REVISION OF SOME CHESTERAN INADUNATE CRINOIDS

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ABSTRACT


INTRODUCTION

In a paper entitled “Mississippian Inadunata—*Eupachycrinus* and related forms,” Sutton & Winkler (1940) reviewed the genera *Eupachycrinus* and *Phanocrinus* and introduced new genera named *Pentaramicrinus* and *Intermediacrinus* and a collective group called *Ageneracrinus*. Their publication was intended to aid in classifying inadunate crinoid genera with basally invaginated bowl-shaped cups. Our paper is largely an evaluation of the species studied by Sutton & Winkler. The material used by these authors was obtained from collections held at the Walker Museum, Illinois State Museum, and the University of Illinois. Most species were represented by only a single specimen, and most were poorly recorded as to horizon and locality. Many were simply labeled “Chester Series, Randolph County, Illinois.” Topotypes cannot be established for these specimens and populations are needed to distinguish many of the forms properly.

The generic criteria used by Sutton & Winkler (1940, p. 545) were “the number of rami, the
character of the rami, and the number of plates in the posterior interray of the dorsal cup.” Cups with biserial arms were placed in *Eupachycrinus* if they had three plates of the anal series within the cup, and in *Intermediacrinus* if only two plates were present. Cups with three anal plates, and uniserial arms were placed in *Phanocrinus* if the first primibrach was axillary and in *Pentaramicrinus* if the first primibrach was not axillary.

Cups with three anal plates but without associated arms could not be identified using Sutton & Winkler’s classification and so such specimens were assigned to a collective group which they named *Ageneracrinus*. Because *Intermediacrinus* was the only genus of this group known to have two anal plates within the cup, species with two anal plates in the cup and lacking arms were placed in *Intermediacrinus*.

Based on some new materials, additional stratigraphic information, and a study of type specimens, the present paper provides additional discussion and reassignment of some of the species and genera covered in Sutton & Winkler’s study. Species of the collective group *Ageneracrinus* are assigned to valid genera.

The criteria for restriction and revision of the genus *Eupachycrinus* by Kirk (1937, p. 599) are largely accepted by us. Kirk predicted that forms would be found showing derivation of *Ethelocrinus* from *Eupachycrinus*. Sutton & Winkler also believed that *Ethelocrinus* evolved from *Eupachycrinus*, and further interpreted their new genus *Intermediacrinus* as an evolutionary step between the two. They stated (1940, p. 546), “This therefore represents a stage in the progression from forms with three anal plates in the dorsal cup to those in which but one remains. Species in this stage of the evolution of this group are placed in a new genus *Intermediacrinus*.” Bassler & Moodey (1943, p. 524) listed *Intermediacrinus* in synonymy with *Eupachycrinus*. If only the anal plates were involved in the differentiation between *Eupachycrinus* and *Intermediacrinus*, we would agree. However, the arm structure of *I. asperatus* (Worthen, 1882), the type species of the genus, varies from that of typical *Eupachycrinus* (type species, *Graphiocrinus quatuordecembrachiatius* Lyon, 1857). *Intermediacrinus* is accepted as a valid genus in our study based on characters of the arm structure in the type species, and is discussed later in this paper.

*Eupachycrinus spartarius* Miller (1879), was assigned to *Intermediacrinus* by Sutton & Winkler because it has only two anal plates in the dorsal cup. This species has the arm structure of *Eupachycrinus*, and is probably synonymous with *E. irregularis* Sutton & Winkler (1940), *E. germanus* Miller (1879), and *E. durabilis* (Miller & Gurley, 1895). These species are reported from the Chester Series of Pulaski County, Kentucky. They are probably from the well-known Glen Dean horizons of that area from which most of the early collections were made. *E. spartarius* would be the senior synonym. Specimens of *E. durabilis* probably represent juvenile forms of *E. spartarius*. Recent collections have shown that members of *Intermediacrinus*, as restricted here, come from lower Chesteran horizons. The lower stratigraphic occurrence of *Intermediacrinus* does not supply evidence that the genus may be an intermediate step from *Eupachycrinus* to *Ethelocrinus*.

Previous authors have noted that the number of arms in *Phanocrinus* is variable. Kirk placed five- and ten-armed forms in the genus. Sutton & Winkler allowed both nine- and ten-armed forms to be placed in *Phanocrinus*, but assigned five-armed forms to *Pentaramicrinus*. They stated (1940, p. 546), “These nine-armed forms are considered to be so closely allied to the ten-armed that it is unnecessary to place them in another genus. If there were a definite progression in arm number from five to nine, it would be impracticable to make the proposed division. However, since no six-, seven-, or eight-armed forms are known, it seems feasible and desirable to classify the uniserial forms into two genera, one with five arms and one to include nine- and ten-armed species.”

Particular cup characters have not been considered by previous authors. If all forms having a smooth cup and nearly vertical radial arms were removed from *Phanocrinus*, those left would all have ten arms. Cup characters of the removed group most nearly resemble *Pentaramicrinus* and forms of this assemblage are here referred to that genus.

The anal sac of *Phanocrinus cooksoni* Laudon (1941) is known to terminate with a single long spine. *P. irregularis* Strimple (1951), from the Pitkin Limestone of Oklahoma, and several similar forms found by us in the Golconda Formation of Union County, Illinois, and the Bangor Lime-
stone of Blount County, Alabama, also are terminated by a single long spine. The anal sac of several forms here referred to Pentaramicrinus are terminated by two lateral rows of spines.

Phanocrinus, as presently considered, usually has three anal plates within the cup. However, populations exhibit some variation in number and arrangement of the anal plates. The radial is usually prominent and distally elongate. Pentaramicrinus also has three anal plates in the cup. Populations exhibit little variation in number and arrangement of the plates. The radial is usually the largest plate, but the other anals also are prominent.

Phanocrinus represents a well-established lineage during Chesteran time. All known species of Phanocrinus have ten arms. Pentaramicrinus seems to be a variable stock with abnormalities occurring within its members. Species are known with five, nine, or ten arms. A specimen (SUI 32556) with six radials has been observed from the Bangor Limestone of Alabama. Each radial of this crinoid bears an axillary first primibrach. Another specimen (UMMP 56564) from the Glen Dean of Kentucky has several extra anal plates within the cup. It has six arms, the first primibrach of the ray being axillary.

