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WELL-PRESERVED TREMADOCIAN PRIMITIVE RADIOLARIA FROM THE WINDFALL FORMATION OF THE ANTELOPE RANGE, EUREKA COUNTY, NEVADA, U.S.A.

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With 1 figure and 7 plates

Abstract:
Primitive radiolarians have been found in the upper part of the Windfall Formation (Antelope Range, Nevada), and are dated by conodonts as *Cordylodus angulatus* Zone (early Ibexian in North American usage = early Tremadocian in North Atlantic terms). They are the first radiolarians known from the Tremadocian. Two new families, Echidninidae n. fam. and Protoentactiniidae n. fam. (superfam. Protoentactiniacea n. superfam.), three new genera, *Noblella* n. gen., *Parechidnina* n. gen. and *Protoentactinia* n. gen. and 6 new species, *Echidnina bengtsoni* n. sp., *Parechidnina nevadensis* n. sp., *Protoentactinia gracilispinosa* n. sp., *P. latospinosa* n. sp., *P. minuta* n. sp. and *Noblella tremadociensis* n. sp. are described. In the Echidninidae, the central space inside the loose spongy shell or „protoshell" is hollow. In the most primitive form, *Echidnina*, isolated spicules are interlocked to form a subglobular, hollow „protoshell". In *Parechidnina* the spicules are fused to a loose lattice. The Echidninidae are probably Collodaria and may be the direct forerunner of the Spumellaria through forms similar to *Parechidnina.* The subglobular to globular, loose spongy test of the Protoentactiniidae is formed by repeated branching of a spicule and partial fusion of the terminal branches. The basic spicule consists of a median bar and 3 or 4 terminal rays on both sides of the median bar, as is characteristic for bar-centred Entactinaria. The Protoentactiniidae are apparently the most primitive Entactinaria, but still similar to Collodaria. Echidninidae and Protoentactiniidae are near the common root of skeleton-bearing Radiolaria.

Zusammenfassung:
Die hier beschriebenen primitiven Radiolarien aus dem oberen Teil der Windfall-Formation (Antelope Range, Nevada) lassen sich mit Conodonten in die *Cordylodus angulatus* Zone (unteres Ibexian in der nordamerikanischen Untergliederung = unteres Tremadoc in der Nordatlantischen Gliederung) einstufen. Zwei neue Familien, Echidninidae n. fam. und Protoentactiniidae n. fam. (Oberfamlilie Protoentactiniacea n. superfam.), drei neue Gattungen (*Noblella* n. gen., *Parechidnina* n. gen. und *Protoentactinia* n. gen.) und 6 neue Arten (*Echnidnina bengtsoni* n. sp., *Parechidnina nevadensis* n. sp., *Protoentactinia gracilispinosa* n. sp., *P. latospinosa* n. sp., *P. minuta* n. sp. und *Noblella tremadociensis* n. sp.) werden beschrieben. Bei den Echidninidae ist eine subsphärische, lockere spongiöse Schale oder „Protoschale" vorhanden, die innen hohl ist. In der primitivsten Form, *Echidnina*, sind die Spiculae isoliert, aber dicht ineinander geschachtelt und bilden so eine subsphärische, hohle „Protoschale". In *Parechidnina* sind die Spiculae zu einem lockeren Gitter verschmolzen. Die Echidninidae sind wahrscheinlich Collodaria und könnten auch die direkten Vorläufer der Spumellaria sein (über *Parechidnina*-ähnliche Formen). Das subsphärische bis sphärische lockere spongiöse Gehäuse der Protoentactiniidae wird durch mehrfache Aufgabelung eines Spiculum und teilweise Verschmelzung der Gabelenden gebildet. Das Ausgangsspiculum besteht aus einem Medianbalken mit 3–4 terminalen Strahlen an beiden Enden des Medianbalkes, wie das für Medianbalken-zentrierte Entactinaria charakteristisch ist. Die Protoentactiniidae sind offensichtlich die primitivsten Entactinaria. Die systematische Position der Echidninidae und Protoentactiniidae ist nahe der gemeinsamen Wurzel der Skelett-tragenden Radiolarien.

1. Introduction

Well-preserved conodonts, radiolarians and sponge spicules were recovered from the lowermost Ordovician Windfall Formation in Nevada. The sample, 6-18-76I (USGS locality number 11307-CO), was 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 (Figure 1; see Merriam, 1963, for discussion of stratigraphy of this section). Locality is 39°12'16" N. Lat.; 116°15'25" W. Long., on the Horse Heaven Mountain 15' topographic quadrangle map. The Windfall comprises chiefly dark gray to brown-black thin-bedded shales and fine-grained to silty limestones, and most likely represents

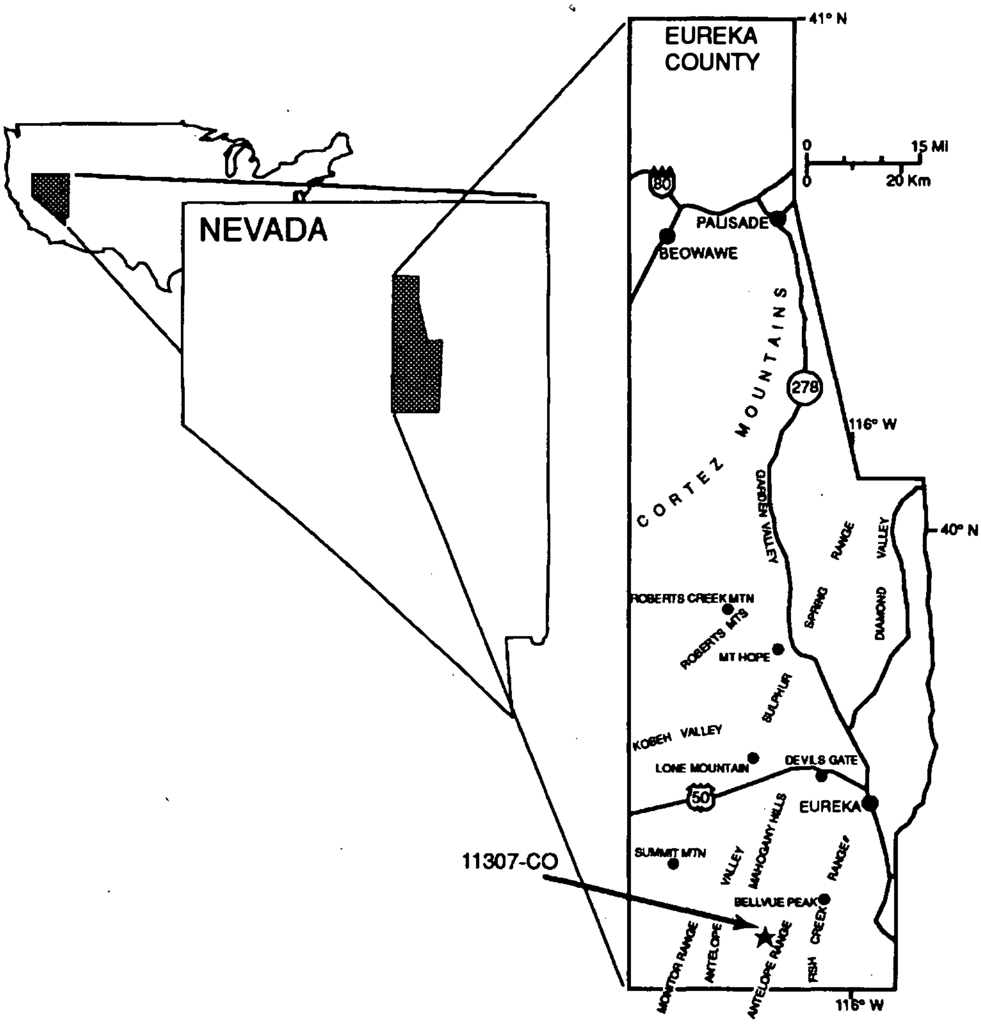

Fig. 1: Map showing location of the Tremadocian radiolarian-bearing sample 6-18-76I (USGS locality number 11307-CO) in Eureka County, Nevada, USA.

outermost shelf or slope facies (TAYLOR & REPETSKI, 1985).

Sample 6-18-76I (11307-CO), from which all figured radiolarians were derived, is from 241 feet (73.46 m) below the top of the Windfall. It contains *Cordylodus 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). This conodont fauna indicates the early Ibexian (North American Series = early Tremadocian in North Atlantic terms) *Cordylodus angulatus* Zone, their age being constrained both by their enclosed faunas and by those of underlying samples (REPETSKI, 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 Limestone (Tremadocian; *Rossodus manitouensis* Zone fauna) which immediately overlies the Windfall, and from the somewhat higher (Arenigian) Ninemile Formation. Conodonts from the Windfall and from the *Caryocaris* Shale Member and overlying limestone member of the Goodwin Limestone also have been treated in REPETSKI & TAYLOR (1982), ETHINGTON & REPETSKI (1984), and TAYLOR & REPETSKI (1985).

Besides rich conodont faunas and primitive radiolarians, numerous spicules of siliceous sponges and of Heteractinida are present that will be described in separate papers by the present authors (in press, this volume, and in prep.).

