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STRATASTER OHIOENSIS, A NEW EARLY MISSISSIPPIAN BRITTLE-STAR, AND THE PALEOECOLOGY OF ITS COMMUNITY

BY

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ABSTRACT—The fortunate discovery of a deposit of densely crowded brittle-stars in a remarkable state of preservation permits description of their morphology and reconstruction of many aspects of their mode of life. All of the hundreds exposed on a bedding plane belong to a new genus and species, *Strataster ohioensis,* which is assigned to the family Protasteridae.

The new brittle-star is characterized by papillose integument on the disk, an inconspicuous madreporite in an oral axil, a large mouth frame, tori bearing three spatulate denticles each, and lateral plates each provided with two stout tapering distal spines and five or six spoon-shaped oral spines. Each arm bears a crest of uniserial aboral spines articulating on tubercles. The circumoral nerve- and water-ring grooves are clearly exposed on several specimens.

The brittle-star species dominated the community. The fossils are distributed in four size groups, thought to represent year stages. Dynamic analysis of the population indicates that annual mortality amounted to 45 percent. Original population density is estimated at 4500 individuals to the square meter, and the duration of the colony as recorded in the deposit is estimated at about 30 years. From the absence of very young specimens, the overturning of some dead individuals, and the successful annual recruitment necessary to maintain the colony, we conclude that the brittle-stars lived not far offshore in an area traversed by tidal currents. Complete exclusion of competitors throughout the span of the colony's existence points to the efficiency of the brittle-stars as filter-feeders. Absence of predators may be the result of secretion of acidic mucous by *Strataster ohioensis,* which may have been as efficient a repellent for that species as similar secretions are for modern brittle-stars. A catastrophic termination is postulated for the brittle-star community; because the uppermost layer appears to contain a natural mortality sample rather than a census group, we believe the last living population was swept forever from the area.

INTRODUCTION

MOST OF THE TIME *Lethaia,* the legendary goddess of the world of fossils, is frugal with her treasures. Paleontologists who work with brittle-stars might claim that she is downright miserly. On rare occasions, however, seized by an uncontrollable feminine impulse to spend some of her wealth, she showers some fortunate collector with a profusion of beautifully preserved specimens of a new species. It is such an occasion that we are celebrating here.

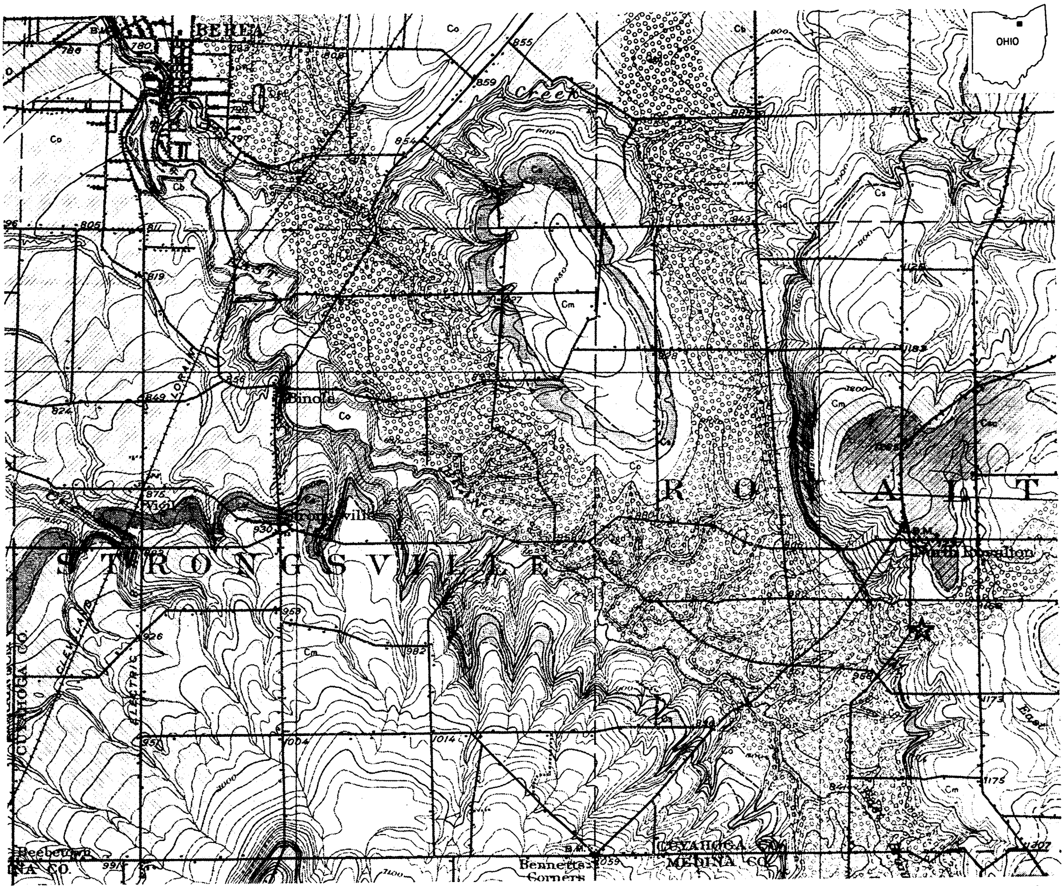
Of a new kind of brittle-star from Mississippian strata of Ohio, we have thousands of specimens, hundreds of them exposed on the upper bedding plane of the deposit. We have no worry about the oral or aboral side of the species, no worry about the nature of the disk, arm plates, ornamentation, or spines. Nor do we have any question about the tori and denticles in the mouth area. Our only problem is the delightful one of selecting the holotype from among the multitude of qualified individuals.

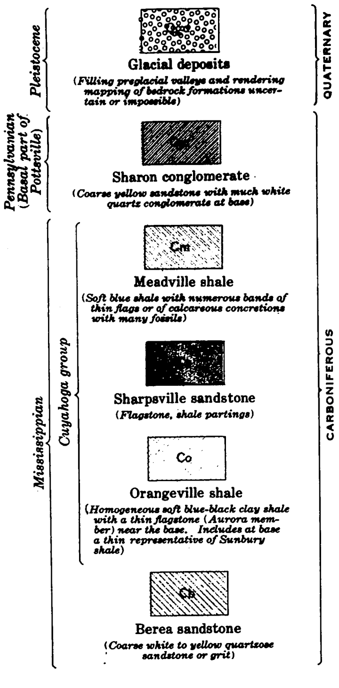
Several years ago, when paleoecology was receiving its first belated attention, Cooper wrote (1957, p. 973):

> The starfishes and brittle stars of the Paleozoic are rare and highly prized fossils. Because these animals were fragile they readily disintegrated after death into heaps of isolated plates and consequently were seldom preserved in their entirety. As with most rare fossils, little attention has been paid to their ecology . . .

These remarks have a degree of validity today, even though the compendium of Boolootian (1966) has helped greatly our understanding of living brittle-stars. With the new discovery we have an opportunity to contribute some observations on these fossil brittle-stars and to speculate on their ways of living.

Special thanks are extended to the staff of



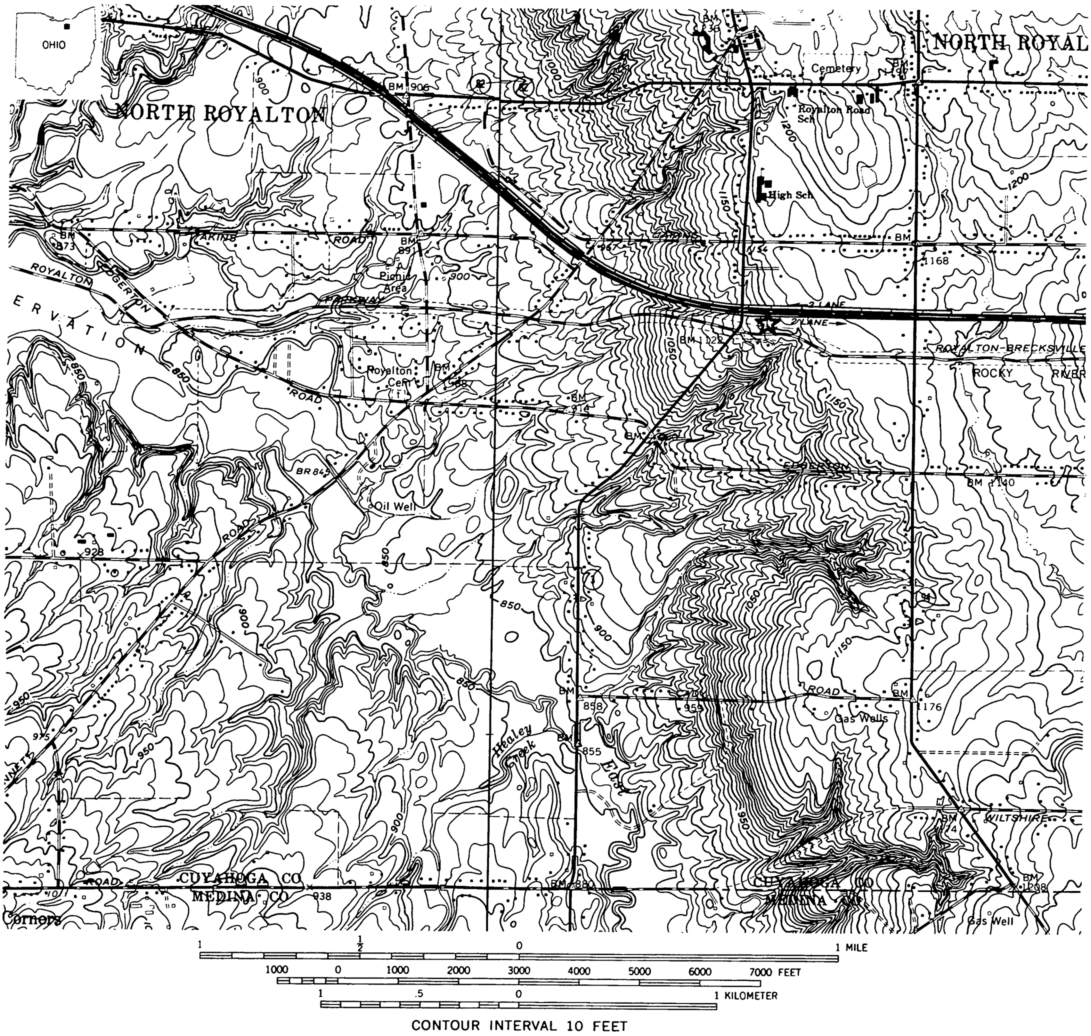


TEXT-FIG. *1*—Geologic map of part of Cuyahoga County, Ohio. Small star marks the locality yielding brittle-stars. From Cushing, Leverett, & Van Horn (1931).

the Ohio Turnpike Commission, who generously permitted the collections to be made.

In preparation of this paper we enjoyed the competent assistance of several friends. Professor Aurèle La Rocque, of Ohio State University, inspected the discovery site and offered helpful suggestions on interpretation of the occurrence. Professor Chester A. Arnold, of our Museum of Paleontology staff, prepared samples and tried to identify plant remains associated with the brittle-stars. Mr. Karl Kutasi photographed the specimens, Mrs. Helen Mysyk typed the manuscript, and Mrs. Gladys Newton read proof. We appreciate all of these valuable contributions.

The type specimens are divided between the collections of the Museum of Paleontology



TEXT-FIG. 2—Topographic map of part of Cuyahoga County, Ohio. Small star marks the locality yielding brittle-stars. From USGS Berea and Broadview Heights quadrangles (both 1963).

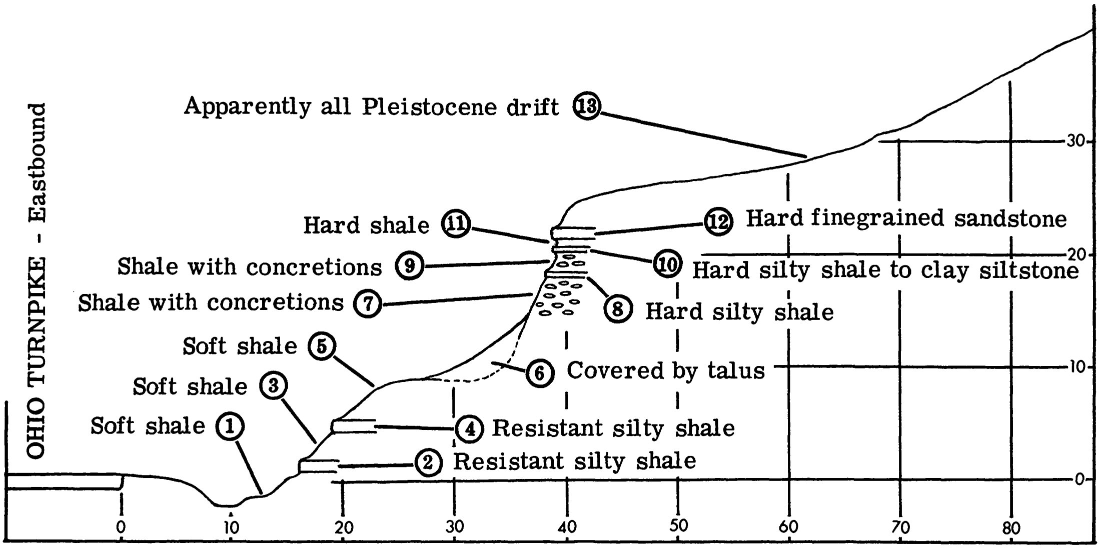
(UMMP) and the collection of the junior author (L).

LOCALITY AND OCCURRENCE

The locality yielding the brittle-stars is in the S½ of T 5 N, R 13 W, in Royalton Township, Cuyahoga County, Ohio (text-figs. 1, 2). It is a road cut along the Ohio Turnpike about 600 feet east of the overpass of Ohio State Route 3. It lies about ¾ mile south of Royalton, 3¼ miles northeast of Bennetts Corners, 5¼ miles east-southeast of Strongsville, and 7½ miles southeast of Berea. It is about 14 miles south-southwest of the main port facilities at Cleveland.

The layer containing densely packed and excellently preserved brittle-stars is unit 10 in the road-cut exposure (text-fig. 3). Slabs and smaller pieces were found scattered on the slope below this unit, many of which could be fitted onto slabs obtained in place. The unit is a lens (text-figs. 4, 5) about 18 feet long in exposed section and reaching a maximum thickness of 2 cm only at its center; for most of its extent it is 1.5 cm thick and averages about 1 cm. We cannot determine how far it extended in the north-south directions. The overburden is too great to quarry very far into the hillside.

The hard noncalcareous matrix contains both clay and silt. Although micaceous flakes of silt size and larger are very conspicuous in microscopic examination, they probably consti-



TEXT-FIG. 3—Sketch of strata exposed in road cut. Brittle-stars were found in unit 10. North is at left in the cross section.

tute less than 2% of the matrix. The clay content makes the layer nearly impervious, and samples dissolve very slowly in HF acid. Much of the unit is dark red, but some parts are lighter red and even approach neutral gray where the iron content is reduced by plant fragments. The black carbonized fragments left after maceration of a sample were examined by Professor C. A. Arnold, who could only state that they seemed to be derived from ferns and were definitely not marine algae. Most of the plant material is concentrated in the basal lamina, but here and there black flecks are present throughout the rest of the unit, including the upper surface. Only a very few other invertebrates can be found associated with the multitude of brittle-stars in the unit; these are crinoidal and bryozoan fragments.

The underlying shale (unit 9) contains other marine fossils, particularly crinoids and fenestrate bryozoa. Blocks quarried near the edge of the lens show disarticulated columnals overlain by better-preserved crinoids, including some heads retaining arms and long sections of column; this part of unit 9 is overlain by a thin veneer of unit 10, a dark red lamina with a few brittle-stars. Some brittle-stars in this part of the deposit lie directly on top of the crinoids. The uppermost 4 cm of unit 9 and the whole of unit 10 together exhibit a notable decrease in the energy of deposition.

Some loose slabs contain a few brittle-stars admixed with crinoids. The former seem to be the same species as the brittle-stars in unit 10, but they are not nearly as well preserved. Some arms appear to have been broken off before burial. The occurrence differs so much from that of unit 10 that we suspect that some brittle-stars, perhaps dead at the time, were washed in from other areas by currents and deposited before the main colony became established. The presence of a concretion in one of these slabs points to unit 7 or unit 9 as the source.

All strata in the road cut to the top of unit 12 are characteristically red, although some subdued tints and gray color can be seen locally. Above unit 12, all or nearly all of the hill is formed by glacial drift. To the south, the hillside rises 65 feet above the turnpike at a distance of about 160 feet from the edge of the pavement, and continues higher for a short distance to the crest of a ridge. Obviously, the whole exposure of the Mississippian red strata was made by the excavation for the roadway (compare text-figs. 1 and 2).

STRATIGRAPHY

Geology of the area was competently treated in 1931 by Cushing (*in* Cushing, Leverett, & Van Horn). To him we owe the revision of regional stratigraphy, determination of faunal lists, and detailed mapping of this part of Ohio. Later, Holden (1942) analyzed facies of the Mississippian rocks throughout Ohio.