We presently consider Phanocrinus fragosus Sutton & Winkler (1940), P. compactus Sutton & Winkler (1940), P. nitidus (Miller & Gurley, 1894), P. inflatoramus Sutton & Winkler (1940), and P. petalloformis Sutton & Winkler (1940), as species of Pentaramicrinus.

Pentaramicrinus magnaradianalis Sutton & Winkler (1940) and P. pulaskiensis (Miller & Gurley, 1895) are here considered to be synonyms of Pentaramicrinus gracilis (Wetherby, 1880). The forms vary only in arrangement of plates in the anal series. Holotypes of each species are reported from the Chester Series of Pulaski County, Kentucky. The specimens are probably from the very fossiliferous and well-known Glen Dean horizons of that area.

Webster & Lane (1967, p. 26), recently have described and assigned a form from the Permian of Nevada to Phanocrinus as Phanocrinus? insolitus. Since the genus is not known at all in the Pennsylvanian, it is not likely to have survived to Permian time. Some Pennsylvanian forms with ten uniserial arms, low cup, and retaining three anal plates appear to be related to the decadocrinids. Until more information is available, the species are questionably left under Phanocrinus.

Ageneracrinus was established as a collective group for the reception of "those forms in which a definite type of dorsal cup occurs but for which no arms are known" (Sutton & Winkler, 1940). The type of dorsal cup referred to is a simple invaginated bowl which incorporates three plates of the anal series within the cup. Specimens with only two plates and without any brachial series were placed in Intermediacrinus. The species I. pentalobus (Hall, 1858) and I. tumidus Sutton & Winkler (1940), were the only cups without arms that Sutton & Winkler assigned generically. Ageneracrinus thus received a variety of similar but unrelated cups and a redundancy of some previously described species which were based on more complete specimens and assigned to valid genera.

Ageneracrinus basalis Sutton & Winkler (1940) and A. altacalyx Sutton & Winkler (1940) are considered in this paper to be species of Pentaramicrinus. A. basalis may be synonymous with P. petalloformis (Sutton & Winkler, 1940). Both are from lower Chesteran horizons in the same region. A growth series of specimens will have to be collected before this can be established definitely. A. altacalyx is here assigned to Pentaramicrinus because it has a smooth cup with erect sides and a deep basal invagination. The cup is proportionally deeper than other species assigned to Pentaramicrinus.

Ageneracrinus subtumidus (Worthen, 1873), A. platycalyx Sutton & Winkler (1940), and A. basalotumidus Sutton & Winkler (1940), are now assigned to Intermediacrinus, because they have tumid basal and radial plates, and because they share general cup characters with I. variabilis. A. subtumidus is reported from a lower Chesteran horizon, as are other known occurrences of species here assigned to Intermediacrinus.

Ageneracrinus parvaradialanlis Sutton & Winkler (1940) has a very low dorsal cup with outward-sloping radial facets. The basal and radial plates are ornamented by granulations and ridges, and a few proximal columnals appear to be pentagonal. The species is here tentatively placed in Linocrinus Kirk, 1938.

Ageneracrinus parvabasalis Sutton & Winkler (1940) is considered to be synonymous with Phanocrinus parvaramus Sutton & Winkler (1940), both described in the same paper. P. parvaramus is a more complete specimen and we
TABLE 1. Generic Assignments Made in This Paper of Species Studied by Sutton & Winkler (1940).

<table>
<thead>
<tr>
<th>SPECIES RECORDED BY SUTTON &amp; WINKLER</th>
<th>GENERIC ASSIGNMENT HEREIN</th>
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<tbody>
<tr>
<td>Ageneracrinus altacalyx Sutton &amp; Winkler, 1940</td>
<td>Pentaramicrinus</td>
</tr>
<tr>
<td>Ageneracrinus basalis Sutton &amp; Winkler, 1940</td>
<td>Pentaramicrinus</td>
</tr>
<tr>
<td>Ageneracrinus basaltotumidus Sutton &amp; Winkler, 1940</td>
<td>Intermediacrinus</td>
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<tr>
<td>Ageneracrinus parebasisal Sutton &amp; Winkler, 1940</td>
<td>Phanocrinus</td>
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<tr>
<td>Ageneracrinus pareradialantic Sutton &amp; Winkler, 1940</td>
<td>Linocrinus</td>
</tr>
<tr>
<td>Ageneracrinus platycalyx Sutton &amp; Winkler, 1940</td>
<td>Intermediacrinus</td>
</tr>
<tr>
<td>Ageneracrinus subtumidus (Worthen, 1873)</td>
<td>Intermediacrinus</td>
</tr>
<tr>
<td>Ageneracrinus tumidorousis Sutton &amp; Winkler, 1940</td>
<td>Exochocrinus, n. gen.</td>
</tr>
<tr>
<td>Ageneracrinus tumulosus (Miller, 1892)</td>
<td>Exochocrinus, n. gen.</td>
</tr>
<tr>
<td>Eupachycrinus boydii Meck &amp; Worthen, 1870</td>
<td>Eupachycrinus</td>
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<tr>
<td>Eupachycrinus durabilis (Miller &amp; Gurley, 1895)</td>
<td>Eupachycrinus</td>
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<tr>
<td>Eupachycrinus germanus Miller, 1879</td>
<td>Eupachycrinus</td>
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<tr>
<td>Eupachycrinus irregularis Sutton &amp; Winkler, 1940</td>
<td>Eupachycrinus</td>
</tr>
<tr>
<td>Eupachycrinus quatuordecembrachialis (Lyon, 1857)</td>
<td>Eupachycrinus</td>
</tr>
<tr>
<td>Intermediacrinus asperatus (Worthen, 1882)</td>
<td>Intermediacrinus</td>
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<tr>
<td>Intermediacrinus pentalobus (Hall, 1858)</td>
<td>Intermediacrinus</td>
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<tr>
<td>Intermediacrinus spartanus (Miller, 1879)</td>
<td>Eupachycrinus</td>
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<tr>
<td>Intermediacrinus tumidus Sutton &amp; Winkler, 1940</td>
<td>Intermediacrinus</td>
</tr>
<tr>
<td>Intermediacrinus varialis Sutton &amp; Winkler, 1940</td>
<td>Intermediacrinus</td>
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<tr>
<td>Pentaramicrinus gracilis (Wetherby, 1880)</td>
<td>Pentaramicrinus</td>
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<tr>
<td>Pentaramicrinus magnaradianalis Sutton &amp; Winkler, 1940</td>
<td>Pentaramicrinus</td>
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<tr>
<td>Pentaramicrinus pulaskiensis (Miller &amp; Gurley, 1895)</td>
<td>Pentaramicrinus</td>
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<tr>
<td>Phanoerinus bellulus (Miller &amp; Gurley, 1894)</td>
<td>Phanoerinus</td>
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<tr>
<td>Phanoerinus compactus Sutton &amp; Winkler, 1940</td>
<td>Pentaramicrinus</td>
</tr>
<tr>
<td>Phanoerinus cylindricus (Miller &amp; Gurley, 1894)</td>
<td>Phanoerinus</td>
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<tr>
<td>Phanoerinus formosus (Worthen, 1873)</td>
<td>Phanoerinus</td>
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<tr>
<td>Phanoerinus fragosus Sutton &amp; Winkler, 1940</td>
<td>Pentaramicrinus</td>
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<tr>
<td>Phanoerinus inflatoramus Sutton &amp; Winkler, 1940</td>
<td>Pentaramicrinus</td>
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<tr>
<td>Phanoerinus maniformis (Yandell &amp; Shumard, 1847)</td>
<td>Phanoerinus</td>
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<tr>
<td>Phanoerinus nitidus (Miller &amp; Gurley, 1894)</td>
<td>Pentaramicrinus</td>
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<tr>
<td>Phanoerinus paravarius Sutton &amp; Winkler, 1940</td>
<td>Phanoerinus</td>
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<tr>
<td>Phanoerinus petaliformis Sutton &amp; Winkler, 1940</td>
<td>Pentaramicrinus</td>
</tr>
<tr>
<td>Phanoerinus supratumulosus Sutton &amp; Winkler, 1940</td>
<td>Staphylocrinus, n. gen.</td>
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</table>

