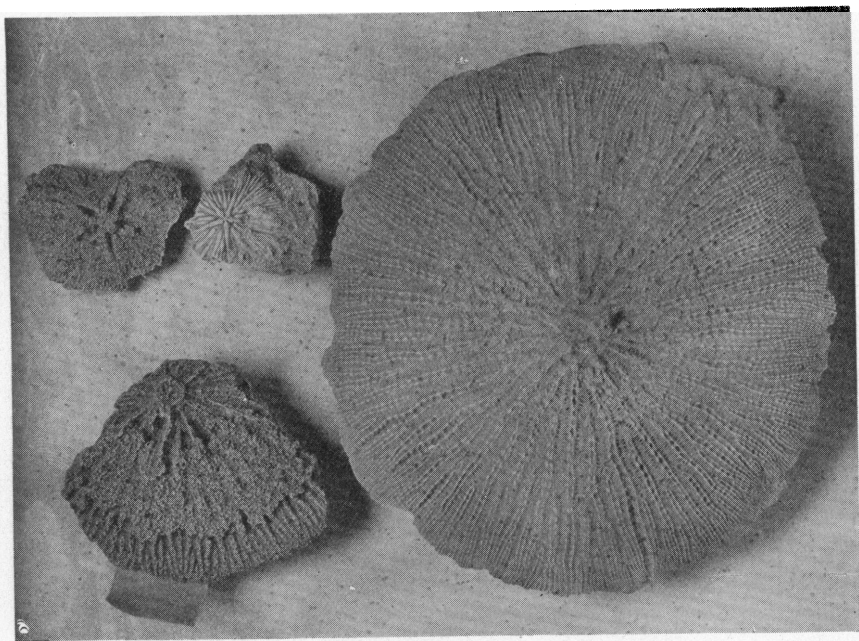


Fig. 37. *Astroporites ottawaënsis* Lambe, and a somewhat similar specimen (the smallest) from the Springer Collection of the U. S. National Museum. About $\frac{3}{8}$. *a* (= the left-hand specimen in the upper row), and *c* (= the specimen below it), from the Trenton Group, High Bridge, Kentucky; *b* (= the smallest specimen), and *d* (= the big specimen) from the Trenton Limestone near Ottawa, Canada.

¹*Op. cit.*, pp. 245, 246, also pp. 239 and 244.

²Springer, F., 1911, Canada Dept. Mines, Geol. Surv., Mem. 15-P, p. 46.

³Springer, 1917, *op. cit.*, p. 10.

certainly with Springer's statements.¹ All these plates are very thin. Their evident under-side is perfectly flat and amorphous, while the upper one (Fig. 37*d*) shows curious radiating structures, starting from a somewhat elevated center. Toward the periphery, smaller radiating structures are successively interpolated, which, like the longer ones, may represent pores or pore-rows, but which may also cause the impression that they could perhaps be interpreted as a special modification from the lamellous structure of the *Lichenocrinus* type. From other fragments (Fig. 37*c*) it may be inferred that this surface was originally roofed over, so that there existed tubular passages between the radiating structures, one close by the other, which ramified through bifurcation at the circumference. Another fragment (Fig. 37*a*) shows only the central part, and from the center slit-like structures diverge. It may be further added that these curious bodies are found sometimes inbedded in shale and sometimes adhering to hard limestone, and evidently rested during life on a flat substratum.² The localities where the specimens have been found are Kirkfield, Ontario; near Ottawa, Canada; and Highbridge, Kentucky. They all belong to the Trenton group.

The question naturally arises: are these bodies really what they were supposed to be? In that regard, without venturing a definite decision, we may mention that the structure so far as known to-day does not preclude a priori an answer in a positive sense. It must be granted that this structure, as has been indicated above, could be understood as a special modification of the lamellous structure frequently occurring among discoid roots. We may further remark the general resemblance to the basal or fixing-plates of such roots, and also mention that there is hardly any other group in the animal kingdom in which these bodies could be placed.

From all these considerations we reach the conclusion that *Astroporites* probably represents, as supposed by Springer, the basal plate of a discoid root which has been adapted to a flat substratum upon which it rested without (?) any decided fixation (cementation), which further points to rather quiet water. Nothing certain can be said about the consistence of the substratum, since its occurrence in shale or in limestone, or both, could be allochthon. Evidently the animals usually became loosened from their roots by breaking off just above them. To what *Pelmatozoan* these discs belong, if they all belong to a single species or genus, must remain an open question. There is something to be said for the opinion that certain diversities may be due only to different

¹Springer, 1911, *op. cit.*, p. 46.