Ordovician radiolarians have been described in rather few papers (FORTEY & HOLDSWORTH, 1971, NAZAROV, 1975, 1977, 1981, DURHAM & MURPHY, 1976, NAZAROV & POPOV, 1976, 1980, HOLDSWORTH, 1977, NAZAROV & ORMISTON, 1984, 1986, 1993, WEBBY & BLOME, 1986, RENZ, 1990 a, b, GOTO & ISHIGA, 1991, GOTO et al., 1992, UMEDA et al., 1992, WANG YU-JING, 1993, GÓRKA, 1994, LI, 1995). Even so, because of good preservation of most of these faunas and the partly monographic character of the above-mentioned papers, the Ordovician radiolarians are rather well known. Arenigian to Ashgillian radiolarians consist mainly of primitive Entactinaria (both spicular types and chiefly forms with well developed shells) and primitive Spumellaria (Inaniguttidae NAZAROV & ORMISTON). Besides these, the doubtful radiolarian genus *Anakrusa* NAZAROV, 1977 (= *Auliella* NAZAROV, 1977) is rather common for the Ordovician. It has a globular test with round perforations, on which spines with hollow central channels are present. Such spines are not known in polycystine radiolarians, but they are typical for sponge spicules and in Muellerisphaerida. Forms with a shell lacking the spines resemble *Blastulospongia* PICKETT & JELL, from the Middle and Upper Cambrian, that was assigned to the sponges both by PICKETT & JELL (1983) and by BENGTSON (1986). Furthermore, primitive Albaillellaria as well as pylomate Entactinaria and primitive ?Nassellaria (*Aciferopylorum* NAZAROV & ORMISTON, *Cessipylarum* NAZAROV and *Proventocitum* NAZAROV) are present in the Arenigian to Ashgillian interval.

No radiolarians have been reported from the Tremadocian. Surprisingly, our Tremadocian radiolarian fauna is totally different from the Arenigian and younger ones and considerably more primitive. One of our Tremadocian genera, *Echidnina* BENGTSON, was first described from the Upper Cambrian of Queensland and regarded as a sponge spicule by BENGTSON (1986), whereas the other genera are new, primitive radiolarians, of which only one genus ranges into the Arenigian.

NAZAROV (1973, 1975) and NAZAROV & ORMISTON (1993) reported poorly preserved Cambrian radiolarians. NAZAROV (1975) established several species (all indeterminable) from thin sections of very badly preserved presumed Middle and Upper Cambrian material. However, it is recognizable in some of these radiolarians that they have a well developed shell and main spines. Therefore, they appear to be more highly evolved than the Tremadocian material. In a subsequent paper, NAZAROV & ORMISTON (1993, Fig. 4) indicated that here are no radiolarians in the interval from the upper part of Lower Cambrian up to the Tremadocian. One of the forms described by NAZAROV (1975), the assumed Upper Cambrian to Upper Ordovician '*Entactinia*' *akdymensis* NAZAROV, was determined by NAZAROV & ORMISTON (1993, Fig. 1) as *Inanigutta akdjemensis* (NAZAROV)*, and restricted to the upper Llandeilian to Caradocian. This latter age assignment explains why the 'Middle to Upper Cambrian' radiolarians of NAZAROV (1975) are more advanced than our Tremadocian material. The Middle and Upper Cambrian radiolarians of NAZAROV (1975) were therefore derived from stratigraphically misinterpreted Middle Ordovician beds. This was not mentioned by NAZAROV & ORMISTON (1993), but in this paper it was pointed out that in the (former) Soviet Union, Cambrian radiolarians are only known from the Lower Cambrian. This refers to Lower Cambrian 'radiolarians' described by NAZAROV (1973) from shallow water limestones with archaeocyathids. One of the figured microfossils, according to NAZAROV (1973) a form of unclear systematic position, is a sponge spicule (*Azyrtalia* NAZAROV). The forms described by NAZAROV (1973) as radiolarians are of doubtful systematic position. '*Lithapium*' *tesiensis* NAZAROV, assigned to *Inanigutta* ? *tessiensis* (NAZAROV)* by NAZAROV & ORMISTON (1993), and „*Lithapium*“ *claviformis* NAZAROV surely are not radiolarians, but rather may be foraminifers. *Palaeoxiphosphaera erbiensis* NAZAROV was tentatively assigned by NAZAROV (1975) to '*Entactinia*', but the same badly preserved specimen was re-figured. The systematic position of this fossil is

* Spelling changed against the rules of the ICZN by NAZAROV & ORMISTON (1993)

unclear; its inner structure is unknown. In a handwritten note on the reprint of the paper NAZAROV (1973), sent to one of the authors (HWK), NAZAROV wrote that he very much doubted that the specimens that he figured on Pl. 1, Figs. 6–8 and possible 5 (*'Lithapium' tesiensis* NAZAROV and *'Lithapium' claviformis* NAZAROV) are radiolarians. We have the same doubt. *Paleocenosphaera magna* NAZAROV, 1973 and *P. parva* NAZAROV, 1973, from the same beds, are badly preserved spherical balls with pores and unknown inner structure. Similar 'balls with pores' occur also in other Cambrian deposits, but it is not even known whether the shell was originally calcitic or siliceous. They were tentatively assigned to *Polyentactinia* by Nazarov (1975), but already BENGTSON (1986) has expressed doubt that the reported inner spicular system (never figured) is present. According to BENGTSON (1986) these forms are very similar to *Blastulospongia* PICKETT & JELL, which belongs to sponges according to both PICKETT & JELL (1983) and BENGTSON (1986). According to these data concerning the previously reported Cambrian radiolarians of Nazarov (1973, 1975), it is probable that the Upper Cambrian radiolarian genus *Echidnina,* published by BENGTSON (1986) as a sponge, and our Tremadocian radiolarian fauna were the oldest skeleton-bearing radiolarians. Former reports of Precambrian radiolarians have never been confirmed (see discussion in NAZAROV, 1973).

About 30 stereo-scan pictures and numerous simple SEM pictures were taken and carefully studied. They show that several different radiolarian taxa are present in our Tremadocian material. These appear to be quite primitive forms of skeleton-bearing radiolarians.

2. Systematic part

Type locality for all new species is the locality at 39°12'16" N. Lat.; 116°15'25" W. Long., on the Horse Heaven Mountain 15' topographic quadrangle map in a section in a tributary to Ninemile Canyon, on the west side of the Antelope Range (USGS locality number 11307-CO). Type stratum is a fine-grained to silty limestone from lowermost Ordovician upper Windfall Formation, Eureka County, Nevada; sample 6-18-76I; 241 feet (= 73.46 m) below the top of the Windfall.

Subclass Radiolaria MÜLLER, 1858
Order Polycystida EHRENBERG, 1838
Suborder Collodaria Haeckel, 1881

Family Echidninidae n. fam.

Diagnosis: Isolated, but interlocked or fused, primary point-centred tetractine, pentactine, hexactine and heptactine spicules form a subglobular, loose, spongy, hollow shell.

Assigned genera:
Echidnina BENGTSON, 1996
Parechidnina n. gen.

Occurrence: Upper Cambrian to Lower Tremadocian. Australia and Nevada.

Remarks: All spicules, both in forms with isolated interlocked spicules and in forms with fused spicules, are situated within the subglobular, loose spongy shell or 'protoshell'. The interior space of the skeleton is hollow. Moreover, none of the isolated or fused spicules that form the spongy, hollow shell has the character of an entactinarian spicule.

Fully preserved Protoentactiniidae have a superficially similar, loose, sponge-like test consisting of fused and partly additionally interlocked spicules. However, the test (also its interior part or much of it) is built up by repeatedly branching entactinarian spicules consisting of a median bar and mainly 3, partly 4, terminal rays. In the outer part of the test only, the branching may be more variable, partly with 2, 4, 5 or 6 terminal rays, a bunch of terminal rays or spines branching away from straight rays in a set of verticiles. Consequently, despite of superficial similarity, the Echidninidae are basically different from the Protoentactiniidae. Transitional forms have not been observed. A small internal part of the test of the Protoentactiniidae may be hollow, but this is caused rather by eccentric arrangement of the entactinarian spicules.

The Echidninidae are the most primitive radiolarians with a shell or a shell-like arrangement of isolated spicules ('protoshell'). In the Upper Cambrian to lower Tremadocian *Echidnina*, the spicules are still isolated and are interlocked only to a subsphaerical hollow shell. In *Paraechidnina*, the spicules are already fused to a spongy lattice. Spines are directed outwards and rarely inwards from this spongy shell, but the inward directed spines (if present) never join to an entactinarian spicule as in the Protoentactiniidae. Therefore, already in the basic group of the skeleton-bearing radiolarians, the Entactinaria seem to be clearly separated from the other radiolarians.

Most similar are those Collodaria that have different types of isolated spicules. However, they are not interlocked to form a loose, spongy shell. Among the shell-bearing Collodaria, some Oroscenidae HAECKEL, 1887 are similar, particularly *Oroplegma* HAECKEL, 1887. Typical Oroscenidae have, however, a regular shell with elevations.

Genus Echidnina Bengtson, 1986

Type species: *Echidnina runnegari* BENGTSON, 1986

Echidnina bengtsoni n. sp.

(Pl. 1, Figs. 1, 3)

Derivatio nominis: In honor of Prof. Dr. S. BENGTSON, Uppsala

Holotypus: The specimen on Pl. 1, Fig. 1, holder-no. 23-6-96/III-135; USNM 494,842.

Diagnosis: Isolated, but densely interlocked, mainly hexactine and heptactine spicules form a subglobular, hollow 'protoshell'.

Description: The subglobular, loose spongy, hollow 'protoshell' has a diameter of 150–200 µm. It consists of isolated, but densely interlocked spicules that are mainly point-centred hexactines, partly heptactines. The rays of the spicules are pointed. One or two rays of each spicule are longer (37–50 µm) than the other ones and mostly slightly curved. The shorter rays (16–27 µm) of the spicules are straight. All rays are in their widest part about 6–7 µm wide.

