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# UNIVERSITY

# **GEOLOGY STUDIES**

Volume 19: Part 1— December 1972

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# Brigham Young University Geology Studies

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# Editor

Jess R. Bushman

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# Cheirocystella antiqua gen. et sp. nov. from the Lower Ordovician of Western Utah, and Its Bearing on the Evolution of the Cheirocrinidae (Rhombifera: Glyptocystitida).

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ABSTRACT.—The family Cheirocrinidae lies at the center of evolutionary radiation within the superfamily Glyptocystitida and evolved from *Macrocystella* the morphology of which is reviewed. Significant trends within the Cheirocrinidae include: loss of R5; development of open plate circlets; decrease in number of pectinirhombs which change from conjunct to disjunct and multi-disjunct; change from discrete to confluent dichopores; increase in length of ambulacra. Other trends lead to other families, including the Glyptocystitidae which, with the Cheirocrinidae, is revised.

Trends are unique or repeated: unique trends lead to the specialized Pleurocystitidae, repeated trends involve increase in functional efficiency. Trends are used to define new taxa. Six genera occur in the Cheirocrinidae. Homocystites Barrande has five radials and confluent dichopores. Acantholepis McCoy has multi-disjunct pectinirhombs; Coronocystis nov. has long ambulacra. All above characters are unique to the genera concerned. Cheirocystella nov. and Cheirocystis nov. have closed plate circlets: the former has conjunct rhombs, the latter disjunct. Cheirocrinus Eichwald has open circlets and disjunct rhombs. The Glyptocystitidae has two genera: Glyptocystites Billings with long ambulacra on thecal plates and Glyptocystella nov. with short ambulacra between thecal plates.

Cheirocystella antiqua sp. nov. is the oldest known cheirocrinid, from the Fillmore Limestone (Tremadoc). Type, or representative, species of other genera are described and figured.

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# INTRODUCTION

Through the kindness of Drs. L. F. Hintze, R. A. Robison and A. J. Rowell, I have been able to examine a collection of echinoderm material from the Lower Ordovician of western Utah, among which were specimens of a new cystoid. The new species, *Cheirocystella antiqua*, is particularly interesting

for the following reasons: (1) It is the first Ordovician cystoid reported from the western United States;<sup>1</sup> (2) it is undoubtedly the oldest pectinirhombbearing cystoid; and (3) it adds new information about the evolution (and hence taxonomy) of the family Cheirocrinidae. Knowledge of evolutionary trends within the Cheirocrinidae is particularly important since this family lies at the center of evolutionary radiation within the Glyptocystitida; the longest ranging of the three rhombiferan superfamilies. Regrettably little detailed information has been published on this subject: partly because many species of Cheirocrinidae have been described from isolated plates and hence are very poorly known and partly because most authors have referred all species to the single genus Cheirocrinus s.l. which has obscured important differences in morphology. In preparing a description of *Cheirocystella antiqua* I have been forced to review current knowledge of evolution within the Cheirocrinidae and to redescribe several other poorly understood species in this family and in the family Glyptocystitidae. For convenience, evolutionary trends are discussed in the first part of this paper and systematic descriptions are grouped together in the second section.

Material mentioned or used in this study is housed in the collections of the following institutions:

Field Museum of Natural History, Chicago (FMNH) Geological Survey of Canada, Ottawa, Canada (GSC) Museum of Comparative Zoology, Harvard University (MCZ) University of Cincinnati, Department of Geology (UC) University of Kansas, Museum of Paleontology (UK) University of Utah, Department of Geology (UU) United States National Museum (USNM).

My grateful thanks go to all those who loaned material for this study. Collections of the Utah materials were made possible by National Science Foundation grant GB-3154 to L. F. Hintze.

# EVOLUTION AND TRENDS

Before any evolutionary trend can be considered to be "well established," three criteria must be met: (1) All species (or specimens) involved in a supposed trend must be closely related; i.e., with regard to cystoids they must belong to the same family or superfamily. (2) A morphological series should be evident or, if just two end members of the trend are known, the trend should be repeated independently in several lineages. (3) The stratigraphic occurrence of the members of morphological series or repeated trends must be in accordance with the directions of the supposed trends. Notwithstanding the imperfections of the fossil record, it is the only independent test of the directions of trends deduced from morphological resemblances.

Strict application of the above criteria indicates that some of the trends outlined below are not "well established." This is largely due to the rarity of adequate specimens but also in some instances to inadequate information about specimens which are available. Hopefully a record of current knowledge will stimulate the search for new material and draw attention to the imperfections of old material.

<sup>&</sup>lt;sup>14</sup>Since this was written Sprinkle (U.S. Geol. Surv. Prof. Paper 750-D) has reported isolated cystoid plates from the Antelope Valley Limestone of Nevada and California."

Text-figure 1 represents a summary of the stratigraphic occurrence and supposed evolution of the superfamily Glyptocystitida, all families of which become established during the Ordovician. Subsequent evolution within the superfamily involved refinement of the more successful lineages. *Macrocystella* Callaway is the oldest known glyptocystitid genus and is taken as the starting point for all evolution within the superfamily. Although Paul (1968a) has described the morphology of *Macrocystella* in detail, a brief summary follows since it is of fundamental importance in glyptocystitid evolution.

# MORPHOLOGY OF MACROCYSTELLA

The skeleton of *Macrocystella* is divisible into a stem, a theca and a sub-vective (or ambulacral) system.

A. The stem consists of a proximal portion near the base of the theca and a distal portion. The former has a relatively large diameter and large lumen, tapers rapidly away from the theca and is composed of two types of *annular* columnals. Outer columnals alternate with an fit outside, inner columnals and have both internal and external flanges. The internal flanges of the outer columnals bear facets for articulation with fulcra on the inner columnals. The orientation of fulcral axes varies systematically in each pair of columnals, thus rendering the proximal stem extremely flexible (Paul, 1968a, p. 585, Text-figs. 1.2). The external flanges of the outer columnals are variously ornamented, a feature which is often useful in speciation (e.g., Chauvel, 1969, p. 28, Text-fig. 4). The distal stem is long, thin, whiplike, tapers relatively slowly and is composed of two types of *cylindrical* columnals. The larger columnals frequently bear external flanges and alternation of columnals becomes less obvious distally. The distal stem tapers to a point  $\frac{1}{2}$ - $\frac{1}{4}$  mm. in diameter; no attachment structure has ever been reported.



TEXT-FIGURE 1.—Stratigraphic distribution of families within the superfamily Glyptocystitida. Dashed lines indicate supposed phylogeny as far as it is known.



TEXT-FIGURE 2.—Analysis of plate arrangement in Macrocystella. A. Reconstruction of lower four circlets (based on Paul, 1968a, Text-fig. 3): B. Reconstruction of oral surface (based on Paul, 1968a, Text-fig. 11a). B1-B4 basals, g, gonopore: h, hydropore: IL1-IL5 infralaterals; L1-L5 laterals: R1-R6 radials: I-V ambulacra. 1-7 orals. Note that the first two brachiole facets branch to the left in ambulacra I and IV.

B. The theca is composed of 27 plates which are arranged in five circlets and are called basals (B, plural BB), infralaterals (IL, ILL), laterals (L, LL), radials (R, RR), and orals (O,OO). Individual plates are numbered clockwise around the theca, starting to the left of the gonopore and hydropore (Textfig. 2a). In *Macrocystella* all five plate circlets are closed, (i.e., they would form a complete ring if isolated from the theca). The plate formula is 4BB, 51LL, 5LL, 6RR, and 7OO. The plates are extremely thin and complexly folded. Folds are often more pronounced on B2 and in radial plates. Other plate "ornament" consists of fine granules. *Macrocystella* lacks pectinirhombs.

The lateral periproct is large and its frame is made by five thecal plates (1L4, 1L5, L1, L4 and L5). In life it was covered by a flexible plated pereproctal membrane within which an anal pyramid was developed. The genopore is a small circular pore and the hydropore a long narrow slit. Both are developed across the suture O1:O7, with the hydropore adoral to the gonopore (Text-fig. 2b).

C. The subvective system consists of five short ambulacra or arms which are confined to the flat, oral surface. They are numbered I-V clockwise, starting with the ambulacrum to the left of the gonopore and hydropore (Textfig. 2b). The ambulacra are composed of flooring plates which lie *between*, not on, the orals and form part of the thecal wall. This has not been reported before but it is evident in Paul, 1968a, p. 592, text-fig. 12, pl. 113, fig. 6. Three to five biserial brachioles arise from each ambulacrum and the first brachiole always branches to the left as viewed from the mouth. The first *two* brachioles branch to the left in ambulacra I and IV while ambulacra II, III, and V have regularly alternating brachioles throughout (Text-fig. 2b). Each ambulacrum is provided with a broad main food groove covered with alternating calcified cover plates in life. The five ambulacra meet at a central mouth.

All later Glyptocystitida are derived from this basic morphology by one or several transitions. The simplest transition is to some species of Cheirocrinidae, typified by the oldest known, *Cheirocystella antiqua*, which differ from *Macro*- cystella only in bearing pectinirhombs and in lacking complexly folded thecal plates.

#### TRENDS WITHIN THE CHEIROCRINIDAE

A variety of evolutionary trends is evident within the family Cheirocrinidae and additional trends lead directly to other families in the superfamily Glyptocystitida. These latter trends are mentioned for completeness but are not described in detail with the exception of those leading to the family Glyptocystitidae, which are particularly well documented in North American material. Parallel or repeated trends occur frequently, and where possible, functional interpretations of trends are offered.

#### Stem

In "pelmatozoans" a well-developed stem has generally been taken to indicate permanent fixture. This was not the case with *Macrocystella* (Paul, 1968a), the distinctive stem of which lacks any attachment structure and continues unchanged throughout the Cheirocrinidae. Although Jaekel (1899, Text-figs. 35, 41) illustrated holdfasts which he claimed belonged to *Cheirocrinus* s.l., there is no evidence that they really belong to this genus and no other worker has described an attached *Cheirocrinus* stem (see Bather, 1913, p. 440 §305). No trends are apparent. Indeed this stem is one of the most characteristic features of the entire superfamily. Holdfasts, which developed in the Callocystitidae (Uppermost Ordovician to Upper Devonian) and in at least one genus of Echinoencrinitidae (*Glansicystis* Paul), enabled cystoids to live in very shallow (?tidal-subtidal) environments with strong currents. However, the original function of the stem in the Glyptocystitida remains unknown.

# Theca

Trends involving the theca affect its shape, the number, arrangement and thickness of thecal plates, and the size of plate R2. Some of these trends, together with most of those affecting the pectinirhombs, can be explained in terms of protection and respiration; others are less readily explained. In cystoids the theca housed and hence protected most of the vital organs, but at the same time it restricted communication with the ambient seawater which provided the food and oxygen necessary for life. For efficient respiration the thecal wall should be as thin as possible; for protection it should be as strong (i.e., thick) as possible. Several trends are attempts to reconcile these conflicting requirements.