²Compare Springer, 1911, *loc. cit.*

states of preservation. In the latter respect, reference may be made to figure 37b. That specimen hitherto has not been placed within *Astroporites*, but, if compared with figure 37a, it could be imagined to be a positive of the latter or of a highly similar type.¹ On the other hand, it could be interpreted that different types of such modified root-discs once existed.

d. Some Further Remarks on Discoid Roots

In the introductory sentence about discoid roots, some general remarks were made on similarities and differences between the forms referable to this group. Now, after the discussion of several examples, we may take up that question again. When we consider an *Aspidocrinus*, a *Lichenocrinus*, a *Calamocrinus*, etc., some diversities between them are very obvious. *Lichenocrinus* undoubtedly possessed a plated upper surface, a lamellous interior and a separate basal plate. In *Aspidocrinus* the presence of a plated integument of a lamellous structure is at least rather doubtful, and a separate basal plate is entirely problematical, while *Calamocrinus*, so far as known, shows nothing of such structures. The same diversity appears when we further consider the other forms mentioned, in this paper, or by Sardeson, as *Encrinus*, *Calceocrinus* (*Cleiocrinus*) *regius* (Fig. 36:4), *Podolithus*, etc. We can generalize the statement in regard to *Podolithus* (page 57) that these forms "show at least partly basal plates, lamellous structures and other characters," which have been mentioned hitherto. It is therefore not possible to-day to trace a common plan of structure for all these discoid roots with certainty. On the other hand, there exists a greater agreement in a biological respect. For if the respective animals rested directly on the sea-bottom or were attached to some foreign bodies, as on shells of *Nautilus*² or on other objects, obviously attachment generally and primarily took place on a rather hard substratum, and fixation must have been usually tight and adapted mostly to moving water. Of course some exceptions may have occurred (page 60) like similar ones met within the cirrus-roots (page 11), but they cannot invalidate the rule. The same thing is also true in regard to another biological consideration: among *Encrinus* there occur some discoid roots in contact with a longer stem-fragment, from which we may have the impression of a maintenance of such sessility during life. But if we compare more of such discoid roots we find as a rule the roots alone, at

¹On that question it may be noted that the specimen of *Lichenocrinus*, which led Meek (*op. cit.*, p. 50) to the supposition that the fixing-plate could be of two different layers, may be explainable in the same way.

²Compare Kieslinger, A., 1925, "Untersuchungen an triadischen Nautiloideen," *Paläontologische Zeitschrift*, Bd. VII, H. 2, pp. 105 ff. Recently many other cases of fixation on foreign objects by discoid roots have come to the writer's knowledge.

best with a few columnals attached, and therefore we must conclude that usually attachment of this kind has been only of limited duration.

A further biological fact may be noted. Among *Lichenocrinus*, *Encrinus*, etc., we met some cases of an accumulated occurrence. Granting that such assemblages must be partly explained as due to allochthony, in other cases we may have to deal with real colonies: cases as shown by figure 38 point in the latter direction, recalling the wicker-work of numerous roots sometimes occurring among the cirrus-root type.

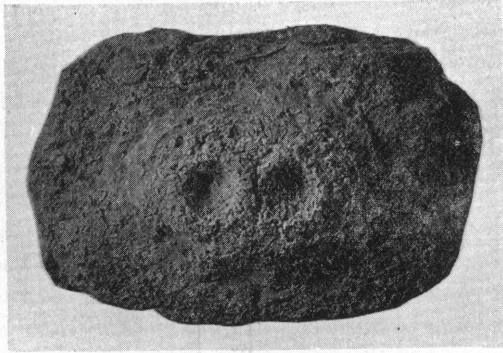


Fig. 38. Two coalesced discoid-roots from the Devonian (Upper. Helderbergian = Onondaga Limestone, State Quarries), Columbus, Ohio. Specimen in the Springer Collection of the U. S. National Museum. About $\frac{1}{4}$.

7. ENCRUSTING ROOTS

The term "encrusting roots" has been used frequently by other authors, and in the foregoing pages it may be found here and there. It is usually employed whenever fixation has been accompanied by a special stereom deposition, so that really a crust has been formed upon both the root and substratum.¹ Of course, such encrusting takes or took place among different root-types and caused a more or less distinct deformation of the respective root. In some cases, however, encrusting reaches such a high degree that the entire root-region looks like an irregular mass, while the original structure is entirely hidden. For such cases alone we intend to use the term "encrusting roots," which, of course, cannot be a morphological term since in many of the cases referable to this group encrusting means only a secondary cover. Whether the latter can be assumed as a rule without exception, in other words, whether there exist

¹So, for example, encrusting roots are represented by figures 3-6, while *Ancyrocrinus* cannot be entered under this term, because during the secondary stereom deposition a crust is formed only upon the root and not upon the substratum.

no such encrusting roots, which would not be referable to any of the previously described types, such as cirrus-roots, discoid roots, etc., I cannot decide, since I personally have not examined enough material of that sort. From my present knowledge I am inclined to regard the encrusting root-type almost always as a secondary character.

Such encrusting roots, to which the specimen appearing in figure 6 could be referred, occur chiefly on forms which evidently were reef-dwellers and lived in moving water. The inclination to form colonies, so that the different roots form a common mass from which the stalks and crowns rise as if sprouting from a common stock like tufts of flowers, frequently seems to be in connection with such encrusting. From the numerous examples at hand, we may first mention the *Apiocrinidæ* about which Quenstedt gave a rather detailed report in regard to the roots.¹ From his account, which is confirmed by Zittel's family diagnosis,² we learn that such encrusting roots seem to be the rule among the *Apiocrinidæ*.

