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ARKONASTER, A NEW MULTI-ARMED STARFISH FROM THE MIDDLE DEVONIAN ARKONA SHALE OF ONTARIO

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Abstract.—Arkonaster topororum, a new Middle Devonian multi-armed starfish from western Ontario, preserves parts of the oral and aboral sides of the arms, the large aboral madreporite, and much of the mouth frame, including large spoon-shaped mouth-angle plates and thick "first" ambulacrals. Associated with its aboral surface are triradiate forcipulate pedicellariae of two sizes. The adambulacral-type mouth frame, large mouth-angle plates, and well-developed pectinate adambulacrals alongside the ambulacrals assure the assignment of this specimen to the order Spinulosida and the suborder Eugnathina, which already contains such multi-armed genera as the Paleozoic *Lepidasterella* and *Helianthaster* and the post-Paleozoic *Solaster*, *Plumaster*, and *Pythonaster*. Certain features of the new starfish, however, distinguish it from forms presently known in the suborder. Its arms bear only radial (carinal) plates and lack both superomarginals and inferomarginals; its mouth-angle plates have only shallow grooves to accommodate the nerve- and water-rings and are not abutted by axillary plates; and its madreporite is aboral. Thus it differs from the family Taeniactinidae, which has superomarginals in addition to radials atop the arms and an oral madreporite (in genera in which it is known); from the Lepyriactinidae, which has smaller mouth-angle plates with deeply incised grooves, no radials, and only one spine per adambulacral; and from the Helianthasteridae, which lacks radials and has only one spine per adambulacral. Accordingly, a new family, the Arkonasteridae, is erected for the Ontario specimen.

INTRODUCTION

Paleozoic starfish preserving essential features of both oral and aboral sides are rare. In many specimens, the arms were contorted in rigor mortis and the whole skeleton was seriously disarticulated before burial. Inasmuch as both oral and aboral sides of arms and disk are needed for accurate classification, Paleozoic starfish are still not well known. By a conservative estimate, the position of the madreporite is definitely known in less than half the Paleozoic species described, and the aboral surface of the disk in far fewer.

Because they must frequently work with poorly preserved and inadequate fossil material, those paleontologists who do specialize in early starfish have had to resort to a great deal of interpretation. As a result, taxonomy in many families, based on incomplete morphologic data and incorrect conceptions, is suspect with good cause. The rarity of good specimens and the instability of the taxonomy combine to discourage most paleontologists from becoming dedicated paleostelleroidologists.

Under these circumstances, presentation of a fairly complete fossil multi-armed starfish to our Museum of Paleontology was very welcome. The specimen was discovered in the Middle Devonian Arkona Shale by John and Michael Topor and Joseph Koniecki. When first exposed to view by hand quarrying, it lay practically complete. In removing the block of soft, wet, crumbly shale containing it, however, the fragile skeleton began to break up. Thanks to the careful handling by the Topor brothers, enough associated parts were retained to demonstrate conclusively the nature of oral and aboral plates of the arms, the mouth-angle plates ringing the oral aperture, and the large madreporite plate. The only large plates on the aboral side of the disk are subpolygonal to subround plates bearing central spines, exactly like those on the tops of the arms; all other parts of the aboral surface of the disk are composed of a thin layer of pyritized granules. Both arms and disk bear pyritized triradiate pedicellariae of two distinct sizes and types.

Shortly after their exhumation, the small slabs of matrix containing starfish remains were coated with white glue to prevent further disintegration. Without this prompt and wise action, all parts of the starfish skeleton would undoubtedly now be reduced to a mass of isolated plates.

At the laboratory, the glue was carefully scrubbed from the specimen parts with a soft brush dipped in acetone. Cleaning proceeded under a binocular microscope with small needles, thin wooden picks, and judiciously brief application of air abrasion with dolomite powder.

For assistance in photography, I am greatly indebted to George Junne, of our Museum of Paleontology. The delicate specimen, lightly sprayed with lacquer after photography, is deposited in the Museum of Paleontology of the University of Michigan, where it is catalogued as UMMP 64450.

OCCURRENCE

Small quarry near the west bank of the Ausable River at Hungry Hollow, about 2 miles east and ¼ mile north of Arkona, Ontario. Specimen from about 25 to 30 feet below the top of the formation, Middle Devonian Arkona Shale. Found by John and Michael Topor and Joseph Koniecki.

SYSTEMATIC DESCRIPTION

Abbreviations.—For convenience, the following abbreviations are used herein. They have already been used widely by previous authors.

Adm (Admm) — adambulacral(s)
Amb (Ambb) — ambulacral(s)
MAP (MAPP) — mouth-angle plate(s)
R (RR) — radial(s) or carinal plate(s) of arm or disk

Subphylum ASTEROZOA Zittel 1895

Class STELLEROIDEA Lamarck 1816

Subclass ASTEROIDEA de Blainville 1830

Remarks.—The differences between the subclasses Asteroidea and Ophiuroidea are not nearly so clear-cut as stated in most paleontology textbooks. It is true that the Recent asteroids (or true starfish), which have the disk merging into the arms, an open ambulacral channel, and tube-feet along the full length of the arms, are readily distinguished from the ophiuroids (or brittle-stars), which have a distinct separation of the circular disk and slender arms, a closed ambulacral channel, and tube-feet developed only in the mouth area as buccal tentacles. Internally, these two subclasses typically differ also: the asteroids, which use their tube-feet for walking, grasping, and (in some) for pulling open their bivalve prey, have Ambb forming an arch to counter the pull exerted by the tube-feet, but the brittle-stars, which have substituted quick, synchronized arm movements for the tube-feet in locomotion, have their pairs of Ambb fused into vertebrae for flexibility. These differences, based on feeding and locomotory habits as well as morphology, led Spencer (1913, p. 9) to characterize the asteroids as the "Graspers" and the brittle-stars as the "Wrigglers."

The distinctions between Asteroidea and Ophiuroidea were less pronounced in early forms. As Spencer (1913, p. 7) observed:

> Among recent Asterozoa there are two types of body-form: the one 'asteroid' (star-shaped), almost without exception characteristic of the Asteroidea, the other 'disc-shaped,' peculiar to the Ophiuroidea. In early Paleozoic times these characters had not the same significance . . . The sharp separation between arm and disc arises later as a secondary modification.

In particular, the asteroids of the order Spinulosida closely resemble the brittle-stars of the order Stenurida in Ordovician through Devonian forms. Both have unfused Ambb and an Adm-type mouth frame; some genera in each have marginal plates; both orders contain some multi-armed genera; and both may lack any aboral arm plates. Further, the Admm plates of the Spinulosida curve around the sides of the arm and can scarcely be distinguished (if at all) from the lateral plates (or side-shields) of the Stenurida; both Admm and laterals bear spines. The supposed internal ampullae of the tube-feet in the Spinulosida and external ampullae in the Stenurida cannot be used as a certain criterion for identification; the position of the ampullae is not clear in most specimens, and its significance is far from established.

Only a few characters are available to indicate the line between these two orders. Paleozoic asteroids of the Spinulosida are, insofar as I can learn, not known to have a torus at the junction of the MAPP, whereas a torus is said to be present in all brittle-stars (even though it is not preserved in the majority of Paleozoic specimens and is not known in many genera). Some genera of the Spinulosida, fortunately including the new genus described here, possess aboral plates on the arms, whereas such plates are not present in the Stenurida. Hence, with some confidence, I assign *Arkonaster* to the subclass Asteroidea.

Order SPINULOSIDA Perrier 1884

Remarks.—Within the subclass Asteroidea the separation of orders is also somewhat confused. For examples, Spencer (1922, p. 178) included *Schuchertia*, *Palasterina*, and *Eoactis* in his family Eoactinidae; but Spencer and Wright (1966) placed *Schuchertia* in the order Spinulosida, *Palasterina* in the order Paxillosida, and *Eoactis* in the order Valvatida! This is but one example of confusion and uncertainty at the ordinal level. Another involves the multi-armed *Devonistella* and *Lepidasterella*; Spencer (1926) included both in his family Taeniactinidae, but Spencer and Wright (1966) assigned *Devonistella* to the order Paxillosida and *Lepidasterella* to the order Spinulosida.

The new genus *Arkonaster* is here placed in the Spinulosida primarily because of its very large

MAPP and its weak aboral skeleton (consisting only of RR plates), even though its madreporite is definitely aboral and the madreporite (where known) is oral in previously described genera of that order.

Suborder EUGNATHINA Spencer and Wright 1966

Remarks.—This suborder is distinguished from the suborder Leptognathina by its large MAPP and its wide ambulacral furrows. Both characters are well shown in the holotype of *Arkonaster topororum.*

ARKONASTERIDAE n. fam.

Type genus.—Arkonaster n. gen.

Diagnosis.—Multi-armed starfish of the suborder Eugnathina having only RR (carinal plates) on aboral sides of the arms. No superomarginals or inferomarginals present. MAPP very large, spoon-shaped, with shallow but distinct grooves aborally for nerve- and water-rings. Mouth frame of adambulacral type, strongly constructed. No axillary plates associated with MAPP. Madreporite aboral, very large and well developed. Pedicellariae atop arms and disk.

Remarks.—This new family differs from the Taeniactinidae in lacking any superomarginals associated with the RR atop the arms. It differs from the family Lepyriactinidae in having much larger MAPP, well-developed Admm, and RR on the arms. It differs from the family Schuchertiidae in having RR in the aboral skeleton and in lacking both inferomarginals and axillaries abutting the MAPP. It differs from the Helianthasteridae and the Solasteridae in having RR present in the aboral skeleton.

In its development of an aboral skeleton in disk and arms, the new family Arkonasteridae seems to be intermediate between the Taeniactinidae and the Helianthasteridae, both of which contain multi-armed genera.

ARKONASTER n. gen.

Type species.—Arkonaster topororum n. sp.

Derivatio nominis.—This genus is named for Arkona, Ontario, a village near the site where the only known specimen was found.

Diagnosis.—Same as for the family.

Description.—A multi-armed starfish of the family Arkonasteridae with 28 arms in only known specimen. Oral opening large, about one-seventh the total diameter, surrounded by close-set pairs of MAPP. Each arm long, from the edge of the disk proximally decreasing slightly to MAPP and distally tapering evenly to rather sharp, narrowly rounded tip.

Arms consisting of Amb and Adm plates surmounted by RR (carinals). Ambb arranged opposite throughout, sharing podial basins equally between adjacent pairs. Admm large, curved along sides of arms, pectinate. MAPP aligned with Admm, each spoon-shaped, large, with shallow grooves for nerve- and water-vascular-rings. "First" Ambb very large and thick, forming essential elements of mouth frame.

Interbrachial areas of disk narrowly triangular, proximally separated from mouth frame by several Admm; each area containing subquadrate alternating plates dividing rather sharply at middle of brachial arc with narrow tapering extension alongside each bordering arm for short distance.

Madreporite very large, irregularly oval with long axis radial, definitely aboral, set above and between MAPP and edge of interbrachial arcs, overlying an arm in only known specimen.

Aboral surface of arms and disk bearing large RR (carinals) and pedicellariae of two distinct sizes.

Remarks.—Parts of the only specimen are pyritized, so that comparisons between pyritized and non-pyritized sections of the skeleton are difficult. All pedicellariae and granules from aboral surfaces of disk and arms are pyritized, but most areas of arms (including RR and Admm spines) are not. Some sections of arms are also pyritized.

Known range.—Middle Devonian (Givetian).

ARKONASTER TOPORORUM n. sp.

Pls. 1–7; Text-figs. 1–6

Derivatio nominis.—This species is named in recognition of the contributions made to the Museum of Paleontology of the University of Michigan by John and Michael Topor.

