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MICHIGANASTER INEXPECTATUS, A NEW MANY-ARMED STARFISH FROM THE MIDDLE DEVONIAN ROGERS CITY LIMESTONE OF MICHIGAN

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VOLUME 23

1. The rodents from the Hagerman local fauna, Upper Pliocene of Idaho, by Richard J. Zakrzewski. Pages 1–36, with 13 text-figures.
2. A new brittle-star from the Middle Devonian Arkona Shale of Ontario, by Robert V. Kesling. Pages 37–51, with 6 plates and 2 text-figures.
3. Phyllocarid crustaceans from the Middle Devonian Silica Shale of northwestern Ohio and southeastern Michigan, by Erwin C. Stumm and Ruth B. Chilman. Pages 53–71, with 7 plates and 4 text-figures.
4. *Drepanaster wrighti,* a new species of brittle-star from the Middle Devonian Arkona Shale of Ontario, by Robert V. Kesling. Pages 73–79, with 2 plates.
5. Corals of the Traverse Group of Michigan. Part 13, *Hexagonaria,* by Erwin C. Stumm. Pages 81–91, with 4 plates.
6. The Pliocene rodent *Microtoscoptes disjunctus* (Wilson) from Idaho and Wyoming, by Claude W. Hibbard. Pages 95–98, with 2 text-figures.
7. A new microtine rodent from the Upper Pliocene of Kansas, by Claude W. Hibbard. Pages 99–103, with 1 plate and 1 text-figure.
8. Evolution of the fern family Osmundaceae based on anatomical studies, by Charles N. Miller, Jr. Pages 105–169, with 2 plates and 10 text-figures.
9. The insectivores of the Hagerman local fauna, Upper Pliocene of Idaho, by Claude W. Hibbard and Philip R. Bjork. Pages 171–180, with 4 text-figures.
10. *Antiquaster magrumi,* a new unusual brittle-star from the Middle Devonian Silica Formation of northwestern Ohio, by Robert V. Kesling. Pages 181–191, with 4 plates and 1 text-figure.
11. Arms of *Decadocrinus hughwingi* Kesling, by Robert V. Kesling. Pages 193–199, with 3 plates.
12. *Dolatocrinus kutasii,* a new crinoid from the Middle Devonian Bell Shale of Michigan, by Robert V. Kesling. Pages 201–211, with 5 plates and 1 text-figure.
13. *Logocrinus brandoni,* a new inadunate crinoid from the Middle Devonian Silica Shale of Ohio, by James P. Sigler, Donald White, and Robert V. Kesling. Pages 213–220, with 2 plates and 2 text-figures.
14. *Agostocrinus* and *Acolocrinus,* two new Ordovician crinoids with peculiar ray and respiratory structures, by Robert V. Kesling and Christopher R. C. Paul. Pages 221–237, with 7 plates and 5 text-figures.
15. Fossil amphibians from the Egelhoff local fauna in north-central Nebraska, by Charles J. Chantell. Pages 239–246, with 1 plate.

MICHIGANASTER INEXPECTATUS, A NEW MANY-ARMED STARFISH FROM THE MIDDLE DEVONIAN ROGERS CITY LIMESTONE OF MICHIGAN

ROBERT V. KESLING

ABSTRACT—*Michiganaster* is the first echinoderm to be described from the Middle Devonian Rogers City Limestone. This new genus of the asteroid order Paxillosida is represented only by the type species. *M. inexpectatus* is characterized by a very large elastic disk including elongate winged and stellate plates, numerous short petaloid arms (perhaps 25 in adult individuals), interambulacral areas bearing ossicles and plates, and long slender keeled mouth-angle plates. Free arms are bordered by conspicuous inferomarginals, which alternate with thick oblong adambulacrals below and with wide superomarginals above. Tiny radials are set into notches between superomarginals without adradial papular areas. Ambulacral plates are strongly arched within the arms. Preservation, associated fauna, and lithology of the matrix suggest that the starfish died in water of low salinity and reduced circulation, possibly in a marginal lagoon where they were entrapped.

INTRODUCTION

FOR MANY YEARS echinoderms were unknown in the Rogers City Limestone. Abundant and diverse brachiopods, gastropods, pelecypods, cephalopods, and corals have been described, as well as some bryozoa and trilobites. The absence of any echinoderms has contrasted strongly with the formations of the overlying Traverse Group.

In July 1970, Robert M. Linsley, Ellis L. Yochelson, and John S. Peel found a fossiliferous bedding plane in the lower part of the Rogers City Limestone at the Calcite Quarry of the Michigan Limestone Operations of U. S. Steel Corporation near Rogers City, Michigan. Believing that all the echinoderms on two slabs were crinoids, they sent them to me at the Museum of Paleontology. After preliminary cleaning, it was apparent that one was a large crinoid root system, a few were scattered crinoid columnals, one was a small section of crinoid arm, and three were starfish. Thus, the discovery establishes that the Rogers City fauna included at least two kinds of echinoderms.

All the starfish are many-armed and appear to fall within the limits of a single species. Two, nearly the same size, are probably adults, and one, much smaller, seems to be a very young specimen. Their preservation leaves something to be desired, but the essential characters can be made out.

Preparation was done slowly. First, the specimens were inspected under magnification. Then the slabs were scrubbed lightly with a soft brush and washed in running water. The slab containing the starfish was three to four inches thick and over a foot square. To enable further cleaning to progress, the specimens were removed in small blocks with a large diamond saw. Many areas of the plates were very fragile. Under a binocular microscope, some surrounding matrix was chipped away by a vibrotool. The areas were cleaned to the level of the plates with short bursts of air abrasion using dolomite powder. An artist's brush and water were sufficient to clean away the abrasive without damage to the plates. In the two adult starfish, only one arm was found to be complete to the end. This area was ground off slowly with emery powder (1000-mesh) on a wet plate for examination of the inner plates of the arm; at intervals, camera lucida drawings were made of the polished surface.

Many people helped in the preparation of this paper. I am greatly indebted, of course, to Linsley, Yochelson, and Peel for their generous permission to study the specimens and for their gift to our Museum of Paleontology. Karoly Kutasi photographed the specimens, Helen Mysyk typed the manuscript, and Gladys Newton read the proof. Their devoted attention to details greatly improved the presentation.

The specimens are deposited and catalogued in the Museum of Paleontology of The University of Michigan as UMMP 57916–57918.

LOCALITY

All starfish originally on a bedding plane of one slab of limestone, found by Linsley, Yochelson, and Peel in the Calcite Quarry of the

Michigan Limestone Operations of U. S. Steel Corporation near Rogers City, Presque Isle County, Michigan. The slab was found in place at the top of the ramp, near the west wall of the quarry, not far from the quarry buildings. The associated fossils show, as Linsley pointed out, that the strata are from Unit 1 of the Middle Devonian Rogers City Limestone. This unit was described by Ehlers & Kesling (1970, p. 22, 24) as the lower bed of the *Emanuella* zone:

> Magnesian limestone, finely crystalline, thin bedded, each bed with discontinuous, alternating bands of dark brownish gray and light buff arranged parallel to the bedding planes. Limestone cut by two sets of closely spaced joints; weathers into blocks or thin slabs that become light yellow in a few years. *Emanuella* sp. aff. *E. meristoides* (Meek) abundant; *Carinatina dysmorphostrota* (Crickmay) and a productid relatively common. Specimens of the pelecypods *Actinopterella calliotis* LaRocque and *A. peninsularis* LaRocque, *Leptodesma furcistria* LaRocque, *Limoptera* (sec. *Myalinodonta*?) *mygrans* LaRocque characteristic of the unit ..... 6 feet 2 inches.

To this I may add that the fossiliferous units in the slab are restricted to two light layers, each about an inch thick, and that the darker interbeds are barren. The dark unfossiliferous layers have a basal lamina of very dark, almost black, fine-grained limestone and the starfish lie on a bedding plane that retains here and there the same dark material, which laps onto the edges of the specimens themselves. Fossils are densely packed in the light layers, and include, in addition to the above-mentioned species, a small *Brachyspirifer* sp. and the uncoiled gastropod *Mastigospira intermedia* LaRocque.

