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'MODERN' SILICEOUS SPONGES FROM THE LOWERMOST ORDOVICIAN (EARLY IBEXIAN – EARLY TREMADOCIAN) WINDFALL FORMATION OF THE ANTELOPE RANGE, EUREKA COUNTY, NEVADA, U.S.A.

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With 1 figure and 5 plates

Abstract

Siliceous sponge spicules occur abundantly in the upper part of the Windfall Formation, Antelope Range, central Nevada, U.S.A., and can be dated by conodonts as Cordylodus angulatus Zone (early Ibexian in North American terms – early Tremadocian in North Atlantic usage). Spicules of hexactinellid sponges prevail; they are mostly simple smooth hexactines. Hexactines and pentactines are similar to Cambrian morphotypes, but some new sclerite types are developed by atrophy. The discovery of scopules in the lowermost Ordovician is surprising because this requires an early separation of Clavularia and Scopularia. Until now, the oldest scopules were known from the Middle Triassic. The Demospongiae of the investigated samples are characterized by diverse microscleres. The occurrence of numerous sigmatose microscleres is remarkable. Not only were numerous sigmata and toxa found, but also sclerites of the forceps type that appear in the Upper Cambrian. Discovery of discorhabds with verticillate arrangement of spines, a spicule type that is restricted to representatives of the family Latrunculidae is very surprising. Until now the oldest known fossil representatives of this family were known from the Tertiary. However, according to our investigations, the Latrunculidae were already present in the lowermost Ordovician. The discovery of micro- and megascleres of „modern" Hexactinellida and Demospongiae in the lowermost Ordovician, their absence in the Silurian to Early Triassic time interval, and their iterative appearance during the Middle Triassic may be explained by a repeated convergent development of scopules, sigmata, toxa, and forcipes. Another explanation would be a very long survival in so far unknown refugia, especially for those forms that appear suddenly in the Middle Triassic with highly diverse forms.

Zusammenfassung

Die hier beschriebene Kielselschwammfauna bzw. deren Spicula aus dem oberen Teil der Windfall-Formation von der Antelope Range, Nevada, U.S.A., lassen sich mit Conodonten in die Cordylodus angulatus Zone (unteres Ibexian in der Nordamerikanischen Untergliederung = unteres Tremadoc in der Nordatlantischen Gliederung) einstufen. Spicula hexactinellider Schwämme überwiegen; es handelt sich vor allem um einfach ausgebildete glatte Hexactine. Sowohl Hexactine als auch Pentactine schließen eng an die Bauformen jener des Kambriums an; z.T. kommt es durch Atrophie zur Bildung neuer Sklerentypen. Überraschend kommt der Nachweis von Scopulen aus dem basalen Ordoviz, zumal dadurch die frühe Trennung von Clavularia und Scopularia gefordert werden muß. Der Erwerb von Scopulen wurde bisher in der Mitteltrias festgestellt. Die Demospongien sind durch eine diverse Mikrosklerenführung ausgezeichnet. Bemerkenswert sind die vielen sigmatosen Mikroskleren. Es wurden nicht nur viele Sigmen und Toxe gefunden, sondern auch Skleren vom Typus Forceps, die übrigens schon im Oberkambrium einsetzten. öberraschend ist auch der Nachweis von Discorhabden mit einer verticillitiden Anordnung der Dornen, ein Spicula-Typ, der ausschließlich auf Vertreter der Familie Latruculidae beschränkt ist. Die bisher ältesten fossilen Vertreter dieses Formenkreises stammen aus dem Tertiär. Nach unseren Untersuchungen muß das Einsetzen der Latrunculidae auf jeden Fall bis in das Ordoviz zurückgenommen werden.

Unser Nachweis von „modernen" Hexactinelliden und Demospongien aus dem basalen Ordoviz auf Basis von Mikro- und Megaskleren und das Fehlen dieser Formen im Zeitraum Silur bis Untertrias sowie deren Wiederauftreten in der Mitteltrias kann dahingehend gedeutet werden, daß sich Scopulen, Sigmen, Toxa und Forcipes zweimal konvergent gebildet haben. Rückzug in unbekannte Reliktareale, aus denen in der Mitteltrias eine Neubesiedlung erfolgte, kann jedoch nicht in jedem Fall ausgeschlossen werden, vor allem bei jenen Formen, die in der Mitteltrias unvermittelt in großer Formenfülle neu einsetzten.

Introduction

Well preserved conodonts, radiolarians and sponge spicules were investigated from the lowermost Ordovician Windfall Formation in central Nevada, U.S.A. Samples 6-18-76 H and 6018-76 I (USGS locality numbers 11306-CO and 11307-CO, respectively) were collected by JER from the upper part of the Windfall Formation in a section in Ninemile Canyon, on the west side of the Antelope Range (see MERRIAM, 1963, for discussion of stratigraphy of this section). Locality for both is 39°12'16" N Lat.; 116°15'25" W Long., on the Horse Heaven Mountain 15' quadrangle map. The Windfall comprises chiefly dark gray to brown-black thin-bedded shales and fine-grained to silty limestones, and most likely represents outermost shelf or slope facies (TAYLOR & REPETSKY, 1985).

Sample 6-18-76 H (11306-CO) was collected at 280 feet below the top of the Windfall Formation. Its conodont fauna includes *Cordylodus caboti* BAGNOLI, BARNES & STOUGE, *C. lindstromi* DRUCE & JONES, *C. proavus* MÜLLER, *Eoconodontus notchpeakensis* (MILLER), *Utahconus utahensis* MILLER, and the para- and protoconodonts *Phakelodus elongatus* (AN), *Ph. tenuis* (MÜLLER), *Prooneotodus gallatini* (MÜLLER), and *Pr. rotundatus* (DRUCE & JONES).

Sample 6-18-76 I (11307-CO) is from 241 feet below the top of the Windfall. It contains *Cor-*

