

# Review of family Entactiniidae (Radiolaria), and taxonomy and morphology of Entactiniidae in the late Devonian (Frasnian) Gogo formation, Australia

Mun-Zu Won

Marine Science Department, Natural Science College, Pusan National University, Pusan, Korea 607-735

**ABSTRACT:** This is the first of two publications dealing with a study of the family Entactiniidae and the taxonomy of a diverse assemblage of Late Devonian spumellarians. A well-preserved radiolarian fauna from the Gogo Formation, Western Australia, has made it possible to clarify the relation of the shell wall and internal structure in this family. The entactiniid shell is of two types: spongy and latticed. The former has apophyses on rays of the internal spicule, whereas those with latticed shells have an internal spicule without apophyses. On the basis of the internal spicule structure the Entactiniidae can also be divided into four types: (1) six-rayed spicule without a median bar, (2) four-rayed spicule without median bar, (3) six- to eight-rayed spicule with a median bar, and (4) twelve- to twenty-rayed spicule with a median bar.

The Gogo fauna includes more than 100 species. Entactiniids or taxa having characteristics similar to Entactiniidae are treated here. They comprise 17 genera and 72 species and subspecies, of which 13 genera and 66 species and subspecies are new. *Bisphaera*, *Radiobisphaera*, *Plenoentactinia*, *Apophysisphaera*, *Retentactinia*, *Retisphaera*, *Spongospaera*, *Duodecimentactinia* and *Multientactinia* belong to the Family Entactiniidae. *Apophysactinia*, *Magnisphaera*, *Magnentactinia*, and *Intracarpus*, are of uncertain taxonomic position. Entactiniid genera of this fauna are tentatively classified into two subfamilies: (1) Entactiniinae, which has a latticed shell(s) and lacks apophyses, and (2) Retentactiniinae n. subfam., characterized by a spongy shell and possessing apophyses. Taxa belonging to subfamily Entactiniinae plus taxa having characteristics similar to Entactiniidae, and subfamily Retentactiniinae are described respectively in this paper and in a second paper in this volume (Won 1997).

## INTRODUCTION

Upper Devonian radiolarian faunas have been described previously from two different areas in the Gogo Formation, a basinal succession interfingering with marginal slope facies of a barrier-reef complex along the northern margin of the Paleozoic Canning Basin, Western Australia. The first reports described material collected in the vicinity of Longs Well, northern Emanuel Range (Nazarov, Cockbain and Playford 1982; Nazarov and Ormiston 1983). The samples from the Longs Well area were initially said to have come from two widely separated localities (Nazarov and Ormiston 1983), but according to Aitchison (1993) they are not more than a few hundred meters apart, and are stratigraphically close. The material described by Nazarov and Ormiston (1983) was originally collected from the upper Gogo Formation during a conodont study, as sample G1/6 of Glenister and Klapper (1966, p. 837, text-fig. 1, section G1/G). This sample also yielded conodonts indicative of lower to middle *asymmetrica* zone, of lower Frasnian (basal Upper Devonian) age. According to Aitchison (1993), this age probably applies also to the sample described by Nazarov, Cockbain and Playford (1982), which is lower in the section by a small but undetermined distance.

A similar but better-preserved fauna was subsequently described by Aitchison (1993) from carbonate concretions in the Gogo Formation exposed in the Pillara Range, on the west side of Menyous Gap 20km north-northwest of Longs Well. I report here on additional material from the same locality (18° 25.8' S, 125° 54.3' E), extracted from limestone sent to me in 1982 by A. F. Trendall, Geological Survey of Western Australia. The material in this samples is even more diverse than in the sam-

ples analyzed by Aitchison (1993), and re-emphasizes a closer similarity between the Menyous Gap fauna and the upper Longs Well fauna described by Nazarov and Ormiston (1983), compared to the lower fauna described by Nazarov, Cockbain and Playford (1982).

Not all taxa from this fauna are treated in this paper. Specifically, all taxa belonging to Palaeoscenediidae and Ceratohiscidae are excluded. The composition of the species belonging to these two families in the present fauna is the same as that reported by Aitchison (1993).

The main purpose of this paper is to clarify and refine the previous definition of the Entactiniidae. Many taxa belonging to this family were defined on numerical characteristics and inner structures that were incompletely studied due to their moderate to poor preservation. The internal structure of many Paleozoic species can not be observed because of their preservation and has therefore been deduced from the outer shell characteristics, such as outer spine number. Thus, many species were classified by inference, and very important diagnostic features were hypothetically illustrated.

The excellent preservation of the radiolarians in this Gogo fauna has revealed inner structures. The relation between skeletal structural elements can now be clarified. In addition, the appropriate criteria for classification and the relative ranking of the criteria, as well as the range of variation in structure elements in a species, genus, or even higher taxon in the family Entactiniidae, may be determined. Some previously misidentified species and genera are revised.

Conodonts, mainly transparent juvenile and some milky colored elements of adults, together with abundant silicified tentaculids of one species were also recovered from the sample.

## COMPOSITIONAL CHARACTERISTICS OF THE GOGO FORMATION FAUNA

Unlike the previously studied Paleozoic radiolarian faunas, this Gogo Formation fauna is diverse, including more than 100 species. It consists mainly of Entactiniidae Riedel 1967, Paleoscenidiidae Riedel 1967, and Ceratoikiscidae Holdsworth 1969. Among these, the Entactiniidae are most diverse and abundant. In particular, specimens belonging to the new subfamily Retentactiniinae, characterized by spongy shell wall structure and internal spicule having apophyses, are much more diverse but much less plentiful than those of the subfamily Entactiniinae, which is characterized by latticed shell wall structure and internal spicule without apophyses. The diversity of the Retentactiniinae tends to decrease in the Devonian faunas younger than the Gogo fauna. In fact, in Lower Carboniferous faunas, species of Retentactiniinae are very rare, and most entactiniid species belong to the Entactiniinae.

Among families in the present fauna, the family Paleoscenidiidae show the lowest diversity, but they are extremely plentiful, consisting mostly of species of *Palaeoscenidium* Deflandre 1953. However, *Palaeoscenidium* includes very diverse forms to compare to that of other faunas. Some specimens belonging to *Palaeocephippium* Goodbody 1986 were recovered. The family Ceratoikiscidae is much more diverse than that in any previously reported fauna, but the number of specimens for any one species ranges from very plentiful to scarce.

Because of enormous quantity of individuals and picking bias, the percentage of each member of the fauna was not calculated. The numbers recorded for each species simply indicate relative abundance.

## SPECIES CHARACTERISTIC OF THE GOGO FORMATION FAUNA

In this fauna many species show a wide range of variation and can be subdivided into two or rarely three to four morphotypes. It is not known whether these morphotypes (1) are ecomorphs, (2) indicate different ontogenetic steps, or (3) are due to dimorphism resulting from alternation of generations. Also, the degree of and features involved in the differentiation in a species differ among the taxa. For example, in most species of *Radio-bisphaera* n. gen. and *Bisphaera* n. gen., shell wall structure and outer spine number, length, and thickness, as well as by-spine density, are generally of two types in a species, and these differences may be due to different characteristics of water mass reflecting changes in ecological factors like water density, silica content, etc. In contrast, the difference between forms appears more gradual in some species of *Spongospaera* n. gen. and *Retisphaera* n. gen. And, as a last example, even though the basic skeletal elements have the same structure, the detailed structure of some elements, for instance, the presence or absence of a basal layer, can also be somewhat different. This variation is discussed in detail in the corresponding taxa.

## TERMINOLOGY

**Apophyses:** Three, less frequently four, much less frequently two or five bars as one set that arise radially on the rays or spines. (See text-fig. 1a, b in this paper and also Won 1997, text-fig. 1, this volume, p. 373).

**Inner apophyses:** apophyses that arise on the rays of internal spicule in the inner shell. (See text-fig. 1.)

**Outer apophyses:** apophyses that lie or between inner and outer shell or between outer shell walls or free on the spines without connection to any skeletal element. (See text-fig. 1.)

Apophyses can, by means of intervening bars or their branches, form a complex N-frame (network frame; text-fig. 1b in this paper; see also Won 1997, text-fig. 1h, this volume p. 373). They can also be very short on the rays very near the inside of the shell wall (Won 1997, text-fig. 1d, this volume, p. 373), or very near the inside of the basal layer (Won 1997, text-fig. 1b, c, this volume, p. 373), or be present only as traces (Won 1997, text-fig. 1a, this volume, p. 373). They can also be free without connection to any other elements (Won 1997, text-fig. 1e, this volume, p. 373) or represented by linear elements (Won 1997, text-fig. 1f, this volume, p. 373). Or they can be a part of shell wall (Won 1997, text-fig. 1g, this volume, p. 373).

This structural element was named spinules or branches and used first by Foreman (1963) and then diversely termed as apophyses or branches. Because the term might be confused with spine or spicule, the term apophysis(-es) is used herein. The term apophyses was used by Nazarov for other projections. However, the term used in this paper is limited only to the cases as defined in this text.

**Axis bar:** A long bar passing through the spherical shell (Won 1997, text-fig. 1c, this volume, p. 373). From two points on the bar two sets of rays arise. The distance between those two points appears as a median bar. When both distal parts of the axis bar are bent in the opposite or same direction at the two points where two sets of rays arise, then all rays appear to be connected by a median bar.

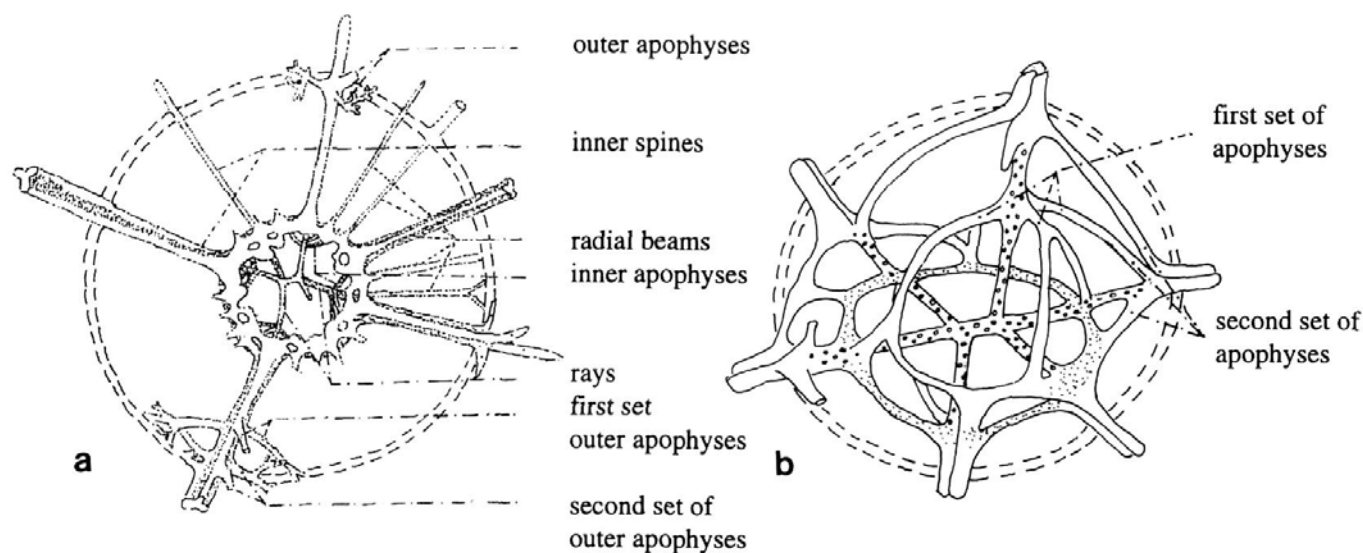
**Basal layer:** A innermost layer of a spongy shell which is distinct and distinguished from its overlying tissue (Won 1997, text-fig. 1b, c, this volume, p. 373). It can be separated from the overlying shell tissue or integrated into the shell wall tissue. The basal layer has been described as an inner shell (in an English translation of Nazarov's report) and even regarded as an inner shell. However, a true inner shell lies far from the outer shell and its diameter is much smaller than the basal layer diameter. In addition, the inner shell is connected with the outer shell by inner spines and can also be connected with radial beams.

**Inner layer:** The innermost layer of spongy shell wall which is not distinguished or not separated from its overlying tissue and has the same structure like the overlying tissue.

**Inner spines:** Spines that lie between inner and outer shells; they are the continuations of the rays of an internal spicule and generally extend beyond the outer shell surface as main or, rarely, much less prominent spines. They can be thin or thick and rodlike or three-bladed, even have the same size and shape as radial beams. (text-fig. 1.)

**Internal spicule:** The internal structural element consisting of several rays connected by a median bar or a median microbar or radiating from a single point within the shell.