Occurrence: Only known from the lowermost Tremadocian of the type locality in Nevada.

Remarks: The Upper Cambrian *Echidnina runnegari* BENGTSON, 1986 is somewhat larger, and the isolated interlocked spicules of the loose, spongy 'protoshell' are tetractines, pentactines and hexactines. The rays of the spicules of *E. runnegari* are distinctly longer (100–150 µm).

Genus *Parechidnina* n. gen.

Type species: *Parechidnina nevadensis* n. sp.

Derivatio nominis: The assumed derivation from *Echidnina* is expressed.

Diagnosis: Heptactine, hexactine, pentactine and tetractine spicules are fused to a loose, hollow, irregular latticed shell with large, triangular to rectangular or rhombohedral pores and numerous needle-like outward-directed spines. Connecting bars between these spines and further fused spicules above the shell form an imperfect, loose spongy shell. In the largest part of the test both shells are united to a single, loose spongy shell.

Assigned species:
Parechidnina nevadensis n. sp.

Occurrence: Lower Tremadocian of Nevada.

Remarks: In *Echidnina* BENGTSON, the spicules are isolated and only interlocked to form a loose spongy shell. *Parechidnina* is a transition form to latticed or spongy primitive Spumellaria described as non-spiculate spumellarians by FORTEY & HOLDSWORTH (1971) or Palaeoactinommids by HOLDSWORTH (1977) from the Arenigian of Spitsbergen. In these forms a regular latticed shell already is present, and the spines are distinctly differentiated from this shell. An imperfect outer spongy shell still may be present. These forms are the most primitive Inaniguttidae Nazarov & ORMISTON, 1984, that comprise very primitive Spumellaria. Particularly similar is the specimen figured by HOLDSWORTH (1977, Pl. 1, Fig. 1). In this form the coarse latticed shell is large and close to the outer imperfect spongy shell. The lattice shell, however, already is regular, and the spines are clearly differentiated from the lattice. In typical Inaniguttidae, the central shell is very small, but in the beginning still has a very coarse lattice (Arenigian forms figured as Palaeoactinommids by HOLDSWORTH (1977, Pl. 1, Figs. 2, 3).

As shown above, the Echidninidae are connected with the most primitive Spumellaria, through *Parechidnina*. Consequently, the Echidninidae as the oldest true radiolarians are the common root of the Collodaria (to which this family belongs) and of the Spumellaria, which developed from the Echidninidae through *Parechidnina*-like forms.

Parechidnina nevadensis n. sp.

(Pl. 1, Fig. 5; Pl. 2, Figs. 1, 3)

Derivatio nominis: Referring to the occurrence in Nevada.
Holotype: The specimen on Pl. 1, Fig. 5; holder-no. 23-6-96/III-104; USNM 494.846.
Diagnosis: As for the genus.
Description: The subglobular test consists of an inner, irregular, latticed shell with very large rectangular, rhombohedral, or triangular pores. This shell is formed by fused heptactine, hexactine, pentactine and tetractine spicules. As the spicules are not arranged totally parallel to the surface of a sphere, this causes an irregular surface for this shell. Numerous needle-like spines radiate outwards from this shell. As they have the same diameter as the fused rays of the spicules, the spines are not yet differentiated from the shell except in their centrifugal arrangement and in that they are partly not fused within the outer spongy shell. Connecting bars between these spines, and also irregularly arranged further fused spicules above the surface of the latticed shell, form an imperfect spongy shell that is united with the inner shell to form a single, loose spongy shell. Therefore, the irregular inner shell is only separated in those parts where the outer spongy shell is not present. In the largest part of the test, the inner shell cannot be separated from the outer loose spongy shell and both together form a loose spongy shell.
Diameter of the test (without spines): 86–130 μm
Length of the spines: 30–34 μm
Occurrence: Lower Tremadocian of the type locality in Nevada.
Remarks: See under the genus.

Suborder Entactinaria
KOZUR & MOSTLER, 1982

Superfamily Protoentactiniacea n. superfam.

Diagnosis and occurrence: As for the family.
Assigned family: Protoentactiniidae n. fam.
Remarks: The basic spicule corresponds to a bar-centred entactinarian spicule of the Hexastylacea. However, in most of the Hexastylacea the shell and the spicular system are clearly separated from each other, or, if only a spicule is present, it does not branch repeatedly to form a subsphaerical 'protoshell' as in the Protoentactiniidae. Moreover, in some Protoentactiniidae the spicular system is partially modified to an asymmetric spicular system, being on one side more robust, and having there on one side of a median bar two branched terminal rays and two unbranched terminal rays with 3–4 verticiles. This modified spicular system is reminiscent of the Palaeoscenidiacea. The Protoentactiniidae are Entactinaria based on their spicular system, but they have features of both Hexastylacea and Palaeoscenidiacea, and they differ from both superfamilies by their subglobular test without clearly differentiated shell and spicular system. Therefore, they are assigned herein to a separate superfamily of the Entactinaria that is the ancestral group of both the Hexastylacea and the Palaeoscenidiacea (see under Protoentactiniidae).

Family Protoentactiniidae n. fam.

Diagnosis: The rarely fully preserved subglobular test consists of a repeatedly branched entactinarian spicular system that forms a spongy network. The inner part of this network is very loose; the outer part is somewhat denser, but still is also loose. A small empty space may be present inside the test, but often this space also is filled by the spicular system.

The spicular system consists basically of a median bar and 3, rarely 4, terminal rays that branch again in 3, rarely 4, terminal rays. In the outer part of the test, both the median bar and the terminal rays are mostly shorter and only a little outward-directed. The ends of the branches there are fused or interlocked. In this part not only 3 or 4, but partly also 2, and rarely more than 4, terminal branches or a bunch of radially arranged short terminal rays occur. In rare cases, some isolated but interlocked spicules also are present in the outer part. In general, all the branches of the spicular system have the same diameter. Only in the outer part they are somewhat more slender, but in general, there is no distinct separation between an inner spicular system and an outer shell. Only with rare exceptions are the inner branches much thicker than the outer one. This development indicates the beginning of a differentiation between an outer shell and an inner spicular system. In exceptional cases, the spicular system is differentiated in such a way that it becomes asymmetrical, with thicker rays on one side. At this side four terminal rays are differentiated into two thick terminal rays that are branched in the typical *Protoentactinia* manner, and two other ones that are straight, unbranched, and have 3–4 verticiles, from which several spines (mainly 3) originate. This differentiation of the spicular system leads toward that of the Palaeoscenidiacea.

A few, corroded rays of the spicular system may be hollow. Despite the fact that this is a secondary feature indicating post-mortem dissolution, there may be some structural or material differences between the outer and central parts of the rays.

Assigned genera:
Protoentactinia n. gen.
Noblella n. gen.

Occurrence: Tremadocian-Arenigian, Nevada and Spitsbergen.

Remarks: The basic spicule form is a typical bar-centred entactinarian (hexastylacean) spicule with median bar and 3, on one side sometimes also 4, terminal rays. In the spicular system, the terminal rays branch again in 3, more rarely 4, terminal rays. As in the largest part of the test (except the outermost part) all rays of the spicular system have the same diameter. Therefore, it is not clear whether this spicular system has developed by repeated branching of the terminal rays of a single primary spicule or whether several spicules with median bar and 3-4 terminal rays are at first interlocked but not fused (as in *Echidnina*) and subsequently fused. The first possibility corresponds to the assumed hypothetical development of shell-bearing Entactinaria from a single spicule as assumed by Goodbody (1986, Fig. 7); that development is achieved in some Triassic Entactinaria. As isolated interlocked spicules may be present in the outer part (very rare), it is possible that the complex spicular system was formed by fusion of primary, isolated, interlocked single spicules. There is also one fragment of the test of *Protoentactinia* sp. C that consists of both branched and isolated interlocked spicules. This form, and the fact that most of the rays of the spicular system (except the outermost ones) have an equal diameter, favors the second model, i.e., that the forerunner of Protoentactinia had isolated, interlocked spicules that subsequently fused into a single spicular system, but that additionally, braiding of the terminal rays of the spicules also occurred, at least in the outer part of the test.

More advanced Entactinaria evolved from the Protoentactiniidae in three ways: (1) Differentiation of the spicular system into an outer shell (or several shells) and an inner spicular system. By this, shell-bearing Hexastylacea with an inner spicular system evolved. This trend can be observed in *Protoentactinia latospinosa* n. sp., in which the spicular system already is differentiated into a robust, somewhat reduced inner spicular system, and fragile, denser outer branches that form a 'protoshell'. (2) Reduction and strengthening of the inner part of the spicular system and disappearance of the outer branches. By this, spicular Entactinaria, mainly Palaeoscenidiacea, evolved. This trend (reduction and strengthening of the inner part of the spicular system) is partly realized in *Noblella* n. gen. (3) The spicular system with equal rays becomes asymmetrical, with thicker and fewer branched rays on one side. On that side, 4 terminal rays are differentiated into 2 terminally branching rays and 2 stout, straight rays with verticiles, from which thin spines branch. The terminal branching either disappeared or is rudimentary in these two rays. These forms (*Noblella*) are already somewhat similar to those Palaeoscenidiacea with loose imperfect shell. The two thick rays with verticiles correspond to the apical rays, the branching rays to the basal rays. *Noblella* may be the ancestor of the Palaeoscenidiacea, but most of the rays still have the branching typical of the Protoentactiniidae. It is possible that this genus belongs to a separate family within the Protoentactiniacea. At present, only one species of *Noblella* is known. For this reason, we retain only one family in Protoentactiniidae.