Thecal Shape.—Within the Cheirocrinidae the thecal shape varies only in the development of a domeshaped oral surface in *Coronocystis angulatus* (Wood). A significant trend toward thecal flattening occurs in the line which leads to the family Pleurocystitidae. This is correlated with the trend toward periproctal enlargement (see below) and the specialized mode of life of *Pleurocystites* (Paul, 1967b).

Plate Number.—Within the Cheirocrinidae the number of radial plates is reduced from six to five in the genus *Homocystites* Barrande (Text-figs. 3i, 16). Outside the family a similar reduction occurs within the Pleurocystitidae and in the line leading to the Echinoencrinitidae. The functional significance of this repeated trend is unknown. Plate Arrangement.—Two separate lines with open plate circlets become established in the evolution of the Cheirocrinidae. Macrocystella has all plate circlets closed and so does the oldest known cheirocrinid, Cheirocystella antiqua nov. However, the type species of Cheirocrinus, C. penniger (Eichwald), has open lateral and infralateral circlets (Text-fig. 3c) and Coronocystis has an open lateral circlet (Text-figs. 3f, 11, 13). These two developments of plate arrangements with some circlets open are apparently independent of each other. Other features of plate arrangement, and other trends, suggest that the family Glyptocystitidae was derived from the Coronocystis line but the Cheirocrinus s.s. line was apparently a blind offshoot. Increased knowledge of European species might reveal unsuspected descendants however.

Enlargement of R2.—This trend is correlated with the development of an open lateral circlet. It is apparently initiated within the Genus *Cheirocystis* nov. C. radiatus Jaekel (Text-fig. 3d) has a plate arrangement virtually identical to that of *Cheirocystella antiqua* nov. but *Cheirocystis anatiformis* (Hall) has a modified arrangement (still with all circlets closed) in which R2 is the largest radial (Text-fig. 3e). In *Coronocystis angulatus* (Text-fig. 3f) R2 meets IL2 along a common suture and hence the lateral circlet is open. In both *Glyptocystella* and *Glyptocystites* (Text-figs. 3g-h) R2 is greatly enlarged and the infralateral



TEXT-FIGURE 3.—Evolution of plate arrangements in the Macrocystellidae, Cheirocrinidae and Glyptocystitidae. A. Macrocystella mariae Callaway, B. Cheirocystella antiqua nov., C. Cheirocrinus penniger (Eichwald), D. Cheirocystis radiatus (Jaekel), E. Cheirocystis anatiformis (Hall), F. Coronocystis angulatus (Wood), G. Glyptocystella loeblichi (Bassler), H. Glyptocystites multiporus Billings, I. Homocystites alter Barrande. Basals white, infralaterals stippled, laterals horizontally ruled, radials white except that R5 is black. B, D-G represent new genera described herein and all but D are type species of their respective genera. (A based on Paul, 1968a, Textfig. 3; C based on Jaekel, 1899, Text-fig. 36b; E. based on Kesling, 1962, Text-fig. 2). circlet is also open as B2 meets L2 along a common suture. This trend is repeated in *Cheirocrinus penniger* (Text-fig. 3c) where R2 is not so markedly enlarged but shares a common suture with IL2. In *C. penniger* the infralateral circlet is also open at *two* points. The functional significance of enlarging R2 is unknown. Indeed the resulting plate arrangement seems to be structurally weaker than the more regular arrangement of *Macrocystella* and *Cheirocystella*, and there is no significant increase in the length of rhomb-bearing sutures (as occurs in the Callocystitidae). Such lengthening enables larger pectinirhombs to develop and hence increases the amount of respiratory exchange.

Plate Thickness.—While this hardly constitutes a trend, there is a significant structural advance between Macrocystella and the Cheirocrinidae. The plates of M. mariae are very thin (0.1 mm., Paul, 1968a) and are thrown into many folds which stiffen and strengthen them. Even so the delicacy of the theca in Macrocystella undoubtedly accounts for the rarity of whole specimens. In Cheirocystella the plates are thicker (approximately 1 mm. in C. antiqua, thinner in C. languedocianus) but are seriously weakened by the abundant conjunct pectinirhomb slits. However, thick axial ridges (which run from plate center to plate center) and corresponding folds in the plates form a triangulation structure which stiffens and strengthens the theca (Pl. 1, fig. 1, Text-fig. 7). Axial ridges divide all pectinirhombs into a pair of demi-rhombs (see below) and are quite common in the Cheirocrinidae. They are absent, however, from the "advanced" pectinirhombs of Homocystites where additional vestibule rims (Paul, 1968b) surround and strengthen the pectinirhombs (Pl. 4, figs. 1-2, Text-fig. 16). In Macrocystella significant respiration took place through the thecal plates; in the Cheirocrinidae it was restricted to the pectinirhombs.

#### Pectinirhombs

Trends affecting the number, arrangement and type of pectinirhomb and the type and spacing of the dichopores (canals) occur within the Cheirocrinidae. All involve a standardization of design which enhanced the efficiency of the rhombs as respiratory organs (Paul, 1968b).

Number of Pectinirhombs.—Parallel trends toward reduction in number of rhombs per theca occur within almost all lines in the superfamily Glyptocystitida. Within the Cheirocrinidae reduction is most prominent, from 20 or more, to six (Table 1, Text-fig. 4). Similar trends occur in other families (Table 2). This reduction in the number of pectinirhombs is partly correlated with a con-

|                          | Age          | No. of rhombs |
|--------------------------|--------------|---------------|
| Cheirocystella antiqua   | U. Tremadoc  | 19(+)         |
| Cheirocystis radiatus    | U. Arenig    | 16            |
| Cheirocrinus penniger    | Llanvirn     | 15            |
| Coronocystis angulatus   | U. Llandeilo | 15            |
| Cheirocystis anatiformis | Caradoc      | 8             |
| Homocystites alter       | Caradoc      | 6             |
| H. constructus           | Ashgill      | 7             |

 TABLE 1

 Pectinirhombs per theca in the Cheirocrinidae



TEXT-FIGURE 4.—Evolution of pectinirhombs in Macrocystellidae, Cheirocrinidae and Glyptocystitidae. A-I as in Fig. 3. Numbers beside periproct indicate the number of pectinirhombs per theca. Note that *Macrocystella* lacks pectinirhombs and that a general trend toward reduction in number occurs after their initial development.

comitant increase in their individual efficiency and partly with an increase in structural strength of the theca. In addition to reduction in total number, the precise arrangement of pectinirhombs in a theca becomes standardized and characteristic of species, genera or even families. This last feature is not markedly developed within the Cheirocrinidae but is evident in the Pleurocystitidae and Callocystitidae for example.

Arrangement of Pectinirhombs.—In the Cheirocrinidae pectinirhombs are particularly associated with B2 and the radial plates. A similar concentration of plate folds occurs in *Macrocystella* (Paul, 1968a). As the number of rhombs per theca is reduced certain locations are vacated in preference to others. For example, early Cheirocrinids have two demi-rhombs and two complete rhombs associated with B2 (Text-figs. 4b-c). Later species lose the demi-rhombs and

| Family             |                           | No. of rhor | nbs |
|--------------------|---------------------------|-------------|-----|
| Glyptocystitidae   | M. Ordovician             | 9 - 13      |     |
| Echinoencrinitidae | Ordovician                | 7 - 3       |     |
| Echinoencrinitidae | Silurian                  | 3-2         |     |
| Callocystitidae    | U. Ordovician             | 5           |     |
| Callocystitidae    | L. Silurian               | 4           |     |
| Callocystitidae    | M. Silurian - U. Devonian | 3 (rarely   | 2)  |
| Pleurocystitidae   | M. Ordovician - Devonian  | 0-`3        |     |

TABLE 2 Pectinirhombs per theca in the *Glyptocystitida* 

finally *Cheirocystis anatiformis* and *Homocystites* spp. have only rhomb B2:IL2, a pectinirhomb which persists in almost all species of Glyptocystitida. In the Cheirocrinidae rhombs between lateral and radial plates are lost in preference to those across radial:radial sutures (cf. text-figs. 4b and 4e). The opposite trend manifests itself in the Echinoencrinitidae and Callocystitidae. Although the details are not well documented there is a consistent loss of rhombs on lateral and infralateral plates culminating in *Homocystites*, which typically has only one such rhomb, L3:L4.

Type of Pectinirhomb.—Bather (1913) identified three types of pectinirhomb: conjunct, in which the dichopores open as a single slit along their entire length; *disjunct*, in which each dichopore opens in a pair of slits, one at either end; and *multi-disjunct*, in which there is a series of slits, the relationship of which to the underlying dichopores is not yet known. Since the latter type of pectinirhomb is a short-lived evolutionary sideline found only in two or three species of Acantholepis McCoy we need not consider it. Within the Cheirocrinidae conjunct pectinirhombs occur in the oldest known species, Cheirocystella antiqua. Disjunct pectinirhombs appear a little later, both within and outside the family. Functionally disjunct pectinirhombs are more efficient in exchange since the entrance slit is separated from the exit, thus reducing the chances of recycling. Disjunct pectinirhombs also weaken the theca much less than conjunct pectinirhombs. The persistence of conjunct pectinirhombs in the Pleurocystitidae (and possibly in Homocystites also) is correlated with the exceptional mode of life (Paul, 1967b). The conjunct pectinirhombs of both Pleurocystites and Homocystites are composed of advanced dichopores (see below) and are strengthened by vestibule rims (cf. Text-fig. 16).

Demi-rhombs, where only half of a rhomb is developed (Text-fig. 5), occur in most genera of Cheirocrinidae but are not found in *Homocystites*. All rhombs of *Cheirocystella antiqua* nov. are either single or paired demi-rhombs. Where the demi-rhombs are paired they are separated by pronounced axial ridges (Pl. 1, fig. 1, Text-fig. 7).



TEXT-FIGURE 5.—Diagrammatic representation of a demi-rhomb with canals developed only half-way along a suture.



TEXT-FIGURE 6.—Diagrammatic representation of discrete (A) and confluent (B) dichopores as seen in cross-section.

Type of Dichopore.—The dichopores (canals) of both conjunct and disjunct pectinirhombs are of two types. The earliest known species have primitive discrete dichopores which are separated by thin strips of plate material (Text-fig. 6a) and are characteristic of most Cheirocrinidae. Homocystites has advanced confluent dichopores (Text-fig. 6b) which are effectively a series of isoclinal folds of very thin plate material, the dichopore walls. Advanced dichopores replace primitive dichopores in all evolutionary lines which survive into the Upper Ordovician or beyond (Paul, 1968b, Text-fig. 37). At the same time demi-rhombs disappear, the Glyptocystitidae being the only family in which demi-rhombs of advanced dichopores occur. Functionally confluent (i.e., advanced) dichopores are more efficient in exchange (Paul, 1968b).

Spacing of Dichopores.—The spacing of pectinirhomb dichopores becomes standardized, and there is a general trend toward closer packing (Table 3). Incomplete pectinirhombs, with a few rather randomly developed dichopores, are typical of *Cheirocystella languedocianus* (Thoral) and occur occasionally in *Coronocystis angulatus* (Wood) but are unknown in later genera.