Of special interest is the question about the presumable primary root-form (compare page 62). In this regard it is of importance that Quenstedt's figure 17 in table 102 shows a stem-fragment from the middle or from the distal region, with typical cirri. That of course points to a cirrus-root as the ancestral type, and even more does figure 103 in table 103 represent a root-region with undoubted places of cirrus-insertion. On the other hand, he shows in figure 46 in table 103 a stem-fragment on which a root is attached of the discoid type, resembling somewhat our figure 36 (7 and 23), in so far as that root mainly consists of a disc with some processes on the periphery. According to him this root should belong to a young *Apiocrinus*. If the latter were really the case, it would be, of course, quite in contradiction to the cirrus-root previously supposed to be a starting point. Notwithstanding, I am inclined to suppose a cirrus-root as the starting point, because figure 17 of table 102, and still more figure 103 of table 103, are rather convincing, while in the case of figure 46 of table 103 there is no proof that these roots belong to a young *Apiocrinus*.

In regard to the secondary character of encrusting, the description given by Quenstedt on page 354 is of equal importance. Therefore it must be concluded that the encrusting is produced by a secondary stereom

¹Quenstedt, *op. cit.*, pp. 310 ff. In that paper Quenstedt gives an interesting historical report and shows how these roots were originally misunderstood and have been taken for a "Rose von Jerichow" by Guettard and Walch respectively (compare pp. 310 and 350). Besides that, we may further especially mention some cases like Table 102, figs. 16 and 19; Table 103, figs 100-103; and Table 104, figs 1-2, where not only roots but also stems are shown, which have grown together. In the latter regard it may be specially referred to the cited figures on Table 102.

²Compare v. Zittel, *loc. cit.*, p. 187.

deposition, which forms some sort of a "callus."¹ Sometimes the original segmentation of the roots shines through this callus, and sometimes (compare Quenstedt's figure 2 of table 104) it happens that the callus layer drops off, in which case the clearest segmentation appears² beneath it. Finally, the aforementioned structural difference of the "callus" and the proper stem or root are worthy of careful note for the correct interpretation of that encrusting.

The Apiocrinidæ, the Cupressocrinidæ, the Sclerocrinidæ and the Eugeniocrinidæ furnish further examples of reef-dwellers with encrusting

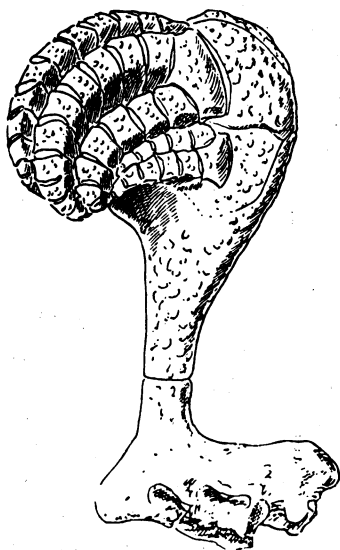


Fig. 39. *Torynocrinus granulatus* Jaekel, Lower Cretaceous (Neocomian), Lattes, Var, France. After Jaekel, 1918. $\frac{3}{4}$.

roots. The compactness of the whole skeleton, the shortening of the column and other adaptations to that peculiar mode of life are common characters to the members of these groups and have produced a structural similarity by convergence. Perhaps the most advanced encrusting is represented within the genus *Torynocrinus*. The encrusting there is not restricted to the root-region, as has been remarked already in the first description by Seeley,³ but the columnals have become coalesced and in some species partly joined with the basal cup as is clearly seen by figure 39 reproduced from Jaekel. Besides these forms, the *Calceocrinidæ* may be added, among which, as Jaekel has made highly probable,⁴ the stem did not rise vertically from the encrusting root, but was lying horizontally on the bottom as expressed by figure 40, a copy after Jaekel's restoration of *Synchiocrinus anglicus*. Also here, as in each of the speci-

mens belonging to this type, the adaptation of the root to the irregularities of the substratum is clearly to be seen.

Regarding all these roots, the question arises anew concerning the primary root-type in these different cases. But because of the fact that I had no chance to examine many roots of that type, and that the figures and descriptions of previous authors do not give sufficient information,

¹ and ² Quenstedt, *op. cit.*, p. 354.

³ Seeley, H. G., 1866, "Notice of *Torynocrinus*," etc., *Ann. and Mag. Nat. Hist.*, pp. 173 ff. Jaekel, O., 1907, "Ueber die Körperform der Holopocriniten," *Jahrb. f. Min., etc., Festband*, 1907, pp. 272-309.

⁴ Jaekel, O., 1918, *op. cit.*, pp. 86 ff.