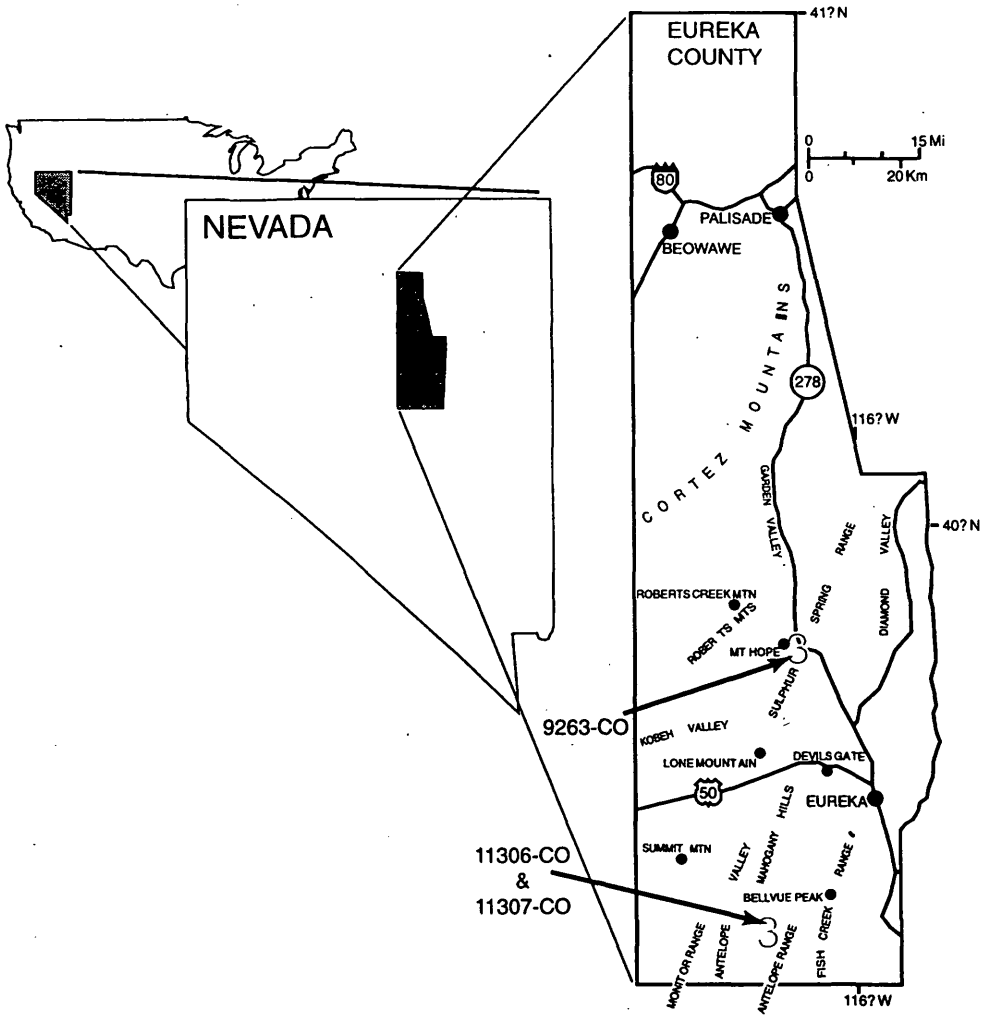

Fig. 1: Location map of Ordovician sponge spicule-bearing samples in Eureka County, Nevada, U.S.A.

dylodus angulatus PANDER, *C. intermedius* FURNISH, *C. lindstromi* DRUCE & JONES, *C. proavus* MÜLLER, *Iapetognathus sprakersi* LANDING, aff. *Laurentoscandodus triangularis* (FURNISH), *Paltodus* sp., and *?Rossodus tenuis* (MILLER).

Both samples from the Windfall are from within the early Ibexian (North American Series = early Tremadocian in North Atlantic terms) Cordylodus angulatus Zone, their age being constrained by their enclosed faunas and by those of underlying samples (JER; unpub. USGS collections).

Previously, ETHINGTON (1972, 1981) discussed the stratigraphy and described conodont faunas from units at this section, from the Caryocaris Shale Member of the Goodwin Formation (early Ibexian/Tremadocian; Rossodus manitouensis Zone fauna) which immediately overlies the Windfall, and from the somewhat higher (late Ibexian/Arenigian) Ninemile Formation. Conodonts from the Windfall and from the Caryocaris Shale Member and overlying limestone member of the Goodwin Formation also have been treated in REPETSKY & TAYLOR (1982), ETHINGTON & REPETSKY (1984), and TAYLOR & REPETSKY (1985).

Along with rich conodont faunas and primitive radiolarians (the latter will be described in a separate paper by the present authors, in prep.), numerous spicules of siliceous sponges and of Heteractinida are present. Sample 6-18-76 I (11307-CO) is especially rich in siliceous sponge spicules. All described forms were derived from this sample, and further sponge spicules will be described in a second paper by the present authors (in press). Sample 6-18-76 H (11306-CO) has an identical, but poorer sponge spicule association and the preservation is not as good.

The Hexactinellida (with a rather monotonous sclerite association) predominate relative to the Demospongiae. The Hexactinellida are represented chiefly by different hexactines that are dominated by morphotypes with inflated rays. Striking among the various forms are echinate pentactines, especially Pinularia, which are similar to the pinule-pentactines or perhaps were derived from them. Kometasters, described by WEBBY & TROTTER (1993) from the Late Ordovician, are present but very rare. Analogous spicula were discovered from the Middle and Upper Cambrian by DONG & KNOLL (1996), who introduced for them a further new genus *Flosculus*, which is a junior synonym of *Kometia* WEBBY & TROTTER, 1993.

The Demospongiae are represented chiefly by different microscleres, both sigmatose and astrose scleres. Also present is a possible representative of the streptastrose morphotype . The common presence of C-shaped sigmata and asters is remarkable . Also surprising is the occurrence of discorhabds, which indicate an early appearance of the Latrunculidae. The sigmatoscleres are represented exclusively by sigmata having C-shapes. It is still open to question whether the C-shaped curved echinate scleres are thorny strongyloxes or moderately curved forcipes. In the latter case, representatives of the taxon *Forcepia* would be present already in the lowermost Ordovician.

The interpretation of the occurrence of C-shaped sigmata in the Early Paleozoic and their absence in the entire Late Paleozoic also is difficult. Although one of the authors (H. MOSTLER) has studied very rich collections of the Carboniferous and Permian sclerites of siliceous sponges, not a single C-shaped sigmatose sclerite nor any other sigmatose sclerite type has been found in this material. Not until the Middle Triassic is an abrupt appearance of very diverse C-shaped microscleres observed. Their maximum occurrence is in the Liassic from our present knowledge (MOSTLER, 1990 a). There are two possible explanations: (1) Siliceous sponges with sigmatoid scleres of the Early Paleozoic retreated in the Late Paleozoic into environments or restricted areas that have not been not discovered yet, and they survived in these refugia until the Middle Triassic, where they spread again over large areas. (2) This type of microscleres developed iteratively during the Middle Triassic, long after the extinction of the Early Paleozoic sponges with these types of microscleres.

Additional skeletal elements of siliceous sponges in our Early Ordovician fauna are rhabdostyles and very thick oxeas. Unusually shaped triodes are difficult to interpret. Only one acanthine protriaen was found.

The Heteractinida, which accompany the siliceous sponges of our fauna, will be described in a separate paper by the present authors.

Description of the Spicula

In this section, first the different types of spicules of the Hexactinellida and the Demospongiae are briefly described, and then their systematic assignments and stratigraphic range are discussed.

