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MOUTH FRAME OF THE OPHIUROID *ONYCHASTER*

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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.

MOUTH FRAME OF THE OPHIUROID *ONYCHASTER*

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ABSTRACT—The three species of *Onychaster* can be readily distinguished by the configuration and arrangement of plates composing the mouth frame. No phylogenetic trends are apparent.

CONTENTS

INTRODUCTION

WHILE we were studying the morphology of ophiuroids in the advanced invertebrate paleontology class at The University of Michigan, Mr. Harrell L. Strimple of the State University of Iowa forwarded a fine specimen of *Onychaster* from the Golconda Formation of Illinois. At about the same time, we discovered the specimen of *Onychaster flexilis* illustrated by Meek & Worthen in their original description in 1868; it was part of the collection of the Museum of Paleontology on display in the Exhibits Museum. Intrigued by the striking differences in the structure of the mouth frame in these two species, we obtained examples of the third species, *Onychaster barrisi* (Hall), for comparison. Since it displayed still another type of mouth frame, we investigated details of the elements composing the frame in the three Mississippian brittle-stars.

Onychaster strimplei Bjork, Goldberg, & Kesling was recently described (1968, p. 197). The holotype has been deposited in the State University of Iowa.

How the specimen described and figured by Meek & Worthen came to reside in our museum is a question belonging to the past. Undoubtedly, it was obtained through Dr. Carl Ludwig Rominger before the turn of the century. Other significant echinoderms of Meek & Worthen are now in the Museum of Paleontology, including the holotypes of some rare species, as reported by Kesling & Ehlers (1958, p. 924). In his journal under "Petrefactorum Catalogus/Merz 1881," Dr. Rominger listed the following items (among others):

28 *Oligoporus coreyi* M & W., Subcarb., Crawfordsville 1 Stk. [German Stück for *specimen*]
29 *Lepidesthes coreyi* M & W., Subcarb., Crawfordsville 2 Stk.
30 *Agelacrinus squammosus*, Subcarb., Crawfordsville 1 Stk.
151 *Onychaster flexilis*, Crawsfordville 5 Stk.

The last item probably included the specimens of *O. flexilis* studied and illustrated in this paper.

For the loan of specimens of *Onychaster barrisi* (Hall) from the Museum of Comparative Zoology at Harvard we are indebted to Prof. Bernhard H. Kummel. For permission to study the holotype of *O. strimplei* we are grateful to Mr. Harrell L. Strimple of the State University of Iowa. Mr. Karoly Kutasi and Mrs. Helen Mysyk assisted us greatly with photography and typing, for which we are most thankful.

TERMINOLOGY

Our terms for plates and structures in the mouth frame are compared with those used by previous authors (insofar as we are able to correlate) in table 1.

PREVIOUS WORK

Onychaster has been investigated by several students of echinoderms because the ambulacral plates of its arms strongly resemble those of modern ophiuroids. Some authors have also drawn attention to the mouth frame in *Onychaster flexilis*. The published accounts, however, do not present a clear understanding of this important structure.

The first account of one of these brittle-stars was by Hall, who described it as "*Protaster* ? *barrisi* (n. s.)" and said of its mouth frame (1861, p. 18):

There are ten oral plates, two from each division of the ray: these plates are expanded vertically; their extreme points have the inner edges slightly curving; the lower external faces are slightly indented, or crenulate; the surface of attachment is wide and strong, and constricted at the base by a distinct groove, beyond which it again expands. This form, if really without a disc, differs essentially from *Protaster;* and there are also other differences, which make it necessary to constitute a distinct genus when better specimens shall be obtained.

The next appearance was in 1868, when Meek & Worthen established the genus *Onychaster* and described their new species *O. flexilis* in considerable detail. On the mouth frame, they stated (1868, p. 526):

On the dorsal side of the body . . . there is seen a comparatively large circular area or disc, composed of an outer circle of ten rather prominent pieces, united together in five pairs by close-fitting sutures, each piece being pierced by a round ovarian ? pore. Immediately within this circle there is, apparently, another circle of ten smaller pieces, also united in five pairs, but without pores; and within this latter circle there is a third range of five still smaller, nonporiferous pieces, surrounding a central anal ? opening;—the whole reminding one of the apical disc of an Echinoid, though differing in structure from this part of the known types of that group. It is also worthy of note, that there is some analogy between this disc and the body of a crinoid, except that there is a central opening . . . Immediately outside of the circle of ten pore pieces, mentioned above, each pair of these pieces is succeded by two or three pairs of differently formed, interlocking, transverse pieces, in direct range, connecting them with the dorsal side of each of the five rays.

In restrospect, the treatment of the mouth frame by Meek & Worthen was not as inaccurate as some later authors implied. Three significant errors were made: (1) their description and figures indicate no hole perforating the frame between the pairs of plates in the middle circle, (2) their figure C shows each plate of the "third range" in a radial instead of interradial position, and (3) the central area is not an opening, but contains five interradially placed denticles; probably, these plates were partly obscured by matrix in their specimens. Their interpretations of an ovarian pore and an anal opening were also incorrect.

In 1873, Meek & Worthen merely listed *Onychaster flexilis* in the fauna of the Keokuk Group; they did present new illustrations (1873, pl. 16, figs. 3a–31), perhaps more artistic but certainly nor more accurate than those of their original article.

Schöndorf (1909, p. 59), after describing details of the ambulacrals in the arm of *Onychaster flexilis,* commented on the mouth frame. He has been the only author to disarticulate a specimen to observe the inner parts of the mouth-angle plates. He wrote (our translation):

TABLE *1*—TERMS FOR PLATES AND STRUCTURES IN MOUTH FRAME OF *ONYCHASTER*

This paper	Hall (1861)	Meek & Worthen (1868)	Schöndorf (1909, 1913)	Sollas (1913)	Spencer (1927)
Mouth frame		Circular area of disc	Mundskelett		Mouth-frame
Am_2 — second ambulacral; probably fused second and third ambulacrals	Ten oral plates	Ten pore pieces	äussere Platte	Jaw	First ambulacral
MAP — mouth-angle plate; = first ambulacral		Circle of ten smaller pieces	Mundeckstück		Mouth-angle piece
Torus		Third range of five pieces	Torus angularis	Torus angularis	Torus
Denticle			Zahn	Tooth	Tooth
Pore of canal to second tube foot (through Am_2)		Ovarian ? pore			Canal to second tube-foot

> Up to now, the mouth skeleton of *Onychaster* was known only very inexactly and only from the dorsal side. Its customary representation as a rosette in no way corresponds to reality and in no manner can be interpreted. In addition, in the previous specimen it was impossible to lay the mouth skeleton entirely free and to clearly study all parts, because the only example in which it could be prepared was very compressed in the central part and no longer possessed any sort of coherence. Nevertheless, it was possible to expose a single mouth-angle piece from various sides, so that the previous representation could be improved in some degree. The mouth-angle pieces are composed of many pieces, which apparently are all bound very tightly one under another. On each mouth-angle piece one can clearly differentiate two kinds of skeletal elements. The outermost are developed in pairs and two unite in an interradius. To the inside, that is, turned toward the peristome, lies an unpaired little plate which holds together both the aforementioned outermost plates exactly interradially. With the particular material at my disposal, it cannot be determined whether this plate is bound to the former plates tightly or only articulated. It is certain that the two outermost plates, which lead off from the ambulacral or adambulacral rows, are not attached in their distal parts but are linked to one another by muscles. The latter are inserted in a broad interradial surface, covered with ridges and corresponding grooves. In all mouth-angle pieces which could be investigated they were tightly united with the unpaired proximal piece. According to what has been said previously, it was nevertheless assumed that their tight union with each other was only apparent and caused by the recrystallization of the calcite. The outermost paired skeletal pieces consist in turn of two parts, a flat interradially lying surface covered by ridges and furrows, with which the two mouth-angle pieces meet interradially, and a small process attenuated in a dorsoventral direction, which fastens onto the distally adjacent ambulacra and bears a corresponding cavity for attachment of the binding longitudinal muscles. The exact form of the mouth skeleton is manifest in figures 13–17.