The Entactinaria are a monophyletic group, as obviously both the Hexastylacea and the Palaeoscenidiacea of the Entactinaria evolved from the Protoentactiniidae. PETRUSHEVSKAYA (1984) assigned the Palaeoscenidiacea to the Albaillellaria and concluded from this unsubstantiated assignment that the Entactinaria are a polyphyletic group that would comprise the Nassellaria, as well as a part of the Collodaria, Albaillellaria and Spumellaria. Albaillellaria and Palaeoscenidiacea are basically different. The rods of the Albaillellaria and the homologous columellae of the advanced Albaillellaria are neither similarly arranged nor homologous to the basic pentactine spicular system of the Palaeoscenidiacea. All shell-bearing Albaillellaria (nearly all Albaillellaria except the most primitive forms) have trabecules between the rods or columellae, and the shell developed between the trabecules, including them in the shell wall. No trabecules are present in the Palaeoscenidiacea. Only the most primitive, Ordovician Albaillellaria have no shell, but also the basic triangular arrangements of the rods present in these forms cannot be found in any other radiolarians. Advanced Albaillellaria are clearly bilaterally symmetrical; such symmetry is never present in Palaeoscenidiacea. The heteropolar shell of the Albaillellaria clearly became subconical in advanced forms, and a distal opening is always present. This shell is similar to that of multicyrtid Nassellaria, but this is only a homeomorphy. Many Palaeoscenidiacea, even advanced Triassic ones, are spicular radiolarians without shells. If a shell is developed, it has the spumellarian geometry and, as in Spumellaria, a medullary shell (or medullary shells) may be present that are never present in Albaillellaria. Thus, neither the most primitive nor the advanced Albaillellaria have any similarity to primitive or advanced Palaeoscenidiacea, and for this reason no one has followed the view of PETRUSHEVSKAYA (1984) that the Palaeoscenidiacea are Albaillellaria. Consequently, the assumed albaillellarian nature is not a reliable argument against the monophyletic character of the Entactinaria.

KOZUR & MOSTLER (1982) have shown that monocyrtid Nassellaria evolved from pylomate Entactinaria, and the cytoplasm of Recent Entactinaria (assigned to the Spumellaria by PETRUSHEVSKAYA, 1984) is very different from that of the Spumellaria but rather similar to that of the Nassellaria (HOLLANDE & ENJUMET, 1960). The Hexastylacea, to which all Recent Entactinaria belong, cannot be assigned to the Spumellaria despite their spumellarian shell geometry (that is typical for all Entactinaria). Thus, not the Entactinaria, but rather the Albaillellaria sensu PETRUSHEVSKAYA (including the Palaeoscenidiacea) and the Spumellaria (Sphaerellaria) sensu PETRUSHEVSKAYA (including the Hexastylacea sensu stricto) are polyphyletic groups, containing parts of the monophyletic Entactinaria.

Clear connections exist between the Nassellaria and Entactinaria, but except for a few spicular forms lacking a shell, all Entactinaria have a spumellarian shell geometry, whereas shell-bearing Nassellaria have heteropolar tests. Moreover, medullary shells, common in Entactinaria, are never present in Nassellaria, and dicyrtid, tricyrtid and multicyrtid forms, common in Nassellaria, are not present in Entactinaria. Thus, the Entactinaria clearly are distinguished from the Spumellaria by the presence of an internal spicular system and this distinction goes back to the oldest differentiated radiolarians in the Tremadocian as well as in the Arenigian and younger Ordovician radiolarians. The Entactinaria also are clearly distinguished from the Nassellaria by the above mentioned features, but despite the spumellarian shell geometry in shell-bearing Enatactinaria, they are more closely related to the Nassellaria because the latter evolved in the early Paleozoic from pylomate Entactinaria (and possibly iteratively during the Scythian, KOZUR et al., 1996).

Recent Collodaria are very different from Recent Entactinaria, mainly by their cytoplasm. Fossil Collodaria are difficult to recognize, if they are not built up by isolated interlocked or fused spicules, as the Echidninidae. As the Echidninidae and the Protoentactiniidae are different in their basic spicular structure, the Collodaria and Entactinaria were probably clearly separated since the appearance of skeleton-bearing radiolarians during the Upper Cambrian and Tremadocian.

Genus *Protoentactinia* n. gen.

1977 Entactiniid Genus Novum 2 – HOLDSWORTH, 1977, p. 170, Pl. 2, Fig. 8.

Type species: *Protoentactinia gracilispinosa* n. sp.

Derivatio nominis: Referring to its systematic position as ancestral to the Entactinaria.

Diagnosis: The rarely fully preserved subglobular test consists of a repeatedly branched entactinarian spicular system that forms a spongy network. The inner part of this network is very loose, the outer part is somewhat denser, but also loose. A small empty space may be present inside the test, but often this space also is filled by the spicular system.

The spicular system consists basically of a median bar and 3, rarely 4, terminal rays that branch again in 3, rarely 4, terminal rays. In the outer part of the test, both the median bar and the terminal rays are mostly shorter and only a little outward-directed. The ends of the branches are fused or interlocked there. In this part not only 3 or 4, but partly also 2, and rarely more than 4, terminal branches occur. Rarely, some isolated, but interlocked spicules also are present in the outer part. In general, all the branches of the spicular system have the same diameter. Only in the outer part they are somewhat more slender, but in general, there is no distinct separation between an inner spicular system and an outer shell. Only in exceptional cases are the inner branches much thicker than the outer one.

A few corroded rays of the spicules may be hollow.

Assigned species:

Protoentactinia gracilispinosa n. sp.

Protoentactinia latospinosa n. sp.

Protoentactinia minuta n. sp.

Protoentactinia spp.

Occurrence: Lower Tremadocian to Arenigian, Nevada and Spitsbergen.

Remarks: *Noblella* n. gen. has a differentiated spicular system that is more robust on one side. On this side, two straight rays have 3–4 verticiles, in which thin spines originated, but no or only a rudimentary terminal branching. All other rays of the spicular system are branched terminally and form a loose spongy test, as in *Protoentactinia*.

Protoentactinia gracilispinosa n. sp.

(Pl. 2, Figs. 2, 4, 5; Pl. 3, Figs. 1–3; Pl. 4: Figs. 1–4; Pl. 5, Figs. 1–4, 6, 7; Pl. 6, Figs. 1–4; Pl. 7, Figs. 1, 2)

Derivatio nominis: Referring to the fragile spicular system.

Holotype: The specimen on Pl. 3, Fig. 1; holder-no. 23-6-96/III-113; USNM 494,853.

Diagnosis: With the character of the genus. Spicular system not differentiated. Only the outermost rays have a somewhat smaller diameter than the rest.

Description: The basic spicule is a bar-centred entactinarian spicule with 3 terminal rays. Rarely, 4 rays may be present on one end of the median bar. In the outermost part of the spicular system two terminal rays may be present in some branches, but in general 3 terminal rays also are present in the outermost part of the test. The loose spongy test, which is formed by the repeated branching of the spicule, has in the rare fully preserved forms a subglobular shape with a diameter of 233–308 μm. The bars of the spicule are 33–56 μm long; only the outermost branches may be distinctly shorter. The width of the bar is 6–8 μm in the largest part of the test . Only the outermost terminal rays are narrower.

Occurrence: Lower Tremadocian of Nevada. ?Arenigian of Spitsbergen.

Remarks: *Protoentactinia* cf. *gracilispinosa* n. sp. from the Arenigian of Spitsbergen has somewhat narrower rays of the spicular system (3.5–5 μm), but is otherwise identical.

In *Protoentactinia latospinosa* n. sp., the rays of the inner part of the spicular system are considerably broader (diameter 11–13 μm) than the outer part (maximum diameter 3–7 μm). Moreover, the entire spicular system is more dense.

Protoentactinia minuta n. sp. also has a denser spicular system; the diameter of the test is smaller (167–185 μm) and the rays are more slender (5–6.5 μm) and are shorter (15-25 μm).

In *Protoentactinia* ? sp. A, from which only small broken pieces are preserved, the length of the rays within the inner part of the spicular system varies considerably (30–75 μm).

Protoentactinia latospinosa n. sp.
(Pl. 7, Fig. 4)

Derivatio nominis: Referring to the broad rays of the spicular system.

Holotypus: The specimen on Pl. 7, Fig. 4; holder-no. 23-6-86/III-57; USNM 494,874.

Diagnosis: With the character of the genus. Spicular system dense, with relatively few branches and broad, robust rays. Outermost branches much narrower.

Description: The basic spicule is a bar-centred entactinarian spicule with 3 terminal rays. The spicular system has relatively few branches and robust, rather short (20–30 μm), and broad rays with 11–13 μm diameter. The outermost branches are distinctly narrower (3–7 μm diameter). The spicular system occupies the entire subglobular, loose spongy test, which has a diameter of 230–250 μm.

Occurrence: Lower Tremadocian of Nevada.

Remarks: *Protoentactinia minuta* n. sp. has also a dense spicular system, but the branches are very thin (diameter (5–6.5 μm) and the test is smaller (167–185 μm).

Protoentactinia gracilispinosa n. sp. has a more strongly branched spicular system with longer (33–56 μm) and narrower rays (diameter 6–8 μm) that are only indistinctly differentiated between the inner and outer part.

Protoentactinia minuta n. sp.
(Pl. 5, Fig. 5)

Derivatio nominis: In reference to the small size of the test.

Holotypus: The specimen on Pl. 5, Fig. 5 ; holder-no. 23-6-96/III-78; USNM 494,864.