**Microsepta:** In some species, a latticed shell is covered by, and the pores of shell wall is filled with delicate threads of spongy tissue (Won 1997, pl. 1, fig. 6, 13, 14, this volume, p. 385). The tissue is usually not preserved but the traces of spongy tissue



TEXT-FIGURE 1

a, Diagram illustrating the terminology used herein. b, Schematic and approximate sketch of one kind of N-frame. The frame is made up of apophyses, their branches and intervening bars. (To simplify the diagram most branches and intervening bars are not drawn in this text-figure, see also Won 1997, Text-fig. 1h, this volume, p. 373). The subcircular R-frame (dotted part) is a portion of the N-frame. The six-rayed internal spicule with a median bar is indicated by open circles. Apophyses can be branched. First apophyses can join either with other first apophyses or second apophyses or even branches of a first apophysis.

can be observable as microsepta, which are connected as a net (Won 1997, pl. 1, fig. 10; pl. 2, fig. 16, this volume, p. 385, 387) that fills the lattice pores or is reduced to spinules that make four to five microsepta that rise from inner sides of each pore-frame and partially cross the pore space (Pl. 1, figs. 17, 18; Pl. 2, fig. 3; also Won 1997, pl. 1, fig. 2, this volume, p. 385).

**Median bar:** A bar joining the rays of an internal spicule where the rays arise at its distal ends. Where this bar is too short to be measured, it can be called a median microbar.

**Median microbar:** An extremely short, or essentially unmeasurable median bar that joins rays of an internal spicule but the rays arise not from a single point. To describe the very short bar, a term median point was used by Foreman (1963), but median point was also used by Riedel in his English translation of Nazarov (1975) to define a single point from which the rays originate. To avoid the confusion, the term median microbar is used herein (Pl. 6, figs. 19, 20).

**N-frame (network frame):** Apophyses that do not join directly to inner shell or to outer shell, but they and intervening bars or branches of apophyses anastomose to form a complex net structure (text-fig. 1b). The N-frame can appear as an inner shell if the elements constituting the N-frame are more densely constructed and the N-frame is separated far from spongy tissue above it (Won 1997, text-fig. 1k, this volume, p. 373). The elements of the N-frame can have a structure like its overlying spongy tissue or can consist of robust and long bars (Won 1997, text-fig. 1i, this volume, p. 373) or delicate bars (Won 1997, text-fig. 1f, j, l, this volume, p. 373). More detailed explanation about N-frame is given in the diagnosis and remarks for *Retentactinia* n. gen.

**One-layered spongy shell:** A spongy shell has one layer consisting of very irregular and fine meshwork with a two-dimensional structure, but it has a three-dimensional structure near inner surface of the shell wall where the apophyses on the rays of an internal spicule or on the inner spines arise (Won 1997, pl. 11, fig. 1, this volume, p. 403).

**Radial beams:** Generally thin, rodlike elements that arise from the outer surface of the inner shell and lie between inner and outer shells, but they can also be three-bladed and thick. They can protrude beyond the outer shell as spines or by-spines (text-fig. 1a).

**R-frame (subrhomboidal, subrectangular, or circular to subcircular frame):** The whole N-frame is in most specimens too complex and too open to make its three dimensional construction readily apparent and it can be extremely difficult to distinguish from overlying spongy tissue. The R-frame is a part of the N-frame. It can be more easily observable than the N-frame and can form a unique subrhomboidal, subrectangular to circular frame (text-fig. 1b; also Won 1997, text-figs. 1i, j, k, l, this volume, p. 373) formed by first set of inner apophyses and intervening bars. Depending on preservation and the direction from which it is viewed, it lies in the middle or eccentrically within the shell, and the unique shape may be or may not be visible.

#### THE RELATION AND DIFFERENCE BETWEEN THE SPONGY SHELL AND LATTICED SHELL

Generally, a spongy shell is easily distinguished from a shell with latticed meshwork by the construction structure of the elements which form the shell wall. The elements of the former are irregular, three-dimensionally interwoven, whereas the elements of latter are two-dimensionally and relative regularly constructed. However, in some spongy shells, the elements are woven two-dimensionally or appear as if they are latticed shells.

(1) As observed in *Retisphaera concinna* (Aitchison 1993; Won 1997, pl. 4, figs. 5-20, this volume, p. 393), and *Spongospaera grandispongiosa* n. sp. (Won 1997, pl. 9, figs. 15-20, this volume, p. 403), as well as in *Multientactinia inconstans* n. sp. (Won 1997, pl. 11, figs. 1-8, this volume, p. 407), some species have a thin one-layered to thick spongy shell. The elements of one-layered spongy shell is two-dimensionally woven. Such a shell wall does not represent the characteristic of those species, and it may be an initial layer of the thick spongy shell. The one-layered spongy shell differs generally from the latticed meshwork by its delicate and/or very irregular or angular meshwork.

(2) Because of their preservation, some spongy shells appear to be or could be considered as latticed shells. Spongy shells can have a basal layer whose meshwork commonly has an indistinct or clear two-dimensional structure. Where the spongy tissue of a shell that overlies the basal layer is not preserved, the meshwork of the shell appears to be two-dimensional as in *Entactinosphaera? riedeli* Foreman 1963, *Entactinosphaera? frederiki* Foreman 1963, and *Spongentactinia flexa* n. sp. (Won 1997, this volume, p. 404) The shells of these species differ from the shells with a true latticed meshwork in having branched by-spines, which imply the presence of delicate spongy material attached to them, and/or in their complicated three-dimensional internal structure including apophyses, even though the spongy tissue is no longer preserved.

Latticed meshwork can also be very irregular. However, the irregularity is generally not so great and the shell wall is not so delicate as in a spongy shell. The difference between a one-layered spongy shell and an irregular latticed shell is easily detected because the former is connected to apophyses in its inner side, whereas the latter has no apophyses. Thus, even though the spongy shell has one layer whose meshwork has a two-dimensional structure as in both these examples, it has a three-dimensional structure near the inner surface of the shell wall where the apophyses on the rays of an internal spicule or on the inner spines arise.

The relation between the latticed shell wall and spongy shell wall in the family Entactiniidae can be deduced as follows:

(1) Compact spongy shell, multi-layered shell, and multi-shelled skeleton:

A series of shell types can be observed in the genus *Plenoentactinia* n. gen. and in *Tetraentactinia* Foreman 1963; it includes a compact nonlayered, faintly layered, and clearly multi-layered shell spongy shell. A multi-layered spongy shell wall to multi-shelled skeleton continuum can be observed in *Meschedea* Won 1983. A multi-shelled skeleton can be found in the type species of *Entactinosphaera* Foreman 1963 and in species formerly assigned to *Belowea* Won 1983 and *Provisocyntra* Nazarov 1981. The multi-layered shell might be a transitional form between the compact spongy tissue and latticed meshwork of multi-shelled skeleton. As examples of these details, in *Plenoentactinia stellata* Won 1997, the compact spongy shell is faintly differentiated radially and concentrically in some specimens (Won 1997, pl. 15, fig. 14, this volume, p. 415) and in *Meschedea crassicortex* n. sp., a few specimens show still less well differentiated layer structure (Pl. 7, fig. 3). Also, in the shell wall of *Entactinosphaera* sp. cf. *E. variabilis* (=former *Belowea* sp. cf. *B. variabilis* Won 1983, pl. 2, figs. 17-22) the distance between layers is very short, unlike typical multi-shelled species, even

though all the other diagnostic characteristics are the same as in *E. variabilis*.

When the layering is well developed, the latticed shell wall structure is dominant. In forms in which layering is less well developed, the spongy structure is dominant. Where layering is better developed, the distance between the layers becomes wider. In addition, when the distance between the layers is wider, the skeletal elements forming the concentric shell layers are more strongly developed than the radial elements (connecting bars between shells). The apophyses are less well developed in the better layered shells, and they can be difficult to distinguish in clearly multi-layered specimens and are absent in all multi-shelled skeletons.

(2) Spongy shell with basal layer, latticed shell, and intermediate shell type:

The meshwork of the basal layer of many of the spongy shelled specimens is two-dimensionally but commonly irregularly constructed. Some basal layers have the same structure as a latticed shell consisting of regularly latticed meshwork. As Foreman described *Tetraentactinia barysphaera* Foreman 1963, there is variation in the development of spongy tissue on a well-latticed layer. In some specimens the spongy tissue is very well developed and the latticed layer can be regarded as the basal layer. The layer was termed lattice-shell by Foreman. In other specimens from one limestone concretion collected by the writer from the Ohio Shale, the spongy tissue is almost completely broken off, or developed only within a small radius around the spines. The same feature was also observed by Foreman (1963). In these forms, it is very hard to define that latticed layer as a basal layer of a spongy shell or a latticed shell. In addition, very well preserved specimens of *Apophysisphaera* n. gen. show spongy tissue on a latticed meshwork (Won 1997, pl. 1, figs. 6, 13, 14, this volume, p. 387). In other relatively well preserved specimens of *Apophysisphaera*, only the traces of the spongy tissue can be observed as microsepta (Won 1997, pl. 1, figs. 2, 10, this volume, p. 387).

Spinule-like microsepta are also observed in *Entactinia* (Pl. 1, figs. 4, 17, 18, pl. 2, figs. 3, 7). One of the main differences between *Entactinia* and *Apophysisphaera* is the presence or absence of inner apophyses. The inner apophyses of *Apophysisphaera* (Won 1997, text-fig. 1d, this volume, p. 373) are very short and lie very close to the inside of the shell wall as they do in *Tetraentactinia*. In these two genera, the degree of their development varies according to shell wall structure; in the more irregular, more spongy shell, inner apophyses are better developed, and they exhibit a tendency to totally disappear in forms where a tight and regularly latticed meshwork having no spongy tissue is present. Many species have very short inner apophyses on each ray or, rarely, some rays have apophyses while the others have none. In other species, there are no traces of inner apophyses. In the more regular, more tightly latticed shell of *Apophysisphaera* species, inner apophyses are less well developed. With a regularly and tightly latticed shell without spongy tissue, inner apophyses do not exist, as in *Entactinia*. From these examples, it appears that shells composed of latticed meshwork and rays with inner apophyses are a construction transitional between spongy and latticed shell walls.

Some very finely latticed shells with or without an unevenly patterned structure have been regarded as spongy shells like specimens identified as *Spongentactinia spongites* Foreman 1963 by Gourmelon (1987, pl. 4, fig. 12) and *Spongentactinia*



*exilis* (Foreman 1963) by Gourmelon (1987, pl. 5, figs. 7, 8, and *Pluristratoentactinia* Nazarov 1981 because their fine surface texture looks like the surface of a compact spongy shell. However, in these finely latticed shells the meshworks are originally two-dimensionally latticed without apophyses. The unevenly patterned structure showing imperfect two-dimensional structure is due to the way in which the base of by-spines and/or of blades of main spines joins the neighboring poreframes or the base of the neighboring by-spines.

#### RANGE OF VARIATION IN SKELETAL STRUCTURE AT THE SPECIES AND GENUS LEVELS IN THE FAMILY ENTACTINIIDAE

##### Shell wall structure

**Basic structure types:** The shell walls of all the entactiniids can be divided into two groups, one consisting of latticed meshwork without apophyses and the other consisting of spongy tissue with apophyses. The basic shell wall structure (spongy or latticed) is constant at the species level and generally also at the genus level. Intermediate or transitional types between the two groups can have characteristics of both and make up a continuum between the end members.

**The variability of shell wall structure:** According to previous studies, the shell wall structure and thickness seemed to be fairly constant. However, the Gogo Formation fauna described in this report shows relatively large variability in the shell wall texture and thickness.

a) The variability in lattice shell (number of shells, meshwork pattern including regularity, pore size or shape).

Generally, the number of shells is constant at the species level and variable at the genus level. However, in multi-shelled species (as in the type species of *Entactinosphaera* Foreman 1963 and in species earlier identified as *Belowea* Won 1983 and *Provisocyntra* Nazarov 1981) the number can vary but within certain limits, but the number can partly also be due to secondary processes such as preservation and preparation. In meshwork pattern, at one end of a spectrum are smooth shell surfaces with two-dimensionally latticed meshwork and at the other end, unevenly patterned or reticulated surfaces, but only at a microscopic scale in certain species. The regularity and pore size or shape can change slightly to moderately or, very rarely, even considerably at the species level.

b) The variability of spongy shell wall (thickness or number of layers, tissue texture).

At the species level, the thickness of the shell wall can, in some taxa, vary from very thin "one-layered" spongy shell to thick typically three-dimensionally interwoven spongy tissue, even though all the other characteristics are constant, as observed in *Spongosphaera grandispongiosa* n. sp. (Won 1997, pl. 9, figs. 15, 16, 17, 19, this volume, p. 403) and *Multientactinia inconstans* n. sp. (Won 1997, pl. 11, figs. 1-8, this volume, p. 405). Tissue texture is generally constant at the species level but can vary within a given species, as in some species of *Multientactinia* n. gen.

##### Outer spine shape, number, and thickness

The number of the outer spines is commonly constant at the species level but variable at the genus level. Nazarov and Ormiston (1983) state that the number of major radial spines depends on the number of rays and branches (referring to

apophyses) in the internal spicule. The main outer spines are normally the continuation of the rays of an internal spicule, and their number generally reflects the ray number of an internal spicule if the number is eight or less. The number of spines in species having numerous radially distributed spines has no relation to the ray number, and the spines arise, except the spines extending from the rays of internal spicule, from the outer or inner shell surface. They are not connected to the apophyses on the rays, despite Nazarov's diagram (1975, p. 15, fig. 5) and Nazarov and Ormiston's statements (1983, p. 457, 459). In some species, there are no outer spines or fewer outer main spines than rays of the internal spicules such as in many specimens of *Entactinia variospina* (Won 1991), *Retentactinia aspinosa* n. sp., and a few specimens of *Bisphaera uniprocera* n. sp.