consider A. parvabasalis to be a junior synonym. P. parvaramus may be synonymous with P. cylindricus (Miller & Gurley, 1894). Populations and growth series have not been studied, and a synonymy cannot be verified or disproved at this time.

Ageneracrinus tumulosus (Miller, 1842) and A. tumidorousis Sutton & Winkler (1940) are presently considered synonyms. The latter is a larger species and bears coarser ornamentation, a character which might be expected on a larger individual. A. tumidorousis is considered to be the junior synonym. The protuberant basals and radials set these forms apart from other described genera. The infrabasals are fused and the stem impression is small, suggesting that it was of little importance. The genus Exochocrinus is here proposed for these forms and A. tumulosus is designated as its type species.

The arm structures of two European species
assigned to *Eupachycrinus* by Wright (1951, p. 91, 92), are not known. Based on general cup characters, the species are better assigned to different genera. *E. vapidus* Wright (1951) has large swollen basals which are coarsely granular. The infrabasal disc is not visible in side view because of the swollen basals. The species shares the above features with *Exochocrinus* the holotype of which has fused infrabasals, and is assigned to that genus. The infrabasals of *E. vapidus* are not described as being fused.

The infrabasals of *Eupachycrinus macneanensis* Wright (1951) are visible in a side view of the dorsal cup, whereas those of *Eupachycrinus* are not. The infrabasals of this species are also much larger than in species now assigned to *Eupachycrinus*. The infrabasals of a new genus described by Strimple & Watkins (in press) are large and sometimes visible in a side view. The genus also has three anal plates within the dorsal cup. Wright's species is tentatively referred to the new genus.

Charles Copeland of the Alabama Geological Survey has sent us a specimen like *Phanocrinus supratumulosus* Sutton & Winkler (1940), collected by M. L. Bulger from Gasper (Chesteran) rocks in Morgan County, Alabama. Further investigations in the area by Copeland, Alan Horowitz of the University of Indiana, members of the Spencer Waters family of Moulton, Alabama, and by us have yielded a dozen good specimens. Several of them have portions of the arms preserved. The arms are known to branch several times above the axillary first primibrachs. The extra branching of the arms and a fused infrabasal disc separates these forms from *Phanocrinus*. We here propose a new genus, *Staphylocrinus*, for the reception of *P. supratumulosus* and *S. bulgeri* Burdick & Strimple, n. sp., the latter being designated as the type species.

Species included in Sutton & Winkler's study of 1940, and members of their collective group *Ageneracrinus*, are arranged in an alphabetical list in Table 1 for correlation with generic assignments of the forms as interpreted in this paper. Additional species not included in their study are similarly recorded in Table 2. The listing is based on some new collections, more precise stratigraphic information, and a study of Sutton & Winkler's types.

**TERMINOLOGY**

Most of the morphological terms used in the present study are fairly well standardized in modern usage. In the dorsal cup the proximal cirlet of plates are infrabasals, followed above

<table>
<thead>
<tr>
<th>Additional Species</th>
<th>Generic Assignment Herein</th>
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<tbody>
<tr>
<td><em>Eupachycrinus macneanensis</em> Wright, 1951</td>
<td>Strimple &amp; Watkins, n. gen.</td>
</tr>
<tr>
<td><em>Eupachycrinus monroensis</em> Worthen, 1882</td>
<td>Intermediacrinus</td>
</tr>
<tr>
<td><em>Eupachycrinus vapidus</em> Wright, 1951</td>
<td>Exochocrinus</td>
</tr>
<tr>
<td><em>Intermediacrinus modernus</em> (Strimple, 1951)</td>
<td>Eupachycrinus?</td>
</tr>
<tr>
<td><em>Phanocrinus alexanderi</em> Strimple, 1948</td>
<td>Phanocrinus</td>
</tr>
<tr>
<td><em>Phanocrinus altus</em> Wright, 1942</td>
<td>Phanocrinus</td>
</tr>
<tr>
<td><em>Phanocrinus ardrosenii</em> (Wright, 1934)</td>
<td>Phanocrinus</td>
</tr>
<tr>
<td><em>Phanocrinus calyx</em> (McCoy, 1849)</td>
<td>Phanocrinus</td>
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<tr>
<td><em>Phanocrinus cooksoni</em> Laudon, 1941</td>
<td>Phanocrinus</td>
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<tr>
<td><em>Phanocrinus gordoni</em> Wright, 1939</td>
<td>Phanocrinus</td>
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<tr>
<td><em>Phanocrinus insolitus</em> Webster &amp; Lane, 1967</td>
<td>Phanocrinus?</td>
</tr>
<tr>
<td><em>Phanocrinus irregularis</em> Strimple, 1951</td>
<td>Phanocrinus</td>
</tr>
<tr>
<td><em>Phanocrinus modulus</em> Strimple, 1951</td>
<td>Pentaramicrinus</td>
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<tr>
<td><em>Phanocrinus ornatus</em> Wright, 1951</td>
<td>Phanocrinus</td>
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<tr>
<td><em>Phanocrinus scotti</em> (de Koninck, 1858)</td>
<td>Phanocrinus</td>
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<tr>
<td><em>Phanocrinus stellaris</em> Wright, 1934</td>
<td>Phanocrinus</td>
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</tbody>
</table>

