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VOLUME 22

SILICASTER, A NEW GENUS OF DEVONIAN STARFISH

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ABSTRACT—*Silicaster esseri* n. gen. and sp., known only from the holotype, is assigned to the Calliasterellidae. It is characterized by rather small disk and long arms. The disk is composed of various kinds of plates, some strongly stellate with long prongs and others blocky, all rather loosely associated in a central papular area; sides of disk are provided with large buttressing axillaries. Arms are composed of rows of radials, inferomarginals, and adambulacrals, with extensive adradial papular areas studded with irregular small accessory plates. Except in the distal ends of the arms, where all plates are subquadrate and closely spaced, the radials are sharply quadristellate, the inferomarginals paddle-shaped (with long adradial riblike extensions), and the adambulacrals provided with robust, longitudinally ridged spines on their oral surfaces. *Silicaster* differs from *Calliasterella* in having large papular areas and more sharply stellate major plates in disk and proximal regions of arms; it differs from *Urasterella* in lacking regular rows of aboral plates between radials and inferomarginals.

INTRODUCTION

MOST PALEOZOIC STARFISH are incomplete, lacking certain details of outer plates of the arms, ambulacrals, disk, or mouth region. The new starfish described here is no exception. The oral sides of disk and arms are known only from a few poorly exposed adambulacral ridges, and many of the disk plates are disarranged. On the other hand, the aboral plates of the arms and some of the distal disk plates are well preserved, retaining their natural association, and the spines of adambulacrals and radials still show their ribbed ornamentation.

The holotype and only specimen was discovered by Joe Esser in the Middle Devonian Silica Shale exposed and dumped in operations of the Medusa Portland Cement Company in their North Quarry, Lucas County, Ohio. Associated fossils reveal that the specimen came from unit 18 (Ehlers, Stumm, & Kesling, 1951) in a small coral bioherm. Four pieces of the starfish were found and presented to the Museum of Paleontology. To my surprise, all pieces fitted together. The remains of the starfish have been replaced as a single unit of pyrite, obscuring all traces of plate boundaries and junctions within the arms and disk. Nevertheless, enough of the morphology can be discerned to place the starfish taxonomically and to determine that it is a new genus.

I take pleasure in naming the starfish in honor of Mr. Esser. I also express my gratitude to Mrs. Gladys Newton for typing, to Mr. Karoly Kutasi for photography, and to Professor C. A. Arnold and Professor E. C. Stumm for their review and editorial work on the manuscript.

ABBREVIATIONS

The following abbreviations are used in the description and text-figures of *Silicaster esseri* n. sp.:

Adm(m)—adambulacral(s).

an—anus.

apa—adradial papular area, radial accessory plates.

Ax(x)—axillary (axillaries), first inferomarginal(s).

C—centrale, centrodorsal plate of disk.

cpa—central papular area, disk accessory plates.

cR—centroradial.

Im(m)—inferomarginal(s).

Im_2, Im_3, etc.—second inferomarginal, third inferomarginal, etc.

M—madreporite.

R(R)—radial(s) or carinal(s).

R_1—primary radial.

R_2, R_3, etc.—second radial, third radial, etc.

Sm(m)—superomarginal(s) or supramarginal(s).

Sm_1—primary superomarginal, primary interradial, or first supramarginal.

Sm_2, Sm_3, etc.—second superomarginal, third superomarginal, etc.

TERMINOLOGY

Terminology of starfish plates is far from standardized, despite the recent treatment of the subclass by Spencer & Wright (1966) in the *Treatise on Invertebrate Paleontology.* Certain plates are particularly difficult to identify because their expression and morphology varies from genus to genus. It is necessary to explain the terms used so that the new genus can be properly compared with other genera.

In each axil, the disk of *Silicaster* is buttressed at the side by a thick large plate. These five plates seem to be homologous to those in similar positions in *Calliasterella* and *Urasterella.* In *Calliasterella* each of these plates was called "Platte No. 7" or "Oralplatte" by Schöndorf (1909), "interradial disk plate" by Schuchert (1915), "odontophor" by Spencer (1918), and "axillary, or odontophore" by Kesling & Strimple (1966). In *Urasterella* it was termed "odontophor" by Spencer (1918). The suborder Uractinina, which includes both *Calliasterella* and *Urasterella* in the *Treatise,* was said by Spencer & Wright (1966, p. 71) to have "odontophore high and wedge-shaped." In genera of the Uractinina and in *Silicaster,* this plate is aboral. Yet in their discussion of morphology, Spencer & Wright (1966, p. 14) use "odontophore" for a plate set orally in the interradius and associated with the mouth frame; they stated, "Presumably this ossicle originally was an inframarginal which in the course of phylogeny became occluded from the margin and adapted as part of the 'jaw' system." These authors then defined odontophore (1966, p. 29) as the "single axillary on distal edge of mouth-angle plates in asteroids." In starfish of the order Valvatida, such as the well-known *Devonaster,* this definition is fitting and precise. But in the starfish of the order Forcipulatida, which has an ambulacral type of mouth frame, the plate called the odontophore has no evident connection with the mouth frame; it is situated aborally and serves to strengthen the sides of the disk. Nevertheless, in both Valvatida and Forcipulatida the plate lies in an interradial position just outside the converging rows of adambulacral plates; although changed in disk location, in form, and in function during the course of its history, the plate seems to have originated as an inframarginal in the remote ancestor. I term it the *axillary* (Ax) in *Silicaster.*