## Periproct

Two opposite trends, toward enlargement and reduction in size, occur in lines leading to other families. The former trend is confined to the line leading to the Pleurocystitidae but the latter is a repeated trend.

| Species                  | Age          | Mean Spacing |
|--------------------------|--------------|--------------|
| Cheirocystella antiqua   | U. Tremadoc  | 0.315 mm.    |
| C. languedocianus        | Basal Arenig | 0.370 mm.    |
| "Cheirocrinus" giganteus | U. Arenig    | 0.273 mm.    |
| Coronocystis angulatus   | U. Llandeilo | 0.358 mm.    |
| "Cheirocrinus" forbesi   | U. Llandeilo | 0.273 mm.    |
| Cheirocystis ardmorensis | U. Llandeilo | 0.2145 mm.   |
| Cheirocystis anatiformis | Caradoc      | 0.257 mm.    |
| Homocystites alter       | Caradoc      | 0.197 mm.    |
| H. constrictus           | Ashgill      | 0.2025 mm.   |

 TABLE 3

 Pectinirhombs slit-spacing in the Cherocinidae

Enlargement.—Macrocystella and all genera of Cheirocrinidae have a moderately large lateral periproct, covered by a plated periproctal membrane and developed within a frame made by five thecal plates (IL4, IL5, L1, L4, and L5). In the Pleurocystitidae the periproct has enlarged so that it almost fills one face of the flattened theca and the frame is made by six plates. This is correlated with the cal orientation and the active mode of life of *Pleurocystites* (Paul, 1967b).

Reduction.-Reduction of the periproct occurs in at least three separate lines leading from the Cheirocrinidae. It is least strongly expressed in the line leading to the Glyptocystitidae. In Glyptocystites (Text-fig. 17) and Glyptocystella (Text-figs. 19-21) the plated periproctal membrane is retained but the periproct is smaller and its frame is made by three plates (IL4, L4, and L5). In the Callocystitidae and at least in Silurian Echinoencrinitidae the periproctal covering is reduced to a valvular pyramid and a circlet of auxiliary plates. The functional significance of this repeated trend toward reduction in size and simplification of the covering of the periproct is not fully understood. However, it may be significant that the families with flexible periproctal membranes (Macrocystellidae, Cheirocrinidae, Pleurocystitidae and Glyptocystitidae) were unattached while the Callocystitidae and at least some Silurian Echinoencrinitidae, which have simplified periproctal coverings, were fixed. Paul (1968a, p. 598) suggested that Macrocystella was partially buoyant and may have had internal gas bubbles. If this was so, a flexible perproctal membrance would have been a useful adaptation allowing for changes in pressure and hence changes in internal volume. This idea is equally valid for the other families of free Glyptocystitidae. In fixed cystoids a flexible membrance would seem unnecessary.

#### Gonopore and Hydropore

As far as is known no trends affect these orifices within the Cheirocrinidae. However, their position in the theca changes in the Pleurocystitidae and the morphology of the hydropore varies within the Callocystitidae.

#### Ambulacra

Trends affecting the number, length and structure of ambulacra occur within the superfamily Glyptocystitida. Only one of these trends is present within the Cheirocrinidae: a trend to increased length of ambulacra seen in Coronocystis. Apparently the peculiar arrangement of brachioles in ambulacra I and IV of Macrocystella persists unchanged throughout the Cheirocrinidae. The trend toward change in ambulacral structure is repeated and is correlated with the

#### **EXPLANATION OF PLATE 1**

#### Cheirocystella antiqua Gen. et sp. nov

FIGS. 1-4 --Holotype UK 49942. 1. Stereophotos of anterior lateral view to show conjunct pectinirhombs, plate ornament and thecal outline 2. Left lateral view showing part of periproct outline. 3. Stereophotos of oral view to show a few preserved brachioles, ambulacral cover plates and orals. 4 Right lateral view. FIG. 5 — Paratype UK 49941. Stereophotos of anterior lateral view.

FIGS. 1-4 X2, fig. 5 X4. All whitened with ammonium chloride sublimate.





trend toward increased length. Together these trends increased food-gathering capacity without weakening the theca.

Number of Ambulacra.—Reduction in the number of ambulacra occurs independently in the lines leading to the Pleurocystitidae (2), within the Echinoencrinitidae (e.g., Schizocystis, 2; Osculocystis, 1), and within the Callocystitidae most genera have 4, Pseudocrinites has 2). Some Callocystitidae develop branched ambulacra.

Increase in Length and Change in Structure.-Macrocystella and all Cheirocrinidae except Coronocystis have relatively short ambulacra which are confined to the flat oral surface and have few brachioles each (3-5 in Macrocystella). In Coronocystis the five ambulacra extend down the theca to the level of the periproct on a dome-shaped oral surface and have 9-13 brachioles each. Since the ambulacral flooring plates lie between, not on, the thecal plates in all Cheirocrinidae this extension of the ambulacra in Coronocystis produces deep clefts in the radial plates (Text-figs. 11, 13). The lengthening trend is repeated independently in lines leading to other families, in particular to the Glyptocystitidae, where a very similar development occurs. Glyptocystella loeblichi (Bassler) has five ambulacra between, not on, the oral plates and again in large individuals the radials are cleft to receive the ambulacra (Text-fig. 21). In Glyptocystites s.s. the ambulacra lie on the thecal plates and some extend almost to the base of the theca (Text-fig. 17). This latter ambulacral structure also characterizes the Callocystitidae, many species of which have long ambulacra reaching the stem.

Long ambulacra of the Cheirocrinid type (i.e., lying between thecal plates) seriously weaken the theca. If such ambulacra reached the stem, there would be ten straight sutures running down the length of the theca from pole to pole. Development of ambulacra with flooring plates *on*, not between, thecal plates allows lengthening (and hence increased food-gathering capacity) without weakening the theca at all.

Decrease in Length.—An opposite trend toward shortening of ambulacra and reduction of the number of brachioles is seen in the Echinoencrinitidae and Pleurocystitidae. All members of the latter family have two simple "arms," while Osculocystis (Echinoencrinitidae) reduces the entire subvective system to one whiplike brachiole. A functional interpretation for this last modification escapes me!

In summary, the following evolutionary trends are associated with the family Cheirocrinidae in that they occur either within it or in lines directly descended from it:

#### **EXPLANATION OF PLATE 2**

Stereophotos of Coronocystis angulatus (Wood).

FIGS. 1-6.—USNM 113309. 1. Anterior lateral view to show long ambulacra, thecal outline and ornament. 2. Left lateral view. 3. Posterior lateral view to show periproct. 4. Right lateral view. 5 Aboral view to show invaginate base of theca. 6 Oral view to show five ambulacra, mouth, gonopore and hydropore.

FIG. 7 --- USNM 93463a. Oral view.

All figures X2, all whitened with ammonium chloride sublimate.

1. Thecal flattening exhibited by the Pleurocystitidae.

2. Repeated loss of one radial plate both within and outside the family Cheirocrinidae.

3. Repeated developments of open plate circlets within the Cheirocrinidae and other families.

4. Enlargement of plate R2 within the Cheirocrinidae.

5. Increase in plate thickness from the Macrocystellidae to the Cheirocrinidae.

6. Reduction in the number of pectinirhombs per theca within the Cheirocrinidae and in lines leading to all other families.

7. Repeated development of specific arrangements of pectinirhombs within the Cheirocrinidae and other families.

8. Change from conjunct to disjunct pectinirhombs within the Cheirocrinidae.

9. Change from discrete to confluent dichopores (canals) within the Cheirocrinidae and in all other lines which survive the Middle Ordovician.

10. A standardization of, and reduction in, spacing of dichopores within the Cheirocrinidae.

11. Enlargement of the periproct in the Pleurocystitidae.

12. Reduction of the periproct in lines leading to all families other than the Pleurocystitidae.

13. Repeated reduction in the number of ambulacra within the Echinoencrinitidae and Callocystitidae and in the line to the Pleurocystitidae.

14. Increase in length of ambulacra within the Cheirocrinidae and in lines to the Glyptocystitidae and Callocystitidae.

15. Repeated change in ambulacral structure within the Glyptocystitidae and in the line to the Callocystitidae. This is correlated with the last trend.

16. Decrease in length of ambulacra in the lines to the Echinoencrinitidae and Pleurocystitidae. This is correlated with trend 13.

# NATURE OF EVOLUTIONARY TRENDS

A number of the trends listed above are apparently unique evolutionary experiments and tend to be associated with highly specialized cystoids. For example, almost all the trends which lead to the Pleurocystitidae are unique and are associated with the unusual, active mode of life of this family. Alternatively, many trends are repeated and usually involve an increase in functional efficiency. Good examples of such repeated trends are the change from discrete to confluent dichopores and the lengthening (and concomitant change in structure) of ambulacra. Trends of a third group are difficult to explain in functional terms; e.g., reduction in the size of the periproct and reduction in the number of ambulacra and brachioles. Finally, one trend (from conjunct to disjunct pectinirhombs) apparently shows a reversal. However, the later conjunct pectinirhombs of the Pleurocystitidae and *Homocystites* are composed of advanced, confluent dichopores and, at least in the case of the Pleurocystitidae, are correlated with a specialized mode of life (Paul, 1967b).

## PHYLOGENY

A tentative phylogeny may be constructed on the basis of the trends recognized. The trends themselves are based on stratigraphic occurrence and morphologic resemblance among the cystoids involved. Preliminary results are shown in Text-figs. 1, 3 and 4. Doubtless, these will require modification or rejection as knowledge increases. Significant stages in any phylogeny are usually deemed worthy of taxonomic recognition. Hence in the next section the most distinct variations found in the Cheirocrinidae and Glyptocystitidae are formalized as genera and, where possible, the type species are described and figured.

# TAXONOMY

A complete taxonomic revision of the family Cheirocrinidae is far beyond the scope of this work even if it were possible. Nevertheless, the preceding account of evolutionary trends emphasized the occurrence of several important morphological variations within the family. Comparison might be made between the Callocystitidae and the Cheirocrinidae. The former has about 40 described species in 16 genera while the latter has about 30 described species in three genera at most and many authors have referred all species to the single genus *Cheirocrinus* s.l. While I do not intend to describe some ten or fifteen new genera of Cheirocrinidae, six clearly defined genera can be recognized using the same criteria on which callocystitid genera are distinguished. These criteria are plate arrangement, ambulacral structure and pectinirhombs. The differences between the genera recognized here are summarized in Table 4.

# Class RHOMBIFERA Zittel 1879 nom transl. Paul 1968b Order DICHOPORITA Jaekel 1899 emend. Paul 1968b Superfamily GLYPTOCYSTITIDA Bather 1899

# Family CHEIROCRINIDAE Jaekel 1899

Definition: A family of Glyptocystitida with well-developed stem which lacks a holdfast; cylindrical theca with large lateral periproct and generally flat oral surface; five usually short ambulacra with 5-15 brachioles each. Plate formula 4BB, 5ILL, 5LL, 5 or 6RR, and 7OO; lateral and infralateral circlets may beopen or all circlets may be closed. Periproct frame always made by five thecal plates (IL4, IL5, L1, L4, L5); periproct covered by flexible plated periproctal membrance. Gonopore and hydropore always across suture O1:O7, latter adoral. Ambulacra I and IV lack brachiole 2, others regular. Pectinirhombs conjunct, disjunct or multi-disjunct, from 6 to 20 or more per theca; demi-rhombs common; dichopores usually discrete but confluent in *Homocystites*.