Description.—This description is based on the holotype and only known specimen, which may or may not be adult.

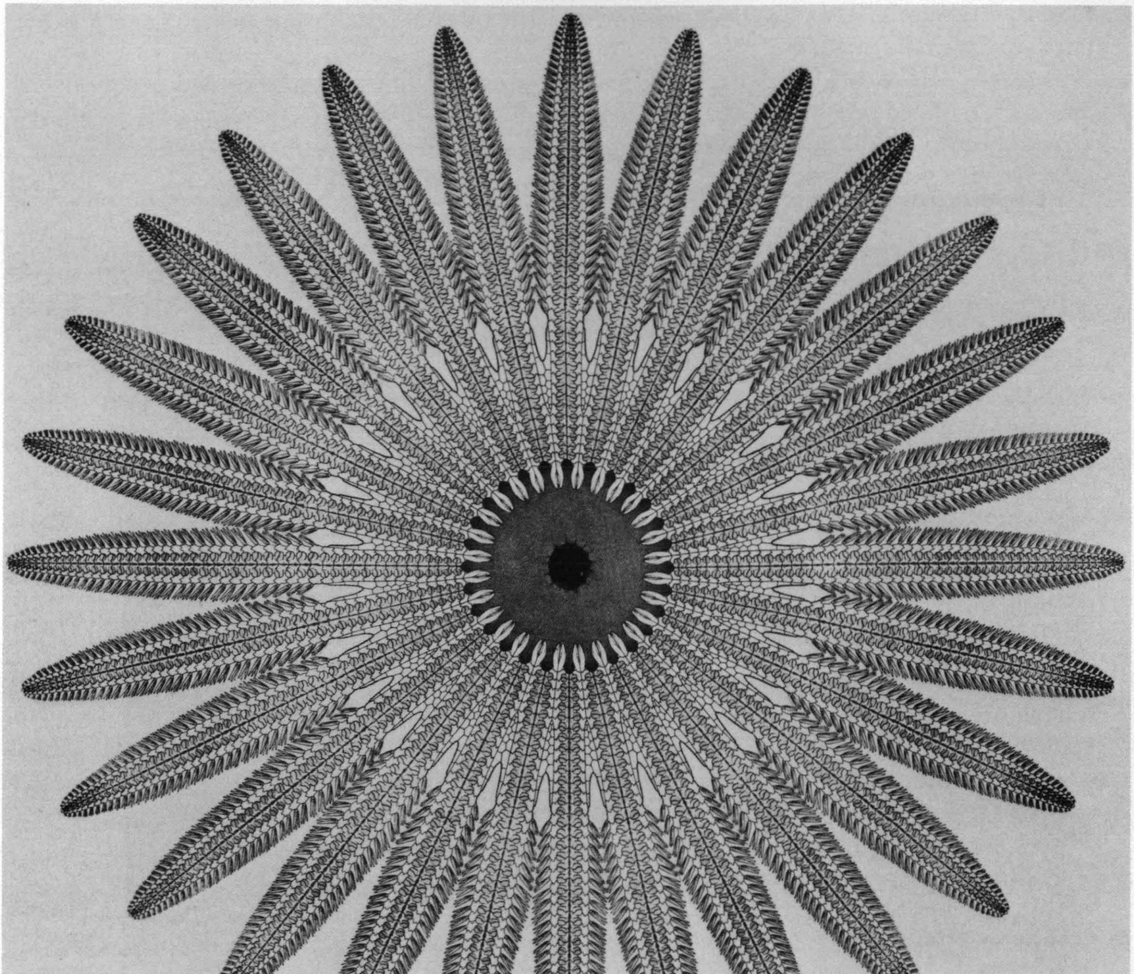
Starfish large for species of suborder Eugnathina, its greatest diameter (between arm tips) about 140 mm and its least diameter (between interbrachial arcs) about 52 mm. Multi-armed, with 28 close-set arms in holotype. Oral opening large, about 20 mm between opposite MAPP, surrounded by large, inwardly directed pairs of MAPP (Pl. 1, fig. 1; Text-fig. 1). Arms long, each extending about 57 mm distally from MAPP.

Each arm only about 3 mm wide at proximal (orad) end, expanding gradually to about 5 mm wide just beyond interbrachial arcs, thereafter tapering evenly to rather sharp, narrowly rounded tip (Text-fig. 3). Arms consisting of Ambb and Admm plates, surmounted by RR (carinals); no inferomarginals or superomarginals present. About 50 opposed pairs of Ambb per arm, making about 2800 podial cups in the animal. Ambb arranged opposite throughout, never alternating, those in each half-arm sharing podial basins equally (Pl. 3, fig. 1; Text-fig. 2.) Median transverse L-shaped ridge on oral side of each Amb, its adradial part directed orad but not reaching ridge of opposite Amb; curved groove behind ridge to accommodate branch water vessel; abradial end of ridge meeting ridge of Adm, the two together forming the wall between podial basins (Pl. 3, fig. 1; Text-fig. 2).

Proximal two pairs of Ambb (not counting MAPP) strongly modified. "First" Ambb (by derivation considered to be fused second and third Ambb) by far the thickest plates of the skeleton, essential elements of the strong mouth frame; each "first" Amb nearly reaching that of the adjacent arm, the 56 plates nearly forming a circlet as viewed from above. Oral and aboral sides of each "first" Amb very different (Text-fig. 6). Aboral side raised into an ovate dome in its adradial part, there adjoining the corresponding "first" Amb of the opposite half of the arm along a corrugated suture (Pl. 2, figs. 6–9). Junction with MAPP much smaller and immovable (Pl. 4, fig. 4; Text-fig. 4), sinuous. Oral side of "first" Ambb rather narrow, forming part of first podial basin (Text-fig. 2). "Second" Ambb sloping upward and backward, their distal edges visible aborally from under the thick "first" Ambb (Pl. 2, fig. 9). Succeeding Ambb essentially unmodified.

Shallow ambulacral groove down middle of each arm to accommodate the radial water vessel, somewhat deeper at midlength of each Ambb pair than at their ends (Text-fig. 3). Aborally, Ambb forming rather flat surface atop arm, each plate with a narrow subtrapezoidal lappet in its abradial-distal half, extending over edge of succeeding plate (Text-fig. 4); this weak imbrication suggesting restricted upward movement of the arms.

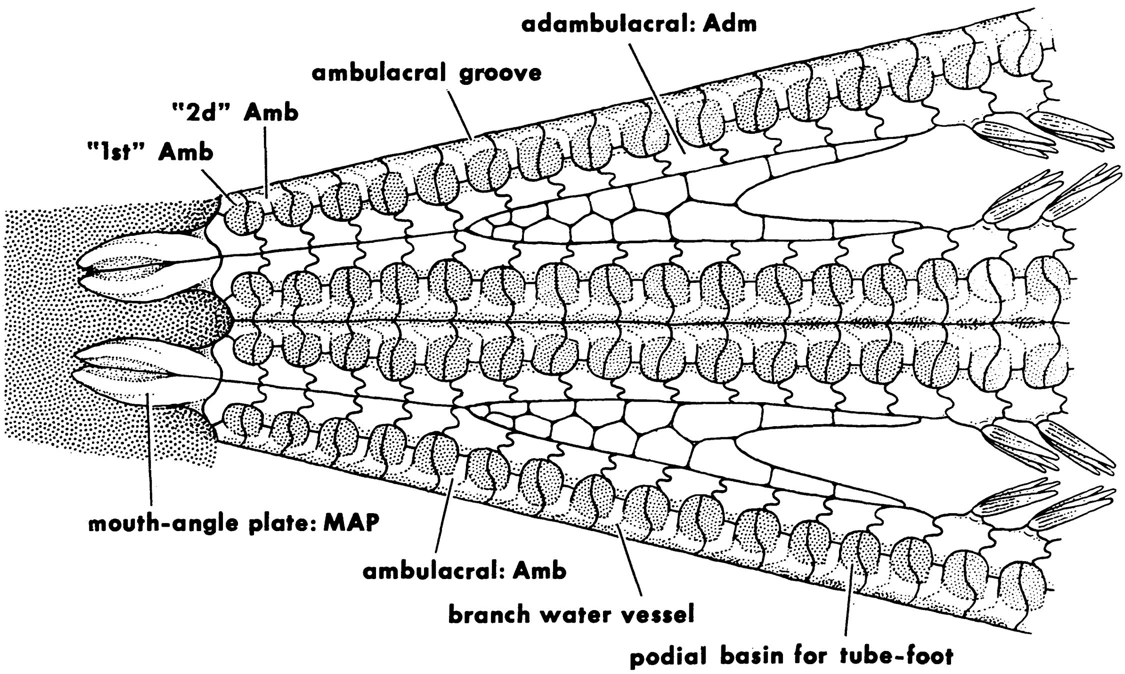
MAPP very large, set closely in pairs directed into the oral opening. Each MAPP spoon-shaped, about 3.6 mm long (Pl. 4, figs. 2, 3). Oral sides of MAPP with a narrow cleft between



TEXT-FIG. 1 — Restoration of oral side of *Arkonaster topororum*. It is presumed that, as in living multi-armed starfish, the mouth was a central opening operated by sphincter muscles and that the surface of the surrounding stomach was visible within the circlet formed by the mouth frame. All hard parts shown in the restoration are represented in more than one arm.

each pair (Text-fig. 2); aboral sides with angular shallow grooves for nerve- and water-rings, and with slightly ovate tips (Pl. 2, figs. 7–9; Text-fig. 4). No evidence of a torus or spines associated with MAPP.

Admm large, curved gently alongside the arms, pectinate, each medially bearing a vertical row of three pustule-like subconical mounds with craters for attachment of spines (Pl. 3, figs. 4, 5). Admm lateral spines long and striate, tapering evenly to narrowly rounded tip, about twice the length of the Adm plate (Text-fig. 3). Each Adm with a median oral ridge adjoining ridge of



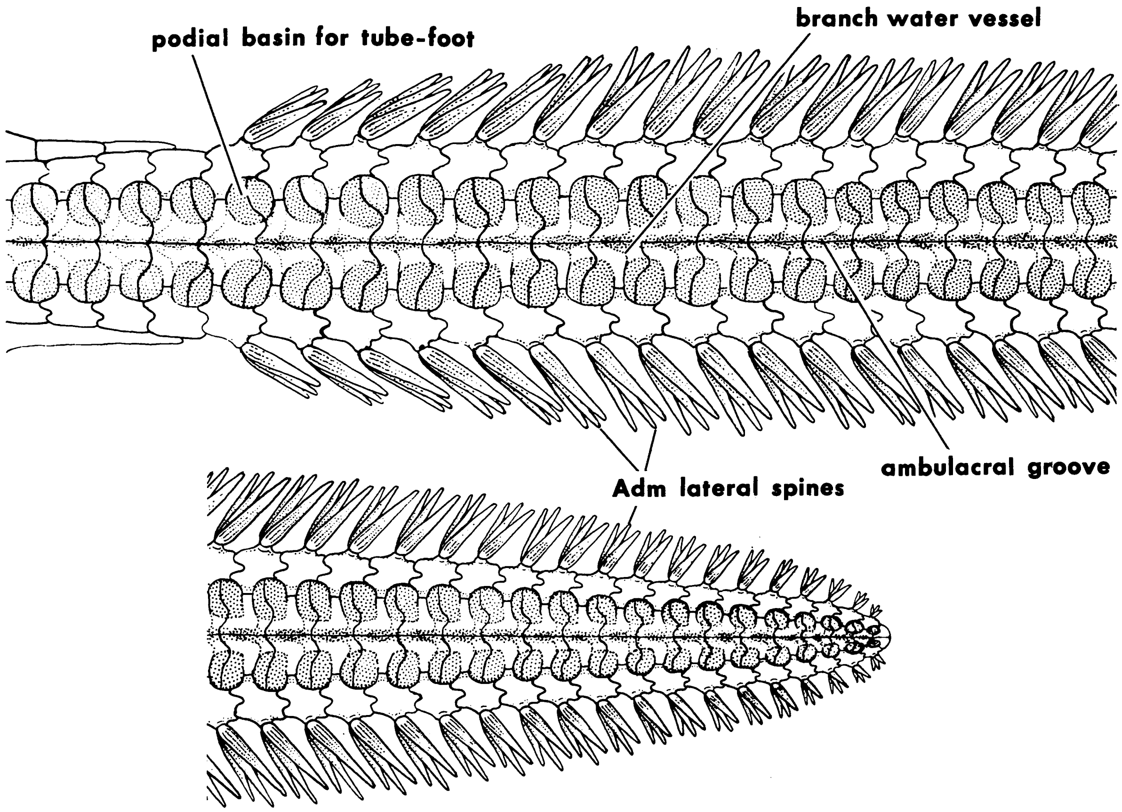
TEXT-FIG. 2 — Oral side of proximal section of arms and mouth frame.