PRESERVATION

From several causes, the plate arrangement of the new starfish is difficult to decipher. The significant contributing factors are: (1) original loose structure of the plates, (2) collapse of the elastic, protrusible disk at death, (3) distortion by muscular contractions in rigor mortis, (4) dislocation and loss of some plates by decay of integument and, possibly, by activities of minute scavengers, (5) distortion by pressure of overlying sediment, (6) uneven and irregular replacement of plates during fossilization, and (7) solution of plates after burial by circulating ground water and during final exposure by weathering. To these might be added the solution of calcareous laminae in the matrix to produce small-scale stylolites, although for the most part, the stylolite seams appear to be restricted to the surface on which the starfish rest.

Original structure.—The body of *Michiganaster inexpectatus* was poorly constructed for fossilization, both disk and arms. The disk was reinforced only by loosely associated stelliform plates. As in any multiarmed starfish, the mouth area was extensive (pl. 1, fig. 3); every arm had to border it. Even the MAPP, therefore, formed a wide circle; and the disk, which necessarily attached to each arm beyond the MAP, had a diameter still greater. Referring to *Palaeosolaster gregoryi* Stürtz, a Lower Devonian species with as many as 29 arms, Spencer (1925, p. 239) stated, "The scattered nature of the disc-skeleton suggests that in life the form was much swollen and high." These remarks apply equally well to *Michiganaster inexpectatus*.

Although composed of much thicker and stouter plates, the arms also lacked rigidity. Each section of an arm was framed by four major plates: two Smm above and two Admm below. The two Smm definitely formed a junction at the aboral midline of the arm (pl. 3, fig. 1); as indicated in a reconstructed cross section of one arm (text-fig. 2a), the Smm extended down around the arm to close proximity if not actual contact with the underlying Ambb. On each side of an arm, the plates of successive sections left a diamond-shaped gap wherein a small Im was inserted; at the top of the arm, a similar gap was filled by an R. Imm and RR, alternating with the larger Smm and Admm plates and not firmly joined to them, seem to have contributed little to the structural strength of the arm.

Collapse of disk.—In one large specimen, UMMP 57916, the early collapse of the disk is evident (pl. 2, fig. 2). The plates, variously stelliform and bladed, lie in such disarray that no original pattern of distribution or symmetry can be discerned. In the immature little specimen, UMMP 57918, the disk plates were not as widely spaced (pl. 1, fig. 1); even so, only

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EXPLANATION OF PLATE 1

Specimens coated with sublimated ammonium chloride

Michiganaster inexpectatus n. gen. & n. sp. *1,* small and presumably immature specimen, paratype UMMP 57918, with 17 arms; × 6. *2,* parts of two arms, holotype UMMP 57916; compare with top of figure 2 in plate 2; × 8. *3,* adult with all upper plates of disk and arms missing, paratype UMMP 57917; specimen probably had 24 or 25 arms; × 3.