1. Hexactinellida

A) Hexactines

All hexactines are smooth. The following types can be distinguished:

1. All six rays have the same length (Pl. 1, Fig. 3).
2. All six rays have the same length, but are strongly thickened or inflated (Pl. 1, Fig. 2).
3. Four rays have the same length, two opposite rays are longer (Pl. 1, Fig. 9).
4. Hexactine with six slender rays; two opposite rays are very long, the second opposite ray pair is somewhat shorter and the third one is very short.
5. Four rays in one plane (paratangentialia, paratangential rays) are proximally constricted (Pl. 1, Fig. 10).
6. Foil-shaped hexactine with or without thickening of the rays (Pl. 1, Figs. 1 and 4).
7. All six rays are variable in length and width (Pl. 1, Fig. 13).
8. Rays variably thickened, distal ray strongly curved (Pl. 1, Fig. 6).
9. Long, thick proximal ray and rudimentary distal ray, paratangentialia very short (Pl. 1, Fig. 11).
10. Pinule-like hexactine; the strongly thickened distal ray reminiscent of a pinule-ray (Pl. 1, Fig. 5).

Discussion

Among the hexactine types mentioned above, those in which the six rays are thickened (inflated) (type 2) are quite remarkable. Their shapes are not as extreme as those of Cambrian forms (*Rigbyella* MOSTLER & MOSLEH-YAZDI, 1976, *Thoracospongia* MEHL, 1996), but they may be derived from *Rigbyella*. Hexactines with strongly inflated rays are known throughout the Paleozoic. They are especially common in the Permian (dermal scleres of Stiodermatidae FINKS; in some only the distal ray is inflated globularly, but in many cases the paratangentialia also are strongly inflated, see MEHL & MOSTLER, 1993, Pl. 5). During the Mesozoic such spicula types seem to be absent.

The type 10 morphology, with inflated distal ray and long paratangential rays, is similar to a pinule-hexactine. The inflated distal ray resembles a pinule ray, but does not have its typical structure. True pinule hexactines are known from the Upper Ordovician (WEBBY & TROTTER, 1993, Figs. 6, 16, 18, 19; VAN HINTE & RUFFMAN, 1995, Pl. 5, Fig. 3). The view that the Lower Cambrian acanthine hexactines (ZHANG & PRATT, 1994, Fig. 3 N) are the ancestors of the pinule hexactines, is rather improbable.

The foil-like, smooth hexactines (type 6) seem to have appeared in the lowermost Ordovician.

Smooth hexactines with rays of unequal lengths and widths also were unknown from the Ordovician until now. Hexactines of this type are unknown in the Upper Paleozoic as far as we know, but they re-appear after the Upper Triassic. The function of the inflated proximal ray of the type 9 hexactine is not clear.

A special type of an Upper Ordovician hexactine was figured by WEBBY & TROTTER (1993, Fig. 3: 1–10). It belongs to *Kometia cruciformis* WEBBY & TROTTER. Very similar Upper Cambrian kometasters were figured by DONG & KNOLL (1996, Fig. 3: 9–16, 19), who assigned them to a new taxon *Flosculus gracilis*. In our opinion, this new genus and species is not justified, the more so as *Flosculus* is based on incompletely preserved scleres (the ends of the umbel-rays are always broken away). The Upper Cam-

brian *Flosculus* most likely is a junior synonym of Kometia. The Middle Cambrian kometaster figured by MEHL (1996, Pl. 3, Figs. 5, 6) belongs to the same morphogroup and probably to the same genus (*Kometia* WEBBY & TROTTER, 1993; by priority).

In our material we have found a form (briefly discussed in the systematics section) that belongs possibly to *Kometia*.

B) Pentactines

In our material, there are smooth acanthine pentactines, pinule pentactines and pentactines with a specially differentiated central ray. The following types can be distinguished:

1. Smooth pentactine with very long central ray (Pl. 2, Fig. 11).
2. Smooth pentactine with very long curved central ray (Pl. 2, Fig. 12).
3. Smooth pentactine with straight long central ray and four, strongly upward-directed paratangential rays of different length (Pl. 1, Fig. 12).
4. Pentactine with short, broad pinule ray and four, thorny paratangential rays of more or less equal length (Pl. 2, Fig. 17).
5. Pentactine with four smooth, slightly upward direced rays and a very long, moderately thorny main ray (Pl. 2, figs. 14, 16).
6. Pentactine with four short paratangential rays and a flag-like, marginally denticulated, but sometimes also smooth central ray (Pl. 2, Figs. 1–6).

Discussion

Smooth pentactines with curved central rays are known from the Middle Cambrian (DONG & KNOLL, 1996). The occurrence of the pentactine of type 5 is documented from the Lower Cambrian (BENGTSON et al., 1990, Figs., 15 A, B, D and F). Pentactines of this type are distributed throughout the entire Paleozoic, but especially common in the Permian (these forms will be described in the systematic part). The pinule-pentactine (type 4) is known from the Upper Cambrian (BENGTSON, 1986, Fig. 8 F). It is still relatively rare during the Lower Paleozoic, but is widely distributed during the Upper Paleozoic. Of note, and surely a new spicule morphotype, is the pentactine of type 6. It has a central „flag" ray and belongs to the morphogroup of *Australispongia* DONG & KNOLL (see systematic descriptions).

Stauractines

Only strongly thorny stauractines were found in our material (Pl. 2, Figs. 13, 15). Bengtson (1986, Fig. 9A) figured a thorny stauractine with numerous small thorns from Upper Cambrian beds.

C) Scopules

Three, unfortunately incompletely preserved, specimens of scopules were found that belong to two morphotypes:

1. Slender scopule that is very similar to a Middle Triassic scopule.
2. A widely projecting spicule with 9 crown-rays and one central ray. Both the central ray and the outer crown-rays are ornamented. Scopules of this type are known from the Lower Liassic (MOSTLER, 1990 b, Pl. 3, Fig. 8).

Discussion

The previous view that scopule-bearing Hexactinellida developed during the Middle Triassic (MOSTLER, 1990 b, p. 156) must be revised. This new evidence of scopule-bearing Hexactinellida within the lowermost Ordovician demonstrates that the Scopularia must have already separated from the Clavularia during the Upper Cambrian.

D) Uncinates

Our lowermost Ordovician material contains three types of uncinate spicules:

1. Uncinate with large distances between the spines (Pl. 2, Fig. 7).
2. Uncinate with narrowly spaced thorns (Pl. 2, Figs. 8, 9).
3. Lanceolate uncinate with glochidiate, narrowly spaced spines.

Discussion

Uncinate spicules are present rarely in the Middle and Upper Cambrian (DONG & KNOLL, 1996, Figs. 7, 31). Upper Ordovician uncinates are common and diverse (WEBBY & TROTTER, 1993, Fig. 5: 17–22). It is probable that the spicule fragments figured by WEBBY & TROTTER (1993, Fig. 5:1–16) also are fragments of uncinates and not acanthostyles of Agelasida, as interpreted by these authors. Lanceolate uncinates (type 3) are similar to Liassic ones figured by MOSTLER (1990 b, Pl. 1, Figs. 12, 15).

