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THREE PERMIAN STARFISH FROM WESTERN AUSTRALIA AND
THEIR BEARING ON REVISION OF THE ASTEROIDEA

BY
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VOLUME 22

1. New species of Porocrinidae and brief remarks upon these unusual crinoids, by Robert V. Kesling and Christopher R. C. Paul. Pages 1-32, with 8 plates and 14 text-figures.
2. Two unusually well-preserved trilobites from the Middle Devonian of Michigan and Ohio, by Erwin C. Stumm. Pages 33-35, with 1 plate.
3. The corals of the Middle Devonian Tenmile Creek Dolomite of northwestern Ohio, by Erwin C. Stumm. Pages 37-44, with 3 plates.
4. Mouth frame of the ophiuroid *Onychaster*, by Philip R. Bjork, Paul S. Goldberg, and Robert V. Kesling. Pages 45-60, with 4 plates and 4 text-figures.
5. Rugose corals of the Silica Formation (Middle Devonian) of northwestern Ohio and southeastern Michigan, by Erwin C. Stumm. Pages 61-70, with 4 plates.
6. A redescription of the Middle Silurian compound rugose coral *Grabauphyllum johnstoni* Foerste, by Erwin C. Stumm. Pages 71-73, with 1 plate.
7. Systematics and faunal analysis of a Lower Pliocene vertebrate assemblage from Trego County, Kansas, by Richard L. Wilson. Pages 75-126, with 17 text-figures.
8. *Gemmaecrinus chilmanae*, a new crinoid from the Middle Devonian Silica Formation in southeastern Michigan, by Robert V. Kesling. Pages 127-131, with 1 plate and 1 text-figure.
9. Note on ontogeny of the Middle Devonian crinoid *Proctothylacocrinus esseri* Kesling, by Robert V. Kesling. Pages 133-138, with 2 plates and 4 text-figures.
10. *Archaeosperma arnoldii*—a cupulate seed from the Upper Devonian of North America, by John M. Pettitt and Charles B. Beck. Pages 139-154, with 6 plates and 3 text-figures.
11. *Ameliacrinus benderi*, a new dicyclic camerate crinoid from the Middle Devonian Silica Formation in northwestern Ohio, by Robert V. Kesling. Pages 155-162, with 3 plates and 2 text-figures.
12. *Logocrinus conicus*, a simple new Middle Devonian inadunate crinoid from Michigan, by Robert V. Kesling. Pages 163-167, with 1 plate and 1 text-figure.
13. Copulatory adaptations in ostracods, Part I. Hemipenes of *Candona*, by Don L. McGregor and Robert V. Kesling. Pages 169-191, with 3 plates and 16 text-figures.
14. A fossil carabid beetle from the Miocene of Montana, by P. J. Darlington, Jr. Pages 193-197, with 2 plates.
15. Two new crinoids from the Middle Devonian Silica Formation, by Robert V. Kesling. Pages 199-206, with 2 plates.
16. Mammalian and other fossils, Early Eocene Pass Peak Formation, central western Wyoming, by John A. Dorr, Jr. Pages 207-219, with 1 plate and 2 text-figures.
17. Copulatory adaptations in ostracods, Part II. Adaptations in living ostracods, by Don L. McGregor and Robert V. Kesling. Pages 221-239, with 17 text-figures.
18. Devonian bioherms of the Michigan Basin, by Erwin C. Stumm. Pages 241-247, with 2 plates and 4 text-figures.
19. *Silicaster*, a new genus of Devonian starfish, by Robert V. Kesling. Pages 249-261, with 4 plates and 2 text-figures.
20. Inarticulate brachiopods of the Silica Formation (Devonian), Ohio and Michigan, by R. D. Hoare and D. L. Steller. Pages 263-272, with 2 plates.
21. Copulatory adaptations in ostracods, Part III. Adaptations in some extinct ostracods, by Robert V. Kesling. Pages 273-312, with 23 text-figures.
22. Growth patterns in *Proctothylacocrinus longus* Kier, by Robert V. Kesling. Pages 313-322, with 14 text-figures.
23. Charles Southworth, fossil collector of Thedford, Ontario, 1880-1968, by Jean D. Wright. Pages 323-338, with 14 text-figures.
24. *Cunctocrinus*, a new Middle Devonian calceocrinid crinoid from the Silica Shale of Ohio, by Robert V. Kesling and James P. Sigler. Pages 339-360, with 1 plate and 13 text-figures.

THREE PERMIAN STARFISH FROM WESTERN AUSTRALIA AND THEIR BEARING ON REVISION OF THE ASTEROIDEA

ROBERT V. KESLING

ABSTRACT—Study of three new Permian starfish from Australia and restudy of other late Paleozoic genera reveal the inadequacy of current classification at suprageneric levels. Orders are revised so that they are distinct from one another and so that the families within each order share common characters.

INTRODUCTION

SOME PERMIAN STARFISH from western Australia are significant for two reasons. First, they constitute new taxa; and second, they lead to re-evaluation of the suprageneric classification of asteroids.

The starfish described here are from Permian strata of Western Australia. They were catalogued in the collections of the University of Western Australia under the number 26992. On his recent visit there, they came to the attention of Professor Donald B. Macurda, Jr., who arranged to borrow them and brought them to our Museum for study.

Cursory inspection showed that the starfish were indeed well preserved and apparently new. Light work with Airdent and fine abrasive cleaned the specimens of limonitic weathered matrix and revealed details of the madreporic plates. Then several pieces were found to fit perfectly, and the larger individuals were carefully re-assembled.

It is not unusual in Paleozoic invertebrates to discover that new specimens lead to new species and genera, and that these in turn lead to new assessments of suprageneric categories. This is the case with the Permian starfish studied here.

At present, it is impossible to assign a specimen to the correct order on the basis of the published accounts. The orders within the subclass Asteroidea are defined on such diverse criteria that they do not appear to be mutually exclusive. To provide an adequate placement of the new starfish, some revisions are suggested at the ordinal level.

Although in the Asterozoans section of the *Treatise on Invertebrate Paleontology* Spencer & Wright (1966) introduced new taxa and shifted assignments of many others, their classification of starfish remains far from satisfactory. Three major deficiencies stand out: (1) des-

criptions are incomplete for fossil genera and completely lacking for most Recent genera, (2) many suprageneric taxa are defined on characters which have never been preserved in fossils, and (3) diagnostic data are insufficient to support any kind of cladistic treatment or phyletic organization.

Terminology and reported observations require careful scrutiny. Original descriptions of species and genera have been written in many languages and spread over many generations. Translation from one language to another, or from older works into more up-to-date terminology, has not, regrettably, always retained the sense of the original author's interpretation—or even of his observations. For example, in the last century some writers used *marginals* to indicate whatever plates formed the border of the arms, whereas recent workers have taken the term to apply only to a series of superomarginals or inferomarginals. The frequency of such misunderstandings emphasizes the need to re-examine type specimens before formulating new classifications.

To classify the new starfish, it is necessary to re-examine the genus *Monaster* and to re-define some of the orders of the Asteroidea.

Abbreviations used in the discussion and descriptions are the same as those used in Kesling (1969); in addition, MAP(s) = mouth-angle plate(s) and Amb(b) = ambulacral(s).

The starfish have been returned to the University of Western Australia (UWA), where they are catalogued as 26992a-e. Plastoholotypes of the new species were prepared, catalogued, and deposited in the Museum of Paleontology of The University of Michigan (UMMP) as 57466-57468.

I am very grateful to Dr. Patrick J. Coleman and Mr. Donald Rhodes, both of the Department of Geology at the University of Western Australia, who permitted me to study the

specimens and publish my conclusions. Mr. Karoly Kutasi photographed the specimens. Mrs. Gladys Newton typed the manuscript. Mr. Peter B. Loomis prepared the camera lucida drawings for the text-figures. Professor E. C. Stumm and Professor C. A. Arnold reviewed the paper. For their help I extend my thanks.

OCCURRENCE OF SPECIMENS

All starfish described here are from the same locality and formation. The label with the specimens states:

Wandagee Stage / Zone: *Calceospongia-Strophalosia*; Large *Spirifer* / Minilya River, Canning Basin, W. A. / NE side of syncline N of Minilya River and E of Coolkilya Pool.

As shown in table 1, the term Wandagee stage was used by Teichert in 1939 and divided into five zones or beds, the middle of which was the

of plates: a median aboral R row, two aboral lateral Sm rows, two oral lateral Im rows forming the borders, and two wide Adm rows on the oral side along the ambulacral groove. This interpretation may be questioned.