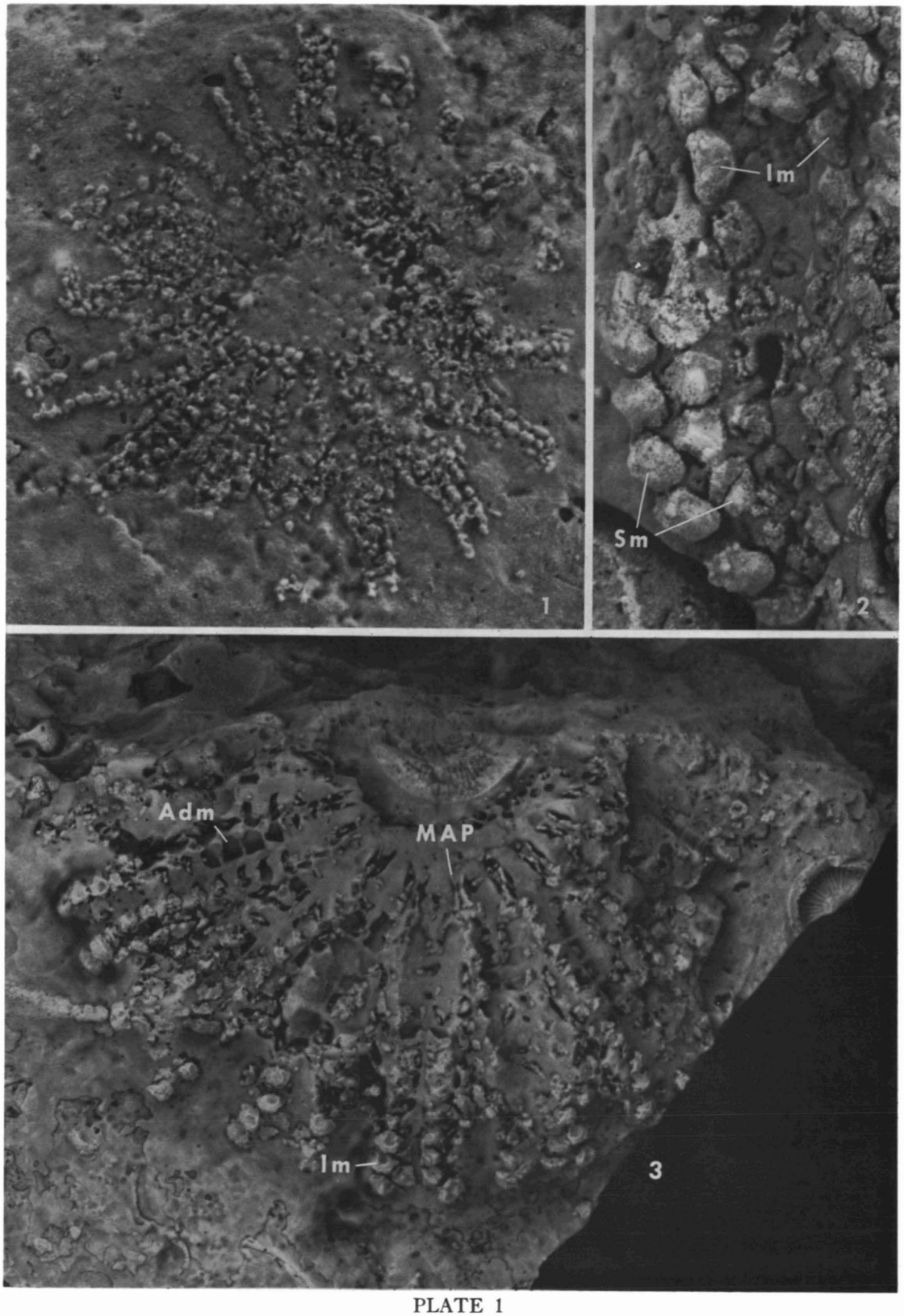


PLATE 1

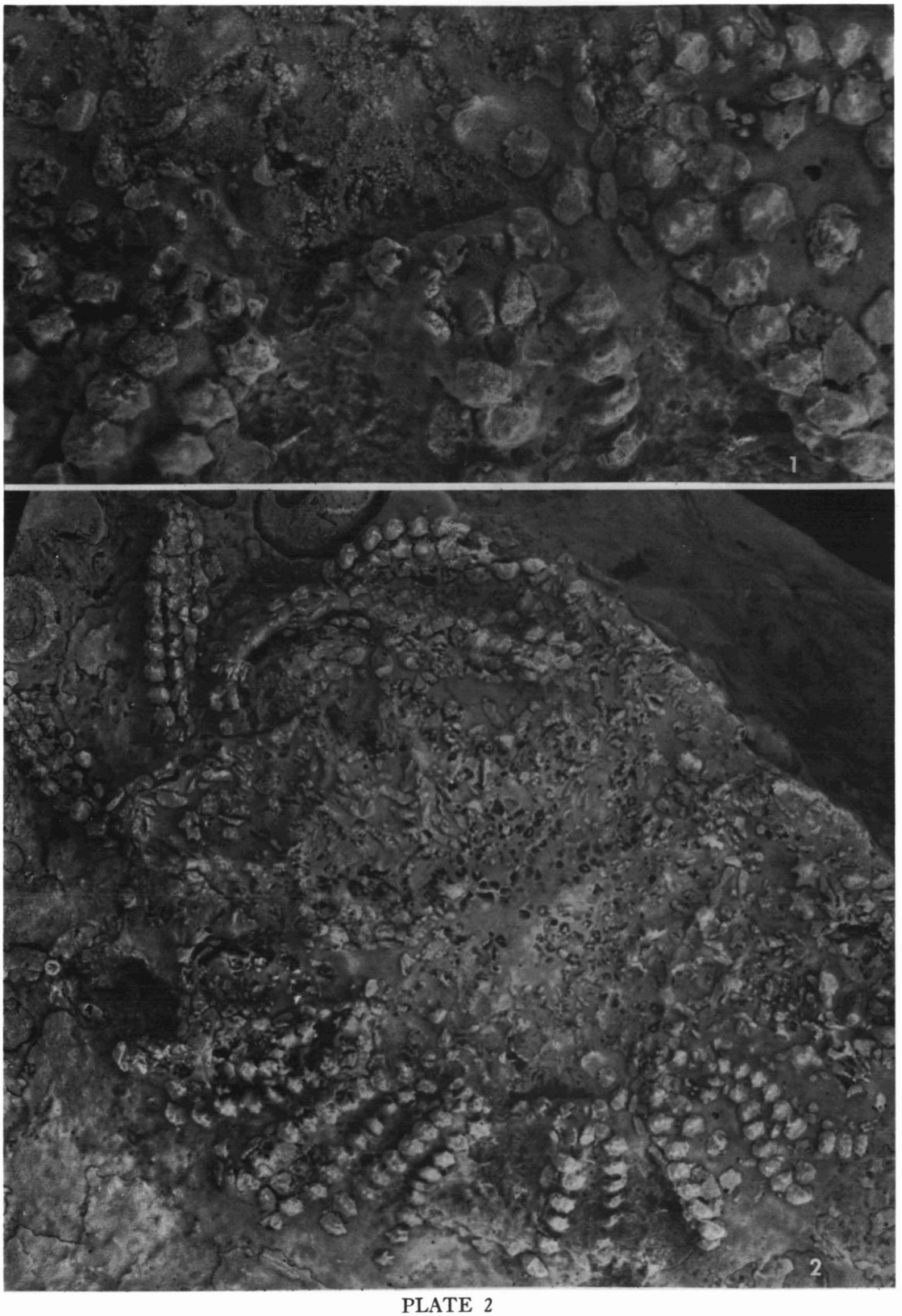


PLATE 2

the central part of the disk (that part overlying the mouth area) is preserved intact and the edges are eroded. Undoubtedly, the crumpled and folded borders of the collapsed disk, lying upon the proximal sections of the arms, were easy targets for post-mortem destruction.

Muscular contractions.—At least some contraction of transverse muscles in the arms took place in rigor mortis. In UMMP 57917, the disk is eroded away to expose the mouth area. Near the MAPP in one arm, the plates have been almost completely dissolved away, leaving their impressions in the underlying matrix (pl. 3, fig. 2). In the area, the impressions of two parallel rows of plates slope down toward the midline but leave a conspicuous flat-topped ridge between them; each plate was flat-bottomed and rectangular except for its outer corners, which were beveled at 45 degrees. These plates cannot be Ambb because they are separated at the midline and possess no bottom relief whatever, such as is universal in asteroid Ambb for accommodation of the tube feet. The plates can only be Admm, and the median ridge is the filling of the ambulacral channel between them. Other examples are known of Paxillosida with closely appressed rows of Admm, even though most specimens are found with the Ambb plates well exposed and the bordering Admm rows widely separated. Spencer illustrated (1918, p. 121, text-fig. 75) a young individual of the many-armed *Lepidaster grayi* Forbes with the Admm rows nearly in contact, and also (1922, p. 233, text-fig. 169) a similar specimen of *Palasterina antiqua* (Hisinger). In the specimen of *Michiganaster inexpectatus,* the proximal parts of at least ten consecutive arms exhibit the same condition, with only a narrow gap between the rows of Admm (pl. 1, fig. 3). The only force which could possibly have laterally compressed this many consecutive arms without dislodging them from the body is muscular contraction within each arm during the death convulsion.

Dislocation and loss of plates.—Most of the arms in the two adults have broken ends that terminate in the matrix (pl. 1, fig. 3; pl. 2, fig. 2). Inasmuch as the ends of these arms were lost before burial, one might wish to know whether the loss occurred before or after the animal died. Because the terminations show no signs of plate regeneration, the arms could not have been severed long before death. Dislocation of plates becomes more pronounced distally in the arms. For this reason I am inclined to believe that the ends of the arms disappeared after the integument decayed. Whether they were carried off by small scavengers or swept away by currents is not evident. They need not have been moved far to be lost from the area exposed on the slab. Probably in the same interval, the disk plates were lost from UMMP 57917. Whatever the agency of their removal, the other remains were left in place and more or less intact.

Post-burial pressure of sediment.—Compression by weight of overlying sediment caused some distortion of the arms. In UMMP 57916, cross sections through the distal part of one arm reveal that the Smm have been shoved laterally and that the plane of symmetry has been shifted from vertical (text-fig. 1).

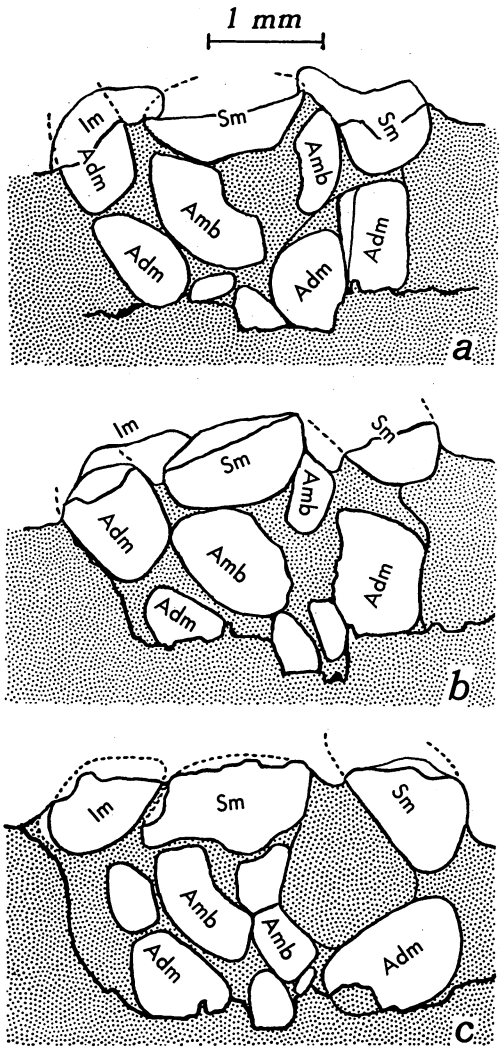
Uneven replacement.—The cross sections of an arm (text-fig. 1) show that replacement of calcium carbonate was not precisely limited to the plates themselves. In some places it seems to have included a little of the matrix as well, whereas in others it failed to include all of the plate. This locally indiscriminate replacement resulted in somewhat ragged and inaccurate sections of the plate outlines. The Ambb, enclosed within the other arm plates, were particularly affected. In most cases, however, the actual boundaries can be established by the "flash" of the cleavage.

Solution of plates.—Several plates around the mouth in UMMP 57917 show evidence of incomplete replacement and differential weathering or solution. In particular, the MAPP and nearby Admm are represented for the most part by cavities (pl. 3, fig. 2). In some places, a central core of calcite is suspended within the cavity by a few fragile connections. In other places, part of the cavity is lined with tiny calcite crystals, like a miniature geode.

EXPLANATION OF PLATE 2

Specimens coated with sublimated ammonium chloride

Michiganaster inexpectatus n. gen. & n. sp. Holotype UMMP 57916. *1,* part of disk showing granular surface presumed to be fossilized integument; most plates shown are Imm; × 8. *2,* top view of specimen showing two types of plates in collapsed disk and some arms; arm at upper left was later sectioned (see text-fig. 1); most arms have Smm and RR missing, enlargements in plate 1, figure 2, and in plate 3, figure 1; × 3.



TEXT-FIG. 1—*Michiganaster inexpectatus*. *a-c,* three successive cross sections of an arm of holotype UMMP 57916, shown in the upper left part of plate 2, figure 2. The specimen is underlain by a stylolitic surface. The arm has the Im row on the right side missing. Admm plates are very imperfectly replaced, and boundaries of these and other plates had to be established by the cleavage "flash."

The plates in the mouth area of this starfish can best be studied as external molds, after all calcite has been carefully removed.