2. Demospongiae

Demospongiae are represented by different microscleres but not diverse megascleres. The following groups are present:

A) Sigmatoscleres

a) Sigmata (Pl. 4, Figs. 1–4, 6–8)
Only C-shaped sigmata are present (sigmatoid sensu RAUFF, 1894). These are exclusively smooth spicules with different radius of curvature. In some specimens, a slight buckle is present in the middle part of the spicule, especially on the outer side. These forms resemble somewhat centroangulate sigmata (Pl. 4, Fig. 3, indistinct also in Figs. 1, 4, 6). In one sigma, a very strong recurvature of the distal ends can be observed (Pl. 4, Fig. 7). Similar sigmata were figured by MOSTLER (1990 a, Pl. 2, Fig. 2) from the Lower Jurassic.

b) Toxa (Pl. 3, Figs. 12, 13)
Our material contains only slighly curved, smooth toxas. Although these spicules are similar to curved oxeas, the upcurving of their distal ends is characteristic for toxas.

c) Forceps ? (Pl. 3, Fig. 11)
A single specimen present is strongly curved in a C-shape, and by this it resembles a sigma. However, our spiculum is strongly thorny, and also the distal ends are characteristic for forcipes of the Recent species *Forcepia topsenti* (see WIEDENMAYER, 1994, Fig. 30–11b).

Discussion

Middle Cambrian sigmatose microscleres were published by KRUSE (1983). The relatively common C-shaped sigmata from our lowermost Ordovician material can be assigned to the taxon Sigmatophora. According to previous works, they occur within the Paleozoic only in the Lower Paleozoic. The rich Carboniferous and Permian spicula associations of siliceous sponges do not contain C-shaped sigmata, and they re-appear only within the Middle Triassic. Since that time they are very common and occur in several genera of Demospongiae.

The accompanying toxas (present both in Haplosclerida and Poecilosclerida) are further evidence for the early occurrence of sigmatosclere-bearing Demospongiae. HAJDU et al. (1994) subdivided the poecilosclerida sponges into three suborders, with more than 300 genera. The suborder Microcyonina has diverse toxas and palmate chelae. Chelate microscleres are absent from the Lower Paleozoic. In our opinion, they developed later (see also MOSTLER, 1990 a).

One spiculum that may be a broken forceps is especially interesting because it coincides well with forcipes of *Forcepia*. DONG & KNOLL (1996) figured U-shaped spicula that can be regarded as forcipes from the middle part of the Upper Cam-

brian. Consequently, those Demospongiae that have microscleres of the forceps type also occur since the Upper Cambrian. However, as such scleres were previously unknown in the entire Paleozoic, we still must be cautious with the interpretation. This also could be an example for a very early development of a type of microscleres which appeared iteratively very much later, e.g., in the Liassic. Only a few living sponges have forcepid microscleres: *Asbestopluma*, *Forcepia*, *Leptolabis*, *Trachyforcepia*, *Clinolabis* and *Labisophlita*. HAJDU et al. (1994, p. 131) questioned the view that the forceps spicula type evolved from a toxon spicula type because most of the forcipes are thorny, whereas acanthine toxa are rare. However, Liassic forcipes are with one exception all smooth. It is our opinion that the smooth forcipes evolved from oxeas, above all because the smooth forcipes, without exception, do not have backward-curved distal ends, in contrast to the thorny forcipes. In addition, the development of the distal ends of many forcepid spicula contradict the view that they have evolved from toxa.

B) Astrose microscleres

a) Oxyaster (Pl. 3, Figs. 1, 2, 4)
Among the astrose microscleres, with one exception, only oxyaster that have 9 to 19 rays are present . The structure observed on the surface of some of these oxyaster is caused by secondary diagenetic process and is not a primary structure.

b) Sterraster
Only one specimen was found. It has the typical bean-like shape of the rhaxe (regarded by most as a synonymous term to sterraster). The typical hilum also is present, but the original structure is no longer recognizable because of strong recrystallization.

Discussion

Astrose microscleres do not have significant diagnostic importance as they occur in many families of the Demospongiae. The oxyaster represent a primordial aster type. The „euaster" collective term sensu GRUBER (1993), which is characterized by the plesiomorph 'protoaster', cannot be regarded as monophyletic. The oldest oxyaster are known from the Lower Cambrian (ZHANG & PRATT, 1994, Figs. 3, 4i). The 'sterraster', which are believed to originate in the 'euaster', also are present since the Early Cambrian (GRUBER & REITNER, 1992). Until the Carboniferous, the sterrasters are relativly rare; since the Permian they became more abundant. In the Middle Triassic, they are present with relatively diverse types and in the Upper Jurassic they are rock-building fossils, as, for instance, in the Suevian and Frankonian Alb (Germany) or in distal turbiditic layers in the Upper Jurassic Oberalm Beds that consist almost exclusively of rhaxes. The sterrasters are typical for the Geodiidae. According to phylomorphogenetic analyses, the Geodiidae are a very early separated taxon.

RÜTZLER & MACINTYRE (1978) regarded the rhaxes as corroded selenaster. Following their view, the rhaxes would have to be assigned to the Placospongiidae, rather than to the Geodiidae with sterraster. In that case the Placospongiidae would be present since the Lower Cambrian.

C) Monaxone microscleres

Discorhabd
Only one specimen was found. It consists of a long rhabd with verticillately arranged thorns (Pl. 4, Fig. 10). One end is nearly blunt and bears indistinct thorn-like elevations. The other end is pointed. The tip lies immediately above the fifth ring of thorns.

Discussion

Discorhabds with the above described morphology occur in living sponges only as representatives of the family Latrunculidae. With the discovery of this spicula type, it can be assumed that the Latrunculidae already had appeared by the beginning of the Ordovician.

The megascleres are represented mainly by very long, straight styles. Such styles, in which a strong break is present somewhat below one rounded distal end (Pl. 4, figs. 5, 14), are present in subordinate numbers. Before, the latter morphotype was known only since the Middle Triassic (MOSTLER, 1976). Some thick oxeas are worthy of comment (Pl. 4, Figs. 12–13, 15). One edge of these spicules has an almost straight margin, the remaining parts of the spicule are convex to different degrees. By this the lateral outline is different in different views. In one view the spicule is straight at one side, but strongly convex on the opposite side (Pl. 4, Figs. 13, 15). In the other views, the spicule is spindle-shaped (Pl. 4, Fig. 13). Irregularly shaped oxeas also occur. Especially striking is an oxea with wavy rhabd, analogous to the rays of a triode, described below. Short, spindle-shaped oxeas and barely curved oxeas also are present. Short, sturdy, smooth strongyles are very rare.

Triode scleres are represented by morphotypes with wavy rays (Pl. 3, Fig. 5) that may have local thickenings (Pl. 3, Fig. 10). Also belonging to this group are those triodes that have a broad encrusted subtriangular central part (Pl. 3, Fig. 6), and morphologically resemble somewhat Radiolaria. The causes of this encrustation are an open question. Similar triodes are known from calcareous sponges.