The original description is not particularly clear as regards plate arrangement. Etheridge (1892) contrasted his specimens with the starfish assigned by James Hall to *Palaeaster*. The latter had on the oral side two series of plates on each side of the ambulacral groove (Adm and Im) and on the aboral side at least three additional series of plates (two Smm and one R). Etheridge stated (1892, p. 70-71):

In the case of our specimens, only one set of plates excepting those of the ambulacral grooves, are, as before stated, absolutely actinal; the marginal are strictly so, or, at the least, sub-dorsal. Under these circumstances, I propose distinguishing our Australian species under the sub-generic name of *Monaster*.¹

TABLE 1—STRATIGRAPHY OF PERMIAN ROCKS IN THE CARNARVON BASIN, WESTERN AUSTRALIA

| | Teichert 1939 | Teichert 1941 | Teichert 1950 | Condon 1954 |
|----------------|--|-----------------------------|---------------------|---------------------|
| | <i>Fenestella-Helicoprion</i> beds | <i>Lino-productus</i> stage | Coolkilya Sandstone | Coolkilya Greywacke |
| Wandagee stage | Lamellibranch beds | Wandagee series | Nalbia Sandstone | Nalbia Greywacke |
| | <i>Calceolispongia-Strophalosia</i> beds | | Wandagee Formation | Wandagee Formation |
| | <i>Calceolispongia-Aulosteges</i> beds | | | |
| | <i>Lingula</i> beds | <i>Lingula</i> stage | Quinnanie Shale | Quinnanie Shale |

Calceolispongia-Strophalosia beds. This unit became part of the *Calceolispongia* stage of the Wandagee Series in Teichert's 1941 revision of stratigraphy, and is now part of the restricted Wandagee Formation (Teichert, 1950, p. 1791; Condon, 1954, p. 79; Smith, 1963, p. 191-192). The locality is near 23°44'S. and 114°25'E., and lies in the Carnarvon Basin rather than the Canning.

THE NATURE OF *Monaster*

Spencer & Wright (1966, p. 54) described the monogeneric family Monasteridae as having Im, Sm, and R plates visible on the aboral sides of the arms and exceptionally wide Adm plates on the oral sides. Thus, they considered that the arms of *Monaster* contained (in addition to the internal Amb plates) seven series

In a footnote (1892, p. 71) Etheridge explained:

¹From the one or single row of adambulacral plates on each side of an ambulacral avenue.

He then compared his subgenus *Monaster* with *Urasterella*, which "likewise only possesses the adambulacral plates on the ventral surface; but in this case neither are there marginal plates."

To his subgenus *Palaeaster* (*Monaster*), Etheridge (1892) assigned *Palaeaster clarkei* DeKoninck (p. 71), *stutchburii* n. sp. (p. 73), and *giganteus* n. sp. (p. 74). This sequence enters into the nomenclatural problem that arose later.

Under *Palaeaster* (*Monaster*) *clarkei*, Etheridge stated 1892, p. 71 in part:

. . . Abactinial plates hexagonal, thick, and convex, arranged in three rows, . . . the median the smal-

lest and alternating with the lateral series, which are transversely elongated. Adambulacral plates . . . large, very transverse, narrow, and convex. Marginal plates subdorsal in position, convex, narrow, and triangular, more or less resembling the plates of the abactinal surface, but differing in ornament . . .

The significant question is what did Etheridge mean by "marginal"?

Schuchert (1915, p. 171) interpreted Etheridge's term *marginal plates* as "having reference to the plates along the margins which consist of adambulacrals, and also form part of the abactinal skeleton." Was this Etheridge's intent, or was it Schuchert's wishful translation? After reviewing the publications many times, I still doubt Schuchert's interpretation—not as regards accuracy of the actual plate arrangement in *Monaster*, but as regards what Etheridge thought about his specimens. Etheridge described *P. (M.) clarkei* as having "very transverse" adambulacral plates and "triangular" marginal plates. I must conclude that he had in mind two kinds of plates, adambulacrals and marginals, and that he did not regard the lateral borders of the adambulacrals as constituting marginals.

Regardless of what Etheridge thought or wrote, the nature of his three specimens of *Palaeaster (Monaster) clarkei* is indicated in his illustrations (1892, pl. 14, figs. 1, 2; pl. 15, fig. 4). All are external molds, one of the oral surface and two of the aboral surface. The mold of the oral surface (his pl. 15, fig. 4) shows the very wide and narrow Adm plates with no definite impression of other plates along the edge. On one of the aboral molds (his pl. 14, fig. 2) edges of narrow plates project beyond the rows of Smm; somehow the central part of the specimen had been removed before the external mold formed, so that impressions of its Ambb appear in this area. The plate edges forming the border beyond the Smm could be Imm—in which case Spencer & Wright are correct—or they could be Admm—in which case Schuchert is correct.

The family Monasteridae was created by Schuchert (1915, p. 170) for starfish "with massive plates, especially the adambulacrals, which are common to the actinal and abactinal areas." The family contained only *Monaster*, of which Schuchert said (1915, p. 170), "Outside of the supramarginals the animal is bounded by single columns of prominent, short, but very wide plates, which are the abactinal aspect of the actinal adambulacrals."

When the Monasteridae came into being, the only species placed in *Monaster* by Schuchert was *Palaeaster clarkei* De Koninck. Etheridge's *P. (Monaster) giganteus* was made by Schu-

chert the type of his new genus *Australaster* (1915, p. 72), to which he with question assigned also *P. (Monaster) stutchburii* (1915, p. 73). Hence the status of the family Monasteridae and the genus *Monaster* rests with *Monaster clarkei* (De Koninck), itself represented by external molds. Little can be learned of this species in De Koninck's original description and figures (1877, p. 166, pl. 7, figs. 6, 6a) and the holotype was destroyed by fire. The most reliable information is contained in Etheridge's (1898) figures and in Schuchert's interpretation.

Meanwhile, however, Gregory (1899, p. 345) had selected *Palaeaster (Monaster) giganteus* Etheridge as the type of *Monaster*, and made (1899, p. 353) *P. clarkei* De Koninck the type of his new genus *Etheridgaster*. Inasmuch as *giganteus* has both Im and Sm plates, and does not fit Etheridge's description of *Monaster*, Schuchert and others claimed that *Etheridgaster* must be a junior synonym of *Monaster*. The case is pending before the International Commission on Zoological Nomenclature.

For this paper, the family Monasteridae, containing only the genus *Monaster*, type species *M. clarkei* (De Koninck), is regarded as having only two rows of plates on each side of the arm. These rows are interpreted as Admm and Imm, not only in *Monaster clarkei* but also in two new species described below.

REVISION OF ORDERS

Evolutionary changes in Asteroidea.—In order to approach phylogeny, any system of classification must take into account the evolutionary changes in each major character and consider each character in the sequence of its importance to the animal. As Fell (1963b, p. 385) pointed out, the geologic record is too incomplete to date the inferred stages of differentiation; other lines of evidence are available in functional morphology and embryology among the surviving forms.

The initial stages of starfish evolution have been succinctly outlined by Fell (1963a, 1963b). From a crinoid-like ancestor, the first starfish evolved as a somasteroid by the pinules developing into virgalia and establishing interpinnular grooves. When terminal plates were established at the ends of the rows of virgalia and the proximal three elements were fused to form MAPs, the stage of the somasteroid *Platasterias* was reached.

The change from somasteroid to asteroid was accomplished by further modification of the virgalia; the critical change was the formation of a fixed ambulacral groove. When elements

could be identified as Amb, Adm, and Im plates, the stage of *Platanaster* was attained. Reduction in length of elements led to the change of arms from petaloid to "strap-shaped" and produced a starfish like *Luidia*. In subsequent evolutionary modifications, primitive pedicellariae were formed, an aboral anus developed at the end of the originally blind gut, the central disk expanded, interpinnular grooves disintegrated, tube-feet grew suckers, and specialized pedicellariae appeared. Other changes occurred which do not concern the discussion here (Fell, 1963b, p. 391, 392, 411-432).