I cannot answer that question now. However, before we leave these encrusting roots, two further remarks may be permitted. First, it may be noted that the encrusting is not exactly the same as cementation. Encrusting can, of course, be accompanied by the latter process, and certainly this companionship occurs frequently. In other cases, however, as is clearly indicated by the inclination to drop off (page 64) or by the general state of preservation, no cementation seems to have taken place. The second fact to which we may refer is the difference in fixation from

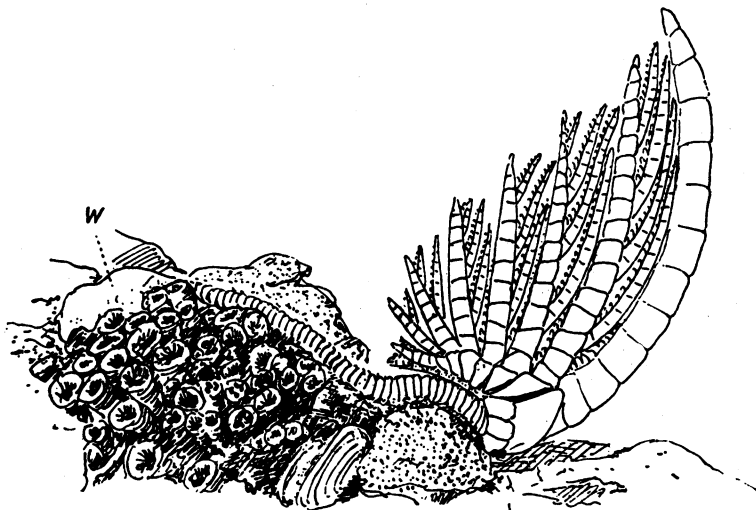


Fig. 40. *Synchirocrinus anglicus* Jaekel. Silurian, Dudley, England. After Jaekel, 1918. See page 64. (W = root).

many of the previously mentioned types. For as by the former, fixation has been often maintained only temporarily, that by encrusting roots seems to have been more frequently maintained throughout life. This is highly probable, since the respective forms were often reef-dwellers and lived, therefore, in water where non-fixation seems rather unfavorable because of the wave-action.

8. FIXATION BY THE BASAL CUP

The discussion of the encrusting roots leads naturally to some Pelmatozoa that are likewise attached to the substratum by so-called encrusting (partly plus cementation), with the difference, however, that the encrusting here occurs on the basal cup (or patina of Jaekel¹) itself, while

¹Jaekel, O., 1891, "Ueber Holopocriniden," etc., *Zeitschr. Deutsch., geolog. Ges.*, Bd., XLIII, H.3, p. 573. Compare also Jaekel, 1907 (footnote 3, page 64) and 1918.

the stem was either totally lost or restricted to few columnals which become entirely coalesced among themselves and with some of the cup plates. The relation of these forms, such as *Holopodidæ*,¹ *Edriocrinus holopoides*, some *Thecoidea*, etc., to the types discussed in the foregoing chapter is yet more intimate. We remarked among the *Cupressocrinidæ*, *Eugeniocrinidæ*, etc., the compactness of the whole skeleton, the shortening of the column, etc. When we now compare these *Eugeniocrinidæ*, etc., with normal crinoids on the one hand, and with forms like *Holopus* on the other, it becomes highly probable that in the ancestry of the *Holopodidæ* a stage has been run through, somewhat resembling a *Cupressocrinus*, *Eugeniocrinus*, *Cyrtocrinus*, etc.²

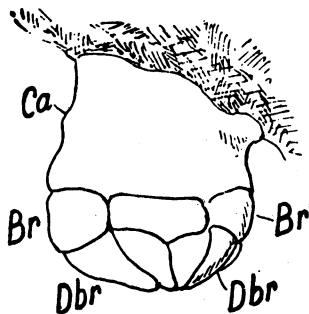


Fig. 41. *Cyathidium holopus* Steenstrup, Upper Cretaceous (Senonian), Faxe, Denmark. After Jaekel, 1918. (Ca = Calyx. Br = Brachialia. Dbr = Dibrachialia).

In other words, the forms in question appear only as the end stage of adaptation to the life on reefs or in the zone of breakers generally, just as the barnacle-type, reached by *Cyathidium holopus*, represents an "ideal adaptation-type" (Fig. 41). That fixation has been of very solid nature and usually has been maintained throughout life, hardly needs to be emphasized in regard to the supposed living-place and mode of life.

9. THE PRIMITIVE "Hohlwurzeln" AND THE ROOTS OF SOME CARPOIDEA

In the foregoing chapter, fixation in the absence of a true stem or root has been considered, but there are some roots which have not been the means, or the chief means, of fixation. These are the so-called "Hohlwurzeln." The forms belonging to this group, including *Cigara dusli*, found in the same locality and horizon as *Acanthocystites briareus* or *Ascocystites barrandei*, respectively, consist of a large internal cavity surrounded by an integument of irregular, polygonal plates. These plates do not form a close pattern and do not touch each other all around, so far as can be judged from the figures of Jaekel. Finally, these "Hohlwurzeln," or "Wurzelblasen," seem not to have been rounded but usually flattened dorso-ventrally (Fig. 42).³

¹Springer, F., 1920, "The Crinoidea Flexibilia," Smiths. Inst. Publ. 2501, pp. 443 ff. Springer, F., 1924, "The genus *Holopus* . . .," Univ. of Iowa Studies in Nat. Hist., X, No. 4. Ehrenberg, K., Paläobiol. Unters. ü. d. Gattung *Edriocrinus*, Paläobiologica, I, Wien., 1928.

²According to Jaekel (1891, *op. cit.*, p. 661), *Holopus* is in close relation to *Cyrtocrinus*.