Amb to form low, narrow wall separating podial basins. Orally, outer margin of each Adm with deep cleft, presumably for attachment of muscles to enroll the arm. Aborally, Adm with a distal subtrapezoidal lappet located near the abradial side (Pl. 3, fig. 3; Pl. 5, fig. 1), sloping distally over the edge of the succeeding plate and forming a shallow imbrication in each row; lappets apparently limiting aboral (upward) movement of the arm. Opening at junction of adjacent Ambb and Admm (at quadruple junction of plates), presumably for passage of nerves and muscles (Pl. 3, fig. 3).

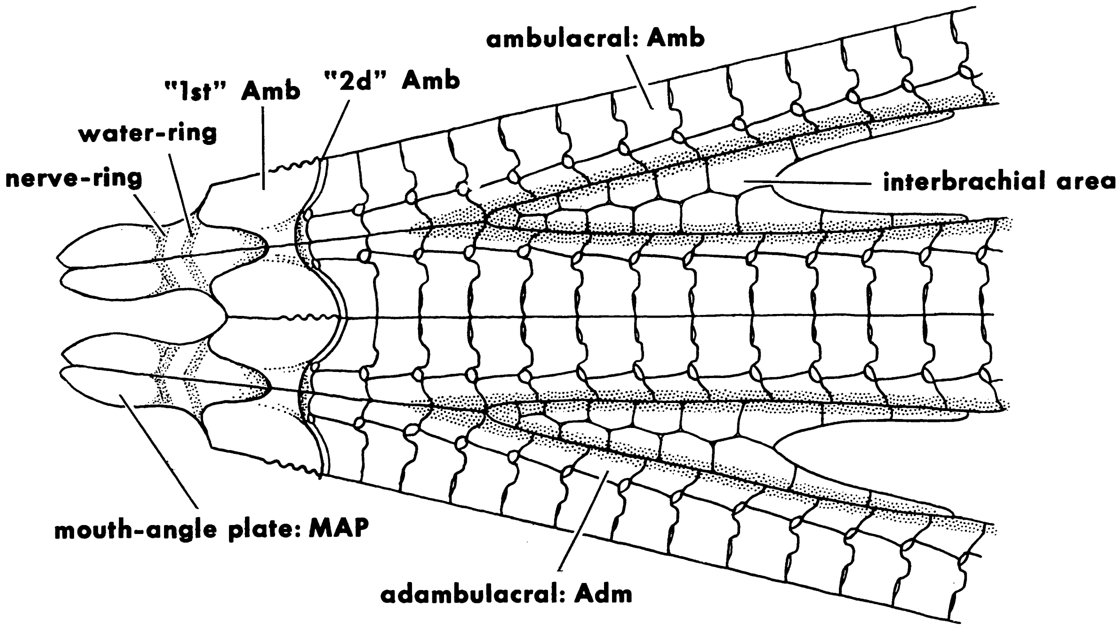
RR (carinals) the only major skeletal elements on aboral side of arms and disk. Each R large, subcircular, with a central concavity surrounded by a rim to accommodate the spine (Pl. 2, fig. 7, Pl. 5, fig. 2); each carinal spine shorter and slightly stouter than any of the Admm lateral spines. RR close-set in a row atop each arm, probably extending onto disk (Text-fig. 5) to judge by positions of some preserved RR now lying upon mouth frame and apparently collapsed from overlying disk.

Pedicellariae of two distinct sizes and shapes found associated with arms, presumably borne on the aboral surface only. Both types forcipulate and triradiate (Text-fig. 5; Pl. 6, figs. 1–15). Larger pedicellariae slender, about 1.3 mm long; each of the three jaws tapering rapidly just above the base, then continuing as a narrow tapered prong to the tip, leaving narrow slits between adjacent jaws in a closed pedicellaria. Smaller pedicellariae much more robust and rotund, only about 0.3 mm long, acorn-shaped, the sides of each jaw convex. In the large pedicellariae, inner face of each of the three movable jaws provided with a marginal row of tiny denticles; each denticle shaped like a rose thorn, its sharp tip directed inward toward the axis of the pedicellaria. No such row of denticles observed in the small pedicellariae.

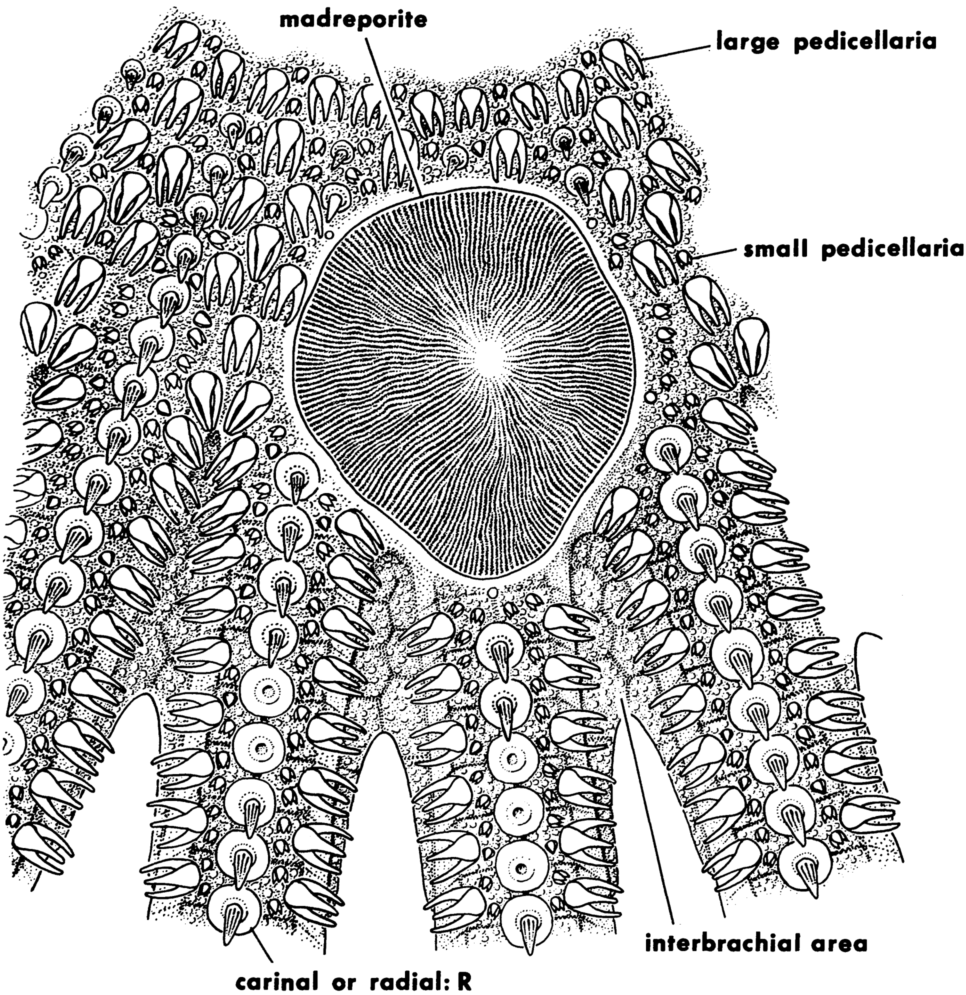
Madreporite very large, irregularly oval, about 10 mm long with its greatest length aligned radially (Pl. 2, figs. 1–3; Text-fig. 5). Madreporite definitely aboral, set above and between MAPP and edge of interbrachial arcs, overlying an arm in the only known specimen (Pl. 2,



TEXT-FIG. 3 — Oral sides of middle and distal sections of an arm. Compare with photographs in Plate 3, figs. 1, 2.



TEXT-FIG. 4 — Aboral side of section of arms and mouth frame.

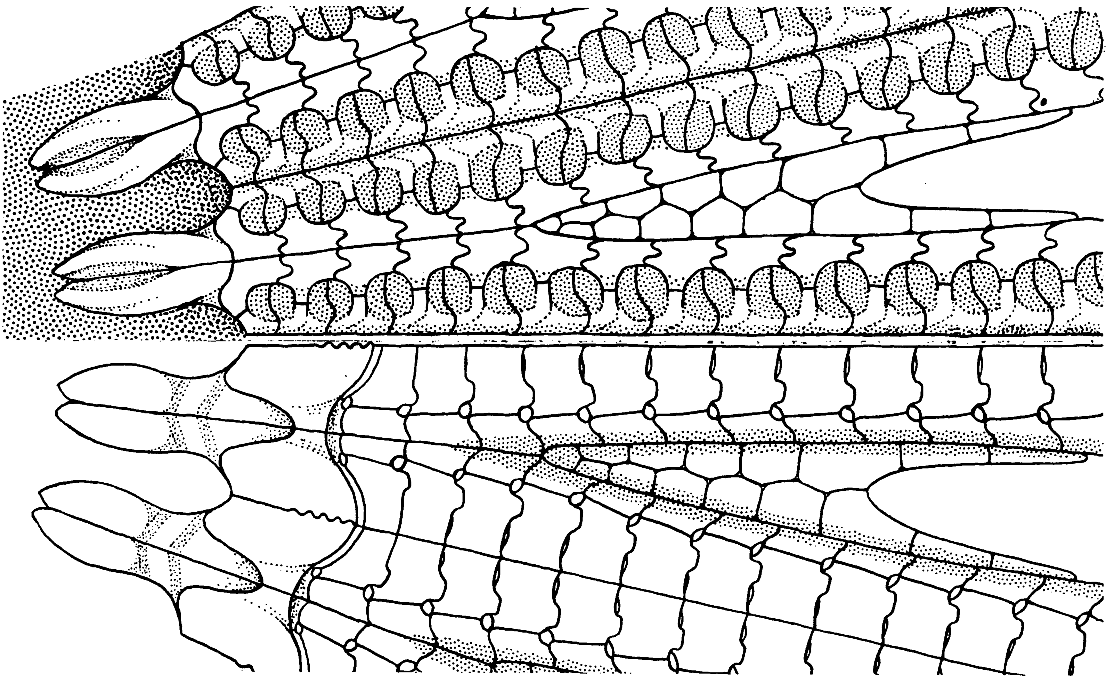


TEXT-FIG. 5 — Aboral side of section of disk and adjoining arms showing the large madreporite and RR (carinals). The disposition of the two kinds of pedicellariae is uncertain; here, the restoration is based on the approximate positions where some have collapsed onto the arms and mouth frame.

fig. 2). Surface of madreporite covered with fine grooves, irregularly radiating and anastomosing from the center of the plate.