Brief Mississippian history of the area.—Mississippian strata in Ohio crop out in a north-south belt through the east-central part of the state, from the Ohio River to within a few miles of Lake Erie; there the belt turns eastward to the Pennsylvania border. In addi-

TEXT-FIG. 4—View of brittle-star locality along Ohio Turnpike, looking south. Dotted line marks course of measured section shown in text-figure 3; small circle marks outcrop of unit 10.

TEXT-FIG. 5—View of brittle-star locality along Ohio Turnpike. Circles mark approximate extent of outcrop of unit 10 from which slabs were obtained in place.

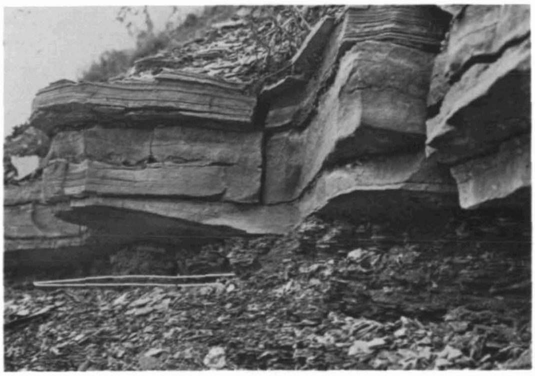
tion to the upper black shales of the Cleveland Shale, the Mississippian rocks are divided into the Bedford, Berea, Sunbury, Cuyahoga, and Logan formations or groups. Of these, the Bedford Shale and Berea Sandstone extend throughout the outcrop belt. The Sunbury Shale is confined to the southern half of Ohio (Holden, 1942, p. 40). The Cuyahoga Group forms a broad zone in all parts of the Mississippian belt, divided into numerous formations. The Logan Group, also divided into several formations, is exposed from the Ohio River as far north as Wayne County; its northern limit lies about 23 miles south-southwest of Cuyahoga County.

The Mississippian period in Ohio was characterized by the shifting and sifting of sands and muds, sometimes on land and sometimes in shallow water. At no time during the period was the area of Cuyahoga County far from shore.

After a brief interruption of black shale deposition, currents stirred up the bottom muds and some organisms were able to establish themselves in the purified water, including brachiopods, small clams, snails, ostracods, and crinoids. They were short-lived, however, as quantities of rapidly deposited mud and sand snuffed out the bottom fauna. Because the Bedford Shale is absent in Pennsylvania, it is presumed that the inundation came from the south and that the area of northern Ohio was landlocked on the west, north, and east sides (Cushing, 1931, p. 89). Cuyahoga County received over 85 feet of argillaceous to arenaceous shales, sandstones, and siltstones at this time. In the eastern part of the county, the sediments are mostly blue-gray, with some maroon and dark red bands, but westward the amount of red coloration increases. Most sandstone layers are ripple-marked (Holden, 1942, p. 37).

At the end of Bedford time, uplift of the lands to the north and west elevated the Cleve-

TEXT-FIG. 6—Close-up of locality. White lines indicate boundaries of part of unit excavated in place. UMMP 58330 and 58332 came from right side of view; UMMP 58331, 58336, and 58337 came from left side of view.



TEXT-FIG. 7—Close-up of locality. White lines indicate boundaries of part of unit excavated in place.

land and Cuyahoga area above sea level. On this low plain, streams channeled into the underlying Bedford muds and filled them to overflowing with sand. The channels were deepest at the northwest sector of this area, where the uplift was greatest. Near the brittle-star locality, the Berea Sandstone reaches 150 feet in thickness. Locally, the formation contains abundant plant fragments. Many specimens of the paleoniscid fish *Gonatodus brainerdi* have been found in the county; invertebrates are rare and badly water-worn. None of the fossils are marine (Cushing, 1931, p. 47). Depression of the bordering lands reduced and finally stopped the sand supply, and Berea deposition came to an end.

Soon the sea returned to northern Ohio, reworking the top layers of the Berea sand. This thin stratum later became cemented with pyrite and constitutes the peculiar black base of the Cuyahoga Group. The formations in the Cuyahoga Group in this area belong to the Tinkers Creek Shale facies of Holden (1942, p. 51–53). They are older than the several facies of the group lying to the south. The basal formation is the Orangeville Shale, about 125 feet of soft blue-black clay shale that weathers rather easily. The Aurora Sandstone Member near the base reaches 10 feet in some exposures but is absent in other places. The Orangeville is barren except for a few scattered fish spines, conodonts, and inarticulate brachiopods. In general, Orangeville sedimentation was like that of the older black shales: uninterrupted accumulation of mud in unoxygenated water.

Another uplift of nearby lands produced a fresh supply of sand and initiated the Sharpsville Sandstone. Currents stirred up and cleared out the foul water of Orangeville time, permitting a marine bottom fauna to settle in the area (Cushing, 1931, p. 90). Near the northern limit of the outcrop belt, land plants are common, indicating nearness to the shoreline. The sandstone varies from 30 to 50 feet, and locally may contain some thin shale units. The sand is typically gray, fine grained, and micaceous; it contains little calcareous matter and considerable marcasite. The middle sections of many thick sandstone units are red, although the margins remain blue-gray (Cushing, 1931, p. 51).

The boundary with the Meadville Shale is transitional. The change in sediment was caused by deepening of the basin. The lower part of the Meadville contains mostly shales interbedded with thin sandstones. In the upper part of the formation, sandstones increase until some exposures show as much sandstone as shale. Invertebrates became more numerous and varied during this interval, but their distribution was irregular and interrupted. The Meadville was the last Mississippian deposit to leave a record in northern Ohio. It probably spanned the boundary between late Kinderhook and early Osage. To the south, younger formations of the Cuyahoga Group were laid down to the Ohio River and beyond.

Occurrence of Meadville Shale.—The stratum bearing the starfish is in the upper part of the Meadville Shale. In Cuyahoga County, the formation consists of 30 to 250 feet of "alternating blue shale, thin sandstone, and sandy limestone" (Cushing 1931, p. 52). The cut along the Ohio Turnpike is probably the best exposure of upper beds in the county. No such extensive section was known in 1931, when Cushing wrote (p. 52):

> The Meadville . . . occupies an area of considerable size between the Cuyahoga River and the West Branch of the Rocky River, in the southwestern part of the Cleveland quadrangle and southeastern part of the Berea quadrangle. Owing to heavy drift covering and to high altitude only the headwater portions of the streams lie across it, so that good exposures are scarce, and no continuous section exists within the quadrangles. The best sections are those on Baker Creek, Big Brook, branches of Chippewa Creek, and small runs tributary to the Rocky River in Royalton Township. East of the Cuyahoga River the formation is much thinner than on the west side, and there are no exposures worthy of the name. The thickness of the formation increases rapidly and unevenly from east to west . . . due to unequal pre-Pottsville erosion.

EXPLANATION OF PLATE 1

Figure × 20

Strataster ohioensis n. sp. Paratype L-25a, juvenile (probably a large yearling) with oral surface exposed. The mouth frame is not completely contracted and the mouth-angle plates (MAP) do not lie parallel in each interray. Alternating lateral plates (L) of the arm form broad shields, with the opposite rows so close together in the distal part of the arm that the ambulacral groove is effectively concealed and the arm becomes terete. Several LL retain the pair of distal spines (ds), but most have lost the oral spines (os) with pustuliform points of attachment marking their former positions. The underside of the disk (Dk) is papillose. Ambulacral plates (Amb) have their oral-side ridges, like those in most other ophiuroids, shaped like "boots" with the "foot" at the proximal end of the plate. A complete view of this specimen can be seen in plate 9 at the right side of figure 1 (× 5) and in plate 11 at the upper left corner of figure 1 (× 2½).

PLATE 1

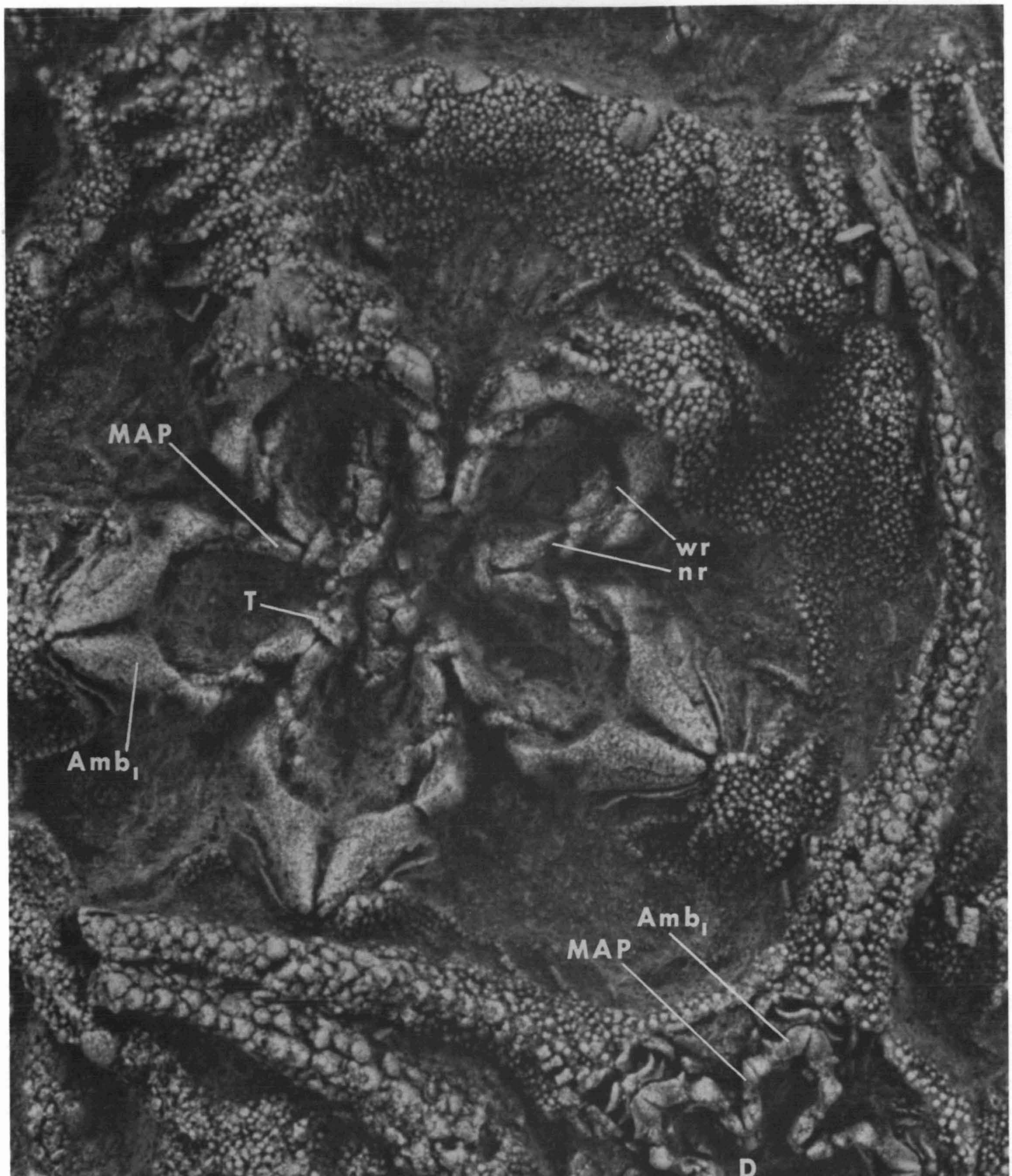


PLATE 2

Character of Meadville Shale.—Cushing (1931) characterized the Meadville as a series of alternating shale and sandstone beds. He did not stress the dark red color, which is very conspicuous in the road cut. He wrote (1931, p. 52, 53):

> The shales range from soft clay shale to very sandy shale. The clay shales are generally blue to blue-black and fissile, but some beds are blocky and show little tendency to split. They are quite like the similar shales of the Bedford and Chagrin formations . . . The sandy shales are grayish blue and well laminated. Many layers of flattened lime-iron concretions, blue within but weathering reddish, alternate with these shales . . . Many of these concretions are exceedingly fine grained and flinty . . .; others are of somewhat coarser texture, and many of these contain excellently preserved fossils.
>
> The flagstones throughout the formation are blue to gray, thin bedded, in places laminated, and generally micaceous. In the lower 100 feet they are subordinate in quantity to the shales, but in the higher part of the formation they equal or exceed the shales. Associated with them are beds of calcareous sandstone or sandy limestone, rather fine grained, usually very hard, gray to blue, but in many places tinged with red and weathering to red or yellow-brown. The more sandy beds weather to brown porous sandstones; the more calcareous beds to weak, friable fragments of iron-stained sand.

Meadville fauna.—Unlike the other Mississippian formations in the area, the Meadville Shale is very fossiliferous. Careful collecting would probably establish several faunal zones. Cushing (1931, p. 53, 54) compiled the following list of fossils from the formation:

Productella newberryi
P. aff. *P. concentrica*
Productus ovatus
Chonetes logani
C. cf. *C. illinoisensis*
Leptaena analoga
Spirifer centronatus
S. aff. *S. centronatus*
S. aff. *S. striatiformis*
Cyrtina burlingtonensis
Cliothyridina cf. *C. obmaxima*
Centronella? cf. *C. julia*
Edmondia burlingtonensis
Cypricardinia consimilis?
Sphenotus cf. *S. valvulus*
Palaeoneilo truncata
Mytilarca cf. *M. occidentalis*
Pernopecten cf. *P. cooperensis*
Pterinopecten cariniferus
Tropidodiscus cyrtolites
Pleurotomaria textiligera
Platyceras cornuforme
Conularia newberryi

In addition, he listed unidentified species of *Productus, Schuchertella?, Rhipidomella, Camarotoechia, Hustedia, Ambocoelia, Reticularia, Cranaena, Grammysia, Edmondia, Palaeoneilo, Nucula, Nuculana, Schizodus, Aviculipecten, Limatulina, Oracardia?, Buchanopsis, Loxonema?, Euomphalus, Platyceras, Orthoceras, Brachymetopus,* and *Dictyospongia.*

Hall & Whitfield (1875, p. 162–179) described the crinoids from "shales of the Waverly sandstone group, at Richfield, Summit County, Ohio." Most and perhaps all of these species are present in the Meadville Shale of the Cuyahoga County region. Hall & Whitfield's species are here followed by the revised classification of Bassler & Moodey (1943) in parentheses:

Actinocrinus daphne (= *Actinocrinites daphne*)
A. helice (= *Aorocrinus helice*)
A. eris (= *Aorocrinus helice*)
A. viminalis (= *Amphoracrinus viminalis*)
Platycrinus contritus (= *Platycrinites contritus*)
P. graphicus (= *Platycrinites graphicus*)
P. richfieldensis (= *Platycrinites graphicus*)
Forbesiocrinus communis
F. tardus (= *Dactylocrinus tardus*)
F. kelloggi (= *Taxocrinus kelloggi*)
Poteriocrinus crineus (= *Cosmetocrinus crineus*)
P. pleias (= *Hypselocrinus pleias*)
P. (*Scaphiocrinus?*) *corycia* (= *Pachylocrinus corycia*)
Scaphiocrinus aegina (= *Decadocrinus aegina*)
S. lyriope (= *Decadocrinus lyriope*)
S. subtortuosus (= *Decadocrinus subtortuosus*)
Zeacrinus paternus (= *Zeacrinites paternus*)
Z. merope (= *Zeacrinites merope*)

In addition, the following species, described by Hall & Whitfield (1875) from the "Cuyahoga shale of Waverly group, at Lodi, Medina County, Ohio" may also be present in the Meadville:

Platycrinus lodensis (= *Platycrinites lodensis*)

EXPLANATION OF PLATE 2

Figure × 20

Strataster ohioensis n. sp. Paratypes L-25b and L-25c, an old adult (probably a four-year-old) and a juvenile (probably a small yearling) with their aboral sides uppermost and the centers of their disks eroded off to expose the mouth frames. In each half-ray the frame consists of the first ambulacral plate (Amb_1) articulated to a mouth-angle plate (MAP). In each interray the MAPP adjoin a torus (T) and, in the smaller specimen, two tori still retain the three denticles (D) each. The upper surface of the mouth frame is incised by two concentric sets of deep grooves, the inner to accommodate the nerve ring (nr) and the outer to accommodate the water ring (wr) or ring canal. $Ambb_1$ of the younger specimen are less acute radially than those of the older. Each shows deep clefts for dorsal muscles of the Ambb. The orientation of the mouth-frame elements clearly indicates that the $Ambb_1$ rode upward and distally on the sloping surface of $Ambb_2$ to open the mouth. Complete views of these specimens in plate 10, figure 4 (× 5), and in plate 11 at the lower right quarter of figure 1 (× 2½).

In unit 9 of the section at the turnpike cut, just below the brittle-star layer, *Actinocrinites daphne* and *Conularia newberryi* are conspicuous faunal elements.

