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NOTES ON *PROTOPALAEASTER NARRAWAYI* HUDSON

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ABSTRACT—In 1912 Hudson described a Middle Ordovician starfish as *Protopalaeaster narrawayi* and made it the type of his new genus. In 1914 Spencer suggested that it was conspecific with *Palaeaster caractaci* Gregory. Also in that year, Schuchert transferred Hudson's species to *Hudsonaster*, for which Stürtz, author of the genus, had selected *Palasterina rugosa* Billings as type species in 1900. In 1916, Spencer followed Schuchert in placing *narrawayi* in *Hudsonaster* and used *Palaeaster caractaci* as the type species for his new genus *Caractacaster*, thereby refuting his previous suggestion of synonymy.

The ambulacral plates of *Protopalaeaster narrawayi* are closely set, so that the "podial openings" (notches for the admission of the ampullae) are mere slits, if indeed they exist at all. In contrast, those in *Hudsonaster matutinus* (Hall) have very large openings. According to Schuchert (1915, p. 62), the ambulacrals of *Hudsonaster incomptus* (Meek) are "so far as can be determined, like those in *P. matutinus*." The ambulacral plates of the type species, *Hudsonaster rugosus*, are still unknown. Because of the strong aboral resemblance of *H. rugosus* to *H. incomptus*, however, it seems likely that these two Richmond contemporaries are congeneric.

Protopalaeaster has not been shown to be the same as *Hudsonaster*, and should be restored, as proposed by Sardeson in 1928. In my present understanding, it is a valid genus—but not because of the characters attributed to it by the original author, who confused oral and aboral sides in the halved, immature holotype.

Details of the aboral side of *P. narrawayi* are revealed in previously unstudied specimens. Its flat-topped disk is surmounted by a coronet of ten stellate plates: five first radials and five first supramarginals. These plates are strongly convex, extending above the general level of the summit. A distinct centrodorsal plate is separated from each first radial by two centroradial plates. Proximal to each first supramarginal and between the centroradial plates of adjacent radii is a centrointerradial. The second supramarginals are also stellate and joined at their tips, except in the interradius containing the madrepore plate.

The madrepore plate fits into a recess between modified second supramarginals and slopes down from its contact with the first supramarginal. It is traversed by numerous small pores spaced along narrow, anastomosing, more or less radial grooves. In the interradius to the right of the madrepore, a low pyramid of triangular plates between the centrodorsal and the centrointerradial plates is interpreted as the anus.

The ambulacral plates form a high vault within each arm, but they are not appressed against the radials or supramarginals.

INTRODUCTION

TO CONNOISSEURS of starfish taxonomy, the title of this paper will suffice to reopen an old controversy and to indicate which side I favor. Investigation of previously undescribed specimens has led to a new interpretation of several structures. The generic assignment of *Protopalaeaster narrawayi* and the details of its morphology are, of course, unseparable.

The problem in classification concerns the criteria for distinguishing genera in the early Paleozoic starfish. It has been made difficult by misidentified specimens, wistful substitution of hypotheses for observation, differences in terminology, and even confusion of oral and aboral surfaces.

Protopalaeaster was described by George H. Hudson in 1912, and the genus was off to a bad start. It was based on one species, *P. narrawayi*, which was represented by one specimen. The holotype has subsequently been proved to be quite immature and incomplete. The preservation led to a serious misinterpretation. The oral side of the inframarginals and adambulacrals is still embedded in the slab of matrix; the aboral plates of the disk, the radials, and the supramarginals have all been eroded away; the inner (aboral) face of the inframarginals and adambulacrals is exposed; and patches of ambulacrals form steep-sided vaults above the adambulacrals. Inasmuch as not a single supramarginal was retained, it is not surprising that Hudson thought the oral face of the specimen was exposed and that the supramarginals, radials, and disk were buried in the slab. The ambulacrals he interpreted as "covering plates" roofing over the ambulacra. Thus, he assumed that the specimen was a very different kind of starfish, in which the ambulacra were covered by movable plates, much like those in edrioasteroids. This description appeared in two parts, one in May and the other in the June–July issue of the Ottawa Naturalist.

In December of the same year, in the same publication, Percy E. Raymond presented a very different analysis of the holotype. Comparing it with a similarly preserved specimen of *Urasterella pulchella* (Billings), he correctly stated (1912, p. 106) that the covering plates were in reality the ambulacrals as viewed aborally. Apparently not wishing to appear to dor the dotterel, Raymond described Hudson's reversed orientation as "our view" (p. 105). He astutely explained the nature of the fossil and portrayed *P. narrawayi* as a starfish exceptional for lacking openings between its ambulacrals.

Whatever Raymond's sincerity and motive, his offer to share the error was not kindly accepted by Hudson, who in October of the following year rather vehemently insisted on his previous interpretation, again in the Ottawa Naturalist. Raymond's statements (1912) were sharply one-by-one rebutted by Hudson (1913*a*), thus:

Raymond: Before the publication of his paper, photographs and descriptions had been seen by three or four paleontologists and students of recent echinoderms, and, it must be confessed, all dissented from our view as to the nature of the "covering pieces" (p. 105).

Hudson: This use of these pronouns is misleading . . . My experience with "paleontologists and students . . . " was not as he unwittingly represents it.

Raymond: The chief reason that Narraway, Hudson and myself had for thinking that *Protopalaeaster narrawayi* was exposed from the actinal side was that the covering pieces did not look like ambulacral plates, and that they made an apparently tight and imperforate roof over the groove (p. 106).

Hudson: Here again I believe the statement would have gained in accuracy had the first two names been omitted. It must be evident at least that Dr. Raymond did not know my reasons (p. 83).

Raymond: The faces actually presented, however, are flat and smooth, as would be expected if they served as a foundation for the plates of the abactinal side (p. 106).

Hudson: I have published stereograms of three different regions from the undoubted oral surface of *Palaeaster niagarensis*, Hall, which show the same smooth surfaces (p. 78).

Raymond: . . . the marginal plates are truncated on the side now exposed to view (p. 106).

Hudson: . . . this is far from being the condition of the interradials and . . . it does not accurately describe the arm marginals (p. 78).

Raymond: . . . each plate [adambulacral] was provided with a cup-like pit into which the proximal end of a covering plate [ambulacral] fitted (p. 105).

Hudson: Now, in the first place, ambulacra never have their adambulacral ends fitting into cup-like pits to form ball and socket joints. In the second place, the ambulacra now in question do not possess "cup-like pits," but they show angular, flat or slightly depressed muscle fields. In the third place, the proximal ends of the epineurals in *P. narrawayi* not only do not "fit" these muscle fields, but they *are in every case placed alternately with them* (p. 79, italics his).

Other specific points of disagreement were expressed by Hudson (1913*a*). Because they do not enter into the basic structure of the starfish, I shall not dwell further on the controversy.

In 1914 (p. 21) Spencer suggested that *Protopalaeaster narrawayi* was conspecific with *Palaeaster caractaci* Gregory, and therefore a junior synonym.

The next tribulation of *P. narrawayi* was its transfer to *Hudsonaster*. The first appearance of "*Hudsonaster narrawayi*" was in the Fossilium Catalogus (Schuchert, 1914, p. 22). This publication was a systematic listing of genera and species without explanation for the generic placements. In the following year, Schuchert again put *narrawayi* into *Hudsonaster* (1915, p. 59), but without strong conviction. He wrote (1915, p. 59), "Ambulacral plates large and solid, rectangular, with slightly rounded ends. As these plates are not T-shaped as in other species of this genus it may be shown that this character is of generic value, in which case *Protoplaeaster* will have to be revived."

Schuchert's skepticism as to the generic value of the differences in ambulacral plates is inconsistent with his preceding statement in the same publication (1915, p. 41): "Undoubtedly the most important skeletal parts of the Stelleroidea are the ambulacrals.

In general they undergo the least alteration during geologic time of the entire asterid skeleton, and therefore any marked variation must be of broad classificatory value."

After reading Schuchert's (1915) paper, Spencer changed his mind about the classification and thoroughly negated his earlier (1914) synonymy of *Protopalaeaster narrawayi* and *Palaeaster caractaci*. The former he included in *Hudsonaster* (1916, p. 77), thus endorsing Schuchert's taxonomy, and the latter he utilized as the type species for his new genus *Caractacaster* (1916, p. 80). He did not elaborate on the reasons why *narrawayi* should be assigned to *Hudsonaster*.

Thus in a span of only four years, *Protopalaeaster narrawayi* was described with an inverted orientation, correctly reversed, again inverted, the species wrongly made a synonym of *Palaeaster caractaci*, the genus made into a junior synonym of *Hudsonaster*, and the suggested synonymy of the species abandoned. This was the status of the starfish—classified as *Hudsonaster narrawayi* (Hudson)—for the next thirteen years.

Then in 1928, Frederick W. Sardeson described some new specimens, presented more details of structure, and commented on the identification of the specimens described by Schuchert in 1915. He made known for the first time the madrepore plate, plates on the aboral side of the disk, and the aboral sides of the arms. His work on morphology was significant and, for the most part, accurate. On only two major points do I not concur: first, that the crescent-shaped space he observed above the "madreporite" is the "anal pore" (1928, p. 105), and second, that the body cavity did not extend into the arms (p. 107).

Sardeson entitled his paper "Star-fish beginnings and *Protopalaeaster*," but he hesitated to take its type species from *Hudsonaster* and restore it to *Protopalaeaster*. For example, he spoke (1928, p. 99) of "having lately found comparatively a wealth of good specimens of the *Hudsonaster narrawayi* (Hudson) . . . " and four times again (p. 105,107,108,110) referred to the species in this manner. Once, however, he used the original name (p. 109), "Formerly only the actinal side of the *Protopalaeaster narrawayi* (Hudson) was known . . . " (incorrect parentheses his).