Diagnosis: With the character of the genus. Spongy test small and globular, consisting of a dense spicular system with very narrow and short rays that have a constant diameter (except the insignificantly narrower outermost branches). Outermost branches differentiated into short, only slightly outwardly-directed rays, and longer, needle-like outwardly-directed spines.

Description: The basic spicule is a bar-centred entactinarian spicule with 3, rarely 4, terminal rays. The rays of the strongly branched spicular system are slender (5–6.5 μm diameter), and because of their small length (15–25 μm), the spicular system is relatively dense. It forms a small, globular, loose spongy test (diameter 167–185 μm) with an eccentrically situated inner hollow space. In the outermost part of the test, often only 2 short terminal rays are present. In this part, an interesting differentiation of the terminal rays can be observed. Except for short terminal rays (7–13 μm), considerably longer (around 30 μm), needle-like, outwardly-directed spines also are present which are homologous to spines on the shell surface of entactinarian radiolarians with a well-developed shell.

Occurrence: Lower Tremadocian of Nevada.

Remarks: *Protoentactinia gracilispinosa* n. sp. has somewhat broader (6-8 μm) and distinctly longer (33–56 μm) rays within its spicular system, which is looser and which forms a distinctly larger test (diameter 233–308 μm).

Protoentactinia latospinosa n. sp. has distinctly broader rays (11–13 µm) in a spicular system having fewer branches, and its test is larger (diameter 230–250 µm).

Protoentactinia ? sp. A
(Pl. 1, Fig. 2)

Remarks: Only a small fragment of the spicular system is present. For this reason it is not clear whether this spicule branches as much as in *Protoentactinia* to form a subglobular, loose spongy test. Unlike all other *Protoentactinia* species, the length of the rays in the inner part of the spicular system varies strongly; some terminal rays are longer (75 µm) than in the other *Protoentactinia* species. Because of the fragmentary preservation it is not clear whether this form belongs to *Protoentactinia.*

Protoentactinia sp. B
(Pl. 1, Fig. 4)

Remarks: A fragmentary test of *Protoentactinia* is present in which the outermost terminal rays end in a radially arranged bunch of 5-11 needle-like, short spines. This fragment probably belongs to a new species.

Protoentactinia sp. C
(Pl. 1, Fig. 6)

Remarks: One fragment of a *Protoentactinia* test consists of partly interlocked, partly fused isolated spicules that are either simple entactinarian bar-centered spicules with 3 terminal rays on each side of the bar, or repeatedly branched spicules, as is characteristic for the Protoentactiniidae.

Genus *Noblella* n. gen

Derivatio nominis: In honor of Prof. Dr. P.J. NOBLE, Austin, for her outstanding work on Paleozoic radiolarians.

Type species: *Noblella tremadociensis* n. sp.
Diagnosis: The robust spicular system is branched in its largest part, in the manner typical of the Protoentactiniidae (median bar with 3–4 terminal rays that branch again in 3–4 terminal rays), and forms an ovoid to subglobular, loose spongy test. The most robust rays of the spicular system are concentrated on one side of the test, and 2 robust terminal rays (out of 4) in this portion of the test are different from all other rays in being straight, unbranched, but having 3–4 verticiles, from which needle-like spines originate.
Occurrence: Lower Tremadocian of Nevada.
Assigned species:
Noblella tremadociensis n. sp.
Remarks: *Protoentactinia* n. gen. has a symmetrical spicular system and no unbranched rays with verticiles. Moreover, in nearly all *Protoentactinia*, the spicular system is undifferentiated, and only in *Protoentactinia latospinosa* n. sp. are the rays of the inner part of the spicular system distinctly broader than the rays of the outer part of the spicular system. The asymmetry of the spicular system and the development of unbranched rays with verticiles in *Noblella* is a trend in direction toward the Palaeoscenidiacea, but in the largest part of the spicular system the Protoentactiniidae branching is still present.

Noblella tremadociensis n. sp.
(Pl. 7, Fig. 3)

Derivatio nominis: Referring to the occurrence in the lower Tremadocian.
Holotype: The specimen on P. 7, Fig. 3; holder-no. 23-6-96/III-22; USNM 494,873.
Diagnosis: As for the genus.
Description: The ovoid to subglobular, loose spongy test has a diameter of 230–250 µm. It consists of a repeatedly branched spicule that is distinctly asymmetrical. On one side, the spicule is strongly branched and the rays have a diameter of 6–7 µm. On the other side, the rays are more robust (diameter approx. 10 µm). In this part of the test there are 4 differentiated terminal rays. Two of them are branched in the manner typical of the

Protoentactiniidae (unbranched part 43 µm long and 11–12 µm wide). The two opposite rays (40–43 µm long and around 10 µm wide) are straight and unbranched, but have 3–4 verticiles, from which needle-like spines originate. The terminal verticile corresponds to a branching point with 3 rudimentary, very short terminal rays.

Occurrence: Lower Tremadocian of Nevada.

Remarks: Most similar is *Protoentactinia latospinosa* n. sp., in which, however, no large, robust, straight terminal rays with verticiles, but without obvious branching, can be observed.

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Explanation of Plates

All figured radiolarians are from a fine-grained to silty limestone from the lowermost Ordovician upper Windfall Formation in Nevada (sample 6-18-76I; 241 feet = 73.46 m below the top of the Windfall) in a section in a tributary to Ninemile Canyon, on the west side of the Antelope Range (USGS locality number 11307-CO) at 39°12'16" N. Lat.; 116°15'25" W. Long., on the Horse Heaven Mountain 15' topographic quadrangle map. Illustrated specimens are catalogued and reposited in the type collections of the Paleobiology Department, U.S. National Museum of Natural History (USNM), Washington, D.C., under the catalogue numbers USNM 494,842- 494,874.

Plate 1

Fig. 1: *Echidnina bengtsoni* n. sp., holotype, x 300, holder-no. 23-6-96/III-137; USNM 494,842; a, b: stereo pair.

Fig. 2: *Protoentactinia* ? sp. A, small fragment of the spicular system that nearly corresponds to the basic spicule, x 200, holder-no. 23-6-96/III-18; USNM 494,843.

Fig. 3: *Echidnina bengtsoni* n. sp., x 3000, holder-no. 23-6-96/III-99; USNM 494,844; a, b: stereo pair.

Fig. 4: *Protoentactinia* sp. B, fragment of the test (part of the inner and outer spicular system), x 300, holder-no. 23 96/III-98; USNM 494,845.

Fig. 5: *Parentactinia nevadensis* n. sp., holotype, x 500, holder-no. 23-6-96/III-104; USNM 494,846; a, b: stereo pair.

Fig. 6: *Protoentactinia* sp. C, fragment of the test, x 200, holder-no. 23-6-96/III-16; USNM 494,847.

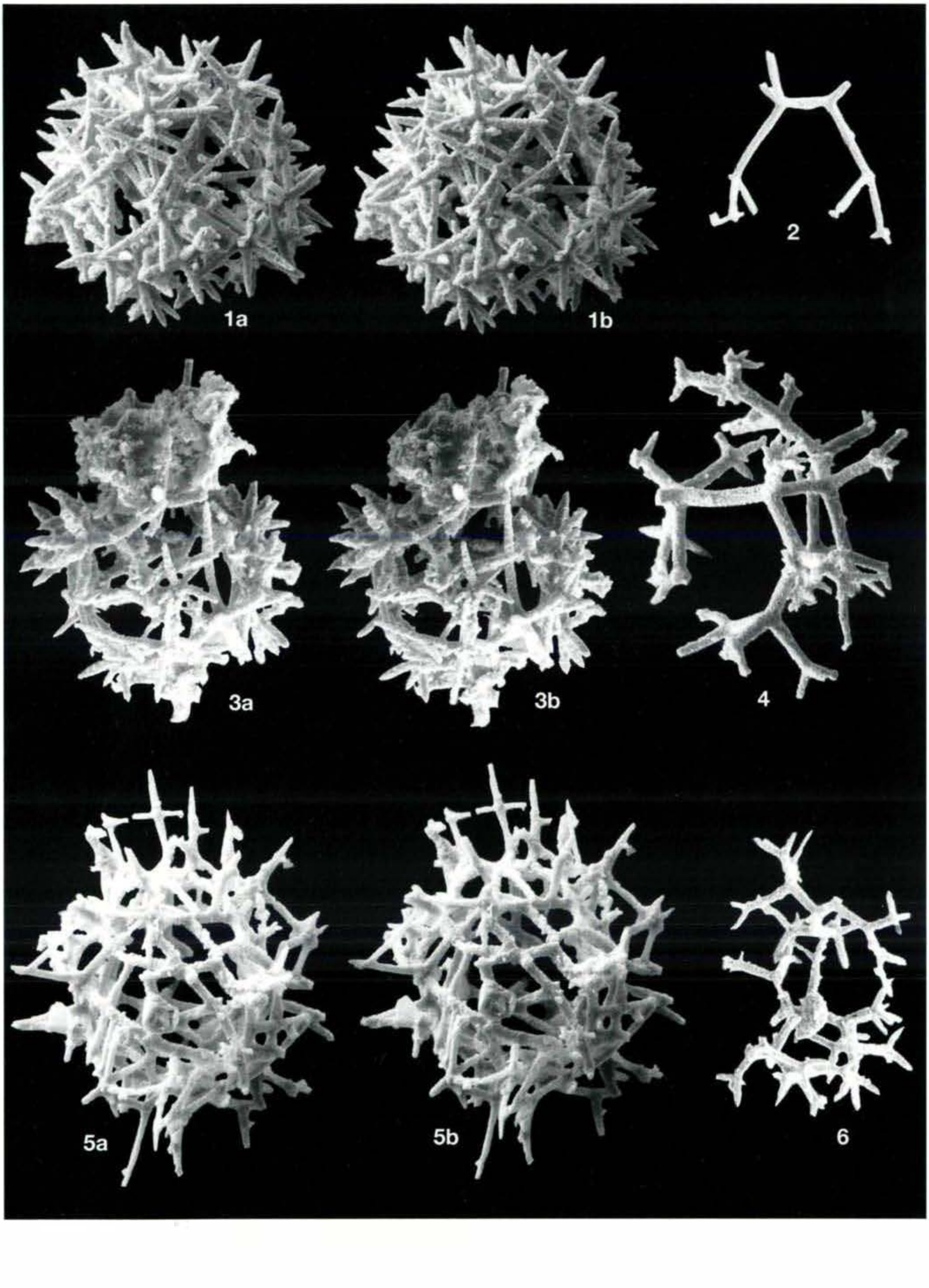

1a
1b
2
3a
3b
4
5a
5b
6

Plate 2

Fig. 1: *Parechidnina nevadensis* n. sp., x 500, holder no. 23-6-96/III-63; USNM 494,848; a, b: stereo pair.