**Table 2. Generic Assignments Made in This Paper of Additional Species Not Reported by Sutton & Winkler (1940).**
by a basal circket and a radial circket. The posterior interray (CD interray) is occupied by extra plates called anal plates, mostly in the radial circket; usually they are three in number and are termed radianal, anal \( X \), and right tube plate. The first brachial of the arm is designated primibrach \( I \). If subsequentbranching occurs, the first plate of the second series is secundibrach \( I \), and that of a third branching tertibrach \( I \). Orientation of the cup follows terminology devised by Carpenter and adopted by Moore (1962), for use in the forthcoming Part T, Echinodermata 2 (Crinoidea), of the Treatise on Invertebrate Paleontology. Looking at the dorsal cup from the summit or upper side, the anterior ray is designated \( A \). Moving clockwise, the next ray is \( B \), and others in succession \( C, \), \( D \), and \( E \).

REPOSITORIES

New material referred to in the present study is reposited in 1) the Repository, Department of Geology, University of Iowa (SUI), Iowa City; 2) University of Michigan, Museum of Paleontology (UMMP), Ann Arbor; 3) Department of Geology, Indiana University (IU), Bloomington; and 4) Geological Survey of Alabama Type Collection (GSATC), University. 5) Other specimens referred to are from the Walker Museum collections (WM), now reposited at the Field Museum of Natural History, Chicago.

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SYSTEMATIC DESCRIPTIONS

Family EUPACHYCRINIDAE Miller, 1889

Genus EUPACHYCRINUS Meek & Worthen, 1865


_Type species._—_Graphiocrinus quatuordecembrachialis_ Lyon, 1857, p. 477, pl. I, fig. 2-26, by original designation.

_Diagnosis._—Dorsal cup low bowl-shaped, with deep basal invagination containing infrabasal circket in its deepest part; normally 3 anal plates in CD interray; anal sac elongate, terminating in single long spine. Arms biserial; primibrach 1 axillary in all rays; secundibrach 1 axillary on right side of \( B \) and \( C \) rays, and left side of \( D \) and \( E \) rays.

_Included species._—Based on assignment of holotype specimens to genus: _Eupachycrinus boydii_ Meek & Worthen, 1870; _E.? modernus_ Strimple, 1951; _E. quatuordecembrachialis_ (Lyon, 1857); _E. asperatus_ Miller, 1879 (=_E. durabilis_ (Miller & Gurley, 1895); _E. germanus_ Miller, 1879; _E. irregularis_ Sutton & Winkler, 1940).

Occurrence.—Upper Mississippian (Chesteran), North America.

Genus INTERMEDIACRINUS Sutton & Winkler, 1940


_Type species._—_Eupachycrinus asperatus_ Worthen, 1882, p. 34; by original designation.

_Diagnosis._—Crown elongate and compact; dorsal cup medium bowl-shaped, with deep basal invagination; anal plates 2 or 3 in CD interray; anal sac elongate, usually terminated by single elongate spine. Rays with 2 to 4 biserial arms (\( C \) ray most commonly with 4 arms and \( A \) ray 2 arms); primibrach 1 axillary in all rays; secundibrach 1 axillary in some rays.

Remarks.—Intermediacrinus was originally defined as part of “an evolutionary series leading from the five-armed uniserial forms [Pentaramicrinus Sutton & Winkler, 1940] with three anal plates in the dorsal cup to the 12- to 18-armed biserial forms with but one anal in the cup” [Ethelocrinus Kirk, 1939] (Sutton & Winkler, 1940, p. 560). Forms assigned to Intermediacrinus...
have 2 plates of the anal series within the cup and were thought to represent an evolutionary series relating Eupachycrinus (3 anal plates), and Ethelocrinus (1 or 2 anal plates). Differentiation between Eupachycrinus, Intermediacrinus, and Ethelocrinus then would rest on supposition that anal plates had migrated to a permanent position outside the dorsal cup or were resorbed during early ontogeny. This is not supported by the stratigraphic occurrence of these forms.

When Kirk described Ethelocrinus, he believed that forms would be discovered which would relate it to Eupachycrinus. He wrote: “Judging by the trend in the derived genus Ethelocrinus, it is possible that within Eupachycrinus forms will be found in which four rami to a ray occur” (Kirk, 1939, p. 599). Sutton & Winkler interpreted Intermediacrinus as representing such transitional forms, for this genus has 4 arms in the C ray and described forms have only 2 anal plates within the dorsal cup.

Sutton & Winkler’s study was based on a few individual specimens. Population studies of some Chesteran (Viséan) crinoid species by Wright (1926, p. 145-164) and Strimple (1948, p. 491-493) have shown a wide variance in the character and arrangement of anal plates within the dorsal cup. Recognition of this variance prompted Moore & Laudon (1943, p. 62), and Bassler & Moodey (1943, p. 470) to place Intermediacrinus in synonymy with Eupachycrinus. Its suppression was also prompted by the fact that Sutton & Winkler included Eupachycrinus spartarius in Intermediacrinus. E. spartarius is contained in many crinoid collections as a common and typical representative of the genus. The species is referred to Eupachycrinus in this study also.

Strimple (1961, p. 79, 80, 81) accepted Intermediacrinus as a valid genus because he considered the arm structure of the type species, I. asperatus (Worthen, 1882), to be different from that observed in species assigned to Eupachycrinus. Strimple’s representation of the arm structure of I. asperatus is erroneous, for the left posterior (D-ray) position should read 2-1, and the right posterior (C-ray) should read 2-2. He noted (1961, p. 81) that “the new generic concept does not allow for the inclusion of Eupachycrinus spartarius Miller which has bifurcation of the arms that is typical of Eupachycrinus.” Strimple thought that Intermediacrinus evolved into Ethelocrinus, and that Eupachycrinus represented another related lineage.