# Genus CHEIROCRINUS Eichwald 1856

1856 Cheirocrinis Eichwald: 69.

1860 Cheirocrinus Eichwald, Eichwald: 645, pl. 32, fig. 1.

1899 Chirocrinus (Eichwald), Jaekel: 212, Text-fig. 36b (p. 196).

1900 Cheirocrinus Eichwald, Bather: 63, Text-fig. 32.

1913 Cheirocrinus Eichwald, Bather: 434.

- 1943 Cheirocrinis Eichwald, Brassler and Moodey: 5, 142.
- 1945 Cheirocrinus Eichwald, Regnéll: 68.

1968 Cheirocrinus Eichwald, Kesling: S182, fig. 87, 1a-b.

(non Cheirocrinus Salter, in Murchison 1859, nec Cheirocrinus Hall 1860 = Calceocrinus s.l.)

| Genus          | Ambs. | RR       | Circlets      | Rhombs         | Dichopores | Oral<br>Surface |
|----------------|-------|----------|---------------|----------------|------------|-----------------|
| Cheirocrinus   | short | 6 normal | ILL & LL open | dısjunct       | discrete   | flat            |
| Cherroystis    | short | 6 normal | all closed    | disjunct       | discrete   | flat            |
| Cherrocystella | short | 6 normal | all closed    | disjunct       | discrete   | flat            |
| Coronocystis   | long  | 6 cleft  | LL open       | conjunct       | discrete   | domed           |
| Homocystites   | short | 5 normal | all closed    | conjunct       | confluent  | flat            |
| Acantholepis   | ?     | ??       | ? open ?      | multı-dısjunct | ?          | ?               |
| *Leptocystis   | ?     | ??       | 2             | conjunct       | ?          |                 |

# TABLE 4GENERIC CHARACTERS IN THE CHEIROCRINIDAE

\*This genus is indeterminate in my opinion.



TEXT-FIGURE 7.—Analysis of plate arrangement in holotype of *Cheirocystella antiqua* gen. et sp. nov. UK 49942. Plate symbols as in Text-fig. 2, Br brachioles, Pe periproct, plate ridges stippled.

Type species: Cyathocrinitis penniger Eichwald 1842.

Diagnosis: A genus of Cheirocrinidae with open lateral and infralateral circlets and six radials; with short ambulacra confined to flat oral surface; with disjunct pectinirhombs.

Remarks: C. penniger (Eichwald) and C. granulatus Jaekel are the only species which can definitely be assigned to the genus Cheirocrinus as here restricted (see Jaekel, 1899, Pl. 11, figs. 1-4). However, since the plate arrangements of very few species of Cheirocrinidae are known in detail more species are likely to be assigned to this genus in the future. No specimens of Cheirocrinus s.s. were available to me, but the characters of the type species, C. penniger, are adequately described and figured by Jaekel (1899) and Bather (1913). For once these two authorities agree on most characters of the species, especially the open infralateral and lateral circlets, and it may be assumed that their independent descriptions are essentially accurate.

# Genus CHEIROCYSTELLA gen. nov.

# Cheirocrinus Auctt. (in part)

Type species: Cheirocystella antiqua gen. et sp. nov.

Diagnosis: A genus of Cheirocrinidae with all plate circlets closed and six radials; short ambulacra confined to the flat oral surface; many (15-20 or more) conjunct pectinirhombs with discrete dichopores.



TEXT-FIGURE 8.—Analysis of plate arrangement in paratype of *Cheirocystella antiqua* gen. et sp. nov. UK 49943. Plate symbols as in Text-fig. 2. Plate ridges stippled.

Remarks: Cheirocystella is proposed for a group of early Ordovician (Tremadoc-Arenig cheirocrininds which closely resemble Macrocystella but possess pectinirhombs. In several respects they appear to be primitive members of the family Cheirocrinidae which agrees with their low stratigraphic position. Five species including the type can be assigned to Cheirocystella on the basis of present knowledge. These are C. antiqua nov, C. lanquedocianus (Thoral), C. atava (Jaekel), C. holmi (Regnéll) and C. leuchtenbergi (Angelin).

Cheirocystella antiqua gen. et sp. nov.

# Plate 1, Text-figs. 3b, 4b, 7-9.

Diagnosis: A species of *Cheirocystella* with plate ornament of prominent axial ridges, occasional accessory ridges and fine granules, pectinirhomb slit spacing averaging one slit per 0.315 mm.



TEXT-FIGURE 9.—Reconstruction of plate arrangement and pectinirhomb distribution in *Cheirocystella antiqua* gen. et sp. nov. Plate symbols as in Text-fig. 2 (Plates L5, R4 and R5 not seen). Note that all plate circlets are closed.

Types: Holotype UK 49942. Paratypes UK 49941, 49943.

Horizon and locality: Types were collected (by P.V. Bitter) from ten feet above the base of the Fillmore Limestone, northwest of Red Tops, House Range, Utah. NE<sub>4</sub>, NW<sub>4</sub>, Section 31, T. 22S, R. 13W. The horizon is in Hintze's trilobite zone "D", characterized by *Apatokephalus* and *Leiostegium* (Hintze, 1952) and is Tremadoc in age. Whittington (1966) suggested that zones "A" to "F" inclusive were Tremadoc and hence the cystoid horizon is well below the Tremadoc-Arenig boundary. Hitherto the oldest known cheirocrinid was *Cheirocystella languedocianus* (Thoral) from the basal Arenig of the Montaigne Noire, France (Paul, 1967a).

# Description:

A. Stem: Typically glyptocystitid as far as known. Proximal portion has wide lumen, tapers rapidly and has alternating inner and outer columnals. The latter have external flanges which are curved down away from the theca. Some flanges bear about ten irregular tubercles. Distal stem unknown.

B. Theca: Cylindrical, typically cheirocrinid with flat oral surface. Plate arrangement is shown in Text-figs. 7-9. Plate ornament of prominent axial ridges, with some parallel accessory ridges and fine granules. Pectinirhomb slits are narrow and slightly raised. Oral plates have fine granular ornament.

Pectinirhombs: All conjunct, 19 positions confirmed on types (Table 5), and more possible since not all plates are known. Most rhombs occur across inter-circlet sutures, and are pairs of demi-rhombs separated by the axial ridges. Demi-rhombs have from one to seven slits and hence no rhomb has more than 14 dichopores. Slit-spacing averages one slit per 0.315 mm. (Table 6).

| Rhomb          | UK49942 | UK49941 | UK49943 | UU C-8 |
|----------------|---------|---------|---------|--------|
| B1:B2          | D       |         |         |        |
| B2:B3          | D       |         |         |        |
| B2:1L1         | +       | +       |         | +      |
| B2:1L2         | +       | +       |         | ;+     |
| 1L1:L1         | D       |         |         |        |
| 1L1:L2         | D       | D       |         | ?      |
| 1L2:L3         | +       |         |         |        |
| L1:R6          | +       | +       |         |        |
| L1:R1          | +       | +       |         |        |
| L2:R1          | +       | +       |         |        |
| L2: <b>R</b> 2 | +       | +       |         |        |
| L3:R2          | D       |         |         | +      |
| L3:R3          | +       |         |         |        |
| L5:R6          | +       |         |         |        |
| R1:R2          | D       |         |         | D      |
| R2:R3          | D       |         |         | +      |
| 1L3:1L4        |         |         | D       |        |
| 1L3:L4         |         |         | D or +  |        |
| 1L4:L4         |         |         | D       |        |
| 1L1:1L2        |         |         |         | +      |
| L2:L3          |         |         |         | +      |
| L3:L4          |         |         |         | +      |
| R1:R6          |         |         |         | D      |

 TABLE 5

 Pectinirhombs present in Cheirocystella from Utah

+ = two demirbombs present, D = one demirbomb present, - = rhomb definitely not present, blank = no information (not preserved, buried in matrix, et cetera).

Periproct: Large, presumably with plated membrane in life.

Gonopore and hydropore: Not detected.

C. Subvective system: Five ambulacra confined to oral surface. Probably with 6-7 brachioles each. Brachioles up to 7 mm. long and with about 40 brachiolar plates. Cover plates of main food grooves ornamented with fine ridges.

# Remarks:

C. antiqua is the oldest known cheirocrinid cystoid and displays a number of primitive characters (e.g., six radial plates, a large number of conjunct pectinirhombs with discrete dichopores which are in fact pairs of demi-rhombs). It is also the only species of *Cheirocystella* in which the precise plate arrangement and the number and arrangement of pectinirhombs are reasonably well known. Even so, not all plates are visible in available material of *C. antiqua*. The distribution of pectinirhombs is interesting in that sutures between plates of different circlets (inter-circlet sutures) more commonly bear pectinirhombs than sutures between plates of the same circlet (intra-circlet sutures). In the type material there are no pectinirhombs across ILL:ILL and LL:LL sutures. However, in the University of Utah collections is a single, well-preserved theca of *Cheirocystella* (Pl. 4, fig. 5) which has pectinirhombs IL1:IL2, L2:L3 and

| TABL | E | 6 |
|------|---|---|
|------|---|---|

| UK             | 49942      | UK49941 |        |     |  |  |
|----------------|------------|---------|--------|-----|--|--|
| Rhomb          | Spacing    | Rhomb   | Spacin | ng  |  |  |
| B2:1L1         | 0.2603 mm. | B1:B2   | 0.2857 | mm. |  |  |
| 1L1:L2         | 0.3810 mm. | B2:1L1  | 0.2857 | mm. |  |  |
| 1L2:L3         | 0.3386 mm. | B2:1L2  | 0.2857 | mm. |  |  |
| L1: <b>R</b> 6 | 0.3302 mm. | L2:R1   | 0.2857 | mm. |  |  |
| L1:R1          | 0.3175 mm. | L2:R2   | 0.2730 | mm. |  |  |
| L2: <b>R</b> 1 | 0.3492 mm. |         | 0.2603 | mm. |  |  |
| L2: <b>R</b> 2 | 0.3386 mm. |         |        |     |  |  |
| L3:R3          | 0.3227 mm. |         |        |     |  |  |
| R2:R3          | 0.3810 mm. |         |        |     |  |  |

Pectinirhombs slit-spacing in Cheirocystella antiqua gen. et. sp. nov.

Mean = 0.315 mm.

Slit-spacing is usually determined by measuring 10 slits and 10 spaces between the slits and dividing by 10 to give mean spacing of one slit per 0.xxxxmm. In *Cheirocystella antiqua* all measurements were taken from one demi-rhomb so that slit-spacing does not include the thick axial ridge in a rhomb. However, this means that all determinations are based on six or less slits.