Interbrachial areas narrowly triangular, separated from the mouth frame by several Admm, composed of subquadrate, alternating thin plates in two rows (Pl. 2, figs. 4–6; Pl. 5 fig. 2; Text-figs. 2,4). At the middle of the interbrachial arc, the two rows diverge rather sharply (Text-fig. 1) with a uniserial extension on each side tapering alongside each bordering arm for about three or four Admm lengths (Pl. 2, fig. 4). No enlarged marginals in the interbrachial area. Proximal to the interbrachial areas, several Admm of adjacent arms in contact, evidently a necessity for accommodating arms of this number and width below the disk. Admm beyond interbrachial arcs bearing lateral spines (Text-fig. 1).

Holotype.—UMMP 64451.



TEXT-FIG. 6 — Oral (above) and aboral (below) sides of section of mouth frame and arms; the two views are shown together to emphasize the drastic differences in aspect of the mouth frame and adjacent Ambb on the opposing sides.

PALEOECOLOGY

Inasmuch as no traces of food remains were found associated with *Arkonaster*, its diet and habits can only be inferred by comparing its morphology with those of living Asterozoa, which have various foods and feeding methods.

Feeding in living forms.—Food and feeding methods in asterozoans are difficult to classify, not only because many species are omnivorous but because the same species may utilize several ways of securing food and conveying it to the digestive system. For convenience of discussion, the asterozoans are here divided into the macrophagous (feeding on fairly large prey), the microphagous (feeding on microscopic prey and particles), and the scavengers (cleaning remains of dead organisms from the sea floor). Recently, in the same volume (Boolootian, 1966), feeding in starfish was discussed by Feder and Christensen and in brittle-stars by Fell.

Predation on macroscopic animals is more characteristic of the Stelleroidea than the Ophiuroidea. Three main methods of feeding on such prey may be distinguished: (1) extra-oral digestion of very large prey, (2) biting off parts of the prey, with internal digestion, and (3) ingestion of the entire prey with later ejection of undigestible remains. Each of these is well known and documented.

1) The tenacity of starfish in opening large bivalves has been described many times. A particularly good account is given by MacBride (1906, p. 439) for *Asterias* (order Forcipulatida):

> The starfish seizes its prey by the tube-feet and places it directly underneath its mouth, folding its arms down over it umbrella-fashion. The muscles which run around the arms and disc in the body-wall contract, and the pressure thus brought to bear on the incompressible fluid in the coelom forces out the thin membranous peristome and partially turns the stomach inside out. The everted edge of the stomach is wrapped around the prey. Soon the bivalve is forced to relax its muscles and allow the valves to gape. The edge of the stomach is then inserted between the valves and applied directly to the soft parts of the prey, which is thus completely digested.

Later experiments and observations have concerned the functional morphology by which the starfish is consistently able to open large bivalves. The pull of the tube-feet in bivalve predators can support 3 to 5 kilograms. Unless the starfish can hump its body and get firm anchorage by the tube-feet in the distal parts of its arms, it is totally ineffective in opening the prey. The arm structures which withstand prolonged pulls of as much as 5 kg probably involve both Ambb and Admm plates and strong musculature joining them. Spencer (1913, p. 11) stated, "This method of feeding was possible only when the ambulacral arch had become sufficiently strong to withstand powerful lateral pull." Nearly all starfish preying upon large bivalves are five-armed.

Some starfish use extra-oral digestion on prey which cannot readily be conveyed into the stomach. Thus, Feder and Christensen (1966, p. 104) report starfish everting the stomach to digest attached barnacles. The notorious destroyer of modern coral reefs is the multi-armed *Acanthaster planci*, (order Spinulosida), known as the "Crown-of-thorns." This carnivore evidently utilizes extra-oral digestion, for there is no report of its dislodging the polyps before digesting them, and the coral heads, stripped of all organic matter, are left behind. The giant multi-armed *Pycnopodia helianthoides* (order Forcipulatida) from the coastal waters of the northern Pacific digests animals too large for its mouth opening by extrusion of the stomach, although in many cases it does not actively catch such food but merely acts as a scavenger on dead fish and other animals; regularly, it swallows smaller prey whole. Spencer and Wright (1966, p. U25) state, "This form of external digestion is applied to a variety of other prey [than bivalves], such as brachiopods, sickly fish, or coral polyps."

2) Biting off small pieces of the live prey may occur in starfish eating the tubiculous annelids, bryozoans, or coral polyps, but presumably most such predation involves some extra-oral digestion.

As reported by Feder and Christensen (1966, p. 104), however, some multi-armed starfish of the family Solasteridae (order Spinulosida) actually eat away at the arms of other starfish. *Crossaster papossus* attacks *Asterias rubens* in such a way as to induce the latter to autotomize an arm, which the *Crossaster* proceeds to feed upon. *Solaster dawsoni* similarly feeds upon *Evasterias troschelii.* As an "ectoparasite," small specimens of *Solaster endeca* may cling to an arm tip of *Asterias* for days, continuously eating it until the diameter of the *Asterias* arm becomes too big for the smaller carnivore to hold in its mouth opening.

The ophiuroid *Astrohamma* is said by Fell (1966, p. 132) to be an active predator on corals, but its feeding method is not described.

3) Ingestion of whole macroscopic prey is common among shallow-water starfish, including many multi-armed genera. As reported by Spencer and Wright (1966, p. U25):

> . . . prey is passed to the mouth by the tube feet or the sea star positions itself with the mouth directly over the prey and the lips of the stomach are everted through the mouth and draw the prey into the stomach. Living *Astropecten* [order Paxillosida] has been observed to fill itself so full of small mollusks by this method that the upper

> surface is distended . . . Many modern asteroids eat other asteroids, ophiuroids, and echinoids. The predator digests the soft parts and ejects the hard remains.

The giant multi-armed *Pycnopodia helianthoides* (order Forcipulatida) regularly swallows small prey in great quantities.

Two main methods of conveying food to the mouth were described by Jennings (1907, p. 93):

> Large objects are usually carried by the active bending of the ray beneath the body, till the object is applied to the mouth . . . Small pieces of flesh are transported in a somewhat different manner. After being carried to the ventral side of the ray, near its tip, perhaps, the ray bends downward and under at precisely the point where the food body touches it, so as to bring the food into contact with a point on the lower surface of the ray nearer the disc. The tube-feet of this nearer point then seize the flesh, while the more distal ones release it . . . Thus the food is passed from one set of tube-feet to another, slowly along the under side of the ray, till it reaches the mouth.

Spencer (1913, p. 12), postulated that the latter method (tube-foot transfer) was probably a survival of the earliest manner of feeding of starfishes, but did not explain the reasons for his conclusion.

Some brittle-stars also feed in part by ingesting whole prey. According to Fell (1966, p. 132), *Ophiura* twists the arms to bring food to the mouth, including small worms, crustaceans, molluscs, and other echinoderms. He also says that *Amphiura belgicae* in Antarctic waters apparently feeds on bryozoan polyps, although its method of obtaining them is not discussed. *Ophiothrix*, which forms extensive colonies, is said to eat small clams, echinoderms, foraminifera, and other invertebrates, extracting them from currents.

Asteroids which feed upon microscopic organisms also use a variety of feeding methods, including (4) entrapment of food by mucous secretions, (5) conveyance by ciliary currents or tube-feet to the mouth, and (6) mucous feeding directly by the stomach.

4) A variety of forms use mucous secretions to entrap microscopic prey or organic particles, which are then carried by ciliary action to the mouth, the whole being ingested. Rasmussen (1965) classifies *Odontaster* (order Valvatida) as one which "feeds by flagellary mucous means." According to Spencer and Wright (1966, p. U24):

> A development of this ciliary feeding is seen in mud-eating asteroids; *Ctenodiscus* [order Paxillosida] plows through the upper layer of mud of the sea floor, entangling material in threads of mucus, which are then swept by ciliary action along channels on the oral surface to the radial groove and then to the mouth.

Such feeding is reported in several ophiuroids by Fell (1966) and by Reese (1966). *Ophiocomina* and *Ophiocoma* eat leaves of laminarian sea plants, dead small animals, and particles "entangled in slimy secretions of tube feet" (Fell, 1966, p. 132). *Ophiocoma scolopendrina* uses threads of mucus to entangle selected material, moving the resulting mass along the ciliated ambulacral groove. *Ophiothrix fragilis* maintains dense populations by its efficient catch of small worms and other little bottom forms in mucus from its tube-feet. Presumably, because their gut ends blindly, brittle-stars are somewhat more selective in food-gathering than are starfishes.

5) Tube-foot or ciliary capture of microscopic prey or extraction of organic particles from sea water is apparently now common among brittle-stars. Nevertheless, they exhibit a variety of adaptations in feeding.

Asteronyx loveni climbs up onto slender pennatulid corals, clinging with two or three arms and sweeping the surrounding area with its other arms to intercept the fall of small nektonic and planktonic animals. *Astrotoma* lies on its back, mouth upwards, its arms sweeping and collecting plankton, which are conveyed to the mouth by tube-feet. The Basket-star, *Gorgonocephalus*, has arms branched many times to form a huge network for intercepting plankton and organic detritus borne by currents. Species of *Amphiura* lie with the body buried and the arms upright; *A. filiformis* holds the ends of its arms erect in the current, whereas *A. chiajei* has the protruding arms horizontal. (See Fell, 1966, and Reese, 1966).

One starfish is reported to mimic this feeding method. Rasmussen (1965) lists the slender-armed *Henricia* (order Spinulosida) as a true ciliary feeder on micro-organisms. However, Spencer and Wright (1966, p. U24) state that "the frequent multi-armed forms among Paleozoic asteroids may also have been suspension-feeders, since the arms could constitute an effective net to catch drifting particles of food."

6) The Cushion-star, *Patiria* (order Spinulosida), uses its stomach as a direct ciliary mucous feeding organ (MacGinitie and MacGinitie, 1949).

Scavengers involve (7) the selective feeders and (8) the presumably non-selective mud swallowers.

7) The largest known starfish, the multi-armed *Pycnopodia helianthoides* (order Forcipulatida), is a scavenger on dead animals, as well as an ingestor of whole prey. Numerous other living starfish, including *Solaster* and other genera of the order Spinulosida, are known to supplement their diet with dead organisms.

8) Some question exists about the selectivity of the mud-eating starfishes, whether they ingest random quantities of mud or extract mainly organic matter with some adhering mud. Feder and Christensen (1966, p. 96) report:

> Mud swallowers . . . may be found with their stomachs fully distended with bottom material which, however, always contains many foraminifera, diatoms and radiolarians . . . their stomachs may also contain minute snails, bits of worm tubes and remains of sea urchins.

Noted mud eaters include *Porania* (order Spinulosida), *Sphaerodiscus* (order Valvatida), and *Thoracaster* and *Ctenodiscus* (order Paxillosida).

In summary, neither multi-armed starfish nor the starfishes of any one order are restricted to any particular feeding method. Those of the order Spinulosida, to which *Arkonaster* is assigned, seem to feed by extra-oral digestion of large prey (*Acanthaster*), eating of large macroscopic prey by gnawing off parts (*Crossaster* and *Solaster*), ciliary extraction of micro-organisms (*Henricia*), direct application of the stomach as a ciliary mucous feeding organ (*Patiria*), scavenging of dead organisms (*Solaster*), and ingestion of mud (*Porania*).

Habitat of Arkonaster.—Whereas most living species with multiple arms live among rocks exposed to the surf (Verrill, 1909), there is no evidence whatsoever for supposing that *Arkonaster* lived elsewhere than on the muddy, shale-forming bottom of the Arkona sea. The specimen was found far below the top of the shale and its skeleton was practically intact.