He strongly inferred that *Protopalaeaster* was a valid genus, stating (1928, p. 109), "As to this matter of name, Schuchert makes the suggestion, in fact, that in case the ambulacral plates of this species prove to be different from those of *Hudsonaster matutinus* (Hall) the name *Protopalaeaster* be restored to it. The ambulacralia *are* different" (his italics), and again (p. 110), in appraising Schuchert's work, " . . . the whole of the confusion appears to be thrown off by putting *Protopalaeaster* in synonymy, where it may not belong."

Sardeson seems to have vacillated also on the suprageneric significance of this starfish. He compared it with cystoids, ophiuroids, echinoids, and asteroids (1928, p. 106):

> This species has structurally in it other features than those of the Asteroidea and may be rather the ancestor of Ophiuroidea. On the other hand it has ancestral characteristics in common with certain cystidea with a suggestion of relationship to the ancestral Echinoid stock."

Impressed with the structures called tori, which are present in the mouth region of *P. narrawayi*, Sardeson considered that they might be compared with an Aristotle's lantern, and offered the following cryptic pronouncement (p. 108), "If so, these structures indicate that a yet unknown Cyst-Echinoidean ancestor is the stock from which this Aster-Ophiuroid ancestor is derived."

In the Museum of Paleontology at the University of Michigan are five starfish catalogued under the number 11043. Labels accompanying them state that they were collected by F. W. Sardeson from "Beloit fm., bed #2, Platteville ls. 2" at Minneapolis, Minnesota, and purchased by the University in 1928. Other Museum records show no such transaction, but it probably was overlooked and not entered under "Accessions." I carefully compared the specimens against the drawings of Sardeson (1928, pl. 5) in hope that they would match. They do not, although the type of preservation is like that described by Sardeson. Presumably, the UMMP starfish were part of the "wealth of good specimens" referred to by Sardeson.

After prolonged work with Vibrotool,

needles, and ultrasonic vibrator, I further exposed the specimens to the state shown in the photographs (pls. 133–134). Three of the starfish have both sides, one has only the aboral side, and the last one only the oral side revealed. Only the oral part of the disk is not well represented by any of the UMMP specimens. For information on structures in this region, I have had to rely on the accounts of previous authors, particularly Sardeson, in making the restorations (text-figs. 1–2).

ABBREVIATIONS

In discussion of skeletal parts, the names are long and cumbersome. In the involved parts of the description and remarks, I will resort to abbreviations as follows:

Ad—adambulacral.
Ad_1—first adambulacral, part of oral armature.
Am—ambulacral.
aAx—accessory axillary.
C—central, commonly called the "centrodorsal."
cI—centro-interradial, also known as "interradial plate."
cR—centroradial, small plate between *C* and R_1, also known as "proximal radial."
cR_1—first or inner centroradial.
cR_2—second or outer centroradial.
Im—inframarginal.
Im_1—first inframarginal or axillary.
R—radial.
R_1—first radial, also known as "primary radial."
R_2—second radial.
Sm—supramarginal.
Sm_1—first supramarginal, interradial in position, also known as "primary supramarginal."
Sm_2—second supramarginal.

The plurals of each of these terms is indicated by adding—'s to the abbreviation.

NEW DESCRIPTION

Subclass ASTEROIDEA

As recognized by Schuchert (1915, p. 60) and by Sardeson (1928, p. 108), *Protopalaeaster* is the oldest and most primitive starfish. Although it displays certain unique characteristics, it is clearly a starfish rather than an ophuiroid, auluroid, or echinoid. The arms lack accessory plates or ossicles and the disk is a more solid, plated structure than that in later asteroids, but the basic pattern of arm plates is the same.

Order PHANEROZONIA

The large marginal plates along the borders of the arms identify this starfish as a phanerozonian.

PROTOPALAEASTERIDAE, n. fam.

Type genus.—*Protopalaeaster* Hudson, 1912, p. 25, here designated.

Diagnosis.—Phanerozonia with the ambulacrals in each of the five arms set so closely that the openings for insertion of ampullae are either very constricted or completely inadequate. First inframarginals (axillaries) marginal. Madrepore plate well developed, aboral. Disk heavily plated. No accessory plates or ossicles in the arms.

Remarks.—The relationship of the water-vascular system to the ambulacral plates forms the basis of separation for the subclasses Asteroidea, Auluroidea, and Ophiuroidea. I consider the lack of so-called "podial openings" (more properly ampullar openings) in the ambulacrals sufficient for at least familial rank, despite the resemblance of *Protopalaeaster* to *Hudsonaster* in the general arrangement of plates.

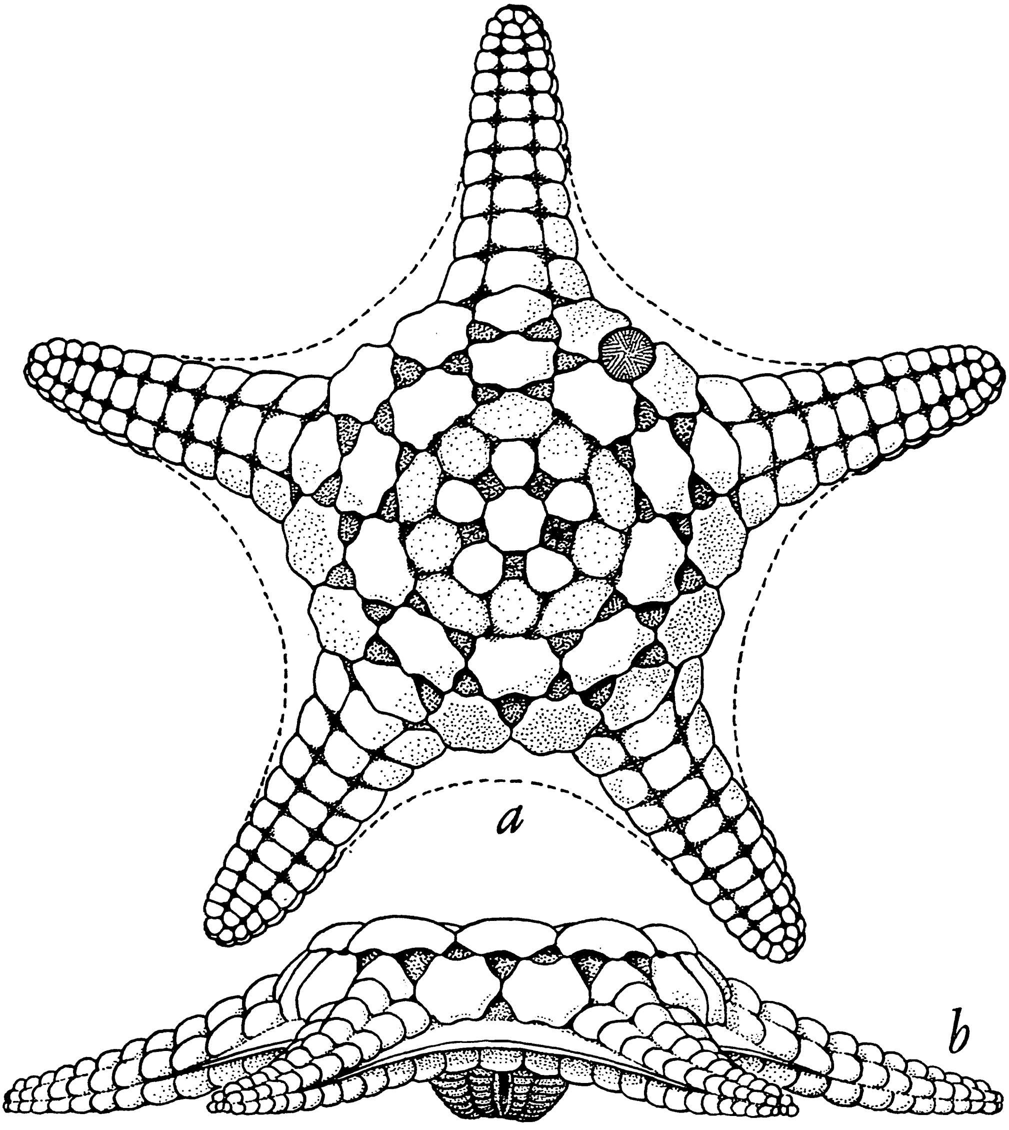
The status of this family depends upon the standing of its type genus, as discussed below. I believe that *Protopalaeaster* is distinct.

The outlines of classification for Palaeozoic phanerozonians has been given by Schuchert (1915, p. 52–53) and by Spencer (1916, p. 65). The chief characteristics of the families, including the new one, are summarized in Table 1.