Aligned with the axillary and extending along the sides of the arms are rows of large imbricating plates set just above the marginal rows of adambulacrals. Each of these aboral plates in the proximal region of the arms is paddle-shaped, with a broadly expanded ovate base and a riblike adradial shaft. The shaft shows no connection or articulation with the radials, and the alignment of the plate with Ax at the axil indicates that it is an *inferomarginal* (Im), homologous with inferomarginal plates in *Protarthraster* and *Urasterella.* The median side-arm plates in *Calliasterella,* however, fit closely with the radials; whether they should be regarded as inferomarginals with exceptional adradial development (as by Spencer, 1918, and by Spencer & Wright, 1966) or as superomarginals with admarginal expansions (as by Kesling & Strimple, 1966) is not readily decided. If *Calliasterella* really belongs in the same family as *Protarthraster* and in the same suborder as *Urasterella,* as assigned in the *Treatise,* then the plates must be interpreted as inferomarginals which extended so far adradially that they established contact with the radials.

On certain matters of terminology I depart from the *Treatise.* One concerns the plates associated with the madreporite. *Silicaster* has a structure which I believe is the *madreporite* (M), closely surrounded and supported by three plates. The location on the disk and the arrangement of plates seems to me to be identical in *Silicaster, Calliasterella,* and *Protopalaeaster.* Spencer (1918, p. 166) proposed that the major interradial plate of the disk in *Calliasterella* originated by fusion of "adradialia" plates; this is the plate immediately proximal to M. Spencer & Wright (1966, fig. 64, *5*) term the plate in *Protarthraster* the "interradial." The plates at the sides of M in *Calliasterella* were called "paired inframarginals" by Schuchert (1918, p. 191) and "infero-marginalia" by Spencer (1918, p. 163). Kesling (1962, p. 936, text-figs. 1–2) called the plates around M in *Protopalaeaster* "Sm_1" and two "Sm_2's," and Kesling & Strimple (1966, p. 1160, text-fig. 1c) applied the same terms to the plates in *Calliasterella.* In all starfish, growth and addition of plates proceeds distally from the primary circlet of the disk. I find it difficult, therefore, to believe that the Imm extended up and over the Ax toward the center of the disk, for such an arrangement would involve the disruption of the primary circlet and distal migration or disappearance of the interradial elements. In starfish of the suborder Pustulosina (order Valvatida), in which Imm are prominently developed, the plates never extend around and beyond Ax; instead, even if Ax migrates from the margin far into the oral surface, the rows of Imm always extend distally from it. It is logical to assume that the Imm in the order Forcipulatida similarly extend only distally from Ax. As for the plates around M, those in *Protopalaeaster* are unquestionably aligned with the Smm of the arms and can be classified as Smm plates of the disk; those in *Calliasterella* and *Silicaster* have the same position, arrangement, and function as in *Protopalaeaster*. It seems unnecessarily complicated to suppose that the original plates around M disappeared and their place was taken by other plates having the identical form and placement in the disk. Instead, the plates seem to be homologous in all respects, and even though in *Silicaster* they are not succeeded on the arms by Smm plates, the three can be designated as the *primary superomarginal* (Sm_1) and two *second superomarginals* (Smm_2).

To emphasize the distinction between disk and arms, Spencer & Wright (1966) call the major radial plate of the disk the "primary radial" and the radially placed plates of the arms the "carinals." Nevertheless, in such well-known starfish as *Devonaster* the radial series of plates continues from arm onto disk without change in form, so that the division between arm and disk is difficult to place. A more logical analysis would extend the terminology of plates across the arbitrary disk-arm boundary as far as they can be traced. The median aboral quadristellate arm plates in *Silicaster* are called *radials* (RR), and the disk plates with which they are aligned are also called RR as far proximally as the major plate of the corona.

SPECIMEN

The assembled fragments of the holotype and only specimen measure about 59 mm long, 44 mm wide, and 6 mm thick. They include identifiable sections of four arms and part of the disk. One side of the strongly compressed specimen (text-fig. 1a) which can be called the obverse, shows a long section of one arm (at left) with an axillary (Ax) on each side marking its junction with the disk. This can be referred to as arm II. The madreporite (M) is in the adjacent interradius. The stellate plates of the disk lie in considerable disarray, and identification of central disk plates must be regarded as tentative. Another arm on this side of the specimen (text-fig. 1a, top) can be called arm I. It is laterally compressed and crushed, with radial (R), inferomarginal (Im), and edges of adambulacral (Adm) plates exposed on the obverse side. The remainder of this side of the specimen (text-fig. 1a, lower right) is a jumble of various kinds of plates, probably all from one arm (arm IV) but possibly containing also some plates of arm III.

On the reverse side (text-fig. 1b), the terminal section of another arm (arm V), aboral side out, is flattened and pressed against the oral surface of the long arm (arm II) on the obverse. A continuation of this arm covers over the oral side of the disk. At the proximal end of the preserved part of this arm (text-fig. 1b, left), the large size of R plates as compared with those in the proximal part of arm II (text-fig. 1a, left) indicates that arm V must be nearly complete and that only a small part of the disk is missing at the right, the part to which the missing arm (arm III) was attached. From the sides of arm V, spines of its Admm are spread out but do not completely obscure what appear to be the spine-bearing transverse oral ridges of some Admm of arm II. The reverse side also shows the rest of the aboral surface of the laterally compressed arm I (text-fig. 1b, bottom), consisting of a row of Imm and a row of the lateral edges and oral spines of Admm. In arm IV (text-fig. 1b, upper right), Admm plates and spines converge with those of arm V and the outer edge of the specimen in this region consists of a row of Imm and intervening adradial papular areas; no part of arm IV shows any certain RR. Plates bearing each a row of short double ridges can be seen near the junction of arms IV and V; these may be the oral ridges of Admm in arm IV, or they could possibly be dislocated Admm of arm III.