In these figures, Schöndorf showed that the depth (vertical) of each mouth-angle plate was more than twice its width.

This article was followed four years later by a truculent exchange between Miss Igerna Sollas of England and Professor Schöndorf of Germany. It was 1913. Breaching the language barrier, they came through implacable and clear. Sollas examined each item reported by Schöndorf, and as she dissected, she dissented. Her criticism was brash, disputatious, and ruthless. His reply was indignant, contentious, and sardonic. Now, over half a century later, perhaps we can look at the evidence calmly.

In the early part of her article, Sollas stated (p. 52), "We cannot refrain from an expression of regret that three specimens of this rare and interesting species should have been sacrified [by Schöndorf] to methods now out of date. Nevertheless, however much we deplore this waste of time and material . . ." Thereupon, Sollas proceeded to relate how she destroyed two specimens by sectioning. Her description is quoted here at length not because it is lucid but because it is the original source of information on the oral features of the mouth frame; she wrote (p. 55–56):

> Sections and reconstructions show that they [the jaws] have a structure very similar to that of the jaws of modern brittle-stars, oral angle pieces traversed by the usual suture being recognizable and presumably formed, like that of modern types, of a modified vertebra fused with the first adambulacral plate. At the apex of the jaw a *torus angularis* is present, bearing teeth. Dorsally the two halves of the vertebra which contributes to the formation of the oral angle piece are fused together, forming a solid piece, which projects very near to the centre of the disc and overhangs the oral tentacle spaces which are situated further outwards from the centre. This peculiar arrangement produces the very misleading appearance which led Meek & Worthen, who had only seen the dorsal aspect, to mistake these radially placed pieces for the jaws themselves . . . The outer and posterior angles of these ossicles are produced backward as long slender laminae . . . two tentacle spaces are clearly seen, and presumably justify us in regarding the vertebra involved in the oral angle as A_2, just as in modern forms. One of the dorsal and radial tori spoken of above bears a cup-like structure, and in the concavity of the cup is a tooth . . . A pair of minute ossicles is situated just below the level of the second tentacle pore and suturally attached to the oral angle piece, between and below the two tentacle pores. Still further ventrally a row of teeth seems to have been borne by the jaw proper (ad_1) at the side of the oral angle (mouth papillae). Signs of a canal perforating the oral pieces can be made out . . .

We decipher her account with some difficulty. Our second ambulacral appears to be her "oral angle piece" formed by fusion of a "modified vertebra" and "first adambulacral plate." With her statement that "the two halves of the vertebra . . . are fused together" we cannot agree; in fact, we consider that fusion would have rendered the entire mouth frame useless in mastication. Nor do we agree with her that the tori are "radial"; they are interradial, as can be seen in our photographs (pl. 2, figs. 2–3; pl. 3, fig. 6). Sollas also seems to have classified the mouth-angle plate as the first adambulacral, which she claimed lay below the level of the "two tentacle pores" (presumably the cups for the tube-feet); although the mouth-angle plates have considerable vertical extent, as shown by Schöndorf, they do not lay wholly below the cups for the tube feet, for this would place the cups atop the mouth frame rather than below it.

On the mouth frame, Schöndorf replied (1913, p. 112, our translation):

> Miss Sollas devoted a detailed consideration to the mouth skeleton of *Onychaster* and came to the conclusion that it essentially coincided with that of the living ophiuroids. With *Onychaster* there is already a torus angularis with teeth; in addition, the fusion of adambulacral and ambulacral elements to form the jaw is similar. With these concepts one can agree in general. Earlier it was not possible for me to study these relationships so precisely as was desirable. Nevertheless, I was able to lay free a mouth-angle piece and to describe and figure it from varous sides (1909, p. 59, pl. 6, figs. 13–17), which Miss Sollas again completely overlooked with silence. As one compares, for example, the earlier illustration of the mouth-angle piece (1909, pl. 6, fig. 13) with the model constructed by Miss Sollas (1913, pl. 8, fig. 6), a striking similarity becomes evident, which in reasonable manner would be worth a mention, especially since thereby the old false rosette interpretation of Meek & Worthen was corrected.

As we study the articles of Schöndorf and of Sollas, we find points on which we agree and points on which we disagree. As for their methods of investigation, information can be gained on external form and surface features by disarticulation, as done by Schöndorf, and on internal structures by serial sections or surfaces, as done by Sollas. Each method should make its contribution, and one method should complement the other. Schöndorf made an original discovery of the depth of the mouth frame and the form of the mouth-angle plates. He failed to demonstrate clearly how the various parts of the mouth frame fitted together. Sollas established the presence of cups for the tube-feet under the mouth frame and she attempted to explain the association of elements in the frame. Her drawings lack clarity and her description is hard to understand.

Schuchert (1915) contributed little to the knowledge of *Onychaster,* taking most of his presentation from previous authors and quoting their works at length.

In his long-continued monograph in the *Paleontographical Society,* Spencer expressed an opinion in the Schöndorf-Sollas affair. He said (1927, p. 338) of the former that "neither his drawings nor his description afford much detail of structure"; and of the latter, "A clear account of the frame was given by Miss Sollas." Spencer studied specimens of fossil brittle-stars from the Skateraw Quarry in Scotland and the Braunton Down locality in Devon, which he assigned respectively to *Onychaster flexilis* and to *O. barrisi.* His remarks and illustrations are far from convincing with respect to the specific determination. Obviously, however, he had closely related ophiuroids. Spencer's important contribution was his concern for the entire mouth frame. He wrote (1927, p. 339):

> The mouth-frame in general build is very similar to that of the recent Ophiuroidea:
> (1) The first ambulacral and the mouth-angle plate of each are fused to form a solid jaw, which is built high and has the cup for the first tube-foot well within the mouth-cavity.
> (2) This jaw has a rocking motion on the proximal vertebra, not a sliding motion as in *Lapworthura.*
> (3) The radial components of the jaw are not arranged in a V as in *Lapworthura,* but the trap is closed by interradial muscles placed on a prominent backward prolongation of the jaw.
> (4) There seems to be a distinct vertical row of teeth.

Spencer also (1927, text-fig. 218A) reconstructed an oral view of the mouth frame of *Onychaster flexilis* from a re-examination of one of Sollas' models. In the figure, he portrayed the cup for the second tube-foot below the plate which we term Am_2 (his "first ambulacral").

Insofar as we know, Spencer was the last investigator to study specimens of *Onychaster.* Later workers have based their treatment of this fossil brittle-star upon published descriptions and figures.

Because *Onychaster* has a compact and constricted mouth frame and lacks an expanded disk, paleoecological notes assume special significance. In 1897 Wachsmuth & Springer reported *Onychaster flexilis* atop the tegmens of two crinoids. At the Indian Creek locality of the Keokuk, the ophiuroid was found between the arms and coiled around the long anal tube of their *Actinocrinus multiramosus,* as Wachsmuth & Springer illustrated (1897, pl. 55, fig. 3). They said that *Onychaster* was rarely discovered by itself and never was observed on other crinoid species at Indian Creek. At the Canton (Indiana) locality, *Onychaster* appeared on most specimens of *Scytalocrinus robustus* (Hall, Wachsmuth & Springer stated (1897, p. 566):

> The fact that this Ophiuroid is only found associated with certain species, and there always under similar conditions, and the frequence of

> this occurrence, would seem to indicate that the position between the arms of these Crinoids was its favorite resting place, in which it either found protection, or some special facility for obtaining nourishment. Nobody, however, who is acquainted with the anatomy of the Crinoids, and their mode of living, will entertain for a moment the notion that the Crinoid preyed . . . on the Ophiuroid, . . . as suggested by the earlier writers.