That some of the solution took place after lithification is indicated by small-scale stylolites. One lies immediately below the specimen in UMMP 57916 (text-fig. 1). Probably, the same seam extends under the other two specimens, which were discovered on the same slab.

DISK PLATES

Plates of the disk are preserved in only one adult, where they are considerably disrupted (pl. 2, fig. 2). Nevertheless, the size and shape of certain plates indicate that at least some of the primary disk plates grew and were retained by the many-armed adult.

The key to deciphering the original arrangement of disk plates is a couple of bladed plates at the margin and aligned with the axis of an arm. From each side of the thick central part of the plate, a flat slatlike blade extends laterally normal to the arm axis; from the central part also a much shorter blade extends distally and a still shorter blade or lobe extends proximally. Each plate resembles in general a long-bladed propeller. From their position, these plates must be radials of the disk. Broken plates and detached larger blades can be discerned in the disk area (text-fig. 3a-c; pl. 2, fig. 2).

One plate of this type is exceptionally large (text-fig. 3d). Part of the carbonate is corroded or dissolved away, but the extent can be determined by the plate's impression. In a disk about 40 mm in diameter, this plate has a blade nearly 4 mm long. A plate of these dimensions can logically be interpreted as a primary radial.

Another kind of plate occurs in considerable numbers (text-fig. 3e-k). It is stellate with tapered extensions. Many are five-rayed with one ray much shorter than the others, some have five nearly equal rays, and a few have only four rays. These plates are probably interradials. In addition, some irregular ossicles are scattered through the remains of the disk in UMMP 57916 (pl. 2, fig. 2). Granulose areas in this specimen are thought to be fossilized integument (pl. 2, fig. 1).

Some of the larger disk plates still show a central depression, probably the socket for a spine. Although no spines were preserved, they may have been present and provided protection for the weakly plated disk.

DISK SYMMETRY

Someday a perfectly preserved disk of *Michiganaster inexpectatus* may be discovered, at which time the arrangement of disk plates will be known for certain. Meanwhile, the combination of multiple arms and large disk plates of two types raises the question of the persistence of pentameral symmetry in the adult starfish. A small specimen with a disk diameter of about 10 mm, paratype UMMP 57918, has 17 arms (pl. 1, fig. 1), whereas a large specimen with a disk diameter of about 40 mm, paratype

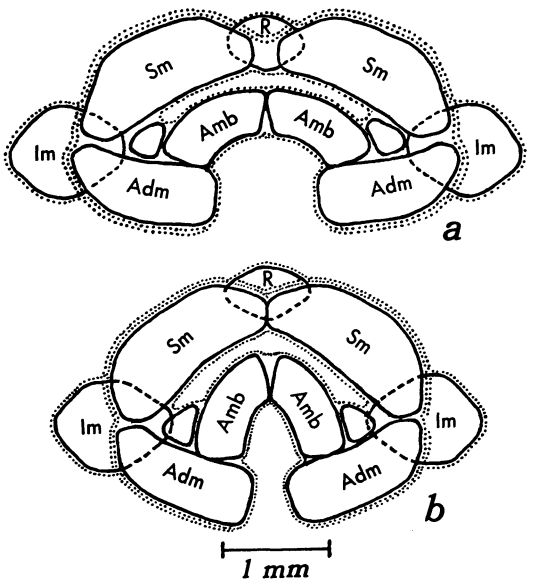
UMMP 57917, has about 25 arms (pl. 1, fig. 3). If, as I believe, both belong to the same species, then *Michiganaster* added arms during its postembryonic ontogeny.

The growth of living many-armed starfish offers some points of comparison with the new starfish described here. It must be understood that none of the Recent many-armed species that have been investigated possesses a system of large regularly arranged disk plates. Hence, the comparison is limited in application. Nevertheless, modern starfish are known to achieve the many-armed adult stage in three ways: (1) the full complement of arms appears very early in development, so that young and adults have the same number of arms, (2) arms are added until late in adult life, first one in addition to the original five, and then all others in opposite pairs issuing from two symmetrical spots on the disk edge, and (3) arms are intercalated at various places around the perimeter of the disk during ontogeny.

The second method has received most attention of zoologists, stemming from the observations of Ritter & Crocker (1900, p. 250–253) on *Pycnopodia helianthoides,* the 20-rayed sun star of our Pacific coast. In this species, metamorphosed with five arms, a sixth arm is soon added clockwise from the bivium (the two rays enclosing the M). Afterward, late into adulthood, additional arms bud off in pairs, first on either side of the sixth arm and henceforth inserted between the last-formed pair and the adjacent original arms. Thus, *Pycnopodia* has two spots on the disk edge which simultaneously give forth new arms at intervals until the full number is reached. This conclusion was confirmed by Verrill (1909, p. 545, 546) and endorsed by Kjerskog-Agersborg (1922), Tortonese (1934), and Greer (1962).

The last method is not so well known, but deserves our particular attention. Perrier (1888, p. 764) reported that in *Labidiaster radiosus* new arms were added until late in life, distributed at rather regular intervals around the entire circumference; in some newly added arms, the ambulacral groove did not reach the buccal membrane. Perrier also stated that *Brisinga mediterranea* has all nine arms by the end of its larval period, no more being added during its lifetime. Perrier elaborated on his work later (1891). A. M. Clark (1967, p. 154) reported that intercalary arms are added after metamorphosis in *Labidiaster* and the 50-armed *Heliaster.*

If *Michiganaster* developed in the same manner as *Pycnopodia,* adding a pair of arms at a time from the two productive spots on the disk edge, then disk symmetry could scarcely be maintained; the original five arms of the baby starfish would end up all adjacent at one side of the adult. If, however, *Michiganaster* grew like *Labidiaster,* distributing its new arms around the circumference, then it would be quite possible for the growing disk plates to maintain their original pentameral symmetry. This is presumed in the reconstruction of *Michiganaster inexpectatus* (text-fig. 4a).

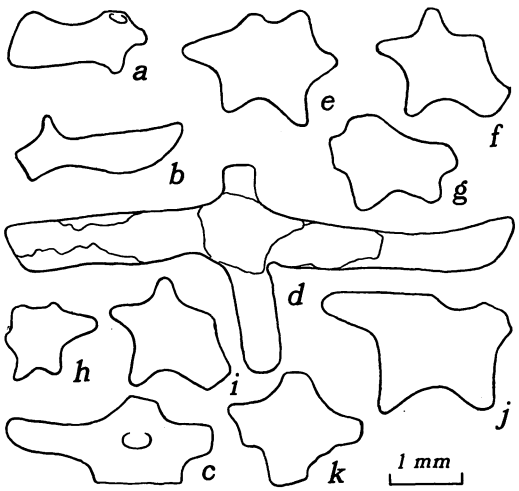


TEXT-FIG. 2—*Michiganaster inexpectatus. a, b,* reconstructions of cross sections of the free arm, based on the sections shown in text-figure 1 and on exposed plates in UMMP 57916 and 57917; *a,* probable positon of plates in life; *b,* position of plates at time of burial (compare with Admm in pl. 1, fig. 3).

CLASSIFICATION

The new starfish does not possess a combination of characters which can be readily fitted into the existing suprageneric taxa. A few notes on the asteroid orders are required to explain why the starfish is considered a new genus of the Paxillosida.

The orders are used here as previously (Kesling, 1969, p. 365–367) modified from the *Treatise on Invertebrate Paleontology* (Spencer & Wright, 1966). The characters are summarized in table 1. My former key (1969, p. 365–366) is revised to correctly place the Pustulosida, which have marginal plates larger than Admm in most genera.



TEXT-FIG. 3—*Michiganaster inexpectatus. a-k,* camera lucida sketches of various disk plates preserved in holotype UMMP 57916.