A single specimen of acanthine protriaene was discovered (Pl. 3, Fig. 3); the entire spiculum is thorny. The oldest triaenes (Middle Cambrian) were described by VAN KEMPEN (1990). They represent smooth plagiotriaene transitional to protriaene. The same author also reported Upper Ordovician smooth triaenes. Therefore the acanthine protriaene reported herein is the first spiculum of this type discovered in Paleozoic strata (see also MOSTLER, 1996). Similar spicules are known from the Middle Triassic and were described under Costamorpha MOSTLER. They are similar to calthrops type of spicula and unrelated to our form from the lowermost Ordovician.

Systematics section

Class: Hexactinellida SCHMIDT, 1870

Genus: *Kometia* WEBBY & TROTTER, 1993
Synonym: *Flosculus* DONG & KNOLL, 1996

Remarks: The diagnosis of *Flosculus* DONG & KNOLL, 1996 is only slightly different from the diagnosis of Kometia WEBBY & TROTTER, 1993. The spicula of *Flosculus* figured by DONG & KNOLL (1996) appear somewhat different from those of *Kometia*, but this is caused by the bad preservation of the *Flosculus* spicula (terminal rays broken away). However, if badly preserved spicula of *Kometia* (WEBBY & TROTTER, 1993, Figs. 3-3 and 3-6) are compared with the likewise badly preserved spicula of *Flosculus*, no difference between these two genera can be observed. Consequently, *Flosculus* is a junior synonym of *Kometia* and the differences are due to preservation.
Assigned species:
Kometia cruciformis WEBBY & TROTTER
Kometia? sp.
Stratigraphic range: Middle Cambrian to Upper Ordovician.

Kometia? sp.

Remarks: If the present spiculum really belongs to *Kometia*, it must be assigned to a new species. However, as only one incomplete spiculum is present (the paratangential rays are missing), this new species cannot be established confidently. Moreover, incomplete preservation makes its interpretation doubtful; relations to a scopule cannot be excluded.

Genus: *Australispongia* DONG & KNOLL 1996 emend.

Type species: *Australispongia sinensis* DONG & KNOLL, 1996
Emended diagnosis: Siliceous spicules of pentactine morphologies, with a propeller-like struc-

ture of four lateral rays, diverging approximately at right angles or larger than 90 degrees from the uppermost part of the central ray. The length of the four lateral rays varies considerably, in contrast to that of the central ray. The central ray is either flat, flag-like, or elaborated into three or four longitudinal flanges (the flag-like central ray has two longitudinal flanges), the edges of which are smooth or serrated. The central ray may be nearly straight, curved, or slightly to moderately twisted.

Assigned species:

Australispongia sinensis (DONG & KNOLL, 1966)

Australispongia compressa n.sp.

Occurrence: Upper Cambrian to Middle Permian. In the Upper Cambrian only forms with tricarinate or tetracarinate central rays are present; the latter type also was found in the Permian (Guadalupian) of Texas. Forms with flattened, thin central rays with two edges are only known from the lower Tremadocian of Nevada.

Remarks: In its original diagnosis, *Australispongia* comprised only forms with three or four flanges at the central ray, whereas in our material the central ray is flat and has only two serrated flanges. Because all other features are identical, the original diagnosis is extended to forms with a flag-like central ray with two serrated flanges.

Australispongia compressa n.sp. (Pl. 2, Figs. 1–6)

Derivation of the name: Referring to the laterally strongly compressed, entirely flattened central ray.

Holotype: The specimen figured on Pl. 2, Fig. 2

Diagnosis: Pentactines with mainly very short paratangential rays and a long, flattened central ray having two, mostly serrated edges ('flag'-ray).

Description: Pentactine spicule with small, mostly very short paratangential rays. The slender to broad central „flag"-ray is entirely flattened and thin; its two margins are mostly serrated, rarely smooth.

Occurrence: So far known only from the lower Tremadocian of the Windfall Formation in Nevada.

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Explanation of Plates

All figured material is from sample 6-18-76I (USGS locality number 11307-CO), upper part of Windfall Formation, 241 feet (72 m) below the top, in a section in Ninemile Canyon, on the west side of the Antelope Range (Text-Fig. 1) All figured material is reposited in the type collections of the U.S. National Museum of Natural History (USNM), Washington, D.C.

Plate 1

Fig. 1: Hexactine of type 6, with proximal constriction of the long proximal ray, and very small distal ray, x 150; USNM 494,036.

Fig. 2: Hexactine of type 2, in which all six rays are inflated, x 200; USNM 494,037.

Fig. 3: Hexactine of type 1, with six rays of nearly equal length, x 200; USNM 494,038.

Fig. 4: Hexactine of type 6, a foil-like hexactine with extremely long proximal ray, x 130; USNM 494,039.

Fig. 5: Hexactine of type 10, with pinule-like, tumid, terminally rounded distal ray, x 200; USNM 494,040.

Fig. 6: Hexactine of type 8, in which all six rays are inflated; the distal ray is strongly curved, x 300; USNM 494,041.

Fig. 7: Ordinary hexactine, x 200; USNM 494,042.

Fig. 8: Hexactine of type 4 with especially slender rays, the three ray pairs (consisting of two opposite rays of equal length) have very different lengths; one is very long, the second is moderately long and the third is very short, x 200; USNM 494,043.

Fig. 9: Hexactine of type 3, the four paratangential rays have equal lengths, the two rays perpendicular to the paratangentialia are longer, x 200; USNM 494,044.

Fig. 10: Hexactine of type 5, with proximally constricted paratangential rays, x 100; USNM 494,045.

Fig. 11: Hexactine of type 9, with long thick proximal ray, rudimentary distal ray and very short paratangentialia, x 100; USNM 494,046.

Fig. 12: Pentactine of type 3 with partly broken central ray. It is characterized by a massive, probably long central ray and four obliquely upwards-directed rays of inequal length, x 200; USNM 494,047.

Fig. 13: Hexactine of type 7, in which all six rays are different in length and width. x 150; USNM 494,048.

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Plate 2

Figs. 1–6: Australispongia compressa n.sp. (Fig. 2 = holotype; = USNM 494,050); the flattened, very thin „flag"-ray above the short neck is broad and lanceolate (Figs. 3 and 4), high, slender, parallel-sided over a long distance (Fig. 5), or transitional between these two morphotypes (Figs. 2 and 6). In Figs. 1, 3 and 6 the central channel is partly recognizable (dissolved from the very thin flattened central rays due to diagenetic corrosion). Figs. 1, 3, 4: x 300; Figs. 2 and 6: x 150; Fig. 5 x 100; USNM 494,049-0554.

Fig. 7: Uncinate spiculum, alternating spines arranged with wide distances, x 100; USNM 494,055.

Figs. 8, 9: Broken parts of uncinate spicula, with narrowly spaced spines; Fig. 8: x 100; Fig. 9: x 150; USNM 494,056, -057.