L3:L4 among others. While it is quite likely that the arrangement of pectinirhombs was not fixed and varied from specimen to specimen in C. antiqua, much more material is needed before this can be established. Hence for the present this last specimen is not assigned to C. antiqua.

# Genus CHEIROCYSTIS nov.

Cheirocrinus Auctt. (in part)

Type species: Echinoencrinites anatiformis Hall 1847.

Diagnosis: A genus of Cheirocrinidae with all plate circlets closed, six radial plates; short ambulacra confined to flat oral surface; 8-16 disjunct pectinirhombs.

Remarks: Cheirocystis is proposed for a group of species which have most features identical to Cheirocystella but possess more efficient disjunct pectinirhombs. This may well prove to be the genus with the largest number of species but at present only the following can definitely be assigned to Cheirocystis: C. anatiformis (Hall), C. radiatus (Jaekel), C. hyperboreus (Regnéll), C. merrileesei (Browne), C. ardmorensis (Bassler) C. walcotti (Jaekel) and C. insignis (Jaekel). These species are from the Lower and Middle Ordovician of North America, Europe and Australia. Kesling (1962) gives an excellent synonymy and description of C. anatiformis which it is unnecessary to repeat here. On the basis of this description, C. anatiformis is selected as type species of Cheirocystis.

Cheirocystis ardmorensis (Bassler) 1943.

Pl. 7, fig. 8, Text-fig. 10.

1943 Cheirocrinus ardmorensis Bassler: 699, Pl. 1, fig. 6.

Diagnosis: A species of Cheirocystis with plate ornament of axial ridges and



TEXT-FIGURE 10.—Analysis of plate arrangement in holotype of *Cheirocystis ardmorensis* (Bassler), USNM 93471. Plate symbols as in Text-fig. 2, plate ridges stippled.

fine growth lines, proximal stem flanges ornamented with vertical ridges separated by fine pits; slit-spacing of pectinirhombs averages one slit per 0.2145 mm.

Type: Holotype (monotype) USNM 93471.

Horizon and locality: Middle member of the Simpson Formation (Bromide), north end of Hickory Creek Gap in the Criner Hills, 8 miles SSW of Ardmore, Oklahoma.

| TABLE | 7 |
|-------|---|
|-------|---|

| Rhomb  | Spacing    |  |
|--------|------------|--|
| B2:1L1 | 0.2222 mm. |  |
| L1:L2  | 0.2413 mm. |  |
| L5:R6  | 0.2041 mm. |  |
| R6:R1  | 0.1905 mm. |  |
|        |            |  |

Pectinirhomb slit-spacing in Cheirocystis ardmorensis (Bassler)

Mean = 0.2145 mm.

Material: the holotype is the only known specimen.

Description:

A. Stem: Proximal stem is typical, tapers from 5 to 3 mm. in approximately 16 mm. length and has 12 or 13 pairs of columnals. External flanges of outer columnals are thick with small vertical ribs separating fine pits. Distal stem is incomplete, about 10 columnals preserved which change from annular to cylindrical distally and have delicate flanges.

B. Theca: Shape is typical. Plate arrangement (as far as is known) shown in Text-fig. 10. Plates are ornamented with strong axial ridges and fine growth lines. Oral plates unknown. All pectinirhombs are disjunct (six seen); slitspacing averages 0.2145 mm. (Table 7). Periproct is crushed, 5 by  $2\frac{1}{2}$  mm., covering plates are not preserved. Gonopore and hydropore are not seen.

C. Subvective system: not preserved.

# Remarks:

The periproct of C. ardmorensis is visible and although distorted by crushing it is undoubtedly surrounded by five the cal plates. Hence the specimen is a cheirocrinid. The plate circlets are all closed as far as it is possible to tell from



TEXT-FIGURE 11.—Analysis of plate arrangement in Coronocystis angulatus (Wood), USNM 113309. Plate symbols as in Text-fig. 2, stippled area damaged. Note the deeply cleft radials and open lateral circlet.



TEXT-FIGURE 12.—Ambulacral structure in *Coronocystis angulatus* (Wood), USNM 113309. A. oral area, B. Detail of ambulacrum, G. gonopore, H. hydropore, M. mouth, OI-O7 orals, I-V ambulacra, I<sup>1</sup>, I<sup>3</sup> et cetera, briochioles in ambulacrum 1. Note that in this interpretation brachiole I<sup>2</sup> is undeveloped which may explain the additional ambulacral flooring plate between O2 and brachiole I<sup>4</sup>.

an incompletely exposed theca. All the pectinirhombs visible are disjunct. Thus *C. ardmorensis* is a species of *Cheirocystis*. It is redescribed here because the original description is inadequate by modern standards and because three other "species" which Bassler described in the same work are also redescribed here as a species of *Glyptocystella* gen. nov. One of these latter "species" was originally referred to as *Cheirocrinus* s.l. along with *C. ardmorensis*.

# Genus CORONOCYSTIS nov.

Type species: Cheirocrinus angulatus Wood.

Diagnosis: A genus of Cheirocrinidae with open lateral circlet, six radial plates; long ambulacra extending from dome-shaped oral surface down into enlarged radial plates, five of which are deeply cleft to receive the ambulacra; with 15 disjunct pectinirhombs.

Remarks: Coronocystis is proposed for a single species, C. angulatus (Wood) 1909, in which the ambulacra are greatly lengthened and which has an open lateral circlet with an enlarged R2. C. angulatus is from the Middle Ordovician of N.E. Tennessee and S.W. Virginia, USA.

Coronocystis angulatus (Wood) 1909. Plate 2, figs. 1-7, Plate 3, figs. 1-5, Text-figs. 3f, 4f, 11-13.

1849 Cyathocrinites sculptus Troost: 61 (nomen nudum).

1909 Chirocrinus angulatus Wood: 7, Pl. 8, figs. 9-10.

1943 Cheirocrinus angulatus (Wood), Bassler and Moodey: 27, 142.



TEXT-FIGURE 13.—Analysis of plate arrangement in *Coronocystis angulatus* (Wood), USNM 93463a. Plate symbols as in Text-fig. 2, stippled area damaged. Note that Pl. L5 is missing.

Diagnosis: As for genus.

Type: Troost's original specimen (USNM 39951) is accepted as holotype (monotype). It is incomplete and has apparently been lost. However, two other specimens in the USNM collections (113309 and 93463a) are complete and were to be made types of a new species, "Cheirocrinus coronatus" by Bassler in an unpublished manuscript. There is little doubt that these specimens are identical with Troost's original specimen, and they all come from approximately the same horizon and locality.

Horizon and locality: Troost's specimen probably came from the Benbolt or equivalent horizons near Knoxville, Tenn. (see Wood, 1909, p. 8). Bassler's material came from the Benbolt formation near Hansonville, Va. (Kesling & Paul, 1968 p. 21 give the precise location of the outcrop). Isolated fragments and plates of this species are very common indeed in the Benbolt, Ottossee and Wardell formations and their equivalents in N.E. Tennessee and S.W. Virginia.

Material: Two complete thecae, six partial thecae and many isolated plates (USNM, FMNH).

Description:

A. Stem: Proximal stem typical. External flanges of outer columnals with vertical ridges (Pl. 2, fig. 1). Outer columnals reach 4 mm. in diameter in USNM 93463a. Distal stem unknown.

B. Theca: Ovoid with portion above periproct dome shaped. Plate arrangement shown in Text-figs. 11 and 13. Plate ornament consists of prominent axial

| US                     | SNM 113309 | USNM   | 39463a     |
|------------------------|------------|--------|------------|
| Rhomb                  | Spacing    | Rhomb  | Spacing    |
| B2:1L1                 | 0.3206 mm. | B2:1L1 | 0.3365 mm. |
| B2:1L2                 | 0.3306 mm. | L1:L2  | 0.3302 mm. |
| IL4:L4                 | 0.3746 mm. | 1L4:L4 | 0.3683 mm. |
| L3:L4                  | 0.3162 mm. | R1:R2  | 0.3270 mm. |
| <b>R</b> 1: <b>R</b> 2 | 0.3968 mm. | R3:R4  | 0.3429 mm. |
| R2:R3                  | 0.3905 mm. | R6:R1  | 0.3460 mm. |
| R3:R4                  | 0.4063 mm. |        |            |
| R4:R5                  | 0.3746 mm. |        |            |
| R5:R6                  | 0.3905 mm. |        |            |
| R6:R1                  | 0.3810 mm. |        |            |

TABLE 8 Pectinirhomb slit-spacing in Coronocystis angulatus (Wood)

Mean = 0.358 mm.

ridges, numerous accessory ridges, growth lines and fine granules. Oral plates (Text-fig. 12a) ornamented with fine granules. Mouth oval about 2 mm. wide. Pectinirhombs disjunct with discrete dichopores, demi-rhombs common. Slit-spacing averages one slit per 0.358 mm. (Table 8). Periproct large,  $5\frac{1}{2}$  by  $3\frac{1}{2}$  mm. in USNM 113309, surrounded by prominent rim. Periproctal membrane unknown. Gonopore small, circular, 0.3 mm in diameter. Hydropore slitlike, 1.4 mm. long.

C. Subvective system: Ambulacra unusually long for a cheirocrinid, extending down to the level of the periproct into deeply cleft radial plates. All five ambulacra well developed with 9-13 brachioles each (Table 9). Ambulacra I and IV lack brachiole 2 as in *Macrocystella* (Text-fig. 12).

# Remarks:

Dr. Porter M. Kier and Mr. T. Phelan of the United States National Museum kindly undertook an extensive but unsuccessful search for Troost's original specimen. In the absence of the type, which was incomplete, some doubt may remain as to the identity of the complete specimens upon which the above description of *Coronocystis* is based. Hence the evidence for my interpretation and a brief history of the species follow.

#### **EXPLANATION OF PLATE 3**

Stereophotos of Coronocystis angulatus (Wood).

- FIGS. 1-4.—USNM 93463a. 1. Posterior lateral view to show periproct. Note plate L5 is missing. 2. Anterior lateral view to show weathered basal pectinirhombs and demirhomb IL1:IL2. 3. Left lateral view. 4. Right lateral view.
- FIG. 5.—USNM 113309. Detail of ambulacrum I to show arrangement of brachiole facets (cf. Text-fig. 12b).

FIGS. 1-4 X2, fig. 5 X4. All whitened with ammonium chloride sublimate.