Fig. 2: *Protoentactinia gracilispinosa* n. sp., fragment of the inner part of the test, x 300, holder no. 23-6-96/III-20; USNM 494,849.

Fig. 3: *Parechidnina nevadensis* n. sp., x 700, holder no. 23-6-96/III-59; USNM 494,850; a, b: stereo pair.

Fig. 4: *Protoentactinia gracilispinosa* n. sp., fragment of the inner test, x 300, holder no. 23-6-96/III-23; USNM 494,851.

Fig. 5: *Protoentactinia gracilispinosa* n. sp., x 300, holder no. 23-6-96/III-117; USNM 494,852; a, b: stereo pair.

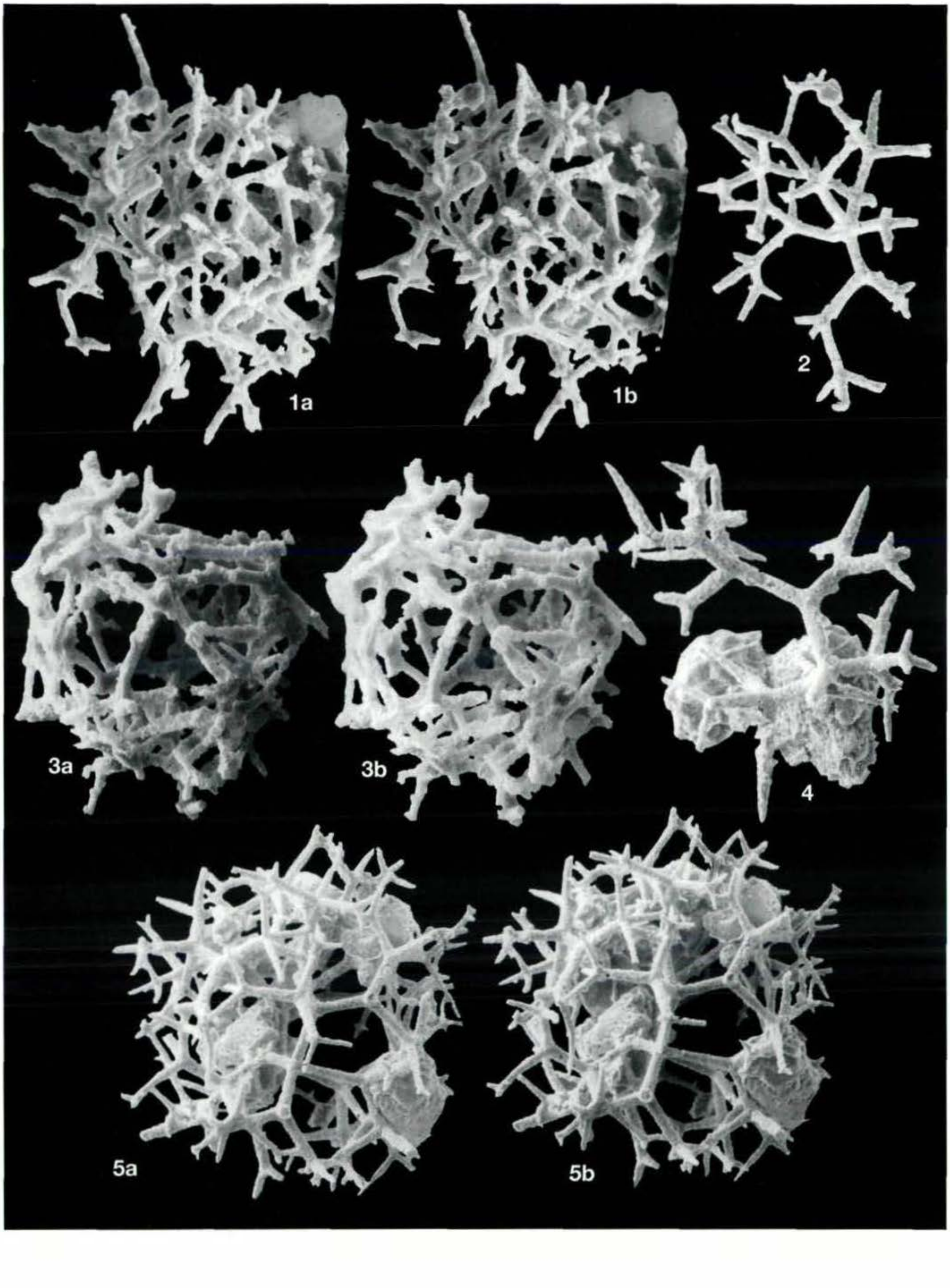

1a
1b
2
3a
3b
4
5a
5b

Plate 3

Fig. 1: *Protoentactinia gracilispinosa* n. sp., holotype, x 300, holder no. 23-6-96/III-113; USNM 494,853; a, b: stereo pair.

Fig. 2: *Protoentactinia gracilispinosa* n. sp., x 300, holder no. 23-6-96/III-83; USNM 494,854; a, b: stereo pair.

Fig. 3: *Protoentactinia gracilispinosa* n. sp., x 300, holder no. 23-6-96/III-68; USNM 494,855; a, b: stereo pair.

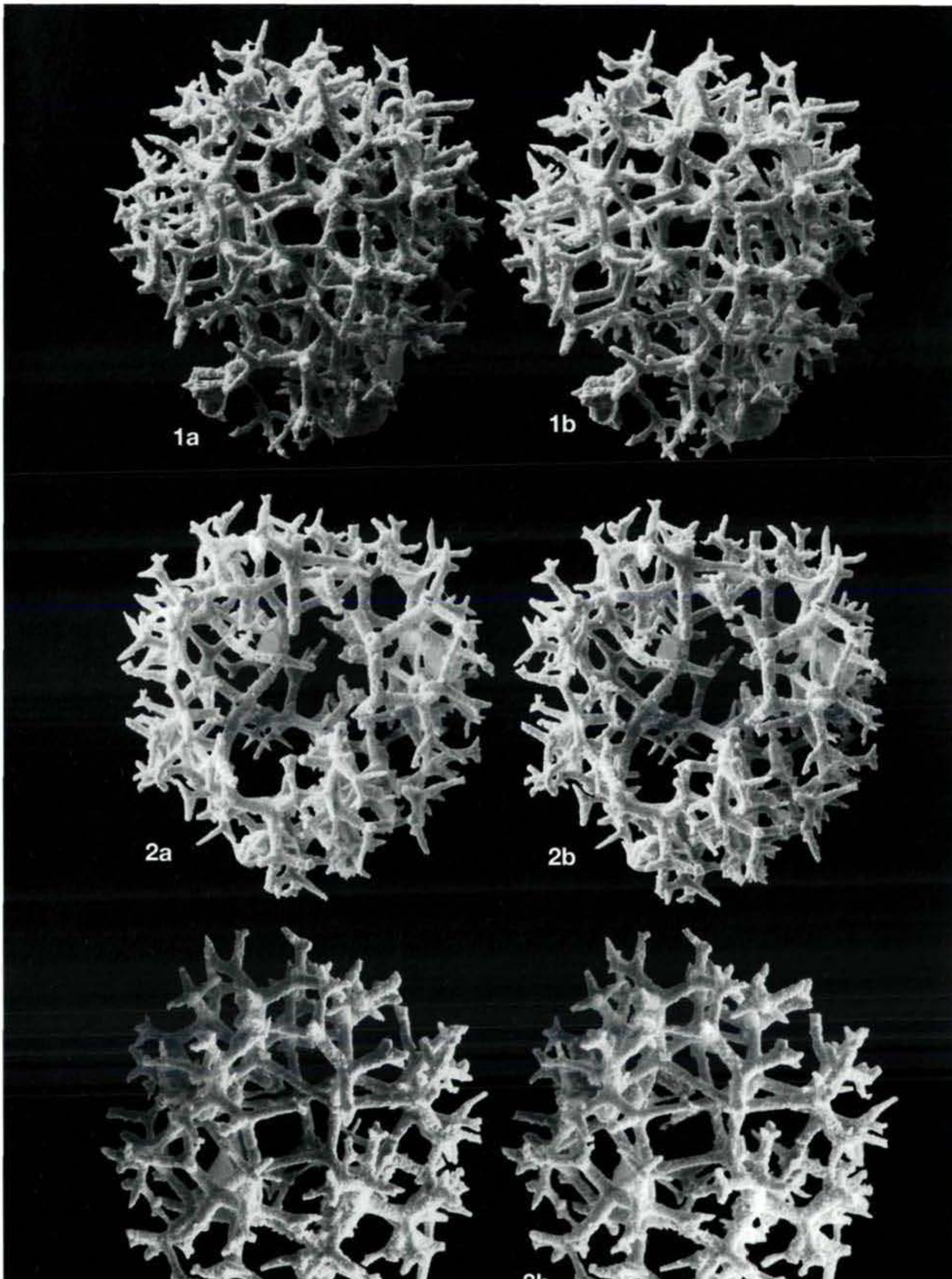

1a
1b
2a
2b
3a
3b

Plate 4

Fig. 1: *Protoentactinia gracilispinosa* n. sp., x 300, holder no. 23-6-96/III-79; USNM 494,856; a, b: stereo pair.

