MORPHOLOGY AND TAXONOMY OF THE MIDDLE DEVONIAN CRINOID *ANCYROCRINUS BULBOSUS* HALL 1862

BY

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ABSTRACT—A young specimen of *Ancyrocrinus bulbosus* from the Dock Street Clay Member of the Four Mile Dam Formation, which retains the entire column and primary root system, has altered some of the previous concepts on the development of the peculiar grapnel-like root structure of this crinoid. The grapnel in *Ancyrocrinus* consists of the lower portion of the stem and the cirri covered over by a layer of secondary stereom. The primary root system may be incorporated into the grapnel, although this is not always the case.

The present paper also attempts to consolidate all the information presently known about *Ancyrocrinus,* including taxonomy, morphology, and the geographic and stratigraphic distributions of the crinoid.

INTRODUCTION

ESSENTIALLY COMPLETE crinoids are one of the rarest finds in paleontology. A great deal of interest was aroused, therefore, when one of the authors, while cataloguing part of the Pettyes Collection at The University of Michigan, found a crinoid specimen which retained the base of the arms, calyx, stem, and holdfast. Upon further investigation the crinoid proved to be an immature specimen of *Ancyrocrinus bulbosus* Hall 1862. The specimen, from the Dock Street Clay Member of the Four Mile Dam Formation, represents the only calyx of this species ever found in Michigan. More importantly, however, it clarifies for the first time the early developmental stage of this crinoid's peculiar anchor-like holdfast. Based on this specimen, as well as others in The University of Michigan Museum of Paleontology, the University of Cincinnati Museum, and the New York State Museum collections, an accurate developmental history of the *Ancyrocrinus* grapnel has now been determined.

One unfortunate feature of the crinoid calyx is its marred surface. Apparently, in an attempt to clean the specimen, someone ground the exterior of the crinoid so deeply that all of the original ornamentation and surface features were obliterated. For this reason it was necessary to photograph the specimen in xylol. Several thin sections of the *Ancyrocrinus* grapnel in other specimens were made by the authors. The best method of photographing these specimens was to moisten the ground surface with xylol and then cover this in turn with a cover slip.

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OCCURRENCE

Ancyrocrinus bulbosus occurs in rocks of the Middle Devonian, Hamilton Group, which is distributed in a broad belt from Indiana and Michigan to Pennsylvania and New York (text–fig. 1).

New York.—If the inclusion of *Ancyrocrinus quinquepartitus* into the genus *Ancyrocrinus* is accepted, the earliest occurrence for the genus is the Glenerie Limestone (Lower Devonian). In western New York *Ancyrocrinus bulbosus* ranges from the lowest (Centerfield Limestone) member to the highest (Deep Run) member of the Ludlowville Formation. A report by Goldring (1943, p. 260) would place *Ancyrocrinus bulbosus* in the Marcellus Formation of eastern New York

Seven specimens of *Ancyrocrinus* are in the Kopf Collection at the University of Cincinnati, all labeled as occurring in the Centerfield Limestone of New York. Although we have studied these specimens, we have not discovered any others in this formation. *Ancyrocrinus* is apparently absent in the Ledyard Shale Member, which directly overlies the Centerfield, but it does occur abundantly in several zones of the

Wanakah Shale Member. The first of these zones, the *Pleurodictyum* bed (Grabau, 1899, p. 58), occurs approximately one foot above the base of the Wanakah Member. We have studied four incomplete calyxes as well as numerous grapnels from this horizon in Erie County, New York. The University of Michigan alone has approximately 200 grapnels from the *Pleurodictyum* bed and it appears that this is by far the most prolific occurrence of *Ancyrocrinus* known.

Although distributed sporadically throughout the member, *Ancyrocrinus* is not found commonly again until near the top of the Wanakah. Here, in a zone ranging from three to five feet below the top of the member, grapnels are again numerous. Goldring (1942) based her original calyx description upon three calyxes, two of them complete, from this horizon.

Ancyrocrinus occurs sparingly in the Tichenor Limestone of western New York. We have observed only two or three grapnels from this member. Although grapnels have been reported from the Deep Run Member of the Ludlowville Formation (Clarke & Luther, 1904, p. 52; Goldring, 1923, p. 457), we have neither collected nor seen any specimens from that member. Grabau (1899, p. 146,147) reported *Ancyrocrinus* in the "Moscow shale, three to five feet above the Encrinal [Tichenor] limestone" in Erie County, New York. Six years of collecting in Erie County has failed to turn up a single specimen of *Ancyrocrinus* in the Moscow Formation at this horizon and we suspect that the above-mentioned specimens were actually found three to five feet below the Tichenor Limestone.

Pennsylvania.—*Ancyrocrinus* has been reported by Goldring (1942, p. 17) from the "Ludlowville Formation" (Mohantango Formation) at Deer Lake, Schuylkill County. It was represented by several grapnels and a calyx. This horizon may be equivalent to either the Wanakah or the Centerfield.

Ontario.—*Ancyrocrinus* is found in the Arkona Shale (Whiteaves, 1887, p. 103,104) and the Ipperwash Limestone (Whiteaves, 1898, p. 375). The genus does not seem to range throughout the Arkona Shale; rather it appears to be restricted to a zone occurring from twenty to thirty feet below the top of the formation. Although environmental conditions were favorable for a large number of stemmed echinoderms, *Ancyrocrinus* is not known to occur in either the Hungry Hollow Formation or the Widder Formation. Grapnels are rather common in the Ipperwash Limestone where it outcrops at Stony Point Park on the shores of Lake Huron.

Michigan.—*Ancyrocrinus* is found in the *Sieberella romingeri*-large *Atrypa* zone of the Genshaw Formation and the Dock Street Clay Member of the Four Mile Dam Formation. To our knowledge only five grapnels have been collected from the Genshaw Formation of which three are in The University of Michigan Museum of Paleontology collections and two are in the United States National Museum. *Ancyrocrinus* is relatively common in the Dock Street Clay. In addition to the complete specimen which initiated this study, The University of Michigan collection contains approximately 100 grapnels from this member.

Indiana-Kentucky.—*Ancyrocrinus* is apparently restricted to the Beechwood Limestone Member of the Sellersburg Limestone. Although not uncommon on the limestone surface, complete undamaged grapnels are difficult to collect. We saw several specimens which retained the long spurs but they could not be removed from the outcrop without serious damage. The Borden Collection in the Field Museum does contain approximately three hundred specimens from Clark County, Indiana (Roy, 1929, p. 204,205).

LOCALITIES

Ancyrocrinus has been studied from the following Devonian formations and localities:

New York
Oriskany (Glenerie) Limestone
  1. Glenerie, Ulster County.
Hamilton Group, Marcellus Formation
  2. Quarry just south of Westerloo, Albany County.
Hamilton Group, probably Ludlowville Formation, probably Wanakah Shale Member
  3. Shales of the Lake Erie shore and elsewhere.
Hamilton Group, Ludlowville Formation, Centerfield Limestone Member
  4. East Alexander, Genesee County.
Hamilton Group, Ludlowville Formation, Wanakah Shale Member, *Pleurodictyum* bed
  5. Bay View Quarry, ½ mile north of Bay View, Erie County.
Hamilton Group, Ludlowville Formation, zone 3 to 5 feet below top of Wanakah Shale Member
  6. South branch of Smoke's Creek at California Road, Windom, Erie County.
  7. Tributary to the south branch of Smoke's Creek at California Road, Windom, Erie County.
  8. Cazenovia Creek at Northrup Road, Springbrook, Erie County.
Hamilton Group, Ludlowville Formation, Tichenor Limestone Member

◎   Mohantango, Ipperwash, Wanakah

O   Centerfield, Beechwood, Four Mile Dam

★   Genshaw, Arkona

□   Marcellus

●   Glenerie
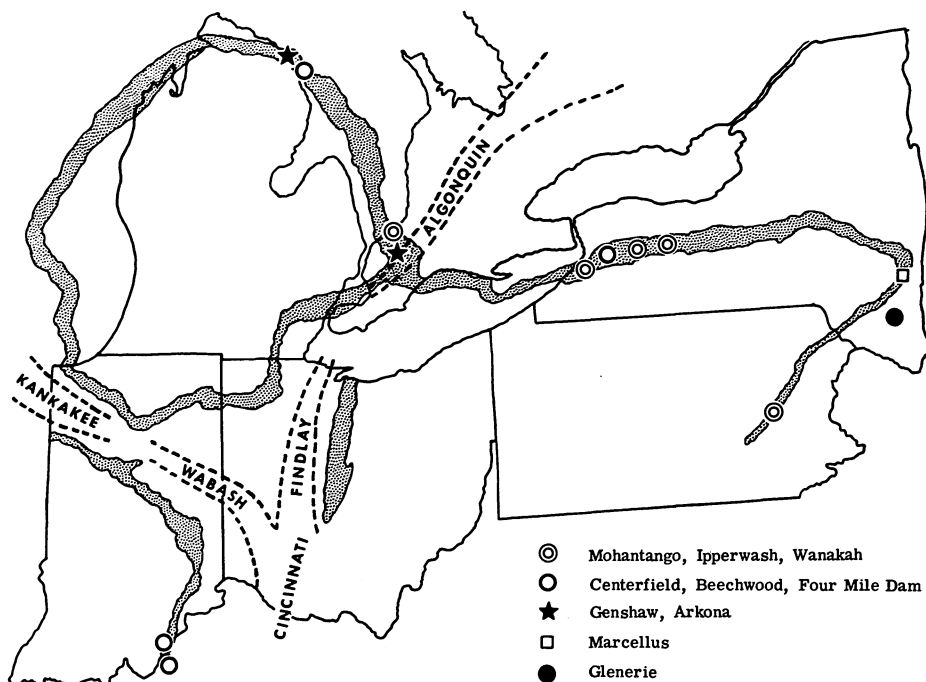
TEXT-FIG. 1—Map illustrating the occurrences of the genus *Ancyrocrinus*. Note that occurrences of similar age have been distinctly marked. The arches, which were major structural features during the Devonian, and the outcrop pattern of Middle Devonian rocks are also denoted.