Genus PROTOPALAEASTER Hudson

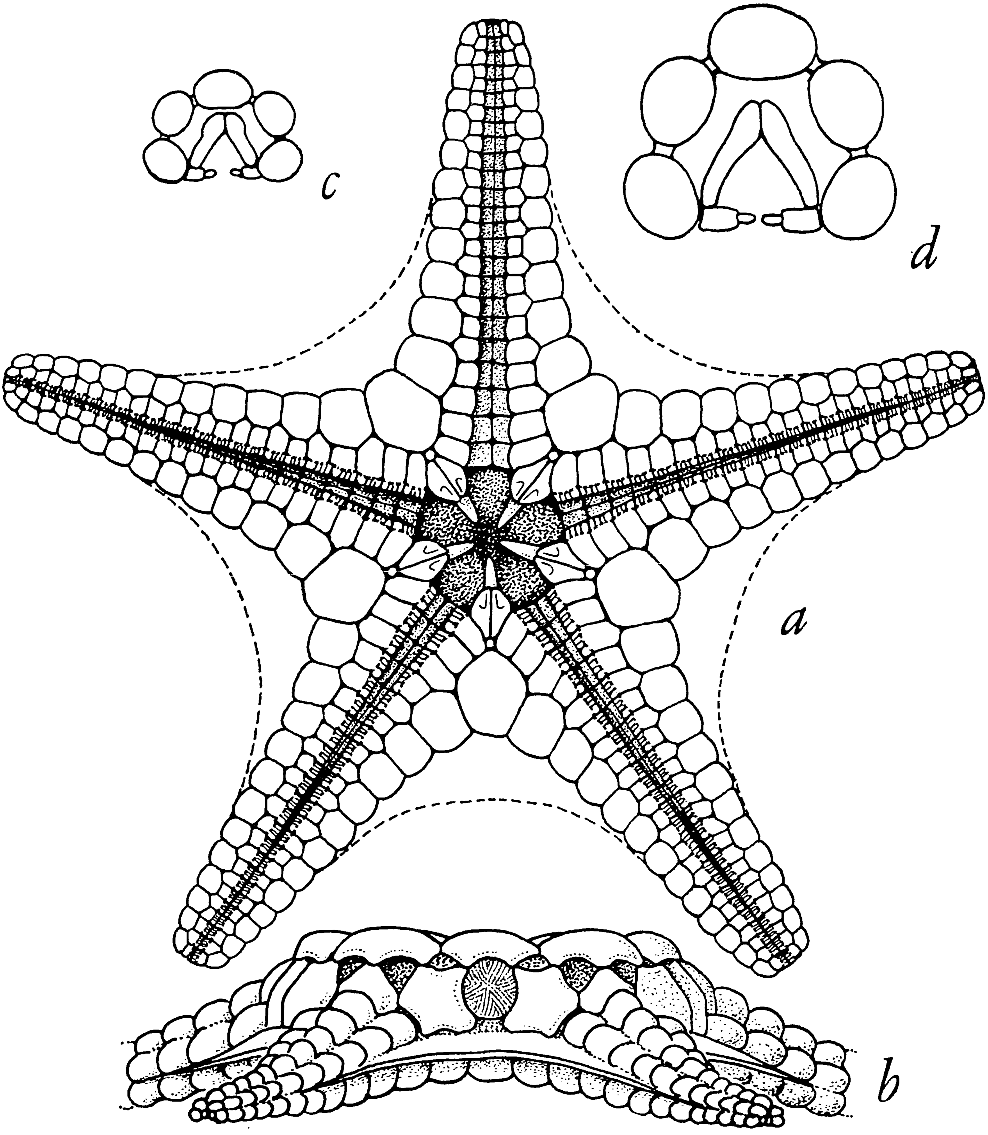
Protopalaeaster Hudson, 1912, p. 21–52; 1913a, p. 77–84; Raymond, 1912, p. 105–08; Sardeson, 1928, p. 109.
Palaeaster (in part), Spencer, 1914, p. 21.
Hudsonaster (in part), Schuchert, 1914, p. 21; 1915, p. 53–57; Spencer, 1916, p. 77; Sardeson, 1928, p. 99–108.

Remarks.—As acknowledged by Schuchert (1915, p. 55), Stürtz, the author of *Hudsonaster*, made an unfortunate selection of the type species, *Palasterina rugosa* Billings. The definition of *Hudsonaster* is



TEXT-FIG. *1*—*Protopalaeaster narrawayi* Hudson restored. *a*, aboral view; the dashed lines indicate the extent of the interradial membranes inferred from the hard laminae discovered while cleaning the specimens; the upper and upper right arms are the bivium; the madrepore plate and the second supramarginals are shown somewhat less steep than in reality, so that their shape could be indicated. *b*, side view. Based on specimens described here and upon the sketches of Sardeson (1928, pl. 5).

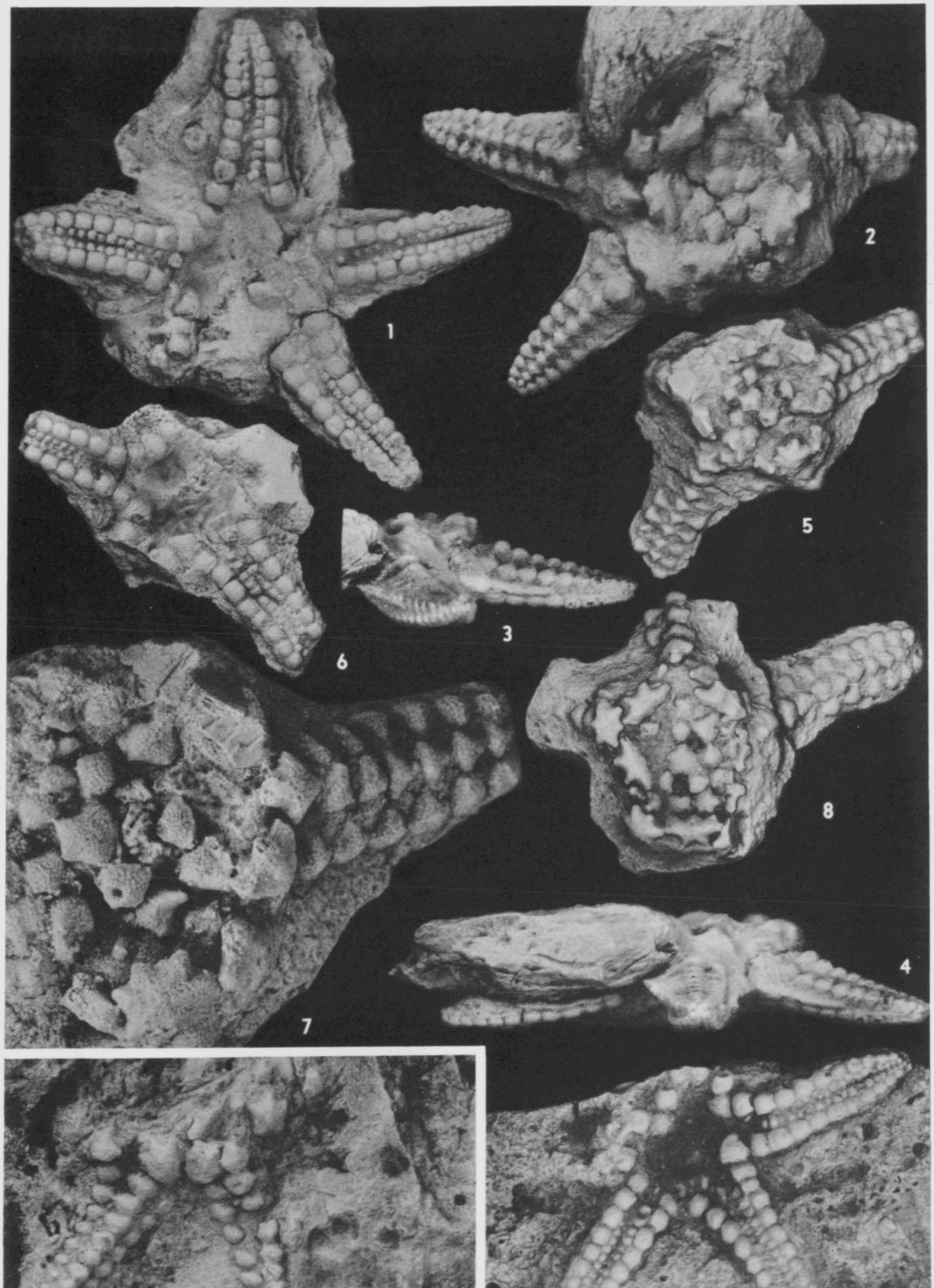
incomplete and full of errors. The orientation is muddled. Turning to the designated type, we learn that no details of the ambulacrals have been observed. Both Schuchert (1915, p. 64–65) and Sardeson (1928, p. 109–10) point out the close aboral resemblance of *Hudsonaster rugosus* to *H. incomptus* (Meek), its Richmond contemporary. The ambulacrals of *H. incomptus* are "so far as can be determined" (Schuchert, 1915, p.



TEXT-FIG. 2—*Protopalaeaster narrawayi* Hudson restored. *a*, oral view; the dashed lines indicate the extent of the interradial membranes inferred from hard laminae in the specimens; the short blunt spines along the proximal edges of the adambulacrals are omitted in the upper arm to better show the ambulacrals. *b*, side view of madrepore plate. *c*, enlarged cross section of distal part of an arm. *d*, enlarged cross section of proximal part of an arm. Based on specimens described here and upon the sketches of Sardeson (1928, pl. 5).

EXPLANATION OF PLATE 133

FIGS. *1–10*—*Protopalaeaster narrawayi* Hudson. *1–4*, oral, aboral, and two side views, ×2, UMMP 11043*a*. *5–7*, aboral and oral views, ×2, and part of aboral view, ×5, UMMP 11043*b*. *8*, aboral view, ×2, UMMP 11043*c*. *9*, aboral view, ×2, UMMP 11043*d*. *10*, oral view, ×2, UMMP 1043*e*.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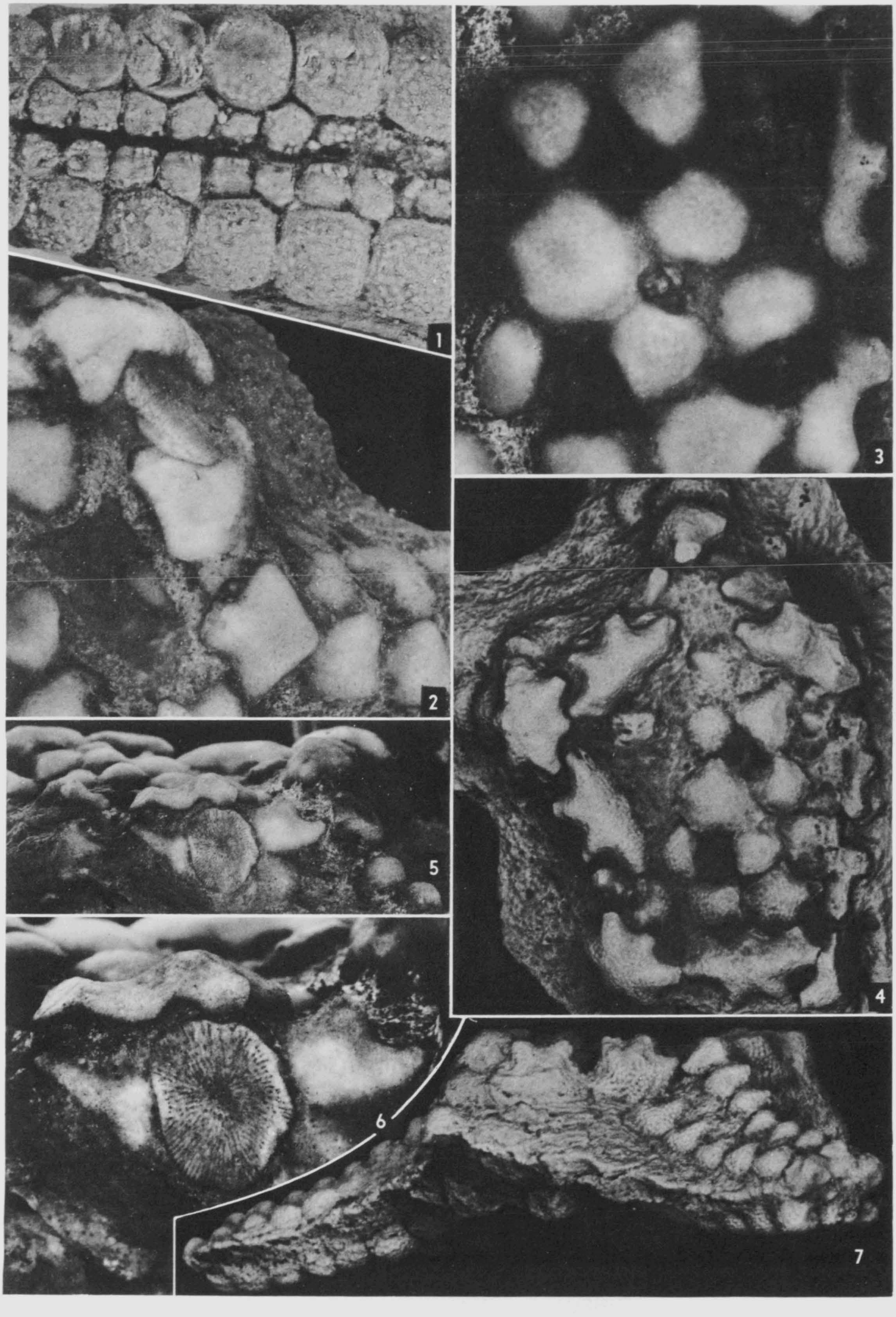