Summary.—The Lower Mississippian in northern Ohio was a period of numerous topographic fluctuations. The shoreline shifted many times. Uplift brought sands and slight downwarping brought muds into the area from nearby sources to the northwest. Some of the sands were laid down on land and some in shallow water. The deepest and most persistent marine basin was formed in Meadville time, but even then pulsations in the neighboring source region resulted in alternating shales and sandstones. Low marshes and marginal swamps provided appreciable plant debris from time to time.

In this unsteady area, bottom-dwelling invertebrates encountered difficulty in establishing themselves. Migrations were commonplace, with entrepreneurs moving in to exploit each new ecological situation. Frequently, whole faunas were blotted out by the quick change in depth and sediment or forced to emigrate to places with more hospitable conditions.

Although the fluctuations in the area were of small magnitude, probably amounting to tens of feet, the changes wrought in sedimentation and in environments were drastic. It was in this setting that the brittle-stars founded their successful colony.

SYSTEMATIC DESCRIPTION

Subclass Ophiuroidea Gray
Order Oegophiurida Matsumoto
Suborder Lysophiurina Gregory
Family Protasteridae Miller

The suprageneric classification used here follows that proposed by Spencer & Wright (1966) in the *Treatise on Invertebrate Paleontology*. At the generic level, however, we have some reservations about the very long ranges assigned to most asterozoans in this standard work; perhaps, these ranges reflect deficiencies in preservation, inaccuracies in published descriptions, or an aversion for close discrimination on the part of the specialists.

The characteristics exhibited by our brittle-stars fit the description of the family Protasteridae. The Ambb alternate, LL are wrapped around the sides of the arms to form side shields, the disk lacks a well-developed marginal frame, M is oral, and the LL bear both distal ("vertical") and oral ("groove") spines. Within the family, our species fits *Drepanaster* and *Mastigophiura* in having deep depressions for aboral muscles in the arms, according to the *Treatise* definitions. It lacks large spines on the disk, differentiating it from *Mastigophiura;* and its arms are not extremely long and narrow, differentiating it from *Drepanaster.*

According to the brief description in the *Treatise,* our new ophiuroid would lie in the genus *Taeniaster,* in which case it would extend the range of that genus. However, the recent review and clarification of *Taeniaster* by Hotchkiss (1970) proves that the genus is very different from the interpretation set forth by Spencer (1934) and by Spencer & Wright (1966). Hotchkiss (1970, p. 61, 63) found that *Taeniaster* does not have deep excavations in the Ambb for insertion of dorsal longitudinal muscles; the aboral outline of its Ambb is quadrate instead of trapezoidal or triangular. He confirmed that *Protaster* also lacks excavations for dorsal muscles. *Protasterina,* placed in synonymy with *Taeniaster* by Spencer & Wright (1966), was resurrected by Hotchkiss (1970, p. 63) for brittle-stars having deep aboral excavations. The nature of *Drepanaster* was strongly questioned by Hotchkiss, inasmuch as most of the characteristics attributed to it by Spencer and by Spencer & Wright were based on *D. grayae,* which is very different from the type species, *Protaster scabrosus;* according to Hotchkiss (1970, p. 63), ". . . *D. grayae* is akin to *Protasterina.*"

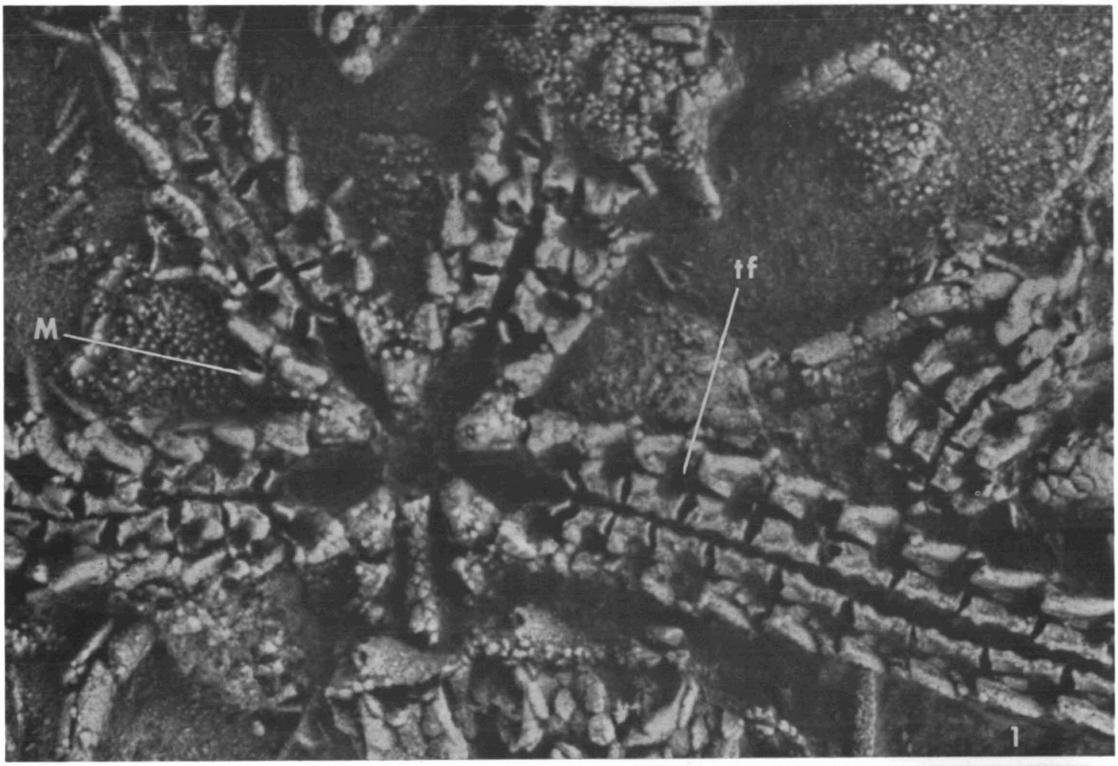
From our search of literature, it seems to us that the genus most like our brittle-star is *Protasterina.* The differences, insofar as we have been able to interpret them from various accounts, are summarized in table 1. Of the contrasting character states, we would place most emphasis at this time upon the aboral shape of Ambb, the extent of the articulating "nose" of L, and the relative size of MAPP.

Explanation of Plate 3

Figure × 20

Strataster ohioensis n. sp. Paratype L-25d, an old adult (probably a four-year-old) with its oral surface exposed. Around the mouth (mo) the MAPP still retain a thin covering of papillae-studded integument, like that over the rest of the underside of the disk (Dk). The LL are very well preserved, showing the spoon-shaped oral spines (os) as well as the long conical distal spines (ds). The madreporite (M) is a small plate crossed by a deep slot set close beside one arm. A view of the entire specimen can be seen in plate 11 at the lower right quarter of figure 2 (× 2½).

PLATE 3



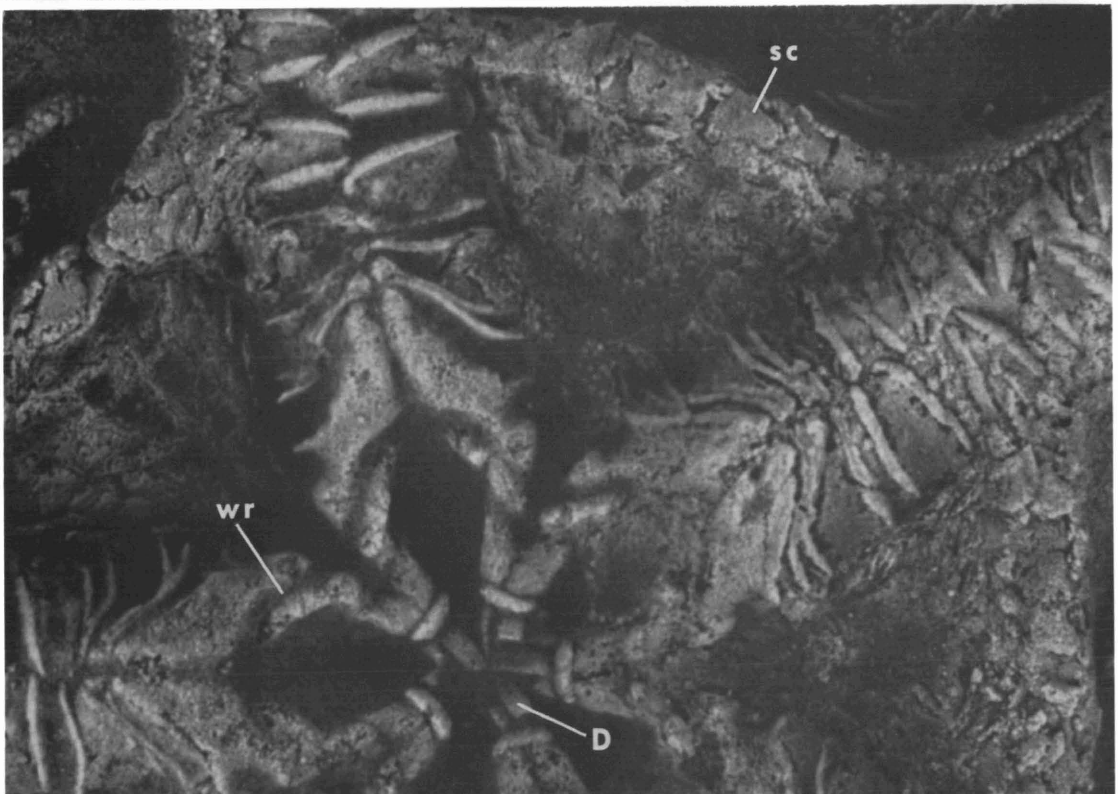


PLATE 4

TABLE 1—DIFFERENCES BETWEEN *Protasterina* AND *Strataster*. Based on information in Spencer (1934), Spencer & Wright (1966), and Hotchkiss (1970).

	Protasterina	*Strataster*
Aboral shape of Ambb	Subtriangular	Trapezoidal
Aboral ridges of Ambb	Close-set, only a narrow groove between them	Subterminal, convergent from midline toward side, but even there separated by deep channel
MAPP	Small	Large
Articulating "nose" of L	Small, subround	Large, elongate
Taper of arms	Abrupt, end whiplike	Uniform

STRATASTER n. gen.

Type species.—By monotypy, *Strataster ohioensis* n. sp.

Diagnosis.—Protasterid brittle-stars with disk covered by integument bearing internal thin irregular mosaic plates and external papillae. Oral surface of disk and aboral surfaces of arms also papillose. Mouth frame large and set upon appreciable incline of Ambb_2. Tori bearing a few large but delicate denticles. Ambb "boots" with a thin shallow groove across the "leg" and a longitudinal groove from the "ankle" to the "instep." Ambb trapezoidal in aboral outline; the two subterminal ridges convergent away from the aboral midline, but separated by a deep channel, leaving space for dorsal musculature. Junction between alternating Ambb in two halves of arm slightly sinuous. LL not overlapping, each provided with several oral spines and a few distal spines; L "nose" ridgelike, its articulation with Amb nearly straight and half as long as the plate. Cupules for tube feet well defined and fairly deep. Arms tapering evenly to terete tip; in distal section of arm, LL usually contracted orally to effectively obscure ambulacrum. M small and inconspicuous, crossed by a slot.

Remarks.—Whether the derivation of the generic name is regarded as from Latin or from Greek, it seems fitting for the only known occurrence of these brittle-stars. If derived from Latin *stratum,* n. ("layer, blanket"), it can refer to the density of specimens in the layer of Lower Mississippian silty shale. If derived from Greek *stratos,* m. ("encamped army, host"), it can refer to the dominance of the area by the brittle-stars. Hence, the name is appropriate either as "layer-star" or as "army-star."

STRATASTER OHIOENSIS n. sp.

Text-fig. 8; pls. 1–13

General shape.—The disk is subround (pl. 1; pl. 3) to subpentagonal (pl. 5, fig. 2), the preserved shape seemingly dependent upon the manner in which the disk is compressed in the interrays (axils) during fossilization. Arms are long and evenly tapering to a small diameter near the tip (pl. 1; pl. 8, fig. 2; pl. 10, figs. 1, 2). Regardless of size, the arm radius (from center of disk) is slightly more than 5 times the interradial disk radius. The distribution of disk radius in 100 well-preserved specimens is shown in text-figure 9. The smallest measured specimen has a disk about 1.2 mm in radius and the largest about 4.0 mm. Arms in the latter extend nearly 22 mm from the center of the disk. Where the arm becomes free, its diameter is about one-fourth that of the disk.

Disk.—All specimens are preserved with the oral or the aboral side up; none are at an angle to the bedding plane. Undoubtedly, the disk is much flatter than it was in life, and the living brittle-star may have possessed a rather rotund disk. In fossilization, the disk has been pressed down onto the mouth frame so firmly that the form of the latter shows clearly through the integument (pl. 5, fig. 2). As a result, weathering exposes the mouth frame aborally in many specimens (pl. 2), greatly facilitating its study.

The integument covering the aboral surface of the disk and extending onto the axils of the oral surface has no frame of marginal plates whatever. Instead, it is studded with numerous

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EXPLANATION OF PLATE 4

Both figures × 20

Strataster ohioensis n. sp. *1,* paratype L-25e, a late juvenile (probably a two-year-old) with oral side exposed. The Ambb are particularly well exposed to show the cupules for tube feet (tf). Alongside one arm on the underside of the disk is a small madreporite (M), an oval plate crossed by a deep slot. Other views of the specimen in plate 10 at the top of figure 4 (× 5) and in plate 11 at the lower right margin of figure 1 (× 2½). *2,* holotype UMMP 58329a, a large adult (probably a four-year-old) with the aboral side uppermost. Integument has been eroded away to expose the scales of the disk (sc), the mouth frame, and the alternating Ambb. The tori retain denticles (D), and the mouth frame shows clearly the groove for the water ring (wr) outside and concentric to the groove for the nerve ring. Other views of this specimen can be seen in plate 8, figure 3 (× 5), and in plate 13 at the lower left quarter of figure 1 (× 2½).

small papillae, varying somewhat in size but lacking any discernible pattern. An adult specimen has about 200 papillae on each square mm of its integument. The papillae extend onto the tops of the arms without interruption; they even cover the MAPP around the mouth in exceptionally well preserved specimens (pl. 3).

Where the outer layer of integument has weathered away, a mosaic of irregular scales is exposed (pl. 4, fig. 2). These thin plates are not joined by sutures, but they probably served to impart whatever rigidity the disk possessed.

Arms.—Each arm extends free for a distance greater than twice the diameter of the disk. The arm tapers distally to a very narrow diameter at the tip, yet it tapers evenly. At its junction with the disk, the arm is grooved on its oral side by the wide ambulacrum; near the end, the arm is terete because the LL converge from its two sides to effectively close off the ambulacrum (pl. 1). At any rate, this is the manner in which the arms are fossilized; we suspect that much of this contraction, perhaps all of it, took place in rigor mortis and that the full length of the ambulacrum was available for feeding in the living animal.

The aboral sides of the arms are covered by integument like that of the disk, studded with papillae. These papillae extend down the sides of the arms, except on the distal edges of the spine-bearing LL (pl. 7, fig. 2).

Along the axis of each arm and encroaching onto the disk for a short distance is a single row of close-set erect spines (pl. 8, figs. 1, 3; pl. 10, fig. 2). Proximally, these spines are nearly as high as the arm is wide, but distally they decrease in height and none are present on the thin terminal section of the arm. Each spine articulates by a ball-and-socket joint, its condyle fitting onto a tubercle in the integument (pl. 7, fig. 2), precisely like the spine of an echinoid. We have no doubt that these spines were movable and functional. Where spines are missing, the tubercles on which they articulated are conspicuous because they are larger than the papillae and are surrounded by a circular groove (pl. 2).

Mouth frame.—Ambb$_1$, MAPP, tori, and denticles comprise the mouth frame. The first element beyond the MAP in each half-ray is here called Amb$_1$, as it is for all oegophiuridan brittle-stars in the *Treatise* (Spencer & Wright, 1966). Actually, the history of Asterozoa indicates that this element may be fused Amb$_2$ and Amb$_3$, as suggested by Bjork, Goldberg, & Kesling (1968) for *Onychaster.*

Structure of the mouth frame can be better studied in aboral view than in oral view. Fortunately, a number of specimens have the top of the disk weathered off to expose the frame and still preserve excellent details of the plates (pl. 8, figs. 2, 3; pl. 10, fig. 4).

Tori are small subelliptical plates with convex proximal surfaces (pl. 2). Each torus is interradial and articulated to two MAPP, one from each side of the adjacent rays, as in other ophiuroids. Proximally it bears three denticles (pl. 2; pl. 4, fig. 2), of which the middle one is longer than the two lateral, its length exceeding the width of the torus. Each denticle is spatulate, with parallel sides and a slightly convex aboral surface. In biting, the 15 denticles met in the center of the mouth, as can be seen in specimens which died with the mouth contracted (pl. 4, fig. 2). As in related fossil brittle-stars, the tori and denticles of *Strataster ohioensis* readily dislodge in weathering. As a result, very few individuals with their oral sides exposed retain any trace of the tori or denticles (for example, pl. 1; pl. 3; pl. 4, fig. 1; or pl. 5, fig. 1).