The specimen is sufficiently complete to permit an estimate of the original size. The radii appear to have been about 60 mm radially and 20 mm interradially. The lateral spread of each arm is difficult to determine. From the flattening of arms and from the folding over of arm V onto the oral side of disk and arm II, it would seem that Admm actually formed the margins of the arms, extending out beyond the border of Imm.

All of the specimen is pyritized. Part of the matrix in the disk region is calcareous, but plates and at least part of the integument are solid pyrite. The pyritization brought about some advantages and some disadvantages in fossilization. The spines are particularly well preserved, not only the long spines of the Admm but also the short spines that were probably attached to the middle of the RR. The replacement has faithfully reproduced the longitudinal ridges of the spines; it has also made a finely verrucose texture on the major plates which may be a reproduction of their original surface.

Two disadvantages concern plate boundaries. First, the complete outlines of major plates cannot be determined because the pyrite also replaced the integument in which parts of the plates were still embedded at time of burial. Second, the replacement of arms was total, so that the outlines of the ambulacral plates are not revealed at the ends of broken arms. Similarly, the pyrite replaced the adpressed arms II and V as one unit, leaving no clear-cut separation between them. In calcareous replacement, it would be possible to determine the extent of ambulacrals by grinding down the end of one of the incomplete arms; because of the pyritization in the only specimen found, this information is denied.

SYSTEMATIC DESCRIPTION

Subphylum ASTEROZOA

Class Stelleroidea

Subclass Asteroidea

Order Forcipulatida Perrier

Suborder Uractinina Spencer & Wright

The suprageneric classification of the *Treatise* is followed here, even though some taxa are based on very limited knowledge of morphology and few specimens.

By its high, strong Axx and median row of stout spines on Admm, the new genus can be assigned to the Uractinina. Nothing can be said with certainty about "paxillae set on shafts in diagonal rows" (Spencer & Wright, 1966, p. 71) on aboral ossicles of the arms. On the other hand, these cannot be discerned in specimens of *Calliasterella americana* either. The mouth frame of the new starfish is hidden so that it is not possible to classify it as ambulacral or adambulacral. The exceptional development of the Admm, however, seems to indicate that the organization of oral ossicles is like that in *Urasterella* or *Calliasterella,* in which an ambulacral type of mouth frame has been demonstrated.

Family Calliasterellidae Schöndorf

The new starfish has some characteristics in common with both the Urasterellidae and the Calliasterellidae: arms are well produced from the disk, the plates of the arms occur in series of equal numbers (one each per skeletal segment), and Admm have well developed transverse ridges bearing long spines. However, genera of the Urasterellidae have very closely spaced skeletal segments in the arms, and many have regular rows of plates between RR and Imm on the aboral sides of the arms. Schuchert (1915, p. 173) described his Urasterellidae as having "Adambulacrals many, like coins set on edge."

The arm segments of *Silicaster* are much fewer than those of *Urasterella,* for example, more nearly equal to those in *Calliasterella americana* Kesling & Strimple. In addition, the RR and Imm rows are the major plates on the aboral side of the arms in both *Silicaster* and *Calliasterella.*

The family was diagnosed by Spencer & Wright (1966, p. 74):

> Disc small; arms long and straight-sided; oral face of adambulacrals with prominent transverse ridge; aboral ossicles of arms transversely elongate and bearing median ridge; with 5 primary radials.

The new genus agrees in all except the median ridge of aboral arm plates. Whereas the proximal section of the arm has RR with lateral pronglike extensions, and the adradial parts of Imm are drawn out into riblike processes, none of the aboral arm plates in *Silicaster* has a transverse median ridge raised above the general rounded outer surface; the same could be said of the aboral arm plates in *Calliasterella americana.* Nevertheless, the closest affinities of the new genus lie with the calliasterellids.

The discovery of *Silicaster* extends the range of the family from Lower Carboniferous-Cretaceous back to Middle Devonian.

Subfamily Calliasterellinae Schöndorf

As the calliasterellids are divided in the *Treatise, Silicaster* must be assigned to the Calliasterellinae, which has the "aboral ossicles of arm reduced to 3 rows" (Spencer & Wright, 1966, p. 74). It should be noted that these authors did not account Admm as aboral arm plates, so that their diagnosis of the subfamily says in effect that the arms are bordered by RR, Imm, and Admm—not by Smm. The only genus previously placed in the subfamily is the type genus, *Calliasterella* Schuchert.

Explanation of Plate 1

Both figures × 4, lightly coated with ammonium chloride

Figs. *1, 2*—*Silicaster esseri* n. gen. and n. sp. Holotype UMMP 57371. *1,* aboral side of disk (compare with text-fig. 1a). *2,* proximal part of arm V adpressed on oral side of disk (compare with text-fig. 1b).