In 1908, John M. Clarke reported and figured (p. 165, pl. 7, figs. 1–2) *Onychaster flexilis* upon *Barycrinus hoveyi* (Hall) from the famous Crawfordsville locality, the arms of ophiuroid and crinoid intertwined. He suggested, without strong conviction, that perhaps *Onychaster* was coprophagous, feeding upon excrement of its crinoid host. One of Clarke's figures (pl. 7, fig. 2) has been copied by later authors to illustrate the association (for example, by Spencer, 1927, text-fig. 216, by Ubaghs, 1953, fig. 48A, and by Spencer & Wright, 1966, fig. 36).

Many years later (1921, p. 78–80) Clarke again referred to the relationship of *Onychaster* and crinoids, and concluded (p. 79) that it "may have been an attack upon the crinoid animal through its oral aperture." He expressed uncertainty as to whether the affiliation was "an actual state of dependence or might under favorable circumstances have developed into true parasitism."

Spencer (1927, p. 338) thought that *Onychaster* was sessile, and (p. 334) considered it to be ancestral to the recent Euryalae, all of which he described as "epiphytic" in habit.

Van Sant & Lane (1964, p. 34) reviewed the paleoecology of the Crawfordsville fauna and concluded, "Muddy bottom conditions . . . at least in part probably caused such forms as *Onychaster* to seek a more desirable habitat than found on the sea floor."

Recently, Spencer & Wright (1966, p. 28) in the *Treatise* stated: "[*Onychaster flexilis*] had arms that could climb up and grip onto hosts such as crinoids by means of the vertical rolling of the arms and small hooked spines (fig. 36). This group [*Phrynophiurida*] consists of suspension-feeders, collecting organic particles of their own ciliary action, aided by that of their hosts."

MORPHOLOGY

For many paleontologists, homology of echinoderm plates is a fascinating field. Admittedly, however, the older the fossil the less reliable its comparison with other forms. Any homology concerning an extinct organism is suspect, at best, and for Paleozoic genera it becomes highly speculative. Yet the subject demands attention. Every description, every discussion, involves morphologic terms; and, by its very nature and form, each term implies some sort of homology. This is a problem for *Onychaster*.

Of the four kinds of plates in the mouth frame of this fossil brittle-star, the largest is the most complex. This plate, ten of which form the outermost circle of the frame, we call Am_2, the second ambulacral (text-figs. 1, 3, 4). Actually, it is probably a fusion of the second and third ambulacral elements.

Our interpretation of this complex plate is based on its supposed ancestry. As Fell has convincingly argued (1963a, 1963b), the ophiuroids appear to have descended from the somasteroids. In one of the very old and primitive somasteroids, *Chinianaster* of Cambro-Ordovician age, Fell says (1963b, p. 400) that "the angle-plate of the jaw is formed from the first ambulacral" and (1963a, p. 472) that the second and third ambulacrals are fused together to make a syzygy. The arrangement in *Chinianaster* is exactly paralleled by that in *Onychaster,* in which the proximal ambulacral element, the MAP, is followed by a compound plate, the Am_2 (perhaps more accurately, the Am_{2+3}).

Our reasons for regarding the Am_2 as a compound plate, derived from the fusion of two ambulacral elements are: (1) each plate consists of two parts, a distal subquadrate promnent part elevated above the rest of the mouth frame and a proximal small part set well below the distal and extending to the MAP, and (2) near the boundary between the two parts, *Onychaster flexilis* has a distinct pore, presumably the opening of a canal leading to the second tube foot (pl. 2, fig. 2). The fusion of the two elements is strong, for all specimens studied have them still united. The Am_2 in *Onychaster barrisi* (pl. 2, fig. 1) and in *O. strimplei* (pl. 4, fig. 3) has the same general configuration as that in *O. flexilis;* however, we have been unable to detect any trace of the pore in the former two species.

In each radius of the animal, the Am_2 plates are paired. Their broad distal surfaces articulate with the ambulacral plates of the arm (pl. 1, fig. 1). The proximal part of each plate projects inward near the interradius, so that the adjoining MAP is separated from the other MAP of that radius (pl. 2, fig. 2). The large side of each Am_2 facing the interradius is slightly concave and rugose (pl. 3, fig. 6). We presume that this surface, like that in living ophiuroids, accommodated the strong thrusting muscle, the *musculus interradialis externus* (text-fig. 2). The musculature of the mouth frame in ophiuroids was thoroughly discussed and figured by Spencer (1925, p. 265, text-fig. 186c).

Because each MAP lies close alongside an MAP of the adjacent radius, some workers have considered that pairs of MAP are interradial. This cannot be defended. The arrangement of plates, even with grooves to accommodate nerve and water-vascular rings, is the same in Paleozoic ophiuroids as in recent forms, such as *Ophiothrix,* illustrated by Cuénot (1948, fig. 290). This was repeatedly emphasized by Spencer. As preserved in each *Onychaster* examined, two MAP meet in each interradius, one from each radial pair, and the denticles nearly or quite meet in the center of the frame (pl. 2, fig. 2). This contracted condition may well be the result of rigor mortis, which seems to have drawn the ambulacrals of the arms into such a severely abnormal enrolled state that various writers have compared the arms with the talons of a bird (pl. 1, figs. 1–4). The fossil state of *Onychaster flexilis* is shown in text-fig. 1. For its mouth frame to have functioned, we presume that this species, like its living relatives, must have had adjacent MAP joined proximally to the torus by a thin but powerfully elastic binding muscle, the *musculus interradialis internus inferior.*

Between the paired MAP and the proximal extensions of the radial pair of Am_2, *Onychaster flexilis* (text-fig. 1) and *O. strimplei* (text-fig. 4) have a spacious opening through the mouth frame. In the contracted state of the fossils, this opening is almost completely cut off from the center of the mouth frame by the close-set tori and denticles (pl. 2, fig. 2). We have termed the opening, therefore, the proximoradial foramen or hole. In such Paleozoic brittle-stars as *Lapworthura,* the proximal part of each ray is flared to form a V, the buccal slit. The configuration of plates in *Onychaster,* whereby the tori can be drawn into a tight circle, renders the term buccal slit rather inappropriate. We presume that radial muscles, the *musculus radialis superior,* extended across the proximoradial hole and served to draw the two halves of each jaw together (text-fig. 2). Nevertheless, such muscles may have been insignificant in *Onychaster* in view of the apparent large size of the thrusting muscles and the long radial suture between pairs of Am_2; contraction of the thrusting muscles would serve to bring all mouth frame plates together and the two Am_2 plates would be in contact at the end of the thrust. In fact, the suture between Am_2 plates is noticeably crenulate in many specimens (pl. 2, fig. 2; pl. 3, fig. 6), so that the surface itself may have provided an effective fulcrum and decreased the need for radial musculature.

Tori are variously developed in the three species of *Onychaster.* All these plates, however, are wide, as are the adjoining denticles. There is a suggestion that the mouth frame of all three species did not function in the same manner. In *Onychaster flexilis* (pl. 3, fig. 6), the tori rise sharply above the adjacent MAP, their proximal surface is notably concave, and the denticles are set well below the upper floor of the mouth frame—so far below that they were overlooked by early investigators. In this species, perhaps, muscles may have connected torus and denticle to impart a sawing motion up and down. Although these muscles would have lain in the same position as those in certain living ophiuroids, in which the *musculi interradiales interni superiores* impart such a motion to the denticles, there is no indication that the muscles in *Onychaster flexilis* passed through the substance of the torus like those used in mastication by modern brittle-stars with stout denticles (Spencer, 1925, p. 265).