The Ambb$_1$ and MAPP served to impart movement to the tori and their attached denticles. In this species, the amplitude of movement seems to have been very small. In each half-ray, the Amb$_1$ and MAP are firmly joined at an angle of about 120°, forming a geniculum directed distally and toward the interray.

The oral and aboral surfaces of each MAP are very different. On the oral surface of the specimen, the MAPP are covered with a thin layer of integument which, like the rest of the oral surface of the disk, is papillose (pl. 3). The majority of specimens with this orienta-

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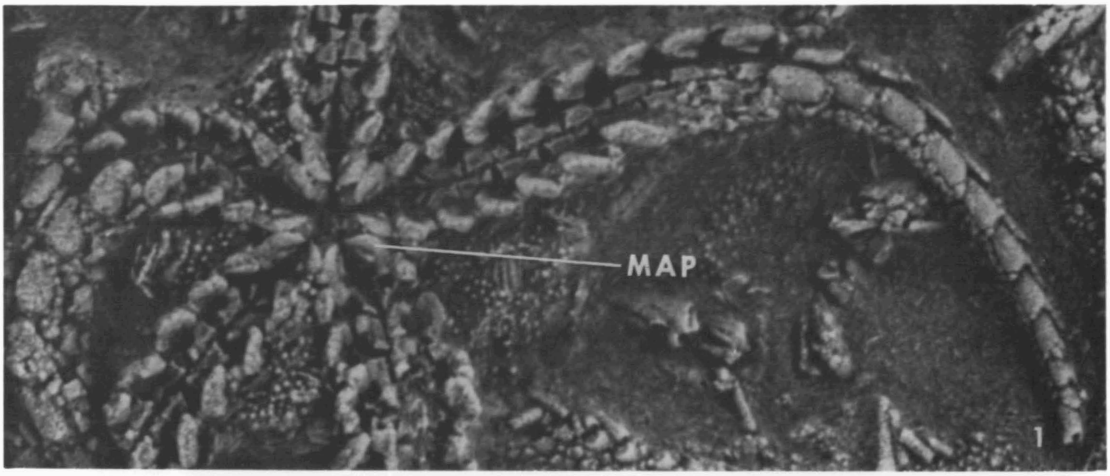
EXPLANATION OF PLATE 5

Both figures × 20

Strataster ohioensis n. sp. *1,* paratype L-25f, a juvenile (probably a yearling) with the oral surface exposed. The ten MAPP around the mouth are in place, with the mouth frame contracted. Alternation of Ambb distinct in each arm. The arm at the right tapers to a terete distal section in which LL of the two sides nearly meet. Other views of this specimen shown in plate 9 at the upper margin of figure 1 (× 5) and in plate 11 at the left margin of figure 1 (× 2½). *2,* paratype L-25g, adult (probably a three-year-old) with its aboral side exposed. The disk is entire, showing the studding of the integument with papillae. The form of the mouth frame can be seen where the disk has collapsed around it. Along the axis of each arm and extending onto the disk is a uniserial crest (c) of spines. Another view of this specimen can be seen in plate 11 at the upper left corner of figure 2 (× 2½).



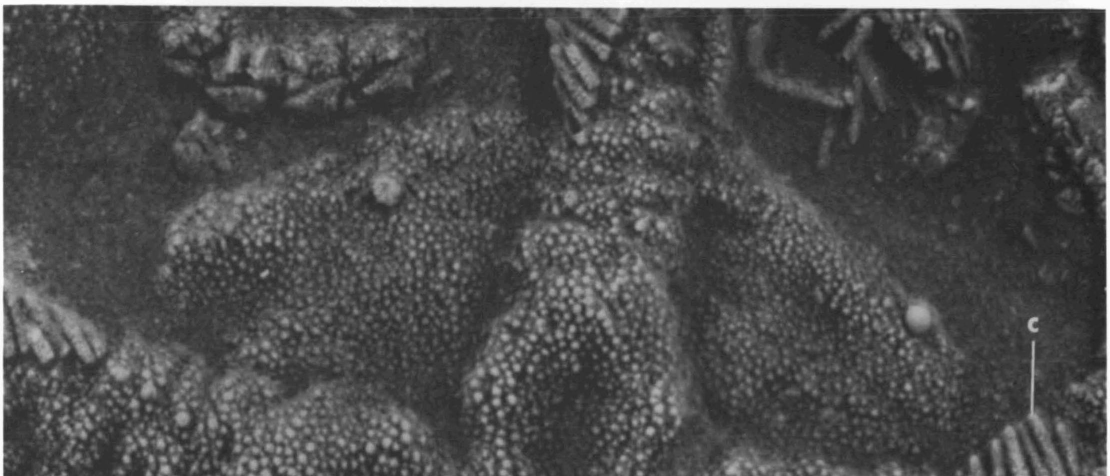


PLATE 5

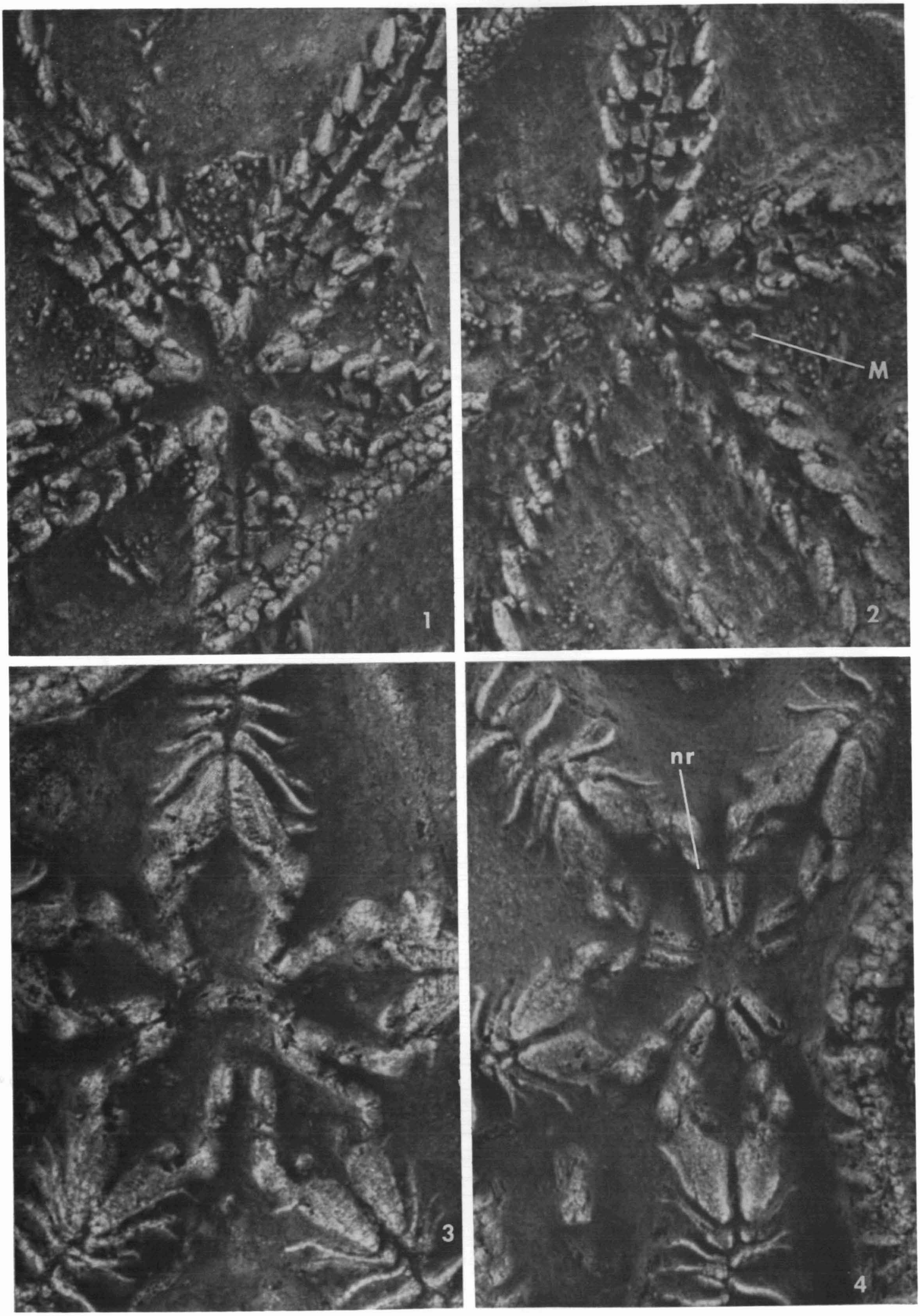


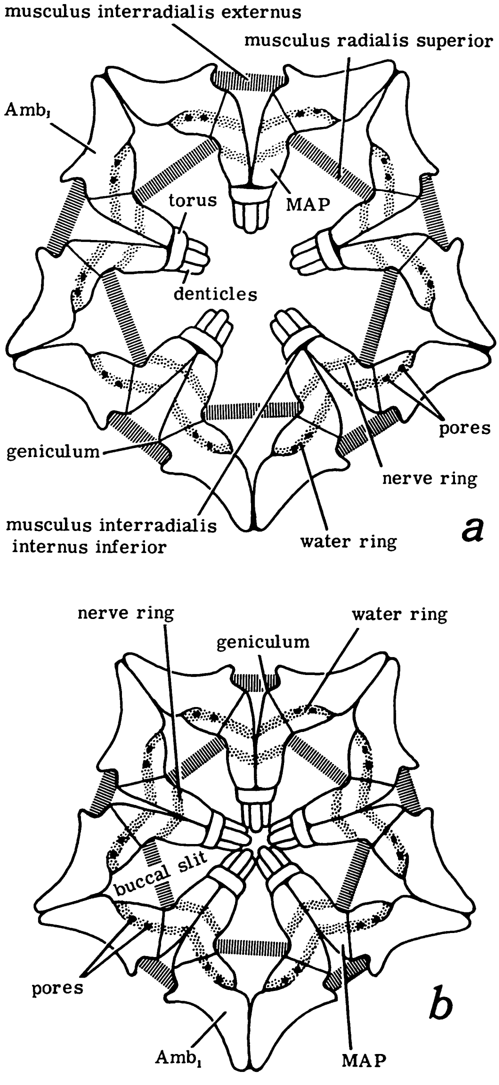
PLATE 6

tion, however, have most or all of the integument weathered off (pl. 5, fig. 1; pl. 7, fig. 4). In these, the oral exposure of each MAP is appreciably longer than that of the adjacent Amb. The proximal two-thirds of its interradial side is nearly straight and fits closely against the adjacent MAP of the interray; from this side, the surface curves rather evenly radially and then aborally, to form a subcylindrical surface bordering the buccal slit. Across the beveled proximal ends of the interradial pair of MAPP the torus fits like a cap (pl. 7, fig. 4).

Aborally (pl. 2; pl. 4, fig. 2; pl. 6, figs. 3, 4) the curvature of the radial side of each MAP continues to the upper edge of the plate, which faces the edge of the other MAP in the interray. This curvature is interrupted and distorted by the grooves to accommodate the circumoral nerve ring (pl. 6, fig. 4) and the concentric water ring or ring canal (pl. 4, fig. 2).

Like the MAPP, the Ambb$_1$ have different oral and aboral aspects. On the oral surface, each Amb$_1$ contains a cupule for a tube foot which is offset from the other cupules of the half-ray, lying closer to the ambulacral axis. The cupule is bordered by only an angular bar instead of the "boot"-shaped ridges possessed by the other Ambb (pl. 4, fig. 1; pl. 6, fig. 1). In each ambulacrum, the pair of bars forms a distally directed V which terminates the buccal slit.

The aboral extent of the Ambb$_1$ is much greater. Each radial pair of Ambb$_1$ bears the overall shape of a triangle, with one of the apices directed distally. Actually, each Amb$_1$ is nearly trapezoidal, with the longer side facing outward and the shorter side bordering the buccal slit (text-fig. 8). The groove for the water ring, which crossed the top of the MAP, continues onto Amb$_1$ where it curves to the end of the buccal slit; there the ring canal gave rise to the radial water vessel, which extended at a lower level between succeeding Ambb in the arm. Each section of the water ring groove has a pair of pores (text-fig. 8; pl. 2; pl. 6, figs. 3, 4), the entries to canals from the water ring



Text-fig. 8—*Strataster ohioensis.* Mouth frame in open or extended position (a) and in closed or contracted position (b), with restoration of inferred musculature. Compare with plate 2; plate 4, figure 2; and plate 6, figures 3, 4.

Explanation of Plate 6

All figures × 20

Strataster ohioensis n. sp. *1, 2,* paratypes L-25h and L-25i, two juveniles (probably yearlings) with the oral sides exposed. In each ray, the oral exposure of Ambb$_1$ is very small as compared with that of the succeeding Ambb. Maximum length of Ambb is attained beyond the edge of the disk. Other views of the first specimen in plate 9 at the lower margin of figure 1 (× 5) and in plate 11 near the center of the upper left quarter of figure 1 (× 2½). *3, 4,* paratypes UMMP 58330a and 58330b, two adults (probably three-year-olds) with aboral sides exposed and integument eroded off to reveal the mouth frames. Mouth frame is expanded in figure 3 and contracted in figure 4. The groove for the nerve ring (nr) is sharply defined in figure 4. Other views of UMMP 58330a in plate 8 at the bottom of figure 2 (× 5) and in plate 12 at the lower margin of figure 1 (× 2½); other views of 58330b in plate 8 at the top of figure 2 (× 5) and in plate 12 at the lower right quarter of figure 1 (× 2½).

to the tube feet in the first two cupules of the half-ray; these canals pass completely through Amb_1.

The grooves for the nerve ring and water ring are concentric. The nerve ring lies inside, and the water ring outside (pl. 2). In general plan, both are pentastellate with apices in radial positions, although each is interrupted by the five buccal slits (the groove for the nerve ring having wider interruptions because of its proximal location).

Biting movements involved the shape and position of the elements of the mouth frame as well as the musculature linking the parts together. The upper surfaces of $Ambb_2$ are beveled to slope downward to the mouth area, like grandstands around a pentagonal arena (pl. 4, fig. 2; pl. 6, figs. 3, 4). Atop their sloping surface are the inclined $Ambb_1$. Only the distal tips of $Ambb_1$ and $Ambb_2$ reach the top of the arm. Because of the sloping position of Amb_1, the tip of the plate actually lies above the proximo-oral end of Amb_3. As the mouth opened, Amb_1 slid out and up on the beveled upper surface of Amb_2, possibly overriding the edge of Amb_3 as well; this action raised the denticles as they diverged from the center of the mouth. As the mouth closed in biting, Amb_1 slid down and in, lowering the denticles as they came together.

The mechanics of the biting action involved rigid units, pivots, and muscles to provide force. In each half-ray, Amb_1 and MAP remained firmly joined at all times, acting as a single unit. The mouth frame was constructed of ten such rigid units, arranged in a pentagram or star in which the distal tips of $Ambb_1$ articulated as outer pivots and the junctions of MAPP and tori served as inner pivots. The mouth apparently opened by longitudinal aboral muscles which pulled each Amb_1 distally in the ray; the disto-oral (lower) surface of Amb_1 is hidden from view, so that the existence of muscle scars there cannot be confirmed in any of the specimens without careful removal and cleaning of the plate. The mouth was apparently closed by contraction of the *musculi interradiales externi* and the *musculi radiales superiores* (text-fig. 8), all acting as third-class levers on the mouth frame. Each *musculus interradialis externus* linked the $Ambb_1$ of adjacent rays, apparently inserted in a slight lateral depression of each Amb_1 just proximal to a small spinelike projection of the plate. Each *musculus radialis superior* was situated across the top of the ambulacrum, serving to pull the $Ambb_1$-MAPP units together; it was apparently inserted in a slight lateral indentation near the junction of the two plates. To judge from the small areas of muscle attachment, the bite of *Strataster ohioensis* was rather weak. The *musculus interradialis internus inferior* was small but powerful, hinging the torus to the two MAPP in each interray and holding it in position during the bite; possibly, the two halves of the muscle could act independently, imparting a slight lateral swing to the denticles.

Contraction of the mouth was mechanically restricted. As the tori moved toward one another, the two MAPP in each interray came to lie side-by-side, preventing any additional thrusting inward of the tori and denticles (text-fig. 8b; pl. 6, fig. 4); hence, it was impossible for the brittle-star to break off its teeth against one another. In expansion of the mouth, the MAPP in each interray diverged to form a V with the apex at the torus (text-fig. 8a; pl. 6, fig. 3). We presume that the outer pivots of the mouth frame were formed by muscular or ligamental connections at the tips of $Ambb_1$.