9. Banks of pond in meadow 1 mile west of the Tile Yard, East Bethany, Genesee County.

Pennsylvania

"Ludlowville Formation"

10. Deer Lake, Schuylkill County.

Ontario

Hamilton Group, Arkona Shale, zone 20 to 30 feet below top of formation

11. Thedford region, Lambton County.
12. Tile and Brick Yard, about ½ mile north of Thedford, Lambton County.
13. East bank of Ausable River at Lot 8, about 2 miles south of Sylvan, Middlesex County.

Ipperwash Limestone

14. Shore of Lake Huron at Stony Point Provincial Park, Bosanquet Township, Lambton County.

Michigan

Traverse Group, Genshaw Formation, lower part, *Sieberella romingeri*–large *Atrypa* zone

15. Ditch along East Grand Lake Road (County Road 405) about ½ mile north of the south line of Presque Isle County; east line of SE¼ sec. 34, T 33 N, R 8 E.

Traverse Group, Four Mile Dam Formation, Dock Street Clay Member

16. Abandoned quarry of Thunder Bay Quarries Company, eastern edge of Alpena, Alpena County; SE¼ sec. 14, T 31 N, R 8 E.

Indiana

Hamilton Group, Sellersburg Limestone, Beechwood Limestone Member

17. Along the electric line ¼ mile west of Watson Junction, Clark County.
18. Louisville Quarry, Speed, Clark County.

PREVIOUS WORK

The genus *Ancyrocrinus* was erected by James Hall (1862, p. 117, 118) to accommodate some "crinoidal bodies which, at one extremity, have the form of a bulb or thickened column, with lateral ascending processes and a central ascending column of greater or less length," The "body and arms" of the crinoid were unknown to Hall.

Hall commented on the spinelike processes which have "the character of a crinoid column, but tapering to an obtuse point, or sometimes truncate." He also observed that,

The central portion [of the root] continues above these divisions [lateral cirri], and is marked by the

transverse joints, while the part below and the lateral processes are rarely thus marked. As the development progresses, this lower portion, and the part around and above the lateral processes, becomes enlarged and swollen in the form of a bulb.

Hall found the column to be round in its lower part, becoming quadrangular above. In summation, Hall believed that,

> These bodies seem to have been the base, and indicate the existence of a free floating crinoid, with the thickened bulb below serving as a balance for the column and body above. The articulating scar on the lower extremity of the smaller ones indicates that the animal was fixed in its young state.

The two species established by Hall, *Ancyrocrinus spinosus* and *Ancyrocrinus bulbosus,* were apparently based solely on geographic considerations; their descriptions and illustrations are essentially the same except that *Ancyrocrinus bulbosus* was found in the "shales of the Hamilton group" along the Lake Erie shore, whereas *Ancyrocrinus spinosus* was found in the "Limestone of the Upper Helderberg group: Falls of the Ohio, and elsewhere."

In discussing the stalked crinoids collected by the Challenger Expedition, Carpenter (1884, p. 19) stated in a footnote:

> The unusual enlargement of the lowest nodal joint in this individual suggests the idea that the structures which have been described by Hall under the name *Ancyrocrinus* ... may be the detached stems of a Palaeocrinoid in the semi-free condition ... The four lateral spine-like processes may very well have been cirri, the jointed structure of which has become obliterated by a calcareous overgrowth, just as in the lower part of the tetramerous stem.

He based his statement on the fact that two living crinoids, *Isocrinus (Annacrinus) wyvillethomsoni* (Jeffryes) and *Annacrinus alternicirrus* (Carpenter), which live on ooze and bluemud bottoms respectively, apparently break loose from their original holdfast. The nodal joint from which the separation takes place "is in all smoothed and rounded, evidently by absorption, showing that the animal had for long been free." This joint, however, "sometimes loses its ordinary characters altogether, becoming much enlarged and rounded below as to be almost hemispherical in appearance."

Wachsmuth & Springer (1886, p. 79,80) in discussing the family Gasterocomidae suggested for the first time that *Ancyrocrinus* might actually be the root of *Myrtillocrinus* or some other genus of this family. This was based on the fact that *Ancyrocrinus* has a stem with four peripheral canals. Wachsmuth & Springer also stated, "There are at the lower end four lateral appendages, which in our opinion are a kind of radicular cirrhi."

Several years later, in their monograph *The North American Crinoidea Camerata,* Wach-

smuth & Springer (1897, p. 50) quoted Carpenter and agreed with his interpretation of the *Ancyrocrinus* root. They felt that the distal end of *Ancyrocrinus* is provided with a small, rounded tubercle, closing the opening of the central canal exactly as in some cases of *Pentacrinus* and said, "That this stem is morphologically in the same condition as that of *Pentacrinus,* nobody will deny after examining the specimens."

In 1887 Whiteaves (p. 103,104) reported and figured the first specimen of *Ancyrocrinus bulbosus* from the Township of Bosanquet, Ontario, Canada. He did little more than give a cursory description and illustrate the specimen.

Twelve years later, Whiteaves (1898, p. 375) described numerous specimens of *Ancyrocrinus bulbosus* collected at Stony Point, Lake Huron, by the Rev. Hector Currie. Whiteaves was the first to point out the variation found in the spur level of *Ancyrocrinus*. Of the four specimens he mentioned, in two "these processes originate at about the same height and are arranged in a rather regular cruciform manner, but in the other two they originate at different heights and are very irregularly disposed."

Grabau (1899, p. 146,147) illustrated seven specimens of *Ancyrocrinus bulbosus,* one of which showed the irregular distribution of the lateral processes just previously described by Whiteaves. Grabau also gave stratigraphic information on the distribution of *Ancyrocrinus bulbosus* in Erie County, New York.

Bather (1900, p. 134,177), apparently basing his judgment on the work of Wachsmuth & Springer (1886), briefly stated in his section on the Crinoidea in Lankester's *A Treatise on Zoology,* "In the Devonian *Myrtillocrinus* the stem ended in a four-fluked grapnel (*Ancyrocrinus,* ...)." Later he simply listed *Ancyrocrinus* Hall as a junior synonym of *Myrtillocrinus* Sandberger 1855.

Kirk (1911, p. 46) was the first of several authors to attack Bather's rather capricious assignment of *Ancyrocrinus* to *Myrtillocrinus,* pointing out that the two genera were in no way stratigraphically related to each other. (This dispute was not settled until 1942, when Goldring described a calyx of *Ancyrocrinus* which still retained the quadrangular stem.) In the same article Kirk suggested that perhaps there really was some geographic control over the distribution of *Ancyrocrinus* when he stated that "spurs may be short and stout, as is characteristic of the Hamilton of southern Indiana, or long and slender, as is shown by the New York specimens." He reported for the first time that the lateral processes are "per-

forated through the center by a very small canal which apparently does not communicate with the exterior." He also pointed out that the arrangement of the cirri is variable but their canals always come off the elongation of the axis of the quadrilobate axial canal. The variation in the root, first mentioned by Whiteaves, was also commented upon by Kirk, who stated, "At times the spurs depart from the normal arrangement, where all are in the same plane, and are variously situated at different levels. Occasionally more than four [spurs] are present." Kirk thought it was obvious that the lateral processes were modified radicular cirri in which all traces of the original segmentation as a rule have been obliterated by secondary deposition of stereom. Kirk envisioned that the

> grapnel of *Ancyrocrinus* served rather as a drag and ballast than as a true anchor. In a quiet sea, the animal no doubt was steadied and maintained in a fairly stable state by the weight of the terminal organ. If affected by current or wave activity, however, the grapnel might be dragged along the bottom and aid appreciably in controlling the motion of the animal.

Springer (1917, p. 10; pl. 5, figs. 7–10) presented the first illustration of a specimen of *Ancyrocrinus* which had its stem extended to the bottom of the terminal structure. Springer also entered the dispute over which calyx should be assigned with the root of *Ancyrocrinus* by suggesting that perhaps it really belonged with *Arachnocrinus,* a crinoid which had a quadrangular canal and which also occurred in the Beechwood Limestone of Indiana.