In this study, Intermediacrinus is accepted as a valid genus because of its arm structure, with 4 arms in the C ray, instead of 3, as in Eupachycrinus. Forms with 4 arms in the C ray are known also from Gasper strata in Alabama and Illinois. The number of arms and the pattern of branching varies slightly within the population from Illinois, but the character of having 4 arms in the C ray is consistent.

The arm structure of Eupachycrinus modernus Strimple, (1951b), does not allow it to be placed readily either in Eupachycrinus or Intermediacrinus. The form may not be a typical individual or it may be indicative of a lineage which paralleled Eupachycrinus and developed into an ethelocrinid stock, as postulated by Strimple. Collection of further specimens will be necessary before this can be determined.

In species of Intermediacrinus in which the nature of arm branching is known (I. asperatus, I. variabilis Sutton & Winkler, 1940, and I. davidsoni Burdick & Strimple, n. sp.), its pattern seems to be unstable. Normally, arm characters are paired, with features of the B ray a mirror image of the E ray, and those of the C ray matched by the D ray. Abnormalities may occur in the A ray. In Intermediacrinus, the C and D rays are not paired, for 4 arms occur in the C ray and only 3 in the D ray.

Most likely, a species of Eupachycrinus did not evolve into Intermediacrinus. Known stratigraphic occurrences of the two genera do not support the evolutionary series postulated by Sutton & Winkler, for Intermediacrinus is found lower than Eupachycrinus. Intermediacrinus is known from the Renault and Paint Creek Formations (Gasper age) and Eupachycrinus has been reported definitely only from the Glen Dean (Horowitz, 1965, p. 12, 34-35). Other specimens referred to Eupachycrinus are reported from Sloans Valley, Pulaski County, Kentucky, and most likely are from the well-known Glen Dean horizons of that area.

Intermediacrinus davidsoni Burdick & Strimple, n. sp., comes from Gasper strata in Colbert County, Alabama. The species is represented by three specimens in which the arms have a characteristic pattern of branching. The species could have evolved into a eupachyrinid by losing one of the posterior arms in the C ray. The C and D
rays would then be paired and the form would seem more stabilized. Specimens of *I. variabilis*, collected from lower Paint Creek strata on Carr Fic., forms stabilized a eupachycrinid branching pattern and others went on to develop into an ethelo-

and going through a variable adaptive radiation. Some variable pattern of branching in the arms. It is probable that forms assigned to *Intermediacrinus* went through a variable adaptive radiation. Some forms stabilized a eupachycrinid branching pattern and others went on to develop into an ethelo-

*Intermediacrinus davidsoni* would then be paired and the form would seem more stabilized. Specimens of *I. variabilis*, collected from lower Paint Creek strata on Carr Fic., forms stabilized a eupachycrinid branching pattern and others went on to develop into an ethelo-

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diagrammatic representation of arm structure of *Intermediacrinus davidsoni* Burdick & Strimple, n. sp. [Axillary secundibrachs stippled. Letters indicate Carpenter designations of rays.]

**Fig. 1.** Diagrammatic representation of arm structure of *Intermediacrinus davidsoni* Burdick & Strimple, n. sp. [Axillary secundibrachs stippled. Letters indicate Carpenter designations of rays.]

Included species.—Here assigned to *Intermediacrinus* are: *I. asperatus* (Worthen, 1882); *I. basaltotumidus* (Sutton & Winkler, 1940), Burdick & Strimple, n. comb.; *I. davidsoni* Burdick & Strimple, n. sp.; *I. monroensis* (Worthen, 1882), Burdick & Strimple, n. comb.; *I. pentalobus* (Hall, 1858), Burdick & Strimple, n. comb.; *I. platycalyx* (Sutton & Winkler, 1940), Burdick & Strimple, n. comb.; *I. subtumidus* (Worthen, 1873), Burdick & Strimple, n. comb.; *I. tumidus* Sutton & Winkler, 1940; *I. variabilis* Sutton & Winkler, 1940.

**Occurrence.**—Upper Mississippian (Chesteran), North America (United States).

**INTERMEDIACRINUS DAVIDSONI** Burdick & Strimple, n. sp.

*Figure 1; Plate 1, figures 10-12*

**Diagnosis.**—Cup plates slightly tumid. Two arms in *A* ray, 3 in *B* ray, 4 in *C* ray, 3 in *D* ray, and 3 in *E* ray.

**Description.**—Crown elongate, compact; dorsal cup medium bowl-shaped, with deep basal invagination, appearing slightly constricted distally, cup plates thick, smooth, and slightly tumid; depth of basal invagination equivalent to about 0.5 height of cup; infrabasals small, downflared, and confined to proximal portion of basal invagi-

**Intermediacrinus davidsoni** Burdick & Strimple, n. sp., differs from *I. asperatus* (Worthen, 1882) in characters of the dorsal cup and nature of the arms (Fig. 1). *I. davidsoni* has cup plates that are only slightly tumid, whereas those of *I. asperatus* are extremely tumid. The arms in the *B* and *E* rays of *I. asperatus* do not branch on secundibrach 1 as in *I. davidsoni*.

**Name.**—This species is named for DONALD B. DAVIDSON, presently of Cedar Rapids, Iowa, who collected the types.

**Occurrence.**—The types are from the Southward Pond Formation (Gasper age, Morse, 1930) and were collected about 1.5 miles southwest of Margerum, Alabama, on the north side of Pennywinkle Creek. The locality is an eroding hillside, in the woods and to the west of the blacktop road which leads to Allsboro, Alabama (W 1/2, SW 1/4, SE 1/4, Sec. 34, T. 3 S., R. 15 W., Margerum, Ala.-Miss. 7%4' Quad.)

**Types.**—The holotype (SUI 32469) consists of a nearly complete, but crushed crown. One paratype (SUI 32470) consists of a crushed dorsal cup with the proximal portion of the arms attached and another (SUI 32471) of a dorsal cup slightly deformed by compaction.

**Measurements of holotype in millimeters.**—Height of crown (as preserved), 44.8; maximum width of cup, 18.6; minimum width of cup, 10.8; height of cup (slightly distorted), 5.2; length of *AB* basal, 4.7; width of *AB* basal, 4.7; length of *A* radial, 4.6; width of *A* radial, 7.4.
Family ERISOCRINIDAE Miller, 1889

Genus PHANOCRINUS Kirk, 1937


Type species — Zeearinus formosus Worthen, 1873, p. 549, pl. 21, fig. 2, by original designation.