Arm plates.—The arms are constructed of Ambb, LL, and the covering integument. In an adult, each half of an arm contains about 30

EXPLANATION OF PLATE 7

All figures × 20

Strataster ohioensis n. sp. *1,* paratype UMMP 58331a, oral surface of a large adult (probably a four-year-old). Ambulacral "boots" are large and sharply delineated. Although oral spines are missing, the edge of each L plate bears a row of pustules to which the spines were attached. *2,* paratype UMMP 58331b, aboral surface of a late juvenile (probably a two-year-old), showing edge of disk and part of attached arm. Some of the spines forming the uniserial crest are dislodged, showing the recessed ball on which each articulated. The arm is twisted, showing the LL plates with their pairs of distal spines. Another view of this specimen in plate 10 at the center of figure 2 (× 5). *3,* paratype L-25j, oral surface of an adult arm. Ambb are shorter than those in UMMP 58331a (fig. 1), apparently indicating younger age at death. The distal spines extend as far as the end of the next Amb plate. Another view of this specimen in plate 11 at the upper right corner of figure 2 (× 2½). *4,* paratype UMMP 58332a, oral surface of an adult (probably a three-year-old). MAPP are well developed, but the tori and denticles have been lost in erosion. The M is an inconspicuous structure, as in other specimens. Some of the LL retain oral spines (os), but they are not as well preserved or exposed as in some other specimens. $Ambb_1$ show only a thin wedge-shaped bar in place of the "boots" exhibited by other Ambb. The cupule for the first tube foot is much smaller than the succeeding cupules. Other views of this specimen in plate 9, figure 4 (× 5), and in plate 13 at the right side of figure 2 (× 2½).

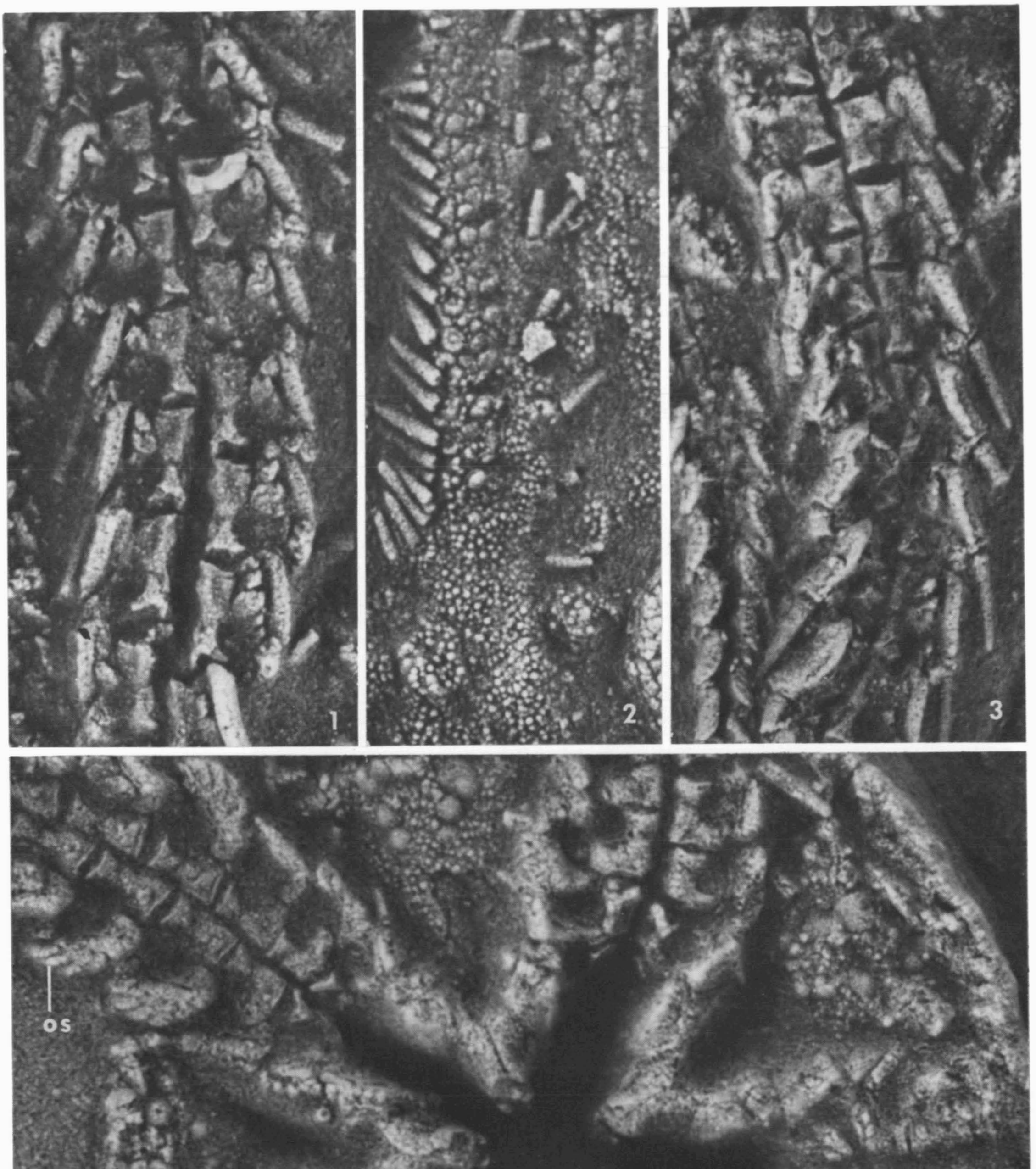
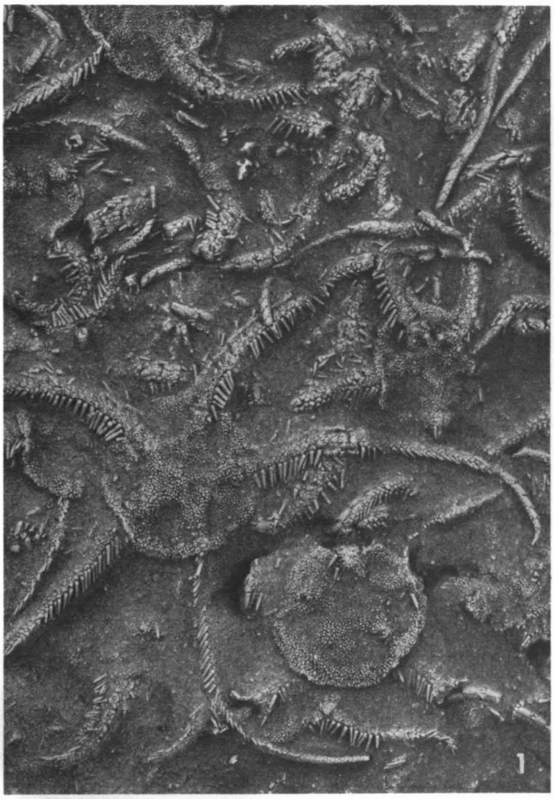


PLATE 7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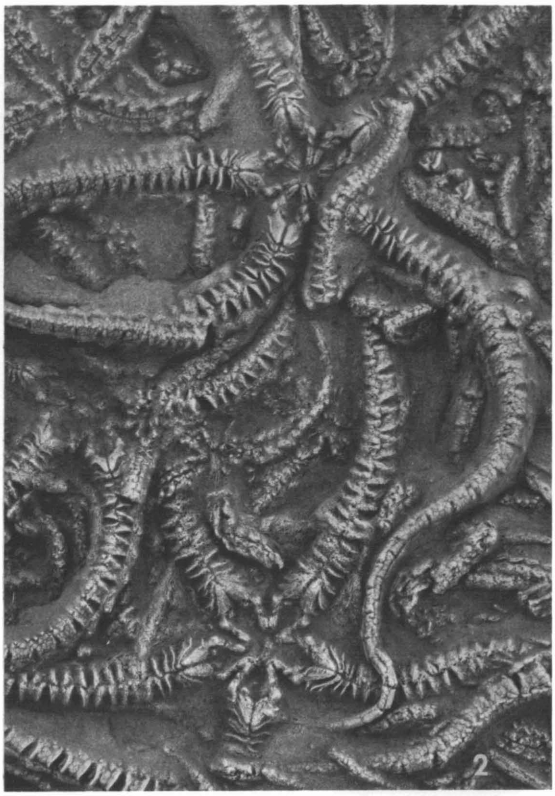
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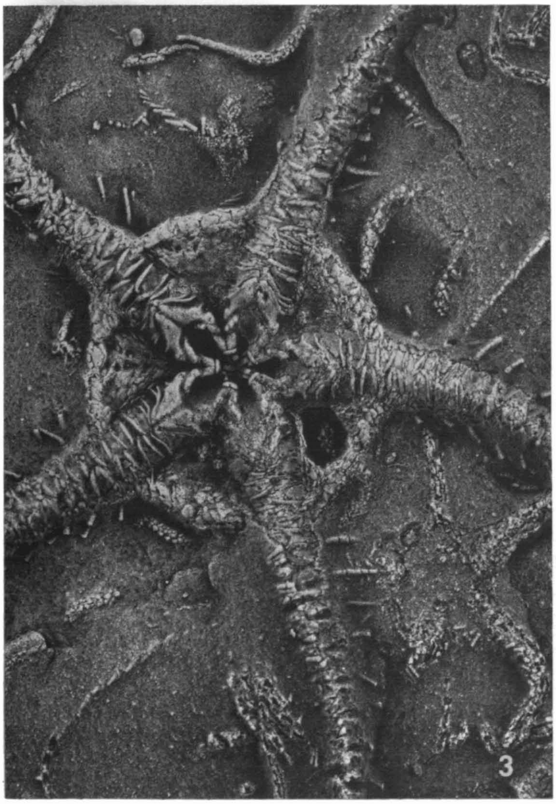
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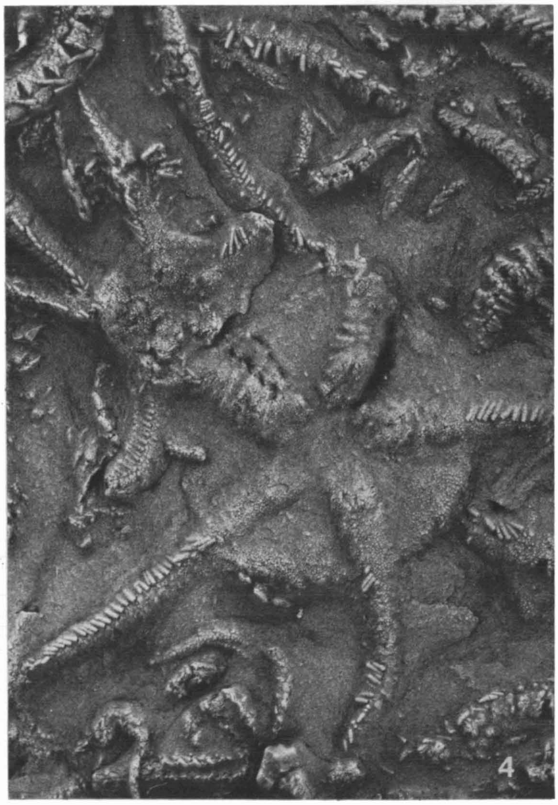
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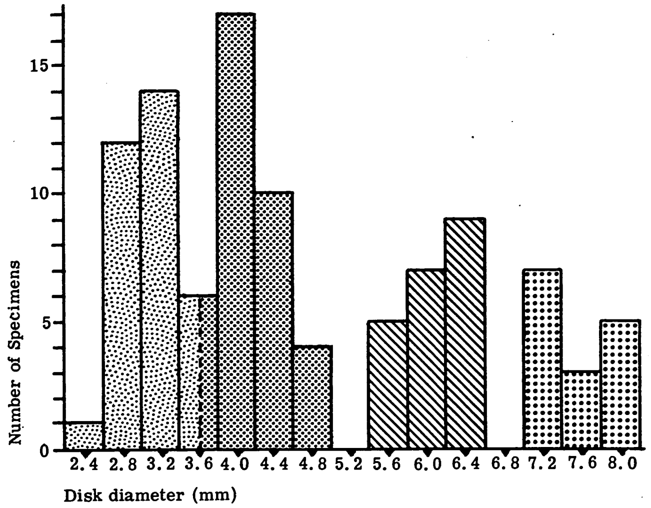
PLATE 8



TEXT-FIG. 9—*Strataster ohioensis.* Distribution of 100 specimens by diameter of disk. Specimens selected for good preservation. Disks measured to nearest 0.4 mm.

each of Ambb and LL plates; a juvenile may contain less than 20 plates in each series.

Ambb in the proximal half of the arm are exposed orally along the ambulacral groove (pl. 4, fig. 1). Their aboral sides, however, can be seen only where the integument has been weathered off (pl. 8, fig. 2). Except in the oral region, where they are involved in the mouth frame, the Ambb of the left and right sides of an arm alternate. Each Amb is a rather thick plate, shaped more or less like a short section of cylindrical rod cut in half longitudinally and beveled along the oral edge.

Even though the Ambb of the two sides alternate, they fit snugly together. Aborally, the adradial articulating face of each Amb is slightly concave to accommodate the ends of the two opposite Ambb (pl. 4, fig. 2; pl. 8, fig. 2). Orally, the same arrangement prevails, the concavity of the adradial articulating face of each Amb making the median groove of the ambulacrum slightly sinuous (pl. 5, fig. 1; pl. 6, fig. 2; pl. 7, figs. 3, 4).

The raised ridges on the oral surface of ophiuroid Ambb have been referred to by many authors as the "boots" or "bootlegs" because of their fancied shape. In most ridges the resemblance leaves much to the imagination. If there are indeed boots shaped like some of the ridges, we offer sympathy for the unfortunate creature who wore them. In many species the ridge has the form of a squared-up C in which the concavity borders the adradial half of the cupule for a tube foot, the back of the C borders the midline of the ambulacrum, the top and bottom of the C accommodate short ventral muscles to roll up the arm, and one end of the C articulates with a process of the bordering L plate. In such ridges, a certain resemblance to a boot can be seen with the "foot" at the proximal end (as most authors interpret it) or at the distal end. We follow the common usage of the term "boot" but acknowledge the inappropriate comparison where the "toe" is thick and blunt to articulate with the L process.

In living brittle-stars, new elements are added at the end of the arm, and presumably this pattern of growth existed in extinct forms.

EXPLANATION OF PLATE 8

All figures × 5

Strataster ohioensis n. sp. *1,* paratype UMMP 58331c (at left), aboral side of late juvenile (probably a two-year-old) preserving crest of spines atop each arm. These spines decrease in height distally, and the end of the arm is covered with scales bearing no spines. *2,* paratypes UMMP 58330b (above) and 58330a (below), two adults (probably three-year-olds) with the aboral side uppermost. Both have the proximal parts of the arms denuded of integument, revealing the deep clefts in the Ambb series for insertion of dorsal muscles. Enlarged views of these specimens shown in plate 6, figures 3 and 4 (× 20); reduced views shown in plate 12 at the lower right quarter of figure 1 (× 2½). *3,* holotype UMMP 58329a, aboral side of old adult (probably a four-year-old). Disk scales show where integument is eroded away. Enlarged view of specimen shown in plate 4, figure 2; reduced view in plate 13, figure 1. *4,* paratype UMMP 58332b, aboral side of old adult (probably a four-year-old), retaining nearly all integument on the disk. Reduced view shown in plate 13 at the lower left corner of figure 2.

Therefore, the full development of the characteristic "boot" for a species is encountered in the proximal section of the arm, which is ontogenetically older than the distal section.

As stated above, the oral ridges of $Ambb_1$ in *Strataster ohioensis* are expressed only as short oblique bars closing off the buccal slits (pl. 4, figs. 1, 2; pl. 7, fig. 4). Other Ambb ridges in the proximal section of the arm form distinctive "boots"; distally these "boots" become narrower, and in the most recently formed terminal section of the arm they are bars lying alongside the median groove of the ambulacrum. In young individuals of *Strataster ohioensis,* the "leg" of the boot is very narrow, the "boot-top" is only slightly flared, the "foot" is extremely thick, the "toe" terminates very bluntly, and a shallow longitudinal groove extends from the "ankle" to the "instep"; an inconspicuous narrow groove crosses the "leg" between the "foot" and the "boot-top" at about two-thirds the length of the ridge from its proximal end (pl. 1; pl. 4, fig. 1; pl. 5, fig. 1). Presumably, this shallow groove marks the course of the little branch from the radial nerve and pseudohemal canal to the tube foot, as suggested by Spencer (1925, p. 254) and Hotchkiss (1970, p. 71) for other species of fossil brittle-stars. In old adults, the "foot" of the "boot" is extremely short and thick and the "boot-top" is flared and notched (pl. 7, fig. 1); actually, the shape of the Amb ridge in these specimens strongly resembles a jackboot with the foot directed distally, complete with heel and toe, the opposite orientation from that normally used.

Proportions of the "boots" vary by the position of the Amb in the arm and by the age of the individual. That of Amb_2 is markedly shorter than that of Amb_3; then the "boots" become progressively longer and attain their maximum length at about Amb_8; thereafter they gradually diminish in length to the tip of the arm. The distal "boots" are reduced to narrow bars bordering the median groove; in most specimens, they are concealed by the oral enrollment of LL from each side, which closes over the ambulacral groove (pl. 1), but in a few individuals they are visible. At about the same position in the arm, "boots" in older brittle-stars tend to be a little more elongate.