TABLE *1*—CHIEF CHARACTERISTICS OF FAMILIES AND SUBFAMILIES OF PALEOZOIC PHANEROZONIA

Family or subfamily and range		Ampullar openings between ambulacrals in each row	Number of arms	Accessory interradial plates between inframarginals and adambulacrals on oral surface	Border plate(s) of interradius on oral surface	Inframarginals enclosing axillary on oral surface	Inframarginals enclosing other inframarginals in interradius	Adjacent supramarginals and inframarginals fused
Protopalaeasteridae (Blk. R.)		Very narrow or none	5	None	Axillary	None	No	No
Hudsonasteridae (Trent.-Rich.)		Large, center of suture	5	None	Axillary	None	No	No
Promopalaeasteridae	Promopalaeasterinae (Blk. R.-Rich.)	Outer, proximally in 2 rows	5	None	Inframarginals	More than one pair	Yes	No
Promopalaeasteridae	Mesopalaeasterinae (Trent.-U.Dev.)	Center of suture	5	None	Inframarginals	One pair only	No	No
Promopalaeasteridae	Anorthasterinae (Rich.)	Outer, every 2d suture	5	None	Adambulacrals	No inframarginals	No	No
Palasterinidae (Trent.-U.Sil.)		Outer edge of suture	5	Present	Inframarginals	None	No	No
Palaeasteridae (Sil.-"Permo-Carb.")		?	5	None	Axillary	None	No	No
Lepidasteridae (Sil.-U.Dev.)		?	More than 5	?	Infra- or supramarginals	?	?	No
Xenasteridae (L.Dev.)		Outer, shared with adambulacrals	5	Present	Inframarginals	More than one pair	Yes	No
Neopalaeasteridae (Miss.)		Center of suture	5	None	Fused infra- and supramarginals	?	?	Yes

62) like those of *H. matutinus* (Hall). The ambulacrals of *H. matutinus* are T-shaped, with large ampullar openings between them. Both *H. incomptus* and *H. matutinus* are better understood than *H. rugosus*, so that Schuchert (1915, p. 55) admitted basing most of his revised generic definition of *Hudsonaster* upon them.

Assuredly, *Protopalaeaster narrawayi* is generically different from *Hudsonaster matutinus*, and the available evidence indicates that *Hudsonaster rugosus* is congeneric with *H. matutinus*. I endorse Sardeson's statement (1928, p. 110) that "it is not easy for me to understand why this rather unique species has been referred to *Hudsonaster* so

EXPLANATION OF PLATE 134

FIGS. *1–7*—*Protopalaeaster narrawayi* Hudson. *1*, oral view of part of an arm, showing inframarginals and adambulacrals, lightly coated with sublimated ammonium chloride, ×10, UMMP 11043*a*. *2*, part of aboral surface, showing broken cross section of madrepore plate and bordering second supramarginals, submersed in xylol, ×10, UMMP 11043*b*. *3*, part of aboral surface, showing pyramid (probably anus) at the right of the central plate, submersed in xylol, ×10, UMMP 11043*c*. *4*, part of aboral surface lightly coated with sublimated ammonium chloride, ×5, UMMP 11043*c*. *5–6*, side views of madrepore plate, submersed in xylol, ×5 and ×10, UMMP 11043*c*. *7*, side view, showing relationships of second supramarginals, coated with sublimated ammonium chloride, ×5, UMMP 11043*b*.

that *Protopalaeaster* is thus reduced to synonymy." Final verdict, nevertheless, must await discovery of the ambulacrals in *Hudsonaster rugosus*, the critical species for comparison.

PROTOPALAEASTER NARRAWAYI Hudson
Text-figs. 1,2; pl. 133, figs. 1–10;
pl. 134, figs. 1–7

Protopalaeaster narrawayi Hudson, 1912, p. 21–26, 45–52, pls. 1–3; 1913*a*, p. 77–84, pls. 8–9, text-fig. 1; 1913*b*, pl. 5; Raymond, 1912, p. 105–08, pl. 6; Sardeson, 1928, p. 109.
Palaeaster caractaci (in part), Spencer, 1914, p. 21, text-fig. 19.
Hudsonaster narrawayi, Schuchert, 1914, p. 22; 1915, p. 50,54–56,59–60, pl. 1, fig. 1; pl. 2, fig. 1 (not pl. 4, fig. 1); Spencer, 1916, p. 77; Sardeson, 1928, p. 99–108, pl. 5.

Aboral side of disk.—Disk relatively flat-topped (pl. 133, figs. 3–4) surmounted by a coronet of ten slightly elevated, stellate plates—five first radials (R_1's) and five first supramarginals (Sm_1's)—joined at their projecting apices (text-fig. 1*a;* pl. 134, fig. 4). Each R_1 strongly convex or tumid, wider than long, with each of its six apices in contact with an apex of a bordering plate: distal apex with R_2, proximal apex with cR_2, each distolateral apex with an Sm_2, and each proximolateral with an Sm_1. Each Sm_1 with seven apices, joined distally to two Sm_2's, laterally to two R_1's, proximolaterally to two cR_2's, and proximally to a cI.

Area enclosed by coronet containing 16 smaller plates, joined only at their apices: one C, five cR_1's, five cR_2's, and five cI's (text-fig. 1*a*). Plate C subpentagonal with concave sides and truncated apices, joined rather firmly to five clavate cR_1's to form a conspicuous central rosette (pl. 133, figs. 2,5,7,8; pl. 134, figs. 3–4). Each cR_2 low, wider than long, linking cR_1 to R_1 along a radius (pl. 134, fig. 3). Each cI low, proximal to Sm_1 and between four cR's.

Anus apparently a low pyramid of triangular plates adjoining C in the first interradius to the right of the bivium (pl. 134, fig. 3).

Sides of disk declivitous, steeper in interradii than in radii (pl. 133, figs. 3,4; pl. 134, fig. 7). Sm_2's stellate, adjacent plates joined at their lateral apices (text-fig. 1*b;* pl. 134, fig. 7) except in bivium, where interrupted by madrepore plate (text-fig. 2*b;* pl. 134, figs. 5,6). Madrepore plate large, suboval, lens-shaped, slightly concave in its outer face, convex on its inner, set as a sieve-plate across a funnel-like opening between Sm_2's. Madrepore plate apparently laid down as thin laminae and perforated by numerous pores (pl. 134, fig. 2) spaced along narrow, anastomosing, more or less radial grooves on the surface (pl. 134, fig. 6).

Each R_2 in contact with laterally adjacent Sm_2's, thus seemingly more an integral part of the disk than of the arm. R_2 shaped somewhat like a stylized arrow, with the triangular head pointing down and distally and the short, stubby shaft directed upward to its contact with R_1 (pl. 134, figs. 2,4).

Oral side.—Oral surface slighly concave. All Im's in rows leading imperceptibly into the arms. Im_1's, or axillaries, larger than other Im's, forming the margins of the interradii on the oral surface. Proximal to each Im_1 is a tiny accessory plate, aAx, circular as seen orally (Sardeson, 1928, pl. 5, fig. 2) and also as seen aborally (Schuchert, 1915, pl. 1, fig. 1), presumably shaped as a short rod with hemispherical ends.

Ad's more numerous than Im's, in a ratio of about 25 to 13. Ad_1's narrow, subtriangular, forming the oral armature, separated from Im_1's by the tiny aAx's. All other Ad's in contact with Im's (text-fig. 2*a*). Narrow dentate processes, interpreted as tori, partly concealed by armature in oral view, extending inward in interradial positions (Schuchert, 1915, pl. 2, fig. 1; Sardeson 1928, pl. 5, fig. 2).

Arms.—Each arm relatively short, slightly concave as seen laterally, turned up rather sharply at its junction with the disk (pl. 134, fig. 7) and tangent to a plane surface near its end (text-fig. 1*b;* pl. 133, fig. 4). Arm tapering gradually throughout its length to subround end, suboval in all cross sections (text-fig. 2*c–d*).