Key to Orders of Asteroidea

1. Ossicles on oral side of arm in transverse gradients ..... PLATYASTERIDA
   Ossicles not in transverse gradients 2
2. Subspherical disk inflated, arms not protuberant ..... TUMULOSIDA
   Stellate, disk not permanently inflated (although it may be protrusible), arms protuberant 3
3. Mouth-frame of ambulacral type ..... FORCIPULATIDA
   Mouth-frame of adambulacral type 4
4. Marginals large, outlining extensive interbrachial area of small ossicles or plates, separated from most of other arm plates; invariably fewer than Admm ..... VALVATIDA
   Marginals (Imm and/or Smm) small in most forms, closely associated with other arm plates, at least in distal part of arm; may be as numerous as Admm; interbrachial area, if any, not extending to ends of arms 5
5. Accessory interbrachials forming conspicuous field; superambulacrals in arms ..... PAXILLOSIDA
   No field of accessory interbrachials; no superambulacrals 6
6. MAPP large, spade- or plowshare-shaped; M oral ..... SPINULOSIDA
   MAPP not large, like adjacent Admm; M aboral ..... PUSTULOSIDA

In tracing the new starfish through the key, we can easily determine that it does not belong to the Platyasterida, Tumulosida, or Forcipulatida, for it has no transverse alignment of ossicles on the oral surface, the body is not subspherical to incorporate the arms, and the mouth-frame is adambulacral. Inasmuch as the marginals do not outline extensive interbrachial areas to produce a pentagonal (or polygonal) outline, the new form may be excluded also from the Valvatida. The Spinulosida may be eliminated from consideration because the ambulacral groove of the new starfish is very narrow; even with allowance for contraction during the final paroxysm, the Ambb do not seem to have been capable of forming a broad channel. The aboral adaxial plates, Smm and RR, are elements rarely found in the Spinulosida; and the narrow keeled MAPP are foreign to all Spinulosida.

In deciding between the Paxillosida and Pustulosida, one may focus upon the following characters of the Rogers City starfish: numerous arms, Imm and Smm alternating with Admm and about as numerous, MAPP clearly differentiated from adjacent Admm, disk with scattered stellate plates rather than well-developed coronet, and interbrachial arcs with accessory ossicles. The Pustulosida are not known to have more than five arms, and Imm and Smm are commonly larger and fewer than the Admm which they border, the disk is typically framed by a coronet of strong plates, interbrachial accessory ossicles are unknown (although marginals may be crowded into the axil region), and the MAPP are bordered by an odontophore or axillary plate. On the other hand, the prominent Admm rows bordering the ambulacral groove in such typical genera of Pustulosida as *Protopalaeaster, Hudsonaster, Girvanaster, Lepidactis, Mesopalaeaster,* and *Devonaster* are strikingly similar to those in the new starfish. All characters considered, the affinities of *Michiganaster* lie with the Paxillosida, despite the relatively small Ambb set well within the arm frame. The Paxillosida already contains many-armed starfish, including *Lepidaster, Devonistella,* and *Palaeosolaster.* It also contains starfish with superambulacral plates within the arms; if my interpretations of plates encountered in the cross section of an arm in UMMP 57916 is correct, *Michiganaster inexpectatus* also has superambulacral plates (text-figs. 1, 2).

SYSTEMATIC DESCRIPTION

Class STELLEROIDEA Lamarck
Subclass ASTEROIDEA de Blainville
Order PAXILLOSIDA Perrier
Suborder HEMIZONINA Spencer
Family LEPIDASTERIDAE Gregory
MICHIGANASTER n. gen.

TABLE 1—CHARACTERISTICS OF SOME ORDERS OF ASTEROIDEA

Character	FORCIPULATIDA	VALVATIDA	PAXILLOSIDA	SPINULOSIDA	PUSTULOSIDA
Mouth-frame	Amb-type	Adm-type	Adm-type	Adm-type	Adm-type
Imm and Smm compared with Admm	Same size	Much larger	Same or larger	Same size	Commonly larger
Field of interbrachial accessories enclosed by marginals	None	Very large in most	None or small	None	None
Coronet of well-developed disk plates	Present or absent	Absent	Present or absent	Absent	Present, usually strongly developed
MAPP	Large or small	Small	Large	Large	Small, like Admm
M	Aboral	Aboral	Oral or aboral edge	Oral invariably	Aboral, firmly framed
Superambulacrals	Absent	Absent	Present	Absent	Absent

Type species.—By monotypy, *Michiganaster inexpectatus* n. sp.

Diagnosis.—Arms numerous, mouth area large, interbrachial areas small. Free arms aborally bearing very large Smm and small RR without intervening adradial papular areas. Admm very large, oblong, thick. Ambb arched within arm. MAPP long, slender, keeled. Disk with distinct plates loosely fitted.

Remarks.—As indicated in table 2, the new starfish differs from previously described many-armed genera of Paxillosida. It can be differentiated from *Devonistella,* in which the aboral surface of the arms is still unknown, by its smaller plates in interbrachial areas, broader Admm, more slender MAPP, and well-developed Imm in the free arm. *Palaeosolaster* is known from the Lower Devonian Hunsrück Shale of Germany, and, like other fossils from this formation, suffers from compaction and compression. Nevertheless, this genus seems to lack Imm along the free arms and to have only small ossicles and spines on the aboral surface of the arms.

The many-armed genus to which *Michiganaster* can be compared most closely is *Lepidaster,* from the Middle Silurian of England, best described and figured by Spencer (1918, p. 116–123, text-figs. 75–78). The two genera are similar in having RR and Smm plates on the upper sides of the free arms, wide oblong Admm, slender keeled MAPP, and well-developed Imm along the borders of the arms. The small ossicles or plates in the interbrachial areas are not very different in the two. The chief difference lies in the aboral arm plates. In *Lepidaster* the Smm are small, with adradial papular areas bearing scattered tiny plates between them and the RR; in contrast, in *Michiganaster* the Smm are very large, occupying most of the aboral surface and beveled at the corners just enough to permit the insertion of small RR plates along the midline.

MICHIGANASTER INEXPECTATUS n. sp.

Text-figs. 1–5; pl. 1, figs. 1–3; pl. 2, figs. 1, 2; pl. 3, figs. 1, 2

Description.—Medium-size starfish; holotype and one paratype, thought to be adults, with overall diameter estimated at nearly 70 mm and disk diameter at about 40 mm; small paratype, thought to be juvenile of species, with overall diameter estimated at 17 mm and disk diameter at about 10 mm. Arms numerous, 24 or 25 in adult and 17 in the juvenile paratype, closely set, with narrow sector of interbrachials between each pair (text-figs. 4c, 5a). Mouth opening large because of number of arms radiating from it, about 14 mm between opposite MAPP in adult (text-fig. 5a; pl. 1, fig. 3). Disk extending about halfway between MAPP and distal ends of arms. Disk domed in life, perhaps hemispherical, rising from narrow axils.

Disk containing rather large plates of two types (text-figs. 3, 4a; pl. 2, fig. 2), one type propeller-shaped with opposite blades long and nearly straight and perpendicular blades much shorter, the other type variously stellate. Some

TABLE 2—COMPARISON OF SOME MANY-ARMED PAXILLOSIDA

	Lepidaster	*Devonistella*	*Palaeosolaster*	*Michiganaster*
Interbrachial areas	Small ossicles	Few large ossicles	Small plates bearing large spines	Small plates
Aboral arm plates	RR and small Smm	Unknown	Small ossicles and spines	RR and large Smm
Admm	Wide, oblong	Narrow, subhexagonal	Narrower than Ambb, blocky	Wide, oblong
MAPP	Slender, keeled	Stout, broad keel	Narrow and high, not conspicuously keeled	Long, slender, keeled
Imm in free arm	Well developed	Very small	None known	Well developed
Adradial papular areas	Present, small scattered plates between RR and Smm	Unknown	Whole area with small ossicles	None, RR fit close within notches of Smm

marginal bladed plates aligned with arm axis, hence considered RR; stellate plates considered interradial disk plates. Size of large disk plates indicative of irregular growth and maintenance of original symmetry. All plates apparently embedded in granuliferous integument (pl. 2, fig. 1). No anal opening preserved.

MAPP elongate, narrow, keeled; each MAP longer than the two adjacent Admm (pl. 3, fig. 2). Admm rather large, the two rows of each arm set close together, perhaps due to muscular contraction, leaving only narrow ambulacral channel between them (pl. 3, fig. 2). Each Adm thick, wide, quadrate in section under disk; adult starfish with about 10 Admm in each row proximal to axils.

Interbrachial arcs narrow, containing variously shaped small plates, bordered distally by at most three Imm and laterally by Admm. No M discerned.