These ridges are important functional elements of the arm. Recently Hotchkiss (1970) has paid particular attention to their shape and sculpturing in redefining *Taeniaster.* This work is exceptional, and most authors have not awarded the ridges the consideration which they deserve. In *Strataster ohioensis,* the "boot-top" of one ridge and the "instep" of the next have their ends excavated for the insertion of ventral muscles, which during the animal's life served to bend the arm down and enroll it. The "shin" of the "boot" is a concavity bordering the cupule for the tube foot (pl. 4, fig. 1). The blunt end of the "toe" articulated with the inner proximal process or "nose" of the L plate (pl. 6, fig. 1). In old individuals, these "toes" are exceptionally large and concave (pl. 7, figs. 1, 3).

On the aboral side, each Amb is trapezoidal. Vertical ridges near its proximal and distal edges are separated by a deep concavity, giving the plate the appearance of a half-vertebra (pl. 4, fig. 2; pl. 8, fig. 2). From the midline of the arm, these subterminal ridges converge slightly toward the side of the arm. On each side of the arm, this arrangement leaves deep V-shaped clefts for the insertion of dorsal muscles, although not as extensive as those shown for "*Taeniaster spinosus*" by Spencer (1934, text-fig. 317) or described for *Drepanaster grayae* by him (1940, p. 496). Nevertheless, the space available for dorsal muscles in *Strataster* indicates that its arms were highly flexible, particularly from side to side; even though the Ambb in each half of the arm fit closely against those in the other half, forming a sinuous junction, the arm was probably capable of elevating its tip high above the substrate.

Cupules for all tube feet except the first are rather well defined and fairly deep. Each cupule has a diameter equal to about half the length of the Amb which it borders. Cupules for the first tube feet in each arm are smaller and closer

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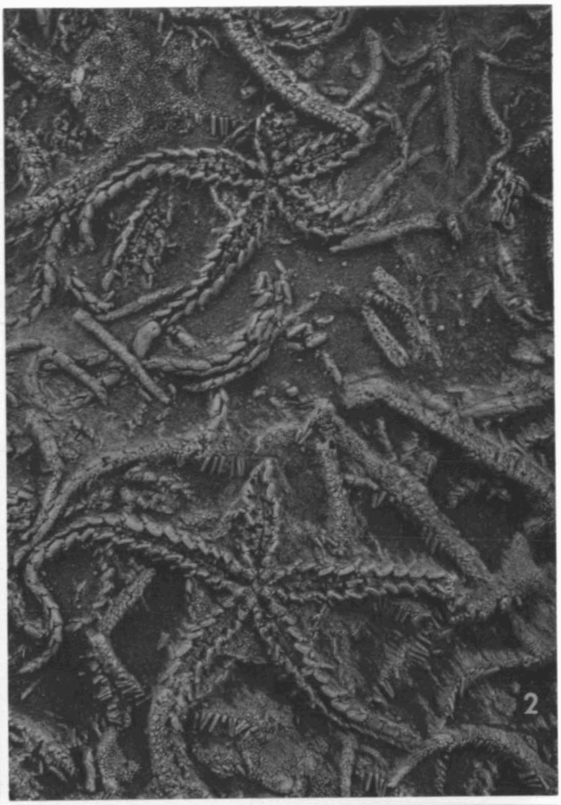
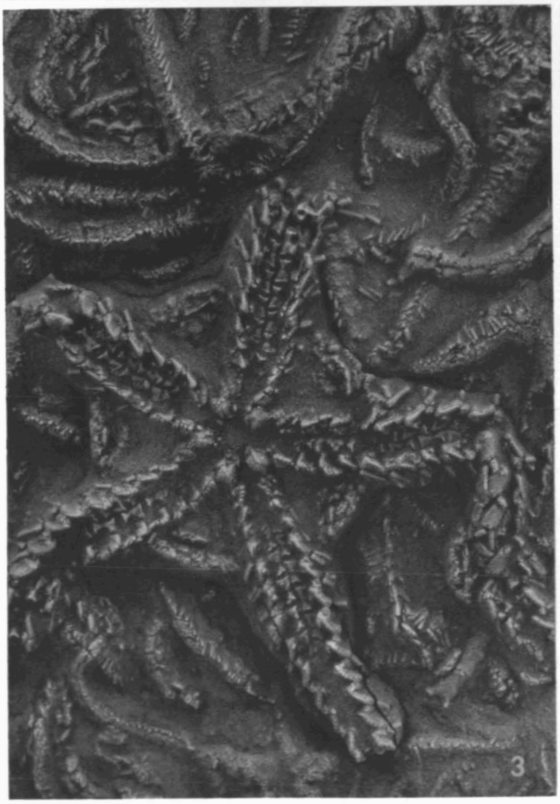
EXPLANATION OF PLATE 9

All figures × 5

Strataster ohioensis n. sp. *1,* paratypes L-25a (lower right), L-25f (upper left margin), and L-25h (lower left margin), all juveniles (probably yearlings) with oral sides exposed. Reduced view shown in plate 11 at the upper left corner of figure 1. *2,* paratypes L-25k (above) and L-25l (below), two juveniles (probably a yearling and a two-year-old), both with oral sides exposed. Distally in each arm the ambulacral groove narrows to a slit and the curved LL produce the characteristic terete shape of the arm tip. *3,* paratype UMMP 58332c, oral surface of an old adult (probably a four-year-old). Ambulacral "boots" are exceptionally large and long. Reduced view of this specimen in plate 13 at the left side of figure 2. *4,* paratype UMMP 58332a, oral surface of an adult (probably a three-year-old). Enlarged view shown in plate 7, figure 4; reduced view in plate 13 at the right side of figure 2.





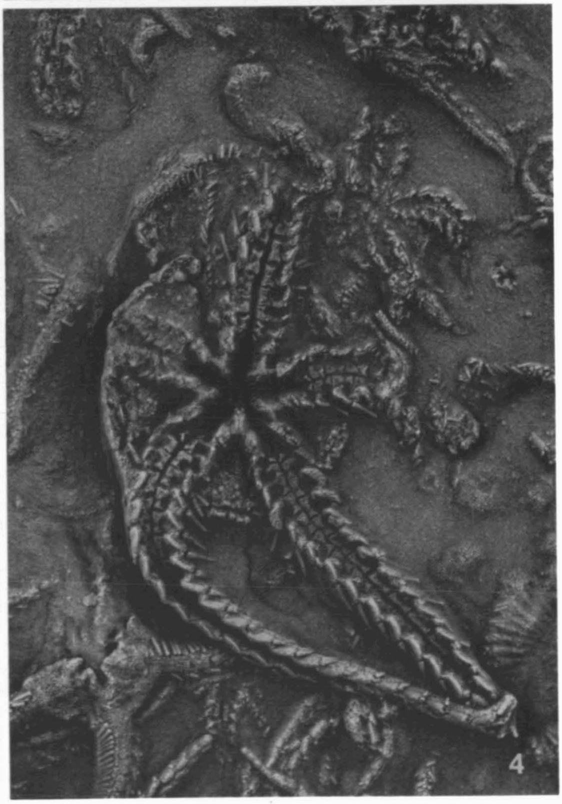
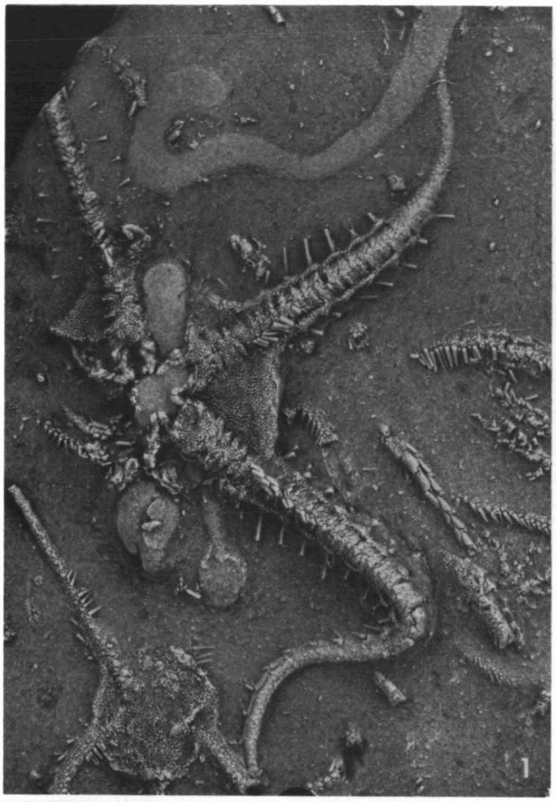


PLATE 9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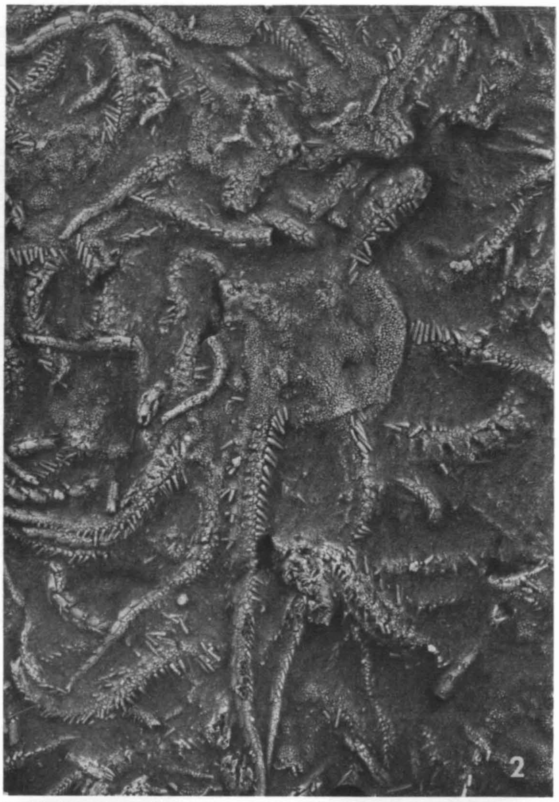
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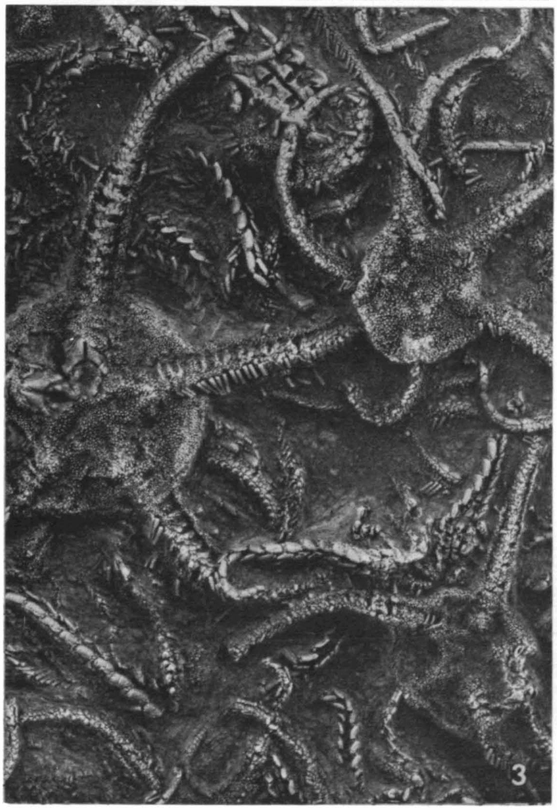
3


4

PLATE 10

together than the next cupules; each is bordered on its inner edge only by the end of the small barlike ridge of Amb_1 (pl. 4, fig. 1; pl. 7, fig. 4). Other cupules are enclosed on all sides, shared about equally by Ambb and LL. Each is bounded on the inner side by its Amb ridge, on the outer side by the edge of its L, and on the distal side by the front edge of the next L in the series.

LL are subcylindrical, curved around the sides of the arms. In the proximal region, the left and right series are separated both orally and aborally by a wide gap, which is filled by the Ambb; in the distal region, the two series fail to meet aborally, but can be turned in to cover the ambulacrum (pl. 1). Each L expands slightly toward the end of the arm but does not itself overlap the next L in the series. On the inner concave side of the L and lying parallel to its lower edge, a ridge extends from the proximal end of the plate about half way to the distal end. This ridge is the so-called "nose" of L, which articulates with the "toe" of the boot-shaped process of the Amb (pl. 4, fig. 1; pl. 7, fig. 3). It is one of the largest Amb-L articulations of any oegophiuridan brittle-star, in some plates extending more than half the length.

The distal end of L is directed obliquely outward from the arm and rather bluntly rounded. There it bears two large spines (pl. 1; pl. 3) in the position of the "vertical" spines of previous authors. It seems fitting to refer to them as distal spines because of their location on L. In specimens that have been weathered deeper than the level of the spines, the ends are almost invariably broken off; only in specimens that have weathered to the exact level of the spines can their full extent be observed (pl. 8, fig. 3; pl. 10, fig. 1). In these the maximum extent of the distal spines is at least the diameter of the arm at their point of attachment. In some individuals the spines are directed distally alongside the next L (pl. 1; pl. 7, figs. 1, 3), whereas in others they are erected at a steep angle to the arm (pl. 10, fig. 1). Each of the two stout spines is articulated with L in a U-shaped indentation, with one spine set immediately above the other and the two close-set spines occupying most of the distal border of the plate (pl. 3, at upper left).

Along the oral edges of LL are spines in the position called "groove" spines by previous writers because in some species they are set into a groove along the oral edge of the plate. In *Stratraster ohioensis* this term is particularly inappropriate, for the spines articulate with raised tubercles along the L edge. We call them oral spines because they are situated on the oral edges of LL. Where spines are missing, as in the majority of specimens that are well weathered, the tubercles are clearly displayed (pl. 7, fig. 1). The spines are perhaps the most fragile structures of the entire brittle-star, but some LL can be found which retain them (pl. 3). Where unaffected by weathering or breakage, the oral spines can be seen to be spoon-shaped, with a series of five or six on each L arranged in echelon with their concave faces directed orad. Each oral spine articulated by a large condyle, and we have no doubts about its being movable. In the living animal, the ambulacra were fringed with these closely spaced spoon-shaped oral spines, which lay just outside the tube feet and may have played a particular role in feeding.

Madreporite.—The M plate in this species is a small inconspicuous structure situated on the oral side of the disk in one of the axils. It lies close to the right side of an arm near the MAP-L_1 junction (pl. 3; pl. 4, fig. 1; pl. 6, fig. 2; pl. 7, fig. 4). It is an oval to round convex plate with a conspicuous median slot, strongly resembling the top of a round-head screw. Upturned lips of the plate border the slot on each side. In young specimens, the slot is clearly exposed, parellel to the axis of the arm which it borders (pl. 3; pl. 4, fig. 1); in an old specimen, however, one of the lips appears to be greatly extended, lapping over the slot (pl. 7, fig. 4). The internal structure of M

EXPLANATION OF PLATE 10

All figures × 5

Stratraster ohioensis n. sp. *1,* paratype UMMP 58334a, an adult (probably a three-year-old) with the aboral side exposed. Each of the very long distal spines on the LL extends to or beyond the base of the next spine in the series. The irregular light bands above and under the specimen may be worm castings; they are the only such structures encountered on any of the numerous slabs. *2,* paratype UMMP 58331b (center), aboral surface of a late juvenile (probably a two-year-old). Enlarged view of part of specimen can be seen in plate 7, figure 2. *3,* paratypes L-25m (left), L-25n (upper right), and L-25o (lower right), three specimens (probably a three-year-old adult and two late yearling juveniles) with aboral sides exposed. Reduced views of these shown in plate 11 near the center of figure 1. *4,* paratypes L-25b and L-25c (center and bottom), aboral sides of adult (probably a four-year-old) and juvenile (probably a yearling), and paratype L-25e (top), oral side of late juvenile (probably a two-year-old). Enlarged views in plate 2 and in plate 4, figure 1; reduced views in plate 11 at the lower right corner of figure 1.

TABLE 2—COMPARISON OF TWO ECOLOGICALLY DISTINCT LIVING SPECIES OF *Amphiura*. Based on data from Buchanan (1967)

Character	*A. filiformis*	*A. chiajei*
Depth	Shallow inshore	Deeper offshore
Substrate	Muddy sand	Silt and mud
Feeding	Suspension	Mud-surface collecting
Growth rate	Rapid, near maximum weight in 2 years	Slow, continuous growth over many years
Breeding	Once only (monotelic)	Several times (polytelic)
Age groups	Very distinct year groups	Indistinct boundaries
Longevity	3 years (rarely 4)	Perhaps 15 years
Recruitment	Consecutive annual	Sporadic, surviving as community for many years from one larval settling
Adult mortality	Very high	Low
Maximum population density (per m^2)	300 to 400	20
Community stability	Low, dependent upon annual larval settlement	High, dominating an area for many years without larval addition

is unknown in this species, as it has been in other Oegophiura. Very careful sectioning of an excellently preserved specimen would be necessary to reveal the inner straining device of the plate and, possibly, its connection with the stone canal.