The thickness and length of the spines can also vary widely. End members in a species or in a group can appear very differently; compare Plate 4, figures 1-8. The expressions used by researchers to describe main spines, minor spines, and rarely also by-spines can simply be a relative order of the size in a specimen.

The shape of spines can be varied but within certain limits. The spines can be straight or twisted even in one specimen. The shape of their cross section is generally constant, but it varies according to the width of the grooves. Very rarely, spines can be rodlike or three-bladed even in a single specimen.

For classification, the presence or absence of by-spines is probably useless because it depends first on ecologic and second on diagenetic factors and preparation processes. However, in some taxa, by-spine thickness, density, shape, and the relation to the meshwork of the shell can be diagnostic at the species level.

##### Inner shell and basal layer

The absence or presence of the inner shell is always constant at the genus and species levels. The elements forming inner shell can be two-dimensionally latticed or three-dimensionally constructed; these features are constant at the genus level. However, a three-dimensionally constructed inner shell that consists of an N-frame, displays a wide range of variation in shell wall outline, mesh shape, size, tightness etc., even in a given species as in species of *Retisphaera* n. gen. (Won 1997, this volume) The latticed inner shell can show variations in the regularity of the meshwork.

In some taxa, the general tendency for presence and absence of a basal layer of spongy shell can be constant at the genus level. In others, it is variable not only at the genus level but also at the species level. Some basal layer have been misconstrued as an inner shell, and extremely rarely, the difference between them is very difficult to discern. However, the general difference between them is clear: the basal layer is contiguous with or slightly separated from the neighboring shell wall tissue, whereas the inner shell is connected with outer shell by the long inner spines and/or radial beams.

##### Inner spines and radial beams

In entactiniids, inner spines are three-bladed or rarely rodlike, and radial beams are rodlike or rarely faintly to clearly three-bladed. The shape and thickness of both can also be the same in a species. The shape of inner spines or radial beams is generally constant in a species. The number of inner spines is constant, but the number of radial beams seems to range within certain limits. In some genera, like *Radiobisphaera* n. gen., the shape

and number of inner spines and radial beams can be good criteria to classify species. On the other hand, in some taxa having spongy shells, radial beams can be present or absent, or their number can vary, and even the inner spines can rarely have different shapes and thicknesses.

#### Internal spicule (ray number, median bar length)

In the family Entactiniidae all the taxa can be classified into four groups on the basis of the ray number and presence or absence of a median bar: (1) four-rayed internal spicule without median bar, (2) six-rayed internal spicule without median bar, (3) six- to eight-rayed internal spicule with a median bar, and (4) twelve- or more than twelve-rayed internal spicule with a median bar. Most entactiniids have an internal spicule structure of the third type. As far as is currently known, the first, second, and fourth types occur only within a very short stratigraphic interval. (See remarks on family Entactiniidae, p. 343)

The number of rays can be variable at the genus level. If it is variable, then it varies within certain limits. For example, a genus belonging to the third group can have six or, less frequently, eight rays, and a genus belonging to the fourth group can have a twelve- to twenty-rayed internal spicule. Generally the number of rays is constant at the species level. However, it too can be rarely variable within certain limits. For example, species with a six-rayed internal spicule can have an eight-rayed variant. Species having an eight-rayed internal spicule can rarely have a six-rayed internal spicule. Many eight-rayed internal spicules can appear seven-rayed because of preservation and of their orientation when being examined. An odd-numbered variation form is much rarer than an even-numbered one.

The median bar length is generally constant at the species level. The median bar length can be used as good criteria for identification. However, the median bar (including internal spicule) structure is hard to observe even if it is preserved. Also, the length often cannot easily be measured because the length appears to change with the angle of observation.

#### Apophyses

Spines and internal spicules in subfamily Entactiniinae have no apophyses, whereas those in the Retentactiniinae n. subfam. have apophyses. However, in "intermediate" genera, those that have both subfamily characteristics, apophyses can be present or absent. In those taxa, apophyses are less well developed, remain as traces, or do not exist. In some intermediate taxa, apophyses are present only on some rays even in a single specimen.

#### Internal structure

The general internal structure, that is, whether the internal spicule has a median bar or a median microbar or arises from a central point, and presence or absence of an inner shell with or without inner apophyses, as well as whether the apophyses form a network frame (N-frame) or not, is constant at the genus level. Exceptionally, there are a few taxa whose internal structure is somewhat variable in their detailed structure within certain limits.

#### RECONSIDERATION OF THE FAMILY ENTACTINIIDAE

Nazarov (1975) divided family Entactiniidae into two subfamilies, Entactiniinae, and Polyentactiniinae. According to Nazarov (1975, p. 45), the Entactiniinae differs from the Polyentactiniinae in the structure of the internal skeleton. The Entactiniinae have a tetra- or hexaradiate internal skeleton, which in Polyentactiniinae is represented by a polyhedron or a

multiradiate spicule. Nazarov and Ormiston (1984) removed *Polyentactinia* from the Entactiniidae, and they (1984) tentatively assigned the genus to family *Orosphaeridae*. Subsequently, Nazarov (1988) established a new family Polyentactiniidae. Instead of Polyentactiniinae Nazarov and Ormiston (1984) established the subfamily Astroentactiniinae. Nazarov (1988) stated that the Entactiniinae is characterized by an internal skeleton in the form of a four- to six-rayed internal spicule, whereas the Astroentactiniinae is characterized by a six-, seven-rayed, or more multi-rayed internal spicule, commonly with two or three groups of apophyses on each ray which join the bases of the radial outer spines. From this, the difference between the two subfamilies became obscure, and the diagnosis of both subfamilies partially overlaps (i.e., number of rays and presence or absence of apophyses). It is also unclear whether the criterion on which to subdivide the family Entactiniidae is the ray number of the internal spicule or the presence or absence of the apophyses, because in contrast to his definition, he reported that some taxa that belonged to his Entactiniinae have apophyses, and some taxa that belonged to Astroentactiniinae have no apophyses.

Whatever Nazarov's criteria to classify the family Entactiniidae are, the occurrence and character of the internal spicule structure can be examined. Through the relation between the internal spicule and the other structural elements, or through the distinct internal spicule structure, the range of variation in the ray number of an internal spicule is shown in the following examples.

Example 1: *Multientactinia* n. gen. consisting of a spongy shell bears a unique internal structure having a very thick internal spicule with a very thick and long median bar; the ray number varies between 12 and 20 as an even number.

Example 2: *Entactinia* and *Apophysisphaera*, which display the same microscopic shell wall structure termed microsepta in well-preserved specimens, bear a six- to eight-rayed internal spicule. A species bearing a six-rayed internal spicule can have a variant with eight rays, and a species with eight-rayed internal spicule can have a variant with six rays. Besides the above two genera, *Bisphaera* n. gen., emended *Spongactinia* Nazarov 1975 in Won 1997 (this volume, p. 400, *Spongosphaera* n. gen., and *Plenoentactinia* n. gen. have a ray number that varies – six to eight.

Example 3: *Callella* Won 1983 has a characteristic twin-layered shell wall structure (Won 1983, see also 1990). The six rays arise from a point.

Example 4: *Tetraentactinia* is characterized by a four-rayed internal spicule without a median bar.

Consequently, even if the ray number might be a basic criterion to subdivide Entactiniidae, they can be grouped as the above four types (Table 1) by combining number of rays and ways in which rays are connected and by considering the characteristics of the other structural elements.

Nazarov (1988) grouped *Entactinia*, *Entactinosphaera*, *Tetraentactinia*, *Thecoentactinia*, *Spongactinia*, *Pluristratoentactinia*, and *Helgeria* together into the subfamily Entactiniinae, and *Astroentactinia*, *Helioentactinia*, *Spongactinella*, *Somphoentactinia*, *Provisocyntra*, *Copicyntra*, *Copiellintra*, *Copicyntroides* into the subfamily Astroentactiniinae. Of the genera assigned to Entactiniinae, *Thecoentactinia* and *Spongen-*

TABLE 1

Classification of family Entactiniidae by shell wall and internal spicule structure. \*Genera between double lines are taxa intermediate between genera having latticed shells without apophyses and genera having spongy shells with apophyses.

Med. bar & ray no.  Shell wall type and apophyses	Genera having six-rayed internal spicule without median bar	Genera having four-rayed internal spicule, no median bar	Genera having six- to eight-rayed internal spicule with median bar	Genera having twelve- to twenty- rayed internal spicule with median bar
Genera having latticed shell without apophyses	<i>Callella</i> Won 1983	<i>Trienosphaera</i> Deflandre 1973	<i>Entactinia</i> Foreman 1963	
	<i>Duplexia</i> Won 1983		<i>Entactinosphaera</i> Foreman 1963  <i>Bisphaera</i> n. gen.  <i>Radiobisphaera</i> n. gen.	
			<i>Meschedea</i> * Won 1983	
Genera having spongy shell with apophyses		<i>Tetrentactinia</i> * Foreman 1963	<i>Plenoentactinia</i> * n. gen.  <i>Apophysisphaera</i> * n. gen.	<i>Multientactinia</i> n. gen.  <i>Duodecimentactina</i> n. gen.
		<i>T. quadrispinosa</i> Foreman 1963  <i>T. gracilispinosa</i> (two-shelled) Foreman 1963	<i>Spongentactinia</i> Nazarov 1975  <i>Spongospaera</i> n. gen.  <i>Provisocyntra</i> Nazarov and Ormiston 1987  <i>Retentactinia</i> n. gen.  <i>Retisphaera</i> n. gen.	
Remarks	Twin-layered latticed shell			Reported only in the Gogo Formation

*tactinia* have apophyses, and the genera assigned to *Astroentactiniinae* such as *Helioentactinia* (some species, including the type species) and *Astroentactinia* (most or all(?) the species) have no apophyses. Nazarov (1975) himself reported the presence of apophyses in the description of *Spongentactinia fungosa* Nazarov 1975, *S. indisserta* Nazarov 1975, and *Thecoentactinia riedlei* (Foreman 1963). Even though Nazarov's criteria are not well defined or even expressed, according to his diagrams (1988, figs. 18, 19), the classification seems to be based on the presence or absence of apophyses and the

number of outer spines, except in *Copiellintra* Nazarov and Ormiston 1985. This classification may result from his belief that the number of outer spines depends on the number of rays and apophyses in the internal spicule (1975, 1988). Nazarov and Ormiston (1983, p. 457) state that "the number of major radial spines depends on the number of rays and branches [referring to apophyses] in the internal spicule (Nazarov 1975, 1981)."

Through the examination of all well-preserved specimens belonging to the Entactiniidae from this Gogo Formation fauna, it

TABLE 2

Summary of characteristics of the genera of the Family Entactiniidae.

ENTACTINIA Foreman 1963

Synonyms: PALAEOXYPHOSTYLUS Won 1983; INAEQUALIENTACTINIA Won 1991; ?ASTROENTACTINIA Nazarov 1975

Original diagnosis: A single well-developed latticed or spongy shell (sometimes with external spongy material) with an internal six-rayed double spicule more delicate than the main spines.

Emended diagnosis: A latticed shell and a six- to eight-rayed internal spicule with a median bar.

Type species and its diagnosis: *E. herculea* Foreman 1963, a latticed shell with a six-rayed internal spicule with a median bar.

ENTACTINOSPHERA Foreman 1963

Synonyms: PLURISTRATOENTACTINIA Nazarov 1981; BELOWIA Won 1983

Original diagnosis: Two or more well-developed spherical or subspherical shells and an internal six-rayed double spicule.

Emended diagnosis: Generally three to five latticed shells with a six-rayed internal spicule with a median bar, second shell is the most robust or all shells have same thickness, shell wall thin and delicate, commonly with unevenly patterned surface structure, radial beams generally present between shells.

Type species and its diagnosis: *E. esstrongyla* Foreman 1963; three or four latticed shells, second shell most robust, and a six-rayed internal spicule with a median bar, secondary radial beams between the inner and second shell in some specimens.

Remarks: Foreman (1963) reported that she had never observed a complete fourth shell. Its absence is due to poor preservation. See also remarks on *Bisphaera* n. gen.

TETRENTACTINIA Foreman 1963

Synonym: SOMPHOENTACTINIA Nazarov 1975; SPONGENTACTINELLA Nazarov 1975

Original diagnosis: Internal spicule with four rays originating in a point and arranged like the axes of a tetrahedron, around which is developed a complete or incomplete spherical or subspherical shell, frequently spongy and frequently with secondary spines.

Emended diagnosis: A spongy shell with or without a latticed basal layer and a four- rayed internal spicule with or without traces of apophyses, no median bar.

Type species and its diagnosis: *T. barysphaera* Foreman 1963; one lattice-shell with a spongy layer developed from the by-spines, a tetrahedral internal spicule.

Remarks: The diagnosis of this genus was redefined by Nazarov (1988) so that the genus is characterized by an internal skeleton represented by a four-rayed spicule, the rays of which disperse from a short (not more 5mm) bar. It is unreasonable to change one of the most important parts of a diagnosis without any foundation. See also the section titled Reconsideration of the family Entactiniidae, especially the discussion of *Tetraentactinia*.

TRIENOSPHERA Deflandre 1973

Original diagnosis: A perforated shell with four multicostulated spines which are tetrahedrally arranged.