Free arms stubby, petaloid (pl. 2, fig. 2; pl. 3, fig. 1). All plates thick and stout. Adult with 12 or 13 plates in each row of Admm, Imm, Smm, and RR in free part of arm. Ambb set well within frame of arm, rather large, orally concave (text-figs. 1, 2), associated with small plates interpreted as superambulacrals. Coelom of arm very narrow. Admm blocky, wider than long, with blunt adradial ends bordering the ambulacral groove and beveled outer (abradial) ends to accommodate Imm. Smm set immediately over corresponding Admm, arched over top of arm and meeting or nearly meeting at midline of arm (pl. 3, fig. 1). Smm set close together in rows, their outer (lower) ends beveled to accommodate alternating Imm and their inner (upper) ends beveled for insertion of alternating RR.

Each Im large, blocky, alternating with Admm below and Smm above, its outer free end bluntly acuminate and probably bearing a short thick spine, its inner end tapered to fit into diamond-shaped space between two Admm and two Smm. Each R of free arm small, lozenge-shaped, inserted in space left by beveled corners of four Smm at midline of arm.

Small short spines observed detached in lower part of arm, apparently associated with Admm.

Remarks.—The immature specimen, about one-fourth the size of the adults, has a disk composed mostly of rather close-fitting polygonal plates (pl. 1, fig. 1). A few of the marginal disk plates tend to be laterally extended, as though starting to grow blades. Unfortunately, the overall symmetry cannot be distinguished in this specimen. Development of 17 arms by this stage indicates that insertion of additional arms began very early in ontogeny.

It is presumed that the Amb, superambulacral, Adm, Im, and Sm plates in the arm were laced together by muscles similar to those found in *Luidia ciliaris* and *Astropecten irregularis* as described by Duncan Heddle (1967, p. 131–135). Even though the plates of *Michiganaster* are thicker and its Smm extend much farther across the top of the arm, it would seem that strong contraction of the marginal muscles, linking the inside of Smm with the outer edges of Admm, might swing the Admm plates into the position found in the large paratype (pl. 1, fig. 3) and reconstructed in text-figure 2b. The rows of Admm as preserved resemble the bomb-bay doors of a plane that have started to open.

Types.—Holotype UMMP 57916 (pl. 1, fig. 2; pl. 2, figs. 1, 2; pl. 3, fig. 1), presumed adult with some disk plates and arms preserved. Paratype UMMP 57917 (pl. 1, fig. 3; pl. 3, fig. 2), presumed adult with upper plates missing to reveal the mouth frame. Paratype

UMMP 57918 (pl. 1, fig. 1), presumed juvenile with parts of disk and proximal parts of all arms. All found with oral surface downward, in living position.

PALEOECOLOGY

Physical circumstances.—The slab bearing the three starfish described herein records two cycles of sedimentation, each characterized by an unfossiliferous layer overlain by an abundantly fossiliferous light-colored layer. The unit from which the slab was obtained shows numerous, perhaps as many as 40, such cycles during its deposition. Hence, during early Rogers City time, the site of the Calcite Quarry was in an area where periodic fluctuations were common. One might suspect that the area was near the shoreline, and certain evidence supports this idea.

Each dark barren layer has a somewhat irregular basal lamina that is commonly darker than the overlying material. All features point to restricted circulation, either in a marginal lagoon or in the shoreward waters of a sea with very low tidal range. The entire region was then near base level. Stagnation, probably in a lagoon, was responsible for the organic-rich basal lamina. This was followed by the slow accumulation of argillaceous lime mud brought in by runoff from the bordering flats and perhaps by slow-moving streams and currents. The whole unit was underlain by a thick sequence of limestones and dolomites, so that any erosion of local low uplifts would have produced only limy sediment. The upper surface of the layer shows no burrows or trails, such as might be recorded if the overlying clams had lived there.

The lighter-colored fossiliferous layer of the cycle contains numerous fossils, approaching a coquina in places. Brachiopods and clams are the most abundant, but uncoiled gastropods, bryozoa, and trilobites also occur. The layer has fossils densely packed, helter-skelter, in the lower part and grades upward into sparsely fossiliferous limestone at the top. The somewhat irregular uppermost surface bears the starfish and crinoid remains, including roots, scattered columnals, and an arm fragment. Of all the fossils, only the starfish and crinoid roots are definitely in the living position. The layer is overlain by the very dark lamina of the next cycle, which passes immediately over the starfish and conveys a first impression of fossilized integument.

The sequence of nonfossiliferous and fossiliferous layers can scarcely be explained as the result of ocean swells and winnowing, for such a process would not leave an organic-rich lamina at the bottom.

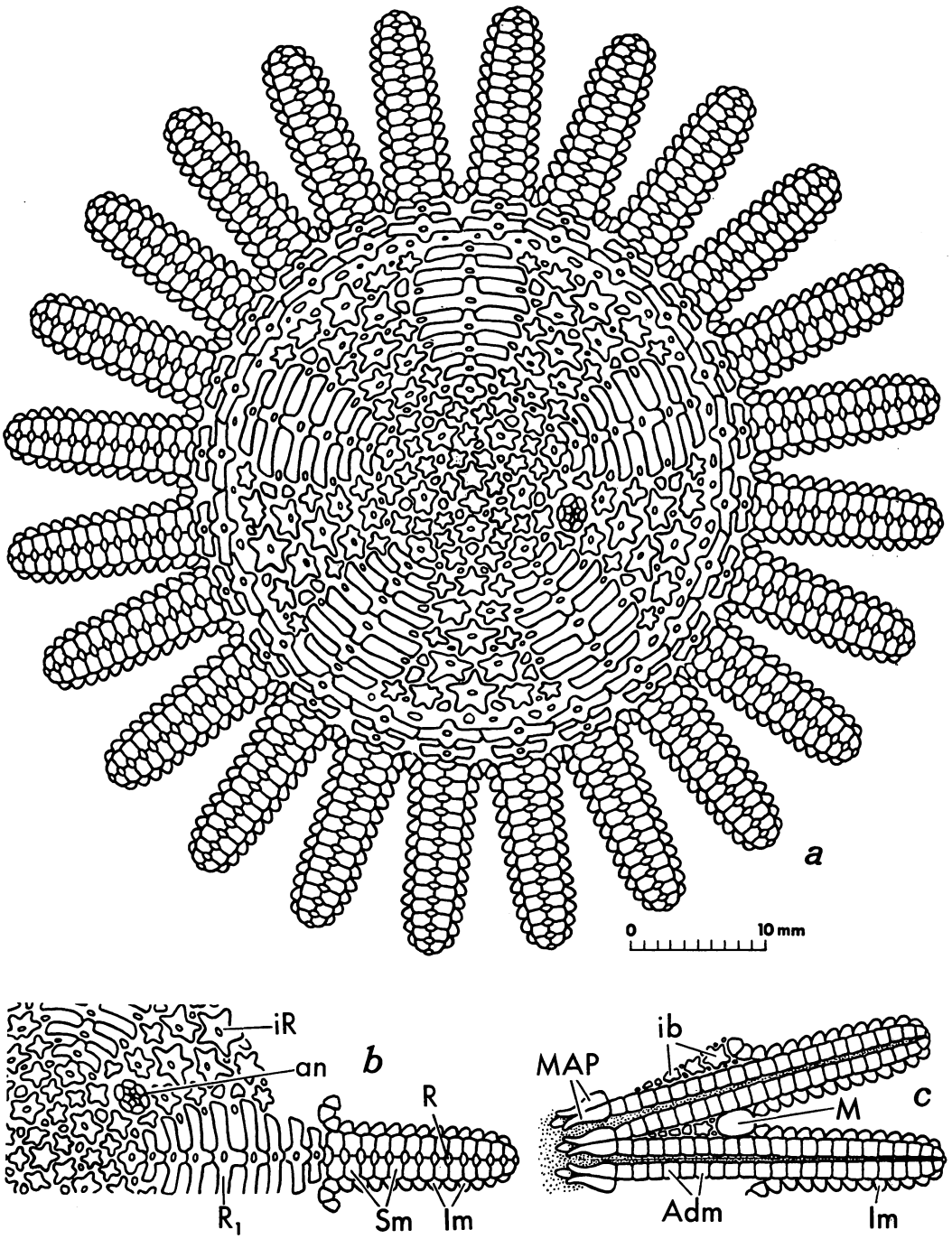
The sudden influx of animals and the sharp reduction of dark coloring matter point to a resumption of active circulation, probably by a renewed connection with the open sea. The mass of jumbled invertebrates first brought in, many disarticulated, seems to indicate a severe storm, which dislodged them from nearby bottom areas and cast them into the marginal lagoon at the same time that it tore out the barrier and allowed a new supply of sea water to pour in. Very soon thereafter, no doubt, the starfish began feeding on the survivors or on the remains of the dead.