According to Fell's analysis, based on comparative morphology, the calyx plates of the crinoid gave rise to the disk plates of the starfish, and crinoid pinnulars became somasteroid virgals and thence evolved into starfish arm plates. Thus, biserial arm Br of the crinoid became the Amb of the starfish, the basal pinnular became the Adm, the second pinnular became the superambulacral, and the distal pinnular became the Im. The Sm is said by Spencer & Wright (1966, p. 30) to be a modified ossicle of "extraxial skeleton in origin," meaning that it was secondarily formed from elements in the aboral integument of the arm. Similarly, the carinal (commonly called an arm R) and the distal arm plates were added after the evolution of the starfish and have no ancestral homologues in the crinoid.

These inferences explain the origin of asteroids, but they do not cover all the subsequent changes which occurred in the subclass. Fell (1963b, p. 393) stated, "Schuchert's (1915) belief in the archetypal nature of the Hudsonasteridae cannot be maintained." This is true insofar as the Asteroidea are concerned as a group; but there is still no evidence that *Hudsonaster* and its contemporary near relatives were not ancestral to most of the later Paleozoic asteroids. It is certainly possible that Fell was correct in pre-Ordovician evolution and that Schuchert was correct in post-Ordovician evolution of asteroids.

In this connection, the evidence from fossil forms is not clear cut. Structures may evolve, serve the animal for a time, and degenerate and disappear when their function is no longer needed. For example, *Neopalaeaster* has no RR (carinals) in its arms; but did it evolve from an ancestor which had not yet produced RR, or did it evolve by loss of RR from an ancestor which had them? Further, the new genus *Permaster* lacks Smm in its arms; were these plates always absent in the ancestors, or were they lost in later stages of evolution? In such cases, the chronological sequence of taxa may offer some guidelines.

Protopalaeaster and *Hudsonaster* have the following characters which persisted in numerous later Paleozoic asteroids: (1) coronet atop the disk composed of ten strong plates, of which five were radial and five interradiial, (2) M aboral, framed by three well-developed plates, the proximal of which is one of the coronet, (3) Ax in each interradius, forming an outer buttress against the pair of MAPs, (4) Admm as tiled margins along both sides of the ambulacral channel, (5) Imm just outside the Adm rows, forming the edges of the arms, and (6) mouth-frame adambulacral. Characters which were maintained in some lineages and lost in others include: (1) C and surrounding plates within the coronet, (2) RR (carinals) along the middle of the aboral side of the arm and aligned with R₁ (primary radial) of the disk, and (3) Smm between RR and Imm of the arms and aligned with Smm₁ and Smm₂ of the disk.

The basic plan of *Protopalaeaster* was modified in some of its Paleozoic successors. (1) Diminution of major plates of the disk and intercalation of little accessory ossicles led to an integumental covering studded with tiny irregular granules. In the plate reduction, the coronet was more persistent than the central plates, giving considerable rigidity to the disk and acting as a frame around the soft, flexible central integument. Perhaps this influenced Spencer & Wright to call the central region a "protrusible cone." (2) All or most Smm in the arms were secondarily eliminated. When the Sm rows became limited to a few proximal plates associated with the disk, the Imm tended to move out and upward to form lateral shields alongside the arms, and their former positions on the oral surface were taken up by expanded Admm. (3) RR or carinals on the arms were less stable than the marginals, and in various genera were replaced by little insignificant scalelike ossicles. (4) RR and Smm, as well as other adjacent plates, became separated by the intercalation of accessory ossicles to form papular areas. This was particularly true in old individuals. (5) Ax became modified in various ways and shifted from its alignment with the Im rows; in some it migrated from the oral surface to the sides of the disk. In a few it became massive, but in others it dwindled or even disappeared as an identifiable entity.

These modifications occurred in different degrees and in various combinations. In separating the Asteroidea into lower taxonomic categories, we find that the fossil record is disappointing for many lineages and fails to show clear trends or progressions. Information is too fragmentary at this time to support a reliable

cladistic treatment of the asteroids. Nevertheless, the general organization of the orders is indicated.

Present classification.—Some orders of the Asteroidea encompass an assortment of starfish so diverse that their close relationship must be questioned. As taxa are constituted in the *Treatise* by Spencer & Wright (1966), this applies particularly to the Valvatida; it is this order which seems inconsistent by including the suborders Pustulosina, Tumulosina, and Granulosina.

Inasmuch as pedicellariae are not fossilized, the term *valvate* can only apply to living starfish. The inclusion in the Valvatida of the Paleozoic suborder Pustulosina and the extinct families Monasteridae and Stauranderasteridae of the suborder Tumulosina must be based on other characters. There is doubt that such characters exist.

Differences between the Pustulosina and the Granulosina are obvious and extend to such basic characters as MAPs and disk. The MAPs are not extremely large in any of the Pustulosina, but they are more developed and more clearly differentiated from adjacent Admm than those living genera of the Granulosina. The Pustulosina preserves a coronet of primary RR and Smm throughout its history, but the Granulosina has the disk covered only by small ossicles embedded in the integument stretched across the frame of marginals.

The suborder Tumulosina seems to fall short of Spencer & Wright's expectations for a unified taxon. They wrote (1966, p. 54):

This suborder is erected for a presumed phyletic assembly of peculiar forms characterized by a high swollen disc covered with rather large ossicles notched in one way or another to allow for extrusion of papulae.

Actually, each of its three families differs significantly from the other two. Further, there is no known sequence leading logically from one family to another, and no starfish of the suborder is known from Triassic or Lower Jurassic strata.

The family Monasteridae, based on the one genus *Monaster*, is by my understanding a far different starfish from the interpretation of Spencer & Wright (1966, p. 54, 55), as explained above. Its arms are composed externally of Adm, Im, and R plates, and lack Sm rows. Although it is true that the disk is "high" and "covered with rather large ossicles," in this character it is essentially like many of the order Pustulosida, such as the Ordovician *Protopalaeaster*, the Silurian *Cocaster*, the Devonian *Clarkeaster*, or the Mississippian *Neopalaeas-*

ter. In lacking Smm in the arms, it resembles *Silicaster* Kesling and *Neopalaeaster* Schuchert. I regard *Monaster* as the culmination of a lineage of Pustulosina in which the Sm plates were eliminated from the arms and persisted only in the structure of the disk.

As for the Stauranderasteridae, they appear to be Mesozoic derivatives of the early Pustulosina, retaining the basic arm organization of the Ordovician Hudsonasteridae. They differ from *Monaster* in having Sm series extending the full length of the arms.

The Sphaerasteridae, however, are bizarre starfish in which the arms have been incorporated into the disk region. The mosaic of plates seems to be arranged in a definite pattern of radial and interradial series. Of all the starfish included by Spencer & Wright in their Tumulosina, the Sphaerasteridae are the only ones so far removed from the Pustulosina by specialization as to warrant a separate suborder. They extend from Middle Jurassic to Recent, but their origin remains obscure.

Revised orders.—The following key and diagnoses are presented here to provide a taxonomic framework for the new starfish described below. It is assumed that refinements will follow future discoveries.

KEY TO ORDERS OF ASTEROIDEA

1. Ossicles on oral side of arm in transverse gradients PLATYASTERIDA
Ossicles not in transverse gradients 2
2. Subspherical, disk inflated, arms not protuberant TUMULOSIDA
Stellate, disk not strongly inflated, arms protuberant 3
3. Mouth-frame of ambulacral type FORCIPULATIDA
Mouth-frame of adambulacral type 4
4. Marginals large, invariably fewer than Admm VALVATIDA
Marginals (Imm or Smm) at least as numerous as Admm 5
5. Accessory interbranchials forming conspicuous field between bordering Imm and Admm PAXILLOSIDA
No field of accessory interbranchials 6
6. MAPs large, spade- or plowshare-shaped; M oral SPINULOSIDA
MAPs not large; M aboral PUSTULOSIDA

KEY TO SUBORDERS OF PUSTULOSIDA

- Arms aborally bearing well-developed rows of Smm and RR (carinals);
Imm oral, alongside
Admm BIMARGINALINA
- Arms aborally bearing (at most) only a few Smm; RR (carinals) absent in some; Imm at sides, forming lateral shields and extending high up on arms MONOMARGINALINA

Order PLATYASTERIDA Spencer 1951

Diagnosis.—Stellate asteroids, arms petaloid or strap-shaped. Arms consisting of transverse rows of Amb, Adm, and Im plates. Ambulacral groove present, but shallow. Transverse grooves between sets of ossicles on oral surface. Mouth-frame adambulacral. MAPs well developed, associated with Ax in each interradius. Amb arched slightly above oral surface; Adm short, broad in forms with petaloid arms and narrow in forms with strap-shaped arms. Im conspicuous in all except *Palasteriscus*, in which it is replaced by marginal strip of integument with imbedded tiny ossicles. Aboral side of arm provided only with ossicles, no Sm or R plates. No coronet or strongly developed calycinal skeleton in adult, the disk covered only by integument bearing small ossicles. M variously placed from aboral near the margin to oral near the mouth-frame. Well-developed spines borne by Im and, in forms with petaloid arms, by the broad Adm, proximally arranged in a median row. Aboral surface covered by paxillae, more or less distributed in numerous parallel rows.