Emended diagnosis (Gourmelon 1987): A spherical latticed shell, in which the four rays of the internal spicule converge at a single point and are connected with four tetrahedrally arranged outer spines.

Type species and its diagnosis: *T. sicarius* Deflandre 1973; the pores of meshwork are round and relative large. Spines are strong, multicostulated at their bases, and thin out constantly toward their tips.

SPONGENTACTINIA Nazarov 1975 (see also Nazarov 1988)

Diagnosis (Nazarov 1988): Internal skeleton in the form of a four- or six-rayed spicule, the rays of which disperse from a median (5-8mm) bar. A spongy outer shell, contiguous with or slightly separated from an inner porous shell, diameter up to 110mm. Six outer radial spines are three bladed, rarely rarely rodlike in form.

Emended diagnosis: Spongy shell commonly with a basal layer, a six- to eight-rayed internal spicule with apophyses, no N-frame and R-frame present.

Type species and its diagnosis: *S. fungosa* Nazarov 1975; shell with a spongy layer and slightly (2-7mm) separated from a very thin latticed base, a six-rayed internal spicule with apophyses.

Remarks: Even though the diagnosis of the genus was expressed as if the test consists of two shells, the inner shell is different from that of *Bisphaera* n. gen. and *Radiobisphaera* n. gen. According to the description of all his species (except for *Spongentactinia nupera* Nazarov 1981), Nazarov's use of the term "latticed inner shell" for this genus is actually a reference to the basal layer of a spongy shell.

CALLELLA Won 1983 (see also Won 1990)

Original diagnosis: Double-layered shell, an outer thick and inner very delicate layer, with six to fourteen outer spines.

Emended diagnosis: Twin layers of a spherical shell, hexagonally latticed, outer thick and inner very delicate layer; a six-rayed internal spicule arises from a single point.

Type species and its diagnosis: *C. stellaesimilis* Won 1983, a double-layered hexagonally latticed shell, fourteen outer spines with wide bases.

Remarks: This genus differs from *Entactinia* by its double-layered shell and the six rays of the internal spicule diverging not from both ends of median bar but arising from a single point.

DUPLEXIA Won 1983

Diagnosis: Double-layered (=twin layers) outer latticed shell, in which the outer layer is thick and the inner layer is very delicate, and an inner shell, six inner spines.

Type species and its diagnosis: *Duplexia foremanae* Won 1983; double-layered, hexagonally latticed outer shell with six inner spines, and hexagonally latticed inner shell.

Remarks: The internal spicule structure of the genus was not observed; however, from the unique twin-layered structure, it might perhaps have an internal spicule structure like that of *Callella*

is clear that the rays of the internal spicule and/or inner spines of the spongy shell have apophyses, whereas those forms with latticed shell(s) have none. However, one of the main problems in subdividing the Entactiniidae by these criteria is the genus *Astroentactinia* Nazarov 1975. According to Nazarov's description *Astroentactinia* has a latticed shell and an internal spicule with apophyses. However, it is doubtful that Nazarov's species of *Astroentactinia* or at least the type species, *A. stellata*, really have apophyses for the following reasons:

1) As yet, no apophyses have been observed in entactiniids consisting only of latticed shell(s).

2) Specimens identified as *A. stellata*, the type species of *Astroentactinia*, were reported from the Gogo Formation fauna (Nazarov and Ormiston 1983), and specimens also occur in the fauna being described in this paper. However, no apophyses were observed. Nazarov and Ormiston (1983) described the rays as branching dichotomously or trichotomously (referring to



TABLE 2  
Continued.

## MESCHEDEA Won 1983

Original diagnosis: A spherical skeleton consisting of three shells with a very short distance between the outer shells, and a large inner shell.

Emended diagnosis: Two-shelled or two-layered outer shell (with or without (?) outermost spongy material, a relatively large inner shell, and a six-rayed internal spicule with a median bar, no apophyses)

Type species and its diagnosis: *M. pyramispinosa* Won 1983; three shells with six outer spines, a very short distance between two outer shells, and a large inner shell.

Remarks: In diagnosis of this genus and the type species, the three shells refer to the two-shelled or two-layered outer shell and inner shell.

## PROVISOCYNTRA Nazarov and Ormiston 1987 (see also Nazarov 1988)

Diagnosis (Nazarov 1988): Entactiniidae? with radially differentiated spongy layers and numerous (up to 20 or more) main spines of rodlike form, probably combined with very fine rays of an internal framework, whose structure is not entirely clear. It [=the framework, internal spicule] is likely situated eccentrically inside small porous sphere (60-80mm).

Emended diagnosis: Large spherical skeleton consisting of spongy tissue which is interwoven among numerous densely and radially distributed spines, having an eccentrically located six-rayed internal spicule with a median bar and apophyses on each ray forming an R-frame.

## HAPLENTACTINIA Foreman 1963

Remarks: The genus is characterized by inner and outer apophyses, and one-layered inner shell showing partly three-dimensional structure. The outer shell is not preserved except for its bases (=outer apophyses). Its systematic position is unclear because the structure of the outer shell (even if it was originally present) is uncertain. Also, the six rays of the internal spicule join with a median microbar and are unusually massive compared to those of entactiniids.

With the reclassification of family Entactiniidae by Nazarov and Ormiston (1984), they removed *Haplentactinia* and established a new family Haplentactiniidae. According to Nazarov's description, the latter family is characterized by a internal skeleton represented by a four- to six-rayed internal spicule dispersed from "single center (a point articulation)", whereas family Entactiniidae has an internal structure represented by a four- to six-rayed or more multi-rayed internal spicule with a median bar. The type species of *Haplentactinia*, *H. rhinophyusa* Foreman 1963, has an internal spicule with a very short median bar; thus, it does not agree with the familial diagnosis given by Nazarov from the Haplentactiniidae. Even if the term "a single center (a point articulation)" included also the very short median bar (=median microbar) *Haplentactinia* has no relationship to other genera assigned by Nazarov to Haplentactiniidae. Either the family or the genus includes heterogeneous taxa. Further study of this matter is necessary.

## THECOENTACTINIA Nazarov 1975 (see also Nazarov 1988)

Remarks: *Thecoentactinia* was established by Nazarov (1975) based on *Entactinosphaera riedeli* Foreman 1963 because it has a greater number of spherical latticed shells than *Entactinosphaera*, in spite of the fact that the type species of *Entactinosphaera*, *E. esotrongyla* Foreman 1963, has three to four lattice-shells. *Thecoentactinia* includes heterogeneous taxa that have no common characteristics except for the shell number. In reality, the meshwork of the intermediate shell of *E. riedeli* is very irregular and differs from the typical latticed shell of entactiniids. Also from the intermediate shell arises a thin spongy layer, and it has outer and inner apophyses, according to author's observation. Thus, this species may be compared to species of *Retisphaera* n. gen. However, the type species, *E. riedeli* has the distinctive intermediate shell. It is unclear whether the two genera are synonyms.

## POLYENTACTINIA Foreman 1963

Remarks: This genus was moved to Family Polyentactiniidae by Nazarov (1988). However, the genus includes heterogeneous taxa. Further study of this matter is necessary.

## ASTROENTACTINIA Nazarov 1975

Remarks: This genus seems to be a synonym of *Entactinia*. See the section titled Reconsideration of the family Entactiniidae, and the remarks on *Entactinia* in this paper

## HELIOENTACTINIA Nazarov 1975

Remarks: This genus is an invalid taxon. See the remarks on *Radiobisphaera* n. gen.

## SOMPHOENTACTINIA Nazarov 1975

Remarks: A synonym of *Tetraentactinia*. See the section titled Reconsideration of the family Entactiniidae in this paper.

## SPONGENTACTINELLA Nazarov 1975

Remarks: A synonym of *Tetraentactinia*. See the section titled Reconsideration of the family Entactiniidae in this paper.

## PLUISTRATOENTACTINIA Nazarov 1981

Remarks: A synonym of *Entactinosphaera*. See the remarks on *Bisphaera* n. gen.

## PALEOXYPHOSTYLUS Won 1983

Remarks: A synonym of *Entactinia*. See the remarks on *Entactinia* Foreman 1963 in this paper

## BELOWEA Won 1983

Remarks: A synonym of *Entactinosphaera*. See the remarks on *Bisphaera* n. gen.

## INAEQUALIENTACTINIA Won 1991

Remarks: A synonym of *Entactinia*. See the remarks on *Entactinia* Foreman 1963 in this paper.

apophyses), but no branching can be observed in the specimen that they show in their plate (Nazarov and Ormiston, 1983, pl. 1, figs. 8-9).

3) According to Nazarov's description (1988) of the subfamily Astroentactiniinae, apophyses join with the bases of the radial outer spines. Also, Nazarov (1975) stated that *A. stellata* has a spherical shell with two kinds of numerous spines, the larger

and longer spines extend immediately from the ends of the apophyses and the rays of the inner spicule. However, there are no apophyses extending to the outer spines. Generally apophyses form the base of the spongy shell wall or are connected or united to the shell wall (Won 1997, text-fig. 1, this volume, p. 373). Except for the spines that extend from the rays of the internal spicule, all the other outer spines arise from the shell surface (in the case of *Astroentactinia*-like forms) or are the extension of

numerous radial beams arising from the inner shell surface (as in the case of *Radiobisphaera*, including some taxa which have been assigned to *Helioentactinia* and its type species).

4) Most of the *Astroentactinia* species were assigned to that genus because of their similar outer appearance — numerous radial spines as in the type species, *A. stellata*. The complete internal spicule structures of Lower Carboniferous species that have been assigned to *Astroentactinia* have not been observed, but the partially preserved rays bear no apophyses. (See remarks on *Astroentactinia*? Won 1991.)

(5) There are no differences in the internal structure or even detailed microscopic shell wall structure between species of *Entactinia* without apophyses and those species having multiple outer spines that have been classified as *Astroentactinia*. [See the relation between *Entactinia* and *Astroentactinia* forms (*E. sexradiata* n. sp. and *E. octaradiata* n. sp., respectively, p. 348, 349) and their intermediate form (*E. mediforma* n. sp., p. 348)] The differences are only in the spine characteristics.

Generally, it is easy to recognize in well-preserved specimens whether a taxon has a spongy shell with apophyses or a latticed shell(s) without apophyses. However, there are taxa that have characteristics intermediate between the two groups. They have generally both characteristics of latticed and spongy shells with or without apophyses. The relation between the two groups can be deduced from the intermediate taxa, which are described as follows:

#### 1) Genus *Apophysisphaera* n. gen.

This genus consists of species having a latticed shell with outer apophyses on the outer spines, and most of them have inner apophyses. In very well preserved specimens the surface of the latticed shell is covered by thin, fine, spongy tissue and the pores of shell wall are also filled by it (Won 1997, pl. 1, figs. 6, 13, this volume, p. 387). In some specimens, traces of the spongy tissue can be observed because the bases of the spongy tissue remain as connected or spinule-like disconnected microsepta in each poreframe (Won 1997, pl. 1, fig. 10, and pl. 1, fig. 2 respectively, this volume, p. 387). The lattice structure of *Apophysisphaera* varies from very irregular to hexagonal. As a general trend, in more regular and tightly latticed shells, the inner apophyses are less well developed, and in most tightly and regularly latticed shell, the apophyses are not present.

#### 2) Genus *Plenoentactinia* n. gen.

Species of *Plenoentactinia* encompass a series of shell wall structures whose end members range from a compact spongy shell to a well-layered spongy shell. However, they are well linked one by one through intermediate forms or change gradually even in a single species. The multi-layered shell may be a transitional form between spongy tissue and the latticed meshwork of multi-shelled entactiniids. Where the layering is well developed, the latticed shell wall structure is dominant and the basal layer is more regularly latticed. However, where the layering is less well developed, the spongy structure is dominant and the basal layer is less distinct. Where the spongy tissue is better developed, the traces of the apophyses are slightly more clearly developed, while where the latticed shell wall structure is more well developed, then the traces of the apophyses are less well developed or not observed.

#### 3) Genus *Tetrentactinia* Foreman 1963

The shell wall structure of *Tetrentactinia* is very similar to that of *Plenoentactinia*. Where the shell wall is more typically spongy, then more clear traces of apophyses are present, and where the shell has a more latticed character or where the basal layer is more typically latticed, then the apophyses remain as traces that are hardly visible or do not exist. Except for the difference in ray number, both genera have almost the same characteristics. A few species assigned by Foreman to *Tetraentactinia*, which either have an inner shell (like *T. gracilispinosa* Foreman 1963, although she did not observe the inner shell) or consist of a loose spongy shell with well-developed apophyses (as in *T. quadrispinosa* Foreman 1963), do not belong to the genus, in my opinion. All the other species characteristically have spongy tissue on a latticed base, a strong to very faintly layered shell wall on a latticed base, or a very fine and compact spongy shell.

#### 4) Genus *Meschedea* Won 1983

This genus has also characteristics intermediate between taxa having a multi-layered spongy skeleton and those having a multi-shelled one. The outer shell ranges from two layered to two latticed with or without(?) an additional spongy tissue or layers. Not only the meshwork of two latticed forms but also that of each of the two layers of the outer shell is tight and there are no apophyses.