# CHEIROCYSTELLA ANTIQUA





PLATE 4

| Number of brachioles per ambulacrum in <i>Coronocystis angulatus</i> (wood) |                  |                   |  |  |
|---|------------------|-------------------|--|--|
| Ambulacrum  | USNM 113309      | USNM 93463a       |  |  |
| I   | 10               | 11+               |  |  |
| II  | 7 visible (9-10) | 13                |  |  |
| III   | 9                | 12                |  |  |
| IV  | 8 or 9           | 9 visible (13-14) |  |  |
| V   | 9                | 13                |  |  |

TABLE 9

Figures in parentheses are estimated totals

Troost (1849) published a list of fossil echinoderms from Tennessee which included "Cyathocrinites sculptus". In 1850 he submitted a monograph to the Smithsonian Institution describing all the species listed in 1849. Due to his death and other events beyond his control (Schuchert, 1904, p. 219-221, gives a detailed history of the case), Troost's manuscript was not published until Elvira Wood (1909) gave a critical summary of it. Wood realized that Troost's "Cyathocrinites sculptus" was an incomplete cheirocrinid cystoid and described it as "Chirocrinus angulatus" since the trivial name "sculptus" was preoccupied. Wood published Troost's original description and figures (Wood, 1909, p. 7, Pl. 8, figs. 9-10) both of which are inadequate by modern standards. Wood also added a description of her own and more information about the locality and horizon. Wood's description of the thecal sculpture, basal invagination, stem and four basal pectinirhombs all agree well with the specimens described here. However, Wood also mentions pectinirhombs IL1:L2 (L1:L'2) and IL2:L2 (L2:L'2) which do not occur on any specimens I have seen (cf. Bather, 1913, p. 439, §300). Since Wood does not give a plate analysis, I wonder if she misidentified pectinirhombs IL1:IL2 and L1:L2. Alternatively the original specimen may have had an unusual distribution of pectinirhombs. In either event I think Wood's description is adequate to identify additional material from the same general locality and horizon, even in the absence of Troost's type. I prefer, therefore, to use Wood's name rather than to erect a new species as Bassler proposed to do in his unpublished manuscript.

# EXPLANATION OF PLATE 4

Homocystites alter Barrande and Cheirocystella sp.

- FIGS. 1-4.-Homocystites alter Barrande.
- FIGS. 1 and 4.—Latex impression of lectotype, original of Barrande, 1887, Pl. 28 (II), fig. 8. 1. Stereophotos of theca to show ornament and conjunct pectinirhombs. Note strongly developed rim to rhomb in L3. 4. Stem to show proximal (above) and distal portions.
- FIG. 2.—Latex impression of paralectotype, original of Barrande, 1887, Pl. 28 (II), fig. 3. Stereophotos of anterior lateral view.
- FIG. 3.—Latex impression of paralectotype, original of Barrande, 1887, Pl. 28 (II), figs. 14-16. Stereophotos of partly disarticulated theca.
- FIG. 5.—Stereophotos of *Cheirocystella* sp. UU. Right lateral view of theca to show pectinirhombs.
- All figures X2. All whitened with ammonium choloride sublimate.

1.

# Genus HOMOCYSTITES Barrande 1887

1887 Homocystites Barrande: 77, 160. 1889 Homocystis Bather: 269. Cheirocrinus Auctt. (in part)

Type species: Homocystites alter Barrande 1887.

Diagnosis: A genus of Cheirocrinidae with all plate circlets closed, five radial plates; with short ambulacra confined to the flat oral surface; with few (6-7) advanced conjunct pectinirhombs with confluent dichopores.

#### Remarks:

Homocystites alter, the type species of the genus, differs from almost all other Cheirocrinidae in having only five radial plates and advanced conjunct pectinirhombs. "Cheirocrinus" constrictus Bather is the only other described species to share these characters although another undescribed species occurs in Britain. Homocystites is late Middle to Upper Ordovician in age and occurs in Britain and Bohemia.

Homocystites alter Barrande 1887

Plate 4, figs. 1-4, Text-figs. 3i, 4i, 14-16.

1887 Homocystites alter Barrande: 160, Pl. 28 (II), figs. 1-21.

1896 Homocystis altera (sic) Barrande, Haeckel: 150, Pl. 4, figs. 26-27.

1899 Chirocrinus alter (Barrande), Jaekel: 221, Pl. 10, fig. 14, Pl. 11, fig. 8.

1943 Cheirocrinus alter (Barrande), Bassler & Moodey: 34, 142.

1968 Homocystites alter Barrande, Kesling: S183-4, fig. 87, 2a-b (non figs. 2c-d).

Diagnosis: A species of *Homocystites* with plate ornament of prominent axial ridges (occasionally with accessory ridges) and fine granules or fine growth lines; outer columnals with double-rimmed flanges; pectinirhomb slit-spacing averages 0.1972 mm.

Type: Original of Barrande 1887, Pl. 28 (II), fig. 8, is here selected as lecto-type.

Horizon and locality: Barrande's material came from Zahorzan, Bohemia, from band d4, which is Caradoc (high Middle Ordovician).

Material: Five more or less complete but crushed thecae were available to me. They are from Barrande's original collection and the Schary collection, MCZ, Harvard.

Description:

A. Stem: Proximal stem typical, with about 15 pairs of columnals, external flanges of outer columnals ornamented with a double rim connected by very fine vertical ridges (Pl. 4, figs. 2, 4). Distal stem typical, about 23 columnals preserved on lectotype. Columnals change from annular to cylindrical distally, the external flanges broaden, become smoother and finally indistinct about halfway along the preserved portion.

B. Theca: Shape typical. Plate arrangement shown in Text-figs. 14-16. Plate ornament varies from specimen to specimen but all show prominent axial ridges which may be beaded (Pl. 4, fig. 3) or accompanied by accessory



TEXT-FIGURE 14.—Homocystites alter Barrande. A. Original of Barrande, 1887, Pl. 28 (II), figs. 9-10, B-C. Counterparts of original of Barrande, 1887, Pl. 28 (II), figs. 14-16. Plate symbols as in Text-fig. 2 except that symbols in parentheses indicate missing plates. Pe periproctal plates, plate ridges stippled. Note that in C only two radials are adjacent to L5 (cf. Text-figs. 2, 9, 10, 11 and 13). IL1-IL3 seen in internal view in C and in external view in B.

ridges (Pl. 4, fig. 2). Fine granules (Pl. 4, fig. 1 at base) or fine growth lines (Pl. 4, fig. 3) may also be developed. Oral plates are apparently smooth. Pectinirhombs are conjunct with confluent dichopores and not more than six per theca as far as known. Pectinirhombs have vestibule rims which are distinct from the plate ornament of axial ridges in some cases (Pl. 4, fig. 2, at top). Slit-spacing averages 0.1972 mm. (Table 10). Periproct surrounded by five plates, covered with membrane armed with small smooth periproctal plates. Gonopore and hydropore are unknown.

C. Subvective system: Not preserved on available material.

Remarks:

The absence of one radial plate (R5) and the advanced conjunct pectinirhombs separate *H. alter* from all other described species of the Cheirocrinidae except "C." *constrictus* Bather. It is distinctly possible that these two forms are conspecific, but as yet I have been unable to compare them directly. *H. constrictus* is younger (Ashgill, Upper Ordovician) than *H. alter* and is accompanied by another undescribed species of *Homocystites*.

# Genus ACANTHOLEPIS McCoy 1846

1846 Acantholepis McCoy: 7.

Cheirocrinus Auctt. (in part)

(non Acantholepis Krøyer 1846, nec Acantholepis Mayr 1861, nec Acantholepis Newberry 1875)

Type Species: Acantholepis jamesii McCoy, by monotypy.

Diagnosis: A genus of Cheirocrinidae with multi-disjunct pectinirhombs.



TEXT-FIGURE 15.—Homocystites alter Barrande. A. Original of Barrande, 1887, Pl. 28 (II), fig. 3, B. Lectotype original of Barrande, 1887, Pl. 28 (II), fig. 8, C. MCZ 23 (Schary collection, approx. X3). Plate symbols as in Text-fig. 2, Cr crack, plate ridges stippled

# Remarks:

McCoy (1846) described *A. jamesii* as a fish scale. Examination of material from the type locality shows that *A. jamesii* is based on isolated plates of a cheirocrinid with multi-disjunct pectinirhombs, a feature which is mentioned in the original description. *Acantholepis* McCoy is apparently an available name despite the fact that Krøyer (1846, p. 97) proposed the name for a recent fish genus in the same year. Although Krøyer's work (Danmarks Fiske, vol. 3, part 1) was issued in parts, the precise date of issue of the relevant part is unknown. I am indebted to Mr. Gordon Howes of the Fish Section, British Museum (Natural History), for attempting to date Krøyer's work. According to the ICZN rules *Acantholepis* Krøyer must be taken as dating from 31 December 1846, in the absence of evidence to the contrary. McCoy's paper contains a letter dated 5 August 1846, is recorded (Anon. 1847, p. 131) as having been received by the library of the Geological Society of London before 4 November 1846, and must have been published between these two dates. Hence *Acantholepis* McCoy is taken as dating from 4 November 1846 and takes precedence over

| Specimen              | Rhomb | Spacing    |  |
|-----------------------|-------|------------|--|
| MCZ 23 (Schary coll.) | L5:R6 | 0.1926 mm. |  |
| MCZ 23 (Schary coll.) | R2:R3 | 0.1894 mm. |  |
| MCZ 23 (Schary coll.) | R : R | 0.1697 mm. |  |
| Barrande coll.        |       | 0.2050 mm. |  |
| Barrande coll.        |       | 0.2250 mm. |  |
|                       |       |            |  |

|               | TA           | BL | E 10         |       |          |
|---------------|--------------|----|--------------|-------|----------|
| Pectrinirhomb | slit-spacing | ın | Homocystites | alter | Barrande |

Mean = 0.197 mm.



TEXT-FIGURE 16.—Reconstruction of plate arrangement in *Homocystites alter* Barrande based on all available material. Plate symbols as in Text-fig. 2, vestibule rims and plate ridges stippled and somewhat idealized. Note that there are only *five* radial plates.

Acantholepis Krøyer. No taxonomic changes are necessary since Acantholepis Krøyer is already preoccupied by Argentina Linné.

"Cheirocrinus" interruptus (Jaekel) is the only other described species of Acantholepis. The genus is confined to the Middle Ordovician of Britain (Scotland and Ireland) and the Baltic States.

# Genus LEPTOCYSTIS Jaekel 1899

- 1887 Homocystites Barrande: 77 (in part)
- 1899 Leptocystis Jaekel: 222.
- 1968 ?Leptocystis Jaekel, Kesling: S184 (non Text-fig. 87, 3a-c = Cheirocystella nov.)

Type Species: Homocystites tertius Barrande 1887.

# Remarks:

Jaekel's original diagnosis of *Leptocystis* is inadequate, but apparently he thought that the nature of the stem and the distribution of the pectinirhombs separated it from *Cheirocrinus* s.l. and that the presence of *conjunct* pectinirhombs separated it from other Silurian rhombiferans. In short, he said what it was not, rather than what it was, and admitted that his name was provisional. I have been able to examine latex impressions of Barrande's original material through the kindness of Professor K. E. Caster, University of Cincinnati. The larger of the two specimens is the original of Barrande, 1887, Pl. 31 (V), fig. 6, and is here selected as lectotype. It is poorly preserved but apparently a

cheirocrinid. It bears pectinirhombs B2:IL1, B2:IL2 and L1:L2 and may have closed plate circlets but virtually nothing else can be determined. The presence of two pectinirhombs on B2 suggests a fairly primitive cheirocrinid, yet the horizon (E2) is Middle to Upper Silurian. If the stratigraphic position is correct, this is the youngest cheirocrinid since all other known specimens are Ordovician (the report of "cf Cheirocrinus giganteus" from the Lower Devonian of France [Pruvost and Le Maitre, 1943, p 88] may be discounted). Indeed it is the stratigraphic position which is the most remarkable feature of *Leptocystis*. Until more and better preserved material which confirms the stratigraphic horizon has been located it is best to restrict the name "*Leptocystis tertius*" to Barrande's original material.