R's subrhombic at junction with disk, gradually modified distally to oval (pl. 133, fig. 2). Each R strongly convex (pl. 134, fig. 7). An arm 18 mm. long with about 12 radials, including the R_1 and R_2 in the disk. Terminal R small, subovate, apparently bordered laterally by two Sm's and distally by two other Sm's (text-fig. 1*a,b;* pl. 133, fig. 2).

Sm's in rows atop Im's but slightly within their borders (text-fig. 2*c,d*). As viewed aborally, each *Sm* at the side of an *R* (pl. 133, figs. 5,7–9); as viewed laterally, approximately above an *Im* (pl. 133, figs. 3,4). Aboral and lateral framework of each arm, therefore, composed of a series of segments, each having two *Im*'s, two *Sm*'s, and one *R*.

Im's forming border of arm, extending laterally slightly beyond corresponding *Sm*'s (text-fig. 2*a*,*b*). Each *Im* subovate, almost flat at its junction with adjacent *Im*'s (pl. 133, figs. 1,6,10).

In each specimen cleaned, a thin hard sheet, thought to be a calcified membrane of integument, inserted between *Sm*'s and *Im*'s and extending as a concave weblike connection from one arm to the next (text-figs. 1*a*,*b*, 2*a*,*b*; pl. 133, figs. 1–8), similar to "interbrachial arcs" known in certain more recent starfish and in the position of ambital accessory plates. No ossicles discerned in hard laminae.

Ad's smaller, shorter, and thinner than *Im*'s (text-fig. 2*a*–*d*). Those on opposite sides of an arm separated by a narrow channel (pl. 133, figs. 1,6,10), their facing edges lined with short, blunt, quadrate spines. Each *Ad* bearing three (some possibly four) narrow spines and one very broad distal spine (pl. 134, fig. 1). Inner (spine-lined) edges of *Ad*'s nearly straight, outer edges variously modified to fit against *Im*'s.

Am's clearly seen only on broken ends of arms, forming a high vault within the arm, not in contact with *Sm*'s or *R*'s but leaving a very restricted space for the body cavity (text-fig. 2*c*,*d*). *Am*'s apparently spaced exactly as *Ad*'s.

End of arm (text-fig. 1*b*; pl. 133, fig. 4) with roof of two *Sm*'s, sides of two *Im*'s, and floor of two *Ad*'s, leaving a minute space in the center, suggesting that another plate (possibly an ocular) fitted therein.

Remarks.—My interpretation of certain features differs from previous accounts. In comparison:

(1) In the adoral region of the disk, Sardeson (1928, pl. 5, fig. 4) presented a restoration in which *C* was followed by two *cR*'s and the Sm_1's formed a ring within the R_1's. I find the *cR*'s in positions he indicated, but different in shape and size (see pl. 134, fig. 4). In addition, as clearly discernible in pl. 134, fig. 3, there are interradial *cI*'s. The Sm_1's alternate with the R_1's (as can be seen in the lower part of pl. 134, fig. IV), although in many specimens the arrangement in this region has been disturbed by compression.

(2) Sardeson (1928, p. 105) thought that a "small crescentic lacuna above the madreporite" might be the "anal pore." According to my analysis, the anus does not lie within the bivium at all; instead, as in many modern starfish, it is in the first interradius to the right, and it is a low pyramid of triangular plates (pl. 134, fig. 3). The small "lacuna" above the madrepore plate (pl. 134, fig. 6) probably represents integument which originally filled the gap between the plates here, as elsewhere in the skeleton. Although small calcareous bodies, possibly tiny ossicles, may be found in other interradial spaces around *C*, they are neither as prominent nor in the form of a pyramid.

(3) The *Am* plates are not attached to the inner walls of the arms, as Sardeson (1928, pl. 5, fig. 3) portrayed them to be. Rather, they form a high, steep-pitched vault (text-fig. 2*c*,*d*), just as exposed in the type specimen (Raymond, 1912, pl. 6, figs. 2–4; Schuchert, 1915, pl. 1, fig. 1; and other published figures).

(4) Sardeson stated (1928, p. 107), "As in the case of the Cystidea the mouth strand appears to be covered by covering plates, the precursors of the adambulacrals of the Asteroidea." The plates in question (pl. 133, figs. 1,6,10; pl 134, fig. 1) do not cover the groove, and undoubtedly are *Ad*'s.

Through an accident of preservation, one of the specimens, UMMP 11043*b*, shows a cross section of the madrepore plate and the bordering Sm_2's. The modified Sm_2's form a funnel-shaped opening leading to the interior of the starfish. Across this opening is inserted the perforated disklike madrepore plate, much like the fixture in the bottom of a sink and presumably fulfilling a similar function in straining the water taken in.

"Primitive" characteristics of *Protopalaeaster narrawayi* include the shortness of the arms, lack of accessory aboral plates in the arms, and the large marginal axillaries (Im_1's).

The evolution of the Stelleroidea cannot be determined, even generally, at this time. Several families, as classified by Schuchert, include few genera. The family Neopalaeasteridae is based on two specimens of the type species of the type genus. The rarity of Paleozoic starfish and the sporadic geologic record within families point to incompletely known, indeed very fragmentary, ranges. Without knowledge of the chronological sequence of development, it is obviously speculative to outline the evolutionary relationships of the families.

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ISCHADITES IS A DASYCLADACEAN ALGA

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ABSTRACT—The lower Paleozoic fossil *Ischadites* is distinctly a dasycladacean alga. Its numerous branches are simple, extending from the non-calcified central axis to the periphery. Near the base of the thallus the branches are lateral and possess thick proximal calcifications, but around the apex they are radial and acicular; presumably, addition of branches was apical. Each branch bears a distal and a subdistal expansion, so that the thallus is provided with a double-walled exterior. Gametangia developed between the two walls. During the life of the alga they were evidently lime-encrusted to form gametocysts; they are preserved as small calcareous spheres.

The presence of undoubted gametocysts in a specimen from the Trenton rocks of Michigan dispels all question of the affinities. No longer need *Ischadites* be placed in "Incertae Sedis" at the end of the Porifera chapter in textbooks.

INTRODUCTION

FEW LOWER PALEOZOIC fossils have inspired more speculation or more fantastic interpretations than *Ischadites*. With other problematica it was placed in the family Receptaculitidae, which was interpreted by various authors as calcareous algae, pine cones, foraminifers, sponges, corals, cystoids, tunicates, or transitional forms between sponges and corals, or an independent extinct phylum (de Laubenfels, 1955, p. 109; Easton, 1960, p. 116).

Confusion may be attributed, at least in part, to the several modes in which these fossils are preserved. Deformation during fossilization has produced a variety of shapes, and many specimens have been studied from oblique sections. The radial structures have been interpreted as "spicules" in fossils in which they were preserved and as "canals" in those from which they were dissolved. The inner wall has been thought to be the outermost. In some specimens its elements have been correctly identified as plates, but in others from which the plates were dissolved, the matrix filling the former sutures has been considered to be radial spicules. Insofar as we have learned from published descriptions, the outer wall of *Ischadites* was not previously recognized as such.

Undoubtedly, the development of the thallus at the time of burial also contributed to misunderstanding of its nature. Living dasycladaceans differ in their ontogenetic stages, and certain features appear only in maturity. It seems probable that some of the described specimens of *Ischadites* were killed and fossilized while immature.

We gratefully acknowledge the advice and assistance of Prof. W. R. Taylor of the Botany Department, University of Michigan.

SYSTEMATIC DESCRIPTION

Subkingdom THALLOPHYTA
Phylum CHLOROPHYTA
Class CHLOROPHYCEAE (SIPHONOCLADALES)
Family DASYCLADACEAE (Siphonae verticillatae)

The family Dasycladaceae, by some paleobotanists called the "Siphonae verticillatae," is represented in the modern flora by about ten genera. All are marine and limited to warm tropical and subtropical waters.

The living plants are sessile, attached to the substratum by branched, non-septate rhizoids. The siphonaceous thallus consists of a central upright axis with lateral whorled branches. These branches vary from one genus to another. In some they are simple, extending from the central axis to the periphery, whereas in others they bear secondary and tertiary branches. In some dasycladaceans the branches are clavate. Pressure resulting from growth compresses the clavate parts of the branches, producing a hexagonal surface pattern.

Some branches are sterile, others are fertile. In fertile ones, short-stalked, spherical to ovate gametangia are formed at or near the apices of the branches. Biflagellate haploid gametes develop within the gametangia and are released through an operculum.

Many genera are characterized by the formation of encrusting layers of lime. Because this resistant material promotes preservation, the Dasycladaceae are abundantly represented in the fossil record.

Pia (1927, p. 61) and Engler (1954, p. 104) each list 10 genera limited to Recent and 58 genera mostly fossil. The geological history of these plants is comparatively well known. Dasycladacean algae appeared in the Ordovician, contributing to limestone formation in formations in England, Norway, Sweden, Texas (Ellenburger limestone), and other places. They are also known from Silurian and Permian deposits. They reached their zenith of development during Triassic and Jurassic, decreased in numbers and geographic range during Cretaceous and Tertiary, and continue today as a few relic species.

The vegetative and reproductive morphology of the Dasycladaceae is distinctive among lower plants. The upright central axis-bearing branches, reproduction by gametes released from lime-encrusted gametangia (gametocysts), calcification, and marine environment characterize these algae.

Genus Ischadites Murchison

The synonymy of this genus was given by Bassler (1915, p. 668). It would be difficult today to trace all of the type specimens requisite for establishing an accurate list of synonyms. Many were described more than a century ago.

The taxonomic placement of *Ischadites* has been a challenge since the creation of the genus. In the original description, Murchison (1839, p. 697) quoted a statement of König that the fossils are "a group of globular, coriaceous, and, it may be added, pedicled bodies, for in one of them the cicatrix for the insertion of the pedicle distinctly appears." On the following page (1839, p. 698) Murchison said, "Unable to acquire more knowledge concerning the affinities of this fossil, I simply refer to the figure, in which the beautiful tesselation of its surface is expressed; and feeling that any name, which does not mislead, is better than no name, I have called it *Ischadites*. . . ." As noted in Table 1, Murchison assigned the genus to "Nondescripts" and to "Sedis incertae."