PLATE 1

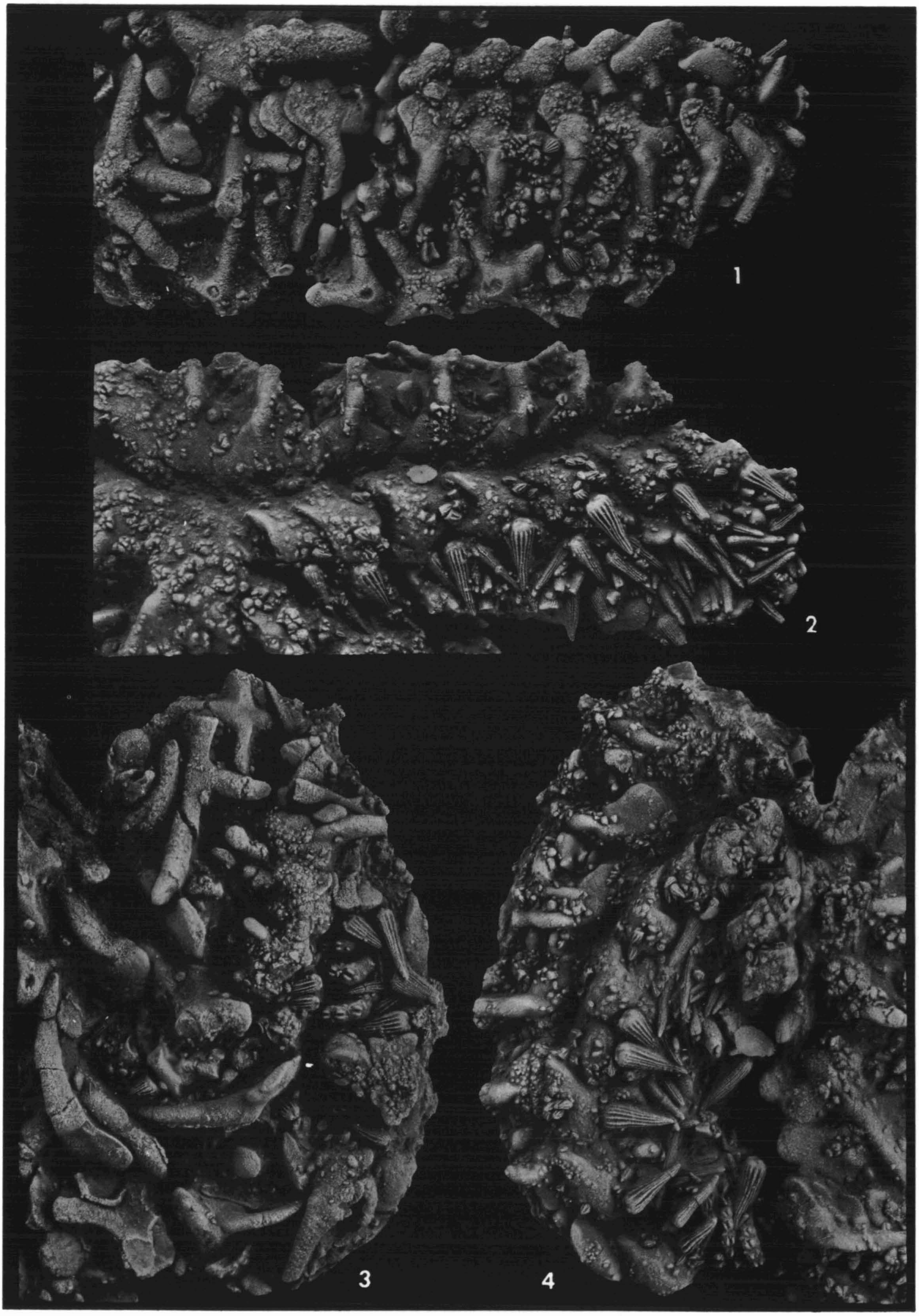


PLATE 2

SILICASTER n. gen.

Type species.—by monotypy, *Silicaster esseri* n. sp.

Diagnosis.—Calliasterellinae with rather extensive adradial and central papular areas containing scattered irregular small accessory ossicles.

Remarks.—*Silicaster* and *Calliasterella* appear to agree in having (1) stellate disk plates, (2) R_1 different from R_2 and succeeding RR, (3) Axx on side of disk in axils, (4) Imm of arms transversely elongate (presuming the lateral plates of *Calliasterella* to be Imm), (5) aboral arm plates consisting of one row of RR, two rows of Imm, and two of Admm, and (6) long spines on oral ridges of Admm. Differences between the two genera are outlined in table 1.

TABLE *1*—ESSENTIAL DIFFERENCES BETWEEN *SILICASTER* AND *CALLIASTERELLA*

Character	*Silicaster*	*Calliasterella*
Central papular areas	Extensive	Practically absent
Adradial papular areas	Extensive	Practically absent
Arm section	Probably low	High
Arm Imm	Paddle-shaped, not in contact with RR	Subpyriform to subquadrate, in contact with RR
Arm RR in proximal part of arm	Quadristellate, central spine	Quadrate, no central spine
Admm spines	Robust, vertically ribbed	Slender, smooth

SILICASTER ESSERI n. sp.

Text-figs. 1, 2; pls. 1–4

Description.—Disk fairly small, arms tapering very gradually to rather bluntly rounded tip. Sides of disk buttressed by large Ax in each axil (text-figs. 1a, 2a,c; pl. 1, fig. 1); top covered by stellate major plates in extensive central papular area, with numerous small accessory ossicles. Ax strong and robust, vertically elongate, the base extending to or nearly to oral surface and the top bifurcate at a broad angle, tapering to rounded tips, and the two flat wings extending laterally from the upper third; on each side of Ax, edge of basal section of Im_2 (first Im of arm) fitting closely below lateral wing (text-fig. 2a,c). Plate interpreted as R_1 (text-fig. 1a, 2a) strongly pentastellate with two long slender prongs diverging distally, two directed laterally and opposite, and a shorter prong directed proximally. Plate possibly representing cR also sharply pentastellate, similar but smaller than plate interpreted as R_1 (text-figs. 1a, 2a; pl. 1, fig. 1).