Fig. 2: *Protoentactinia gracilispinosa* n. sp., somewhat fragmentary, x 250, holder no. 23-6-96/III-101; USNM 494,857; a, b: stereo pair.

Fig. 3: *Protoentactinia gracilispinosa* n. sp., large fragment of the test, x 300, holder no. 23-6-96/III-21; USNM 494,858.

Fig. 4: *Protoentactinia gracilispinosa* n. sp., fragment of the inner test, x 340, holder no. 23-6-96/III-1968; USNM 494,859.

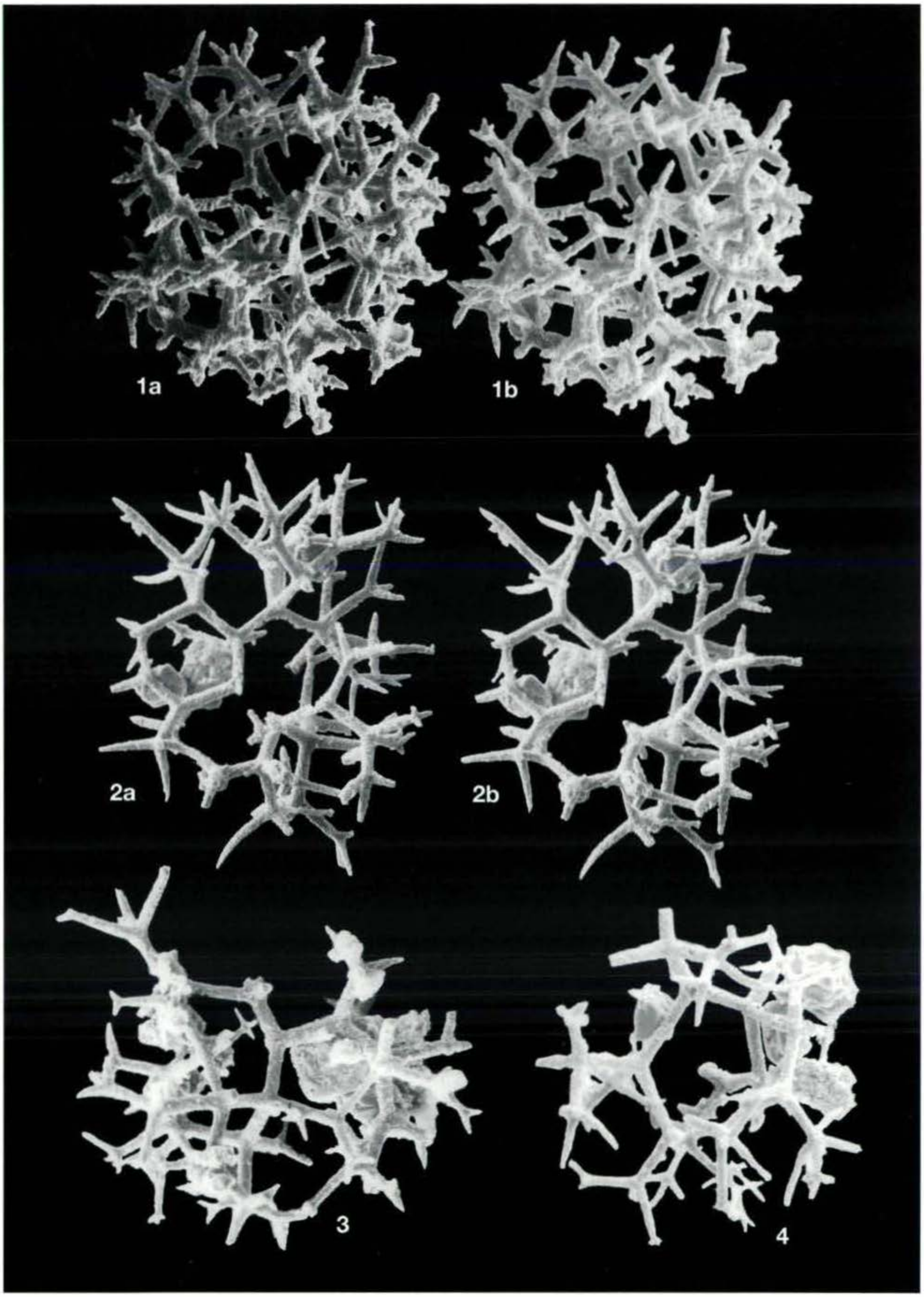

1a
1b
2a
2b
3
4

Plate 5

Fig. 1: *Protoentactinia gracilispinosa* n. sp., x 200, holder no. 23-6-96/III-126; USNM 494,860; a, b: stereo pair.

Fig. 2: *Protoentactinia gracilispinosa* n. sp., x 300, holder no. 23-6-96/III-55; USNM 494,861.

Fig. 3: *Protoentactinia gracilispinosa* n. sp., x 300, holder no. 23-6-96/III-117; USNM 494,862; a, b: stereo pair.

Fig. 4: *Protoentactinia gracilispinosa* n. sp., large fragment of the test, x 300, holder no. 23-6-96/III-46; USNM 494,863.

Fig. 5: *Protoentactinia minuta* n. sp., holotype, x 300, holder-no. 23-6-96/III-78; USNM 494,864; a, b: stereo pair.

Fig. 6: *Protoentactinia gracilispinosa* n. sp., x 300, holder no. 23-6-96/III-69; USNM 494,865.

Fig. 7: *Protoentactinia gracilispinosa* n. sp., x 250, holder no. 23-6-96/III-89; USNM 494,866.

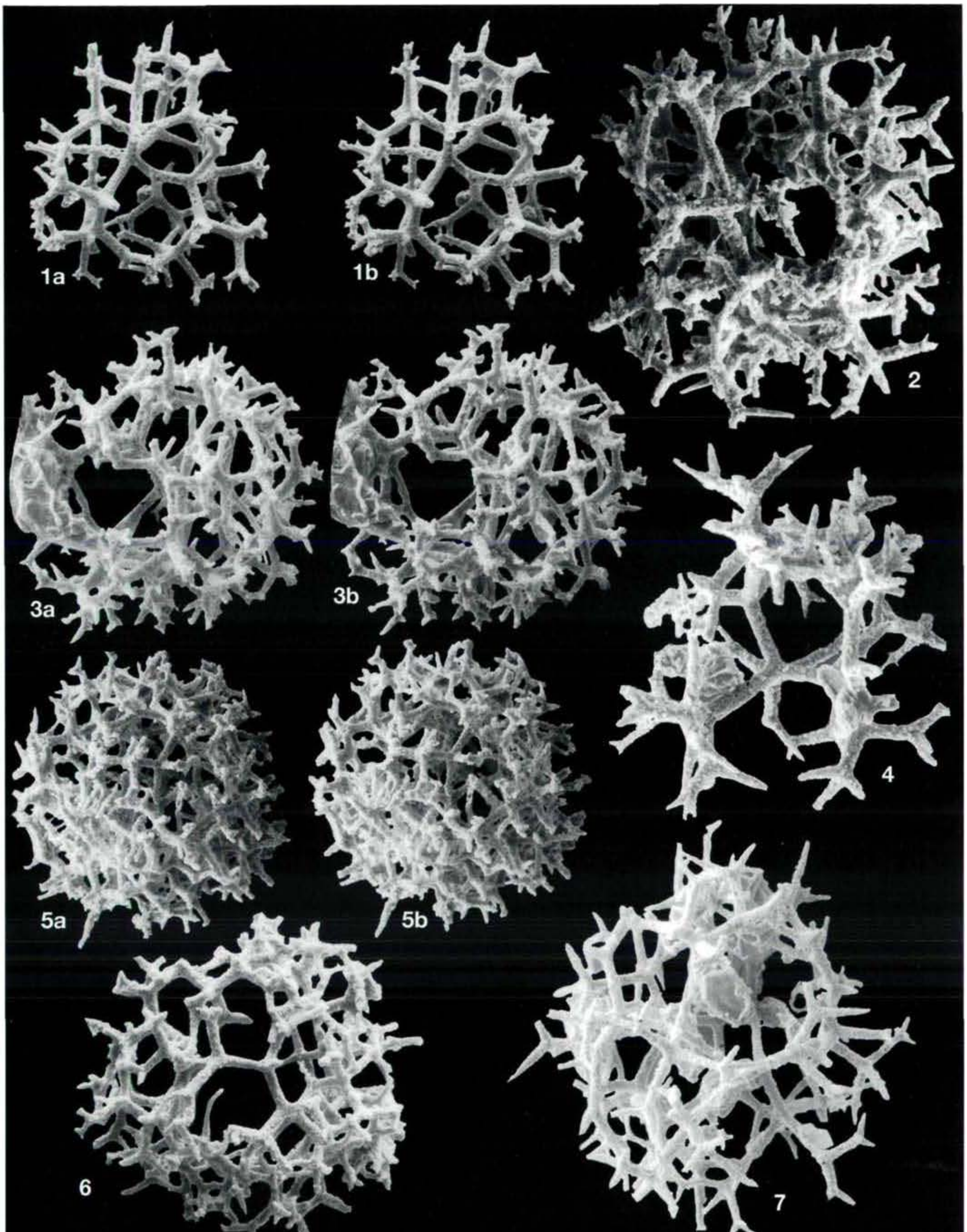

1a
1b
2
3a
3b
4
5a
5b
6
7

Plate 6

Fig. 1: *Protoentactinia gracilispinosa* n. sp., large fragment of the test, x 300, holder no. 23-6-96/III-76; USNM 494,867; a, b: stereo pair.