Insofar as we have found, Austin in 1845 was the first to conclude that *Ischadites* is a sponge. This assignment was also followed by Bigsby (1868), Hinde (1884), James (1886), Nicholson & Lydekker (1889), and others, recently including Weiss (1954), and Lowenstam (1957).

In 1852 Owen created the genus *Selenoides* based on the "*Orbitolites reticulata*" which he figured but did not describe in 1844. He assigned it to the Foraminifera. Although they called the fossil by other names, Billings (1865), Winchell & Marcy (1865), Zittel (1880), and Roemer (1880) agreed with this classification.

Salter (1865, in Salter & Blanford, as quoted by Reed, 1912) compared the form of *Ischadites* (which he called *Sphaerospongia*) to that of freshwater plants: "The areolae . . . are simply convex, and the edges are greatly sinuated, inosculating with those of the neighbouring mammillae in a way which would remind a botanist of the proteiform cells of some water-plants." He went on to say that the structure was illustrated by *Callitriche verna* of the British ponds. He did not, in any way, state that *Ischadites* was related to the plants; he only used the example of structure in *Callitriche* as an illustration of the arrangement in the fossil.

Gümbel (1875, p. 172) compared *Ischadites* with the Dactyloporidae of calcareous algae, but he did not definitely state that it was part of that taxon. In the same work (p. 212) he referred to *Ischadites* as one of the "Zwischenformen."

Kiaer (1932) assigned *Ischadites* to the calcareous algae with question. Most other authors have admitted uncertainty and placed the genus in "Incertae sedis."

It is interesting to note the confused terminology arising from the differences in preservation. The account of structure by Nicholson & Lydekker (1889, p. 172) is clear, although it is readily apparent that their specimens lacked the outer wall:

> The wall of the organism is composed of cylindrical, pillarlike spicules, arranged at right angles to the surface, and in most respects similar to the corresponding structures in *Receptaculites*. The outer ends of these hexactinellid spicules are modified to form rhomboidal

TABLE *1*—TAXONOMIC ASSIGNMENTS OF *Ischadites*

Year	Author	Assignment
1839	Murchison	"Nondescripts" (p. 697–8); "sedis incertae" (p. 712).
1842	Archiac & Verneuil	*Receptaculites neptuni = Ischadites königii*, Incertae sedis (p. 407).
1845	Austin	Sponge (p. 407)
1848	Bronn	= *Receptaculites*, incertae sedis (p. 614, 1079).
1850	Orbigny	Palaeospongia, sponge (p. 26).
1852	Quenstedt	Problematical (p. 671).
1852	Owen	Selenoides, Foraminifera (p. 587).
1861	Hall	No assignment (p. 14–15).
1863	Hall	No assignment (p. 67–69).
1865	Billings	"Foraminifera near Orbitolites" (p. 386).
1865	Winchell & Marcy	Foraminifera (p. 85–6).
1868	Bigsby	"Clearly a regularly formed sponge with roots, J.W.S." (p. 3).
1875	Gümbel	Dactyloporidae of calcareous algae (p. 172); "Zwischenformen" (p. 212).
1877	Miller	= *Receptaculites*, Protista (p. 43).
1880	Zittel	Foraminifera (p. 728).
1880	Roemer	Foraminifera (p. 291–2).
1884	Hinde	Proifera, Order Hexactinellidae, Suborder Lyssakina (p. 836).
1886	James	Sponge (p. 249).
1887	Schlüter	No assignment (p. 7,25).
1888	Geinitz	Sponge (p. 19).
1888	Hinde	Family Receptaculitidae in sponges (p. 119).
1889	Nicolson & Lydekker	Lyssakine hexactinellid sponge (p. 172–3).
1891	Rauff	*Palaeospongia* is a sponge (p. 92).
1892	Rauff	Not a sponge, position uncertain.
1893*a*	Rauff	Not a sponge, position uncertain
1893*b*, 1895	Rauff	Not a sponge, position uncertain.
1895	Winchell & Schuchert	Poriferra, Order Hexactinellida, Suborder Lyssakina (p. 63–6).
1897	Whiteaves	Family Receptaculitidae, no assignment (p. 143–4).
1900	Schuchert	Family Receptaculitidae, class uncertain (p. 153).
1900	Zittel	Questionable position (p. 67).
1909	Grabau & Shimer	Porifera (p. 19).
1910	Zittel	Receptaculitida, uncertain position?
1912	Reed	No assignment (p. 117–8).
1915	Bassler	No assignment (p. 668).
1932	Kiaer	"Calcareous alga (?)" (p. 104).
1938	Twenhofel	Porifera (p. 36–7).
1941	Roy	Incertae sedis (p. 59–61).
1944	Shimer & Shrock	Incertdae sedis, spongelike (p. 57).
1948	Wilson	"Appendix to Spongiae, Incertae sedis" (p. 24–5).
1952	Moore, Lalicker, & Fischer	Not Porifera (p. 87).
1952	Moret	Position uncertain (p. 358).
1953	Shrock & Twenhofel	Spongelike, unknown affinities (p. 92).
1954	Weiss	Porifera (p. 427–8).
1955	Laubenfels	"Kingdom, Phylum, Class, Order uncertain" (p. 108).
1957	Lowenstam	" 'aberrant' sponges" (p. 236–7).
1958	Fenton & Fenton	Problematica (p. 65).
1960	Easton	Incertae sedis (p. 118).
1960	Ehrenberg	Uncertain position (p. 38).
1960	Beerbower	"Spongelike" (p. 230).

summit-plates, which are nearly in contact, and are arranged in obliquely curved intersecting rows, giving the external surface of the fossil very much the appearance of the engine-turned case of a watch. Internal to the summit-plate, each radial spicule gives off four transverse or horizontal rays, as in the genus *Receptaculites;* but the inner ends of the radial spicules simply terminate in pointed extremities, and there is, therefore, no internal plated membrane such as characterizes the latter genus.

The "radial spicules" were undoubtedly the ridges on the proximal side of the inner wall. In other respects, this is an exceptionally good description of the form.

The statements by Wilson (1948) are very difficult to follow. She said (p. 24) that "Each ridge [on the surface] contracts irregularly in width and height near each canal opening [actually cavity left after solution of a branch], around which it swerves." Yet on the following page (p. 25) she stated, "*Ischadites* has often been confused with *Receptaculites*, but it definitely differs from that genus in its outer surface, having ridges protecting the canal openings in place of plates." The "cloaca" to which she refers seems to have been the central axis which we infer gave rise to the branches.

Weiss (1954) correctly interpreted the radial elements as solid structures, which he termed "spicule rays," and described for the first time "superficial spines" along the periphery of the surface of a broken specimen. The latter elements are not present in our specimen, and will be discussed later.

ISCHADITES IOWENSIS (Owen)
Text-figs. 1,2; pl. 135, figs. 1–5;
pl. 136, figs. 1–5

Synonymy.—Some of the synonyms are listed in Table 2, together with the taxonomic assignment of the species. The synonymy up to 1915 is listed by Bassler (1915, p. 669). The only subsequent junior synonym, insofar as we know, is *I. ottawaensis* Wilson (1948, p. 26–7), as recognized by Weiss (1954, p. 427).

General form.—Only the thallus is presently known, but presumably the organism was anchored by a rhizoidal system such as is present in living dasycladaceans. The thallus consists of a group of branches, presumably radiating from an uncalcified original central axis, near the distal ends of which were formed the gametangia. Gametangia calcified to form gametocysts. Branches bear distal and subdistal expansions to form two walls, between which the gametocysts lie (text-fig. 1).

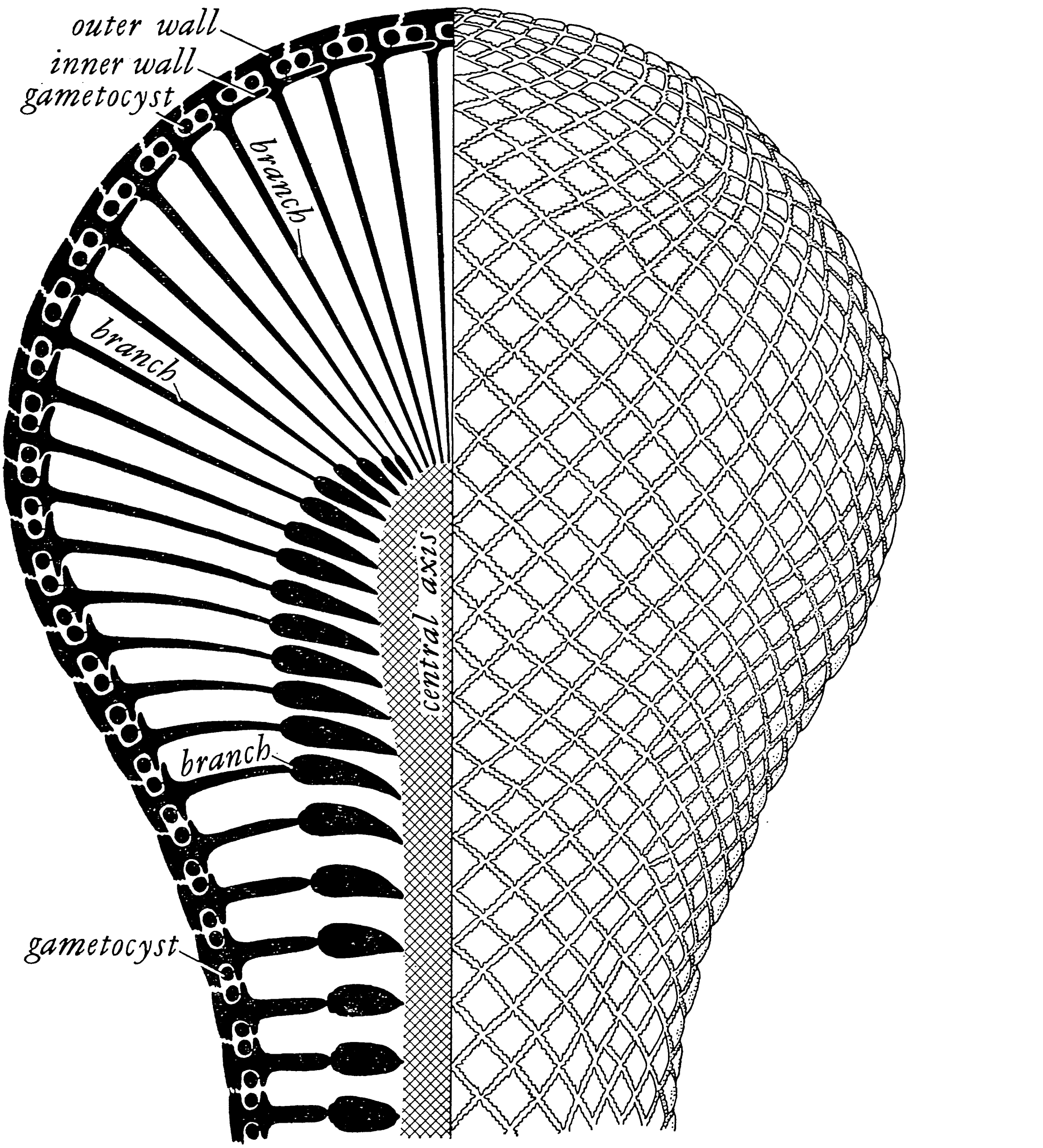
Shape of thallus.—From the variations in shape of the specimens that have been illustrated previously, it is obvious that this alga (1) originally grew in a variety of external forms, or (2) after burial was deformed in many ways due to the lack of calcification in the central axis. Possibly both factors contributed to the variations. We can only agree with Wilson (1948, p. 24) that the fossils are "subglobular, cone, biscuit, or irregularly horn-shaped forms," to which we might add bulbous as best describing our specimen (pl. 135, fig. 3). Inasmuch as our specimen has the best preservation of any yet found, we would venture to assert that it probably represents the original shape rather faithfully.