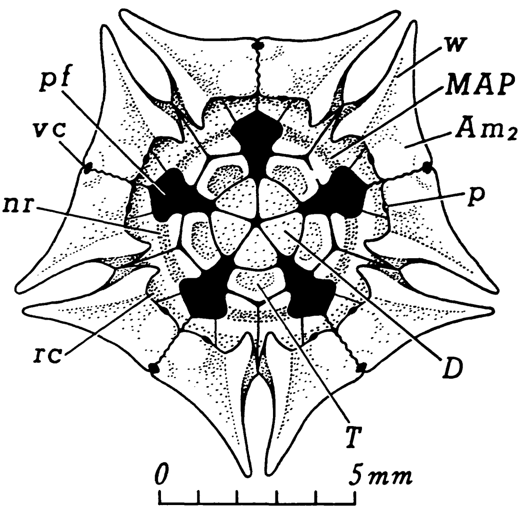
As demonstrated by Schöndorf (1909, pl. 6, figs. 13–17), the MAP are deep plates and their junction with the torus is long. We have not been so fortunate as to have a specimen available to disarticulate, but it seems that the vertical extent of the torus is adequate to have accommodated several denticles, as suggested by Spencer (1927, p. 339), and demonstrated to be present in the modern genus *Ophiura* by Berry (1934). The large size of the denticles leads us to believe that they played an important role in mastication.

In *Onychaster strimplei* (pl. 4, fig. 3) and in *O. barrisi* (pl. 2, fig. 1) the tori are not elevated at their upper extremities, their inner surface is not concave, and the denticles are not depressed. The tori and denticles in *O. strimplei* seem to be firmly united. The structure of this part of the frame suggests that these two species did not have any appreciable sawing action of the denticles, such as appears likely in *Onychaster flexilis.*

Outside the circle of tori, extending across the middle of each MAP, is a circular depression, particularly developed in *Onychaster flexilis* (pl. 2, fig. 2). We believe it held a nerve ring, homologous with that occurring in living ophiuroids (Cuénot, 1948, fig. 290). This depression is very shallow in *Onychaster barrisi* and intermediate in *O. strimplei.*

Concentric to the nerve ring depression and extending along the junction of Am_2 and MAP is a second circular furrow, without doubt to accommodate the ring canal of the water-vascular system (text-fig. 2). The distal part of the Am_2 forms a stout rampart around the outside of the mouth frame, and the ring canal furrow lies along the base of the inner steep wall. Within the furrow, each Am_2 of *Onychaster flexilis* has a distinct pore (text-fig. 1; pl. 2, fig. 2; pl. 3, fig. 6), presumably leading to the second tube-foot below. An indentation at the junction of the paired Am_2 seems to have served as the passage for the radial vessel from the ring canal. We have been unable to determine if the radial vessel of the arm was in an oral groove, as set forth by Schöndorf (1909), or within the ambulacrals, as proposed by Sollas (1913) and Spencer (1927).

In comparison with *Ophiura,* a modern ophiuroid genus whose mouth frame was studied by Berry (1934) from isolated plates, *Onychaster* has a frame that is simpler, much more compact and apparently less flexible.



TEXT-FIG. 1—*Onychaster flexilis* Meek & Worthen. Aboral plate diagram of mouth frame. Plate symbols: *Am_2*—second ambulacral; D—denticle or tooth; *MAP*—mouth-angle plate; *nr*—furrow for nerve ring; *p*—pore of canal to second tube-foot; *pf*—proximoradial foramen or hole (= buccal slit); *rc*—furrow for ring canal; *T*—torus; *vc*—vertical canal between pairs of Am_2; *w*—wing of Am_2. Based on UMMP 6196a (pl. 2, fig. 2) and other specimens.

DESCRIPTIONS

Order PHRYNOPHIURIDA Matsumoto 1915

Suborder EURYALINA Lamarck 1816
Family ONYCHASTERIDAE Miller 1889
Genus ONYCHASTER Meek & Worthen 1868

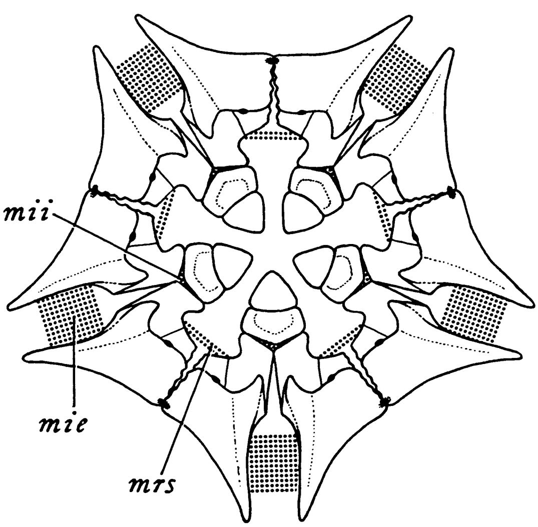
With regard to the five species assigned in 1915 by Schuchert, we agree with Spencer (1927) that only *Onychaster flexilis* and *O. barrisi* qualify as species of *Onychaster*. To these, we recently added *O. strimplei,* so that there are now three distinct species.

In each of the following descriptions, we confine our observations to the aboral part of the mouth frame. Although vertebrae of the arms are also characteristically developed, the mouth frame is sufficient to distinguish each of the three species. Furthermore, it is the feature most often preserved and exposed in fossils, since the arms are invariably enrolled under the mouth and the integument of the disk (with rare exception) is not retained. In table 2 the differences in the mouth frames of *Onychaster* species is summarized.

ONYCHASTER FLEXILIS Meek & Worthen

Text-figs. 1, 2; pl. 1, figs. 1–4; pl. 2, figs. 2, 3; pl. 3, figs. 1–6

Am_2.—Major (distal) part of a pair of second ambulacrals subtrapezoidal in dorsal view and subovate in distal view; articulating surface with arm vertebra very gently concave, nearly flat; wings acuminate, extending more in lateral than in distal direction. Vertical interradial-facing surface with large, rugose concavity, apparently for attachment of a great thrust-



TEXT-FIG. 2—*Onychaster flexilis.* Aboral plate diagram of mouth frame in expanded position, with dotted areas to represent supposed musculature. Muscle symbols: *mie—musculus interradialis externus; mii—musculus interradialis internus inferior; mrs—musculus radialis superior.*