Families.—Palasteriscidae Gregory 1900, Luidiidae Verrill 1899.

Order PAXILLOSIDA Perrier 1884

Diagnosis.—Stellate asteroids. Arms five or many, tapering. Mouth-frame adambulacral. MAP prominent, in many genera with keel and median furrow. Ambulacral areas broad; Adm recognizable in fossil forms. Plates called Imm proximally separated from Admm by intercalation of accessory ossicles, in many forming a frame around a plated interbrachial arc (large in some forms). No Smm associated with disk; in a few forms the aboral arm plates have been termed Smm, but they do not show close association with Imm. M oral or aboral; if aboral it is not framed by Sm disk plates and seems to have been free to shift over the edge onto the oral surface by supplanting small plates of the arc. Each interradius filled with interbrachial plates or ossicles between bordering Imm and Admm. Tube feet present, in two rows. Some

genera have marginals channeled, presumably to conduct water from aboral to oral surface. Paxillae common on aboral surface. *L. Ord-Rec.*

Suborders.—Hemizonina Spencer 1951, Diplozonina Spencer & Wright 1966, Cribellina Fisher 1911, Notomyotina Ludwig 1910. The content of suborders and families accepted as given in the *Treatise*.

Order VALVATIDA Perrier 1884
[= Granulosa Perrier 1894]

Diagnosis.—Stellate to pentagonal asteroids. Mouth-frame adambulacral. Marginals large, blocky, fewer than Admm. Sm plates normally equal in number and immediately overlying corresponding Imm, but in some advanced families the distal Smm of each arm may fuse whereas the Imm remain discrete. No coronet or conspicuous disk plates in adult, the calycinal system of the young being supplanted by mosaic of small platelets, irregular ossicles, or granules. Pedicellariae common, generally valvate and sunk into ossicles; paxillae and/or spines common on aboral plates. MAPs triangular, relatively small. *L. Jur-Rec.*

Families.—Goniasteridae Forbes 1841, Archasteridae Viguier 1878, Odontasteridae Verrill 1889, Oreasteridae Fisher 1911, Ophidiasteridae Verrill 1867, Chaetasteridae Sladen 1889.

Order PUSTULOSIDA Spencer 1951

Diagnosis.—Stellate asteroids. Mouth-frame adambulacral. Ax associated with each pair of MAPs. Adm and Im rows of plates in all forms. Central R row and two lateral Sm rows on aboral side of arms in some but Sm or R and Sm rows absent in others. Coronet well developed. Sm plates in each interradius of disk. M always aboral, set within three Smm. Aboral center of disk with C and surrounding plates within coronet, or covered with small irregular ossicles. Proximally on each arm, accessory ossicles may occupy a papular area and extend distally between R and Sm rows. Aboral anus. Basins for tube feet large in some genera, minute or absent in others. Pedicellariae unknown. *L. Ord-U. Cret.*

BIMARGINALINA n. suborder

Diagnosis.—Arms aborally bearing well-developed rows of Smm. RR (carinals) rudimentary or absent in only a few genera. Imm on oral side, set in row alongside Admm, and commonly extending out beyond row of Smm to form actual margin. *L. Ord.-U. Cret.*

Families.—Palaeasteridae Miller 1889, Hudsonasteridae Schuchert 1914, Mesopalaeasteridae Schuchert 1914, Xenasteridae Gregory 1899, Promopalaeasteridae Schuchert 1914, Eoactinidae Spencer 1919, Stauranderasteridae Spencer 1913. This content differs from that of Spencer & Wright (1966) for their suborder Pustulosina in excluding the family Neopalaeasteridae and in adding the family Stauranderasteridae. Thus, the range of the suborder is extended beyond the Lower Carboniferous to include the Mesozoic starfish of the Stauranderasteridae, which have little in common with the family Sphaerasteridae and seem to be the last survivors of a flourishing Paleozoic stock.

MONOMARGINALINA n. suborder

Diagnosis.—Arms aborally bearing (at most) only a few Smm and these associated with the disk. RR (carinals) absent in some. Imm well developed, forming lateral shields for the arms and extending high up on arm, commonly occupying the positions of the Smm in the Bimarginalina. Admm broad, tending to extend to or nearly to the margin, filling the space released by the Imm. *Miss.-Perm.*

The upward displacement of the Imm and their expansion make them take the form of the lateral shields in ophiuroids. This is regarded as convergence, and evolved in asteroids much later than it did in ophiuroids.

Families.—Neopalaeasteridae Schuchert 1915, Monasteridae Schuchert 1915.

Order TUMULOSIDA Spencer & Wright 1966

Diagnosis.—Dome-shaped to subspherical asteroids; arms not produced, incorporated in disk. Covered with mosaic of close-fitting plates. *M. Jur.-Rec.*

Family.—Sphaerasteridae Schöndorf 1906.

Order SPINULOSIDA Perrier 1884

Diagnosis.—Stellate asteroids. Mouth-frame adambulacral. MAPs prominent but not keeled. Arms commonly long and narrow, several genera with multiple arms. Marginals rare in adult; aboral side of arm with numerous reticulate or imbricate small scalelike ossicles except in Taeniactinidae, which retains three rows of distinct plates on each arm. No strong coronet, the aboral plates of the disk in rather loose association. Ax present, bordering MAPs. Aboral skeleton consisting mostly of paxillae, arranged in regular rows, in most families. M oral and large in fossil starfish. Pedicellariae, if present, developed as grouped spines. *M.Ord.-Rec.*

Suborders.—Eugnathina Spencer & Wright 1966, Leptognathina Spencer & Wright 1966. Classification of families as in the *Treatise* (1966, p. 65–71).

Order FORCIPULATIDA Perrier 1884

Diagnosis.—Stellate asteroids. Mouth-frame ambulacral. Ax or O set commonly on side of disk and forming an interradiial buttress. Aboral surface of both arms and disk variously developed, from coronet and regular rows of plates on arms to irregular array of dermal ossicles. In many older representatives, Admm very short and wide, like a stack of coins on edge; if Admm well developed, Im rows set on side and shoulder surface of arm. Smm, if present, normally confined to disk. M aboral but not always set within well-defined Smm. Pedicellariae, if present, forcipulate, either straight or crossed. *L.Ord.-Rec.*

Suborders.—Uractinina Spencer & Wright 1966, Asteriagina Fisher 1928, Brisangina Fisher 1928. Content of suborders and families as in the *Treatise* (1966, p. 71–78), with some exceptions.

SYSTEMATIC DESCRIPTIONS

Order PUSTULOSIDA Spencer 1951

Suborder MONOMARGINALINA n. subord.

Family MONASTERIDAE Schuchert 1915

Diagnosis.—Monomarginaline Pustulosida in which RR (carinals) are developed along the aboral median line of each arm, tending to alternate with aboral ends of Imm.

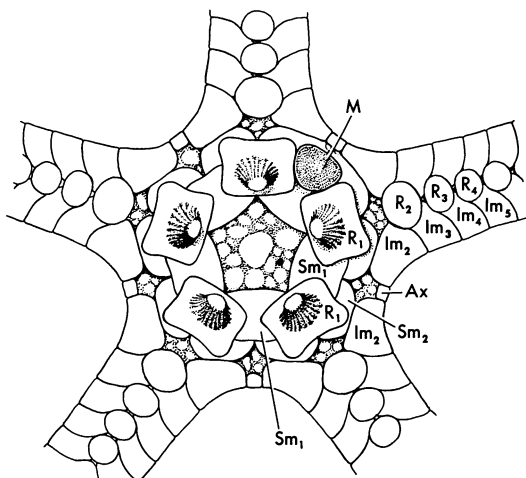
Remarks.—This family differs from the Neopalaeasteridae in having RR in the arms. Like other starfish of the Pustulosida, the Monasteridae have an adambulacral mouth-frame and an Ax abutting against each pair of MAPs. The coronet is well developed with alternating RR₁ and Smm₁. One Sm₁ lies proximal to M and two Smm₂ hold M rather firmly ventrolaterally. Within the coronet, the top of the disk may be plated or covered with irregular ossicles. The aboral plates of arms (and in some of the coronet) are pustulose.