In her memoir on Devonian crinoids of New York, Goldring (1923, p. 456–458) contributed little to the knowledge of *Ancyrocrinus*. She did establish *Ancyrocrinus quinquepartitus* as a new species, based on a single root from the Glenerie Limestone, thus making it the oldest occurrence of the genus. The new species was distinguished from *A. bulbosus* by the presence of five spurs in the grapnel, versus four in *A. bulbosus,* and the rounding of the column above the spur level. The column is usually quadrangular in *A. bulbosus.*

In the same memoir she summarized the known geographic and stratigraphic range of *Ancyrocrinus* in New York.

Ehrenberg (1929, p. 11–20) was the first author who seriously studied *Ancyrocrinus* and attempted to speculate on its development. In his paper on pelmatozoan root forms, he suggested that *Ancyrocrinus* was derived from a *Rhizocrinus* root type, the grapnel being nothing more than the end of the stem and radicular cirri modified by the secondary deposition of calcite. The deposition of calcite stereom, he thought, made the movement of one cirrus joint

against another impossible. Ehrenberg also observed that the cirri were not always completely calcified, and illustrated a specimen (1929, fig. 8) which shows the single joints fairly well. More than any other author up to his time, Ehrenberg noted the great variability of the *Ancyrocrinus* grapnel due to the irregular cirri development and secondary calcite deposition, and quite accurately stated that "the repeatedly mentioned variability of the *Ancyrocrinus* species clearly indicates that form and detail structure have not become fixed hereditarily." In his figure 11 (1929) Ehrenberg illustrated two specimens which "are remarkable because they are so distinctly curved" and also three other specimens "in which the underend is somewhat flattened and truncated, suggesting that it [the root] rested on a rather solid surface." According to Ehrenberg one of the latter specimens, which were in the Springer Collection, was labeled "fixed." The illustration would indicate the root is still attached to the original surface. In summation, Ehrenberg said, "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." The remaining portion was modified by the secondary deposition of stereom into a grapnel which either served as a drag, as was suggested by Kirk, or more probably served as an anchor whenever the animals "according to their semi-sessile habits, wanted rest." The latter position was postulated as being unstable and occurring only on a bottom surface of loose mud or sand in quiet water. The fact that no crowns were found associated with the anchors indicated to Ehrenberg that there was a further change during later life in which the anchor was cast off.

In the same year, Roy (1929, p. 204,205) illustrated several specimens of *Ancyrocrinus bulbosus,* one (1929, fig. 10) being a longitudinal section and another (1929, fig. 9) being a cross section through four regularly arranged "hook-like projections" in a single plane.

In 1942 Goldring (p. 13–18) gave the first account of the calyx of *Ancyrocrinus* based on three specimens in the Kopf Collection (now in the University of Cincinnati paleontology collection). These specimens were found in the Wanakah Shale of Erie County, New York. Goldring did such a commendable job of describing the calyx that only minor changes have been made in this paper. She placed *Ancyrocrinus* in the family Botryocrinidae because of the quadrangular RA and the arm structure. Thus, eighty years after Hall's original description, the taxonomic position of the *Ancyro-*

crinus grapnel was established. The geographic range of *Ancyrocrinus* was also extended by Goldring to include the Ludlowville Formation of Pennsylvania, from which she described several grapnels as well as a single calyx.

In the same bulletin Lowenstam (1942, p. 21–36) dealt with the development of the *Ancyrocrinus* root. For the first time, a detailed study involving several hundred specimens, eighteen of which were thin-sectioned, was carried out. Lowenstam essentially agreed with Ehrenberg that *Ancyrocrinus* was derived from the proximal section of a crinoid root of the *Rhizocrinus* type. Lowenstam found the grapnels to consist of two parts. The primary part was composed of the original stem and radicular cirri, and the secondary part consisted of a secreted covering of stereom with a secondary canal system. The stereom was derived from two centers of secretion, one at the base of the grapnel and the other at the junction of the cirri with the stem.

Lowenstam believed that the initial process in the grapnel formation was a violent mechanical disruption within the primary root. This disruption would trigger immediate regeneration of the axial gland organ along with stereom secretion at the detached distal end. The stereom would envelop the axial gland organ and stiffen the primary radicular cirri in an upward position. Since no kind of root is known whose radicular cirri trunks point obliquely upward, Lowenstam (1942, p. 31) postulated that this position was acquired subsequent to the disruption of the proximal root part but prior to the stiffening of the cirri by stereom. The latter upward position was produced either by (1) the gradual overlap and building up of stereom at the distal junction of the cirri and stem, forcing the cirri to turn in the direction of minimum stress, or possibly by (2) the weight of the crinoid resting on the two cirri and the stem base, causing the cirri to turn in their sockets to the maximum degree of movability in order to gain a stable position. In either case, the cirri would then be held in place by secondary stereom secretion.

In studying the frequency of unilevel-type individual roots as compared to the number of multilevel forms, Lowenstam (1942, p. 35) found that the former were by far the most common. He rejected, therefore, the hypothesis that the unilevel forms were derived polyphyletically from several multilevel forms.

His thin-sectioned specimens confirmed the belief of most previous authors that *Ancyrocrinus* represents a heterogeneous body with respect to the origin and formation of its skeletal elements. Morphological variability was

regarded by Lowenstam (1942, p. 35) as a function of the flexibility of the stem and the degree of secondary stereom secretion, the number of spur levels in the grapnel being completely dependent on the number of primary radicular cirri retained by the crinoid after the break within the primary root. The preponderance of unilevel forms over multilevel forms, in his opinion, was related to a critical point of weakness between the first and second cirri nodal. He could not, however, distinguish any skeletal structure or columnal articulation surface in the stem which could be considered "weak."

An interesting series of structures were first seen by Lowenstam (1942) in his thin sections. Within the grapnel he discovered a secondary canal system which branches off the axial canal at its distal terminus and from the cirri canals. He found (1942, p. 30) that,

> The canals pass along the articulation surfaces of the columnals and cirri joints, pierce the stereom layers and extend to the body surface. Commonly the canals branch off in irregular intervals within the stereom layers. The axis of orientation of the canals shows a radial arrangement in regard to the stem and cirri surfaces. The course proper is commonly undulating, though straight canals were observed.

No evidence of wall deposition was observed but "tubercle-like protuberances in a number of specimens were found to be the result of local bulging of the uppermost stereom layer around the canal ends." Lowenstam regarded the secondary canal system as being derived subsequent to the loss of the distal portion of the primary root.

A second interesting structural feature first noted by Lowenstam (1942, p. 25) was a

> wrinkled fold series arranged peripherally around the spur bases and the proximal body portion, overlapping at the junctions of the body and spurs. Fold-like stereom masses were observed on the body and on the spurs. The folds follow each other at equal distances, the axes being vertical to that of the covered skeletal elements.

On the distal end of the *Ancyrocrinus* grapnel in a New York specimen Lowenstam noted a bryozoan colony. He thought, however, that the colony grew there prior to root disruption. Although confirming Ehrenberg's observation that some grapnels possessed bent stem portions, Lowenstam regarded as untenable Ehrenberg's interpretation that the flat distal ends resulted from resting on a solid surface. He explained the observed structures as the product of fracturing at these points.

Lowenstam also substantiated Kirk's observation that spurs in the grapnel were arranged with respect to the axial canal. Several specimens which appeared to be exceptions to

this rule were proven to be properly oriented by thin sections, their true origin being obscured by the secondary stereom layer.

In 1943 Goldring merely listed *Ancyrocrinus bulbosus* in a faunal list from the Marcellus in a quarry just south of Westerloo, New York. If this age is correct it represents the oldest known occurrence of the species.

Ubaghs (1953, p. 727) reconstructed *Ancyrocrinus* in the living position based on Goldring's specimens. He illustrated the crinoid with its arms roughly forming a food-gathering cone or funnel.

In 1967 Pierre Morzadec described the interesting occurrence of *Ancyrocrinus amoricanus* in the Givetian of France. His specimens, roughly equivalent to *A. bulbosus* in age, differ from the latter species in possessing five cirri in the grapnel, all of which apparently arise from the same level.

Most recently, Breimer (1969, p. 146), in his paper on the paleoecology of Paleozoic stalked crinoids, drew attention to an alternative living position for *Ancyrocrinus* which differed from that of Ubaghs. Breimer suggested that perhaps *Ancyrocrinus* extended its arms until they lay in a single plane which was at a right angle to the cup proper, all arms being equally spaced around the cup. The structure formed would be a two-dimensional circular fan. In flowing water, he expected, this fan would be turned from the horizontal to the vertical and directed normal to the current direction; the aboral side of the arms could thus face into the current in the same manner as living crinoids. The anchor served to keep the crinoid in place amidst stronger currents and perhaps allowed it to take advantage of the currents around it by allowing itself to be passively transported to another place to begin a new anchoring period.

SYSTEMATIC DESCRIPTIONS

Class CRINOIDEA
Subclass INADUNATA
Order CLADOIDEA Moore & Laudon 1943
Suborder DENDROCRINOIDEA Bather 1899
Family BOTRYOCRINIDAE Bather 1899

Ancyrocrinus belongs to the Order Cladoidea because of its dicyclic cup, firm junction of plates, and free arms above the radials.

The thin flexible anal tube which occupies almost the entire ventral surface of the crinoid and the dichotomy of the arms restrict *Ancyrocrinus* to the suborder Dendrocrinoidea.