TABLE 2—COMPARISON OF MOUTH FRAMES IN *ONYCHASTER* SPECIES

Character		*O. barrisi*	*O. flexilis*	*O. strimplei*
Second ambulacral — Am_2	Surface articulating with arm vertebra	Concave with central convexity	Shallowly concave, nearly flat	Strongly concave
	Topography of aboral surface	Low relief	Intermediate	Very strong relief
	Interradial margins	Not delineated	Tapering distally	Narrow band, sides parallel
	Inner face of major part	Low	Very steep	Intermediate
	Vertical canal along radial suture	Shallow pit but no canal	Distinct pore for canal	None found
	Direction of wings	Distal	Lateral	Distal
	Proximointerradial projection	Small, bluntly rounded	Large, acuminate	Small, acuminate
Pore for canal to second tube-foot		None found	Present	None found
Furrow for ring canal		Shallow	Sharply defined	Intermediate
Furrow for nerve ring		Shallow	Deeply incised	Intermediate
Proximoradial hole		Very small, slot	Very large, kite-shaped	Intermediate, keyhole-shaped
Mouth-angle plate—MAP		Very large, subparallel sides	Small, subparallel sides	Intermediate, sides not parallel
Torus	Outline formed by tori	Pentagonal, apices radial	Pentagonal, apices interradial	Circular
	Elevation above MAP	Low	Very strong	Low
	Proximal concavity	None	Well-developed	None
	Fusion with denticles	None	None	Apparently fused
	Size	Very large	Large	Narrow band
Denticles		Small, slightly depressed	Small, deeply depressed	Large, raised in low dome
Age		Burlington	Keokuk	Chester (Golconda)

ing muscle, the *musculus interradialis externus* (pl. 3, fig. 6). Aboral surface of plate with considerable relief, rising to rounded peak near radial suture, the slope laterally decreasing to a V-shaped groove subparallel to the interradius, thence rising to an upper sharp edge. Marginal area between groove and sharp edge tapering distally, extended proximally into a prominent subtriangular projection overhanging the furrow for the ring canal (pl. 2, fig. 3). In each pair of ambulacrals, an opening between the peaks and along the radial suture, evidently for a vertical canal leading down between the pair of plates (pl. 2, fig. 2; pl. 3, fig. 6). Radial suture distinctly serrate. Inner face of main part of Am_2 declivitous, nearly vertical, with furrow for ring canal along its base. Minor part of Am_2 small, tapering inward, its junction with MAP nearly parallel to interradius; between this suture and the radial suture, a pore present in the furrow for the ring canal, the inner opening of a canal leading

EXPLANATION OF PLATE 1

(All figures stereograms, × 2, photographed in xylol)

FIGS. *1–4—Onychaster flexilis* Meek & Worthen. Lectotype, UMMP 6197. *1–3,* lateral views; *4,* aboral view.