From these examples, the apophyses seem to be associated with the looseness of the shell wall in Entactiniidae, and there are general relations between shell wall structure and the apophyses. Thus the family Entactiniidae could be classified into two groups linked by an intermediate group—one group characterized by a latticed shell without apophyses and the other one having a spongy shell with apophyses, as treated in Table 1.

Except for the four genera, *Hegleria* (Nazarov and Ormiston 1985), *Copicyntra* (Nazarov and Ormiston 1985), *Copellintra* (Nazarov and Ormiston 1985), and *Copicyntroides* (Nazarov and Ormiston 1985), whose internal structures are unknown and included species are very few, all the genera that belong to family Entactiniidae which have been described are treated in this paper in the systematics or briefly in Table 2. However, I would like to discuss specifically *Tetrentactinia*, *Spongactinia*, *Somphoentactinia* and *Spongactinella* in more detail to clarify the relation among genera assigned to Entactiniidae.

*Tetrentactinia* was erected by Foreman (1963) because of its characteristic four-rayed internal spicule. The genus was reviewed and its species were reclassified by Nazarov (1975) into several genera; he established the Tribe Spongactiniini for forms with a four- to six-rayed internal spicule and the Tribe Spongopolentactiniini with a multi-rayed internal spicule. The former tribe is subdivided into two genera, *Spongactinia* and *Tetraentactinia*, by the presence or absence of an "inner latticed shell", respectively. The latter tribe was likewise separated into two genera, *Somphoentactinia* and *Spongactinella*, on the same basis — presence or absence of the "inner latticed shell".

Aside from the question of the validity of Nazarov's criteria for classifying forms at the generic level, there are also several other problems:

#### a) The inner shell of *Spongactinia* and *Somphoentactinia*:

In contrast to Foreman's description, there are two species having an inner shell that were assigned to *Tetraentactinia*, but the

type species of *Somphoentactinia*, *Tetraentactinia somphozona* Foreman 1963, has no inner latticed shell. In addition, according to Nazarov's description, the type species of *Spongentactinia*, *S. fungosa* Nazarov 1975, has a spongy layer which is slightly separated (2-7µm) from a very thin latticed base with a diameter of 116-132µm. Nazarov described the latter feature also as a "inner latticed shell" in the measurements. Even though he showed the latticed base as an inner shell in his schematic diagrams (1988, figs. 18d, 19d) of *Spongentactinia* and *Somphoentactinia*, he used the term "inner latticed shell" interchangeably with "latticed base" or "inner shell". Such a large latticed base separated from the spongy shell by such a short distance cannot be treated as an inner shell. Even if the term "inner shell" as used for *Spongentactinia* and *Somphoentactinia* has the same meaning as a latticed basal layer of a spongy shell, the presence or absence of a latticed basal layer can not be a critical criterion for classification at the generic level. Rarely, the latticed basal layer can be present or absent even at the species level.

b) The spine and ray number of an internal spicule of *Spongentactinella* and *Somphoentactinia*:

Despite Nazarov's definition (1975, 1988), the type species of *Somphoentactinia* Nazarov 1975, *T. somphozona*, and other undescribed species (observed by the writer) bearing numerous outer spines from the Ohio Shale have a four-rayed internal spicule. The ray number of the internal spicule of the type species of *Spongentactinella*, *Tetraentactinia veles* Foreman 1963, could not be seen because of the thick spongy shell wall and there was no appropriately broken specimen to determine the correct ray number of the internal spicule. However, species (i.e., *T. teuchestes* and cf. *T. somphozona* Foreman 1963) having numerous outer spines may have a characteristic outer appearance, but many of them also resemble *T. veles*. Only when the specimens are broken can we see whether there is a latticed basal layer and whether the basal layer is contiguous with or slightly separated from the spongy shell wall. Only in such instances is it possible to determine to which species they belong. Those species have a four-rayed internal spicule.

According to Nazarov (1988), the numerous outer spines of *Spongentactinella* and *Somphoentactinia* join with the apophyses. Traces of apophyses on the partially preserved rays are present in *T. veles* (*Spongentactinella*), but not in *T. somphozona* (*Somphoentactinia*). In addition, they connect to the spongy shell wall without continuing as outer spines. Also, in contradiction to his statement, the type species of *Spongentactinia*, *S. fungosa* (Nazarov, 1975, p. 76), also has apophyses.

Consequently, *Spongentactinella* and *Somphoentactinia* have no unique diagnosis with which to separate them from *Tetraentactinia*. The case of *Spongentactinia* is discussed in the systematics section of this paper.

## SYSTEMATIC DESCRIPTION

### Family ENTACTINIIDAE Riedel 1967

**Diagnosis:** One or more spherical to subspherical spongy or latticed (exclusive of shaply angular meshwork) shells having an internal four-, six-, eight-, or twelve- to twenty-rayed spicule located eccentrically. Apophyses on the rays of the internal spicule and/or on the spines may be present or absent.

**Remarks:** The presence or absence of apophyses is apparently related to shell wall structure in the Family Entactiniidae. As

mentioned in the section titled Reconsideration of Family Entactiniidae, it can be easily recognized in well-preserved entactiniids specimens that the taxa characterized by a spongy shell have an internal structure having apophyses and the taxa having a latticed shell(s) have an internal structure without apophyses. Thus, the family is here subdivided into subfamily Entactiniinae, which has a latticed shell(s) without apophyses, and the Retentactiniinae n. subfam., which has a spongy shell with apophyses.

Even though I propose establishing the new subfamily Retentactiniinae, it is uncertain how important apophyses are to systematics. In latticed shells, three or four meshwork bars attached to spines seem to be equivalent to the apophyses. In *Magnetactina fragilis* n. sp. and *Polyentactinia* aff. *suave* (Nazarov, 1988, p. 87, fig. 27v) whose familial assignment is unclear, three meshwork bars arising on spines are thicker than those bars in other positions. Additionally, except for the family Entactiniidae, not all spongy shells have an internal spicule with apophyses, nor do all taxa having apophyses possess a spongy shell. Furthermore, not every kind of latticed shell has an internal spicule without apophyses.

This classification on the basis of presence or absence of apophyses is still tentative because if considered from a different point of view, the critical criterion for classifying the family Entactiniidae might be the internal spicule structure (Table 1). The family Entactiniidae might then be subdivided into four groups on the basis of the internal spicule structure. The first group is characterized by a six- to eight-rayed internal spicule with a median bar. The second group comprises the species that have a by six-rayed internal spicule without median bar, the third the species that have a four-rayed internal spicule without median bar, and the fourth, a twelve- to twenty-rayed internal spicule with a median bar. The first and third groups have both spongy and latticed shell wall structures and in these groups, the relationship (in some genetic and morphological respect) among taxa in the same group is apparently closer than that between taxa belonging to a subfamily, that is classified by shell wall structure.

However, most entactiniids have an internal spicule structure of the third group, and except for this group, as far as is known, the other groups occur rarely and within a very narrow stratigraphic interval. The second group has been occurred from Lower Carboniferous Viesen Faunas, the third group from Frasnian to Famennian except one genera and one species, and the fourth group only from the Gogo Formation fauna. Thus, further studies are needed.

### Subfamily ENTACTINIINAE Riedel 1967

**Emended Diagnosis:** Entactiniidae with one or more well-developed spherical or subspherical latticed (exclusive of shaply angular meshwork) shells, a four-, six- or eight-rayed internal spicule and no apophyses present.

**Remarks:** The taxa belonging to the subfamily Entactiniinae are distinguished from those of subfamily Retentactiniinae by possessing the latticed shell without apophyses.

In entactiniids, apophyses seem to have a role in supporting the shell wall. Not every but in many taxa in more loosely interwoven shells, apophyses are more strongly developed. They are not detectable in the shells that consist of extremely fine and compact spongy tissue. In a spongy shell with a distinct basal layer, if the basal layer of the spongy shell is more tightly and



regularly latticed, the apophyses are less well developed and remain as traces or are not present.

Genus *Bisphaera* Won n. gen.

Derivation of name: bi (Lat.), two; sphaera (Lat.), sphere.

Type species: *Bisphaera solidispinosa* n. sp.

**Diagnosis:** Two spherical latticed shells with six to eight inner spines as well as a six- to eight-rays of an internal spicule with a median bar. No radial beam between the shells.

**Remarks:** Many species assigned to *Entactinosphaera* Foreman 1963 belong to *Bisphaera* n. gen. *Entactinosphaera* was established by Foreman for species consisting of two or more shells and a six-rayed internal spicule. Excluding the species whose generic assignment was tentative, twelve *Entactinosphaera* species were reported from the Huron Member of the Ohio Shale (Foreman 1963). These can be grouped as follows.

- a) The type species, *E. esostrongyla*, which consists of three to four shells.
- b) *E. fredricki*, *E. riedeli*, and *E. dystactota* (possibly also *E. cancellicula*), which have an internal spicule with apophyses and a spongy outer shell with or without a latticed basal layer.
- c) *E. euthlasta*, *E. palimbola*, and *E. variacanthina*, which have one or two latticed shells.
- d) The other species having two latticed shells.

The absence of the inner shell in the three species of the (c) group can be due to its having been broken out or dissolved, or they may be heterogeneous. Putting these various species together, *Entactinosphaera* includes spongy or latticed shells and one- to four-shelled forms. In many respects, the genus is a heterogeneous taxon and needs redefinition particularly to clarify the diagnostic characteristics of the type species *E. esostrongyla*.

The establishment of *Bisphaera* to include two-shelled species previously identified as *Entactinosphaera* can also lead to great confusion. Until now most of the species identified as *Entactinosphaera* have had as a diagnostic characteristic a skeleton consisting of two latticed shells, unlike that of the type species. Many taxa which are similar to the type species, *E. esostrongyla*, were reported as species of *Belowea* by Won (1983, 1991) and as species of *Pluristratoentactinia* by Nazarov (1981). Reexamination by the writer of the type species of *Entactinosphaera* and the species of *Belowea* shows that *Belowea* is a synonym of *Entactinosphaera*. According to my observations, unlike the illustrated text-figure of the type species, *E. esostrongyla*, from the Ohio Shale fauna (Foreman 1963, pl. 6, fig. 1a), the type species consists of a maximum of four shells. In addition, the second shell is only slightly more robust than the other outer shells, which are often incompletely preserved. In many specimens assigned to *Belowea* the second shell is also the most robust, but in some individuals in a species and in some species the thickness of all outer shells is the same.

Nazarov (1981) established the genus *Pluristratoentactinia*. According to his description (1988), the internal skeleton is represented by a six-rayed spicule, an inner porous shell which is slightly separated from the spongy layer, and the thick spongy layer, which is differentiated into two to three (or four) shells, with six (rarely less) basic, outer radial spines. However, in con-

trast to his descriptions, the illustrated species (Nazarov, 1981, pl. 1, figs. 4-7; 1988, pl. 16, fig. 1) of the genus has no spongy shell but is typically two-dimensionally latticed and multi-shelled and shows no difference from species assigned to *Belowea* and from the type species of *Entactinosphaera*.

*Entactinosphaera* can also be rarely two-shelled, like *Bisphaera*, partly due to secondary processes. However, the type species of *Entactinosphaera* and the species that had been assigned to *Belowea* and *Pluristratoentactinia* have radial beams between shells. In contrast to this, *Bisphaera* has no radial beam and only six or eight inner spines between the shells.

*Entactinosphaera crassiclathata* Nazarov and Ormiston 1985, *E. strangulata* Nazarov and Ormiston 1985, and *E. cimelia* Nazarov and Ormiston 1985 from Permian faunas cannot belong to *Bisphaera* n. gen. Even though they have two-shelled skeletons, their shell wall structure is quite different from the two-shelled *Bisphaera* in possessing the numerous ridges on the shell surface. The shell number is not a critical criterion for classification. The shell wall structure can vary at the generic level but only within certain limits.

No species similar to the type species of *Entactinosphaera* occurs in the Gogo Formation fauna. All specimens belonging to *Bisphaera* from this Gogo fauna have one outer spine that is larger and thicker than the other spines.

*Bisphaera beniguna* Won n. sp.

Plate 2, figures 9-12

Derivation of name: benigunus (Lat.), abundant.

Holotype: G7304

**Diagnosis:** Large skeleton with an outer spherical shell consisting of an irregular and somewhat coarse meshwork perforated by moderately large, angular to subspherical pores and a hexagonally latticed inner shell. Six long outer spines, one of which is massive, and six inner three-bladed spines, as well as an six-rayed internal spicule with a median bar.

**Description:** The skeleton consists of two shells and six spines. The outer shell is robust and latticed with an irregular and coarse meshwork having pores of various sizes and shapes, rarely, some of which show a hexagonal structure. The many by-spines are thick but vary in length, thickness, and density. Six outer spines have generally three deep grooves or are three-bladed. They are long but vary in thickness and length; one is clearly larger than the other five. The spines are rarely twisted. The hexagonally latticed inner shell is very small compared to the outer shell. The internal spicule with a median bar is six-rayed.

**Remarks:** The specimens of this species have a similar external appearance to one specimen identified as *Entactinosphaera echinata* by Aitchison (1993, pl. 5, fig. 14). However, according to Aitchison's description, the latter has a delicate inner shell. In contrast to this, *B. beniguna* has a moderately robust inner shell. Moreover, the illustrated specimens identified as *E. echinata* by Aitchison (1993, pl. 5, figs. 6, 11, 14; pl. 7, fig. 3) show diverse outer appearances and his description is not detail enough to compare them. Except for the character of the by-spines, many characteristics of this species are same as Aitchison's description about *B. australis* (Aitchison 1993). However, the external appearance of illustrated specimens (Pl. 2, figs. 9-12) from this Gogo fauna is not similar to that of the holotype of *B. australis*.