# Family GLYPTOCYSTITIDAE Bather 1899

Definition: A family of Glyptocystitida with well-developed stem which lacks a holdfast; cylindrical to ovoid or pyriform theca with moderate to small lateral periproct and generally dome-shaped oral surface; five recumbent ambulacra which may be developed on or between thecal plates, in the former case some ambulacra are long and may reach the stem. Plate formula 4BB, 5ILL, 5LL, 6RR, and 7OO; lateral and infralateral circlets are open. Periproct frame always made by three thecal plates (IL4, L4 and L5); periproct is covered by flexible plated periproctal membrane in life. Gonopore and hydropore always across suture O1:O7, latter adoral. Ambulacra I and IV lack brachiole 2, other three ambulacra regular. Pectinirhombs always disjunct with confluent dichopores but with incompletely developed vestibule rims (monti-disjunct), from 9-13 per theca, occasional demi-rhombs present.

The Glyptocystitidae differ from the Cheirocrinidae in the number of plates surrounding the periproct (3 not 5) and in the type of pectinirhomb (Textfig. 17, Pl. 7, figs. 3-4) for which Sinclair (1948, p. 306) proposed the term "monti-disjunct". Hitherto only one genus, *Glyptocystites*, has been attributed to the family. *Glyptocystites* also differs from all Cheirocrinidae in having all its ambulacra developed on, not between, thecal plates. Some of the ambulacra are very long and regularly reach the basal circlet or even the stem. Five species are currently assigned to *Glyptocystites*, and all are from the Trenton Group (Middle Ordovician) of North America. In addition to these, Bassler (1943) described a sixth species from the Bromide Formation of Oklahoma which dif-

#### **EXPLANATION OF PLATE 5**

#### Glyptocystella loeblichi (Bassler).

- FIGS. 1, 3, 6-7.—Stereophotos of holotype, USNM 113107. 1. Right lateral view. 3. Left lateral view. 6. Anterior lateral view. Note small pectinirhomb B2:L2. 7. Posterior lateral view.
- FIG. 2.—Detail of ambulacrum I in USNM 216603/4 to show arrangement of brachiole facets.
- FIG. 4.—Posterior lateral view of USNM 216603/7 to show anal pyramid within periproct.
- Figs. 5 and 8.—Stereophotos of holotype of "Glyptocystites loeblichae" Bassler, USNM 93484. 5. Oblique posterior lateral view. 8. Oblique anterior lateral view.
- FIGS. 2 and 4 X4, all others X2. All whitened with ammonium chloride sublimate.





PLATE 6

fers from all the others in having primitive cheirocrinid ambulacra which are developed *between*, not on, the thecal plates and in having cleft radial plates like those of *Coronocystis*, in large individuals. This species is not a cheirocrinid, however, since it has three plates around the periproct and "monti-disjunct" pectinirhombs. The new genus *Glyptocystella* is proposed for Bassler's species.

## Genus GLYPTOCYSTITES Billings 1854

1854 Glyptocystites Billings: 215.

1858a Glyptocystites Billings, Billings: 280.

1858b Glyptocystites Billings, Billings: 53.

1859 Glyptocystites Billings, Hall: 151.

1879 Glyptocystites Billings, Zittel: 423.

1899 Glyptocystites Billings, Jaekel: 275, Text-fig. 36H (p. 197).

1900 Glyptocystis (sic) Billings, Bather: 64.

1910 Glyptocystites Billings, Grabau & Shimer: 463.

1943 Glyptocystites Billings, Bassler & Moodey: 6, 159.

1944 Glyptocystites Billings, Shimer & Shrock: 128.

1946 Glyptocystites Billings, Wilson: 15.

1948 Glyptocystites Billings, Sinclair: 305.

1968 Glyptocystites Billings, Kesling: S169.

Type Species: Glyptocystites multiporus Billings 1854.

Diagnosis: A genus of Glyptocystitidae with ambulacra developed on, not between, thecal plates; some ambulacra extending to basal circlet.

Remarks: *Glyptocystites* is a distinctive genus which is rarely misidentified except that some species of cheirocrinids were initially attributed to it. Kesling (1961) gives a very detailed description of *G. ehlersi* and sumarizes many of the generic characters. It is unnecessary to repeat these details here but some brief comments on *G. multiporus*, the type species, follow.

Glyptocystites multiporus Billings 1854 Plate 7, figs. 1-6, Text-figs. 3h, 4h, 17-18.

1854 Glyptocystites multipora (sic) Billings: 216, Text-figs. 1-5, 7-8.

1858a Glyptocystites multiporus Billings, Billings: 281.

1858b Glyptocystites multiporus Billings, Billings: 54, Pl. 3 (all figures except fig. 1b).

#### **EXPLANATION OF PLATE 6**

#### Glyptocystella loeblichi (Bassler).

FIGS. 1-4.—Stereophotos of USNM 216603/7. 1. Left lateral view. 2. Anterior lateral view. 3. Oral view to show ambulacra, gonopore and hydropore. 4. Right lateral view.

- FIG. 5.—Stereophotos of right lateral view of USNM 216603/8 to show proximal stem. FIG. 6.— Stereophotos of posterior lateral view of USNM 216603/10 to show anal pyramid within periproct.
- FIG. 7.—Stereophotos of anterior lateral view of USNM 216603/4, a large example showing well-developed ambulacra.
- FIG. 8.—Aboral view of USNM 216603/7.

FIGURE 7 X2, all others X4. All whitened with ammonium chloride sublimate.



- TEX-FIGURE 17.---Analysis of plate arrangement in Glyptocystites multiporus Billings, USNM 18012a. Plate and ambulacra symbols as in Text-fig. 2. Plate ridges stippled, monti-disjunct pectinirhomb ridges black, ambulacra horizontally ruled.
- 1896 Callocystis multipora (Billings), Haeckel: 132, Pl. 3, figs. 18-20. 1899 Glyptocystites multiporus Billings, Jaekel: 277, Text-figs. 54 (p. 268) & 57 (p. 275).
- 1900 Glyptocystis (sic) multiporus Billings, Bather: 64, Text-fig. 33.
- 1910 Glyptocystites multiporus Billings, Grabau and Shimer: 143, Text-fig. 1770.
- 1943 Glyptocystites multiporus Billings: Bassler and Moodey: 30, 160.
- 1944 Glyptocystites multiporus Billings, Shimer and Shrock: 129, Pl. 49, figs.
- 1946 Glyptocystites multiporus Billings, Wilson: 15.
- 1948 Glyptocystites multiporus Billings, Sinclair: 311, Pl. 42, figs. 5, 9.
- 1961 Glyptocystites multiporus Billings, Kesling: Text-figs. 1 (p. 63) and 2 (p. 64).
- 1968a Glyptocystites multiporus Billings, Kesling: Text-figs. 73 (p. S171) and 75, 2a-c (p. S173).

#### **EXPLANATION OF PLATE 7**

Glyptocystites multiporus Billings, Glyptocystella loeblichi (Bassler) and Cheirocystis ardmorensis (Bassler).

- FIGS. 1-6.—Stereophotos of Glyptocystites multiporus Billings, USNM 18012a. 1. Anterior lateral view. 2. Posterior lateral view. Note traces of ambulacra reaching the base of the theca. 3. Left lateral view. 4. Right lateral view. 5. Aboral view. 6. Oral view to show mouth, ambulacta, gonopore and hydropore. FIG. 7.—Holotype of "Echinoencrinites ornatus" Bassler, USNM 113106 (=Glypto-
- cystella loeblichi).
- FIG. 8.—Stereophotos of holotype of Cheirocystis ardmorensis (Bassler) USNM 93471. All figures X2. All whitened with ammonium chloride sublimate.



1968b Glyptocystites multiporus Billings: Paul: 712, Pl. 135, fig. 11.

Diagnosis: See remarks.

Types: GSC 1387c, f-g, k & m are Billings' original cotypes.

Horizon and locality: Cobourg Beds (Trenton), Ottawa.

# Remarks:

G. multiporus is illustrated here simply to facilitate comparison with the new genus Glyptocystella (see below). My observations on G. multiporus have been perfunctory and, I now find, inadequate. For nearly a century G. multiporus was the only known species of Glyptocystites and it is very common in museum collections. Bassler (1943), Sinclair (1945, 1948) and Kesling (1961) added new species of *Glyptocystites*, all of which were originally based on very few specimens. Bassler's species is redescribed here as Glyptocystella loeblichi; the other four species belong to Glyptocystites s.s., but I doubt if they all represent distinct species. The pectinirhomb slit-spacings of G. multiporus Bil-lings, G. ehlersi Kesling and G. regnélli Sinclair do not differ by very much but that of G. batheri Sinclair is apparently somewhat coarser (Paul, 1968b, p. 712). I have no information on slit-spacing in G. grandis Sinclair, G. ehlersi and G. regnelli have much more prominent plate and rhomb ridges than the other species. Apart from these characters, the species were originally distinguished on the distribution of pectinirhombs (summarized by Kesling, 1961, p. 68, Table II) and on thecal size. The number and position of pectinirhombs are known to vary in G. multiporus (see, for example, Sinclair, 1948, p. 311) and this would seem to be an unreliable specific character especially when found in only one or two specimens. For G. multiporus Kesling lists (1961, p. 68) 13 pectinirhombs as "always present" and a fourteenth as "present only in some specimens". However, the specimen which I selected to illustrate in this paper (USNM 18012a, Text-figs. 17-18, Pl. 7, figs. 1-6) has only ten pectinirhombs and they are developed in exactly the same positions as



TEXT-FIGURE 18.—Ambulacral structure in *Glyptocystites multiporus* Billings, USNM 18012a. A. Oral surface, B. proximal portion of ambulacrum I, G gonopore, H hydropore, M mouth, O1-O7 orals, I-V ambulacra, I<sup>1</sup>, I<sup>3</sup> et cetera, brachioles in ambulacrum I.

those of the holotype (and only known specimen) of *G. ehlersi.* USNM 18012a was selected for illustration simply because it is well preserved and relatively free of matrix. I was therefore able to make camera lucida drawings of individual plates and combine them to form an accurate plate analysis (Text-fig. 17). It was not until a year later that I noticed the discrepancy in distribution of pectinirhombs. Clearly a thorough revision of all species of *Glyptocystites* is desirable. Hence I am unable to give a precise diagnosis of *G. multiporus*. Neither can I select a lectotype from Billings' original specimens. Although I have examined the type set I did not do so with the intention of revising *G. multiporus*.

# Genus GLYPTOCYSTELLA nov.

Type species: Cheirocrinus ? loeblichi Bassler 1943.