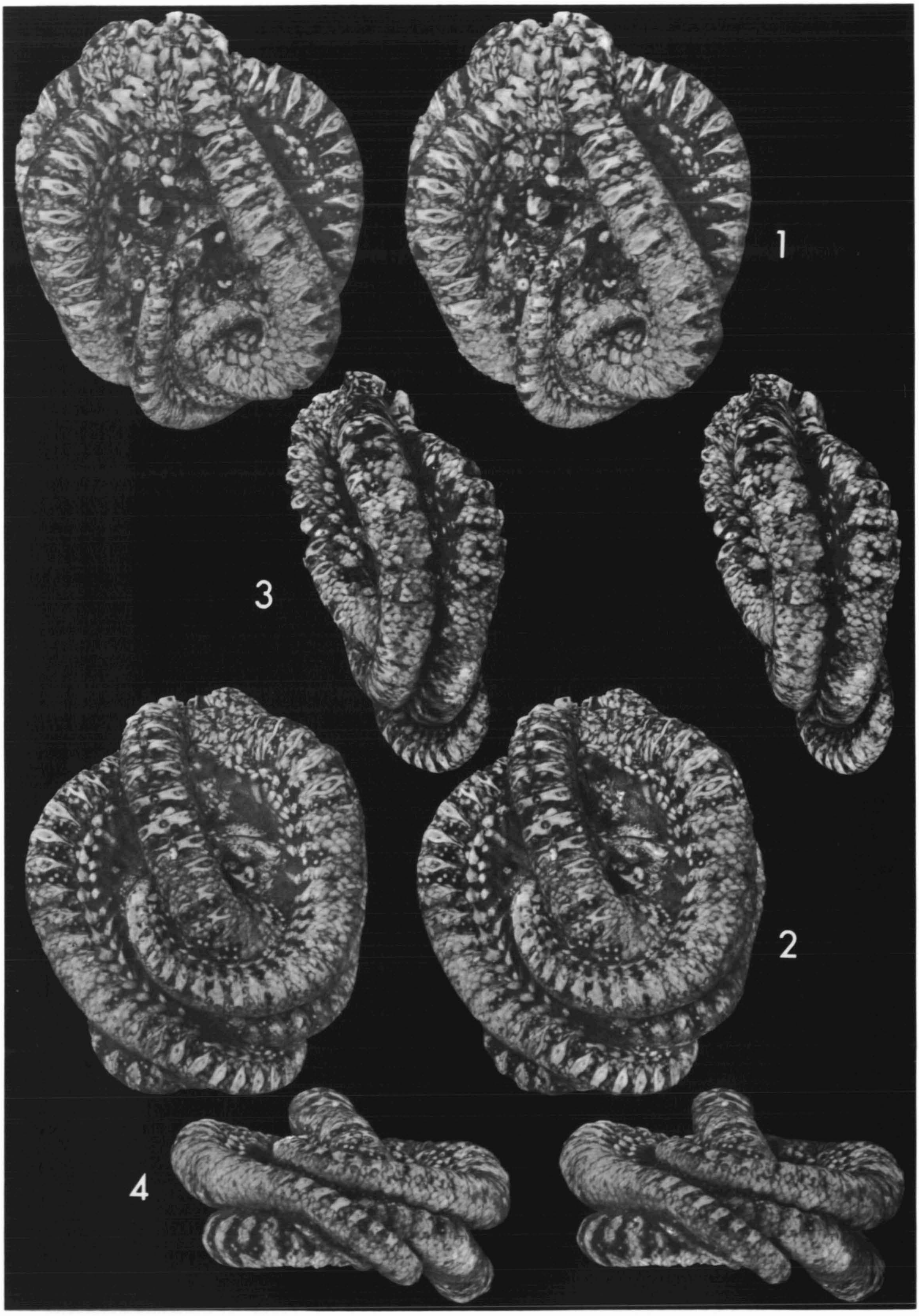


PLATE 1

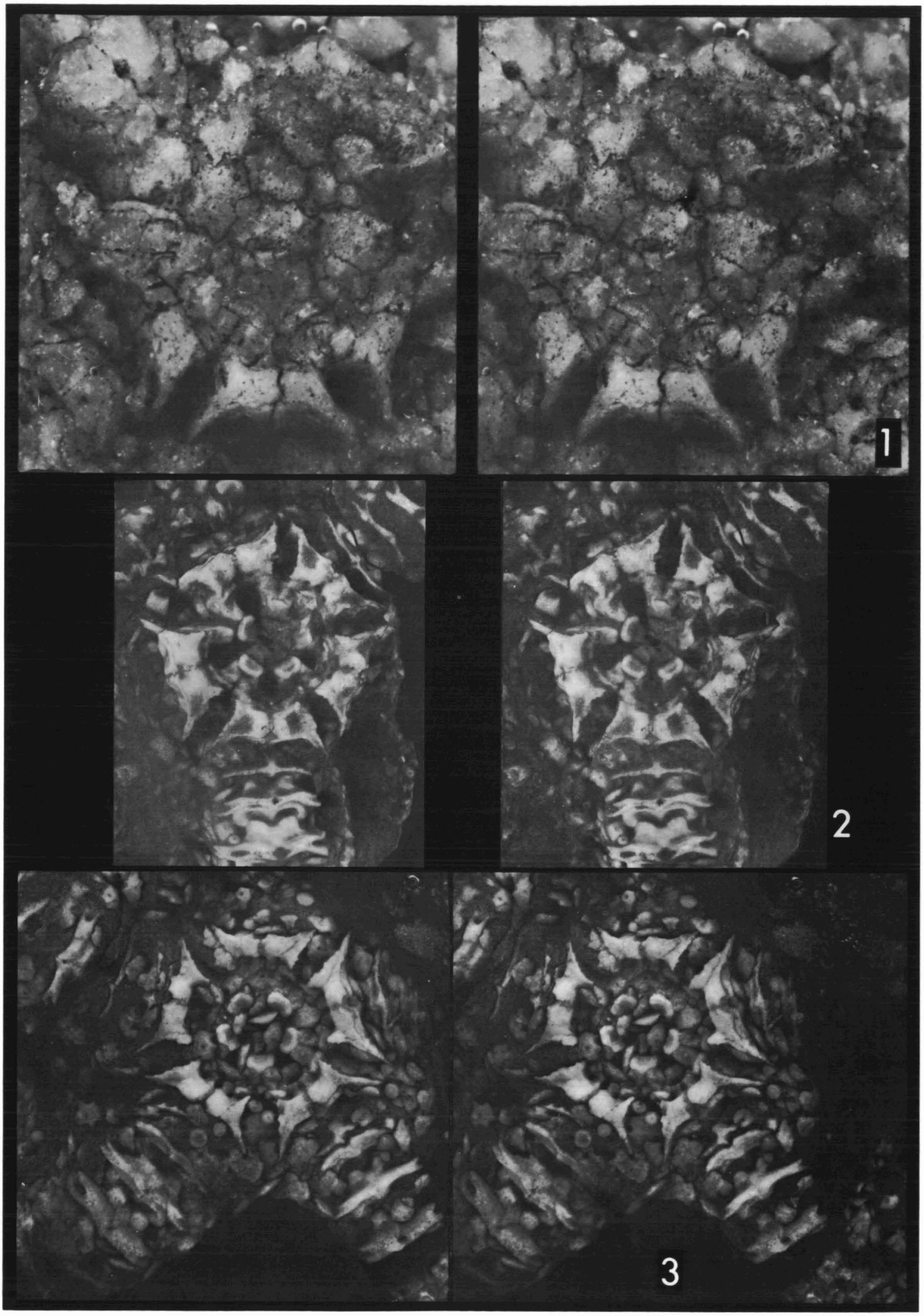


PLATE 2

through the ambulacral plate to the second tube-foot below.

MAP.—Mouth-angle plate with subparallel sides, its radial side with an embayment around the proximoradial hole, its proximal side meeting the torus obliquely, and its distal end extending out under the ambulacral. In the contracted condition of the frame (as preserved in all specimens examined), each MAP in contact with an MAP of the adjacent pair along the interradius. Plate corrugated by two distinct, well-incised, subcircular, concentric furrows, the outer for the ring canal and the inner for the nerve ring; surface rising as a rounded ridge between nerve ring and torus.

Proximoradial hole spacious, kite-shaped, bounded distally by minor extension of Am_2 and laterally by MAP and torus. Widest part of hole between mouth-angle plates in contracted condition (text-fig. 1), and probably in the same postion in the expanded condition (text-fig. 2).

Torus.—In aboral view, smaller than denticle, pentagonal, its two outer sides forming an obtuse angle and meeting at the interradius. Outer sides developed as a thick rim, sharply elevated above the MAP (pl. 3, fig. 6), the inner surface concave and sloping down to contact with denticle; the five tori rising above the central part of the frame like petals of a flower. Concavity of each torus somewhat rugose, suggesting area of muscle attachment.

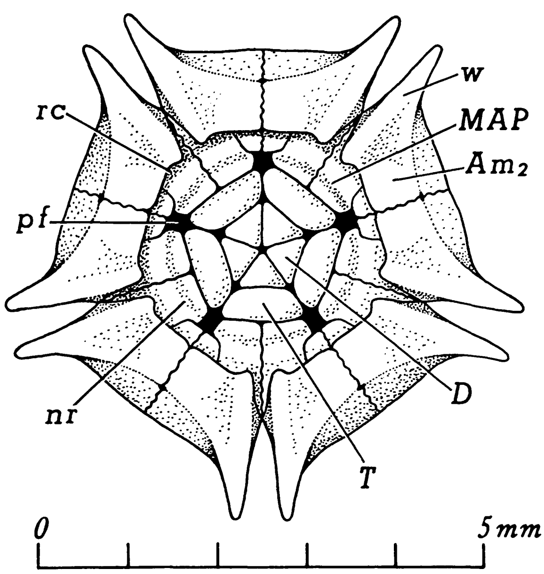
Denticle.—Subtriangular, set well below the tori. In the contracted condition of the frame, each denticle filling a complete interradius and the five denticles forming a circle.

Remarks.—The specimen which triggered this study is UMMP 6197. We discovered it on exhibit in our museum, with a simple label stating that it was from Crawfordsville, Indiana. In all respects it conforms to the original illustration by Meek & Worthen (1868, p. 526). Subsequently, the figure was somewhat modified by Meek & Worthen (1873, pl. 16, fig. 3a), whose illustration has been widely copied. We illustrate the specimen in plate 1. Undoubtedly, it is the best known (from literature) of all specimens of *Onychaster flexilis,* and we designate it the lectotype. Because Meek & Worthen mentioned other specimens, we refain from calling it the holotype. The specimen was photographed in xylol to emphasize the plates, including the integumental ossicles. This was necessary, because the surface was severely prepared by scraping and perhaps by sandpapering to expose the external form. Actually, the mouth frame is intact (pl. 1, fig. 1), but the Am_2 plates seem to be abraded and the denticles are poorly exposed. For that reason, it was necessary to base our description for the most part on better-preserved specimens.

Onychaster barrisi (Hall)

Text-fig. 3; pl. 2, fig. 1

Am_2.—Even in the best-preserved specimen available, the lower part of this plate is not exposed. Major (distal) part of plate massive; articulating surface with vertebra of the arm



TEXT-FIG. 3—*Onychaster barrisi* (Hall). Aboral plate diagram of mouth frame. Same plate symbols as in text-figure 1. Based on MCZ 398 (pl. 2, fig. 1).

EXPLANATION OF PLATE 2

(All figures stereograms, photographed in xylol)

FIG. 1—*Onychaster barrisi* (Hall). MCZ 398, × 10. Aboral view of mouth frame showing close set plates in shallow structure.

FIG. 2–3—*O. flexilis* Meek & Worthen. *2,* UMMP 6196a, × 4; aboral view of mouth frame showing crenulate sutures between paired Am_2, MAP beside each interradius, elevated tori, depressed denticles, and circular furrows for nerve ring and ring canal. *3,* UMMP 56561, × 4; aboral view of mouth frame showing numerous polygonal plates appressed onto central area, evidently from the integument overlying the frame and perhaps with an original arrangement as disk plates.

set in concavity but with convex central part; wings prominent, extending more in a distal than a lateral direction, those of adjacent pairs subparallel; short, bluntly rounded, inward-directed projection at the proximo-interradial corner; whole upper surface rounded, without furrows or peaks. Within the distal part, central area of frame shallow. Minor (proximoradial) part of plate small. Suture between paired peaks irregularly crenulate. Shallow depression in the dorsodistal part of suture, but no indication of vertical canal into plate. Junction with MAP long, extending from interradius nearly to radius. Furrow for ring canal inconspicuous, only overhung at the corners of the paired Am_2 plates by the short projections. No pores observed leading into the plates from the furrow for the ring canal.

MAP.—Mouth-angle plates very wide, not depressed much below Am_2. Those of each pair separated only by a narrow, small proximoradial hole, the only remainder of the buccal slit in the contracted condition of the frame. Each MAP meeting that of the adjacent pair along a crenulate suture; these two plates with nearly straight juncture with the torus. Furrow for nerve ring very shallow.

Torus.—Wide and large, not elevated above MAP. Distal border nearly straight, normal to the interradius. Proximal border apparently convex.

Denticles.—The five denticles in contact in the contracted condition, nearly filling central area of frame. Denticles only slightly lower than tops of adjacent tori, but distinctly set off from them.

Remarks.—Spencer (1927) described and figured an Upper Devonian brittle-star which he assigned to this species. He did not mention the mouth frame, and the vertebrae are so massive that we doubt that his specimen belonged to this species; we are not even certain that it was an *Onychaster*.