It is possible that the central axis was originally much longer than the part represented in any described specimens. A living dasycladacean, *Acetabularia*, gives rise to successive whorls of infertile branches ("sterile hairs") which are shed prior to the formation of the disk of fertile branches (Smith, 1955, p. 119). Some of the specimens of *Ischadites* previously described may have been immature, in which case they would lack gametocysts or any form of gametangia.

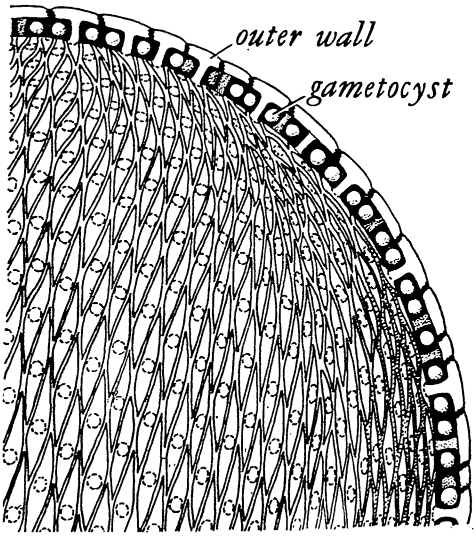
Branches.—All branches are simple in our specimen (pl. 135, fig. 1). The shafts of the branches in the first-formed part of the thallus bear thick proximal califications (text-fig. 1; pl. 135, fig. 3); those near the end have thinner and shorter calcifications; and those around the tip are long and acicular (pl. 136, fig. 2). The older branches are more or less radially disposed around the inferred central axis, so that they are lateral, whereas the younger radiate out from the end region of the axis. Because the terminal branches are longest, we infer that this thallus was fully mature. The thick calcification of the proximal part, noted in longitudinal section (pl. 135, fig. 3) appears to be progressive with the age of the branch.

Each branch bears a distal expansion which forms a unit of the outer wall and a subdistal expansion which forms a unit of the inner wall.

Inner wall.—Each unit doubly lanceolate, scarcely wider than the shaft of the branch of which it is a part (text-fig. 2). Units closely packed (pl. 135, fig. 4). Each tip of a unit projecting well beyond the shafts of the branches in the rows below or above (pl. 136, fig. 3). Each unit set with its long direction at an angle of 25 to 30 degrees to that of the central axis, so that the units



TEXT-FIG. *1.* Reconstruction of thallus of *Ischadites iowensis* (Owen) as seen from the side. The right half of the sketch shows the exterior of the thallus, and the left half shows the longitudinal section. The basal branches of the thallus have thick proximal calcifications; toward the apex the amount of proximal calcification progressively decreases; and the apical branches are acicular, with no trace of proximal thickening. The central axis is not preserved in the known specimens.



TEXT-FIG. 2. Reconstruction of part of thallus of *Ischadites iowensis* (Owen) as seen from the side. The outer wall has been exfoliated from all except the periphery, showing the pattern of plates in the inner wall. Compare with text-fig. 1.

appear to proceed upward in steep spirals; actually, they are parts of branches which more or less alternate in successive rows (text-fig. 2; pl. 135, fig. 1).

On weathered surfaces (pl. 135, fig. 2), the matrix between units remains as narrow crests, forming a rhomboidal network, and the units are sculptured and incised by solution. Further solution would doubtless produce the kind of fossil encountered and described by Wilson (1948).

On a tangential polished surface, the innermost part of each unit extends from the shaft as a narrow needle (pl. 136, fig. 1). From this we conclude that the internal surface of each unit is marked by a median ridge extending from the shaft to each tip of the unit.

Outer wall.—In contrast to the units of the inner wall, which are long and narrow, those of the outer wall are nearly square. The diameter of the thallus was increased by the intercalation of additional branches with irregular or triangular outer-wall units (text-fig. 1; pl. 136, fig. 1); otherwise the branches successively alternate in horizontal rows. Because the square units have their diagonals set vertical, they appear to be disposed in slanting 45-degree "rows" (text-fig. 1; pl. 135, fig. 1; pl. 136, fig. 1). The edges of the units are fimbriate (pl. 136, fig. 1).

Because the units of the outer wall and those of the inner wall have their diagonals set at different angles to the long axis of the thallus, two different patterns of "rows" are produced, approximately 15 degrees apart. Units in each wall fit about equally closely. The gametocysts are too large to pass outward between units of the outer wall or inward between units of the inner wall.

On a weathered surface, the outer face of each unit in the outer wall bears short, irregular, subpyramidal spinose projections. These are neither as long nor as discrete as the "superficial spines" clearly depicted and described by Weiss (1954, pl. 41, fig. 2, p. 427). In the other hand, the branches in the squashed specimen described by Weiss do not show clear differentiation of inner and

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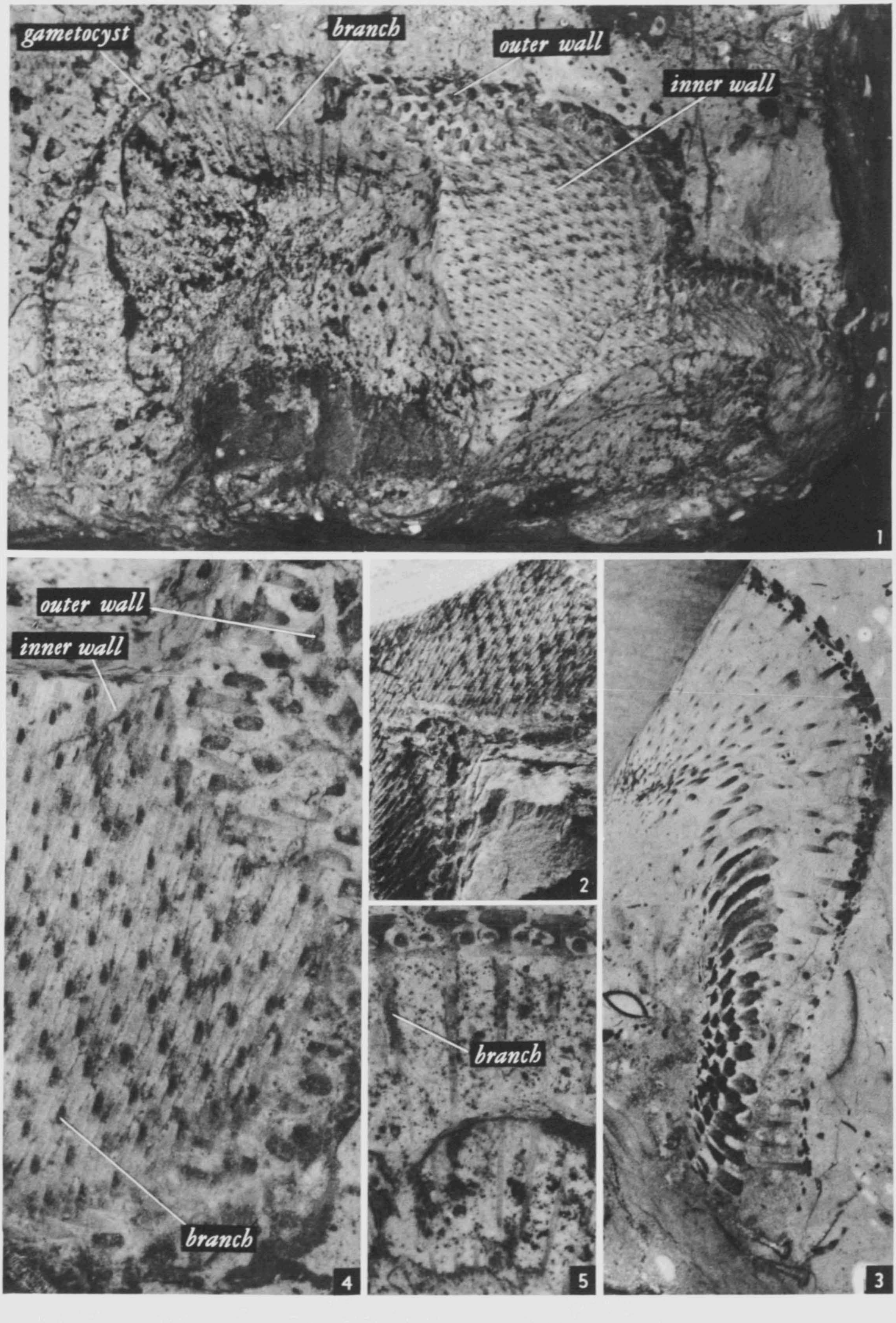
EXPLANATION OF PLATE 135
(All figures of specimen UMMP 30526)