The conical cup, quadrangular RA obliquely below the right posterior radial, X in line with the radials, large anal sac composed of thin plicate plates, horseshoe-shaped radial facets, and the isotomously branching armlets, definitely place *Ancyrocrinus* in the family Botryocrinidae.

Genus ANCYROCRINUS Hall 1862

Diagnosis.—The genus *Ancyrocrinus* was originally established by Hall (1862, p. 117, 118) for the holdfast of this crinoid. The description of the calyx was given by Goldring (1942, p. 13–18). *Ancyrocrinus* is similar to *Botryocrinus* in having five pentagonal radials which are more or less rounded and project from the cup, comparatively narrow radial facets, a quadrangular RA, and an X roughly shaped like the radials and at the same level; nevertheless, we consider it to be a valid genus because it possesses cirri on the stem which are eventually covered by secondary stereom forming a distinctive grapnel, a quadrangular stem with an axial canal and four peripheral canals, and only four infrabasals which are aligned with the four corners of the columnal as well as with the four peripheral canals. The basals of *Ancyrocrinus* also have a different shape from those of *Botryocrinus* as a consequence of their fitting against a reduced number of infrabasals.

Remarks.—Because it possesses five cirrial grapnel appendages originating from the same level the question arises as to whether or not Goldring's *Ancyrocrinus quinquepartitus* actually belongs to the genus. Although *A. quinquepartitus* (pl. 3, figs. 15,16) could conceivably fit into Hall's original description of the genus, the five-lobed axial canal and five spurs in the species would seem to exclude it from a genus whose four-spur grapnel and calyx characteristics in the type species are adapted to a quadrangular stem which possesses only four peripheral canals. Because of the stratigraphic occurrence (Glenerie Limestone = Lower Devonian) of *A. quinquepartitus* and its representation by a single specimen, the relationship of this species with *A. bulbosus* is difficult to ascertain. The grapnel of *A. quinquepartitus* may be an analogous structure developed in a completely different type of crinoid, or it could belong to an ancestral form of *Ancyrocrinus* in which the fourfold symmetry of the grapnel, stem, and lower cup had not yet developed.

Morzadec's recent (1967) study on *Ancyrocrinus amoricanus* appears to indicate that the latter may well be the explanation. His new European species, which is based on 18 specimens, is apparently equivalent in age to *Ancyrocrinus bulbosus* in North America. Although possibly analogous in structure to *Ancyrocrinus*, the internal structure of *A. amoricanus* is iden-

tical to that of *A. bulbosus* except the former develops five cirri per nodal and has a five-lobed axial canal like that in *A. quinquepartitus.* The calyx is unknown in *A. amoricanus.* The occurrences suggest that *A. quinquepartitus* gave rise to *A. amoricanus* in Europe and *A. bulbosus* in North America. The latter species developed a quadrangular stem with the appropriate modifications while the European form retained its "normal" crinoid configuration.

At the present time the characteristics of the genus have been taken from the type species of the genus, which is the only form in which the calyx is known. If the calyxes of *A. quinquepartitus* and *A. amoricanus* are found, the characteristics of the genus may well have to be modified or perhaps a new genus proposed for the two latter forms. At the other taxonomic extreme the question might well be asked: If a large sample of *A. amoricanus* grapnels could be collected, how many "mutant" four-sided forms would it contain?

ANCYROCRINUS BULBOSUS Hall 1862

Text-figs. 2–4; pl. 1, figs. 1–18; pl. 2, figs. 1–17; pl. 3, figs. 1–14,17,18; pl. 4, figs. 1–13

Ancyrocrinus bulbosus Hall 1862, p. 118, pl. 1, figs. 25,26.
Ancyrocrinus spinosus Hall 1862, p. 119, pl. 1, figs. 27,28.

Hall's original description of this species was:

> Bulbiform below, with four lateral, obliquely ascending processes of the character of jointed or solid spines, which more or less thickened according to age. Column above the bulb often elongated, rounded in the lower part and obtusely quadrangular above in older specimens, which preserve but a small part of the column as a thickened process. Body and arms unknown. ... In the shales of the Hamilton Group: Lake Erie shore, and elsewhere.

Due to the morphologic variability of the *Ancyrocrinus* grapnel wherever it is found, we must agree with the implications of several previous authors (Ehrenberg, 1929, p. 17; Roy, 1929, p. 204,205; Lowenstam, 1942, p. 27,28) that Hall's second species, *Ancyrocrinus spinosus,* cannot be justified. In any case *A. spinosus* would be unacceptable if it was Hall's intention to establish a new species solely on its geographic distribution.

General description.—A medium-size inadunate crinoid with a conical cup containing four infrabasals, five basals, five radials, and two anal plates (the X and the quadrangular radianal). Cup approximately as high as wide, as measured across the radials. Sides of the cup straight except for a slight flaring at the radial facets; flaring becoming more pronounced in older specimens. Width at the cicatrix approximately $\frac{3}{4}$ the width as measured across the radials. Plates thick and devoid of any ridging. Ornamentation weakly developed, the calyx plates being slightly granular in appearance. Cup dorsally confluent with the unusually large and stout quadrangular column. Column in immature specimens only slightly tapered from the proximal to the distal end; in more mature specimens, only a slight degree of tapering at the proximal end but pronounced tapering at the distal end, there terminating in a grapnel composed of stem cirri overlain by secondary stereom.

Dorsal cup.—IBB forming a complete circlet, quadrangular in outline and equal in size to the top of the column. Each infrabasal situated over one of the four angles of the quadrangular stem. A, B, and C infrabasals relatively low, wide, and pentagonal; the fourth infrabasal occupying the DE area, polygonal with two peaks, having the appearance and size
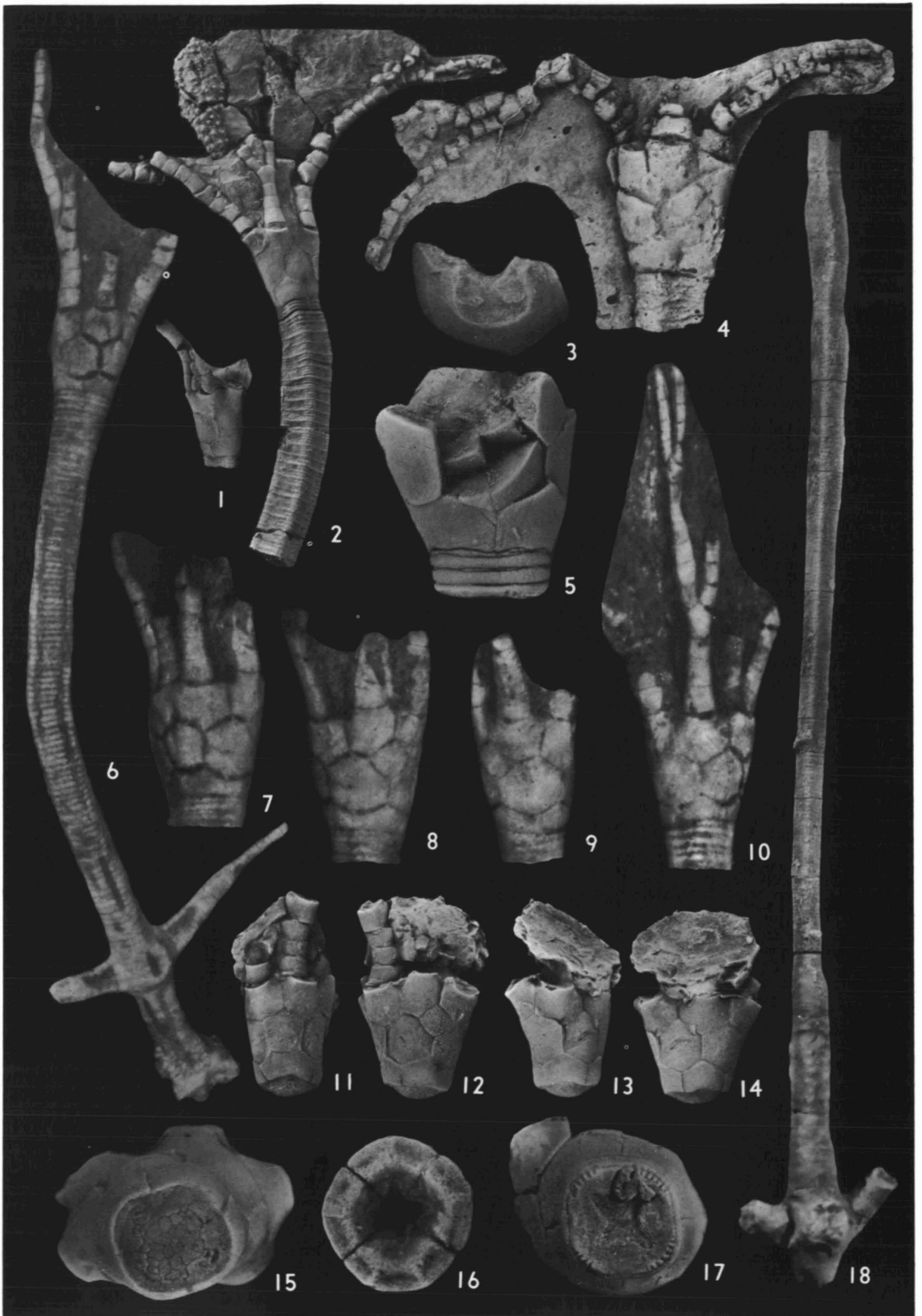
PLATE 1

PLATE 2

of two pentagonal infrabasals fused together. Base of the calyx completely floored by the IBB ring except for a cruciform lumen in the center of the base. Each of the projections of the cruciform lumen directly centered on one of the four infrabasals and continuous with one of the four peripheral canals of the column.