(Aitchison 1993). The latter has very short and delicate by-spines, whereas the specimens in this study have thick by-spines that vary in length, thickness, and density. Moreover, Aitchison described that the inner shell of *B. australis* is approximately one half the diameter of the outer sphere, but the inner shell of *B. australis* is commonly one third the diameter of the outer shell.

**Material:** More than 100 specimens.

**Measurements (in  $\mu\text{m}$ ):** Shell diameter 150-230 (average 185); thickness of outer shell wall average 7.5; pore diameter 5-22; inner shell diameter 50-88 (average 63); inner shell pore diameter 7.5, spine length maximum 325; by-spine length maximum 50; median bar length 7-8.

***Bisphaera cribrisimilis* Won n. sp.**

Plate 3, figures 1-8

*Entactinosphaera? echinata* (Hinde 1899) NAZAROV and ORMISTON 1983, p. 458, pl. 1, figs 6-7.

(?)*Entactinosphaera echinata* (Hinde 1899) AITCHISON 1993, p. 115, pl. 5, fig. 6, pl. 7, fig. 3.

**Derivation of name:** cribrum (Lat.), sieve; similis (Lat.), similar.

**Holotype:** G7106

**Diagnosis:** Skeleton with an outer shell consisting of an irregular, unevenly patterned meshwork with sieve-like pores or a fine and more or less regular meshwork with a thorny surface; an inner shell with hexagonal meshwork. Six outer spines, one of which is thicker and longer than the others; six three-bladed inner spines and a six-rayed internal spicule with a median bar.

**Remarks:** Two morphotypes occur in this species. Except for the two end members, some intermediate forms are difficult to classify. The two end members differ in the shell wall structure, but all the other characteristics are nearly identical. The differences in the shell wall structure depend on whether the bases of by-spines join to their neighboring poreframes and to the bases of the neighboring by-spines, and are well linked by transitional forms (Pl. 3, fig. 3). In both types spine length strongly varies, but it is more pronounced in specimens of *B. c. crassa* n. ssp., which have a more or less regular and evenly latticed meshwork, than it is in *B. c. cribrisimilis* n. ssp., which has an unevenly patterned wall structure with sieve-like pores. Such variation can also be observed in many species of *Radio-bisphaera*.

The two types are here treated as subspecies for the practical use, even though it is not coincident with the definition of subspecies.

***Bisphaera c. cribrisimilis* Won n. ssp.**

Plate 3, figures 1, 2, 6, 7

*Entactinosphaera? echinata* (Hinde 1899) NAZAROV and ORMISTON 1983, p. 458, pl. 1, figs. 6-7.

**Holotype:** G7106

**Description:** The spherical outer shell has a microscopic, unevenly patterned shell wall structure (Pl. 3, fig. 6) due to the connection of the bases of by spines with the neighboring poreframes and the bases of the neighboring by spines; two to five or more pores are commonly grouped in a poreframe that stands slightly higher than the frames of the pores within it. The six

outer spines are commonly long and have three main grooves; one of the spines is longer and thicker than the other five. The thickness and length of the spines varies. The hexagonally latticed inner shell is connected to the outer shell by the six three-bladed inner spines. A six-rayed internal spicule with a median bar is located eccentrically.

**Remarks:** The described subspecies is in essence identical to the specimens identified as *Entactinosphaera? echinata* (Hinde 1899) by Nazarov and Ormiston (1983). However, neither the described species nor the specimens described by Nazarov and Ormiston (1983) from their Gogo fauna can belong to *E. echinata* (Hinde 1899). Each of the two illustrated specimens of *Heliosoma echinata* Hinde (1899, pl. 9, figs. 1, 2), which was reassigned to *Entactinosphaera* by Foreman (1963), shows only one main spine, which is very massive and grooved in one specimen but thin and rodlike in the other. The external appearance of the specimens in his illustration based on thin sections is also quite different from specimens found in the Gogo faunas. Furthermore, Hinde did not describe the number of the spines and simply expressed it as "plural." Thus, no specimens can be correctly identified with *Heliosoma echinata*. In addition, Hinde could not observe whether the species bears only six inner spines between the two shells, as in *Bisphaera* (most of whose species formerly were assigned to *Entactinosphaera*), or have additional numerous radial beams, as in *Radiobisphaera* n. gen. (many of which were formerly assigned to *Helioentactinia*).

**Material:** More than 1000 specimens.

**Measurements (in  $\mu\text{m}$ ):** Shell diameter 120-210; large pore size 6-11; small pore size 1-3; inner shell diameter 42-50; inner shell pore size 8-9; maximum length of strongest spine 275; maximum length of the other five weaker spines 250; median bar length 5-6.

***Bisphaera c. crassa* Won n. ssp.**

Plate 3, figures 4, 5, 8

(?)*Entactinosphaera echinata* (Hinde 1899) AITCHISON 1993, p. 115, pl. 5 fig. 6, pl. 7, fig. 3

**Derivation of name:** crassus (Lat.), thick.

**Holotype:** G11938

**Description:** The detailed meshwork texture of the outer shell cannot be easily observed on those specimens that are densely covered by fine thorn-like by-spines. However, the meshwork is a more or less regular and very densely latticed and at least partially hexagonal. The size of the shell varies greatly. The six outer spines are deeply or widely grooved or three-bladed and are extremely varied in size; one is longer and thicker than the other five. The density and length of the by-spines also varies. The surface of some specimens is virtually smooth because of the weak development of by-spines. The six inner spines between the outer and the inner shell are three-bladed. The small inner shell is hexagonally latticed. A six-rayed internal spicule with a median bar is located eccentrically.

**Remarks:** Aitchison (1993, pl. 5, figs. 6, 11, 14, pl. 7, fig. 3) figured four specimens identified as *Entactinosphaera echinata*. According to the external appearance shown in his photos these can be easily separated into two types: the specimens of pl. 5, fig. 6 and pl. 7, fig. 3, and those of pl. 5, figs. 11 and 14. This subspecies has fairly similar outer appearance as the specimens

of his pl. 5, fig. 6 and pl. 7, fig. 3. However, it is unclear whether Aitchison's description is based on the former type or latter type. Also, he did not describe the relation between the two types, and his description is not detailed enough to unite them into a single species. As explained in the remarks for *B. c. cribrisimilis*, the specimens can not belong to *E. echinata* (Hinde 1899).

**Material:** More than 100 specimens.

**Measurements (in  $\mu\text{m}$ ):** Shell diameter 100-195; outer shell pore size 2-5; inner shell diameter 42-50; inner shell pore size 6-8; largest spine length 150-275; maximum length of the other five spines 250; by-spine length maximum 25; median bar length 5-6.

***Bisphaera dissimilicortex* Won n. sp.**

Plate 2, figures 13-20

?*Spongentactinella* sp. 1 AITCHISON 1993, p. 120, pl. 7, fig. 5.

**Derivation of name:** dissimilis (Lat.), diverse; cortex (Lat.), cortex.

**Holotype:** G11919

**Diagnosis:** Two spherical shells with a very thin and finely latticed outer shell and a hexagonally latticed inner shell; with eight outer spines, one of which is longer and thicker than the others; three-bladed inner spines, as well as an eight-rayed internal spicule with a median bar.

**Description:** The thin and very finely latticed outer shell varies in the surface texture. Some of them are relatively regular and smooth (Pl. 2, fig. 13), and others have a minutely unevenly patterned (Pl. 2, figs. 14, 16, 18) or reticulated (Pl. 2, fig. 15, 17) surface. The inner shell is hexagonally latticed, and its meshwork is coarser and thicker than that of the outer shell. The eight outer and inner spines are three-bladed. One outer spine is thicker and longer than the other seven. The eight inner spines are the continuation of the eight rays of an internal spicule with a median bar. Very fine and short by-spines rise from the surface of the inner and outer shell. On the latter, the density, number, and length of the by-spines vary widely.

**Remarks:** Even though the specimen figured by Aitchison (1993, pl. 7, fig. 5) was tentatively assigned to *Spongentactinella* and he stated that the species consists of spongy shell with several spines, the external appearance is the same as that of *B. dissimilicortex*. When the latticed shell consists of a very fine mesh, it might sometimes be misconstrued as a spongy shell.

Specimens of *B. dissimilicortex* show diverse shell wall structure. The shell wall may consist of a basically fine and regular meshwork, but it appears differently, smooth and regular, unevenly patterned (not observable at the figured scale), or reticulated, according to how strongly the bases of by-spines or of blades of main spines join to their neighboring poreframes. In addition, the presence or absence, and thickness, length, or density of by-spines, which may reflect ecological factors and secondary processes, greatly influence the external appearance of specimens.

**Material:** More than 100 specimens.

**Measurements (in  $\mu\text{m}$ ):** Shell diameter 112-200 (majority 150); outer shell pore size 2-4; inner shell diameter 45-50; inner shell

pore size 6-7; maximum one largest spine length 325; maximum the other seven spine length 225, median bar length 5-7.

***Bisphaera solidispinosa* Won n. sp.**

Plate 3, figures 9-11

**Derivation of name:** solidus (Lat.), massive; spinosus (Lat.), spiny.

**Holotype:** G11931

**Diagnosis:** Small skeleton, the outer spherical shell with a very densely latticed meshwork. Six massive spines, which taper sharply to their tips, as well as six three-bladed inner spines. Inner shell with a hexagonal latticework. Six-rayed internal spicule with a median bar.

**Description:** The densely latticed outer shell seems to consist basically of a hexagonal meshwork, but the poreframes are slightly irregular in their shape. The shell wall is relatively thick compared to its shell size. Extremely fine and short thorns are on the shell surface. The inner shell consists of a coarse, hexagonal meshwork. The inner shell has a large diameter compared to that of the outer shell. The six, massive, deeply grooved spines are symmetrically arranged and tapered to their tips. One of them is somewhat larger than the other five. The internal spicule is six-rayed, and the median bar is eccentrically located.

**Material:** More than 50 specimens.

**Measurements (in  $\mu\text{m}$ ):** Shell diameter 90-130; thickness of shell wall 10-13; pore diameter average 5; inner shell diameter 45-50; pore diameter 5-6; maximum spine length 140; median bar length 6-7.

***Bisphaera uniprocera* Won n. sp.**

Plate 3, figures 12, 13

**Derivation of name:** uni (Lat.), one; procerus (Lat.), long.

**Holotype:** G3401

**Diagnosis:** Two spherical, hexagonally latticed shells, with one strong, sharp main spine, five other poorly developed spines. Six three-bladed inner spines between the two shells. A six rayed internal spicule with a median bar.

**Description:** The outer shell consists of a relatively densely and hexagonally latticed meshwork. The skeleton varies in size. The one main, long, relatively massive spine is sharply pointed at the tip. The main spines are generally widely and smoothly, but rarely deeply or sharply grooved. The other five three-bladed spines are much shorter and weak. By-spines are also developed on the shell surface. The relation between the five weak spines and the by-spines varies according to the shell size. In general, the rare large form has many well-developed by-spines and relatively weak spines; it is difficult to distinguish by-spines from weak spines. On the other hand, most specimens of the small form have five weak spines, and the by-spines are poorly developed. There are intermediate forms between the large and small forms. The internal shell consists of a hexagonal meshwork and is connected to the outer shell by the six three-bladed inner spines. The six-rayed internal spicule is located eccentrically in the inner shell.

**Material:** More than 50 specimens.

**Measurements (in  $\mu\text{m}$ ):** shell diameter, large form 150-160, normal form 120-125; inner shell diameter (both forms) 48-50; largest spine length, large form 275-300, normal form 150-200; largest spine diameter, large form 50-60, normal form 30-33; weak spine length, large form maximum 88, normal form 88-113; median bar length uncertain.

**Genus *Entactinia* Foreman 1963**

*Palaeoxyphostylus* WON 1983

*Inaequalientactinia* WON 1991

?*Astroentactinia* NAZAROV 1975

**Type species:** *Entactinia herculea* Foreman 1963

**Emended Diagnosis:** A single latticed shell and a six- to eight-rayed internal spicule with a median bar. The number of outer spines varies. No apophyses on the rays.

**Remarks:** Even though the diagnosis of *Entactinia* Foreman 1963 was emended by Won (1983) and the genus redescribed by Nazarov (1975, 1988), the genus is still a heterogeneous taxon, and the systematic position of species having one latticed shell with an eight-rayed internal spicule is open. Two species having an eight-rayed internal spicule were discovered in this Gogo Formation fauna. Except for the ray number, all the shell wall characteristics of these two species are the same as in those species of *Entactinia* that bear a six-rayed internal spicule; even the microscopic structure of microsepta is similar (Pl. 1, figs. 4, 17, 18, Pl. 2, figs. 3, 7). Also, a few variants of some species (e.g., *E. hindeiana* n. sp.) normally having an eight-rayed internal spicule have a six-rayed internal spicule, while the group normally having a six-rayed internal spicule [e.g., *E. deflandrei* (Won 1991)] has variants with an eight-rayed spicule. In addition, some genera like *Bisphaera* n. gen., *Plenoentactinia* n. gen., and *Spongentactinia* Nazarov 1975, which is emended in Won 1997 (this volume, p. 400) have a ray number that varies six or eight or ranges from six to eight.