Furthermore, since starfishes of the order Spinulosida now inhabit a variety of depths and bottom conditions, the environment in which *Arkonaster* lived may not be much of an indicator to its life habits except for the availability of food as shown by the associated fauna. In the Arkona Shale, molluscs are relatively rare, crinoid remains are locally common, brachiopods are very common, trilobites fairly common, and micro-organisms (especially Ostracoda) abundant.

Morphology of Arkonaster.—Certain features of *Arkonaster* may be pertinent in inferring its feeding and other habits.

1) The arms are numerous, entailing a very large oral opening.

2) Each arm is long and slender, consisting only of Amb and Adm plates with overlying RR.

3) Each arm contains about 100 small podial basins; whereas the tube-feet were numerous, they were quite small.

4) The mouth frame shows little room for movement in chewing and crushing action. The "first"' Ambb appear to meet (or almost meet) in each ray.

5) The distally directed lappet on the aboral side of each Amb, imbricating over the succeeding plate, would seem to preclude lifting of the arm tip far above the disk. Instead, the arms would readily enroll downward.

6) The arms extend far beyond the disk, allowing more than ample accommodation for the distal part of the arm to reach the mouth.

7) The aboral surface of arms and disk bear both large and small triradiate pedicellariae. By their size and shape, the former would appear to have been rather powerful organs.

Possible life mode of Arkonaster.—Among living starfishes, ossicle morphology seems to bear a significant relation to possible food selection. On the other hand, food choice appears to be related to habitat only insofar as the habitat can provide the desired food; genera of the same family may live in radically different energies, depths, and temperatures, and on very different bottom sediments in order to obtain a supply of their particularly preferred food.

Arkonaster presumably lived at moderate depths on the Middle Devoian mud substrates, which then extended northwestward and westward into Michigan, southwestward into Ohio, and eastward to western New York. This rather uniform realm supported a very rich and diverse fauna.

Arkonaster had no buttressing inferomarginals or superomarginals, like those of living *Asterias*. Its slender arms seem completely inadequate for pulling open large bivalves. Compared to the arms of *Devonaster* (order Valvatida), which occurs in the same formation, those of *Arkonaster* are very weakly constructed. Furthermore, one can hardly imagine how any large starfish could exert enough force to open a bivalve with only soft mud for the tube-feet to brace against.

In view of the rarity of small bivalves in the same strata, it is also doubtful that *Arkonaster* fed mainly upon them, in the manner of some species of Recent multi-armed *Pycnopodia*. The minute quantity of soft parts in each of the abundant small brachiopods in the formation make them unlikely whole prey for such a large animal as *Arkonaster*.

The large circlet around the mouth formed by the 28 pairs of MAPP would seem to have precluded biting off pieces of prey, even if suitable, large, soft-bodied, and defenseless prey were available. In addition, the MAPP do not seem to have been capable of much "spring" in the mouth frame, due to their lateral extent.

From the nature of articulations of its Ambb, *Arkonaster* probably could not have held its arms erect to intercept plankton and organic particles carried by currents. It may, however, have used such food as a mud-eater, ingesting quantities of the organic-rich bottom sediment. Whether the starfish was selective in such a feeding process, passing only nutritive items toward the mouth with its many tube-feet, cannot be logically conjectured.

I would suppose that such a starfish, with many slender arms, was mainly a scavenger. The Arkona Shale contains numerous concentrations of crinoid remains, thoroughly disarticulated and extensively worked over by concentrations of scavengers, such as the gastropod *Platyceras* and the small brittle-star *Eugasterella*, and undoubtedly including the trilobites *Phacops* and *Greenops*.

These layers of crinoidal "hash," forming irregular lenses in the formation, may have been favored feeding grounds of *Arkonaster*, which would have been the largest of the scavengers.

This multi-armed starfish, with about 2,800 tube-feet, may have used them to pull off particles and strands of decaying skin from the crinoid ossicles and pass them along to the mouth; it could similarly have used the array of tube-feet in extracting the soft tissues from other dead animals.

Arkonaster may also have availed itself of the platycerid gastropods attracted to the area by the odor of decay. It could have used its numerous tube-feet and long flexible arms to shove such whole prey into its mouth cavity.

Role of pedicellariae.—Interpretation of the use made by *Arkonaster* of its numerous and prominent pedicellariae is made more difficult because the function of pedicellariae in living starfishes is not fully understood, particularly in relation to feeding. Hegner (1937, p. 515) said that in the living *Asterias* the pedicellariae act "to protect the dermal branchiae, to prevent debris and small organisms from collecting on the surface, and to capture food." Ricketts and Calvin (1968, p. 182) stressed their effectiveness in destroying debris settling on the aboral surface, and stated:

> Considering that sessile animals must struggle for even sufficient space for a foothold, and that seastars live in a region where the water may be filled with minute larvae of barnacles seeking an attachment site, the value of these cleaning pedicellariae is very apparent. It is even possible that they have some value in obtaining food, for, despite their small size, they have been observed to catch and hold very small crabs, which may eventually be transferred to within reach of the tube feet.

Nevertheless, I doubt that *Arkonaster* regularly obtained food by its pedicellariae.

The Middle Devonian fauna of the Arkona Shale includes abundant epizoans, as shown clearly by the inhabitants on the larger brachiopods. These included inarticulate brachiopods, many kinds of bryozoans, and small tabulate corals, among other invertebrates. Probably, the pedicellariae of *Arkonaster* served primarily to keep such epizoan larvae from establishing residence upon its exposed upper surface by grasping, crushing, and killing them. Any use of the remains of epizoans dispatched in this manner as food was probably only incidental.

STELLEROIDEA OF THE ARKONA SHALE

Despite the general rarity of fossil Stelleroidea, the Arkona Shale and its stratigraphic near-equivalents have yielded a remarkably diverse fauna. This includes five starfish of four orders and four brittle-stars of two orders (Table 1). The Arkona Shale itself has produced two starfish—*Devonaster triradiatus* Kesling and Wright and *Arkonaster topororum* n. sp.—and two brittle-stars—*Eugasterella thorni* Kesling and *Drepanaster wrighti* Kesling. *Michiganaster inexpectatus* Kesling (order Paxillosida) is known from the slightly older Rogers City Limestone of northern Michigan; the starfish *Silicaster esseri* Kesling and the two brittle-stars *Antiquaster magrumi* Kesling and *Strataster devonicus* Kesling came from the approximately co-eval Silica Shale of northwestern Ohio; and *Devonaster southworthi* Kesling and Wright was found in the Hungry Hollow Formation overlying the Silica Shale. To date, however, no one of these species is known to occur in more than one formation or at more than one locality. The following key is provided for use in identifying these stelleroids.

TABLE 1 — Known Middle Devonian Stelleroidea of northern Michigan, northwestern Ohio, and southwestern Ontario.

Order	Suborder	Family	Genus and species	Formation
		Subclass ASTEROIDEA		
Forcipulatida	Uractinina	Calliasterellidae	*Silicaster esseri*	Silica Shale
Paxillosida	Hemizonina	Lepidasteridae	*Michiganaster inexpectatus*	Rogers City Ls.
Pustulosida	Bimarginalina	Promopalaeasteridae	*Devonaster triradiatus*	Arkona Shale
			Devonaster southworthi	Hungry Hollow
Spinulosida	Eugnathina	Arkonasteridae	*Arkonaster topororum*	Arkona Shale
		Subclass OPHIUROIDEA		
Stenurida	Parophiurina	Antiquasteridae	*Antiquaster magrumi*	Silica Shale
Oegophiurida	Lysophiurina	Protasteridae	*Eugasterella thorni*	Arkona Shale
			Drepanaster wrighti	Arkona Shale
			Strataster devonicus	Silica Shale

Key to Known Middle Devonian Stelleroidea from Michigan, Ohio, and Ontario

1. Arm skeleton with aboral series of plates, including RR (carinals) and, in some, inferomarginal and superomarginal plates; no torus at junction of MAPP .... Subclass ASTEROIDEA ... 2
   Arm skeleton devoid of aboral series of plates; torus present at junction of MAPP .... Subclass OPHIUROIDEA ... 6
2. Mouth frame of ambulacral type; large axillary plate set at axil between arms, forming interbrachial buttress on side of disk; RR and inferomarginals extremely well developed on top and sides of arms; superomarginals confined to disk ... Order FORCIPULATIDA ... *Silicaster esseri* Kesling 1969a
   Mouth frame of adambulacral type; axillary plate (if present) not conspicuously large; RR small and inferomarginals (if present) more or less confined to oral side of arm; superomarginals (if present) extending onto arms in series 3
3. Accessory interbrachials forming conspicuous triangular field between bordering inferomarginals and the proximal series of Admm of bordering arms .... Order PAXILLOSIDA ... *Michiganaster inexpectatus* Kesling 1971b
   No field of accessory interbrachials if inferomarginals present 4
4. MAPP small; axillary associated with each pair of MAPP; coronet well developed on disk; no multi-armed genera known .. Order PUSTULOSIDA ... 5
   MAPP very large; no axillary associated with MAPP; coronet not developed; several multi-armed genera known .... Order SPINULOSIDA .... *Arkonaster topororum* n. sp
5. Proximal inferomarginals large; Adm series wider than that of inferomarginals .... *Devonaster triradiatus* Kesling and Wright 1965
   Proximal inferomarginals narrow; Adm series narrower than that of inferomarginals .... *Devonaster southworthi* Kesling and Wright 1965
6. Ambb discrete plates; arms capable of only limited movement; disk not raised as round button above arm level; long sublateral plates; Admm developed as rodlike laterals .... Order STENURIDA .... *Antiquaster magrumi* Kesling 1971a

Ambb tending to fuse into vertebrae but without well-developed ventral peg-and-socket joint; arms capable of snake-like movements; disk subround and elevated; no sublateral plates; Admm developed as curved or flat side shields, never rodlike .... Order OEGOPHIURIDA ... 7

7. Admm developed as thin, curved side shields with sharp oral edges; articulating noses of these plates recessed from oral edge; Amb "boot-shaped" ridges very prominent; Adm spines thin and long; MAPP small .... *Drepanaster wrighti* Kesling 1969c

Admm developed as thick lateral plates or side shields, with little if any curvature; articulating noses of these plates near oral edge; Amb "boot-shaped" ridges not particularly thickened; Adm spines stout; MAPP large 8

8. Oral spines of lateral plates (Admm) developed as thin spatulate structures; arm bases thick and arms fairly stout .... *Strataster devonicus* Kesling 1972

Oral spines of lateral plates (Admm) conical and tapered, arm bases rather thin, arms very slender .... *Eugasterella thorni* Kesling 1969b

With the possible exceptions of *Michiganaster inexpectatus*, which probably stuffed whole molluscan prey into its large oral opening, and the two species of *Devonaster*, which may have preyed upon very small clams and/or snails, the stelleroids listed above seem to be morphologically fitted to be scavengers, raking through bottom debris with the lateral spines of the arms or settling directly upon larger deceased organisms. Some may have supplemented their diet with entrapped micro-organisms, but the general picture which emerges is of several kinds of stelleroids competing as scavengers on the shallow-water mud and lime substrates of Middle Devonian time in this region.

LITERATURE CITED

BOOLOOTIAN, R. A., ed. 1966. Physiology of Echinodermata. Interscience Publ., New York 822 pp.

FEDER, H. M., and A. M. CHRISTENSEN. 1966. Aspects of asteroid biology. Pp. 87–128 *in*: BOOLOOTIAN, R. A. (ed.), Physiology of Echinodermata, Interscience Publ., New York.