Remarks.—The only structures to which we have not been able to give adequate attention in this species are the proximal and distal articulating faces of Ambb, the channel between opposing Ambb for the radial water vessel, and the internal structure of M. These can be studied only by disarticulating and sectioning good specimens.

Although we are without question guilty of using more illustrations than are necessary to substantiate the characteristics of the new genus and species, we wish to show the nature of the crowding of specimens and their relationships. This information can best be conveyed by photographs, and provides the background for our discussion of paleoecology.

Types.—Without destroying many other excellent specimens, it would be impossible to remove individuals for type designations. We have numbered the slabs, therefore, and assigned letters to designate particular specimens.

Type-bearing slabs deposited in the Museum of Paleontology have numbers UMPP 58329–58337. Those in the collection of Le Vasseur have numbers L-20, L-21, L-23, L-25, L-45, L-46, and L-79.

PALEOECOLOGY

The paleoecology of *Strataster ohioensis* must take into account the following factors, singly and in combination:

(1) the density of fossilized specimens, suggesting by their numbers that the living population was greatly crowded upon or in the uppermost layer of sediment or that sedimentation was extremely slow;

(2) the remarkable preservation of delicate structures, with no evidence of the breakage that would be expected with even brief transport or with any reworking of an original deposit;

(3) the persistence of the brittle-star community for the period of time necessary for the lens-shaped deposit to accumulate;

(4) the distribution of the specimens in size groups;

(5) the orientation of the specimens, about half buried with the oral side up and the others with the aboral side up;

(6) the sparsity of other invertebrates, none of which appear to have lived in the brittle-star community;

(7) the presence of carbonized plant frag-

EXPLANATION OF PLATE 11

Both figures × 2½

Strataster ohioensis n. sp. *1, 2,* two parts of L-25, a slab with many specimens exposed on its upper surface and many more embedded within it. *1,* part of slab bearing paratypes L-25a (upper left; see pl. 1), L-25b (lower right; see pl. 2), L-25c (lower right; see pl. 2), L-25e (lower right; see pl. 4, fig. 1), L-25f (left margin; see pl. 5, fig. 1), L-25h (upper left; see pl. 6, fig. 1), L-25m (right center, see pl. 10, fig. 3), L-25n (center; see pl. 10, fig. 3), and L-25o (upper right center; see pl. 10, fig. 3). *2,* part of slab bearing paratypes L-25d (lower right; see pl. 3) and L-25g (upper left; see pl. 5, fig. 2).

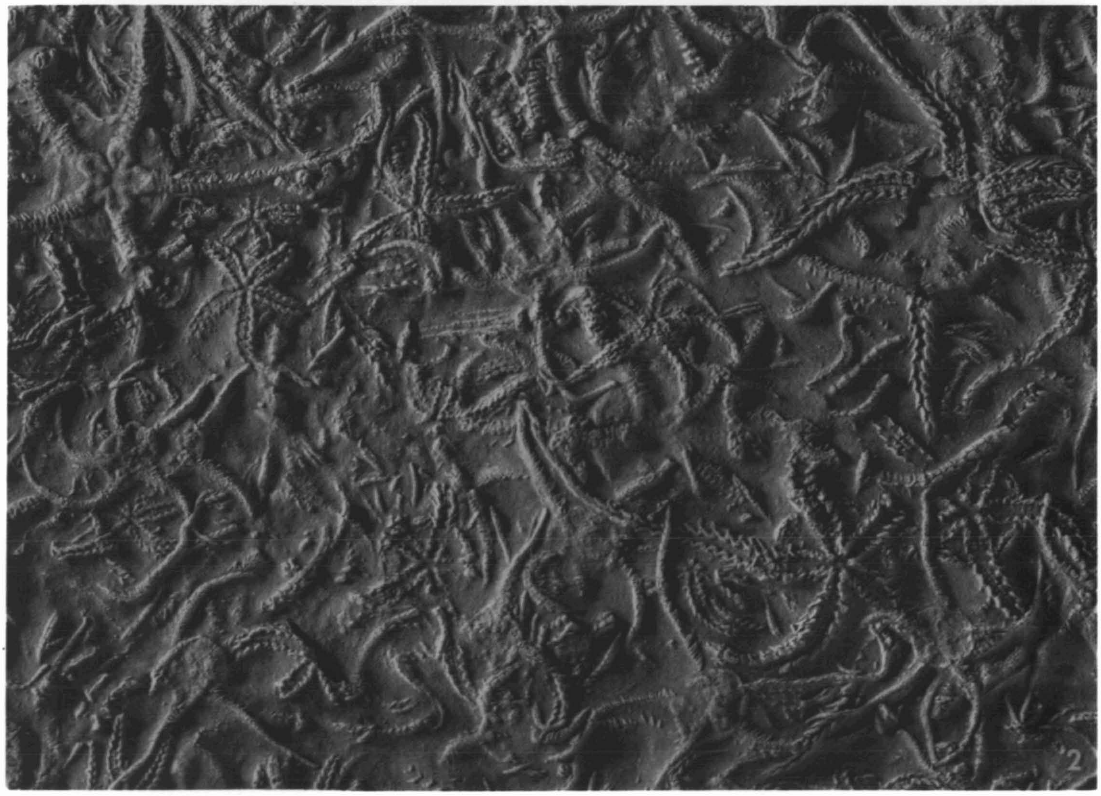

PLATE 11

PLATE 12

ments, mostly concentrated at the base of the lens but with a few particles occurring here and there among the brittle-stars; and

(8) the physical and chemical character of the matrix, which is heavily colored by hematite and composed of noncalcareous clay and silt particles.

Even though some aspects of ophiuroid biology and ecology have not been thoroughly investigated, enough is known of living species to provide comparison with the fossil brittle-stars described above. We have concerned ourselves with the problems of longevity, community structure, phototaxis, salinity, feeding habits, and a few other factors concerning *Strataster ohioensis.* Some questions still have no answers. It seems important to us to document the occurrence as thoroughly as possible, so that other workers can use the information to advance our knowledge of Paleozoic Ophiuroidea.

The occurrence has all the aspects of a long-continued densely populated community in which the specimens represent a natural mortality. As such, the population structure can be analyzed dynamically. From estimates of the original density of the standing population, the duration of the deposition can be postulated. In all the study, we have been astonished at the great similarity of this fossil community to some of the living communities that have been reported.

Longevity.—The longevity of living brittle-stars has not been thoroughly established, and observations are few. Some estimates have been set forth based on natural populations observed over a span of years and upon aquarium specimens.

Swan (1966) believed that *Ophiothrix fragilis,* the common brittle-star found off the British coast, lives at least 5 years. After a review of several records, Fell (1966, p. 130) stated,

> On the whole, then, we may not err on the conservative side if we infer that the average maximum age of an ophiuroid is around 15 years. In the case of a very small species, such as members of the genus *Ophiomisidium,* the life-span may be restricted to only 2 or 3 years, though here again we lack any direct observational basis for the inference.

By far the best references on longevity are those of Buchanan (1964, 1967), who studied *Amphiura filiformis* and *A. chiajei* from samplings of their natural communities off the British coast taken over a span of many years. These two species are contrasted in table 2. Buchanan found that *A. filiformis* shows three distinct year groups in the population and that breeding takes place only in the three-year-olds. Individuals rarely survive to their fourth year. Essentially, the majority of individuals mature in three years, breed, and die. To maintain the population level, the species must have annual recruitment. In contrast, Buchanan recorded, *Amphiura chiajei* has low mortality and lives for perhaps 15 years. For periods up to several years, there may be no recruitment and the individuals of the population simply grow older. One heavy settlement of larvae can form a stable bottom fauna for many years.

From the numerous specimens of *Strataster ohioensis* available, specimens were selected at random and measurements were made of only those which showed no skewing or excessive compression of the disk. Disk diameters of 100 specimens were measured to the nearest 0.4 mm and were found to fall into four distinct stages or groups (text-fig. 9). It is our interpretation that mortality in the community was greatest at some particular period of the year and that these stages represent year groups. The distribution is nearly like that of *Amphiura filiformis* reported by Buchanan. The two groups of juveniles, considered to be yearlings and two-year-olds, are not as sharply separated as are those of the adults. This may be the result of greater endurance of the young during the stress of the annual temperature drop, salinity decrease, or food shortage when the kill was greatest. In contrast to the adults of the living *Amphiura filiformis,* of which very few survive to a fourth year, about 40 percent of the adults of *Strataster ohioensis* lived to another year. We have no evidence on whether these four-year-olds were reproductive or sterile. From the population structure, discussed below, we suspect that they may have been able to reproduce in their final year.

Population structure and community stability.—The slabs containing *Strataster ohioensis* have a basal lamina about one to two millimeters thick of gray siltstone with plant frag-

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EXPLANATION OF PLATE 12

Both figures × 2½

Strataster ohioensis n. sp. *1, 2,* two parts of UMMP 58330, a slab with many specimens exposed on its upper surface and many more embedded within it. *1,* part of slab bearing paratypes 58330a (lower margin; see pl. 6, fig. 3) and 58330b (lower right; see pl. 6, fig. 4).

ments. Where this is chipped away, the lower surface of the red unit shows brittle-stars in apparently the same density and size distribution as the upper surface. As can be seen on the edges of the slabs, the fossils continue through the unit without interruption. The brittle-star community continued to flourish for a fairly long time. We see no indication that the individuals exposed on the upper surface met with catastrophic death. Their age distribution, therefore, may be regarded as a natural mortality sample rather than a census of the population at a moment of sudden extinction. Accordingly, the analysis of data is better made dynamically than time-specifically.

As indicated in table 3, in a population of 221 (yearlings and older) the annual deaths amounted to 100 (or 45%) and the annual recruitment necessary to maintain population density was the same. If larval settling was prevented for one year, the community balance would be greatly affected; if it were prevented for three or four consecutive years, the community would be extinct. The community maintained itself precariously; it persisted for a remarkable period of time against considerable odds.

TABLE 3—DYNAMIC ANALYSIS OF POPULATION OF *Stratdster ohioensis*.

Stage	Disk diam. average (mm)	Growth[1]	Dying during stage	Survivors at start of stage	Mortality rate[2]
I	3.05	37%	30	100	300
II	4.18	45%	34	70	486
III	6.08	24%	21	36	580
IV	7.55	....	15	15	1000

[1] Average growth to the following stage expressed as a percentage of disk diameter.

[2] Mortality rate per 1000 alive at the beginning of the stage.

The short lifetime, high adult mortality, and relative instability of the community postulated for *Stratdster ohioensis* are remarkably similar to those recorded by Buchanan (1964, 1967) for *Amphiura filiformis* and summarized here in table 2. They contrast strongly with Buchanan's findings for *Amphiura chiajei*, the deeper-water species (see table 2).

Population density and duration of the community.—The numbers and concentration of the dead can be calculated for *Stratdster ohioensis* from surface counts and measurements of the slabs, and, as just demonstrated, the proportion of the living brittle-stars to the annual die-off can be deduced; but the actual population density at any one time left no identifiable record to be counted, measured, or calculated. The dead of one generation are just like those of other generations. Obviously, the remarkable deposit could have been made by a populace of only a few starfish over millions of years, or it could be the product of a crowded community which lasted for a much shorter time.

In an area of 250 cm² on three representative slabs, the number of specimens was counted (table 4). The depth to which brittle-stars are exposed on the surface of the slabs is about 1.5 mm. On the average, the deposit exposes about 9000 specimens on each square meter of surface and contains about 6,000,000 specimens in each cubic meter of volume.

TABLE 4—DENSITY OF FOSSILS OF *Stratdster ohioensis* IN ROCK MATRIX.

Slab	Exposed specimens	Area of count (cm^2)	Specs. per cm^2	Specs. per m^2	Specs. per cm^3
L-23	57	71	0.8	8000	5.3
L-25	106	86	1.2	12000	8.2
L-79	64	93	0.7	7000	4.6
Total	227	250	0.9	9000	6.0

To estimate the original population density of *Stratdster ohioensis,* we compare it with some living species which form crowded communities. Buchanan (1964, 1967) reported that *Amphiura filiformis,* an inshore suspension-feeding species, reaches a maximum density of 300 to 400 individuals per square meter at a depth of approximately 30 meters. From submarine photographs, Vevers (1952) calculated the density of *Ophiothrix fragilis* at about 340 individuals per square meter at a depth of 48 meters. Inasmuch as *Amphiura filiformis* has disk diameters twice those of *Stratdster ohioensis,* the latter would reach comparable areal coverage with 4 × 400 or 1600 specimens per square meter. Similarly, since *Ophiothrix fragilis* has disk diameters about 5 times those found in *S. ohioensis,* the latter would attain comparable coverage of the bottom with 25 × 340 or 8500 spe-

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EXPLANATION OF PLATE 13

Both figures × 2½

Stratdster ohioensis n. sp. *1,* edge of UMMP 58329, a slab containing numerous specimens. Holotype 58329a is the large specimen on the left (see pl. 4, fig. 2; pl. 8, fig. 3). *2,* part of UMMP 58332, a slab bearing numerous specimens, including paratypes 58332a (right side; see pl. 7, fig. 4), 58332b (lower left corner; see pl. 8, fig. 4), and 58332c (upper left; see pl. 9, fig. 3).

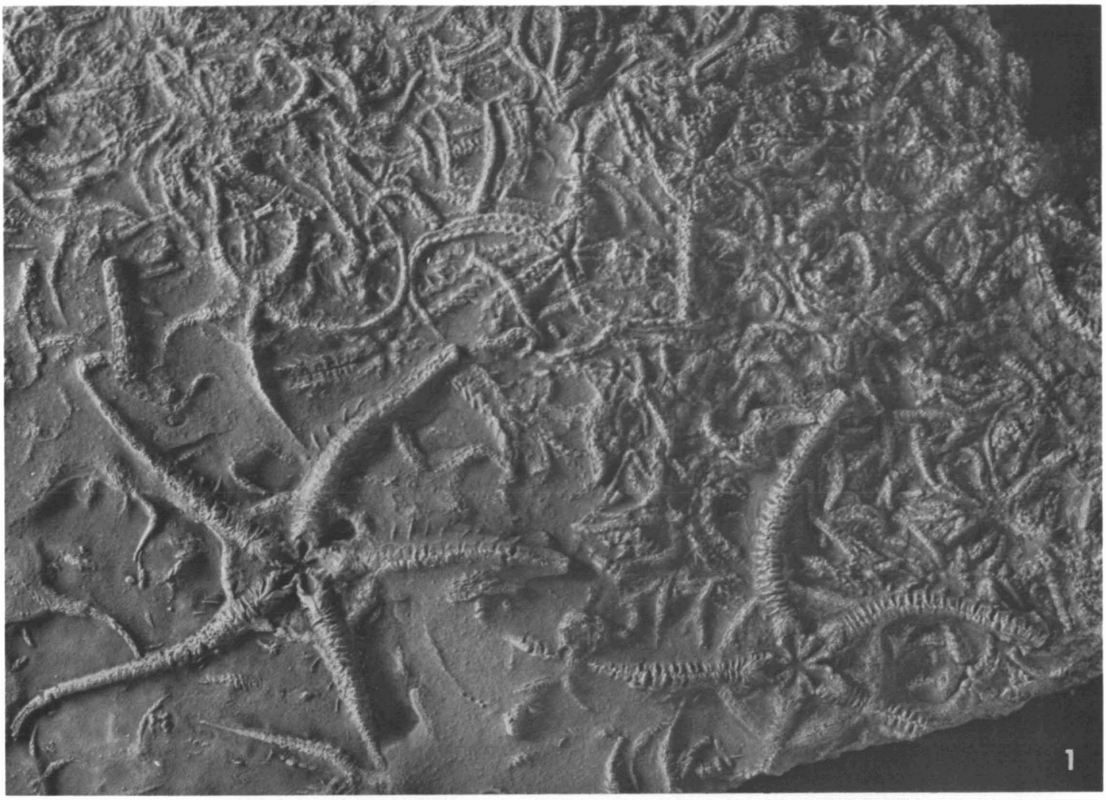

PLATE 13

cimens per square meter. We believe that a density of 4500 specimens per square meter is a reasonable estimate for the population of *Strataster ohioensis*. Hence, of the individuals exposed on the surfaces of the slabs (pls. 11–13), about half are thought to have been alive at one time.

The thin lens containing the fossil brittle-stars is about 1.5 cm thick at the center; it averages about 1 cm in thickness. Therefore, a slab 1 m^2 × 1 cm would contain 60,000 individuals. If the population had a density of 4500 individuals upon this square meter of the Mississippian sea bottom, and if the annual mortality was about 45 percent, then each year about 2025 specimens died. Because even delicate spines are still attached and the arms are entire, even to the fragile tips, we are convinced that the dead were not moved from the area which they had inhabited. With a contribution of 2025 dead per year, the accumulation of 60,000 individuals would require about 30 years. This seems to be a reasonable estimate for the time to deposit the lens as preserved. The original deposit may have been thicker, and its uppermost layer removed by erosion before the overlying stratum was laid down. In fact, the apparent natural mortality represented on the upper surface of the slab leads us to postulate that the final living population was swept away, perhaps along with some of the dead. The species did not return to this particular place, at least not in the interval recorded by several feet of strata overlying the brittle-star lens.