Fig. 10: Broken central ray of a pentactine, 80; USNM 494,058.

Fig. 11: Smooth pentactine of type 1, with very long central ray, x 150; USNM 494,059.

Fig. 12: Smooth pentactine of type 2, with distinct curvature in the proximal part of the long central ray, x 300; USNM 494,060.

Figs. 13, 15: Strongly thorny stauractines; Fig. 13: x 150; Fig. 15: x 200; USNM 494,061, -062.

Figs. 14, 16: Pentactines of type 5, with slightly upwards directed, smooth paratangential rays; the central ray is thorny; Fig. 14: x 300;

Fig. 16: x 150; USNM 494,063. -064.

Fig. 17: Pinule-pentactine of type 4. The four paratangential rays are very long and thorny. The pinule ray is short, with the typical tree-like structure, x 300; USNM 494,065.

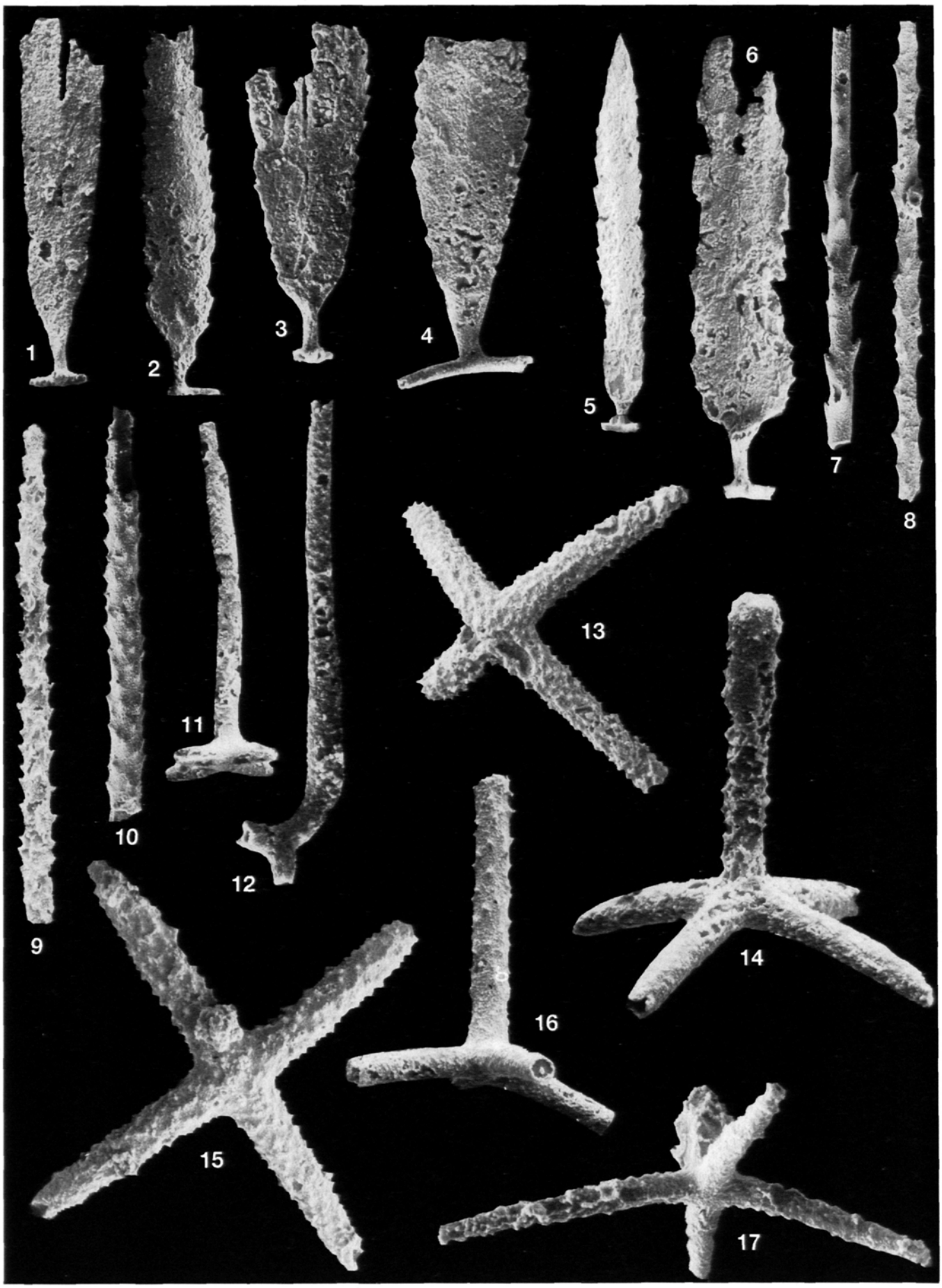
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Plate 3

Figs. 1, 2, 4: Astrose microscleres (oxyaster). These oxaster are smooth, Figs. 1 and 3 have a 'pseudostructure' caused by diagenetic processes. Figs. 1, 4: x 300; Fig. 2: x 410; USNM 494,066-068.

Fig. 3: Acanthine protriaene spicule; x 300; USNM 494,069.

Figs. 5, 10: Triode spicules with wavy rays; in addition, the specimen on Fig. 10 has local thickenings; Fig. 5: x 200; Fig. 10: x 300; USNM 494,070, -071.

Fig. 6: Triode spicule, in which the broad, subtriangular central part is covered by a sponge-like layer, x 500; USNM 494,072.

Figs. 7–9: Broken specimens of echinate ?styles, x 200; USNM 494,073-075.

Fig. 11: Sigma-like spiculum; the button-like end of the rhabd favors an interpretation as moderately curved echinate forceps spiculum, x 200; USNM 494,076.

Figs. 12–13: Slightly curved toxa; evidence for an assignment to toxa type of spicula is the upward flexure at the ends of the rhabd, x 150; USNM 494,077, -078.