Diagnosis. — Dorsal cup low bowl-shaped, with proximal invagination which involves infrabasals and proximal portions of basals, and bears 10 uniserial arms with primibrach 1 axillary in all rays; commonly 3 anal plates within cup; radials generally touching basal plane and curving upward from it (not vertical); distal portion of anal sac bearing single elongate spine.

Included species. — Described holotype specimens referred to Phanocrinus represent the following species: P. alexanderi Strimple, 1948; P. altus Wright, 1942; P. ardrossensis (Wright, 1934); P. bellulus (Miller & Gurley, 1894); P. calyx (M'Coy, 1849); P. cooksoni Laudon, 1941; P. cylindricus (Miller & Gurley, 1894); P. formosus (Worthen, 1873); P. gordonii Wright, 1939; P. irregularis Strimple, 1951a; P. maniforis (Yandell & Shumard, 1847); P. ornatus Wright, 1951; P. parvaramus Sutton & Winkler, 1940 (= P. parvabasalis (Sutton & Winkler, 1940); P. scotica (de Koninck, 1858); P. stellaris Wright, 1934.

Occurrence. — Upper Mississippian (St. Genevieve—Chesterian), North America (United States); Lower Carboniferous (Viséan), Europe (Britain); Upper Carboniferous (Namurian), Europe (Britain).

Genus PENTARAMICRINUS Sutton & Winkler, 1940

Pentaramicrinus Sutton & Winkler, 1940, p. 558.

Type species. — Cromyocrinus gracilis Wetherby, 1880, p. 248, pl. 16, fig. 2-2c; by original designation.

Diagnosis. — Dorsal cup low bowl-shaped, with deep basal invagination, and bearing 5 to 10 uniserial arms; rays that branch axillary on primibrach 1; 3 anal plates in CD interray; radial plates nearly vertical, proximal portion not extending inward toward basal plane; infrabasals completely within invagination; 2 rows of spines extending over distal portion of anal sac.

Included species. — Here assigned to Pentaramicrinus are: P. altacalyx (Sutton & Winkler, 1940) Burdick & Strimple, n. comb.; P. basalis (Sutton & Winkler, 1940); Burdick & Strimple, n. comb.; P. compactus (Sutton & Winkler, 1940); Burdick & Strimple, n. comb.; P. fragusus (Sutton & Winkler, 1940); Burdick & Strimple, n. comb.; P. gracilis (Wetherby, 1880) (= P. magnaradi-analis (Sutton & Winkler, 1940); P. pulaskiensis (Miller & Gurley, 1895)); P. inflatoramn (Sutton & Winkler, 1940), Burdick & Strimple, n. comb.; P. modulus (Strimple, 1951); Burdick & Strimple, n. comb.; P. nitidus (Miller & Gurley, 1894); Burdick & Strimple, n. comb.; P. pittilloformis (Sutton & Winkler, 1940), Burdick & Strimple, n. comb.

Occurrence. — Upper Mississippian (Chesterian), North America (United States).

Family AGASSIZOCRINIDAE Miller, 1889

Two new genera are assigned to the Agassizocrinidae, Staphylocrinus and Exochocrinus. Both, like Agassizocrinus, are known only from Chesteran strata, have thick cup plates, uniserial arms, and a fused infrabasal circle. A rudimentary stem is fused within the infrabasal circle of mature members of Staphylocrinus. Strimple (1962, p. 187) has shown that some representatives of Agassizocrinus also exhibit a small stem fragment completely enclosed by the fused infrabasal circle. Arms of any specimens referable to Exochocrinus are unknown, and the infrabasal disc is not tumid, as it is in Agassizocrinus and Staphylocrinus. However, the infrabasal circle is fused and the very small stem impression indicates a stem which was probably nonfunctional.

Anartiocrinus Kirk, 1940, is probably not correctly placed within the Agassizocrinidae. Members belonging to this genus were once placed in Agassizocrinus. After they were described as a distinct genus, subsequent taxonomists classified them in the Agassizocrinidae without question. The forms have ten uniserial arms, and a smooth cup like some species of Agassizocrinus, but they have a large stem and the infrabasals show no tendency to fuse. Anartiocrinus is probably more correctly related to the Scytalocrinidae of which some members have ten uniserial arms, a smooth cup and a prominent stem.

Genus STAPHYLOCRINUS Burdick & Strimple, n. gen.

Type species. — Staphylocrinus bulgeri Burdick & Strimple, n. sp.

Diagnosis. — Crown consisting of medium, truncate, bowl-shaped cup, composed of very thick, tumid plates, and heavy uniserial, multiple branching arms; infrabasals nearly horizontal but slightly upflared, mature specimens fused and swelled, forming tumid projection below proximal plane of basals; 3 thick and tumid anal plates in CD interray; first bifurcation on primibrach 1.

Description. — Cup truncate medium bowl-
shaped, composed of smooth, very thick, and tumid plates; infrabasals slightly upflared, in mature specimens are fused into a pentagonal disc which approaches the size of basal plate of the same individual; basal plate as long and wide and extend to about 0.8 the height of the cup; radials about twice as wide as long, their length being equivalent to about 0.25 the height of the cup. There are 3 tumid plates in the CD interray. Articular facet slope slightly outward. Arms are stout, uniserial, and axillary in primibrach I and several other times within each ray.

Remarks.—The fused infrabasals and multiple branching of the arms separate this genus from Phanocrinus. The tumid nature of the fused infrabasals and their projection below the basals separate it from Exochocrinus Burdick & Strimple, new genus. It is possible that a specimen found without arms and with a completely fused (rounded) infrabasal disc could be mistaken for certain species of Agassizocrinus which have a low infrabasal circket. Mature specimens of Staphylocrinus have a dorsal cup much larger than that of Agassizocrinus and generally the interior portion of the fused infrabasal disc of Staphylocrinus is much broader. Some infrabasal cirlets show a remnant stem fused within the depression at the center of the infrabasals. Other specimens show the fused infrabasals swelled over a portion of the incorporated stem. A slight depression is still present in these forms. Larger and presumably more mature forms do not exhibit a proximal depression.