³Jaekel, O., 1899, *op. cit.*, p. 78; 1904, *op. cit.*, p. 60; 1918, *op. cit.*, pp. 15-18.

Roots of this sort probably¹ represent the most primitive root-type among the Pelmatozoa. When both the stem and the root are considered, according to Jaekel, as having originated by the restriction of the end of the ancestral, worm-like body, the large internal cavity of the "Hohlwurzeln" perhaps lodged some internal organs. Therefore these roots served in second line for fixations, as may be concluded from the slight firmness of their construction. Regarding the aforementioned flatness, it is probable that they anchored in a soft mud or sandy bottom wherein they lay buried horizontally, or that they merely rested upon the bottom in like orientation. In each case, however, fixation was not solid and the animals may have changed their places easily, at least so far as they were able to do so in regard to their other organization.

The few roots of that type hitherto known have been found isolated. This, according to the statements repeated in the foregoing chapters, could be interpreted as the result of the breaking free from the root during life. Since, however, these roots probably lodged some important organs, the above explanation seems improbable. It is to be supposed, rather, that the separation is due to decay after death, as in *Cigara*, where, between the root and stem, a region, with a few skeletal elements, widely separated from each other, seems to be interpolated. Or it may be due, as Jaekel supposed, to the burial of these roots in the bottom and therefore in a deeper horizon than the stem and theca during fossilization.

Between this type and such roots as are with doubt referred to *Chirocrinus* and *Echinoencrinites*, exists a relationship in the thinness

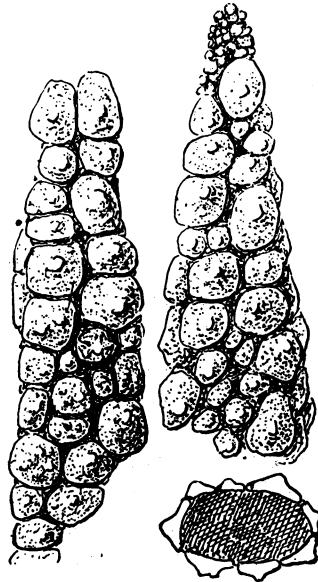


Fig. 42. A root-cyst probably of *Ascocystites barrandei* Jaekel, seen from two sides and section. After Jaekel, 1918. See page 66.

¹Indeed Bather quite recently advanced again the opposite view that pelmatozoan stems (and therefore also roots) in general "have arisen as a downward extension of a many-plated theca," except perhaps the roots of his "Heterostelea" (almost identical with Jaekel's Carpoidea) which he takes for a special branch, widely separated from all other members of the echinoderm-stock ("The Fossil and its Environment," 1928, Quart. Journ. Geol. Soc. London, XXIV, 2, pp. 67 and 71).—Granting a certain (but not a perfect) separation of the "Heterostelea" we cannot agree with Bather in regard to the stem-(root-) origin for some reasons, especially these "Hohlwurzeln," which probably belong to *Acanthocystites* or *Ascocystites* and not to a carpod (see above); the presumable elongate form of the echinoderm-ancestor seems to favor Jaekel's view, which we believe, therefore, at present, the more probable one.

of the walls and their wide lumen. Similar roots are regarded as belonging to Carpoidea. Among the latter group of Pelmatozoa, roots occur, for example, in the *Rhipidocystidæ*, which are, as Jaekel stated, thin-walled, irregularly plated, flat and sac-like structures, agreeing therefore in all important points with the "Hohlwurzeln."¹ Other roots of like general shape and flatness are distinguished by the great compactness of the walls, comparatively small lumen, and by a more regular, biserial arrangement of plates. Of course, roots of this type, referred to the Mitrata subdivision, would scarcely lodge important organs. They may however, be interpreted as modified "Hohlwurzeln," serving for only a temporary and weak fixation, which seems more in accord with the supposed prostrate habit of the forms.

IV. THE PRESUMABLY MUTUAL RELATIONS OF THE DIFFERENT ROOT-TYPES

In the foregoing chapters, the different types of roots or fixation known among Pelmatozoa have been discussed at some length. In that multitude of root-forms (I hope that nothing of general importance has been omitted), some groups seem to contrast rather with one another. Sometimes fixation is effected by the stem itself or by its branches which form a root in the usual sense. Secondly, the so-called discoid roots represent another type, the "Hohlwurzeln" a third one. Further fixation by the basal cup (eventually plus some stem-joints more or less incorporated therein) is distinguishable. Finally the "encrusting" must be added. That diversity naturally leads to the question about the mutual relations of these different types.

Taking first the encrusting, it has been mentioned already (page 63) that it often occurs on roots of different types as a secondary character. In other cases, however (fixation by the basal cup), no relation is to be seen to any of the other root-forms, and the encrusting appears to be a particular type of fixation. Of course, such stemless forms could have forerunners with a stem likewise fixed by encrusting. Especially where a successive shortening of the stem preceded, the encrusting could represent only the last rudiment of the primary fixation. If, however, the ancestral stem has been lost suddenly, and if a period of freedom was intercalated between primary fixation by stem and root and the secondary by the basal cup, an encrusting of the latter is an entirely new thing and bears no relation to any of the other types of root or fixation. Since, indeed, an intercalated freedom (*Edriocrinus holopoides*?,

¹Jaekel, O., 1900, "Ueber Carpoideen, eine neue Klasse von Pelmatozoen," Zeitschr. Deutsch., geol. Ges., 1900, H. 4, pp. 661-77, and 1918, *op. cit.*, pp. 113 ff.