MONASTER Etheridge 1892

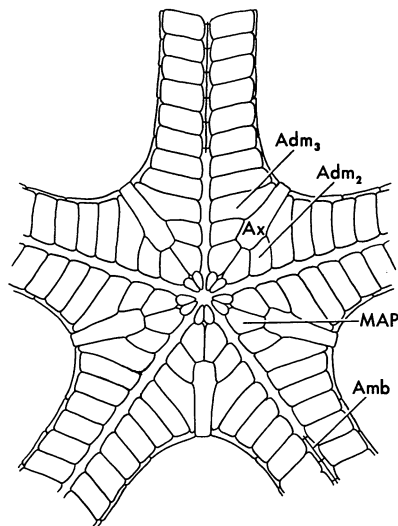
MONASTER WANDAGEENSIS n. sp.

Pl. 1, figs. 1, 2; pl. 3, figs. 2–4; text-figs. 1, 2

Description.—Stellate; arms tapering very gradually, nearly parallel-sided, except proximally, there flared to form a smooth inter-brachial curve. Disk rather strongly constructed, with a prominent coronet. R₁ especially conspicuous; its base blocky and subquadrate, pro-



TEXT-FIG. 1—*Monaster wandageensis* n. sp. Aboral view of disk and arm bases; ornamentation incompletely indicated.



TEXT-FIG. 2—*Monaster wandageensis* n. sp. Oral view.

jecting over margins of adjacent Sm_1 and Sm_2 plates, and its apex strongly produced into a greatly elevated node or blunt spine (pl. 3, figs. 3, 4). Sm_1 incorporated in coronet but overlapped by adjacent RR_1 . Center of disk evidently plated, but details not preserved. Sides of disk formed by Sm_2 plates and by outer end of Ax. M rather large, set somewhat loosely within triad of Sm_1 and Smm_2 , its weathered surface showing subradial striae.

Oral surface exceptionally flat. Mouth-frame adambulacral. Mouth small. MAPs about the same size as adjacent Admm; each subtrapezoidal and bearing a conspicuous orad flattened spine. Ax large, its inner border bluntly acuminate against pair of MAPs and its outer border reaching edge of interradius; proximal half with parallel sides, distal half tapering.

Arms strongly plated. Amb plates, as seen at broken end of arm (pl. 3, fig. 3), small and set well above oral surface of arm. Admm much wider than long (pl. 1, fig. 2), very thick, in lateral view (pl. 3, fig. 3) occupying the oral third of the total arm. Admm extending from ambulacral groove to margin, distally tapering very gradually, the proximal few expanding to

form a smooth interbranchial curve with the Ax; in each half-ray, only the Adm next to the MAP failing to reach the edge of the arm, its distal end acuminate between Ax and the adjacent Adm. Surface of these plates somewhat weathered, but showing traces of a few spines each, probably arranged in a transverse row.

Im plates longer than Admm (pl. 3, fig. 3), more or less subquadrate and close-fitting, the proximal edges of opposing pairs only slightly separated along the aboral midline of the arm (pl. 1, fig. 1). Im rows thus set atop the thick edges of the Adm rows, in about the positions occupied by Sm plates in typical genera of the suborder Bimarginalina.

Arm RR (carinals) rather small, not in contact with adjacent RR, alternating with proximal ends of Imm.

Surface of Imm and arm RR pustulose. Base of R_1 pustulose, its produced apex with striate sides.

Remarks.—This species differs from the type species, *Monaster clarkei* (De Koninck), by its straighter arms and more numerous arm plates. It is named for the Wandagee Formation.

EXPLANATION OF PLATE 1

All figures $\times 2$; specimen lightly coated with ammonium chloride

- FIGS. 1, 2—*Monaster wandageensis* n. sp. Holotype, UWA 26992a (plastoholotype, UMMP 57466). Aboral and oral views. Other views shown in plate 3, figures 2–4.
 3–6—? *Monaster wandageensis*. 3, 4, aboral and oral views of badly weathered disk, UWA 26992b; another view shown in plate 3, figure 1. 5, 6, aboral and oral views of isolated arm, UWA 26992c.
 7, 8—*Monaster carnarvonensis* n. sp. Holotype, UWA 26992d (plastoholotype, UMMP 57467). Aboral and oral views. Other views shown in plate 3, figures 5, 6.
 9–11—*Permaster grandis* n. gen. n. sp. Holotype, UWA 26992e (plastoholotype, UMMP 57468). Aboral, oral, and lateral views. Other views of this specimen shown in plate 2, figures 1–6.

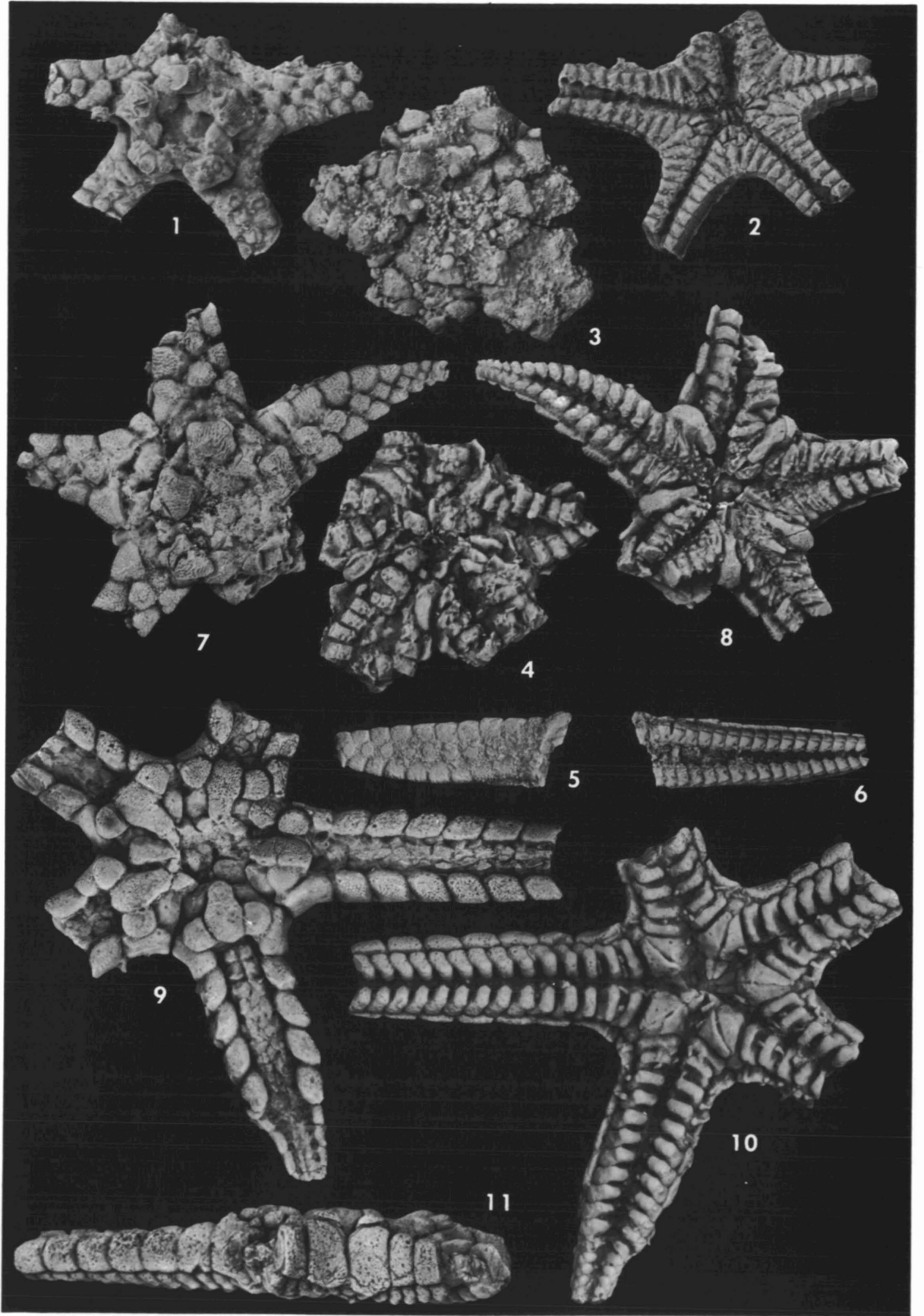


PLATE 1

Type.—Holotype, UWA 26992a; plasto-holotype, UMMP 57466.