FELL, H. B. 1966. The ecology of ophiuroids. Pp. 129–144 *in*: BOOLOOTIAN, R. A. (ed.), Physiology of Echinodermata. Interscience Publ., New York.

HEGNER, R. W. 1937. Invertebrate Zoology. MacMillan and Co., New York. 570 pp.

JENNINGS, H. S. 1907. Behaviour of the starfish *Asterias forreri* de Loriol. Univ. Calif. Publ. Zool. 4(2):53–185.

KESLING, R. V. 1969a. *Silicaster*, a new genus of Devonian starfish. Contrib. Mus. Paleontol. Univ. Mich. 22(19): 249–263, 4 pls., 2 text-figs.

———. 1969b. A new brittle-star from the Middle Devonian Arkona Shale of Ontario. *Ibid.* 23(2):37–52, 6 pls., 2 text-figs.

———. 1969c. *Drepanaster wrighti*, a new species of brittle-star from the Middle Devonian Arkona Shale of Ontario. *Ibid.* 23(4):73–80, 2 pls.

———. 1971a. *Antiquaster magrumi*, a new unusual brittle-star from the Middle Devonian Silica Formation. *Ibid.* 23(10):181–192, 4 pls.

———. 1971b. *Michiganaster inexpectatus*, a new many-armed starfish from the Middle Devonian Rogers City Limestone of Michigan. *Ibid.* 23(16):247–262, 3 pls., 5 text-figs.

———. 1972. *Strataster devonicus*, a new brittle-star with unusual preservation from the Middle Devonian Silica Formation of Ohio. *Ibid.* 24(2):9–15, 2 pls., 3 text-figs.

———, and J. D. WRIGHT. 1965. Two new Middle Devonian species of the starfish *Devonaster* from southwestern Ontario. *Ibid.* 20(2):49–61, 4 pls., 2 text-figs.

MAC BRIDE, E. W. 1906. Echinoderms. Cambridge Nat. Hist.

MAC GINITIE, G. E., and N. MAC GINITIE. 1949. Natural History of Marine Animals. McGraw-Hill, New York. 473 pp.

RASMUSSEN, B. 1965. On taxonomy and biology of North Atlantic species of the genus *Henricia* Gray. Medd. Danm. Fisk.-Havunders. 4:157–213.

REESE, E. S. 1966. The complex behavior of echinoderms. Pp. 157–218 *in*: BOOLOOTIAN, R. A. (ed.), Physiology of Echinodermata, Interscience Publ., New York.

RICKETTS, E. F., and J. CALVIN (revised by J. W. HEDGPETH). 1968. Between Pacific Tides. 4th ed. Stanford Univ. Press. 614 pp.

SPENCER, W. K. 1914–1940. British Palaeozoic Asterozoa. Palaeontogr. Soc. London Monogr., pt. 1, 1913 (1914): 1–56, pl. 1, text-figs. 1–31; pt. 2, 1915 (1916):57–108, pls. 2–5, text-figs. 32–63; pt. 3, 1916 (1918): 109–168, pls. 6–13, text-figs. 64–112; pt. 4, 1917 (1919):169–196, text-figs. 113–138; pt. 5, 1920 (1922):197–236, pls. 14–17, text-figs. 139–171; pt. 6, 1922 (1925):237–324, pls. 18–22, text-figs. 172–212; pt. 7, 1926 (1927):325–388, pls. 23, 24, text-figs. 213–248; pt. 8, 1928 (1930):389–436, pls. 25–28, text-figs. 249–280; pt. 9, 1933 (1934): 437–494, pls. 29–32, text-figs. 281–321; pt. 10, 1940 (1940):495–540, pls. 33–37, text-figs. 322–348.

SPENCER, W. K., and C. W. WRIGHT. 1966. Asterozoans. Pp. U4–U107 *in*: J. W. DURHAM, et al., Echinodermata 3: Asterozoa—Echinozoa. Treatise on Invertebrate Paleontology, (R. C. MOORE, ed.), pt. U.

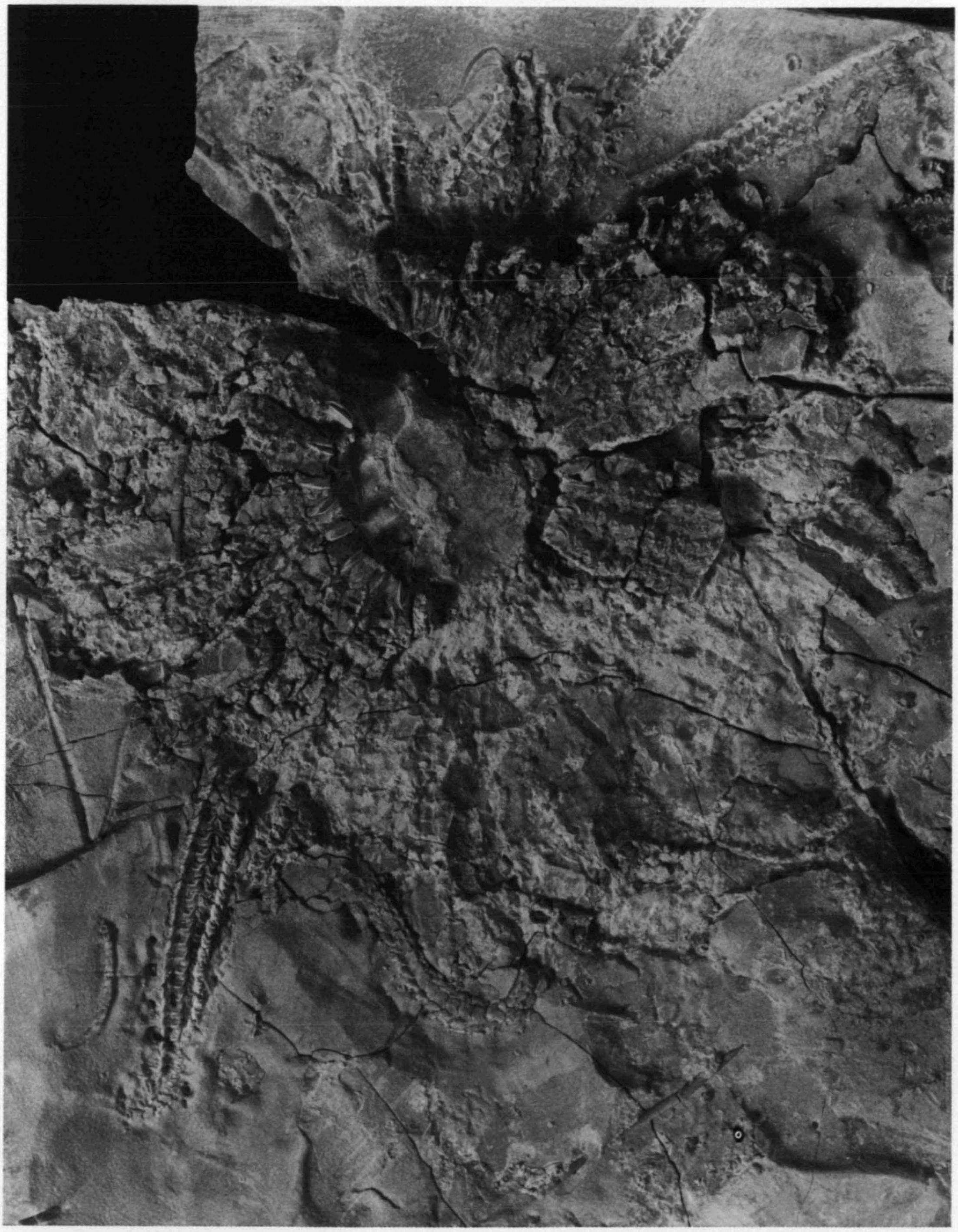
VERRILL, A. E. 1909. Remarkable development of starfishes on northwest American coast; hybridism; multiplicity of rays; teratology; problems in evolution; geographical distribution. Am. Nat., 43(513):542–555.

EXPLANATION OF PLATE 1

(Figure about × 1.6)

Arkonaster topororum n. gen., n. sp.

Oral view of specimen (UMMP 64451, holotype) partly reassembled from fragments. The MAPP in the upper part of the circlet are enlarged in Plate 7, fig. 4, and Plate 4, figs. 2, 3. An impression of the circlet of MAPP is shown at about the same scale in Plate 6, fig. 17, for comparison. The mold of the oval madreporite can be seen here at the upper left near the major crack; an aboral view of this part of the skeleton is shown in Plate 5, fig. 3. The MAPP and "first" Ambb, figured in aboral view in Plate 2, figs. 7–9, and Plate 3, fig. 7, came from the gap in the mouth frame at the right, leaving only a very poor impression to mark their former position. The arm at the upper left can be seen enlarged in Plate 7, fig. 3. Compare this view with the restoration shown in Text-fig. 1.



EXPLANATION OF PLATE 2

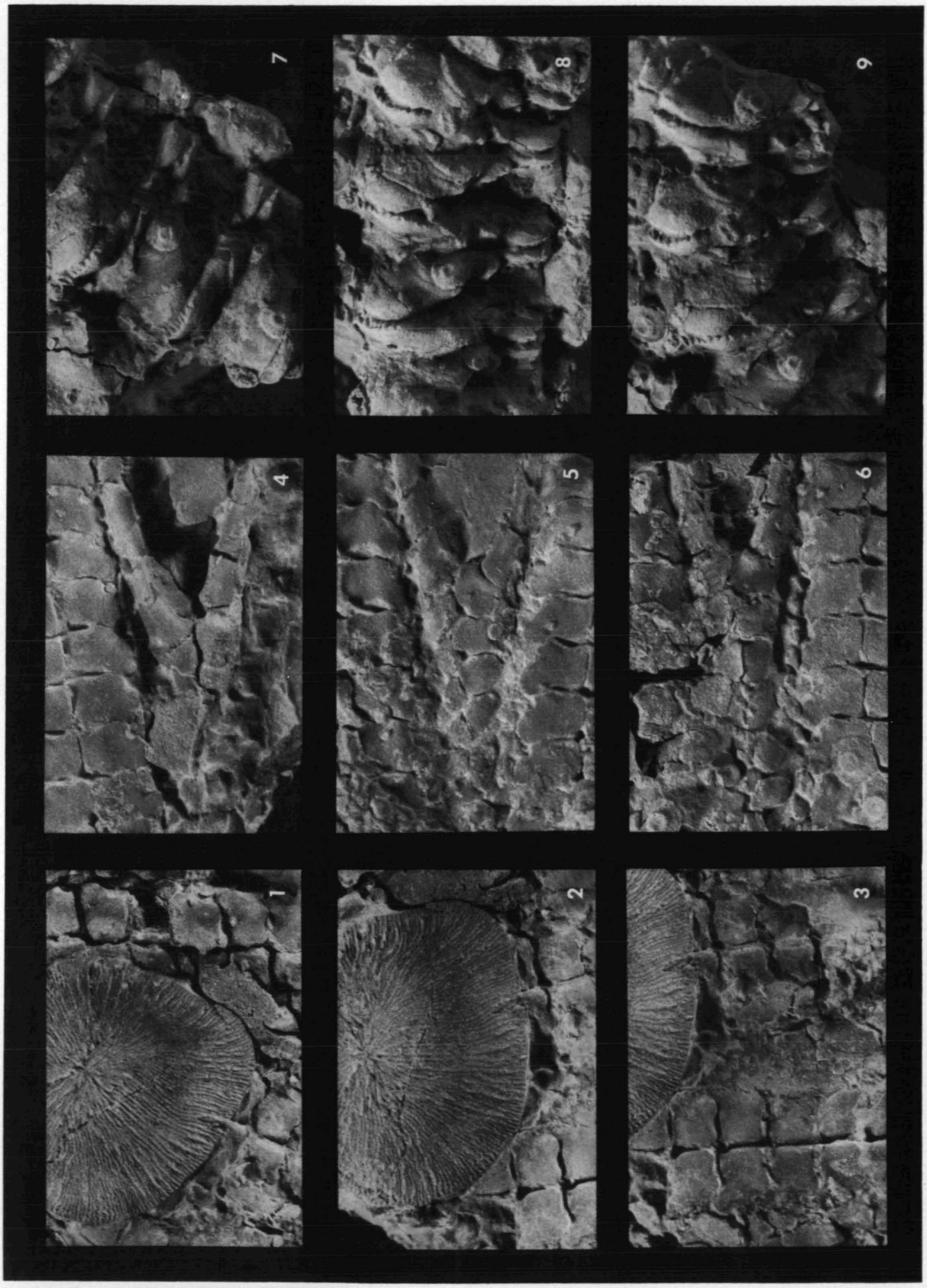
(All figures about × 5; area of specimen covered in each figure about 12 × 8 mm)

Arkonaster topororum n. gen., n. sp.