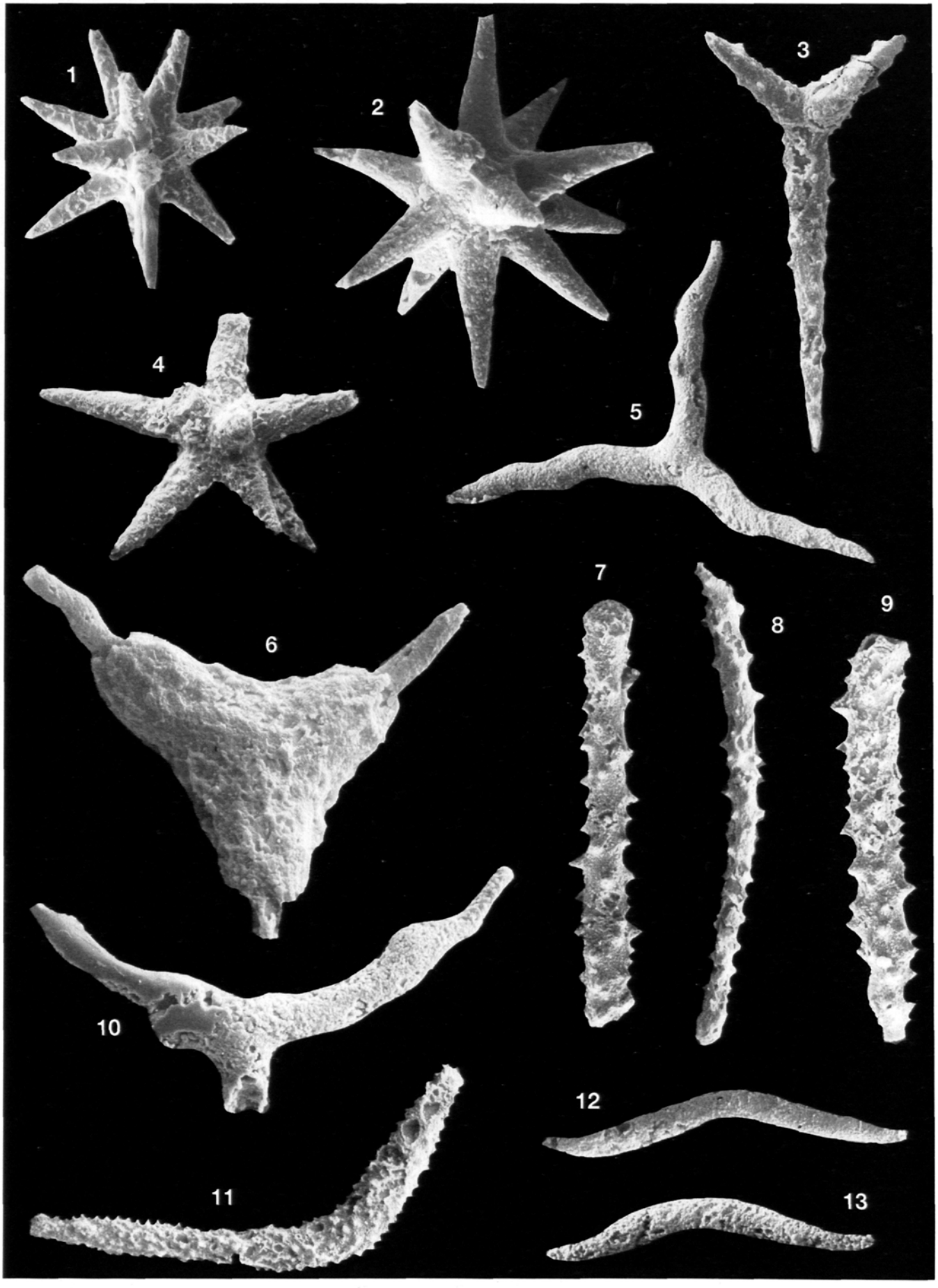
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Plate 4

Figs. 1–4; 6–8: C-shaped sigmata; Fig. 3 shows a slight buckle at the outer side of the mid-curvature, which is analogous to, but stronger, in present-day centroangulate sigmata. The degree of the curvature is different, but hemicircular forms that are known from many Middle Triassic and Liassic sigmata do not occur. Figs. 1-4, 7: x 200; Fig. 6: x 150; Fig. 8: x 100; USNM 494,079-085.

Figs. 5, 14: Long, narrow, straight styles, with distinctly oblique part near the round rhabd end; Fig. 5: x 200; Fig. 14: x 150; USNM 494,086, -087.

Fig. 9: Curved monaxone sclere; x 200; USNM 494,088.

Fig. 10: Discorhabd; remarkable are the five rings of verticillately arranged spines. Such a spiculum type is characteristic for representatives of the Latrunculidae. x 150; USNM 494,089.

Fig. 11: Broken monaxon spiculum, x 200; USNM 494,090.

Fig. 12: Thick oxea, spindle-shaped view, x 200; USNM 494,091.

Figs. 13, 15: Oxeas of different width; views in which the straight side and the opposite convex side is visible, x 300; USNM 494,092, -093.

Fig. 16: Oxea with irregular outer margin, x 200; USNM 494,094.

Fig. 17: ?Oxea with free fill of the axial channel. Many scleres of the investigated samples show strong diagnetic corrosion, as in this example; x 300; USNM 494,095.

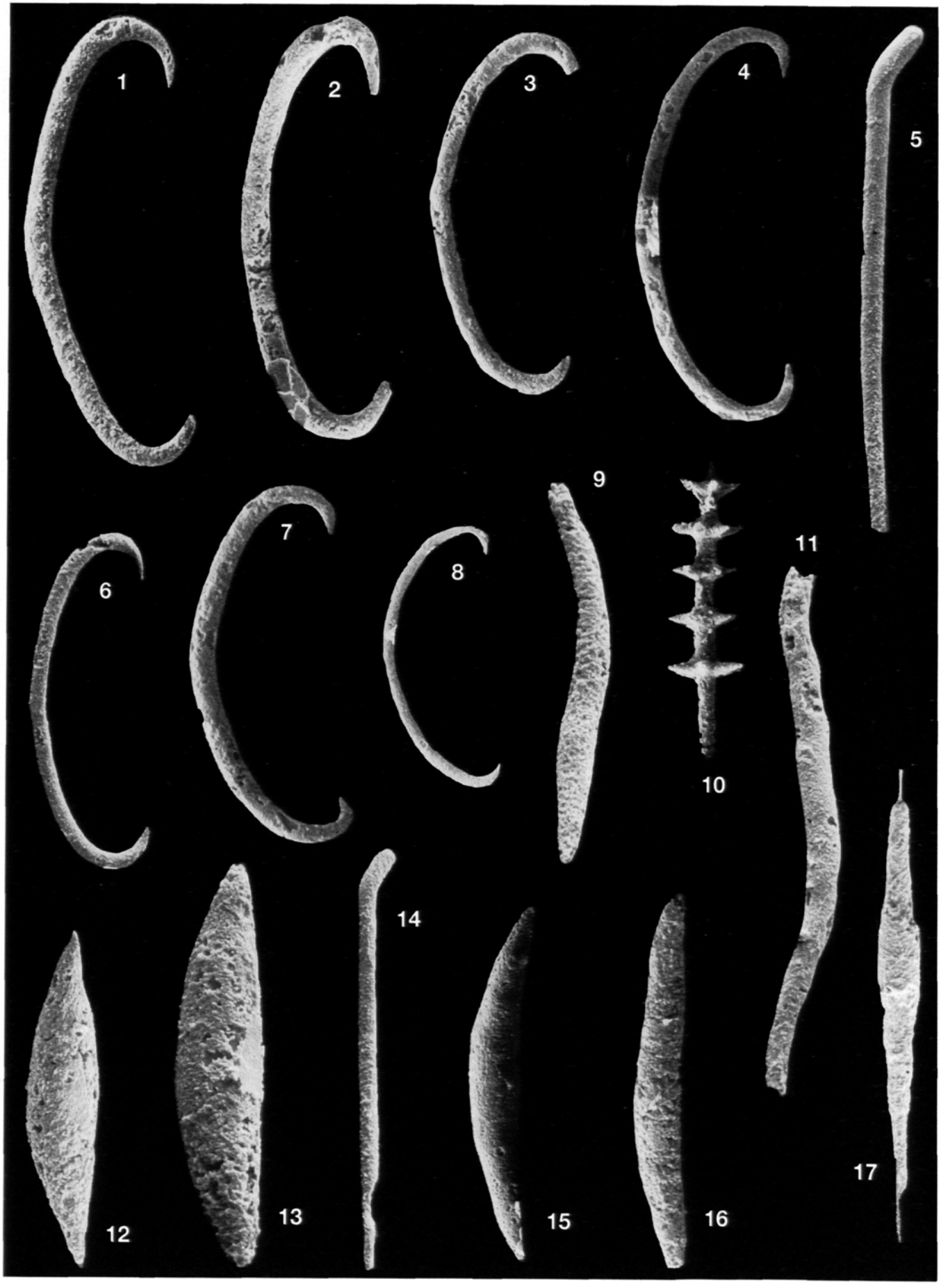
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Plate 5