In one specimen, UC 37125 (pl. 1, fig. 15), the base of the infrabasal circlet not attached to any columnals but instead completely covered by a series of small, polygonal plates. No openings through this covering of plates; presumably, the crinoid, at the time of its death, had no stem.

BB forming a complete circlet, about half the height of the cup. Basals the largest plates in the cup, each higher than wide. BC and CD basals both heptagonal, the former supporting the RA, X, and RR of the B and C rays and the latter supporting the RA, X, and the R of the D ray. AB and EA basals both hexagonal. DE basal pentagonal in outline, its base bulging slightly into the DE infrabasal upon which it rests.

RR circlet composed of five plates interrupted by the X. Each radial pentagonal, although the rounded shoulders on either side of the facet give it a heptagonal appearance. Radials wider than high. The part of the radial plate containing the radial facet protuberant. The radial facet horseshoe-shaped, occupying from 57% to 70% of the width of the radial plate. In the three specimens examined, there is a tendency for the A ray to have proportionally the smallest radial facet and the C and D rays to have proportionally the widest facets.

A small, poorly developed fulcral ridge developed across the face of the radial facet, together with the ambulacral groove dividing the facet into three distinct ligamental areas. The radial nerve does not appear to be separated from the ambulacral groove.

RA quadrangular in shape, the smallest plate in the cup. Approximately square in an immature specimen (UMMP 23867); in a more mature specimen (UC 37125) three of the four sides equal, but the fourth side (in contact with the C radial) 20% to 25% longer than the other sides. RA resting on the left and right posterior basals. The upper right side of the RA helping to support the C radial, and the upper left side of the RA helping to support X.

X approximately the same size as the radials and in line with them, having the outline of a slightly irregular heptagon. The base of X on the left side slightly inclined from the horizontal toward the left posterior basal; the left side of X bounded by the D radial; the base of the X on the right side resting upon RA; and the right side proper of X in contact with the C radial.

None of the specimens observed with any of the plates above the X preserved *in situ*. Facets on the top of the X to accommodate three plates. The widest of these facets occupying approximately 80% of the top surface of the X, forming a slightly curved surface. On each side of this wide central plate, a single facet present to support a small plate. Each of these plates would occupy approximately 10% of the top surface of the X.

Only a small portion of the anal sac visible and this small area, for the most part, in disarray. All plates pyritized making observation

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TEXT-FIG. 2—*Ancyrocrinus bulbosus* Hall 1862. Camera lucida drawing of UMMP 23867, the specimen which initiated this study. Approximately × 3. Note the structure of the grapnel in this immature specimen. Photographs of this specimen in plate 1, figures 6–10; plate 3, figure 17.

difficult. Plates thin and plicate, each with raised central portion; central portion forming a node in the plates of the lower sac (approximately 14 mm from the base) and becoming more spinous near the top of the sac (approximately 35 mm above the base). Sac plates apparently either quadrangular or hexagonal, the latter being the dominant form. In a quadrangular plate, four ridges radiating from the center node, one to each corner. In a hexagonal plate, five initial ridges radiating from the center node, one of which quickly bifurcates; of the six ridges thus formed, one extending to each of the six corners of the plate. Normally, three ridges converging at the junction of three plates; rarely, four ridges meeting at the junction of four adjacent plates, as at the corners of a quadrangular sac plate. End of the anal sac not preserved.

Arms.—These are poorly preserved in the Dock Street Clay specimen. Nothing can be added to Goldring's (1942) study. The following information is essentially from Goldring.

Arms in general long and slender, rounded on the dorsal side. IBrr quadrangular, narrower at the top than at the base. Width of a brachial equal to the height. IBrr series narrowing to the base of the IAx, each being slightly wider at the base than high. In UC 37071 the A ray with five IBrr, but the B, C, and E rays each with four IBrr (pl. 1, figs. 1,2); D ray is covered by matrix. In UMMP 23867 the A and D rays each with four IBrr. The number of IBrr probably of little specific importance. IAx flaring from the base to the top with the height greater than the width at the base, giving rise to two equal arms. IIBrr quadrangular, wider than high; seventh IIBr axillary in the A ray of UMMP 23867 (pl. 1, fig. 10) and the A and C rays of UC 37071 (pl. 1, fig. 2). No other complete IIBr series preserved. IIAx flaring from the base to the top, higher than wide; bifurcations slightly unequal. IIIBrr series preserved only in the A ray of UC 37071 (pl. 1, fig. 2). Each of the eight brachials higher than wide; the eighth brachial axillary; bifurcations unequal. IVBrr higher than wide.

Column.—Quadrangular in the proxistele becoming more elliptical in dististele. Proximal third of stem distinctly heteromorphic with columnals grouped in noditaxes of four. Nudinodals slightly taller and wider than internodals. Distal two-thirds of stem homeomorphic. The lumen quadrilobate with lobes directed toward angles of the columnal. Areola discontinuous, located between angles of lumen lobes. Crenulae short, straight, and well developed in anchor, becoming less well developed in mesistele and proxistele. Crenularium of proxistele confined
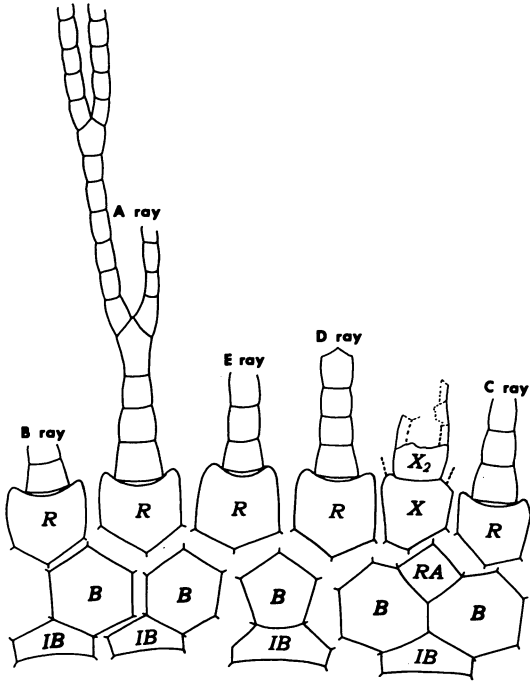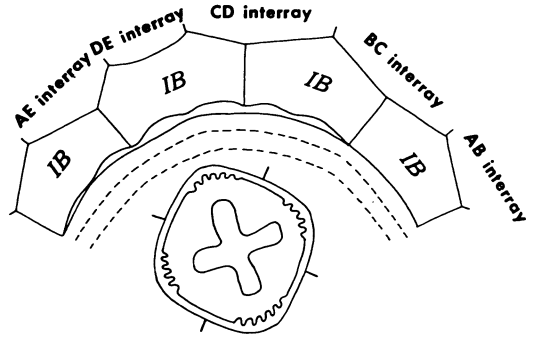
TEXT-FIG. 3—*Ancyrocrinus bulbosus* Hall 1862. Diagram of UMMP 23867 illustrating the thecal plate arrangement and the arm structure. Approximately × 5. Photographs of this specimen in plate 1, figures 6–10; plate 3, figure 17.

TEXT-FIG. 4—*Ancyrocrinus bulbosus* Hall 1862. Camera lucida drawing of the infrabasal ring showing the addition of new columnals at the cicatrix. Note the shape of the DE infrabasal.

solely to angle of columnal. The column has one or more levels of cirri. Proximal cirrials (those nearest the columnal) as high as wide. Cirrials becoming progressively higher, near the distal end twice as high as wide. Each cirrial provided with a dumbbell-shaped lumen for passage of the axial canal.

Holdfast.—The primary holdfast composed of numerous, small polygonal plates. Base of the root covered by secondary stereom but the small polygonal plates still evident farther up the column in young specimens. Similar small plates visible after removal of the object to which the crinoid was attached, as in UMMP 57700 (pl. 3, fig. 8). Very short stumplike radicular cirri present. *Ancyrocrinus* found attached to a wide variety of brachiopods, corals, and bryozoans in the New York and Michigan areas.

PLATE ARTICULATIONS AND GENERAL REMARKS

Plate articulations.—As might be expected, the plate articulations are solely ligamental in *Ancyrocrinus*. Ligamental articulations in crinoids have, to some degree, an active contractile power. In *Ancyrocrinus* any flexing of the columnal, thecal, or arm plates would neces-

sarily be dependent on this active contractile power.