The size of the infrabasal circket apparently has no direct relationship to fusing over of the stem, for infrabasal discs of various sizes are found in all states of fusion. Apparently growth of the infrabasals over the stem depends on when the stem is broken off and how short it is broken. A stem a few millimeters longer will take more time for the infrabasals to grow over it.

Fusion of the infrabasals and thickening of the calyx plates are thought to have been necessary for survival of the crinoids in a wave-disturbed environment. In such circumstances, a stem was a hindrance and the animal had to exist free of a stem. The swelling of the infrabasals over the axial canal probably led to a strengthening of the calyx as well as to sealing off any irritation arising from an open canal.

Our interpretation of the ontogeny of Staphylocrinus is similar to that of some living crinoids which are attached by a column during early stages of development. Upon reaching a mature stage the forms separate from the column and become free-swimming. The presence of a rudimentary stem in Staphylocrinus supports this view. In Staphylocrinus the rapid growth and thickening of the infrabasals seems to have encased the outer diameter of the column. The encasement of the column presumably induced irritation or pressure, which caused the column to drop off, leaving a small portion of it impinged between the fused infrabasals. This was later enveloped by the still-enlarging infrabasals, and is visible only upon internal sectioning of the specimen.

EXPLANATION OF PLATE 1

FIGURE
1-6. Staphylocrinus bulgeri Burdick & Strimple, n. gen., n. sp.—1. Internal cross section of basal plate (SUI 32118) showing external growth rings, ×1.—2. Broken infrabasal circket (SUI 32121) showing fused plates and incorporated stem segment, ×1.5.—3. Paratype (SUI 32115), CD-interray view, ×0.8.—4. Paratype (SUI 32119), basal view of immature individual, ×1.—5. Paratype (GSATC 123), CD-interray view, ×1.—6. Holotype (SUI 32113), BC-interray view, ×1.
The name is derived from *staphyllos* (Greek) meaning a cluster of grapes and refers to the appearance of the dorsal cup.

**Included Species.**—Two species are here assigned to this new genus: *Staphylocrinus bulgeri* Burdick & Strimple, n. sp.; *S. supratumulosus* (Sutton & Winkler, 1940), Burdick & Strimple, n. comb.

**Occurrence.**—Specimens representing this genus are reported from the Chester Series of Randolph County, Illinois, and Gaper strata of Colbert and Morgan Counties, Alabama. The genus is thought to be restricted to lower Chesteran (Gaper).

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**STAPHYLOCRINUS SUPRATUMULOSUS** (Sutton & Winkler, 1940), Burdick & Strimple, n. comb.

Plate 1, figure 9

*Phanocrinus supratumulosus* Sutton & Winkler, 1940, p. 556, pl. 68, fig. 9-10.

**Diagnosis.**—Species of *Staphylocrinus* in which tumidity of each cup plate starts slightly to inside of plate margins. Small nodes or granulations are present on some plates.

**Remarks.**—The holotype is a poorly preserved and slightly disarticulated specimen consisting of a dorsal cup and a few of the lower brachials of several arms. In the original description, Sutton & Winkler stated that the basals were smooth. This is apparently a mistake because the basals and infrabasals bear a few low and irregularly spaced nodes. The radial plates have a large node near each lateral margin. Axillary plates commonly have a large conspicuous node on either side of their exterior, near the lateral margins, and another in distal position. Small nodes also occur on some of the other brachials. The plates of the dorsal cup are very tumid. The tumidity of the plates does not start at the suture as in *Staphylocrinus bulgeri* Burdick & Strimple, n. gen., n. sp., but slightly away from the suture, leaving a shallow trough which parallels all sutures of the dorsal cup. A small stem fragment is fused within a proximal invagination in the infrabasal disc. The holotype is the only known representative of this species.

**Occurrence.**—The holotype is from the Gurley collection no. 19132 in the University of Chicago collections, at the Field Museum of Natural History. The specimen is reported from the Chester Series of Randolph County, Illinois. Probably it comes from a low Chesteran horizon such as that of *Staphylocrinus bulgeri* Burdick & Strimple, n. gen., n. sp.

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**STAPHYLOCRINUS BULGERI** Burdick & Strimple, n. sp.

Figure 2B; Plate 1, figures 1-6

**Diagnosis.**—Tumidity of cup plates starting at their margins.

**Description.**—Dorsal cup medium bowl-shaped and truncate, with smooth, very thick plates, tumid to their margins; 3 anal plates within cup in normal position; infrabasals fused into nearly flat but slightly upflared pentagonal disc, which approaches size of basal plate from same specimen. In smaller and presumably less mature specimens, infrabasal disc is fused, but each infrabasal tumid, surrounding small stem. In larger discs, infrabasals lose their individual identity but depression remains at center of disc (Fig. 2b). In largest discs infrabasals individually tumid, without depression at center and no sign of stem.

Largest elements of cup are basals, about as long as wide and extending to 0.8 of cup height. Radials proportionally small for size of cup, with height approximately 0.25 that of cup, and about 0.5 of radial width; articular facets prominent, sloping outward, not extending full width of plates. Three anal in normal position within cup; right tube plate slightly smaller than anal X, which is about 0.5 size of radianal; nature of anal sac uncertain, but character of some of anal series above CD interray observed, proximal series being composed of large plates which are thick and tumid, size of plates decreasing both in size and thickness toward distal portion of sac.

Brachitaxes composed of thick uniserial segments which are individually tumid. Arms branching on primibrach 1 and several higher axillaries, with 2nd branching usually on secondibrach 6; axillary primibrachs about equal in size to radials of same individual. All facets within brachial series articulated.

**Remarks.**—*Staphylocrinus bulgeri* Burdick & Strimple, n. sp., has less tumid plates and lacks the distinctly arranged nodes of *S. supratumulosus* Burdick & Strimple, n. sp. Also, the tumidity of plates comprising the dorsal cup of *S. supratumulosus* does not start immediately at the sutures as in *S. bulgeri*.

**Name.**—This species is named for M. L. Bulger, of Prattville, Alabama, who collected a paratype and informed the Alabama Geological Survey of the locality.

**Occurrence.**—Types were collected from the Monteagle Limestone (Gaper age) in an inactive quarry on the H. C. Dunaway farm, about 10.5 miles east of Fort Yell, Alabama, and about 2 miles north of Bean Mountain.
Genus EXOCHOCRINUS Burdick & Strimple, n. gen.