Fig. 1: Enlarged magnification of the central ray of the scopule shown on Fig. 2. Only the sculptured part is shown; x 600.

Fig. 2: Scopule with 10 marginal rays and one central ray. As in stratigraphically younger scopules, only the distal part of the rays is sculptured (umbrella sculptures); x 250; USNM 494,096.

Fig. 3: Proximal part of a scopule (8 rays). The rays are broken within the smooth proximal part; x 200; USNM 494,097.

Fig. 4: Fragmentary four-rayed scopule. Whether the distal parts of the lateral rays were sculptured cannot be demonstrated; x 300; USNM 494,098.

Fig. 5: *Australispongia compressa* n. sp., with strong torsion in the flat central ray, x 200; USNM 494,099.

Fig. 6: Strongly upturned stauractine with small thorns and two ray-pairs of different length; x 200; USNM 494,100, -101.

Fig. 7: Stauractine, with rays of equal length that are entirely thorny; x 200; USNM 494,102.

Figs. 8, 9: Typical bean-shaped sterraster with distinct surface structure and well-developed hilum; Fig. 8: x 200; Fig. 9: x 500; USNM 494,103, -104.

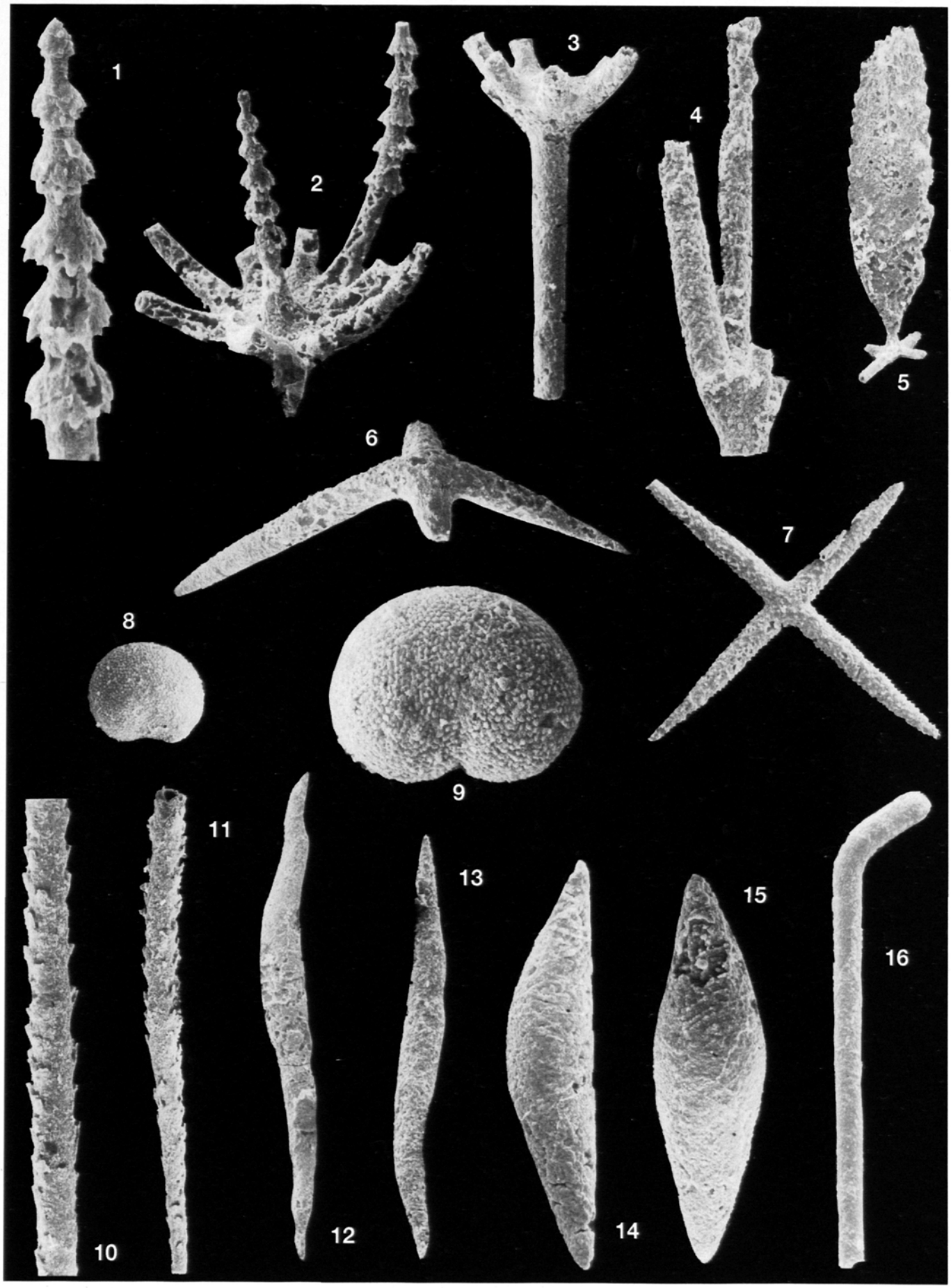
Figs. 10, 11: Uncinate spicules, with marginal denticulation or the basis of thin marginal spines on the rhab, respectively; Fig. 10: x 300;

Fig. 11: x 150; USNM 494,105, -106.

Figs. 12, 13: Wavy, curved oxeas, x 200; USNM 494,107, -108.

Figs. 14, 15: Short, thick oxeas. Fig. 14: Straight side and convex side visible. Fig. 15: View opposite to the straight side. In this view the same oxea type as in Fig. 14 appears biconvex; x 300; USNM 494,109-110.

Fig. 16: Fragment of a style with strongly curved upper third, x 300; USNM 494,111.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