FIGS. 1–3 — Aboral views of the very large madreporite and adjacent area. In this part of the specimen, the pedicellariae and RR (carinal plates) are not preserved; compare with Text-fig. 5. The madreporite clearly overlies the aboral sides of the arms, demonstrating convincingly that it was on the aboral side of the disk. The double rows of subquadrate Amb plates are more clearly defined here than the bordering and intervening Admm and interbrachial plates.

FIGS. 4–6 — Aboral views of three interbrachial areas, filling the narrow arcs between arms. The rows of biserial alternating interbrachial plates diverge at the disk edge, with each row continuing for a short distance alongside the Admm of the adjacent arm; compare with Text-fig. 4. The Admm are here squeezed between the large Ambb and the interbrachials, although their edges are visible in figure 6. Three subcircular RR (carinals), somewhat displaced, can be seen at the left margin of figure 6.

FIGS. 7–9 — Aboral views of parts of the mouth frame. The large "first" Ambb are raised into ovate domes in their adradial parts, with each pair joined along a corrugated suture. Proximal to these plates are the MAPP, set in interradial pairs and showing shallow but distinct grooves to accommodate the nerve- and water-rings. Edges of the "second" Ambb can be seen just beyond the "first" Ambb (figure 9). Scattered subcircular plates, each with a raised and rimmed central concavity, are RR (carinals) which have collapsed from the disk and lost their spines.



EXPLANATION OF PLATE 3

(Figures about × 5 except as noted)

Arkonaster topororum n. gen., n. sp.

FIGS. 1, 2 — Oral and inclined oral views of median section of arm. The curved groove behind the ridge separating podial basins accommodated a branch water vessel. Amb plates share podial basins equally (compare with Text-fig. 3).

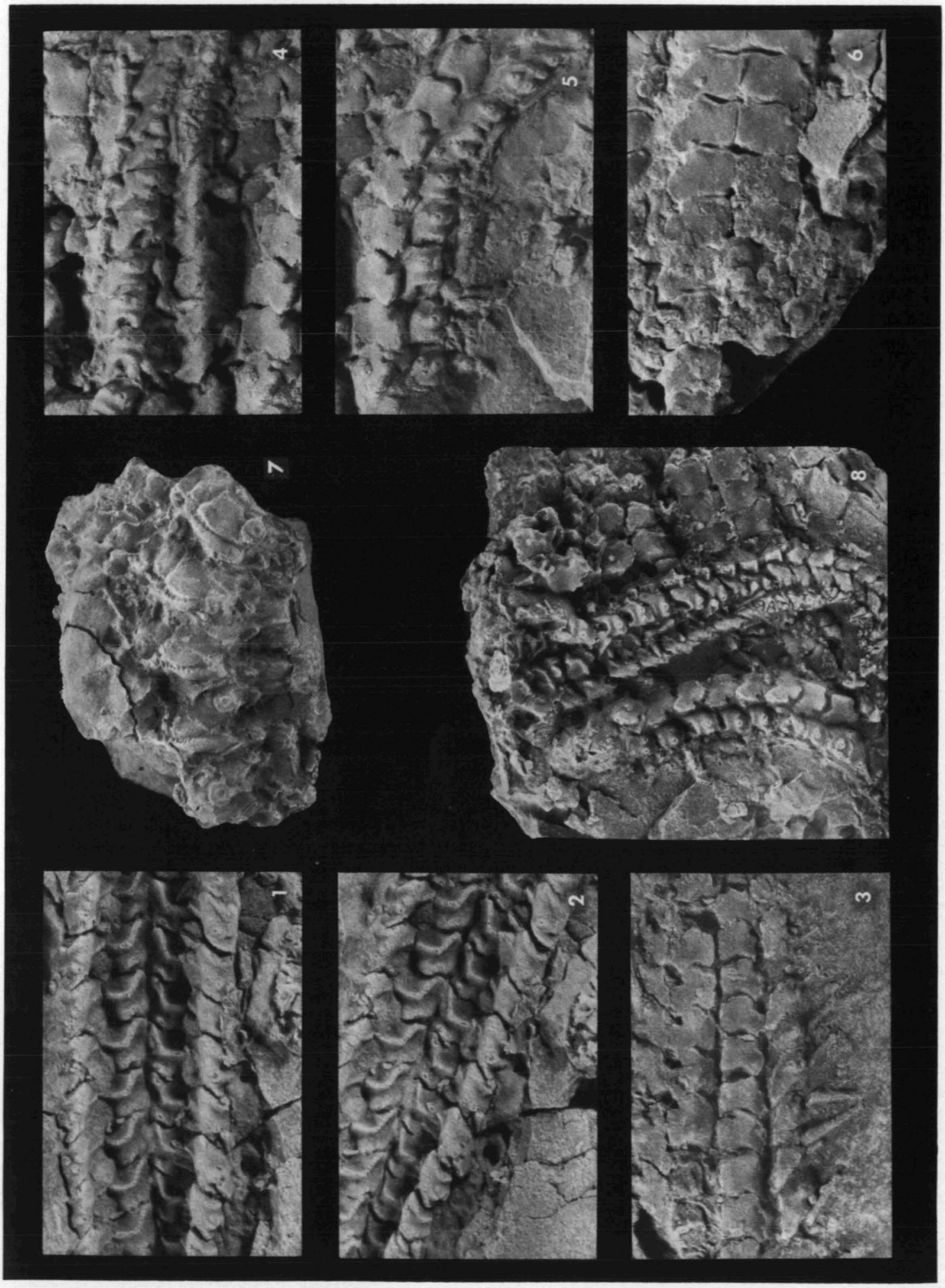
FIG. 3 — Aboral view of section of arm. The Adm spines shown here are incomplete. Distal lappet on each Amb extends over edge of the succeeding Amb, forming an imbrication. Openings at junctions of Ambb and Admm are presumed to have been passages for nerves and muscles (compare with Text-fig. 4).

FIGS. 4, 5 — Inclined aboral views of sections of somewhat twisted arms. The abradial surfaces of Admm bear pustule-like bases for attachment of spines, which extended outward and back.

FIG. 6 — Aboral view of arm section near oral opening. In this area of the skeleton, Admm of adjacent arms lie in contact, without intervening interbrachial plates (compare with Text-fig. 4). A few scattered RR (carinals) from the collapsed and mostly disintegrated disk are atop arm plates.

FIG. 7 — Aboral view of section of mouth frame showing four pairs of "first" Ambb. A few RR (carinal plates) have collapsed onto the mouth frame from the overlying disk. About × 3.5. Compare with enlargement in Plate 4, fig. 4.

FIG. 8 — Inclined view of arm sections showing bases for attachment of Adm spines. About × 3.5. Compare with figs. 4 and 5 on this plate.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EXPLANATION OF PLATE 4

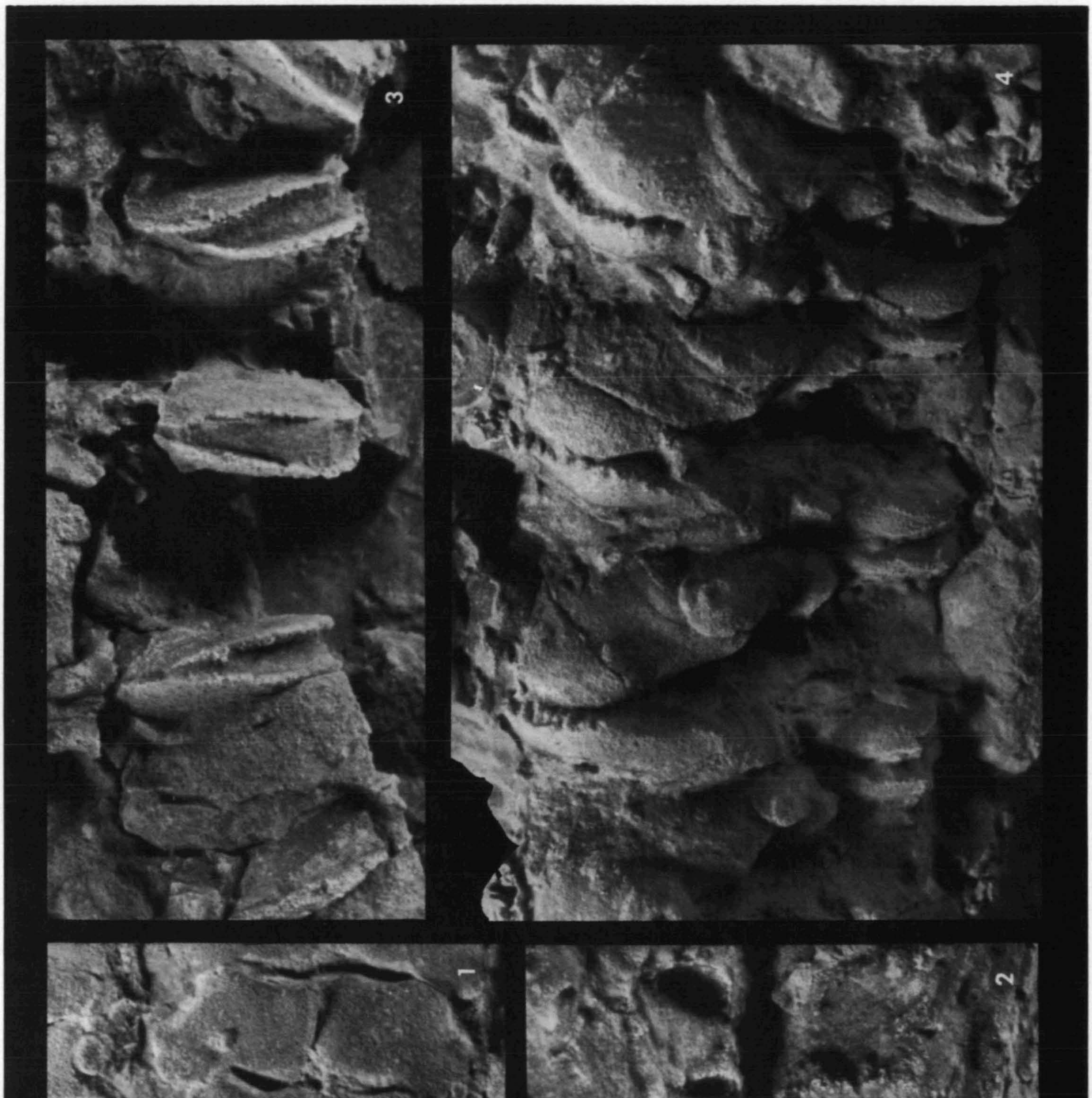
(All figures about × 10)

Arkonaster topororum n. gen., n. sp.