Type species.—Eupachycrinus tumulosus Miller, 1892, p. 680, pl. 9, fig. 9-10.

Diagnosis.—Dorsal cup deep, truncate bowl-shaped, and except for infrabasals composed of very tumid plates; infrabasals fused into flat, nearly pentagonal disc which lies within proximal invagination formed by protuberant basal plates, basals largest elements of cup; 3 anal plates in CD interray.

Description.—See description of Exochocrinus tumulosus (Miller, 1892) below.

Remarks.—Exochocrinus Burdick & Strimple, n. gen., is assigned to the Agassizocrinidae because of its fused infrabasal disc and general resemblance to Staphylocrinus Burdick & Strimple, n. gen. Both are marked by tymid plates, have a similar cup shape, a generally flat-based visceral cavity, and slightly separated and outward sloping articular facets. Exochocrinus and Staphylocrinus seem more closely related to each other than to Agassizocrinus. Reasons for assigning Staphylocrinus to the Agassizocrinidae were stated in the discussion of that genus.

Exochocrinus has a flat infrabasal disc which lies within an invagination, and can be readily separated from Staphylocrinus which lacks such a basal invagination. Basal plates of Exochocrinus are more tymid than those of Staphylocrinus, and most cup plates bear coarse radial ornamentation.

Name.—The name of this new genus, derived from exos (Greek), refers to the extremely tymid nature of the basal and radial plates.

Included species.—Here assigned to Exochocrinus are: E. tumulosus (Miller, 1892), Burdick & Strimple, n. comb. [=E. tumidiorugosus (Sutton & Winkler, 1940)]; and E. vapidus (Wright, 1951), Burdick & Strimple, n. comb.

Occurrence.—Upper Mississippian (Chesterian), North America (United States); upper Lower Carboniferous (Viscan), Europe (Britain).

EXOCHOCRINUS TUMULOSUS (Miller, 1892)

Figure 2A: Plate 1, figures 7-8

Eupachycrinus tumulosus Miller, 1891, p. 70, pl. 9, fig. 9-10 (advance sheets); 1892, p. 680, pl. 9, fig. 9-10.

Ageneracrinus tumulosus Sutton & Winkler, 1940, p. 563-564, pl. 67, fig. 18-19.
Ageneracrinus tumidorugosus Sutton & Winkler, 1940, p. 566, pl. 68, fig. 20-21.

Diagnosis.—Characters of genus.

Description.—Dorsal cup bowl-shaped, truncate, and except for infrabasals, composed of very tumid plates. Cup about 0.6 as high as wide, with greatest width at about 0.5 height of cup, and near top of basals. Except for infrabasals, cup plates bear fine to coarse granules, some of which form confluent ridges exhibiting radial symmetry on each plate. Infrabasals fused into nearly flat pentagonal disc, which lies within proximal invagination formed by swollen basals, and is not visible in side view; dorsal cup about 4.5 times wider than infrabasal disc; circular impression left by proximal columnal occupying less than 0.5 width of infrabasal disc. Distal portions of basals extend to more than 0.7 height of cup. Length and width of basals, measured with calipers, about equal. In side or basal views tumidity of radials not protruding beyond that of basals; radials twice as wide as high, their articular facets sloping outward and separated by enlarged interfacet area. Three plates of anal series within cup in normal position, radianal largest and most tumid.

Remarks.—The radial symmetry exhibited by the granulations and ridges on the basals is not located at the center of the plates, as one may expect, but occupies a more distal and lateral position. This ornamentation is thought to represent rapid and less orderly secretion of calcite by the crinoid. Lateral enlargement of the basals would tend both to lower the center of gravity and provide a large base upon which the organism could rest. Thus, it would be oriented with the oral surface up in normal feeding position.

The stem impression of Exochocrinus tumulosus is very small, indicating a diminutive stem which probably was not functional. The swollen basals held individuals off the sea bottom so that irritation at the attachment was avoided, fusion and growth over the lumen being unnecessary.

The cumbersome shape and heavy nature of this crinoid seem prohibitive to any pelagic movement and probably Exochocrinus was adapted to a benthonic mode of life in its adult stage. The extremely thick plates and rigid nature of the cup probably are indicative of an environment within wave base.

Ageneracrinus tumidorugosus Sutton & Winkler is an incomplete dorsal cup herein considered to be a junior synonym of Exochocrinus tumulosus (Miller), Burdick & Strimple, n. comb. A. tumidorugosus is larger, bears coarser ornamentation, and has a deeper stem impression, such as is to be expected in larger specimens because of tendency for the infrabasals to grow around and over the stem. Larger specimen would then exhibit a deeper cavity if the stem were removed.

Occurrences.—Only 2 dorsal cups of the genus are known although the easily recognized basal plates are very common in some strata. The holotype is from the Chester Series of Breckinridge County, Kentucky, and another was described by Sutton & Winkler from Chesteran strata of Randolph County, Illinois. Basal plates ascribed to the genus occur in the Gasper-age portion of the Monteagle Limestone at several localities around Huntsville, Madison County, Alabama. Several well-preserved plates were collected by T. W. Cornell of Huntsville, Alabama. These specimens are from Chapman Mountain along U.S. Highway 72, about 2.5 miles northeast of Huntsville (NW 1/4, sec. 20, T. 3 S., R. 1 E., Meridianville Quad., Ala). Plates are also known to occur in the Huntsville Limestone of Arkansas and Oklahoma.

Types.—The holotype is no. 6240 in the Gurley Collection, labeled Eupachycrinus tumulosus Miller, now reposited in the Field Museum of Natural History. The second cup, designated Ageneracrinus tumidorugosus Sutton & Winkler, presently considered a junior synonym, is no. 39346 in the Gurley Collection, Field Museum of Natural History. A well-preserved basal plate from Huntsville, Alabama is IU 10580-5. Basal plates from the Huntsville Limestone Member of the Batesville Sandstone Formation, of Oklahoma and Arkansas, are SUI 32927 and SUI 32928, respectively.
SELECTED REFERENCES


Horowitz, A. S., 1965, Crinoids from the Glen Dean Limestone (Middle Chester) of southern Indiana and Kentucky: Indiana Geol. Survey Bull. 34, 52 p., 3 fig., 5 pl.


Wright, James, 1926, Notes on the anal plates of Eupachycrinus calyx and Zeacrinus konincki: Geol. Mag., v. 63, p. 145-164, text-fig. 1-90, pl. 15-17.