*Astroentactinia* was established by Nazarov (1975). According to his description and text-figure, the genus is characterized by an internal spicule having apophyses. Specimens identified as *A. stellata*, which is the type species of *Astroentactinia*, were reported from the Gogo Formation by Nazarov and Ormiston (1983). According to their description the species has eight, rarely seven, or six (?) rays, each of which branches dichotomously or trichotomously (these are the apophyses). However, the figures in Nazarov and Ormiston (1983, pl. 1, figs. 8-9) show no apophyses (= branches). The specimens found in the Gogo Formation fauna reported in this paper have no apophyses (Pl. 1, fig. 14) but have an internal spicule just like that of *Entactinia*. Many species have been assigned to *Astroentactinia* only because of the presence of numerous (greater than eight), radially distributed outer spines. The greater number of outer spines is the only characteristic distinguishing them from specimens of *Entactinia*, which generally have six or eight outer spines. However, the number of outer spines cannot be a criterion to classify taxa (see also section titled Range of variation in skeletal structure at the species and genus levels in the family Entactiniidae, p. 337). Except for the number of outer spines, the two types are very nearly identical, even in microscopic structure (Pl. 1, figs. 4, 17, 19; Pl. 2, figs. 3, 7). The very close relation between these two types can be demonstrated by the presence of intermediate species like *Entactinia mediforma* n. sp. (see remarks on *E. mediforma* n. sp. and Pl. 1, figs. 5-12) and *Entactinia unispina* Won 1991.

No illustrated specimen demonstrates that *Astroentactinia* has an internal structure with apophyses; this is figured only in the schematic diagrams of Nazarov (1975, p. 15, fig. 5v; 1988, p. 59, fig. 19a). Nazarov described the numerous radial external spines of *Astroentactinia* and *Helioentactinia* as the extension of the branches (= apophyses) and rays of the internal spicule. However, in reality, except for the six or eight spines that extend from the rays of the internal spicule, all the other spines arise from the shell surface (as in the case of *Astroentactinia*-like type shells) or are the extension of the radial beams arising from the inner shell surface (in the case of *Radiobisphaera* including type species of *Helioentactinia* and some species assigned to *Helioentactinia* which are belonging to *Radiobisphaera* n. gen. in this paper).

Nazarov established or described more than 30 species of *Entactinia*. Most of the early Paleozoic species were reassigned (Nazarov and Ormiston 1993), and seven species differ from the other species in having outer apophyses on the spines and inner apophyses on the rays of the internal spicule. Those species, *E. diversita* Nazarov 1973, *E. dimidiata* Nazarov 1975, *E. pycnoclada* Nazarov and Ormiston 1985, *E. praepycnoclada* Nazarov and Ormiston 1993, *E. postadditiva* Nazarov and Ormiston 1993, and species identified as *E. additiva* Foreman 1963 from the southern Urals (Nazarov, 1975) and from the Gogo Formation fauna described by Nazarov, Cockbain, and Playford (1982) and by Nazarov and Ormiston (1983) cannot belong to *Entactinia*. (See also remarks on *Apophisphaera* n. sp.)

*Inaequalientactinia* was established by Won (1991). The specimens vary widely in shape and spine number, and some of them occur only in certain stratigraphic intervals. Thus, they were separated into several species, and a new genus was erected for them. However, my continuing studies show that the spine shape is too varied and has too many intermediate forms to differentiate the specimens occurring from the uppermost Devonian to middle Lower Carboniferous. Also, the basic structure of *Inaequalientactinia* is the same as that of *Entactinia*.

The genus *Palaeoxyphostylus* was established by Won (1983) on the basis of the bipolar spines of many specimens. However, the spine number varies from two to six, and the basic structure is the same as that of *Entactinia*.

Generally, the species of *Entactinia* in the Upper Devonian Gogo Formation fauna differ from the Carboniferous species studied previously in having microsepta. The presence of the septa may depend on the preservation of specimens, the preparation, or diagenetic factors.

***Entactinia haeckeliana* Won n. sp.**

Plate 1, figures 19-20; Plate 2, figures 1-4

**Derivation of name:** In honor of Ernst Haeckel.

**Holotype:** G12008.

**Diagnosis:** A small, hexagonally latticed, thin, spherical shell with microsepta and six, very long, faintly to clearly three-bladed spines and generally equally long, thin, needlelike by-spines; a six-rayed internal spicule with a median bar located very eccentrically.

**Description:** The single spherical shell consists of an essentially hexagonal, but slightly irregular meshwork. Very short, delicate microsepta are rarely preserved. The markedly asymmetrically arrangement of the six rodlike long spines, which are the con-

tinuation of the six rays of the internal spicule, is attributed to the very eccentric location of the median bar that connects each pair of three rays of this internal spicule. The spines taper very gently from their bases to the tips. The thickness and the length of the spines vary somewhat even in one specimen. The spines are clearly or faintly three-bladed or are three-bladed only at their lower part and become rodlike distally. Almost all of the very thin, long by-spines are the same length. Many are broken because they are so delicate. The internal spicule with a very eccentrically located median bar is six rayed.

**Remarks:** The spines of this species vary slightly in shape and thickness. Specimens having larger and well-developed three-bladed spines are similar to *E. procaspina* Aitchison 1993, but they differ in having a six-rayed internal spicule. No species of *Entactinia* in the presently studied Gogo fauna is represented by a seven-rayed internal spicule structure.

In one specimen, the six rays of the internal spicule are partly enclosed in tubes (Pl. 1, fig. 20) at the boundary between the internal spicule and the outer spines.

**Material:** More than 50 specimens.

**Measurements (in  $\mu\text{m}$ ):** Shell diameter average 100; pore size 6.5-8; spine length maximum 350; by-spine length 20-35; median bar length 5-6.

***Entactinia hindeiana* Won n. sp.**

Plate 2, figures 5-8

**Derivation of name:** In honor of G. J. Hinde.

**Holotype:** G11993.

**Diagnosis:** The spherical, slightly irregularly latticed shell, por-frames having microsepta. Eight unequal, asymmetrically arranged, unevenly distributed, rodlike spines with microthorns, four of the spines arising on the surface more closely together than the other four, a extremely eccentrically located median bar connecting eight internal rays.

**Description:** The very thin shell seems to be basically hexagonally latticed, but the meshwork is not entirely regular in its shape in a single specimen. The microsepta can rarely be seen (Pl. 2, fig. 7). Parts of some rays lie along and form part of the shell wall (Pl. 2, fig. 8). The eight, long, rodlike spines are the continuations of the internal spicule. Four of these spines are positioned close together on the surface because of the extremely eccentric position of the median bar, which connects the two sets of four rays of the internal spicule. Very fine thorns cover the shell surface, and microthorns are densely developed on the rays and spines. An uncommon variant form has a six-rayed internal spicule and six outer spines.

**Remarks:** This species is most abundant of the entactiniids in the presently studied Gogo fauna. *E. hindeiana* seems to be an ancestral form of *Entactinia*? *inaequopora* Won 1983 and *Entactinia*? *parvipora* Won 1990 of Lower Carboniferous faunas. The latter two species are distinguished from this species by having a much more irregular meshwork and less eccentrically positioned internal spicule.

**Material:** Several thousand specimens.

**Measurements (in  $\mu\text{m}$ ):** Shell diameter 105-120; maximum spine length 400; median bar length 5-6.

***Entactinia mediforma* Won n. sp.**

Plate 1, figures 9-12, 15, 16

**Derivation of name:** medius (Lat.), intermediate; forma (Lat.), form.

**Holotype:** G3505

**Diagnosis:** Shell with a hexagonally latticed meshwork having microsepta, one strong and five weaker rodlike outer spines, numerous radial by-spines, and a six-rayed internal spicule with a median bar.

**Description:** The shell consists of a basically hexagonal meshwork perforated by rounded pores. Microsepta divide each pore. The one main spine is grooved and much stronger than the other five. The five lesser spines are commonly varied in their thickness and length in a given specimen. The one strong grooved spine becomes rodlike at the tip. The other five weak spines are grooved mainly at their bases. In a few specimens, some weak spines are large and grooved like the one large spine (Pl. 1, figs. 11, 12). There are also numerous radial by-spines on the shell surface. The six spines extend to the six rays of the eccentric internal spicule with a median bar.

**Remarks:** *E. mediforma* is easily distinguished from *E. sexradiata* n. sp. by its six spines. However, the other characteristics are very similar. In some specimens of *E. sexradiata*, the six spines that extend to the six internal spicules are stronger than the other radial spines. In addition, there are intermediate forms between the two species (Pl. 1, figs. 6-9). The main difference between them is the gradient of the development of the spines that extend to the six-rayed internal spicule. These species demonstrate also the close relationship between species with radial spines (*Astroentactinia*-like types) and species having generally six or eight main spines (*Entactinia*).

*E. mediforma* is very similar to *Entactinia unispina* Won 1991. However, the latter has a larger shell and the one main spine is three-bladed or deeply grooved for its entire length. See remarks for *Entactinia unispina* for a discussion of the relation between *Astroentactinia*-like type and *Entactinia*-like type.

**Material:** More than 50 specimens.

**Measurements (in  $\mu\text{m}$ ):** Shell diameter 120-135; shell thickness 8-12; pore size 8-10; maximum large and weak spine length 300 (In a few specimens, small spines can be as long as the large spine but much thinner); maximum largest spine thickness at base 40; maximum weak spine thickness at base 20; maximum by-spine length 75; by-spine thickness 12; median bar length 5-6.

***Entactinia sexradiata* Won n. sp.**

Plate 1, figures 5-7, 13, 14, 17

*Astroentactinia paronae* (Hinde 1899) NAZAROV and ORMISTON 1983, p. 459, Pl. 1, fig. 3

*Astroentactinia stellata* Nazarov 1975. – NAZAROV and ORMISTON 1983, p. 459, Pl. 1, fig. 8-9

?*Astroentactinia stellata* Nazarov 1975. – AITCHISON 1993, p. 118, fig. 6, 4.

**Derivation of name:** sex (Lat.), six; radius (Lat.), rayed.

**Holotype:** G12004



**Diagnosis:** A spherical shell with a hexagonal meshwork, several microsepta in each poreframe, and numerous rodlike radial spines with grooved bases, one of which is slightly more robust than the others, as well as a six-rayed internal spicule with a median bar.

**Description:** The single small spherical shell is hexagonally latticed and has four to five microsepta that rise from the sides of each poreframe and partially cross the pore space. About thirty rodlike spines are radially arranged. All spines have short grooves at their bases and thin toward the tips. Spine length is somewhat varied. One spine is slightly longer and stronger than the other spines. However, the differences among spines are not great in most specimens, and when the spines are broken, these differences are not observable (Pl. 1, fig. 5). In a few specimens, several spines are weaker than the one stronger spine but thicker and/or longer than the other numerous radial spines (Pl. 1, figs. 6, 7). These several more robust spines and the single strong spine are the spines that extend to the six-rayed internal spicule. The six-rayed internal spicule with its median bar is located eccentrically.

**Remarks:** Even though this species strongly resembles *Astroentactinia stellata* Nazarov 1975 or *A. paronae* (Hinde 1899) reported from the Gogo Formation by Nazarov and Ormiston (1983), it is established in this paper as a new species, *Entactinia sexradiata*. According to Nazarov's description (1975), *A. stellata* from Aitpaika River, southern Urals, is characterized by the two kinds of numerous spines, the longer and larger spines extending immediately from the ends of the apophyses and the rays of the inner spicule. However, Nazarov and Ormiston (1983) described that the specimens identified as *A. stellata* from their Gogo Formation fauna have main spines all the same size (see comparison on *A. stellata* Nazarov and Ormiston 1983, p. 459). They described also each ray of the internal spicule of *A. stellata* from their Gogo fauna as branching dichotomously or trichotomously, and thus it joins with the bases of the radial spines on the sphere. However, the specimen illustrated by them (1983, pl. 1, figs. 8-9) shows no dichotomously or trichotomously branching internal spicule. Instead, it has an internal spicule without apophyses like the internal structure of *Entactinia*. Thus, *E. sexradiata* and specimens identified as *A. stellata* from Gogo Formation fauna by Nazarov and Ormiston (1983) cannot belong to *A. stellata*.

*E. sexradiata* also has the same external appearance as the specimens identified as *A. paronae* (Hinde 1899) from the Gogo Formation by Nazarov and Ormiston (1983, pl. 1, fig. 3). *Heliosoma paronae* was reassigned by Nazarov (1975) to the genus *Astroentactinia*. However, even though Hinde could not observe the internal structure of the specimens of *H. paronae* (his pl. 8, fig. 3) from New South Wales, he classified it as *Heliosoma* and named it *H. paronae*. One of the characteristic features of *Heliosoma* is that it has two shells. Hinde may have imagined that his *H. paronae* had an inner shell because of its resemblance to specimens of *Heliosoma echinatum* Hinde 1899. Thus, it is not certain if *H. paronae* is one or two shelled, and no specimens can be actually identified as *H. paronae*. Nazarov and Ormiston (1983) stated that a diagnostic character of *A. paronae* is the development of one spine that is larger than the rest, and that *A. stellata* differs from *A. paronae* in having main spines all of the same size, even though in 1975 Nazarov reported that *A. stellata* has two kinds of spines. All the specimens like those identified either as *A. stellata* or *A. paronae* from the Gogo Formation faunas have a spine which is a little bit

larger than the other spines, but the difference between them is very small. Thus, when the spines are broken, this difference can not be recognized. In addition, the spine difference in a specimen identified as *A. paronae* from the Gogo fauna of Nazarov and Ormiston and figured by them in their plate 1, figure 3, is almost undetectable, unlike in the specimens of *A. paronae* from New South Wales (Hinde, 1899).