Thecoidea?) may have happened as likely as a successive stem-reduction, we must calculate with the possibility that the encrusting can also be an entirely new character.

Besides such stemless forms also *Calamocrinus* wants consideration. For if here the "root" is really formed "by the spreading of the last joint encroaching upon a part of the last joints," that could be effected by a mere encrusting process. Therefrom, of course, the question arises, if not other root-discs also, mean only stem-joints likewise enlarged. Indeed, the latter seems to be Bather's view, so far as can be judged from his statements referred to just below (see page 70). Remembering, however, structures like *Lichenocrinus*, such interpretation seems entirely impossible. Therefore, we can at present only state: so-called discoid-roots may sometimes mean only encrusted columnals, but they do not do so always.

Another question concerns the relation between the "Hohlwurzeln" and the other root-types. It already has been referred to such relations in regard to the roots occurring together with some *Mitrata* (compare page 68). Here such a comparison is a simple one. In other cases, however, such relations are not easily traceable. Take, for example, a cirrus-root. Is the "Hohlwurzel" (which undoubtedly means the distal stem-end but no true root) morphologically homologous only to the main trunk of a cirrus-root or to that plus the branches (cirri)? That is only one question arising in that connection, but many others could be added which likewise can hardly be answered at the present time. Notwithstanding that some relations of this sort must exist, if the "Hohlwurzeln" really represent the primitive root-form, they may be of more direct or of more indirect nature.

The main question which needs further discussion concerns the relation between the cirrus- or stem-root and the discoid root. For naturally it must be asked whether these two root-types are in any relation to each other; whether the one could be derived from the other or vice versa; whether the one appears to be more primitive, the other to be more specialized, etc.

Looking around for opinions previously expressed in that regard, it is found (for example) that Sardeson¹ speaks of the "early evolution of crinoidal roots from a primitive conical expansion of distributed polygonal plates, over a large circular fixing-plate, to a lobate form with plates in single rows over a deeply cut fixing-plate. Further reduction of the fixing-plate could produce the commonly known cirri with circular, perforated

¹*Op. cit.* p. 250.

segments." While Sardeson evidently thought the discoid type was more primitive, Clark apparently believed that both types were equally primitive. Indeed, he states that "the columnals of the earlier crinoids typically (though by no means always) terminated in an expanded base composed of a number of enlarged columnals which, in later types, became simplified as a single terminal stem plate from which the column more or less abruptly arises." But he continues: "combined with a broad spreading base composed of a mass of swollen, distorted and overgrown columnals, the early crinoids commonly possessed stout and massive radicular cirri, which were very irregular in position and equally irregular in structure."¹ Bather in 1900² recognized two types of skeletal growth at the distal end of the stem: "1. Deposition of solid unjointed stereom, around the distal columnals, forming an encrusting plate or mass. 2. Outgrowth of jointed branches from the plated end, forming 'radicular cirri'" I inquired whether he meant that both these types were dependent only upon local conditions, so that both may occur within the same species, or whether he had another opinion in this regard.³ Thereupon he kindly answered in a letter, dated January 2, 1926, as follows: "In answer to your question, I would suggest that a good deal depends upon the amount of specialization of the particular species. A primitive unspecialized form could more easily adapt itself to different conditions and environments than could the highly specialized form. For instance I should hardly expect a *Pentacrinus* to develop a solid encrusting base, nor should I expect *Aspidocrinus* to appear in the form of jointed columnals. . . ."

It may be that other authorities are, or have been, of another opinion, but so far as I know, special researches dealing with that problem have never been published. Therefore, the foundations do not seem to be sufficient for a critical discussion of these views, and it may be best to treat it at first hand, as if nothing had been said previously.

From a purely theoretical view-point, the following cases appear to be possible:

1. Between stem- (cirrus-) roots and discoid roots there exists no relation; both represent entirely different things and may be deducible from the "Hohlwurzel" in different ways.

2. Between stem- (cirrus-) roots and discoid roots exists some relation.

- a. Both types are likewise primitive or specialized, the forma-

¹Clark, A. H., 1915, "A phylogenetic study on recent crinoids," etc., Smiths. Misc. Coll., LXV, No. 10, pp. 21 ff.

²*Op. cit.*, p. 107.

³Letter dated 27th December, 1925.

tion of the one or of the other being at least originally dependent upon biological factors (environment).

b. The cirrus-root is the more primitive and the discoid-type deducible therefrom.

c. The discoid-type is the more primitive and the cirrus-root deducible from the former.

