THE PHYLOGENETIC INTERRELATIONSHIPS OF THE RECENT CRINOIDS.

By Austin H. Clark,

Assistant Curator, Division of Marine Invertebrates, U. S. National Museum.

In the present enlightened epoch of comprehensive zoological thought, one is justly considered as antiquated and narrow-minded if, in the study of any group of organisms, careful attention is not given to their fossil representatives. Yet in many cases the combination of recent species with their fossil representatives and near relations forms a mass very difficult of mental digestion, and it is found that the best results are attained by studying each component separately and then combining the acquired data.

The study of the Crinoidea has always been approached from the paleontological standpoint as a natural corollary of the preponderance of the fossil over the recent species; but a comparative study restricted to recent forms alone brings out certain points well worthy of consideration, and emphasizes certain facts not so evident if recent and fossil species are studied all together.

In the present paper all the recent crinoid groups will be taken up and their various interrelationships shown, without reference to any of their fossil relations, as if there were none but recent crinoids, in the hope that this unique and more or less illogical treatment will call attention to certain points hitherto more or less obscured.

In studying the recent crinoids I have become impressed with the fact that the stems offer the best criteria for tracing out phylogenetic relationships; a critical study of the stems has shown that all the types converge, both phylogenetically and (where observations have been possible) ontogenetically to a common center. Next in importance to the stems come the basals, and using these two structures alone we can form a very satisfactory phylogenetic tree.

On the characters offered by the stem and basals, the recent crinoids fall into three sharply differentiated groups, as follows:

a^1. Stem short and stout, unjointed. *Holopus.*

a^2. Stem long and slender, with many joints.

b^1. Stem without cirri or nodes; the basals are inclined upward more or less toward a position parallel to the dorso-ventral axis, enclosing a cup-shaped cavity, and form part of the lateral body wall.

Phrynocrinus; Ptilocrinus; Calamocrinus; Hyocrinus; Cephyrocrinus; Bathycrinus; Rhizocrinus.

b^2. Stem with cirri, forming one or more nodes; the basals are horizontal, or have become metamorphosed, and do not form part of the lateral body wall.

Comatulida; Pentacrinitida.

Were there no such things as fossil crinoids, each of these groups would have the standing of an order; and for the purposes of this paper they may be referred to as (1) the Holopida, (2) the Ptilocrinida, and (3) the Comatulida.

The stem of *Holopus* is of the simplest possible construction, being practically but a simple thickening of the primitive central plate. Our Holopida therefore are a surviving early offshoot from the main line of descent, representing a developmental stage of great antiquity, before the inception of articulations in the crinoidal base.

I have elsewhere shown that the theoretically most primitive type of articulated crinoidal columnar is that found in *Rhizocrinus*, and, especially, *Bathycrinus;* these two genera, therefore, stand at the foot of the Ptilocrinida, though not on the same plane, for the second is much more specialized than the first. The stem of *Phrynocrinus* is a curious and unique adaptation of the primitive articulated columnar to a great increase in size and the necessity of supporting a greatly increased weight; the individual columnars of *Phrynocrinus* are morphologically the same as those of *Bathycrinus*, but modified by being greatly shortened, the diminution in length being correlated with a broadening of the terminal ellipses. The family Phrynocrinidæ therefore marks the furthest development in the line of the simplest possible adaptation to increasing stress of a column of the type found in the Rhizocrinidæ. In very large specimens of *Bathycrinus* we notice that the primitive fulcral ridge on the articular faces of the columnars shows a tendency to form a pair of triangular structures with their apices at the central canal, and these triangular, or more properly fan-like, structures are marked more or less distinctly with radiating lines. This indicates a second line of adaptation to increased stress, which eventually results in the formation of circular articular surfaces uniformly covered with radiating lines. Such articular surfaces are common to *Ptilocrinus*, *Calamocrinus*, *Gephyrocrinus*, and *Hyocrinus*, and therefore we should group these four genera together (a course already in part indicated by Doctor Bather) making of them the superfamily Hyocrinoida which, most obviously on the basis of the arrangement of the brachials, falls into two families, Ptilocrinidæ and Hyocrinidæ.

The great order of the Comatulida, and the family Pentacrinitidæ, to which the vast majority of the recent forms belong, represent a higher state of development and phylogenetic (as opposed to generic or family) specialization than the Ptilocrinida; for we find that the primitively uniform stem of the latter in this group is modified by the development, at regular intervals, of cirriferous nodes; and the basals, which throughout the echinoderms form part of the body wall and in the Heteroradiata lie in the same plane as the radials, forming in con-

junction with them a dorsal cup, here have come to lie horizontally, have moved inward, and have become more or less atrophied or metamorphosed, taking no part whatever in the formation of anything but the bottom of the cup. The Comatulida are sharply divided into two parts: (1) Those species in which the stem is retained throughout life, and (2) those in which it is cast off at an early stage—the Pentacrinitidæ and the Comatulida.