FIGS. *1–5*—*Ischadites iowensis* (Owen). *1*, entire specimen as discovered, submersed in xylol, ×2. *2*, inner wall and a narrow V-shaped band of outer wall, lightly coated with sublimate of ammonium chloride, ×2. *3*, polished longitudinal surface, submersed in xylol, ×2. *4*, part of specimen as discovered, showing area of inner wall at the left and outer wall at the upper right; branches appear on area of inner wall as dark spots; submersed in xylol, ×5. *5*, part of surface as discovered, showing radial arrangement of branches in apical portion of thallus, submersed in xylol, ×5.


gametocyst
branch
outer wall
inner wall
1
outer wall
inner wall
branch
4
2
branch
5
3

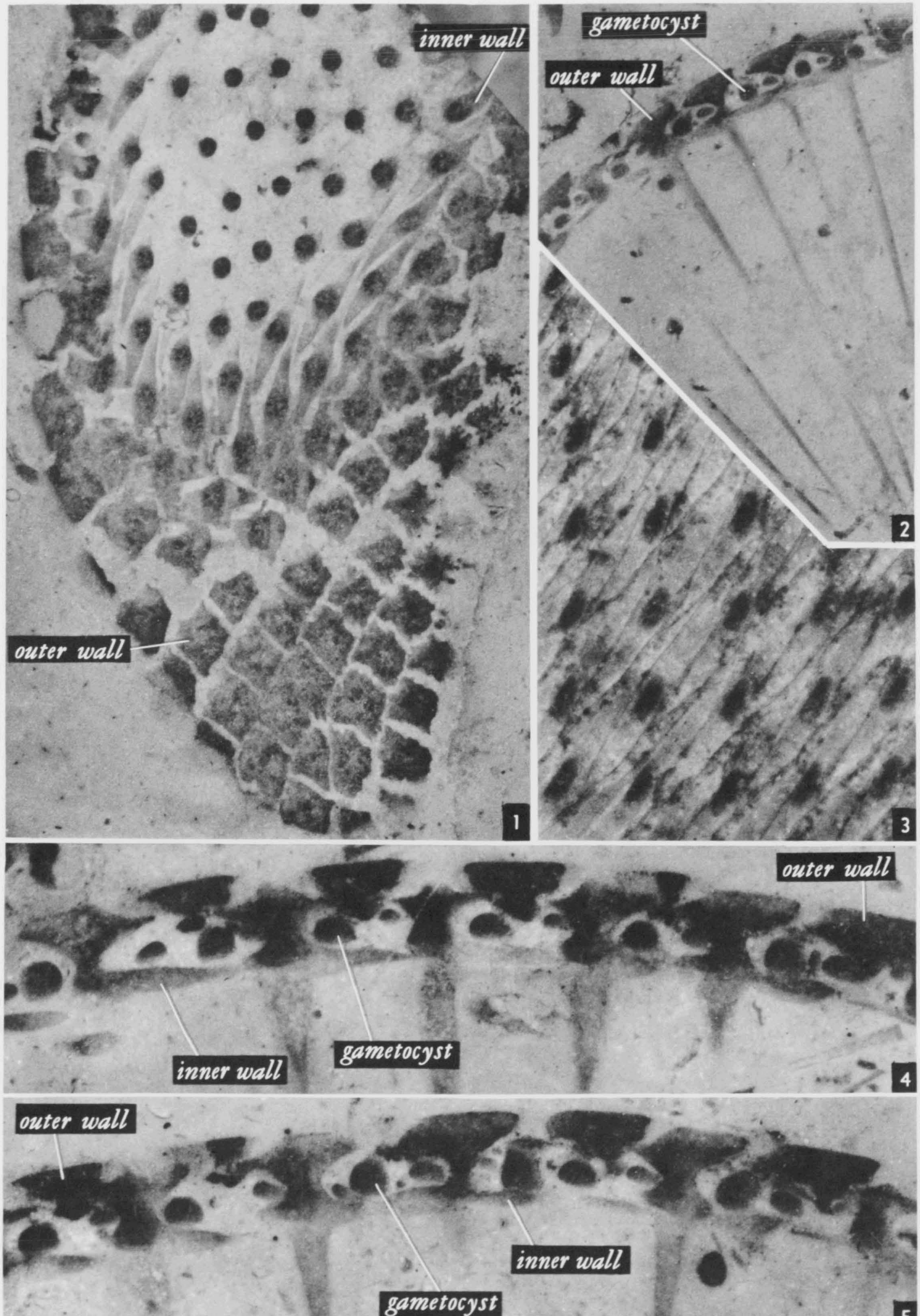

inner wall
outer wall
1
gametocyst
outer wall
2
3
outer wall
inner wall
gametocyst
4
outer wall
inner wall
gametocyst
5

TABLE 2—SYNONYMY AND TAXONOMIC ASSIGNMENT OF *Ischadites iowensis* (OWEN)

Year	Author	Name	Assignment
1844	Owen	*Orbitolites reticulata* (pl. 18, fig. 7)	
1852	Owen	*Selenoides iowensis* (p. 587, pl. 2B, fig. 13)	Foraminifera
1861	Hall	*Receptaculites (Selenoides) iowene* (p. 14–15)	
		R. fungosum (p. 15–16)	
		R. globulare (p. 16)	
1863	Hall	*R. iowensis* (p. 69)	
1865	Billings	*R. iowensis* (p. 385–86)	"Foraminifera near *Orbitolites*"
1868	Bigsby	*R. iowensis* (p. 4)	Sponge
1868	Meek & Worthen	*R. globularis* (p. 301, pl. 2, fig. 2*a*,*b*)	Protozoa
		R. ——— (p. 301–02, pl. 2, fig. 1*a*,*b*)	Protozoa
1877	Miller	*R. iowensis* (p. 44)	
1884	Hinde	*Ischadites koenigii* (part) (p. 836)	Porifera, Hexactinellidae, Lyssakina
1889	Nicholson & Lydekker	*I. iowensis* (p. 172)	Lyssakine sponge
1889	Lesley	*R. iowensis* (p. 852, 1 fig.)	
1895	Winchell & Schuchert	*I. iowensis* (p. 63–66; pl. F, figs. 5,6)	Porifera, Lyssakina
1895	Whitfield	*R. globularis* (p. 44; pl. 5, fig. 7)	
		R. fungosum (p. 45, pl. 5, figs. 5,6)	
1895	Dana	*R. iowensis* (p. 513)	Relation to sponges very doubtful
1897	Whiteaves	*I. iowensis* (p. 143–44)	
1900	Schuchert	*I. iowaensis* [sic] (p. 153)	Class uncertain
1909	Grabau & Shimer	*R. (I.) iowensis* (p. 19, text-fig. 30)	Porifera
1912	Reed	?*I.* ? *inosculans* (p. 117–8)	
1915	Bassler	*I. iowensis* (p. 669)	
1941	Roy	*I. iowensis* (p. 59–61; fig. 29*b–e*)	Incertae sedis
1944	Shimer & Shrock	*I. iowensis* (p. 47; pl. 17, figs. 27–28)	Incertae sedis, "spongelike fossils"
1948	Wilson	*I. iowensis* (p. 25–6; pl. 12, figs. 5,6; pl. 13, figs. 7–8)	Incertae sedis
		I. ottawaensis (p. 26–7; pl. 13, figs. 1–4)	
1952	Moore, Lalicker, & Fischer	*I. iowensis* (p. 87; figs. 3–5, 2*a*,*b*)	Not Porifera
1954	Weiss	*I. iowensis* (p. 427–8; pl. 41, figs. 1,2)	Porifera
1955	de Laubenfels	*I. iowensis* (p. 109)	See Table 1
1958	Fenton & Fenton	*I. iowensis* (p. 65)	Problematica
1960	Easton	*I. iowensis* (figs. 3–8; 2*a–c*)	Incertae sedis

EXPLANATION OF PLATE 136

(All figures of specimen UMMP 30526 submersed in xylol)

FIGS. *1–5*—*Ischadites iowensis* (Owen). *1*, polished tangential surface, showing fimbriate edges of plates in the outer wall, relationship of inner wall to the outer, and spacing of branches (shown in upper part of figure as dark circles), ×5. *2*, polished oblique surface in apical portion of thallus, showing radial arrangement of branches, ×5. *3*, weathered surface of inner wall, with branches appearing as dark spots, ×10. *4,5*, polished oblique surfaces showing distal parts of the thallus, ×10.

outer walls. We suppose that it may have been immature and the branches infertile, like the earlier-formed, compound branches called "sterile hairs" in the living *Acetabularia* (Smith, 1955, p. 119).

Gametocysts.—Numerous gametocysts lie between the inner and outer walls (pl. 135, fig. 1; pl. 136, figs. 2,4–5). None show the attachment clearly, but they appear to lie closer to the inner wall than the outer. Possibly they formed on the inner wall, as portrayed in text-fig. 1, or on the shaft of the branch between the two walls. No evidence of an operculum was seen on any gametocyst, but such a structure would be difficult to decipher from polished surfaces.

Specimen.—UMMP 30526, Trenton rocks exposed in a small quarry known as the Pine Ridge Quarry, operated for road metal, in the SE¼ NW¼ sec. 28, T. 39 N., R. 23 W., about 4 miles west of Escanaba, Delta County, Michigan. Collected by Mr. Arthur Slaughter, of the Geological Survey Division of the Michigan Department of Conservation, while visiting the quarry with Prof. George M. Ehlers and the senior author in 1958.

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