? *MONASTER WANDAGEENSIS* n. sp.

Pl. 1, figs. 3–6; pl. 3, fig. 1

Specimen UWA 26992b.—A crushed and badly weathered disk shows strong resemblances to the holotype of *Monaster wandageensis*, although it is a larger specimen. It has R_1 plates that are subquadrate and bear an apical protuberance, Im plates that are longer than $Admm$, Ax that reaches the edge of the interradius, and $Admm$ that are much wider than long.

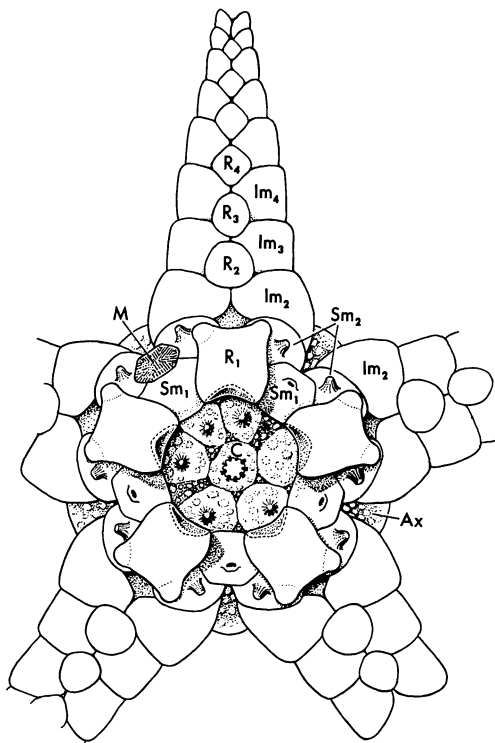
Specimen UWA 26992c.—An arm fragment, its aboral surface crushed and weathered nearly flat, may belong to *Monaster wandageensis*. The arm tapers gradually, and the oral surface shows what may be processes for attachment of spines.

The relative spacing of Adm and Im plates is the same as that in the holotype.

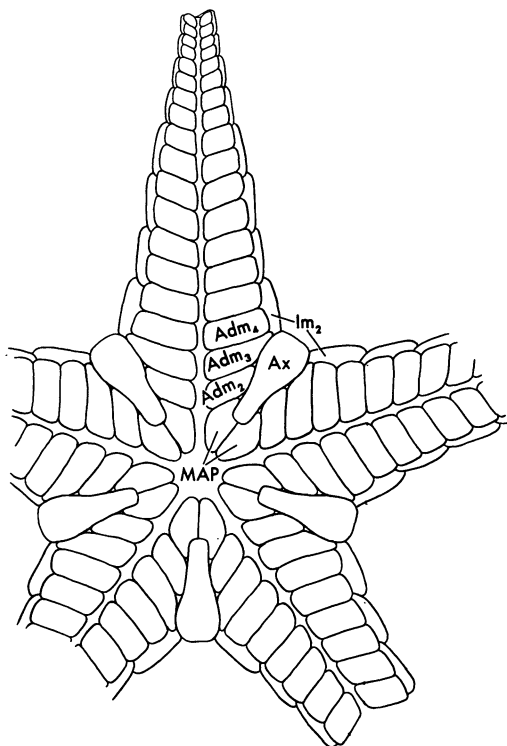
MONASTER CARNARVONENSIS n. sp.

Pl. 1, figs. 7, 8; pl. 3, figs. 5, 6; text-figs. 3, 4

Description.—Stellate; arms tapering rather rapidly; interbrachial regions containing only edges of Ax plates. Disk with coronet, R_1 plates large, thick, unusually shaped; base subquadrate with somewhat protuberant angles, the proximal face raised to an elevated ridge normal to the radius (pl. 3, fig. 5); edges of R_1 overlapping those of adjacent plates. Sm_1 plates fairly well developed but not conspicuous because of elevated intervening RR_1 . Sm_2 plates not well exposed, overlapped by RR_1 . Center of disk containing large plates around C , as well



TEXT-FIG. 3—*Monaster carnarvonensis* n. sp. Aboral view; ornamentation incompletely indicated. Compare with plate 3, figure 5.



TEXT-FIG. 4—*Monaster carnarvonensis* n. sp. Oral view, ornamentation incompletely indicated.

EXPLANATION OF PLATE 2

All figures $\times 6$ except as noted; specimen lightly coated with ammonium chloride

FIGS 1–6—*Permater grandis* n. gen. n. sp. Holotype, UWA 26992e (plastoholotype, UMMP 57468). 1, 2, inclined aboral and lateral views, $\times 2$. 3, oral view showing mouth-frame. 4, end view of broken arm, showing Amb plates with Imm at the sides and $Admm$ below. 5, oral view of disk, showing only preserved Sm_1 (except perhaps that associated with M) at the right. 6, inclined aboral view showing M and associated plates.

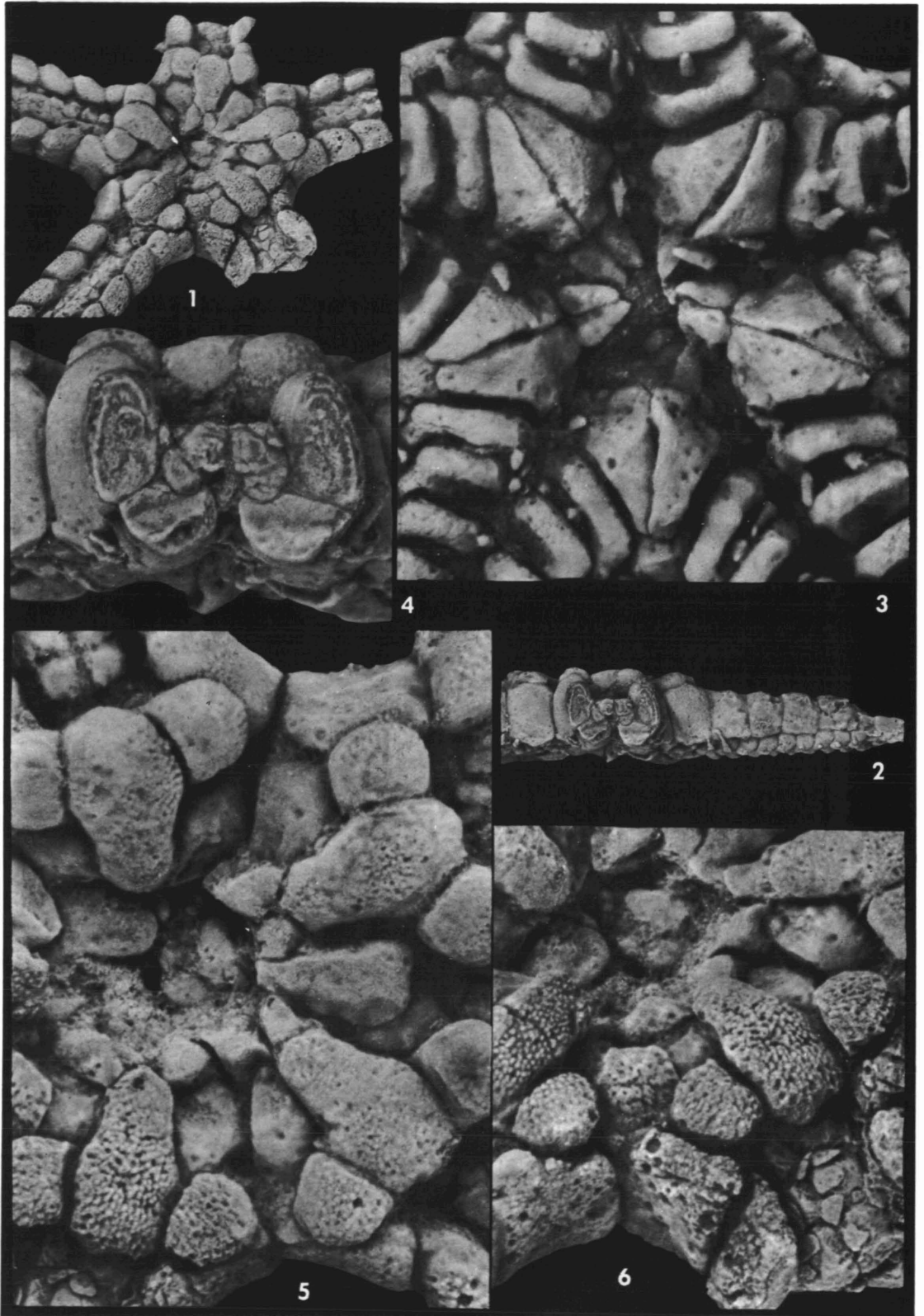


PLATE 2

as some granular ossicles; area fractured and weathered, anus not discernible. M distinct (pl. 3, fig. 5), set in triad of Sm plates as normal in Pustulosida; striae exposed on weathered surface, subradiate and anastomosing, probably connected to exterior through pores (originally forming a sieve).