The condition of the specimens from the Burlington Limestone leaves much to be desired. We have based our description of the mouth frame on the material as preserved. Possibly, details of the plates have been slightly altered in fossilization.

This species has the most compact arrangement of plates of any *Onychaster*. The mouth-angle plates nearly form a wide circular band, being separated only by narrow gaps at the proximoradial holes. The entire aboral surface of the mouth frame is very shallow.

ONYCHASTER STRIMPLEI Bjork, Goldberg, & Kesling

Text-fig. 4; pl. 4, figs. 1–3

Am_2.—In aboral view, major part of plate narrow at junction with other Am_2 of the pair, laterally expanding into sturdy subtriangular wing. In distal view, a pair of ambulacrals subtriangular except for upturned interradial margins set on the sloping shoulders. In aboral view, articulating surface with arm rather strongly concave. Each Am_2 with strong relief, rising to a sharp peak set very close to the radius; surface sloping steeply away laterally to a sharp V-shaped groove nearly parallel to the interradius, thence rising abruptly to form a narrow margin. Inner edge of margin extending inward as a small, acuminate projection, slightly overhanging the furrow for the ring canal. No indentation or pore along the radial suture. Inner face of major part of ambulacral steep but relatively low. Furrow for ring canal moderately developed; no pores detected along furrow. Minor part of Am_2 very small, strongly tapering inward to proximoradial hole.

MAP.—Mouth-angle plate meeting minor part of ambulacral at a strongly oblique suture; inner borders of the plates lying on a circle (text-fig. 4). Each MAP adjacent to one from the adjacent pair, as in other species. Plate corrugated by two distinct, subcircular, concentric furrows, the outer for the ring canal and the inner for the nerve ring; furrows in depth intermediate between those of *Onychaster*

EXPLANATION OF PLATE 3

(All figures stereograms, × 1 except as noted)

FIGS. *1–6*—*Onychaster flexilis* Meek & Worthen. *1, 2,* UMMP 56561; oral and aboral views, photographed in xylol; dark carbonaceous residue still adheres to parts of the arms. *3, 4,* UMMP 6196b, × 1 and × 2; photographed with ammonium chloride sublimate; *3,* excellently preserved integumental ossicles covering the strongly retracted arms; specimen partly embedded in matrix; *4,* mouth frame, exposed by careful removal of matrix covering the oral side; specimen partly pyritized, reducing stray integumental ossicles to disk-shaped particles. *5, 6,* UMMP 6196a, photographed in xylol; *5,* aboral view of complete specimen; *6,* inclined aboral view of mouth frame, emphasizing the elevated tori and showing the pores of the canals supposedly leading to the second tube-feet, × 4.