Beginning with the question, what known facts or considerations point to or against any of the named possibilities, we first mention the fact that discoid roots evidently appear also among young individuals. For example, the description of *Isocrinus* (*Hypalocrinus*) *naresianus* by Carpenter may be remembered,¹ and the young discs adhering to some *Camarocrinus*-bulbs² or to some brachipods (page 51). Further, the observations on some Triassic nautiloid and ammonite shells from Timor may be added. There crinoid roots of discoid-type frequently cover not only both sides of these shells but also the broken walls of the gas-chambers, thereby showing that the occupation by the partly young crinoids took place after the death of the cephalopod, either during the drifting of the empty shell or after the latter had sunken and rested partly on the bottom.³ Such occurrences are somewhat against case 2b (see above). For, if the discoid type should have arisen from the cirrus-root (perhaps by coalescence of the rootlets), it could be expected with some probability that the cirrus-stage would be recapitulated in ontogeny.

We turn now to the chronological sequence of both types. It is true that the discoid roots appear frequently just in the lower Palæozoic, where not much in regard to cirrus-roots is known to-day. It is further true that the highly developed discoid roots, like *Aspidocrinus*, *Lichenocrinus*, etc., are restricted to these early periods. Both facts would seem to confirm the above result and to point to case 2c of our scheme. However, it must be kept in mind that the chronological sequence is never an absolute proof of phylogenetic interrelationship, and therefore it should be used only for re-examination in the field of phylogeny and morphology.

Concerning the problems in question it is of still further importance, whether roots of both types occur together in any species (compare page 70). Unfortunately here also the evidence does not suffice for a definite answer, since both types of roots are found chiefly isolated and therefore admit of no specific determination. It is, however, noteworthy

¹*Op. cit.*, p. 18.

²Compare footnote 3, p. 20.

³Compare Kieslinger, A., 1925, *loc. cit.* It may be specially referred to a specimen of *Paraladiscites timorensis* v. Arthaber, now in the Palæontologisches und Palæobiologisches Institut of the University of Vienna, where some of these adhering discs apparently must have belonged to rather young crinoids.

that among recent crinoids, so far as can be judged from the statements by Clark,¹ only one type seems to occur as a rule, not only within a species, but within the family throughout. Because of the additional fact that in a few fossil instances (*Apiocrinidæ*, page 63, etc.) the root-type appears as a rather constant character, the latter behavior may be supposed to be the rule.

To these observable facts some considerations may be added. After it became known that the *Antedon*-larva has the stem fixed to the bottom by a cribiform plate, the so-called "dorsocentrale," Wachsmuth and Springer² were evidently inclined to ascribe the dorsocentrale as a feature common to young crinoids in general. Owing to the formal similarity between the discoid-roots and dorsocentrales, it needs no discussion to prove that such an assumption could give support to the view of the primitive character of the discoid-types. Besides, it could be also taken for an argument against the primitiveness of the "Hohlwurzel." Is, however, the above generalization correct? In his critical review of Wachsmuth and Springer's great monograph, "The North American Crinoidea Camerata," Bather reached the conclusion that "except as a misleading and highly confusing appellation for the primitive distal end, there is, therefore, no virtue in the term 'dorso-central'."³ But even granting the dorsocentrale for a common character in young crinoids, it must not be interpreted in a phylogenetic sense. It could represent merely a cænogenetic structure, a larval adaptation.⁴ Therefore the dorsocentrale cannot be used in reaching a decision on our problem.

The same conclusion is valid for quite another consideration, which concerns the homology between some of the main root-types. If the cirrus-root is compared with some discoid types, such as the *Encrinus*-root, the *Lichenocrinus*-root or the *Calamocrinus*-root, the possible homology is by no means always the same. For the *Encrinus*-root could be conceived as an enlarged stem-joint alone; in the *Lichenocrinus*-root the radiating lamellæ could be (I do not say must be) interpreted as homologous to the cirri, and the third could be homologous to a single stem-joint, to a cirrus-root, or to a mere encrusting. These examples suffice to show that our present knowledge of these structures needs to be studied further (page 3), before their comparisons can furnish acceptable results. Our supposition concerning discoid-roots seems justified in com-

¹Compare Clark, A. H., 1915, *loc. cit.*

²*Op. cit.*, p. 49.

³Bather, F. A., 1898, *Geol. Mag.*, n.s., Dec. IV, V, p. 329.

⁴Also the interesting report of Clark (1921, *op. cit.*, p. 580 ff.) about the "terminal stem plate" in the comatulids seems to point rather in that direction. Compare further Ehrenberg, K., 1922, *Acta Zoologica*, *loc. cit.*, p. 302, where the dorsocentrale has been comprehended in that way.

prehending morphologically different forms, but nothing can be said about their relations to the cirrus-roots.

Summarizing the above discussions, the result seems not entirely satisfactory. Of course case 2b of our scheme may be eliminated and the apparently never intermingled occurrence of both types could be taken for an argument against 2a, while the stratigraphy seems to favor case 2c. Nevertheless, it must be freely admitted that the above facts and considerations do not suffice for a decision, chiefly because of the fragmentary knowledge about the morphology. The question remains, whether any other method could perhaps bring us a little farther forward.

On page 39 attention has been called to some common characters of all stem- or cirrus-roots, both morphologically and phylogenetically. The cirrus-roots always were easily recognizable as stem-derivates (by ramification and articulation), and primarily they appeared as adaptations to a not very firm fixation on a rather loose substratum and in rather quiet water. Opposing now the discoid-root type to the cirrus-roots, not much can be said about the structure, except that discoid-roots differ structurally from the former. They differ also functionally, since they undoubtedly appear to mean in general an adaptation to a firm fixation on a hard substratum, and in moving water (compare page 61). Keeping that in mind, we may turn our thoughts back to the time when the "Hohlwurzel-stage" had just been reached by the ancient Pelmatozoa.