Oral surface somewhat convex, its plates strongly sculptured (pl. 1, fig. 8; pl. 3, fig. 6). Mouth-frame adambulacral. MAPs small, not much larger than adjacent Admm, each plate with a ridge along the edge facing the other MAP of the interradiial pair, and bearing a few large, irregularly spaced pustules; no MAP spines preserved. Ax plates exceptionally prominent, large, their convex surface projecting out beyond the general level of the oral region; each Ax extending from the paired MAPs to edge of interradius, its distal half broad with subparallel sides and its proximal half narrower with concave sides.

Arms strongly plated. Amb plates, as seen at broken end of arm, set well within the arm; ambulacral groove deep. Admm wider than long, thick, in lateral view extending around lower edges of arm; each Adm extending from ambulacral groove to margin. Main part of arm tapering rather rapidly from axil, its sides somewhat convex; distal end of arm small and tapered, the Admm there quite small. Proximal two or three Admm in each half-ray tapered proximally, abutting against Ax. Oral surface of Adm rounded, evidently bearing a transverse row of spines, somewhat rugose.

Im plates about twice as long as Admm; each Im subquadrate, fitting close against Imm in the row, extending high up on arm and only slightly separated from opposite Im.

Arm RR (carinals) diamond-shaped in distal part of arm, modified to less angular corners in proximal part (pl. 1, fig. 7); no R in contact with succeeding R; each R alternating with proximal ends of Imm.

Surface of RR, Imm, and Smm pustulose. In Imm the pustules in the outer half of each plate tending to align in vertical ridges (pl. 3, fig. 5). R₁ plates with rugose irregular ridges from elevated edge, not attaining the base of the plate; base ornamented with low elevations, perhaps small pustules. C bearing large, low, fluted spine or boss.

Remarks.—This species differs from *Monaster wandageensis* in many characters; perhaps the most conspicuous is the shape of the R₁ plates, which are produced to a ridgelike edge in *M. carnarvonensis* and to a blunt apex in *M. wandageensis*. The arms of the former taper much more rapidly, its oral surface is

more rugose, and its Admm are relatively narrower. Furthermore, in the oral region the Ax of *M. carnarvonensis* is wider distally, whereas that of *M. wandageensis* is wider proximally.

The differences between this species and *M. clarkei* (De Koninck) are not so readily established. Because the latter is represented by external molds, some doubt persists about the shape, position, and surface features of its plates. However, *M. carnarvonensis* seems to have longer arms and less interbrachial spread than *M. clarkei*. It is unfortunate that the disk plates and the oral surface of the latter are so poorly preserved that comparison cannot be made with other species.

Type.—Holotype, UWA 26992d; plastoholotype, UMMP 57467.

Family NEOPALAEASTERIDAE Schuchert 1915

Diagnosis.—Monomarginaline Pustulosida in which no RR (carinals) are developed along the aboral median line of each arm, their position occupied by irregular ossicles.

Remarks.—In the coronet the RR₁ are especially large and robust, tending in known species to be associated each with a pair of distolateral extraneous plates of unknown ancestry. The few remnant Smm are associated with the disk, set above Imm.

PERMASTER n. gen.

Type species.—*Permaster grandis* n. sp.

Description.—Neopalaeasterid starfish with coronet of large RR₁ and Smm₁, the former much higher and overlapping the latter. Imm thick, set along sides of arms atop Admm. MAPs large and conspicuous. M framed by three Smm of the disk.

Remarks.—Only the type species of *Permaster* is known and only the type species and *enigmaticus* are known in *Neopalaeaster*. The comparison of *N. enigmaticus* and *P. grandis* (table 2) may not represent generic differences only, and as more species are known the differentiation may become more refined. Basically, however, *Permaster* is a more strongly constructed starfish, particularly in the coronet and the sides of the arm. In *N. enigmaticus* each R₁ is associated with a distolateral pair of long tapering plates, termed "extraneous plates (X's)" by Kesling (1967, p. 81); in *Permaster grandis* each R₁ is associated with a pair of robust subcylindrical plates in the corresponding positions. These plates have no obvious coun-

TABLE 2—COMPARISON OF *NEOPALAEASTER ENIGMATICUS* KESLING AND *PERMASTER GRANDIS* N. SP.

| Character | <i>Neopalaeaster enigmaticus</i> | <i>Permaster grandis</i> |
|-----------------------------------|--|--|
| Coronet | Plates stellate, small, rather loosely set | Plates blocky, large, set firmly in place |
| Center of disk | Only scattered ossicles | Some definite plates |
| Sm ₃ | Present | Absent |
| Ossicles in aboral channel of arm | Small, rounded | Scalelike, flat |
| Imm | Thin, convex, wrapped around side of arm | Thick, forming dorsal two-thirds of arm |
| Admm | Rhomboid, not extending on side of arm | Short, closely spaced, extending on side of arm |
| Ax | Large, about equal to MAP, reaching border | Small, circular, not reaching interradial border |
| MAPs | Large | Very large |
| Ambb | Relatively small | Robust |

terparts in other starfish, and no hint can be found on their history. Whether they are specialized Smm moved out of association with other Smm of the disk or are symmetrically fused adradial accessory plates, the "extraneous plates" of both *Neopalaeaster* and *Permaster* appear to be homologous.

PERMASTER GRANDIS n. sp.

Pl. 1, figs. 9-11; pl. 2, figs. 1-6; text-figs. 5,6

Description.—Stellate; arms with subparallel sides, very gradually narrowing. No interbranchial arc of plates. Disk with coronet (pl. 1, fig. 9; pl. 2, fig. 1); RR₁ especially thick, radially elongate, more or less rhomboid but with bluntly rounded outer end and bluntly acuminate inner end. Smm₁ large and radially elongate, nearly scalene triangular (pl. 2, fig. 5), set much lower than RR₁ and not quite in contact with them. Smm₂ large, set low atop disk, radially elongate, strongly overlapped by Smm₁ proximally and somewhat overlapped by RR₁ laterally (pl. 2, figs. 5,6). Subpolygonal plates on proximolateral edges of acuminate ends of RR₁, each pair separated from the adjacent pair by the terminal extension of Sm₁; perhaps other plates within coronet but not preserved well enough for definite placement. M subpolygonal, set in triad of Smm plates, its exposed face pierced by numerous small pores (pl. 2, fig. 6).

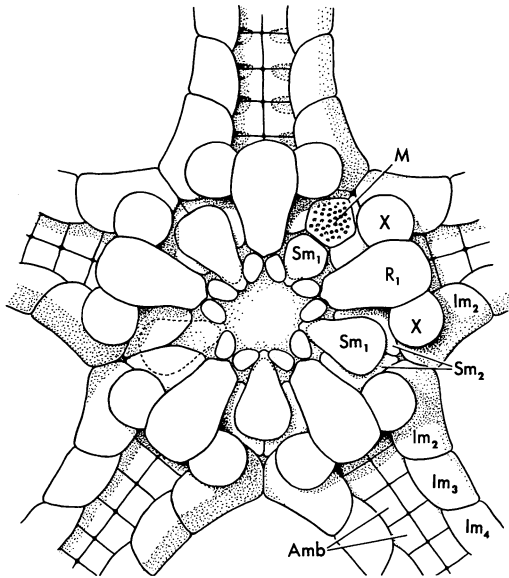
Very thick extraneous plates (XX), semi-circular in outline, one on each distolateral border of R₁, attaining the same height as R₁

and rather firmly attached by an extensive sutural area (pl. 2, figs. 1,5,6); each extraneous plate overhanging part of the proximal Im near the axil, and apparently recessed somewhat into it.