Diagnosis: A genus of Glyptocystitidae with ambulacra developed between, not on, thecal plates. All ambulacra are short, confined to oral surface or extending slightly into radial circlet, plates of which are cleft to receive them. Remarks: *Glyptocystella* differs from *Glyptocystites* s.s. in the structure of the ambulacra (as noted by Sinclair, 1948, p. 312) and from the Cheirocrinidae in the plate arrangement, particularly around the periproct. It is intermediate between the Glyptocystitidae and Cheirocrinidae but has more affinities with the former. Its stratigraphic position, below that of all species of *Glyptocystites* s.s., is consistent with the idea that it is an intermediate step in the evolution of *Glyptocystites* from the Cheirocrinidae.

> Glyptocystella loeblichi (Bassler) 1943 Pl. 5, figs. 1-8, Pl. 6, figs. 1-8, Pl. 7, fig. 7, Text-figs. 19-21.

1943 Cheirocrinus ? loeblichi Bassler: 701, Pl. 1, figs. 1-2.

1943 Glyptocystites loeblichae Bassler: 702, Pl. 1, figs. 8-9.

1943 Echinoencrinites ? ornatus Bassler: 703, Pl. 1, fig. 7.



TEXT-FIGURE 19.—Analysis of plate arrangement in holotype of "Cheirocrinus loeblichi"
 Bassler (= Glyptocystella loeblichi), USNM 113107. Plate symbols as in Text-fig.
 2, plate ridges stippled, monti-disjunct pectinirhomb ridges black. Note the small pectinirhomb across suture B2:L2.



TEXT-FIGURE 20.—Analysis of plate arrangement in holotype of "Glyptocystites loeblichae" Bassler (=Glyptocystella loeblichi), USNM 93484. Plate symbols as in Text-fig. 2 except that symbol in parentheses indicates missing Pl. R4, plate ridges stippled.

1948 Glyptocystites ? loeblichae Bassler, Sinclair: 312.

Diagnosis: As for the genus which is monotypic.

Types: Cheirocrinus loeblichi Bassler USNM 113107, Holotype (monotype). Glyptocystites loeblichae, USNM 93484, Holotype (monotype). Echinoencrinites ornatus, USNM 113106, Holotype (monotype).

Horizon and locality: All specimens are from the Bromide Formation (Middle Ordovician). The type "C." loeblichi is from beside Oklahoma highway 99 in section 12, T. IN, R. 6E, which becomes the type locality. The type of "G." loeblichae is from a hillside above Sulphur Spring, Bromide, Oklahoma, and that of "E." ornatus is from Rock Crossing, Criner Hills, Section 35, T. 5S, R. IE, Oklahoma. Additional material collected by Harrell Strimple (USNM 216603) is from West Branch, Sycamore Creek, Oklahoma.

Material: In addition to the three type specimens, about 30 more or less complete thecae and an equal number of isolated stem fragments (USNM 216603).

# Description:

A. Stem: Proximal portion typical, external flanges of outer proximal columnals thick, with vertical ribs which bear two nodes and an incipient spine at the lower (distal) end. Distal stem unknown.

B. Theca: Roughly cylindrical, with typical smallish lateral periproct surrounded by three thecal plates (IL4, L4, & L5), short ambulacra almost confined to oral surface but extending into notched or cleft radial plates. Plate arrangement shown in Text-figs. 19-21. Plate ornament variable: some plates



TEXT-FIGURE 21.—Analysis of plate arrangement of Glyptocystella loeblichi (Basslet), USNM 216603/4, a large theca with deeply cleft radial plates. Plate symbols as in Text-fig. 2, plate ridges stippled, monti-disjunct pectinirhomb rims black.

smooth except for axial ridges (Pl. 6, figs. 1, 5); others with strongly developed reticulate ornament (Pl. 7, fig. 7). Orals may be smooth or bear ridges or tubercles. Periproct subtriangular, about 3 mm. in diameter in largest example. Frame made by three plates (family character). Periproctal membrance finely plated with small subcentral anal pyramid composed of ten to twelve anal plates (Pl. 5, fig. 4, Pl. 6, fig. 6). Gonopore small, circular, covered with three-valved gonal pyramid. Hydropore a dumbbell-shaped slit. Pectinirhombs "monti-disjunct," one example multi-disjunct (USNM 216603/14). A unique rhomb B2:L2 developed in holotype USNM 113107. Slit-spacing averages 0.2531 (Table 11).

C. Subvective system: Five short ambulacra which extend into cleft radial plates in large examples (Text-fig. 21, Pl. 6, fig. 7). Developed between, not

| Specimen      |        |             |
|---------------|--------|-------------|
| USNM 113107   | B2:1L2 | 02.2730 mm. |
| -             | B2:1L1 | 0.2667 mm.  |
|               | L1:L2  | 0.2222 mm.  |
|               | 1L4:L4 | 0.2889 mm.  |
|               | L3:L4  | 0.2317 mm.  |
| USNM 216603/2 | R1:R2  | 0.2698 mm.  |
|               | B2:1L2 | 0.2476 mm.  |
| USNM 216603/1 | L3:L4  | 0.2730 mm.  |
|               | L1:L2  | 0.2413 mm.  |
| USNM 216603/4 | L1:L2  | 0.2222 mm.  |
|               | R2:R3  | 0.2476 mm.  |

 TABLE
 11

 Pectinirhomb slit-spacing in Glypocystella loeblichi (Bassler)

Mean = 0.2531 mm.

|                  |         |         | Theca   |                       |    | Pectin    | irhombs |       |
|------------------|---------|---------|---------|-----------------------|----|-----------|---------|-------|
| pecimen          |         | H. (mm) | D. (mm) | V. (mm <sup>3</sup> ) | N. | <u>n.</u> | n/N     | V/n.  |
| J <b>SNM</b> 216 | 6603/10 | 8.8     | 5.0     | 172.9                 | 6  | 57        | 9.50    | 3.03  |
| J 9              | / 7     | 8.0     | 5.3     | 176.6                 | 5  | 49        | 9.80    | 3.60  |
| ••               | / 8     | 8.9     | 5.5     | 211.5                 | 7  | 44        | 6.29    | 4.81  |
| ,,               | / 6     | 9.2     | 6.2     | 277.9                 | 6  | 44        | 7.33    | 6.32  |
| ••               | /16     | 12.0    | 8.0     | 603.4                 | 7  | c95       | 13.57   | 6.35  |
| ••               | /12     | 13.1    | 9.0     | 833.7                 | 8  | c75       | 9.38    | 11.12 |
| ,,               | /13     | 13.2    | 9.1     | 858.9                 | 9  | c144      | 16.0    | 5.96  |
| ••               | / 1     | 15.9    | 10.4    | 1351.2                | 9  | c95       | 10.56   | 14.22 |
| ,,               | / 2     | 17.6    | 11.9    | 1958.3                | 8  | 110       | 13.75   | 17.80 |
| ,,               | / 4     | 25.0    | 16.5    | 5347.8                | 12 | 219       | 18.25   | 24.42 |

 TABLE 12

 Relationship of thecal size, number of pectinirhombs and dichopores in Glypocystella (Bassler)

H = Height, D. = diameter, V = volume (calculated as a cylinder), N = number of pectinirhombs, n = number of dichopores

on, thecal plates, as in *Coronocystis* from which *Glyptocystella* probably evolved. Ambulacra have wide main food grooves provided with small ridged cover plates. Brachioles I<sup>2</sup> and IV<sup>2</sup> missing, but ambulacra II, III, and V regular. Up to thirteen brachioles, which reach at least 7 mm. in length and are composed of about 40 brachiolar plates, per ambulacrum.

# Remarks:

Bassler (1943) described three species, each based on a single sometimes incomplete specimen, and all of which I regard as conspecific on the basis of much larger growth series collected by Harrell Strimple from the same formation. Text-figs. 19-21 show the plate analysis for two of Bassler's type specimens and the largest of Strimple's material (USNM 216603/4). Although incomplete the plate analysis of "Cheirocrinus loeblichi" (Text-fig. 19) shows only one infralateral plate (IL4) bordering the periproct and, unless some radically new plate arrangement obtains, only two lateral plates can border the periproct (L4 and L5). The type of "Glyptocystites loeblichae" has just three plates bordering the periproct (IL4, L4 and L5) and Pl. 7, fig. 7, reveals the same three plates bordering the periproct of "Echinoencrinites ornatus." From this I conclude that all three type specimens belong to the same species for which "C." loeblichi is the oldest available name by page priority. Strimple's material reveals the ambulacral structure which necessitates the establishment of a new genus, Glyptocystella, and provides information on growth. Table 12 indicates the relationship between thecal size, number of pectinirhombs and number of dichopores in Glyptocystella loeblichae.

## APPENDIX

Alphabetical list of trivial names of species of *Cheirocrinus* s.l. with their present generic assignments.

| Name                 | Genus                       | Reliability |
|----------------------|-----------------------------|-------------|
| alter                | Homocystites <sup>+</sup>   | 1           |
| anatiformis          | Cheirocystis <sup>+</sup>   | 2           |
| angulatus            | Coronocystis <sup>+</sup>   | 2           |
| antiqua              | Cheirocystella <sup>+</sup> | - 1         |
| ardmorensis          | Cheirocystis                | 1           |
| atavus               | Cheirocystella              | 2           |
| constrictus          | Homocystites                | 1           |
| devener              | "Cheirocrinus" s            | × ×         |
| dilatatus*           | "Cheirocrinus" s            |             |
| torhesi              | "Cheirocrinus" sl           |             |
| eieanteus            | "Cheirocrinus" s            |             |
| granulatus           | Cheirocrinus s.             | 3           |
| eranulosus*          | "Cheirocrinus" s            | 2           |
| ĥolmi                | Cheirocystella              | 1           |
| hyperboreus          | Cheirocystein               | 1           |
| incionic             | Cheirocystic                | 2           |
| interrubtus          | Acantholetis                | 2           |
| iamesii*             | Acanthalepist               | 2           |
| languedocianus       | Chairocustella              | 2           |
| lauchtanharni        | Cheirocystella              | 2           |
| loeblichi            | Gluptocystella <sup>+</sup> | 1           |
| marrilaasi           | Chainacustis                | 1           |
| nodosus*             | "Chairporninus" a l         | 3           |
| nouosus ·            | Cheinoennus 5.1.            |             |
| bonnicon             | Cheirocrinus s.i.           |             |
| penniger<br>radiatus | Cheinocustic                | 5           |
| 74414143             | Chemorysh's                 | 3           |
| 36412143             | Cherrocrinus S.I.           |             |

| striatus<br>tertius | "Cheirocrinus" s.1.<br>"Leptocristis"* | 1 |
|---------------------|--|---|
| volborthi           | "Cheirocrinus" s.l.                    | 1 |
| walcotti            | Cheirocystis                           | 3 |

\*indicates a species described from isolated plates.

\*type species of genus.

Reliability as follows:

1 based on examination of type specimen.

2 based on examination of other specimens.

3 based on description and figures in literature.

All other sources are deemed inadequate for certain generic placement.

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