M somewhat distorted, originally probably subcircular, with no preserved evidence of pores; M held in position by three surrounding plates, interpreted as Sm_1 and two Smm_2. Sm_1 proximal to M small, curved, blocky. Sm_2 at each side of M more or less trapezoidal except for subcircular indentation to accommodate M. Plates interpreted as Sm_1 of other interradii quadristellate, three prongs sharply acuminate and the other longer and flat with broad blunt end. Plate interpreted as Sm_2 of other interradii subquadrate and blocky. Small quadristellate plate between Ax and R_2 regarded as possible Sm_3 (text-figs. 1a, 2a,c; pl. 1, fig. 1).

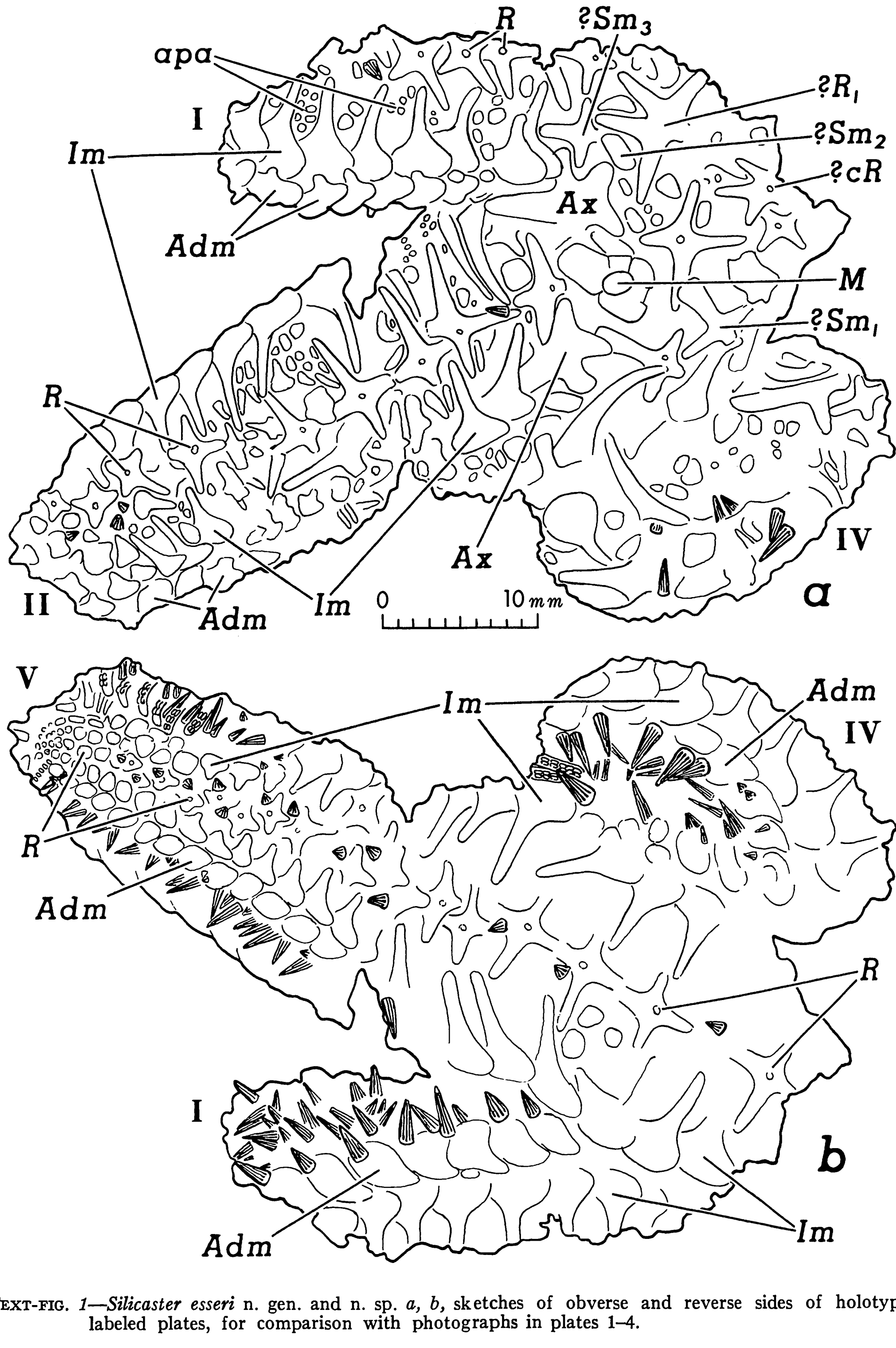
Distal end of arm (text-fig. 2b; pl. 3, fig. 2) with small close-set ossicles representing R, Imm, and Admm rows. Ossicles subcircular at tip of arm, proximally becoming quadrate and thence gradually assuming definitive final ontogenetic shape.

Proximal part of arm with distinctive RR, Imm, and Admm plates. RR sharply quadristellate with long spinelike prongs extending at right angles; central depression to accommodate short robust spine ornamented with about 15 sharp radial (longitudinal) ridges (costae, ribs). Based on fossilized position, RR probably overlapping, with distal prong of each extending free above proximal prong and central spine of next R (text-fig. 2a,c; pl. 1, fig. 2; pl. 3, fig. 2). Ends of lateral prongs probably extending free out over sides of arms in similar fashion and serving a defensive function.