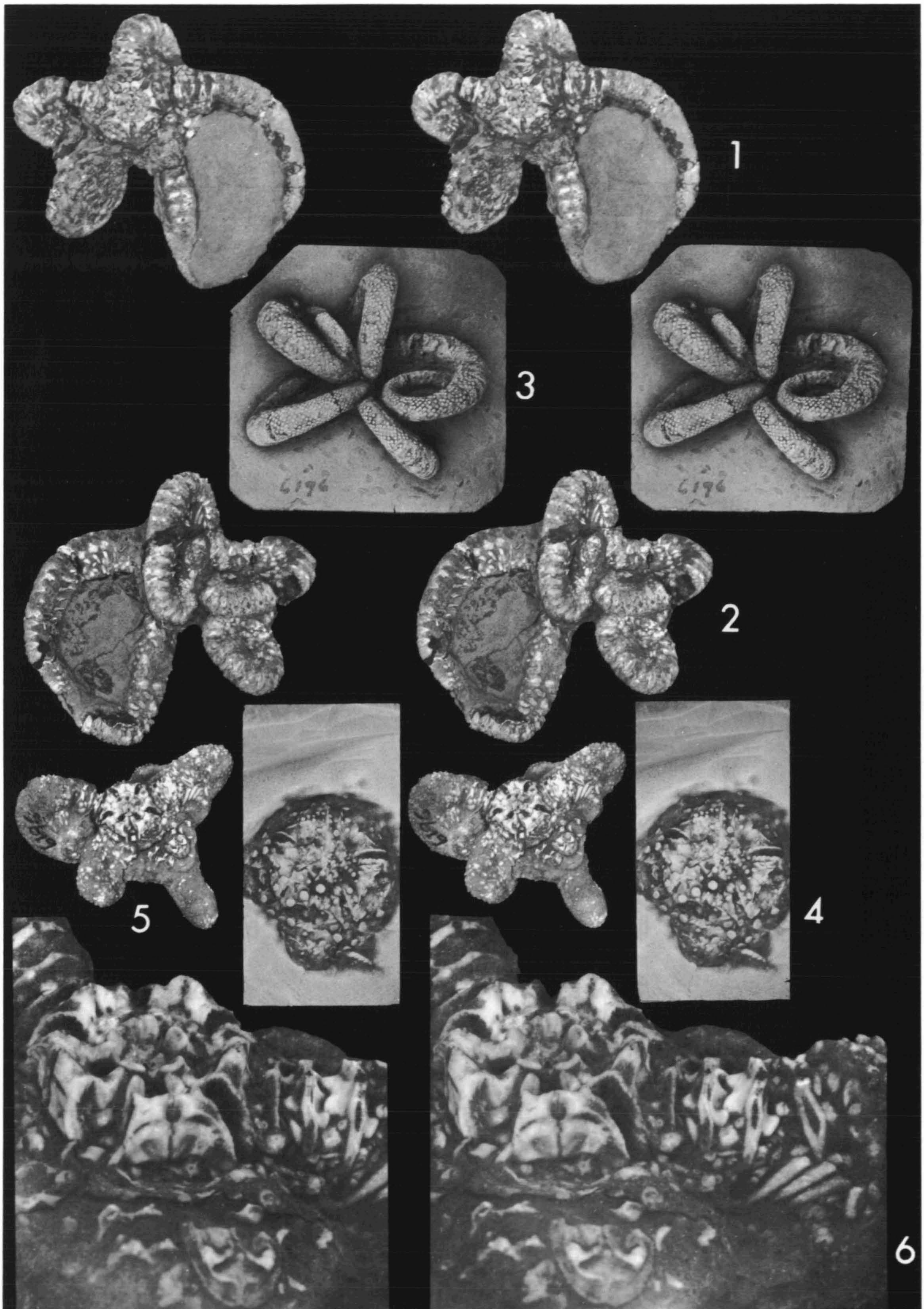


PLATE 3

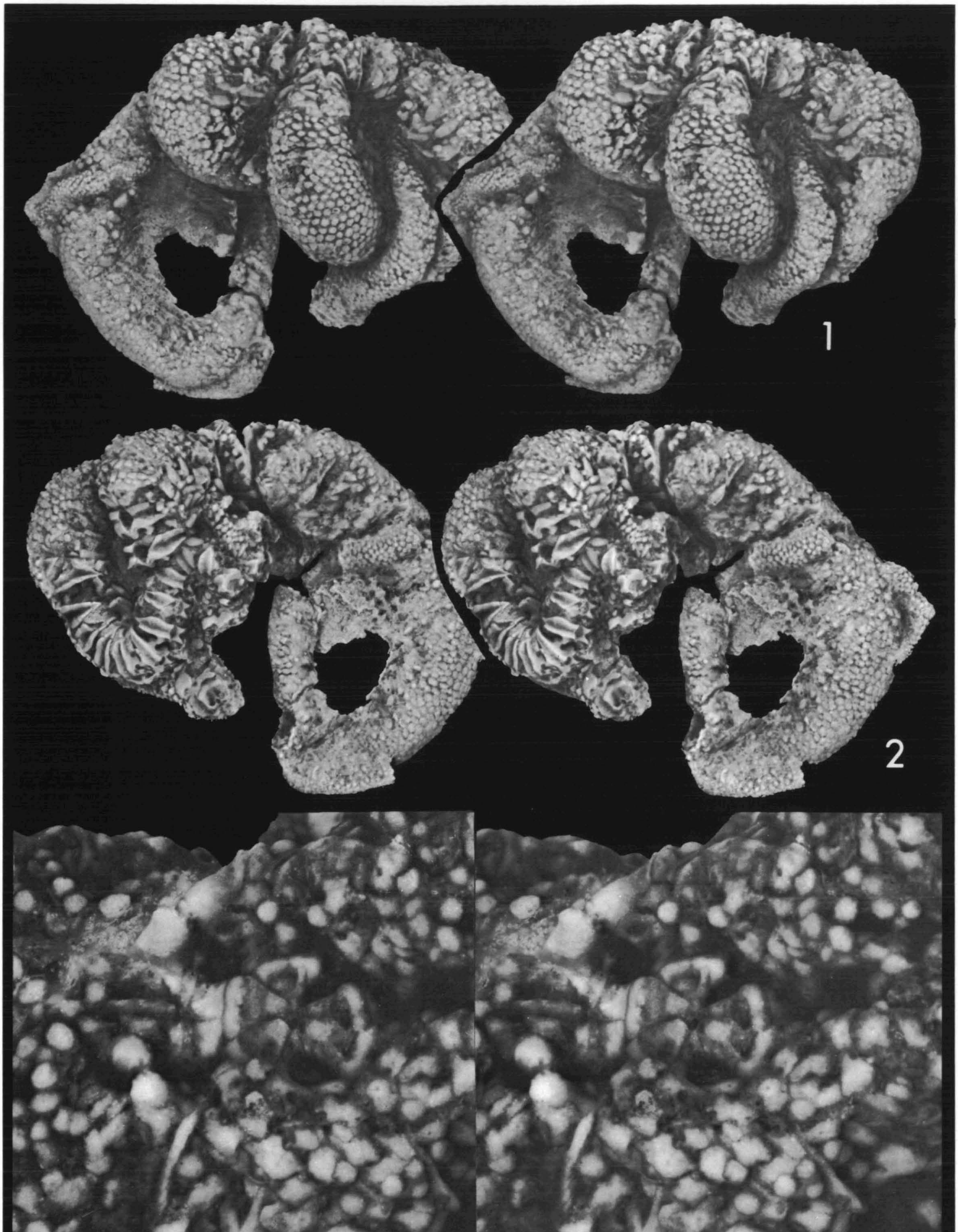
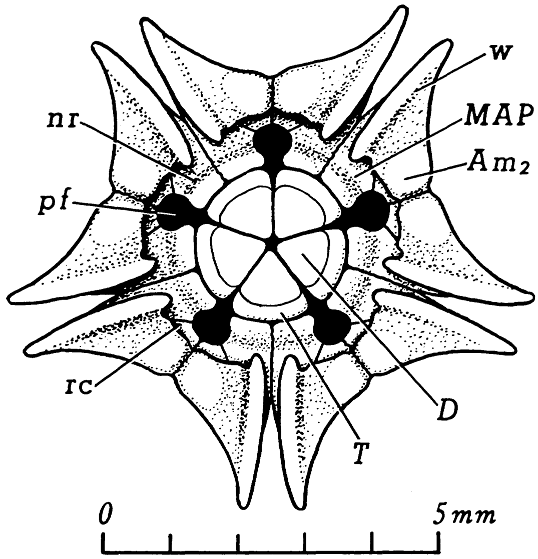


PLATE 4



TEXT-FIG. 4—*Onychaster strimplei* Bjork, Goldberg, & Kesling. Aboral plate diagram of mouth frame. Same plate symbols as in text-figure 1. Based on SUI 32002, the holotype (pl. 4, fig. 3).

flexilis and *O. barrisi;* inner margin of plate developed as low ridge.

Proximoradial hole keyhole-shaped, smaller than that of *Onychaster flexilis* and larger than that of *O. barrisi.* Outer part of hole circular, inner part a broad slot between the inner edges of the mouth-angle plates.

Torus.—Very narrow, not strongly elevated above MAP, the inner and outer borders of the tori forming complete circles. Tori apparently fused to denticles in each interradius.

Denticle.—Denticles forming a central circle developed as a low mound, fused to tori.

Remarks.—At present this species is only known from the holotype. It differs in so many characters from the other two species that it cannot possibly be confused with them.

PALEOECOLOGY

The fossil material gives a rather clear indication of the total animal. The arms were powerful, their articulations somewhat restricting lateral movement. The stomach lay within the central cavity of the mouth frame (as viewed aborally), covered over by an integument studded with small plates or ossicles. Some of the extraneous plates lying upon the mouth frame of UMMP 56561 (pl. 2, fig. 3) seem to have been plates of the overlying integument; their regular positions upon the mouth frame suggest that the disk of *Onychaster* had not completely degenerated. It occurs to us that the vulnerability of the stomach and other internal organs, inadequately armored on the aboral side, may have been a factor inducing *Onychaster* to seek protection within the arms of crinoids.

The heavy construction of the frame, the large attachments for thrusting muscles, and the strong denticles indicate that *Onychaster* was capable of powerful mastication. Nevertheless, it seems highly improbable that large particles were brought into the mouth. In particular, the tight fit of all plates in *Onychaster barrisi* (text-fig. 3) precludes the opening of the jaws more than a few millimeters. The torus is exceptionally wide, and it would seem impossible for the binding muscles there to have stretched to much more than twice their contracted state.

Many of the living ophiuroids have narrow jaws, functioning more like springs than like pile-drivers. The denticles can be opened wide, and thrusting movements may be used to loosen sediment in burrowing (Spencer & Wright, 1966, p. 27). In *Onychaster,* however, the massive jaws and very large denticles appear to have acted more like a battery of millstones in vertical series, thoroughly crushing and macerating small particles before they were eaten.

The association of *Onychaster flexilis* with crinoid calyces has been widely publicized. We have also seen one specimen of *O. barrisi* on a crinoid tegmen. Brittle-stars which do not burrow into the bottom sediments and ingest quantities of mud evolved two methods of acquiring sufficient nourishment. In the keen competition with one another and with other animals for the rain of detritus settling in marine waters, one group developed branching of the arms, wherewith these "basket-stars" proliferated the ambulacral area into a great food-collecting

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EXPLANATION OF PLATE 4

(All figures stereograms, × 3 except as noted, photographed in xylol)

FIGS. *1–3*—*Onychaster strimplei* Bjork, Goldberg, & Kesling. Holotype, SUI 32002. *1, 2,* lateral views of complete specimen; *3,* aboral view of mouth frame, × 10.

network. The other group, which includes *Onychaster* and certain of the living Phrynophiurida, solved the problem by climbing upon crinoids and other sessile bottom forms to intercept the food supply before it reached the congested bottom area and to take advantage of any food-collecting currents set up by their hosts. The well-developed masticatory apparatus and the restricted oral intake argue strongly against *Onychaster* being coprophagous.

On the other hand, the feeding of crinoid and brittle-star were different. Lacking any structures for biting, chewing, or grinding, the crinoid sifted and selected particles of the proper minute size for ingestion. The brittle-star, as indicated by its mouth frame, was equipped to eat large and even hard materials. *Onychaster* may very well have taken up residence on the crinoid calyx both for protection and for taking advantage of large food particles rejected by the crinoid. The relationship appears actually commensal.

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