Calyx.—The articular surfaces of the thecal plates in *Ancyrocrinus* are not simply flat, structureless joint faces; instead, they are rather slightly concave. Such an articulation surface has been described by Van Sant & Lane (1964, p. 62) in *Barycrinus hoveyi*. This type of surface suggests that the connective tissue was not lodged in a distinct fossa. Such an articulation cannot be called a zygosynostial articulation (the most common thecal plate ligamental union in Paleozoic crinoids) but must rather be considered a synostial articulation. In the latter articulation, short ligamental fibers allow a slight degree of movement in all directions.

The largest plate in the infrabasal circlet is undoubtedly the evolutionary end product of ankylosis of the D and E infrabasals, as Goldring suggested (1942, p. 15). These two basals were fused throughout the ontogeny of the crinoid. Of the seven specimens which retain the infrabasal ring observed by the authors, all have a single plate in the DE infrabasal area. In none of the specimens is there a trace of a former suture running down the middle of this infrabasal.

Radial facets.—The ligamental articulation between the radials and the arms at the radial facet is completely different from that of the thecal plate unions. The radial facet is divided into three distinct ligamental areas by a slightly elevated fulcral ridge (pl. 1, fig. 3). This type of movable ligamental union is called a trifacial articulation. Van Sant & Lane (1964, p. 39) have pointed out that such an articulation was antecedent to true muscular unions and that it is "quite probable that some muscle fibers were present in these articulations, thus providing controllable contractile power." Such an articu-

lation would enhance the mobility of the arms in all directions with the greatest degree of mobility occurring along the dorsoventral axis.

Brachial facets.—Some dissociated arm brachials showing the articulation surfaces poorly preserved were found with UC 37125. The brachials in *Ancyrocrinus* have a "ball-in-socket" articulation, the distal brachial surface being slightly concave and the proximal surface being gently convex. Similar articulation surfaces were described by Van Sant & Lane (1964, p. 62) for their crinoids assigned to the Cyathocrinoidea. Such a synostial articulation would allow a slight degree of movement in all directions.

Anal tube.—In living crinoids the anal tube is capable of considerable movement. Unfortunately, in none of our specimens is the anal sac well enough preserved to allow us to make any interpretation of the ligamental articulations in this structure. The facets of X are slightly concave suggesting that a synostial type of ligamental articulation was present at least at the base of the sac.

Column.—As in all other Paleozoic stemmed crinoids, the columnals were held together by symplexial unions in which the opposing articular surfaces have interlocking culmina and crenellae. The short stem composed of quadrangular columnals with symplexial articulations would tend to give a great deal of rigidity to the column. The unusually short height of the individual columnals would, however, allow increased movement, especially in the direction of the flat sides of the column. Some degree of torsion has been observed in the *Ancyrocrinus* stem (pl. 1, fig. 1). Such "twisting" is usually accompanied by some distortion of the stem ossicles and it may well be due in part to diagenesis of the surrounding sediments.

The outer margin of the columnals in the proxistele is characterized by a smooth depressed area (pl. 3, fig. 11). Moore, Jeffords, & Miller (1968, p. 28) called such an area of similar morphology an epifacet but excluded the term from straight- or nearly straight-sided columnals. A new term *allofacet* is proposed to describe a smooth depressed surface, outside of the crenularium, of straight- or nearly straight-sided columnals.

The column could apparently increase its length in several ways. As can be seen in UMMP 57838 (pl. 1, fig. 5), it could add new columnals directly at the cicatrix. Some of the small columnals near the proximal end of the stem appear to have been added between older columnals. The stem was also lengthened by the growth, in height, of the individual columnals.

PLATE 3

PLATE 4

Such growth evidently could not take place where the columnals were covered by secondary stereom in the grapnel area.

Cirri.—The cirrials are initially articulated solely by symplexial unions. With the onset of secondary stereom secretion, apparently at a very young stage, ankylosis takes place. With increasing maturity, ankylosis proceeds from the proximal to the distal end of the cirrus. Initially, the cirri had some degree of mobility, but obviously this mobility was reduced during growth and lost in the mature animal.

The lumen of the cirri in *Ancyrocrinus* is "dumbell-" or "bean-shaped" similar to that found in *Gasterocoma? bicaula* described from Nevada by Johnson & Lane (1969, p. 72). Although most "two-hole" pelma ossicles are probably cirrials as reported by Johnson & Lane (1969, p. 72), it is now evident that this feature is not confined to the family Gasterocomidae, as that family is now defined; hence, we doubt the reliability of these structures to determine age horizons over any great distance until more work is done on the occurrence of such plates.

GRAPNEL DEVELOPMENT

Grapnel development evidently started at a very early stage in *Ancyrocrinus*. Stereom secretion was apparently controlled genetically rather than environmentally. In the youngest specimen observed, a grapnel only 4 mm high, secondary stereom secretion had already commenced at the junction of the cirri and the stem. Disruption at the base or within the base, as was postulated by Ehrenberg and by Lowenstam, was not necessary for the start of stereom secretion, as demonstrated by the attached base of UMMP 23867 (pl. 3, fig. 17) and by a large number of other grapnels which still retain their primary roots as well as the objects to which they were attached.

Lowenstam's violent mechanical disruption within the primary root was proposed to explain the obliquely upward position of what he considered to be radicular cirri. As can be seen in UMMP 23867 (pl. 1, fig. 6), the cirri are not part of the radicular cirri in the original root system, but rather are normal stem cirri. Nor is a mechanical disruption needed to explain the number of grapnel levels or variation in the number of spurs (Lowenstam, 1942, p. 35). Within a population, variations of the distribution of stem cirri would be expected.

Based on the Michigan material two centers of secondary stereom secretion can be distinguished. The first of these centers is at the base of the root where finger-like encrusting radicular cirri attached to the bottom. Secondary stereom secretion in this area can be seen in almost all Paleozoic crinoids. The second center, as stated earlier, is at the junction of the cirri and the stem. If there is more than one level of cirri, secretion occurred at each individual junction. Here, secondary stereom built up on both the stem and each of the four cirri, forming at a very early stage the primary grapnel.

How the secondary stereom was added is still not fully understood. No growth lines are readily apparent and it would seem that the secretion cannot be compared to normal growth of an echinoderm plate. A similar amorphous

EXPLANATION OF PLATE 4

All specimens lightly coated with ammonium chloride. All figures × 2, except where noted

Ancyrocrinus bulbosus Hall 1862—*1,* hypotype UC 40391, Locality 4, New York; lateral view of a highly weathered grapnel, indicating secondary stereom in the column may be due to extensions of the individual columnals. *2,* hypotype UC 37189, Locality 8, New York; side view of grapnel illustrating two cirri levels; in the lower cirri level one cirrus is directed downward, due in this instance to diagenesis of the surrounding rock. *3,* hypotype UMMP 57720, Locality 17, Indiana; lateral view of grapnel with cirri developing at three distinct levels. *4,* hypotype UMMP 57711, Locality 6, New York; lateral view of grapnel with a long segment of stem incorporated into the grapnel; wrinkled areas also well shown. *5,* hypotype UMMP 57713, Locality 6, New York; lateral view of grapnel showing a bend in the stem such that it is parallel to one of the cirrus. *6,* hypotype UMMP 57717, Locality 18, Indiana; side view of grapnel; note the short length of the cirri. *7,* hypotype UC 40392, Locality 16, Michigan; distal view of grapnel showing radicular cirri of the original root encrusting a brachiopod valve. *8,* hypotype UMMP 57836, Locality 5, New York; lateral view of grapnel showing the finger-like radicular cirri of original root. *9,* hypotype UMMP 57714, Locality 6, New York; portion of column encrusted with bryozoan and an inarticulate brachiopod; × 1. *10,* hypotype UMMP 57719, Locality 17, Indiana; lateral view of grapnel, again illustrating a long portion of stem below the cirri level which has been incorporated into the grapnel. *11,* hypotype UMMP 57560a, Locality 6, New York; grapnel sectioned along the axial canal; note extensions of canal near base into the original root and the trace of original columnals near the top; × 2.3. *12,* hypotype UMMP 57963, Locality 5, New York; sectioned grapnel; note the curvature of axial canal indicating the original stem was curved before secretion of secondary stereom; × 3.4. *13,* hypotype UMMP 57718, Locality 18, Indiana; lateral view of grapnel in which the cirri were short; there is also an unusually large amount of secondary stereom secreted around the stem and base of the cirri.

stereom structure in modern echinoderms is caused by infestations of myzostomes or by some other injury. The only statements which can be made with any certainty are that the secondary stereom was mesodermally controlled by the stroma together with calcigenous coelomocytes and that this calcification, genetically controlled, started at a very early stage.

The "wrinkled fold series" observed by Lowenstam (1942, p. 25) was also readily apparent in our specimens. At first we believed these might represent growth lines but thin sections have not corroborated this earlier speculation. We can only say that these wrinkles represent differential rates of stereom secretion.

As the animal matured, secondary stereom secretion took place primarily around the stem-cirri junction. The secondary calcite was built up predominantly around the stem and slowly advanced up and down the stem from the cirri junction. Secondary calcite also built up around the cirri but did not spread out along their entire length; instead, it concentrated around the bases of these structures. As the junctions between cirri and stem ossicles became ankylosed, the enclosed plates ceased to grow in height. Growth in width of the cirrials and columnals may have continued, although the boundary between the original plate and secondary calcite is not distinct.