So far as can be judged from the available facts, the earlier stage of these two groups is the same; a dorso-central like that of *Phrynocrinus*, or a root like that of *Rhizocrinus*, supports a *Bathycrinus*-like stem, which in turn bears a crown in which the basals are large and form part of the dorsal cup exactly as in *Rhizocrinus*, and large orals are present, as in the Holopida and Ptilocrinida generally. But after the formation of a certain number of columnars, approximately definite for each species, a specialized columnar is formed which is united to the preceding by a plane articular surface instead of by an articular surface comprising the usual fulcral ridge and ligament fossæ, and which gives off radially five articulated processes, the cirri. At this stage the basals, at first large and an important and essential part of the wall of the calyx cup, have considerably diminished in their external size, due to having become more recumbent in position, and to having slipped inward under the central part of the dorsal cup.

From this point onward the paths of the Pentacrinitidæ and the Comatulida diverge. In the former a new series of columnars, resembling the first series, is added on top of the cirriferous nodal, this series also terminating, as did the first, in a nodal, a second cirriferous columnar, separated from the first by about the same number of ordinary columnars as separated the first from the dorso-central. This process is continued; new columnars are added one by one, every so often one being formed with a whorl of cirri; with increasing size the columnars gradually become shorter, and the primitive fulcral ridge little by little spreads out into two fan-like figures, which have indicated radiating lines. The structure of the basals has not changed since the formation of the first nodal and its whorl of cirri; they are much reduced in size and lie horizontally so that their sides are dorsal and ventral, and their edges outward. As each columnar is formed, either directly under the basals or, in later life, by intercalation between the upper columnars, it is cast in a mold formed by the under side of the basals, and thereby becomes modified by the acquisition of petaloid markings, more or less obscuring the primitive radiating lines which otherwise would have been formed.

In the Comatulida, stem development ceases when the first nodal is formed; but the nodal itself greatly increases in size, and usually adds several additional rows of cirri to the first; coincidentally the basals slip farther and farther inward, disappearing from sight alto-

gether,[a] and fusing so as to form the so-called rosette; the stem, now become too delicate to support the growing animal, breaks off at the modified articulation just under the nodal, and the animal becomes a so-called free form.

It is interesting to notice that in the adults of the Pentacrinitidæ and Comatulida the radials have undergone a considerable change comparable to that undergone by the basals. Primarily large broad plates forming an important part of the calyx wall, as seen in the Ptilocrinida, they have gradually become recumbent, and have attained an almost or quite horizontal position. Their inferior ends, originally abutting on the superior ends of the basals, with which they form, as in the young of *Antedon*, a smooth, regularly-rounded cup, have, as the basals became more and more recumbent, gradually slipped inward, so as to become attached to what was at first the inner side of the basals. When the radials in their turn became recumbent their lower ends slipped inward along the upper (originally inner) surface of the basals, so that finally the radials come to form a circlet of almost or quite horizontal plates, superposed upon the similar circlet of horizontal basals. The infrabasals long ago underwent a similar transformation, and in the Comatulida and in the pentacrinite genus *Endoxocrinus* have been quite lost. Morphologically, therefore, the calyx of the Comatulida and Pentacrinitidæ is composed of three alternating circlets of five plates each, superposed horizontally upon each other, so that the first two have entirely lost their original function of serving as a protection to the calyx contents, and the third, or uppermost, merely forms the central part of the calyx floor, having for its chief function the support of the arms.

The changes undergone by the plates of the calyx which primarily form a cup about the calyx contents are accompanied by a gradual extrusion of the calyx contents, so that these (the so-called disk) come to be supported more and more by the arm bases, and in the Pentacrinitidæ and Comatulida rest upon the post-radial ossicles to and including the second of the undivided arm. In many cases these ossicles have spread out laterally, and are in close lateral apposition, so that they have taken on the function of the original calyx plates and form a solid calcareous wall enclosing and protecting the "soft parts."

Exactly the same thing has taken place in *Bathycrinus*, but by a radically different process; instead a diminution of the interior volume of the calyx cup by the attainment gradually of a horizontal position and a slipping inward of the calyx plates, the basals and radials have moved inward without at all changing their original relationships, but with the same result of causing the "soft parts" to be extruded and to be supported by the post-radial ossicles.

[a] Except in *Holocrinus*, where the basals are retained in the condition of those of the Pentacrinitidæ.