FIG. 1 — Aboral view of arm sections near mouth frame showing distal lappets of Ambb inbricating on succeeding plates. In this part of the skeleton, interbrachial plates are excluded from between adjacent arms.

FIGS. 2, 3 — Oral views of sections of mouth frame showing large spoon-shaped MAPP. The proximal end of an ambulacral groove can be seen, slightly spread and distorted, in fig. 2.

FIG. 4 — Aboral view of three adjacent sections of mouth frame showing sloping junctions between MAPP and "first" Ambb. Grooves to accommodate nerve- and water-rings around the mouth can be seen on the MAPP. Compare with Text-figure 4.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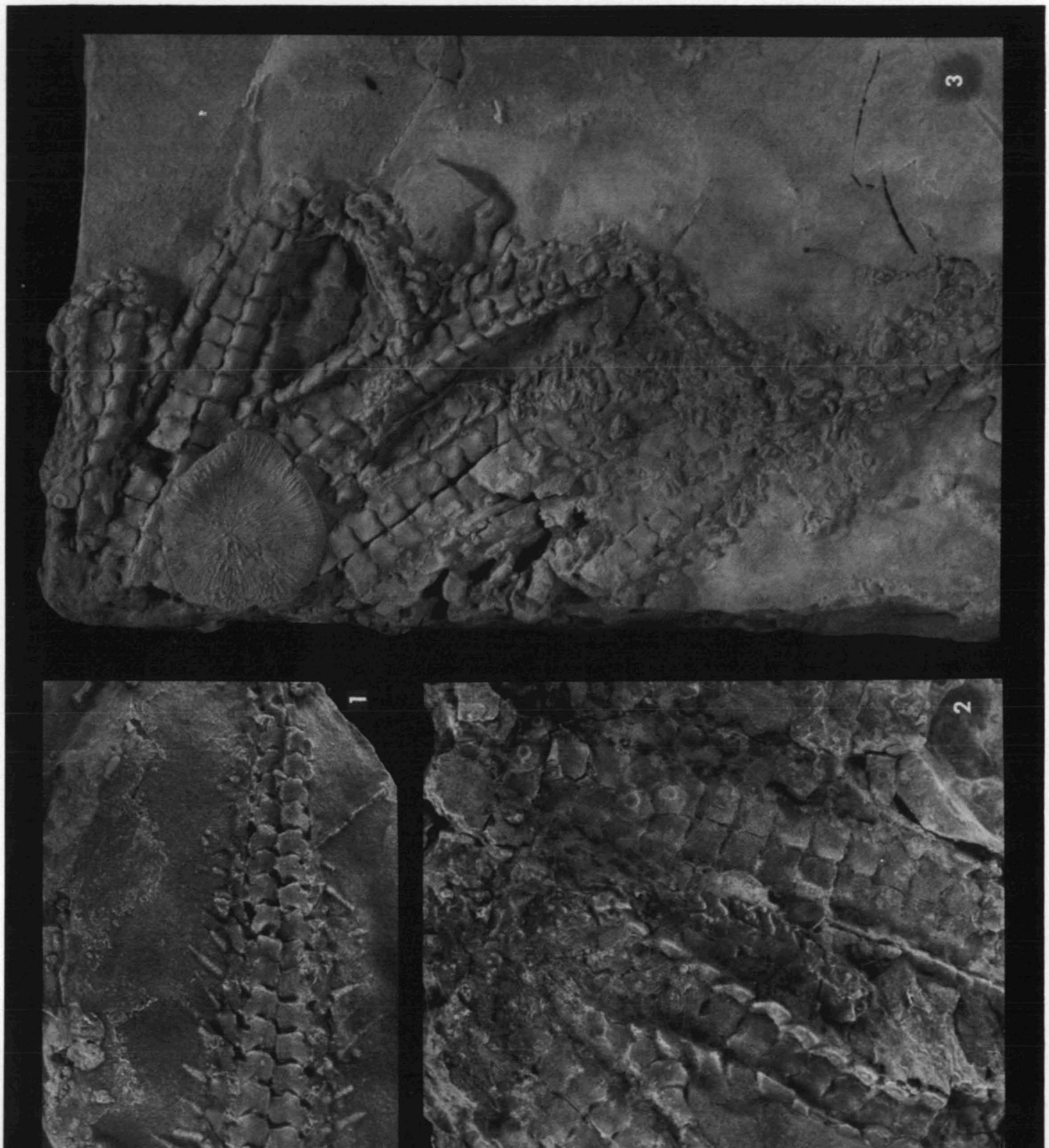
EXPLANATION OF PLATE 5

Arkonaster topororum n. gen., n. sp.

FIG. 1 — Aboral view of distal segment of arm, showing imbricating series of large Ambb bordered by curved Admm bearing long spines. Openings between successive Ambb and adjoining Admm are presumed to be for passage of nerves and muscles. About × 3.5.

FIG. 2 — Aboral view of proximal segments of arms at the edge of the disk, showing narrow triangular fields of interbrachials. Some slightly displaced RR (carinals), collapsed from the overlying disk, lie upon the arm at the right. About × 3.5.

FIG. 3 — Aboral view of madreporite lying upon an arm near the edge of the disk. Narrow triangular fields of interbrachials denote the boundary of the disk, with extensions alongside the adjacent arms. A few large pedicellariae associated with arms can be seen in the lower half of the figure. About × 2.5.



EXPLANATION OF PLATE 6

(Figures about × 17 except as noted)

Arkonaster topororum n. gen., n. sp.

FIGS. 1–15 — Large and small pedicellariae. All those figured here are replaced by pyrite. Many of the large pedicellariae are encrusted with additional pyrite (figs. 1, 2, 11, 13), but some are relatively smooth and clean (figs. 5–8). The small pedicellariae are mostly smooth (figs. 4 at left, 9, 10 at upper left, 15), although a few are encrusted (fig. 4 at top, fig. 10 at center). The triradiate form of the large pedicellariae is indicated (fig. 14 at top) by some with the three tips agape; the three jaws of the smaller pedicellariae can be seen in basal view (fig. 3 at right, fig. 13 at bottom), about of equal size and resembling the fruit of the beechnut tree but more inflated. The apparent small denticles along the inner margin of jaws in the large pedicellariae are visible in figure 1.

FIG. 16 — Part of madreporite, showing radiating and anastomosing grooves. No large pores or perforations can be seen through the bottoms of the grooves, and water seems to have been admitted to the water-vascular system through thin plate material.

FIG. 17 — Impression of oral region, showing spacing of MAPP. At the right in the figure, a segment of arm is seen in aboral view, showing the series of large Ambb. This impression can be compared with the oral view of the specimen in Plate 1. About × 1.7.

EXPLANATION OF PLATE 7

(All figures about × 3.5)

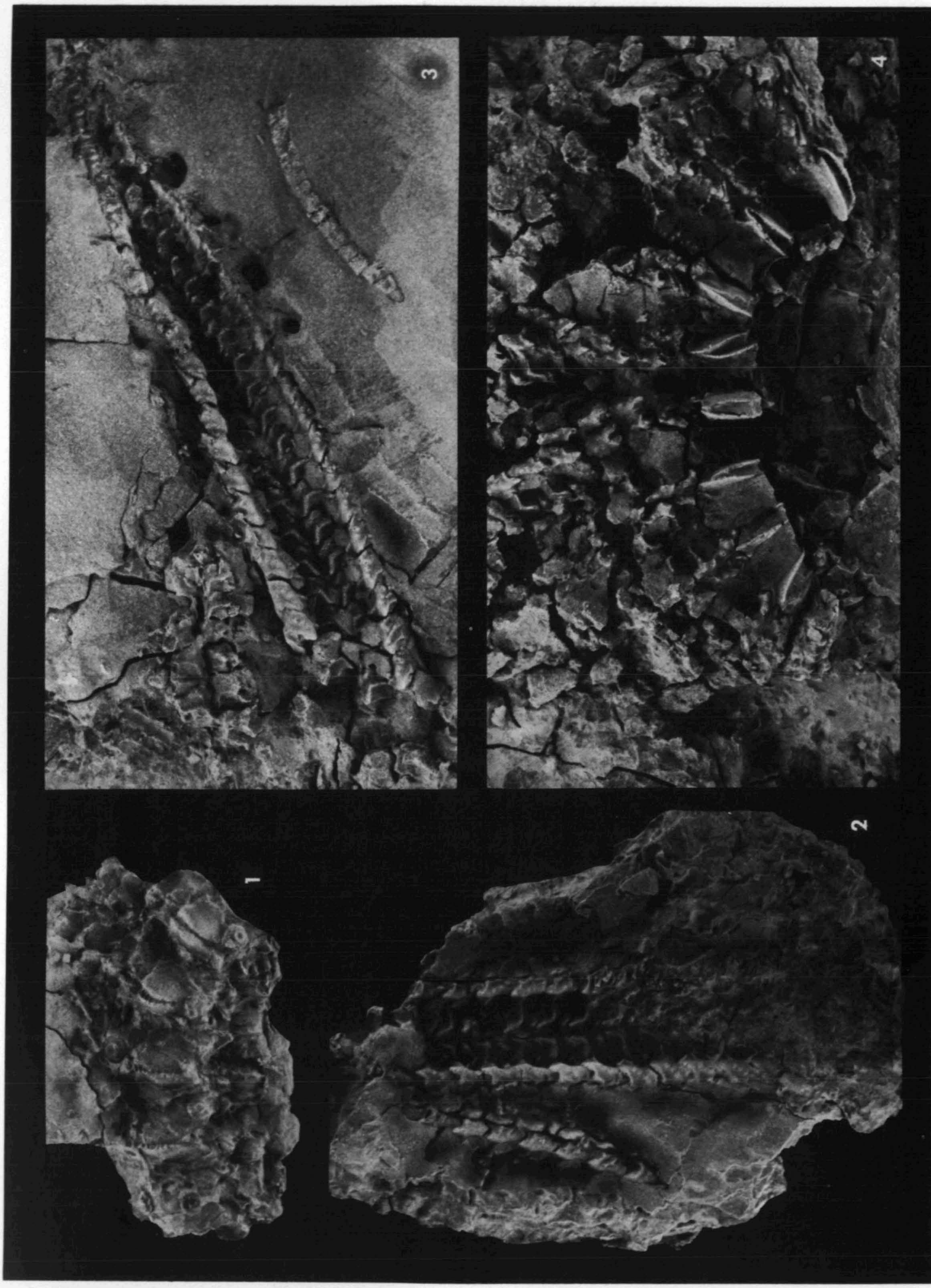
Arkonaster topororum n. gen., n. sp.

FIG. 1 — Aboral view of section of mouth frame showing paired "first" Ambb. This photograph was taken from a slight inclination, inasmuch as the plates are slightly distorted and lie more or less en echelon, to show the symmetry of the pairs. Compare with Plate 2, fig. 7.

FIG. 2 — Oral view of arms at edge of disk. This shows particularly well the deep clefts on the outer margins of the Admm, as well as the adjoining ridges of Ambb and Admm forming walls separating podial basins.

FIG. 3 — Oral view of arm shown at upper left in Plate 1. Very small pustules on edges of Admm may have been attachment points for oral spines, but this is uncertain. The pustule-like mounds for attachment of the lateral spines are considerably larger (compare with Plate 3, figs. 4, 5). The groove behind each median ridge in the Ambb accommodated the branch water vessel.

FIG. 4 — Oral view of mouth region, showing the large spoon-shaped MAPP. The first podial basins of an arm can be seen at the right. Compare with upper part of MAPP circlet in Plate 1.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