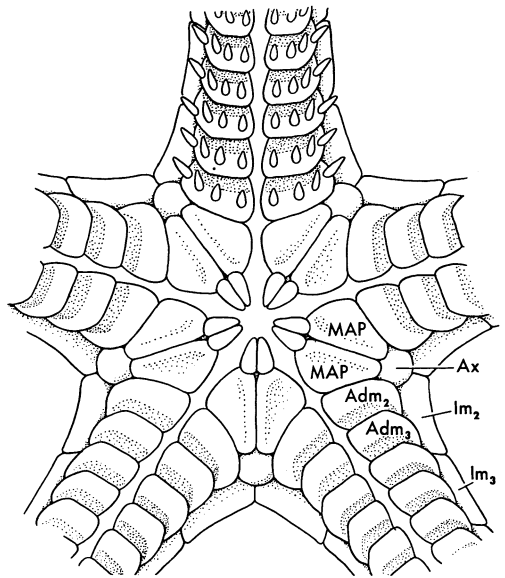
Axx small, exposed section circular, probably rod-shaped (pl. 2, fig. 3); each Ax in contact with outer ends of a pair of MAPs. Mouth rather small, the oral area mostly filled with large MAPs; each MAP subtriangular, radially elongate, with a ridge along its side next to other MAP of the interray and with an elongate stout triangular spine projecting orad; the ten spines of the mouth area forming a tight circle around the mouth.

Ambb exceptionally robust; each plate thinly overlain with arm ossicles, its outer and ventral convex borders closely set against Im and Adm (pl. 2, fig. 4). Admm very short and broad; each plate very thick, semicircular in cross section (pl. 2, fig. 4), its outer part exposed in lateral view as part of side of arm (pl. 2, fig. 2), apparently bearing a few short spines along its median transverse ridge. Imm large and very thick, extending high above Ambb (pl. 2, fig. 4) and forming stout lateral shields for arms. Proximal Im of each half-ray reaching axil, enclosing Ax in interray on oral surface, supporting part of extraneous plate on aboral surface. Each Im about twice as long as underlying Admm, its sutural surfaces large; plate convex and blocky.

Aboral median part of arm forming a deep, wide channel. No RR (carinals), the channel



TEXT-FIG. 5—*Permater grandis* n. sp. Aboral view of disk and arm bases; one Sm_1 removed (at left) to show extent of underlying Sm_2 plates.



TEXT-FIG. 6—*Permater grandis* n. sp. Oral view, short Admm spines shown on base of upper arm. Compare with plate 2, figure 3.

covered with integument bearing thin scale-like irregular ossicles (pl. 2, fig. 6). Proximally, the channel abruptly terminated by high R_1 and XX.

Imm pustulose, RR_1 and extraneous plates coarsely pustulose, the pustules tending to be aligned in anastomosing ridges.

Remarks.—The longest preserved arm (pl. 1, figs. 9,10; pl. 2, fig. 2) has abnormally small plates at the end, showing regeneration after the original end of the arm had been excised (presumably bitten off). From the size of these newly formed arm plates and from the very gradual taper of the arms, one can surmise that the arms of *Permater grandis* were much longer than the preserved section, perhaps three times as long. Hence, the disk is relatively small, and the ratio of the ray radius to the interray radius is extremely large.

The bulk, close contact, and large sutural areas of Ambb, Admm, Imm indicate very re-

stricted but powerful movements of the arms. The short spines attached to the Admm probably rasped and raked through bottom debris. The degree of freedom of the oral spines (attached to the MAPs) cannot be ascertained, but it would seem to be much less than that possessed by the mouth frame of the advanced ophiuroids.

Type.—Holotype, UWA 26992e; plastroholotype UMMP 57468.

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EXPLANATION OF PLATE 3

All figures $\times 6$; specimen lightly coated with ammonium chloride

- FIG. 1—? *Monaster wandageensis*. Part of aboral surface, including M plate; plates with prominent protuberances are probably RR_1 ; UWA 26992b; see also plate 1, figures 3, 4.
- 2-4—*Monaster wandageensis* n. sp. Holotype, UWA 26992a (plastroholotype UMMP 57466). 2, oral view, showing mouth-frame. 3, lateral view showing protuberances on R_1 plates; end of broken arm (lower left in photograph) shows the great lateral extent of Adm plates. 4, part of lateral view showing two RR_1 with protuberances and M plate (right). Other views of specimen in plate 1, figures 1, 2.
- 5, 6—*Monaster carnarvonensis* n. sp. Holotype, UWA 26992d (plastroholotype UMMP 57467). 5, inclined aboral view, showing M and associated plates. 6, oral view, showing part of mouth-frame with Ax at lower center. Other views of specimen in plate 1, figures 7, 8.

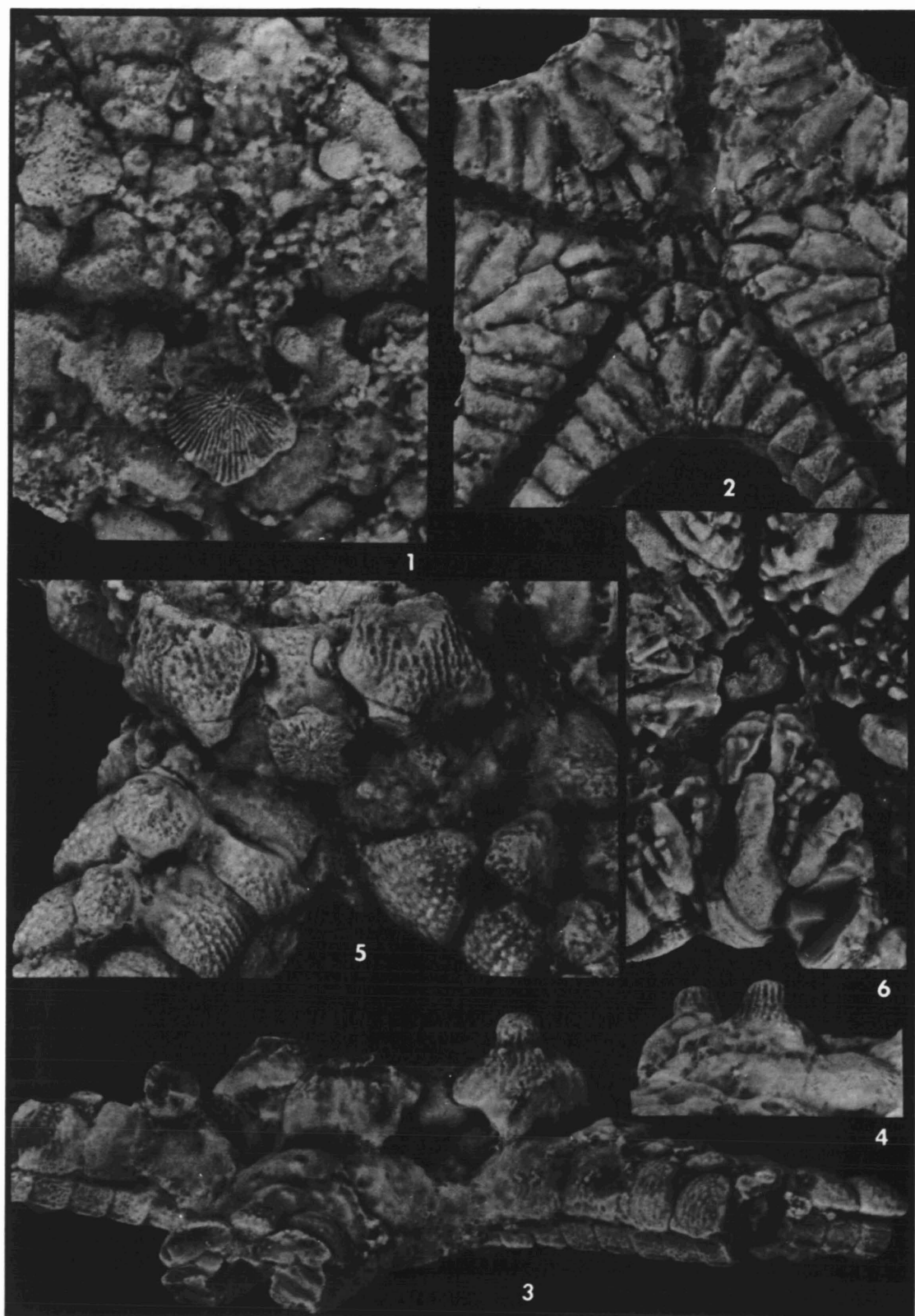


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