At this stage of development, two possible circumstances could arise. In some specimens, secondary stereom secretion continued down the stem, and eventually the grapnel contained all the initial root as well as the stem below the original cirri level. In other specimens, however, it is evident that no original root is present. In these specimens we believe that some outside force broke off the stem above the original root but below the area covered by secondary stereom extending down the stem from the cirri. After this break, the secondary stereom encased the broken end of the stem. We wish to emphasize, however, that the disruption did not initiate the stereom secretion.

If the original root is incorporated into the grapnel, several features reported by both Ehrenberg and Lowenstam can be readily explained. The flattened and truncated grapnel bases were not an attempt by the crinoid to renew a firm base on the bottom as believed by Ehrenberg. Although Lowenstam may be correct in holding Ehrenberg's interpretation "untenable," we prefer to believe the structures could as easily reflect original roots which have been incorporated into the grapnel. In the same manner, the bryozoan colony reported by Lowenstam could be the object to which the original root was attached. That some of the

grapnels are bent is not very surprising. Koch & Strimple (1968) have recently published a description of several cystoids which are attached to the underside of a ledge; although the present authors do not believe *Ancyrocrinus* normally lived in a similar position, we do believe that any position which the young crinoid adopted in the section of the stem below the cirri level became represented in the adult grapnel. If the young *Ancyrocrinus* attached itself to the side of a bryozoan colony or coral, there would have been a tendency for the stem to curve at the distal end so that the cup could be properly oriented. Any change in orientation of the object to which the original root is attached would also be reflected in the grapnel, provided ankylosis did not prevent the movement of the stem between the cirri and the root. Such adaptive pressures during ontogeny could explain many unusual forms and variations in the grapnel.

The height of the cirri above the base of the grapnel is quite variable. At least two factors determine height in *Ancyrocrinus*. The first and most obvious is where the cirri originate. We feel the height represented in UMMP 23867 (pl. 1, fig. 6) is the most common in *Ancyrocrinus*. A second factor is the rate of stereom secretion around the stem below the cirri level. If the secondary stereom secretion progresses slowly a great deal of columnal growth can take place before the stem is completely incorporated into the grapnel. These two factors may lead to forms such as those illustrated (pl. 3, fig. 1; pl. 4, fig. 10).

The length of the cirri in the grapnel is also quite variable. The cirri in modern crinoids grow in such a manner as to have new cirrials added at the distal ends. The short length of some cirri in several of the grapnels observed is undoubtedly due to the fact they never achieved their natural length. This may have been due either to improper growth or to the rapid buildup of secondary stereom around the entire length of the cirri which prevented new cirrials from being developed. This latter process may have taken place at the cost of slower secondary stereom secretion around the stem between the cirri level and the root, producing forms such as UMMP 57641a (pl. 2, fig. 17).

The secondary canal system reported by Lowenstam was very obvious in our thin sections. The secondary canals commonly pierced the secondary stereom up to the very surface where they were sealed by a thin layer of calcite. Weathered specimens often have the appearance of having been bored. As Lowenstam (1942, p. 30) pointed out, this secondary canal system branches at irregular intervals

TABLE *1*—MEASUREMENTS OF CUP PLATES IN *Ancyrocrinus bulbosus* (in mm)

Plate			Infrabasals								
Meas.			Width						Height		
			Ray						Ray		
Spec.	A	B	C	DE			A	B	C	D	E
UMMP 23867	1.41	2.02	2.54	3.55			1.04	1.04	1.20	1.50	1.17
UC 37071	5.32	5.04	..	5.42			3.20	3.60	..	3.50	3.34
UC 37125	3.23	3.55	3.88	7.57			2.20	2.32	2.27	2.51	2.39

Plate			Basals							
Meas.			Width					Height		
			Interray					Interray		
Spec.	AB	BC	CD	DE	EA	AB	BC	CD	DE	EA
UMMP 23867	2.50	2.71	2.67	1.99	2.14	2.59	2.58	2.66	2.09	2.33
UC 37071	4.97	..	..	4.62	4.95	6.21	..	..	5.37	6.05
UC 37125	4.00	3.91	3.99	3.54	3.54	4.28	4.57	4.13	3.53	4.21

Plate			Radials							
Meas.			Width					Height		
			Ray					Ray		
	A	B	C	D	E	A	B	C	D	E
UMMP 23867	2.33	..	2.33	2.25	2.21	1.52	..	1.56	2.00	2.03
UC 37071	5.66	5.11	..	..	5.19	4.19	4.25	..	..	4.01
UC 37125	4.02	4.48	3.87	4.03	4.03	2.76	2.95	2.68	3.29	2.88

Meas.		Radial Facet Width			
			Ray		
	A	B	C	D	E
UMMP 23867	1.42	..	1.50	1.58	1.35
UC 37071	3.22	3.25	..	..	2.99
UC 37125	2.48	2.84	2.51	2.67	2.63

Plate	Radianals			
Meas.	Plate Contact			
	RA-X	RA-DE	RA-C	RA-BC
UMMP 23867	1.36	1.32	1.21	1.31
UC 37071	..	..	..	..
UC 37125	1.89	1.90	2.35	1.92

Plate	X	
Meas.	Width	Height
UMMP 23867	2.09	1.97
UC 37071	..	..
UC 37125	3.37	3.64

	Complete Specimen		
Meas.	Width at Cicatrix	Width at Radials	Height
UMMP 23867	3.09	4.55	4.58
UC 37071	7.05	(9.37–11.9)	11.48
UC 37125	4.88	9.80	8.56

along the axial canal of the stem and the cirri. It is always radially arranged in regard to the stem and cirri joint surfaces. The part of the secondary canal system which extends from the very end of the axial canal of the stem almost certainly represents extensions of that canal into the radicular cirri of the primary root which had been incorporated into the grapnel. The present authors suggest that this secondary canal system is in general an extension of the axial canal and that it served to supply numerous coelomocytes which, in turn, acted as carriers of food and calcigenous cells to this area of concentrated stereom development.

If the adult crinoid lost its entire grapnel, most likely it could grow a new one. Perhaps plate 3, figure 5 represents such an example. If this is the case, however, it is interesting to speculate on how the animal was able to attach itself to the bottom during this period of regeneration.

Throughout its stratigraphic and geographic range *Ancyrocrinus* appears to retain its heterogeneous grapnel form, thus making specific determinations based solely on the grapnel difficult, if not impossible. In no area is there a tendency toward any consistent spur-level distribution in the grapnel or shape of the grapnel which would justify the need for more than one species. In the Ipperwash Limestone the grapnels are consistently larger than in most other areas but, even in this instance, grapnels of at least equal size are to be found in the majority of the other geographic areas. Furthermore, speciation based solely on size, or on morphologic form which is obviously not completely hereditarily controlled, would be deemed unwarranted.

PALEOECOLOGY

The life mode of *Ancyrocrinus bulbosus* and the possible use of the crinoid's peculiar grapnel has long been a question of extensive debate. Hall, Carpenter, Ehrenberg, Lowenstam, and most recently Breimer have all made attempts to interpret the function of the grapnel. We feel that perhaps the environments in which *Ancyrocrinus* lived may shed some new light on this question.

Ancyrocrinus apparently lived in two basic types of environments. The first of these, as represented by the Ipperwash and Genshaw Formations, was a relatively shallow-water moderate-energy environment.

The Ipperwash is predominantly a bioclastic limestone, the matrix in which *Ancyrocrinus* is found being a shell hash. Brachiopods with articulated valves or even single unbroken un-

abraded valves are rare. Argillaceous material is present in small quantities.

The *Sieberella romingeri*–large *Atrypa* zone of the Genshaw Formation was apparently transitional from a rough-water to a quieter-water environment. Deposition took place at a greater depth than that of the Ipperwash and was accompanied by an increase in the supply of argillaceous material. Some current activity is readily apparent from the abraded appearance of some of the fossils, the rolling of some of the corals and stromatoporids, and the large number of single brachiopod valves, most of which are turned over. Since large numbers of complete *Atrypa* and *Sieberella* brachiopods can be found in some layers, currents were not always strong.

In both the Ipperwash and Genshaw Limestones the grapnels of *Ancyrocrinus* are larger on the average than those found in any other area. Only in the Ipperwash are the grapnels at all common, and even in this formation they are not as prevalent as in the Beechwood, Dock Street Clay, or Wanakah.

The second environment, as represented by the Beechwood Limestone, Dock Street Clay, Wanakah Shale (two zones), Centerfield, and Tichenor Limestones, was somewhat deeper and quieter water.

The Beechwood is predominantly a bioclastic limestone. Its agitation during deposition was much less than that in the Ipperwash. Corals occur in living position; and complete brachiopods, small inadunate crinoids, blastoids, and many other forms of animals whose skeletons normally are disarticulated or broken easily are common. It thus appears that the upper part of the Beechwood, which yields *Ancyrocrinus*, was deposited in deeper water than that of the Ipperwash and that there was a dearth of argillaceous material.

Although *Ancyrocrinus* is found in the Centerfield and Tichenor Limestones, it is restricted in both members to the more argillaceous top strata. In both the Centerfield and Tichenor the conditions of deposition are nearly the same as those of the Beechwood Limestone except they contain more argillaceous material.