In accordance with the above statements, it seems highly probable that the two main root-types diverged from each other for biological reasons. As the "Hohlwurzel" became more and more restricted, and the rising of the theca more pronounced, there existed a need for a better anchorage. Forms which happened to be on a sandy or muddy bottom, wherein the distal stem-end may have been buried, probably sought a hold by sprouting short processes which soon formed a "root"; by further ramification and became subsequently¹ jointed like the stem itself. Forms, whose distal end lay on a firmer surface, may have spread out all around according to the aforementioned evolution. Subsequently, the short processes may have been easily transformed again by coalescence into a simple disc, while a broadened base split into processes whenever a change took place in the consistence of the substratum. Later, however, as both types became more highly developed (*Lichenocrinus*-type, *Rhizocrinus*-type, etc.), they became also hereditarily fixed. In that stage, a cirrus-root could adapt itself to a hard substratum only by

¹"Jointing develops gradually"—Bather in a letter to the author, dated January 2, 1926, compare page 70.

becoming a creeping-root-trunk with horizontally spreading rootlets and a flattened and broadened under-surface, or by encrusting.

Stopping here in tracing the history of root-fixation, we hardly need to emphasize the fact that an answer is given to the question of the relation between cirrus-roots and discoid-roots. To some extent, both seem to have been originally in a certain relation, and from the cirrus-root-oriment a disc-root-oriment¹ may have been formed, and vice versa. With the higher specialization (adaptation to environment), however, both lines diverged more and more and became finally separated throughout.²

It is not necessary to add much more concerning the other modifications of root (fixation) among Pelmatozoa. Here also the biological conditions as revealed by palæobiological analysis must be taken as the starting-point, as has already been done in the foregoing chapters.

Taking up again the history of root (fixation) where we just left it, two diverging lines of further evolution seem clearly traceable. On the one hand, freedom was reached in many ways and on different lines (compare page 25). Separation from the fixation took place within the root, just above it, or somewhere else within the stem, or directly beneath the calyx.³ Often that freedom was not long maintained, and a second fixation, frequently in form of semi-sessility (page 12) soon followed. Thus the "*Ancyrocrinus*" was formed as a derivate from a normal cirrus-root, and the stem itself obtained fixative functions, to which it became adapted by a coiling of its distal portion or by winding around the object of attachment to a greater or less degree. *Pleurocystis*, *Acanthocrinus*, *Glyptocrinus*, and *Eifelocrinus* are examples of such modifications, which surely lie partly on different, partly on the same, lines of evolution. Other adaptations to secondary fixation are represented by the peculiar modification in *Lepadocrinus* of a middle stem-section and by the *Drepanocrinus*-calyx (plus uppermost stem-region?) respectively, while the grasping "roots," formed by non-radicular cirri, are something else. To all these adaptations of secondary fixation, the encrusting may be further added. At least in some cases (*Edriocrinus holopoides*, page 68), such interpretation must be admitted.

Mostly, however, the encrusting must be estimated as an adaptation along the second line of evolution. This did not lead to chiefly

¹The term "oriment" was used first by O. Abel (Mitt. naturw. Ver. Univ. Wien, XII, Jahrg., Nos. 4-6, pp. 79-82, Wien, 1914).

²Of highest interest in that connection is the fact that, although adult roots of recent crinoids seem to be always within a species (family) of only one type, there occur among the pentacrinoid larvae of comatulids both root-types and also intermediate forms within the same species. (Compare Clark, A. H., 1915, *op. cit.*, Pl. III.)

³Compare Ehrenberg, K., 1922, *Pal. Z., loc. cit.*, p. 204, and *Acta Zoologica, loc. cit.*, p. 204, etc.

temporary freedom but to a tighter fixation. As already mentioned, encrusting occurs in both main root-types, especially in highly moving water of the shore region (reef-dwellers). Sometimes after gradual reduction of the stem, it remains alone as effecting fixation.

While all these types may be traced back to one of the two main root-types, nevertheless, in special cases it is impossible to decide whether the cirrus-root or the discoid-root represents the ancestral type.

Furthermore the "Hohlwurzel," which is the evident starting-point in general, shows a modified type occurring among the Carpoidea.

What I have summarized in the foregoing pages¹ and have attempted to make plain by the attached scheme (page 75) is not, of course, the true history. It is not the true history, not only because the accurate chronological sequence of the different modifications has been omitted for a better comprehension of the connections, but also because of the missing evidence. Yet it is a history, in so far as it tries to show what happened with the fixation (root) of Pelmatozoa from the early Palæozoic to the present.

¹Compare also: Ehrenberg, K., 1928, *Festheftung und Wurzelbildung bei Pelmatozoen*, *Pal. Z.*, 10, 1, pp. 42-52. (A preliminary report given at the meeting of the Palæontolog. Gesellschaft at Breslau, 1927.)