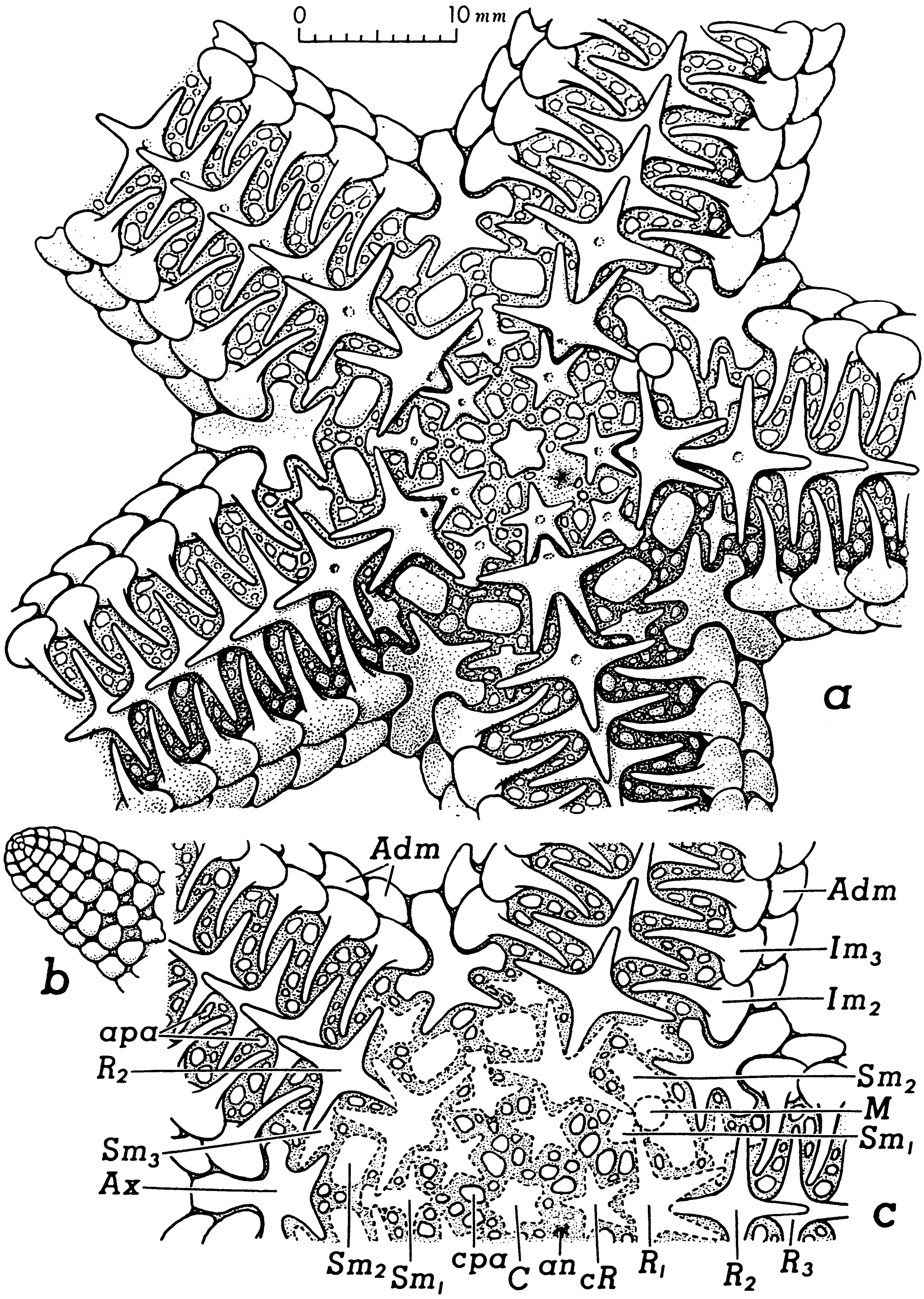
EXPLANATION OF PLATE 2

All figures × 4, lightly coated with ammonium chloride

FIGS. *1–4*—*Silicaster esseri* n. gen. and n. sp. Holotype UMMP 57371. *1, 2,* obverse and reverse sides of laterally compressed aboral surface of arm I (compare with text-fig. 1a,b). *3, 4,* obverse and reverse sides of laterally compressed arm IV (compare with text-fig. 1a,b).



TEXT-FIG. 1—*Silicaster esseri* n. gen. and n. sp. *a, b,* sketches of obverse and reverse sides of holotype with labeled plates, for comparison with photographs in plates 1–4.



TEXT-FIG. 2—*Silicaster esseri* n. gen. and n. sp. Reconstructions. *a,* aboral side of disk and adjacent parts of arms. *b,* aboral side of distal end of arm showing closely spaced RR, Imm, and Admm. *c,* labeled plates of disk and adjacent parts of arms. In the reconstructions, it is presumed that the spines attached to the oral surface of Admm were not visible in aboral view. Roman numerals refer to the numbers of the arms with aboral sides exposed. Abbreviations explained in text. Based on holotype; specimen may not have been flattened quite as much as indicated in reconstructions.

Imm in proximal part of arm paddle-shaped, each consisting of adradially directed thick rib-like shaft and ovate base; shaft curved to conform with sectional outline of arm side, adradially terminating in papular area between lateral prongs of RR, orally extending onto base and gradually tapering to merge with it; base expanded laterally both proximally and distally, tapering to thin edge. Bases of Imm imbricating, the distal margin of each overlapped by the next plate. Oral edges of Imm closely fitting against Admm. First Im of arm (Im_2) fitting against side of Ax.