Fig. 2: *Protoentactinia gracilispinosa* n. sp., x 300, holder no. 23-6-96/III-118; USNM 494,868.

Fig. 3: *Protoentactinia gracilispinosa* n. sp., fragment of the spicular system of a large specimen, x 300, holder no. 23-6-96/III-44; USNM 494,869; a, b: stereo pair.

Fig. 4: *Protoentactinia gracilispinosa* n. sp., specimen with high percentage of bifurcation (bifurcated outer branches of the spicular system), x 300, holder no. 23-6-96/III-66; USNM 494,870; a, b: stereo pair.

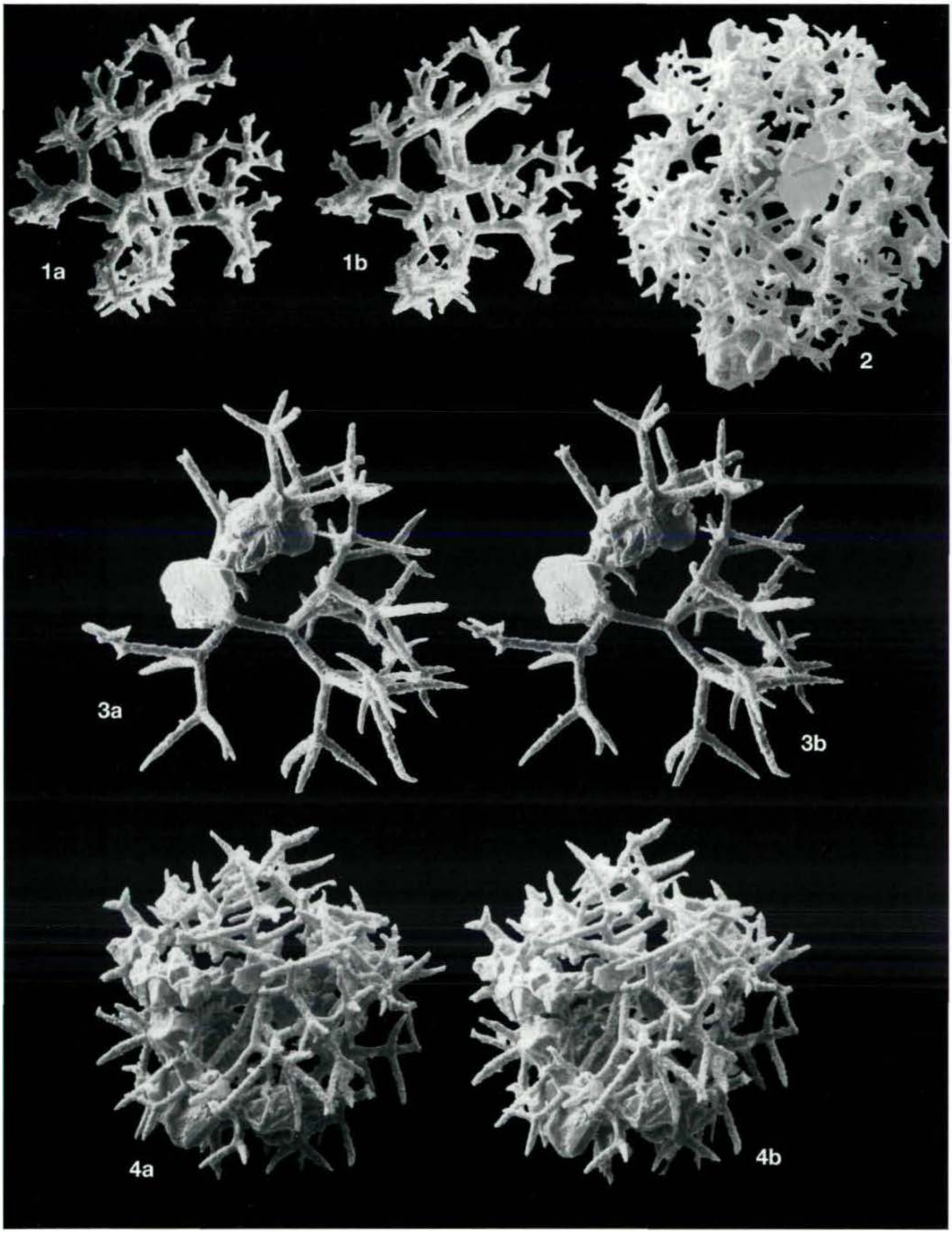

1a
1b
2
3a
3b
4a
4b

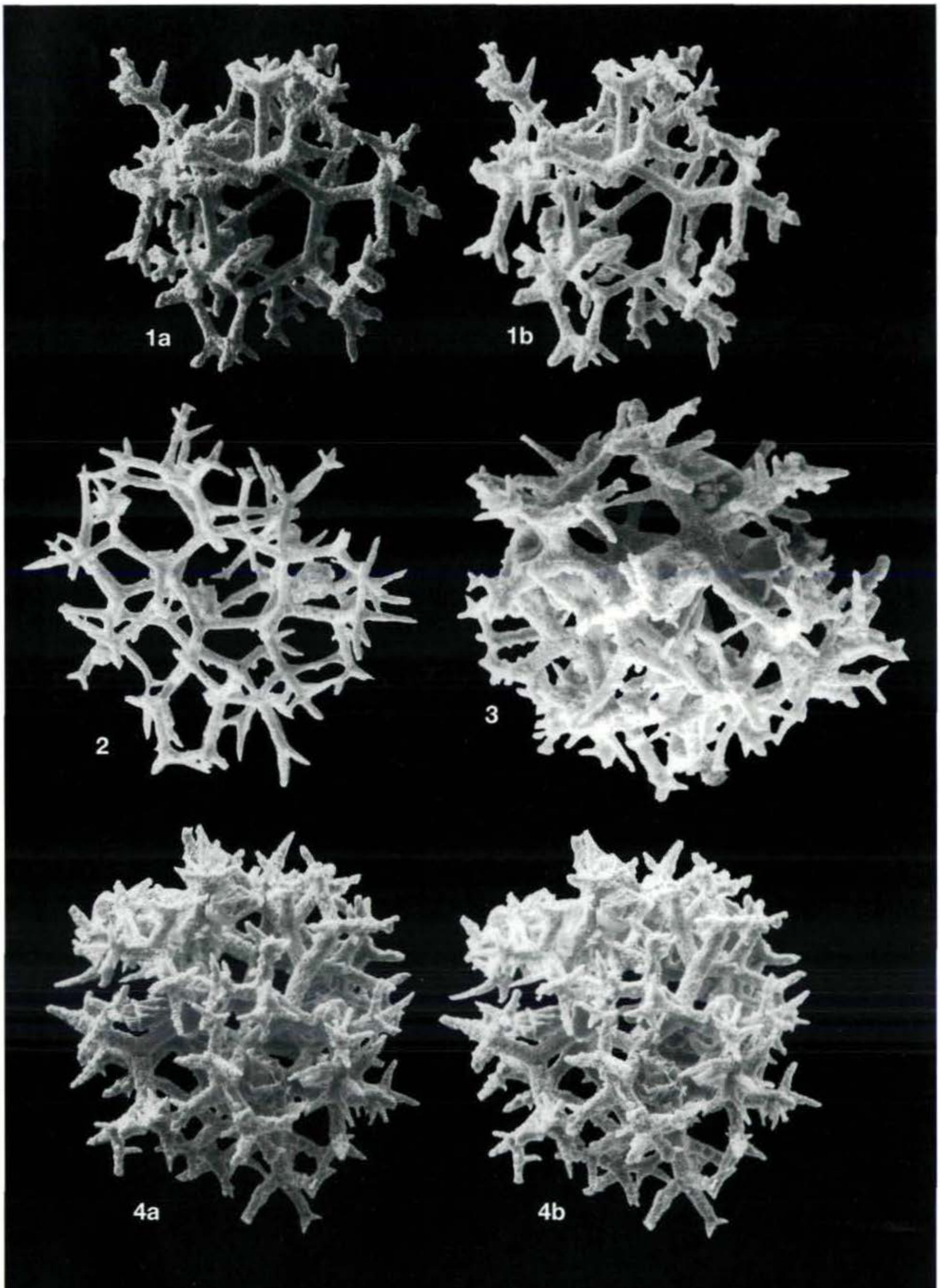
Plate 7

Fig. 1: *Protoentactinia gracilispinosa* n. sp., large fragment of the test, x 300, holder no. 23-6-96/III-58; USNM 494,871; a, b: stereo pair.

Fig. 2: *Protoentactinia gracilispinosa* n. sp., x 250, holder no. 23-6-96/III-116; USNM 494,872.

Fig. 3: *Noblella tremadociensis* n. sp., holotype, x 420, holder-no. 23-6-96/III-22; USNM 494,873.

Fig. 4: *Protoentactinia latospinosa* n. sp., holotype, x 300, holder-no. 23-6-96/III-57; USNM 494,874; a, b: stereo pair.


1a
1b
2
3
4a
4b