During the ensuing period, the lagoon was slowly choked off again, perhaps by longshore currents restoring the barrier. Active circulation lasted long enough for crinoids to establish their root systems, but the clams and brachiopods died soon. Across the surface of accumulating limy mud crawled the last starfish, undoubtedly seeking food in the depleted environment. We can be rather sure that the starfish did not smother in fouled water, for they were already decomposed and partly dismembered when they were buried under the organic-laden sediment of the next cycle.

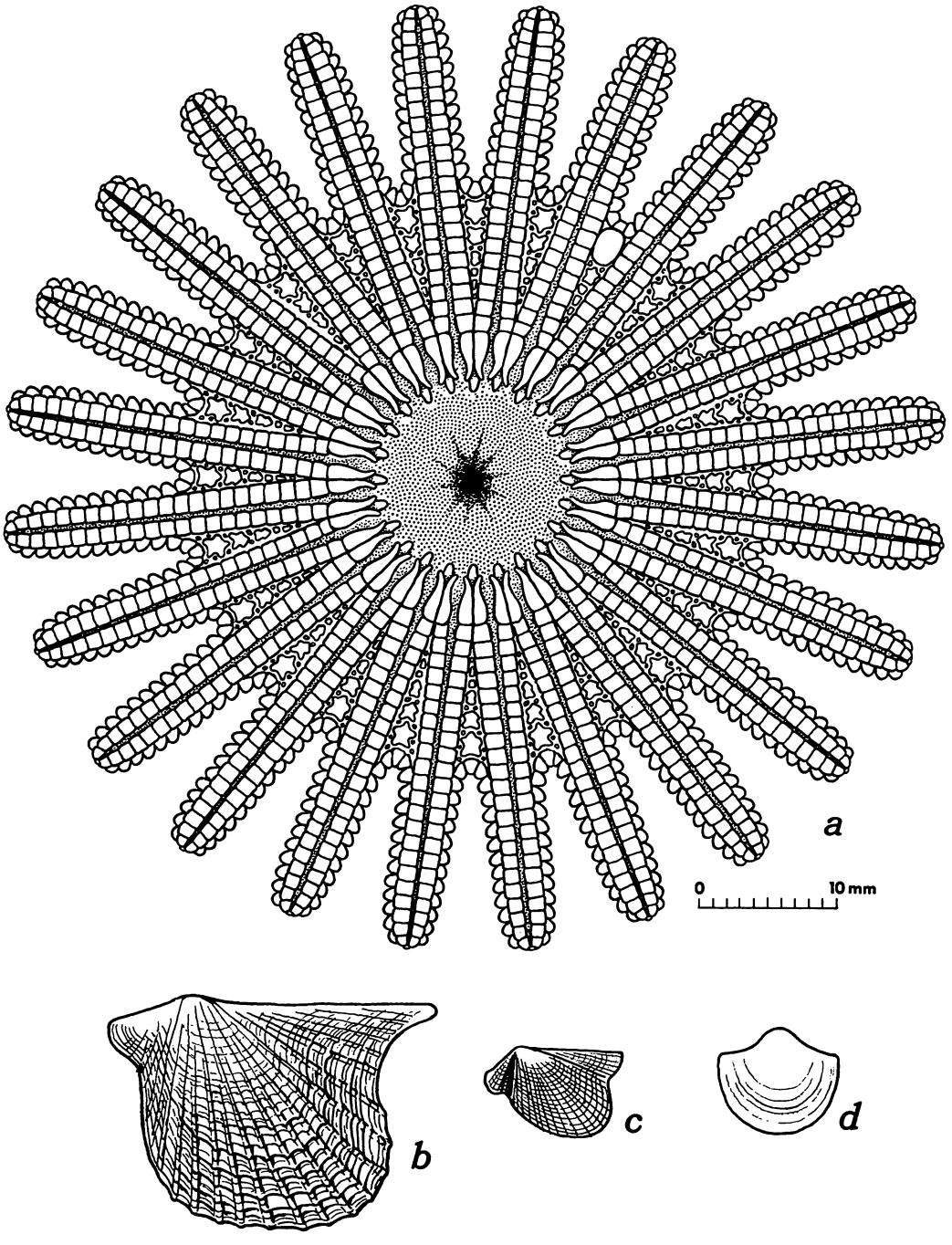
Perhaps the starfish died of starvation, but I suspect that inadequate food was only one factor. The more logical cause was decreased salinity. Some time ago Maloeuf (1937) established that the entire surface of asteroids is freely permeable to water. Decline in salinity results in water intake, swelling, and eventually death. In recent times, sudden influxes of fresh water into Long Island Sound have wiped out entire populations of *Asterias forbesi* (Loosanoff, 1945). The living *Asterias rubens* can tolerate the low salinity of the Baltic, but there it becomes plump, dwarfed, and sterile (Bock & Schlieper, 1953). Runoff and streams into the marginal lagoon could have so diluted the water that *Michiganaster inexpectatus* became abnormally distended. This would explain why the disks of the adult specimens appear to have ruptured and the arms to have come apart with ease.

Biologic circumstances.—In life, *Michiganaster* may have been a combination predator and scavenger. We have no proof of what it ate or how it ate. Comparison with living asteroids, however, does suggest some interesting possibilities.

Modern starfish feed in various ways, as summarized by Feder & Christensen (1966, p. 93–107). The most significant are: (1) ciliary feeders which secrete mucus to entrap suspended particulate material directly from sea water, such as *Linckia guildingi* and *Henricia sanguinolites;* (2) ciliary feeders commonly



TEXT-FIG. 4—*Michiganaster inexpectatus*. *a*, reconstruction of aboral surface of adult; anus (an) and precise arrangement of disk plates hypothetical. *b*, labeled plates of part of aboral surface. *c*, labeled plates of part of oral surface.



TEXT-FIG. 5—*a*, reconstruction of oral surface of adult *Michiganaster inexpectatus;* M and tori hypothetical. *b-d*, abundant invertebrates associated with the starfish; *b*, *Actinopterella peninsularis*, based on UMMP 24544, 24549, and 24545; *c*, *A. calliotis*, based on UMMP 24556 and 24558; *d*, *Emanuella* sp., based on UMMP 57695. All figures to the same scale.

called "mud-stuffers," which distend their stomachs with bottom material and may on occasion act as scavengers, such as *Sphaeriodiscus placenta* and all the deep-sea porcellanasterids; (3) direct mucus feeders, such as the cushion star *Patiria miniata,* an omnivorous scavenger which envelops plant and animal matter with its very large protrusible stomach; (4) carnivores which swallow their prey whole and digest it intraorally, such as *Astropecten;* (5) carnivores which seize bivalved prey with their tube feet and pull them open, digesting the contents extraorally; one example is *Asterias forbesi,* the notorious enemy of mussels, scallops, and oysters, which can exert a pulling force over 5000 grams for extended periods; (6) carnivores which hold fast with tube feet and insert their stomach through a permanent opening in the prey, such as *Evasterias trochelii,* which attacks *Mytilus californicus* through the byssus gape; (7) carnivores which somehow induce bivalves to succumb even though the tube feet are separated from the prey by the greatly distended stomach lobes, such as *Crossaster papposus* eating *Mytilus* (this process is still not fully understood, and even "guile" and "hypnosis" have been suggested); (8) carnivores which eat other starfish by inducing them to autotomize an arm, such as *Crossaster papposus,* which ritually causes *Asterias rubens* to part with one of its arms; (9) carnivores which eat other starfish by direct attack, such as young *Solaster endeca,* which seizes the tip of an arm of *Asterias* and will not be dislodged until it has eaten as far as possible into the flesh of its unwilling host; and (10) carnivores catching small prey with their pedicellariae and transferring them to the mouth by tube feet, such as has been observed in long-spined *Marthasterias glacialis* and *Astrometis sertulifera,* which capture small worms and crustaceans in this manner. Most starfish do not use one feeding method exclusively, but, on the other hand, many are exceptionally adept at capture of one preferred species of prey. With few exceptions, feeding habits do not correlate with taxonomic divisions at the family and order level.