The Wanakah Shale is predominantly a bluish-gray calcareous shale with several thin limestone bands, one to three inches thick, near the base and top of the member. One of these bands is part of the *Pleurodictyum* bed of Grabau. It undoubtedly represents a momentary slowing down in the rate of argillaceous deposition combined with an increase in the numbers and variety of the benthonic fauna. Within this limestone the brachiopods, pelecypods, and crinoid columns are generally dis-

articulated. This was due in part to either slight current action or bioturbation, perhaps both. The *Pleurodictyum* beds extend both above and below this thin limestone band; and although the fossils in it are not as abundant, they are generally better preserved and more often articulated. *Ancyrocrinus* is equally common throughout the bed.

In the zone from three to five feet below the top of the Wanakah a bluish-gray calcareous shale is present at most exposures, although from Locality 6 westward in New York a thin one-inch band of limestone is also found at the very top of this zone. The abundance and variety of fossils vastly increases in this zone compared to the meager fauna of the underlying middle Wanakah. This upper unit represents a mud bottom in moderately deep water. The increase in fauna probably reflects a decrease in the rate of sedimentation.

The Dock Street Clay is a very localized occurrence of blue calcareous shales between reef mounds in the Four Mile Dam Formation. The occurrence of fossils is very "patchy," although where they do occur it is generally in large numbers with the material exceptionally well preserved. This unit suggests a mud bottom in which the rate of sedimentation was generally too rapid for benthonic life. In local sheltered areas, however, where the water was quiet enough to maintain only a moderate amount of fine material in suspension, an abundant benthonic fauna developed. *Ancyrocrinus* is a member of this abundant benthonic fauna.

In both the low- and moderate-energy environments *Ancyrocrinus* occurs with a normal, benthonic marine fauna. This fauna includes camerate, flexible, and inadunate crinoids, blastoids, trilobites, brachiopods, bivalves, bryozoans, sedentary polychaete worms, and gastropods. Tabulate corals more than three inches across are found in the Tichenor, Centerfield, Beechwood, and Genshaw. Smaller tabulates (*Pleurodictyum*) are found in the lower Wanakah. Large rugose corals are found in the same units as the large tabulates. Smaller rugose corals are found with every occurrence. In the Wanakah Shale of New York these smaller corals seldom exceed two inches. Based on the fauna it is apparent *Ancyrocrinus* lived in a well-oxygenated, normal marine environment.

From this discussion it is evident that although *Ancyrocrinus* could and did adapt to moderate turbulence in part by increasing grapnel size, as in the Ipperwash and Genshaw Formations, it was more at home in quieter areas with less current activity. In no instance has *Ancyrocrinus* been found in the high-energy

zone of a reef or very near shore environment.

In trying to explain the use of the grapnel in *Ancyrocrinus* several more factors should also be taken into account. Despite the fact that there are obvious advantages to an eleutherozoic mode of life, modern comasterid crinoids do not, as a rule, move about very much although they have the means of doing so. Once in a favorable environment comasterids tend to stay fixed in one spot for considerable periods of time, moving only because of an excessively strong current or other adverse conditions. In the same manner the feeble swimming powers of the larva tend to keep the young crinoids in the same favorable environment. Living comasterid crinoids move, for the most part, very slowly along the bottom using their anterior arms as pulling tactile organs and their posterior arms for pushing. When one considers that the mobility afforded by the arms of *Ancyrocrinus* must have been considerably less than that of these living crinoids, it becomes apparent that *Ancyrocrinus* exercised little control over its movement.

It is dubious, to say the least, to believe that *Ancyrocrinus* would allow itself to be pulled along by currents and use its grapnel as a drag, as suggested by Kirk and by Breimer. The initiation of movement would depend solely upon the current, not the organism, since mobility at the distal end of the stem was minimal. Once movement began, the crinoid would be completely at the mercy of the prevailing current, unable in any way to control its own motion or stop its progress. Possibly, the current could drag a crinoid from the place where it was growing to a more favorable environment, but the chance seems slight or, at best, not worth the risk.

An investigation of the grapnels themselves indicates that the crinoid gained two advantages from possession of a grapnel. The first of these is the presence of long cirri spurs in some specimens (pl. 3, fig. 9). In living crinoids which live on mud bottoms the radicular cirri have a tendency to be long and straight, thus preventing the sinking of the root into the substrate. We believe the long cirri found in some *Ancyrocrinus* served the same purpose. Long spinelike cirri could give the crinoid a substantial base by being either partially buried in mud or stuck in bottom vegetation.

The second advantage is a product of the secondary stereom secretion around the grapnel. This deposition increased the weight of the distal end of the stem, moving the center of gravity away from the middle of the crown down to the lower part of the stem or perhaps

even to within the grapnel. This feature would also provide a secure base for the crinoid.

Although we do not accept all of Lane's (1968, p. 169) hypothesis on balancing in Paleozoic stalked crinoids, we do agree that it was important for these forms to be firmly fixed to the bottom in order for the base to act as a point of leverage. Why a grapnel would be an advantage over a normal cirri root is not clear. Perhaps *Ancyrocrinus* originally developed in an environment in which large objects for attachment were not readily available; or it may have occupied a niche between large bottom objects where most other crinoids were unable to secure a good hold on the bottom. Not having a *Rhizocrinus*-type root at the start, *Ancyrocrinus* may have developed the grapnel to give it an advantage over those other large crinoids with rigid stems which depended upon large objects for attachment. The fact that the grapnel gave *Ancyrocrinus* a sound base may explain why its stem is from two to three times wider than that of any other inadunate crinoid occurring in the same beds. Once a sound base was formed, *Ancyrocrinus* could concentrate on developing a rigid column and a rigid distal end, which, as Breimer pointed out, would prevent the crown from being forced down to the bottom by strong currents.

Like its modern counterparts, *Ancyrocrinus* was a filter-feeding organism. Although there is no direct evidence, its food supply was undoubtedly like that of living crinoids—composed of diatoms, radiolaria, foraminifera, dinoflagellates, nauplius and veliger larvae, as well as small copepods and ostracods. These organisms, trapped in mucous produced by the crinoid's tube feet, were carried down the ambulacral grooves to the mouth.

Previous authors proposed two hypotheses for the feeding position of *Ancyrocrinus*. In the first method, best illustrated by Ubaghs (1953), the arms of the crinoid formed a collecting bowl and the animal depended on food particles drifting down from above. Such a method of feeding is presently used by rheophobic (current-avoiding) crinoids; although this may have been one method of feeding, it is not believed to be the dominant one.

We agree with Breimer's hypothesis that *Ancyrocrinus*, like most living crinoids, formed a filtration fan. It was thus a rheophilic (current-seeking) crinoid. All the environmental data would indicate that this was the case. The formation of a filter fan as outlined by Breimer (see Previous Work) is by far the most likely feeding position.

A third possible feeding position envisioned by the present authors also involved a filtration fan. In this method, the crinoid held all its arms above the calyx in such a manner as to have the aboral side of the arms face into the current and at the same time form a vertical filtration fan. This method of feeding required the C and D rays to turn almost 180° around the long axis. Although the significance of the proportionally larger radial facets in the C and D rays cannot be fully understood with such a small sample, it seems possible that the radial facets reflect this torsion.

Whatever the position assumed, we believe that *Ancyrocrinus*, for the most part, depended on currents in the surrounding water to supply food. It is quite possible that any one of the above methods of collecting food may have been utilized at one time or another during the life of the crinoid.

The lack of a stem (pl. 1, fig. 15) is not considered normal in *Ancyrocrinus*, although Ehrenberg (1929, p. 19) suggested that the grapnel eventually broke away from the crinoid calyx. We cannot accept this as an explanation for the occurrence of the covered lumen in this specimen. There is no way to determine how well the crinoid fared or how long it survived on the substrate. Obviously, death did not follow immediately after the break, since the crinoid lived long enough to plate over the exposed lumen. Nevertheless, that process may have been accomplished in only a few days. In our opinion, the crinoid was out of its ecologic niche even though it did survive for at least a short period of time. Modern crinoids, if turned over, will right themselves by pushing with some arms against the substrate so as to raise one side of the disk (Hyman, 1955, p. 102). If the abnormal *Ancyrocrinus* used the base of the calyx and the C and D arms to push against the substrate, it could well have formed a filtration fan with the A, B, and C rays. Although possible, there is little likelihood that the crinoid survived very long in this state.

More study is needed on the occurrence of epizoic organisms on crinoids. If Lane's contention on the balancing of crinoid crowns is correct, the growth of a bryozoan colony on a stem (pl. 4, fig. 9) would eventually endanger the life of the crinoid. No epizoic organisms were found attached to the calyxes or crowns of *Ancyrocrinus*. Besides bryozoans, inarticulate brachiopods were found attached to some stems. A slight degree of swelling in the illustrated stem, associated with a breakdown in the orderly pattern of the columnals, may indicate the infestation of a parasitic polychaete worm. This is considered unlikely, however. This disruption in the plate pattern develops on the side oppo-

site to that where an inarticulate brachiopod was attached, and may well be due to the presence of this foreign object to the column. Rofe (1869) has previously described such occurrences.

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