Absence of very young specimens.—No specimens were found with disk diameter smaller than 2.4 mm (text-fig. 9). We believe that some individuals must have died before the end of their first year. The absence of any very young specimens in the deposit may be due to one of two causes. First, currents may have swept away the very small individuals when they died or became too weak to maintain their hold on the bottom. Second, the very young may not have been able to establish themselves in the currents which crossed over the colony; they may have settled nearby, where currents were much weaker, and moved into the area of the main colony as soon as they were large enough to withstand the currents prevailing there. In either case, however, there is no reason to suspect that their absence in the material studied seriously altered the computed mortality rate; the population could have kept its saturation level by additional recruitment, whether it came from larval settling or immigration of young brittle-stars.

Sparsity of fauna.—As already pointed out, the basal lamina of the deposit is nearly gray, perhaps the result of reduction from the concentration of plant fragments. No brittle-stars were found in this thin lamina, but a piece of fenestellid Bryozoa was noted near the contact with the overlying red layer. On several hundred square centimeters examined of the upper surface of the deposit, the only fossils other than brittle-stars are a short section of narrow crinoid stem and a fragment of crinoid arm. No remains are found in sufficient quantities to have served as a food source for the dense colony of *Strataster ohioensis*. If they fed on plankton, no trace of it remains.

The elimination of competitors for the apparently bountiful food supply over a period of years is probably attributable to the feeding efficiency of the brittle-stars. Larval forms of potential competitors appear to have been eaten before they could settle. Any chance larger forms may have been starved out by the more efficient brittle-stars. Such competitive success is attributed to living brittle-stars by D'yakanov, who wrote (1954, p. 17; p. 8 of translation):

> The economic importance of these marine animals is slight . . . But where they abound, their influence on the entire "economy" of the sea floor is evident. Swarming throughout the upper layers of the bottom, they may consume huge quantities of small animals or dig up from the ocean floor all the available food, thus affecting the vital activity of other organisms.

It seems to us remarkable that no predators or scavengers invaded the *Strataster ohioensis* community. With a mass of dead in the sediment and a thick live population upon the surface, the brittle-stars might be expected to attract a host of other marine animals. Fontaine (1964) discovered that the living *Ophiocomina nigra* secretes an acidic mucous with the tube feet as a defense. Similarly, *Strataster ohioensis* may have secreted some kind of repellent with its tube feet, and thus protected its territory against predatory invaders.

Feeding.—Because their stomachs end blindly, ophiuroids must be selective in feeding; because their tube feet lack suckers, they cannot pull open bivalves like the asteriods; and because their arm movements are restricted by vertebral articulations, they have certain limitations in capture of prey.

By and large, brittle-stars are opportunistic omnivores. In the matter of diet, only a few are active predators; some eat detritus directly from sediment; many intercept plankton or detritus from currents or, in quiet water, from the downward "rain" of particles; and others eat carrion or plant material directly. Feeding positions include burrowing with only arm ends exposed, lying with the oral side uppermost, and lying with the oral side down. To these variables in feeding habit are added those of the gathering method. As summarized by Reese (1966, p. 192), macrophagous feeding includes (1) arm-loop capture of large food items, (2) tube-foot capture of smaller particles involving mucous secretion, and (3) direct browsing on plants and carrion. Microphagous feeding methods involve (1) waving arms in the water, (2) raising arms to intercept particles, commonly with a mucous net, (3) sweeping of the surrounding bottom, and (4) cleaning of the surface film in shallow water.

From the various combinations of diet, positions, and gathering methods, numerous feeding patterns have developed in brittle-stars. Many species use more than one, selecting the most advantageous to suit the immediate circumstances. As described by Fell (1966) and by Reese (1966), the following patterns have been observed in living species:

(1) *Astrohamma tuberculatum, Gorgonocephalus caput-medusae,* and *Asteronyx loveni* are carnivorous predators on corals, equipped with prehensile arms for climbing onto the prey;

(2) *Ophiocomina nigra* is remarkably omnivorous, readily climbing laminarian sea plants to browse on the leaves, scavenging on carrion, and capturing live prey in its coiled arms; it prefers stony bottom conditions and strong currents;

(3) *Ophiocoma bollonsi* rests on a hard bottom in rather strong currents, stretching the arms upward to intercept food in secretions of the tube feet;

(4) *Ophiothrix fragilis,* which lives in dense communities, is a very efficient filter-feeder, catching small worms and other little bottom forms in the mucous secretion of the tube feet and passing them to the mouth; it relies mainly on a steady flow of suspended matter;

(5) *Ophiura* species feed on detritus and small worms, crustaceans, and molluscs by bringing the mouth over the food or by wrapping an arm around it and transferring it to the mouth;

(6) *Astrotoma agassizii* lies on the sea floor with its mouth upward, sweeping the surrounding area with its arms for the fall of small nekton and plankton;

(7) *Asteronyx loveni* clings to pennatulid corals with 2 or 3 arms, catching small pelagic animals with the free-waving arms; there is also evidence that it feeds upon the coral polyps from time to time;

(8) *Amphiura chiajei,* like other members of the family Amphiuridae, lies buried in sand or mud with only the ends of arms protruding; it extends the arms tips horizontally to feed upon surface detritus;

(9) *Amphiura filiformis* also lies buried, but it holds its arm ends erect into the current to intercept detritus in transport;

(10) *Ophioglypha texturata* feeds almost exclusively on bottom detritus, in dense populations, in contrast with the carnivorous species of the genus which are less localized;

(11) *Ophionereis reticulata* grazes only on algae; and

(12) *Ophiocoma scolopendrina* adapts its feeding habits to suit prevailing conditions in shallow water. Threads of mucous are used to entangle selected material, and the whole is moved to the mouth along the ciliated ambulacral grooves. When water is quiet, the species collects food from the substrate, tasting with the podia; when water is flowing rapidly, two arms remain anchored in a crevice for quick retreat while the other three extend their podia as filtering combs; and at flood tide, the arms are twisted upward to move back and forth under the water surface to graze upon sun-dried particles floating there.

Vevers (1952, 1956) was convinced that the high density and large areas covered by populations of *Ophiothrix fragilis* are made possible by suspension feeding in a tidal current. Moore (1962) reached essentially the same conclusion for another ophiuroid, *Ophiophragmus wurdemani.* Reese (1966, p. 179, 180) stated the case as follows:

> Although some aggregations are related to reproduction, most appear to be related to feeding. If this is so one would expect grazing, detrital-suspension feeding, and deposit-feeding species to reach the highest populations densities. This is particularly true of the suspension feeders because they are not dependent upon the substratum as a limitation, since the suspended food may be brought to them by currents.

Fell (1966, p. 139) agreed, saying, "Ophiuroids which live in large dense populations on the sea floor evidently rely upon the steady flow of suspended material in bottom currents . . ."

The overall picture of ophiuroid feeding is one of opportunism, with some species better adapted than others for particular foods. It seems clear that particular feeding patterns are not limited to taxonomic groups nor to morphologic types. However, feeding patterns do appear to be directly related to bottom conditions, to intensity of currents, and to density of populations. Hard substrate precludes all burrowing forms, which feed with the exposed distal parts of the arms; strong currents favor those brittle-stars that elevate their arms and intercept food particles with mucous secretions; and densely populated communities depend on a steady supply of detritus or small animals.

In the case of *Strataster ohioensis,* we find no remains of large animals associated with the brittle-star community in sufficient numbers to indicate that they were a major source of food. Hence, the species was not predatory on corals and it did not subsist upon carrion, at least not carrion from any animals with hard parts. The matrix and the burial attitude of the brittle-stars give no suggestion of the burrowing habit; indeed, the fossils are so closely packed in the stratum that any burrowing down from the surface would have necessarily destroyed many of the dead specimens buried below. Plant fragments found with the brittle-stars are all broken with angular edges; none show any signs of having been partly eaten away. It seems likely, therefore, that the herbaceous elements brought in with the sediment were ignored as possible food.

We infer that *Strataster ohioensis* maintained its dense population by feeding upon plentiful small animals or detritus, which were transported by currents. We infer also that this species was an extremely efficient filter-feeder, probably employing mucous secretions of the tube feet to entrap particles. The deep aboral clefts between the Ambb undoubtedly housed large dorsal muscles to facilitate elevation of the arms; it would be possible for *Strataster ohioensis* to hold nearly the full length of the arms vertical while feeding, holding onto the substrate with the proximal tube feet. The conditions of food supply persisted at the site for as long as the community lasted.

Again, as in the case of population structure, this Mississippian brittle-star shows strong ecological resemblance to the living *Amphiura filiformis* (table 2), except for the burrowing reported for the genus by Reese (1966) and others; actually, as shown in an underwater photograph (Woodley, 1967, fig. 1), the arms of *A. filiformis* project upward for most of their length in feeding, and the disk is not buried very deep in the sediment.

Phototaxis.—Living ophiuroids always exhibit negative phototaxis under strong illumination (Fell, 1966). For those living in oceanic depths, no such problem exists, and they have been photographed at various times congregating openly on the floor. Shallow-water species, however, avoid light. Those dwelling on hard substrate hide under stones, shells, or any other available cover during the daylight hours, emerging to feed in darkness of night. Some make their daytime home in rock crevices. On a soft substrate, some forms, like *Ophiura texturata,* bury themselves, leaving star-shaped depressions in the sand to mark their positions; others, such as *Ophiosparte gigas,* are inferred to paddle and flounder over the soft bottom or through the semi-liquid uppermost layers of the substrata, using the tube feet and spatulate spines of the arms as oars (Fell, 1966). Several forms burrow into mud or soft sand to such depth that only the tips of the arms protrude (Mortensen, 1927).

We presume that the brittle-stars of the past may have developed a similar aversion for strong light. If *Strataster ohioensis* was a shallow-water creature and cryptozoic during the day, it must have hidden somewhere. Because the plant material associated with the deposit is fractured and well broken up, much of it nearly macerated, we are led to conclude that it grew elsewhere, presumably on land, and was brought in by currents. No stones or shells were present to provide shade. The only protection capable of housing such numbers of specimens seems to have been the substrate itself. Composed of noncalcareous clay and silt particles, the substrate may have been soft enough for the living brittle-stars to cover themselves with a thin veneer of sediment during the daylight hours, emerging during the night to feed. In fact, the crest of closely spaced spines along the top of the proximal arm sections and extending onto the edge of the disk may have been used for such operations, pulling the surface silt over the brittle-star's body and arms during wriggling movements.

Salinity.—Like other echinoderms, brittle-stars cannot tolerate fresh water. The exchange through the permeable integument invariably leads to fresh-water bloat and death. Some brittle-stars, however, live in brackish water. D'yakonov (1954) reported ophiuroids in the Black Sea, where low salinity precludes asteroids. Brattström (1941) discovered that *Ophiura albida* can live in the Danish waters where salinity is as low as 10 parts per thousand, and Thomas (1961) that *Ophiophragmus filograneus* tolerates the water off the Florida coast where dilution by the discharge from the fresh-water Everglades lowers the salinity to only 7.7 parts per thousand. Fell (1966, p. 139) regards the latter as "a unique low for any enchinoderms."

We conclude that *Strataster ohioensis* was also a marine animal, although it could possibly have lived where estuarine currents lowered the salinity well below normal marine levels.

Depth and currents.—No morphological characters distinguish the shallow-water brittle-stars from the deep-sea forms. For our fossil species we must rely upon indirect evidence.

Three factors indicate that currents were present. First, the thickly populated brittle-star community persisted for many years at the same locality without leaving any fossilized remains of its food supply. Second, about half of the specimens were overturned before burial. And third, the youngest segment of the brittle-star population seems to have been effectively precluded.

Probably, the community was passed over by tidal currents. A reversal of flow is indicated by the admixture of fragments of marine crinoids and land plants. In addition, the persistence of the community of brittle-stars depended upon consecutive annual recruitment; if the current traveled always in one direction, the larvae would be swept out of the area. In our interpretation, the tidal fluctuations replenished the food supply daily and, in the breeding season, washed the larvae back and forth in the vicinity.

Of the plant fragments, Professor Arnold could only tell us that the alignment of cells seemed to indicate bits of fern; the material was definitely not marine algae. If these are indeed fragments of land plants, the locality was probably not far offshore.

Sediment.—The matrix around the specimens is dark red silty shale. Very little calcium carbonate is present, and the only reaction with hydrochloric acid seems to take place along the edges of the slabs, suggesting that the carbonate was deposited along seams after lithification of the bed. Small pieces of the rock dissolve very slowly in concentrated hydrofluoric acid, presumably because the permeability is decreased by a large fraction of clay-size particles. Under a binocular microscope, numerous little flecks of mica can be seen.

The red color seems to be entirely a primary feature of the sediment, and we suppose that the nearby source of the sediment was an exposure of older red beds. Only in the lowermost lamina, where plant fragments are concentrated, has reduction been sufficient to alter the red color.

The concentration of brittle-stars in the sediment, building up a total thickness of only 1.5 cm in a period of perhaps 30 years, is strong evidence that most of the silt and clay particles passed over the area of the colony. Plausibly, the brittle-stars themselves were responsible for the deposition and retention of the sediment, intercepting it while feeding and holding some of it in place by the resistance to the current created by their mass.

Conclusion.—This, then, is our reconstruction of conditions prevailing during the life and times of *Strataster ohioensis*.

At first the locality was not far offshore, perhaps less than a mile, and traversed by tidal currents. Red beds were exposed on the shore, and their weathering and erosion produced the supply of sediment. With each outgoing tide, some sediment was discharged to sea through an estuary. Although the tides surged strongly in and out of the estuary, farther out to sea they became weaker and scoured only a very shallow trough. The current carried most of its load of sediment and debris beyond the locality.

When the water became slightly deeper, perhaps 30 meters at the locality, the shoreline receded inland to lie more than a mile away. Plant fragments, probably first concentrated in a marginal swamp and there partly decomposed, were swept to sea along with sediment by the ebb tide. Tidal currents were no longer able to erode at the offshore locality. Now some sediment and debris settled out and started to fill the shallow trough. Deposition replaced erosion, although much of the finer fraction of sediment continued to be swept to deeper water beyond. With weak tidal currents fetching sediment and debris from the land at ebb tide and bringing marine plankton at flood tide, moving the mixture back and forth over the locality, the stage was set for the brittle-star invasion.

The first *Strataster ohioensis* at the locality may have been some adults walking along the bottom and attracted by the organically charged currents. Or they may have been larvae that settled from the incoming tidal current and prospered. We can be certain that the brittle-stars were the pioneer settlers, probably establishing the nucleus of their colony just after the reduction of current intensity, for no competitors left a record in the deposit.

These brittle-stars were filter-feeders. During the tidal peaks, they flexed their dorsal arm muscles, elevated their arms, and secreted mucous from their extended tube feet. Entrapped particles were moved to the mouth by the tube feet and cilia. Within the limits of the tidal currents, the colony thrived and expanded. The food supply, plentiful enough to support a dense population of around 4500 individuals to the square meter, did not diminish, except perhaps for very brief intervals, for many years.

Although ebb tide and flood tide brought on a frenzy of feeding activity, at other times the colony was quiet and inconspicuous. With just a few wriggles of the horizontal arms, provided with crests of spines, each brittle-star could rake through the top sediment and embed itself to avoid the light of day. Space in the matrix was limited. Much of the sediment passed over the locality, and most of the relatively small quantity retained was probably first intercepted in mucous nets by the feeding individuals. Once a layer of particles was established, perhaps still held together by mucous, it tended to remain.

Territory at the locality was completely dominated by *Strataster ohioensis*. Any larvae of potential competitors were promptly eaten. Adult competitors were soon starved out by the more efficient brittle-stars. Predators were kept from the community, probably repelled by the taste of the acidic mucous which brittle-stars secrete when alarmed.

Each year a crop of larvae was produced at the breeding period. Carried back and forth by tidal fluctuations, they settled down in the vicinity and provided the recruitment necessary to maintain the population at near-saturation level. For two years each crop of larvae grew as juveniles. In the third year they matured and reproduced, after which many of them died. Those that lived to a fourth and final year may still have been reproductive. Hence, at any one time, the population was divided into four age groups, each from the larvae of a different year.

At some season of the year, mortality reached a peak. Probably, it was winter, when cooling of the water placed a direct physiological strain on the brittle-stars and at the same time sharply curtailed the plankton available for food. At any rate, most deaths occurred at one particular season. The result was the distribution of the dead into year stages or groups. On the average, about half the community died off each year and was replaced by young recruits.

It is surprising that the community lasted for as long as the postulated 30 years. Its existence was precarious. For continuity it depended upon annual recruitment. Always it was subject to possible shifting of the tidal currents, storm swells, and other natural catastrophes that would disturb its delicate ecological balance. At the end, some such catastrophe did wipe out the community. Increased currents swept the living population and probably some of the dead out of the locality, presumably into deeper water. Whether any survived we do not know, but we have no record of their return to this particular place.

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