Admm as seen in aboral (more accurately aboral-lateral) view somewhat smaller than bases of Imm, each elongate oval with its long axis set at an angle to the oral surface, its distal end fitted below the proximal end of the next Adm and apparently imbricating when arm enrolled. Blunt aboral projection on each Adm, probably serving as a pivot in articulation of the plates. Admm transversely elongate on oral surface, bearing a narrow ridge for attachment of long stout spines; points of spine articulation consisting of pairs of short curved ridges (one on each side) rather closely spaced along the main transverse ridge, more or less like a vertical series of miniature parentheses (pl. 4, figs. 1, 2). Admm oral spines stout, conical, tapering from circular base to sharp tip, ornamented with about 15 steep, sharp-crested longitudinal ridges. Shorter but similar spines probably attached near outer edge on oral surface or on lateral margin of Admm.

Ambulacrals and mouth frame unknown.

Remarks.—The extensive papular area provided the disk with a "protrusible cone," as that term is used by Spencer & Wright (1966). The flexible dome probably expanded and contracted to assist respiration. The overlapping of RR appears to have seriously restricted aboral enrollment of the arms. Although imbrication of the bases of Imm somewhat restricted lateral movement, the construction of the plates indicates supple arms able to move easily from side-to-side or downward. The curious shafts of Imm may have been for attachment of muscles used in locomotion. Even if little can be deduced from only one specimen, it may be significant that in death the arms were not rolled down and inward like those of *Calliasterella americana* (see Kesling & Strimple, 1966, pls. 151–153). A possible explanation is that the structurally weak adradial papular areas in *Silicaster esseri* did not permit powerful contraction of enrolling muscles in *rigor mortis.*

Morphology and occurrence combine to suggest the paleoecology of the species. The long spines, peculiarly articulated with the oral ridges of Admm, were probably adapted for raking through bottom sediments; they are even more strongly constructed than those of *Calliasterella americana.* Whereas *Calliasterella* was protected aborally by thick close-set plates, *Silicaster* developed spinose projections of disk plates and arm RR, in addition to sharp articulated spines on these plates. Both genera probably lived in about the same ecological niche, scavengers on the organically littered sea floor. *Silicaster* may have flourished in local Middle Devonian reefs, moving among the corals and probing through the debris with its strong spines for particles of food to select and move orad with its elongate tube feet.

Occurrence.—Middle Devonian Silica Formation, unit 18, exposed in North Quarry of Medusa Portland Cement Company in Lucas County, Ohio.

Type.—Holotype UMMP 57371.

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MANUSCRIPT SUBMITTED AUGUST 1, 1968.

EXPLANATION OF PLATE 3

Figures × 4, except as noted; all lightly coated with ammonium chloride

FIGS. *1–3*—*Silicaster esseri* n. gen. and n. sp. Holotype UMMP 57371. *1,* aboral side of arm II (compare with text-fig. 1a). *2,* aboral side of end of arm V, adpressed on oral surface of arm II (compare with text-fig. 1b). *3,* adambulacral spines of arm V, × 12.