It is of further interest to look at the feeding habits of modern many-armed starfish, for the numerous arms and expanded oral opening are functional considerations in eating. Common many-armed species occur in *Solaster, Crossaster,* and *Acanthaster* of the order Spinulosida and in *Coscinasterias, Pycnopodia, Rathbunaster,* and *Heliaster* of the order Forcipulata. The relatively small fast-moving *Solaster dawsoni, S. stimpsoni,* and *S. endica* eat other asteroids, whereas *Solaster paxillatus* prefers the sea cucumber *Molpadia intermedia. Crossaster papposus* has already been discussed, feeding mostly on the asteroid *Asterias rubens* but also on molluscs and bryozoans. *Coscinasterias calamaria* eats brachiopods, small gastropods, and Mytilidae. *Rathbunaster californicus* prefers small crustaceans. The recently publicized destroyer of Pacific reefs, *Acanthaster planci* (called the "crown-of-thorns" because of its poisonous aboral spines), feeds on coral polyps and leaves behind a trail of white skeletons. The giant sun star *Pycnopodia helianthoides* of the Pacific shore of North America attains a weight of 10 pounds and a diameter of 800 mm (32 inches). It swallows small prey and digests larger animals extraorally. Its diet includes clams, gastropods, sea urchins, crustaceans, and even algae and sponges. Fisher (1928, p. 159) describes this very active and voracious starfish in these words: "Intertidally it frequents rocky situations rich in kelp, where it feeds greedily on sea urchins, hermit crabs, or any other creature not too active to escape." *P. helianthoides* has up to 24 arms, and hence is more nearly like *Michiganaster* than are the species of *Solaster* with 7 to 13 arms, *Crossaster* with up to 14, or *Coscinasterias calamaria* with 12.

Verrill (1909, p. 551), said, "It is certainly true that most of the species with multiple rays live among rocks in situations exposed to the surf," and (1909, p. 552), "I am inclined to believe that the increase of rays has been due more to the advantages gained in holding the food securely than for holding to the rocks, though both go together." Of the many-armed asteroids now living, *Pycnopodia helianthoides* regularly inhabits tidal pools, *Acanthaster planci* lives around shallow-water reefs, and *Crossaster papposus, Solaster endeca,* and *Coscinasterias calamaria* migrate into the shallow intertidal areas during the spring breeding season. Hence, there are extant many-armed starfish which are adapted to nearshore environments, many of which are predators on pelecy-

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EXPLANATION OF PLATE 3

Specimens coated with sublimated ammonium chloride. Both figures × 8

Michiganaster inexpectatus n. gen. & n. sp. *1,* two arms and part of disk, holotype UMMP 57916; this part of specimen shown at upper left in plate 2, figure 2. *2,* proximal part of specimen with disk missing, UMMP 57917, showing upper surface of poorly preserved Admm and MAPP.

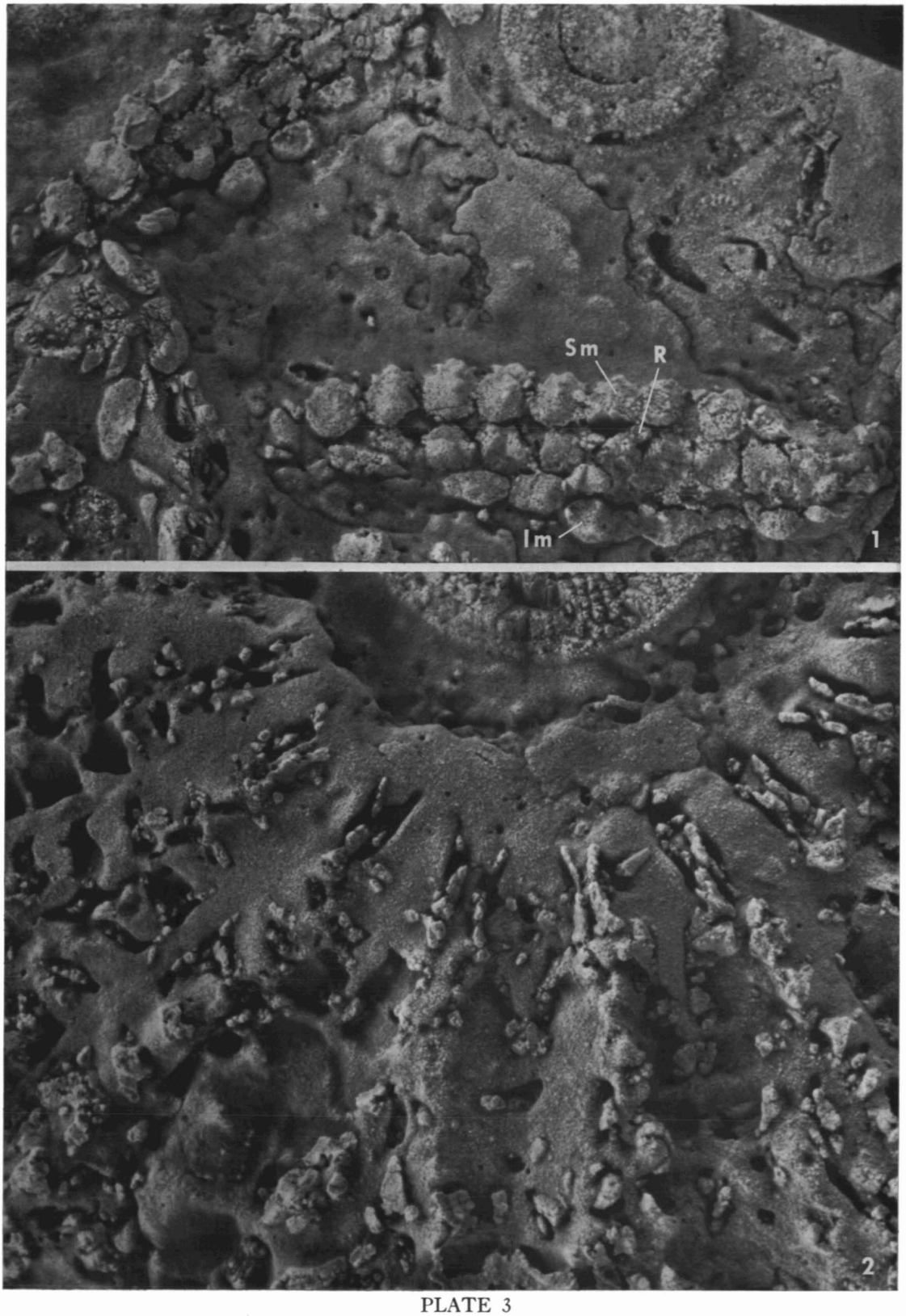

PLATE 3

pods and other echinoderms, and one of which eats brachiopods.

This discussion does not settle the question of the diet or manner of feeding in *Michiganaster inexpectatus*. Nevertheless, it does suggest that the other members of the Rogers City fauna with which it is associated—pelecypods, brachiopods, gastropods, and crinoids—could have served as food. With its stubby arms and large mouth, *Michiganaster* does not appear to have been strong enough to pull apart large bivalves; yet *Pycnopodia,* with a similar number of arms, is successful today even though it has the disadvantage of a weak, obsolescent aboral skeleton. Like *Pycnopodia, Michiganaster* may have thrust most of its prey whole into its large stomach and later ejected the indigestible residue. The exceptionally large protrusible disk was capable of housing a stomach of only slightly smaller dimensions. In this manner of feeding, *Michiganaster* would have been able to ingest adults of the common brachiopod *Emanuella* and younger individuals of the pelecypods *Actinopterella calliotis, A. peninsularis,* and *Leptodesma furcistriata* (see text-fig. 5).

Possibly, *Michiganaster* was a scavenger and facultative predator which was attracted into the lagoon by the odor of decay. However, it seems to me reasonable to believe that this starfish normally inhabited the banks where *Emanuella* and *Actinopterella* flourished, that it was transported into a marginal lagoon with other invertebrates where they all finally died, that lack of circulation and reduced salinity killed off most of the other animals, that the starfish was perhaps the last surviving species in a biologically depleting environment, that it suffered the pangs of fresh-water bloat, and that it expired before organic-rich sediment settled out of the fouled waters of the lagoon.

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