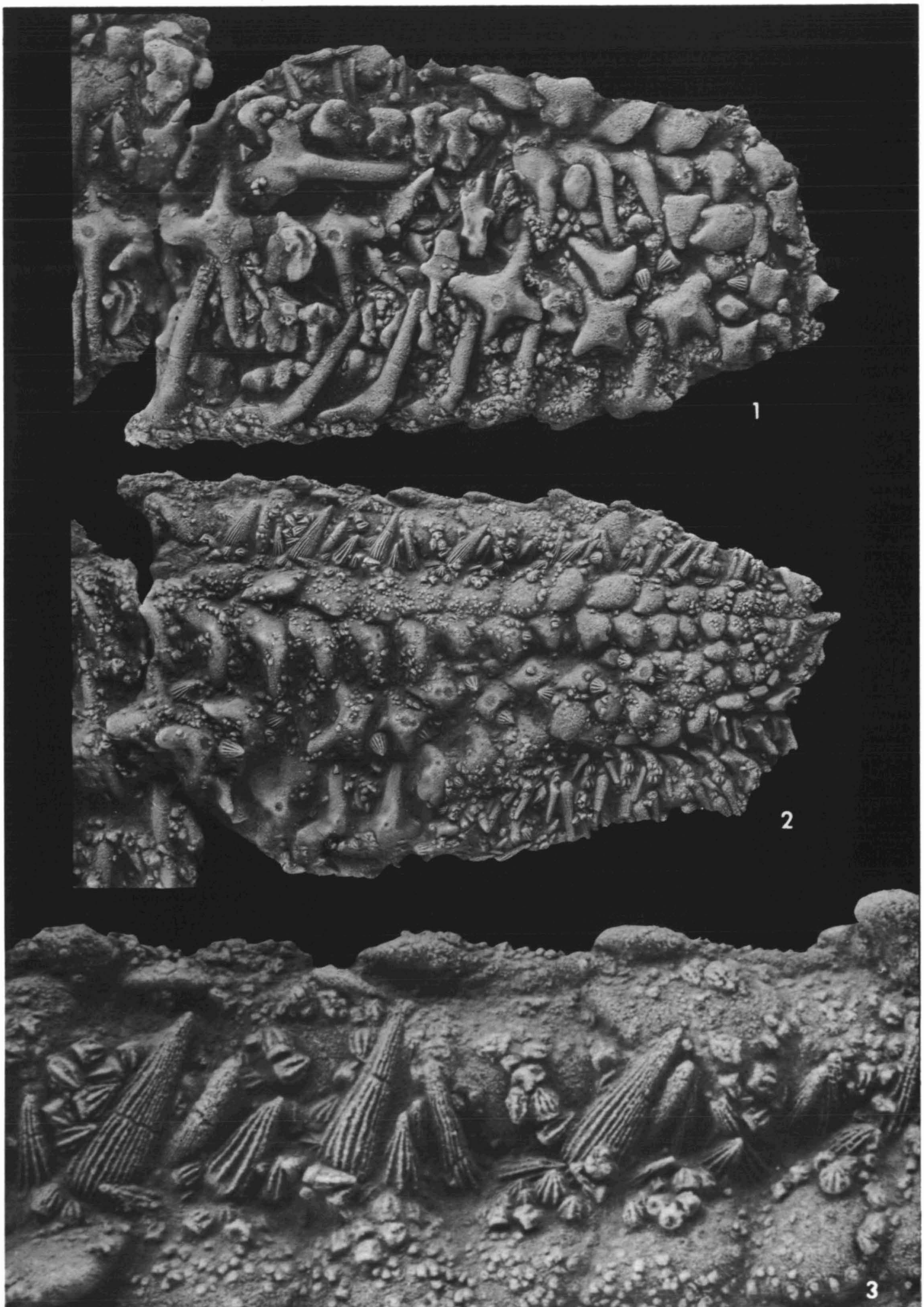

PLATE 3

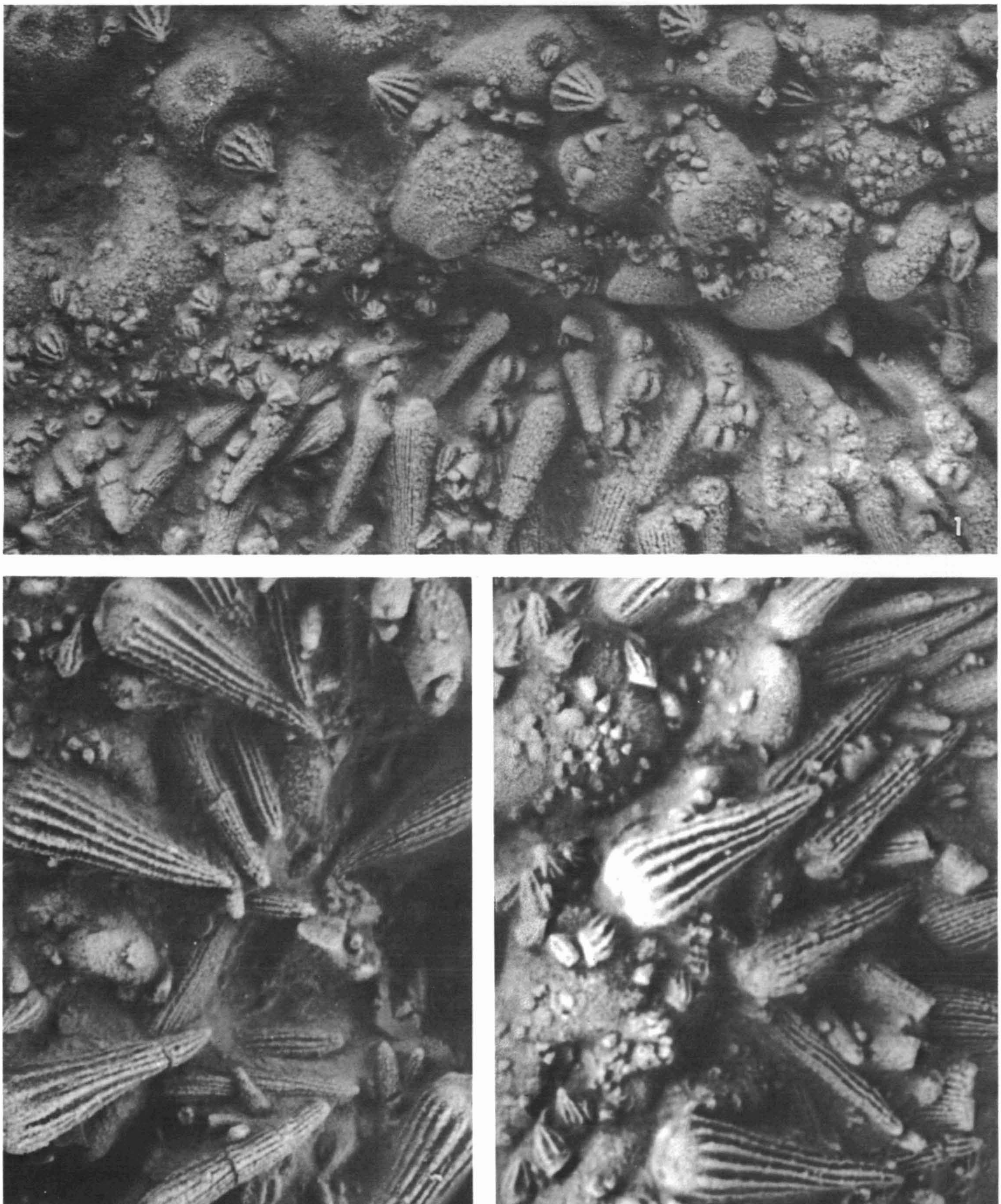

PLATE 4

EXPLANATION OF PLATE 4

All figures × 12, lightly coated with ammonium chloride

FIGS. *1–3*—***Silicaster esseri*** n. gen. and n. sp. Holotype UMMP 57371. *1,* aboral side of distal section of arm V and edge of oral side of arm II, showing adambulacral spines of arm V interspersed with transverse spine-bearing adambulacral ridges of arm II. *2,* adambulacral spines of arm IV with two transverse spine-bearing ridges, possibly from same arm. *3,* adambulacral spines of arm I. (compare all views with text-fig. 1b).