Nazarov did not state how many rays the internal spicule has in *A. stellata* from the Aitpaika River, southern Urals. However, Nazarov and Ormiston (1983) noted that the specimens identified as *A. stellata* from the Gogo Formation have eight, rarely seven or six? rays. They may have included two different species in their description of *A. stellata*, one of which is a species having an eight-rayed internal spicule, the other a six-rayed species; these might belong to *E. octaradiata* n. sp. and *E. sexradiata* n. sp., respectively. Eight-rayed forms can appear to have seven rays, depending on the observation angle and because one of the rays can be very short and attached near the shell wall and often not seen. Or the seven-rayed specimens may be a variant form. The specimens of *E. sexradiata* and *E. octaradiata* are similar in their external appearance, but they differ as described in the remarks on *E. octaradiata*.

The species in the present fauna is very similar to *Entactinia multispinosa* Won 1983 reported from Lower Carboniferous faunas of the Waffenhämmer siliceous shale (Braun and Schmidt-Effing 1988), the Bareilles lydites (Gourmelon 1986), and the Calle fauna (Won 1983), but it differs in being smaller and having microsepta. It is uncertain whether the microsepta disappeared in the younger geologic period or the lack of microsepta is due to secondary processes.

The external appearance of this species is like the previously described species belonged to *Astroentactinia*. However, it is assigned to *Entactinia* because the rays of the internal spicule are not distally branched. Except for the numerous outer spines, there is no difference from *Entactinia* (see remarks on *Entactinia*). The meaning of outer spine number and the relation among species having multi-radiated spines (*Astroentactinia*-like type) and species having six main spines (*Entactinia* type) can be seen in Plate 1, figures 5-12 in this paper. This species is closely related to *Entactinia mediforma* n. sp., which is the intermediate form between species with numerous outer spines and species having six spines. (See remarks on *E. mediforma*.)

**Material:** More than 200 specimens.

**Measurements (in  $\mu\text{m}$ ):** Shell diameter 100-140 (large form 120-140); shell thickness 5-12; pore diameter 8-10; largest spine length maximum 155; largest spine base diameter maximum 20; small spine length of large form 50-80; median bar length 5-6.

***Entactinia octaradiata* Won n. sp.**

Plate 1, figures 1-4, 18

**Derivation of name:** octo(Lat.), eight; radiatus (Lat.), rayed

**Holotype:** G12006

**Diagnosis:** A spherical, hexagonally latticed shell; several microsepta present in each poreframe. More than twenty rodlike, long, thin radial spines; in general, one of these spines slightly larger than the others. Eight rays of an internal spicule with a median bar.

TABLE 3

Classification of genus *Radiobisphaera* in the Gogo Formation fauna

Elements of skeleton	Inner spines	Radial beams	Median bar length (in $\mu\text{m}$ )	Outer shell	Inner shell	Outer spines
Species						
<i>R. acuta</i>	rodlike, thick	rodlike, thin, not numerous	thick six-rayed (2-4)	hexagonal finer than that of inner	somewhat regular	one strongest spines, numerous thin spines, rodlike
<i>R. flamans</i>	rodlike, thick	rodlike, thin, not numerous	thick six-rayed (2-4)	very coarse, very irregular	very coarse, very irregular	one strongest spine, numerous thin spines, rodlike curved by-spines
<i>R. variantia variantia</i>	three-bladed	rodlike	six-rayed (?)	very fine	irregular, coarse	one spine slightly stronger than the others.
<i>R. variantia inaequalis</i>	three-bladed	rodlike	six-rayed (?)	very fine	hexagonal to slightly irregular, coarse	one spine much stronger than the other five
<i>R. multiaculeata multiaculeata</i>	three-bladed	three-bladed	six-rayed (6-8)	very fine	coarse, hexagonal	one spine slightly stronger than the others, all three-bladed
? <i>R. multiaculeata stellaepolus</i>	three-bladed	three-bladed	six-rayed (6-8)	very fine	coarser than that of outer shell, irregular	one spine much stronger than the others, all three-bladed
<i>R. magnifenestra</i>	three-bladed	three-bladed or rodlike	six-rayed (6-8)	irregular, very coarse	very irregular, very coarse	numerous three-bladed long spines, one slightly stronger spine
<i>R. multa</i>	rodlike, the same thickness as radial beams	rodlike, very numerous	six-rayed (5-6)	very fine	hexagonal	one strongest spine, numerous by-spines
<i>R. nazaroviana</i>	three-bladed	rodlike, extremely thin	six-rayed (5-6)	very thin, hexagonal	thick, slightly irregular	six, three-bladed

**Description:** The hexagonally latticed spherical shell with a thorny or, less commonly, smooth surface has more than twenty spines. Each poreframe of the shell wall has four or five microsepta. The length of the spines is two to four times the shell diameter, but many spines are broken. One spine is slightly longer and thicker than the others, but if this more robust spine is broken, it may not be possible to identify it, because the difference between spines is not great. All the spines are rodlike and very thin. The thickness of the spines is almost constant; they taper very gradually to the tip. The numerous by-spines are commonly broken. The internal spicule with a median bar has eight rays.

**Remarks:** This species is very similar in many respects to *E. sexradiata* n. sp. It is distinguished from the latter by the number of rays of the internal spicule and by the structural details of the shell wall meshwork and spines. In *E. sexradiata* the shell is generally larger and thicker and the spines are shorter than those of *E. octaradiata* n. sp. The spines of *E. sexradiata* taper relatively sharply to the tips, and their bases are faintly to clearly grooved. In the *E. octaradiata*, the width of the spines is almost the same from the base to the tip, and their bases are not grooved or are only very faintly grooved for a short distance. However, some small specimens of *E. sexradiata* and *E. octaradiata* cannot be easily distinguished if the spines are broken

and if the number of the rays of the internal spicule cannot be observed.

**Material:** More than 200 specimens.

**Measurements (in  $\mu\text{m}$ ):** shell diameter 95-112, pore size 8-10; shell thickness 4-6; strongest spine length 190-275; length of other spines 100-275; median bar length 8-9.

#### Genus *Radiobisphaera* Won n. gen.

**Derivation of name:** Radio-(Lat.); rays, and the genus name of *Bisphaera* n. gen.

**Type species:** *Radiobisphaera variantia* n. sp.

**Diagnosis:** Two latticed shells, an outer and inner shell; generally numerous outer spines, one or six of these commonly are much or slightly stronger than the others; with six inner spines which are the continuations of the six rays of an internal spicule with a median bar; radial beams arising from the surface of the inner shell and commonly protruding out of the outer shell; no apophyses present.

**Remarks:** This genus has the same characteristics as the type species of *Helioentactinia* Nazarov 1975. According to his (1975) diagnosis of the genus, "Two spherical latticed shells

with numerous outer spines extending from the ends of the multi-rayed spicule or polyhedron." According to his redefinition (1988), "its internal skeleton represented by a seven-, eight-rayed or more multi-rayed, sometimes with apophyses on rays which diverge from a short median bar, two shells, the number of outer spines from eight to twelve, rarely more." His redefined diagnosis of *Helioentactina* does not make it clear whether its shell is latticed or spongy. In addition, according to the diagnosis, the shell structure of *Helioentactinia* overlaps with that of *Somphoentactinia* or *Bisphaera* (two-shelled species formerly assigned to *Entactinosphaera*) having eight-rayed internal spicule. The presence of apophyses in the shell of entactiniids indicates that the shell is spongy. In addition to the early Paleozoic species that have been partly reassigned to the genus *Inanihella* Nazarov and Ormiston 1984 by Nazarov and Ormiston (1984), they or Nazarov reported six *Helioentactinia* species from Upper Devonian and Lower Permian faunas. *H. secutrix* Nazarov 1975 and *H. circumtexta* Nazarov 1975 have branched radial beams (indicating that the shell has no latticed meshwork). *H. ikka* Nazarov and Ormiston 1993 has a thin spongy layer, and *H. biexosphaera* Nazarov 1986 (in Isakova and Nazarov 1986) has a two-layered outer shell. The other two species, including type species, consist of shells with latticed meshwork. Thus, the genus is heterogeneous. Importantly, the establishment of the genus is based on the misidentified (by Nazarov) type species. According to my observations, the type species of *Helioentactinia*, *Entactinosphaera polyacanthina* Foreman 1963, has a six-rayed internal spicule without apophyses. Among numerous outer spines, six of them extend from inner spines, which are the continuation of the six-rayed internal spicule, and the other outer spines are extensions of the three-bladed, thick radial beams arising from the surface of the inner shell. All two-shelled, latticed species having numerous outer spines and/or radial beams in the Gogo Formation fauna being described here have a six-rayed internal spicule and no apophyses, like the type species of *Helioentactinia*. Multi-spine-bearing specimens identified as *Entactinosphaera* cf. *E. assidera* by Aitchison (1993) have the same basic structure as the species of *Radiobisphaera*. Not only the specimens identified as *Entactinosphaera* cf. *E. assidera* but also all two-shelled and latticed species having numerous radial spines in the Gogo Formation fauna have a six-rayed internal spicule. *Radiobisphaera* differs from *Bisphaera* not by the presence of apophyses which it does not have but by the numerous radial beams between the two shells and the generally numerous outer spines which join to radial beams and can be as small as by-spines.

*Radiobisphaera* is one of the most plentiful and diverse taxa in the present fauna. There is much variation in the shape and length of the outer spines, as well as in the shell wall structure. The internal structure is much less varied. The inner spines and radial beam characteristics and median bar length are generally constant at the species level in *Radiobisphaera* (Table 3). Many species belonging to this genus have morphotypes that might be ecomorphs. They are treated here subspecies for the practical use even though it is not coincident with the definition of subspecies.

***Radiobisphaera acuta* Won n. sp.**  
Plate 4, figures 13-16

*Derivation of name:* acutus (Lat.), sharp.

*Holotype:* G3103

*Diagnosis:* Spherical skeleton with a regularly latticed outer shell and a coarsely latticed inner shell; one acuminate main spine and numerous conical minor spines with grooved bases. Rodlike radial beams and six inner spines present, a robust six-rayed internal spicule with a very short median bar.

*Description:* The two spherical shells are a hexagonally latticed outer shell and a coarse, less regular latticed inner shell. There are one main spine and 15 or more minor spines. The main spine has three grooves that extend from the base to the middle or to two-thirds of the spine length, beyond which the spine continues rodlike to the tip. The numerous minor spines are shorter and thinner than the main spine and vary in number, thickness, and length. They are three faceted or slightly grooved at their base, becoming rodlike and tapering rapidly near the tip. The length and thickness of the minor spines can be uniform or varied even in a single specimen. Numerous radial beams and the six inner spines between the two shells are rodlike and are connected to the spines on the outer shell surface. The number of the radial beams is also varied. The six rodlike inner spines are slightly thicker than the radial beams and are the continuation of the six strong rays of an internal spicule that has a very short median bar.

*Remarks:* The specimens are distinguished from those of the other species of *Radiobisphaera* in this Gogo Formation fauna by the hexagonally latticed regular meshwork of the outer shell and by the less numerous radial beams. The species is very similar to the specimen of *R. perjucunda* (Nazarov and Ormiston 1983) illustrated by Nazarov and Ormiston (1983, pl. 1, figs. 14-15). However, according to their description, *R. perjucunda* has numerous main spines. They are similar to the minor spines of the specimens in the present fauna. Moreover, a single larger main spine is not present in *R. perjucunda*. The inner shell structure of these species also differs. The meshwork of the inner shell of *R. acuta* is slightly irregular, and its pore size is much larger than that of the outer shell, whereas the inner shell of *R. perjucunda* consists of regular and small poreframes.

*Material:* More than 50 specimens.

*Measurements (in  $\mu\text{m}$ ):* Outer shell diameter 105-125; outer shell pore size 5-8; outer shell thickness 8-13; inner shell diameter 38-45; inner shell pore size 5-14; main spine length 100-130; main spine base diameter 12-27; minor spine length maximum 100; median bar length 2-4.

***Radiobisphaera flamans* Won n. sp.**

Plate 4, figures 17-20; Plate 7, figures 4-5

*Derivation of name:* flamans (Lat.), blazing.

*Holotype:* G3007

*Diagnosis:* Spherical skeleton with very irregularly latticed outer and inner shells; one faintly grooved, rodlike, acuminate main spine and numerous rodlike minor spines and curved by-spines densely cover the shell surface; rodlike inner spines and radial beams; a robust six-rayed internal spicule with a very short median bar.

*Description:* This species is characterized by very irregular, coarsely latticed inner and outer shells and very closely spaced by-spines on the surface. The irregular latticework of the outer shell is commonly not observed because of the density of the by-spines. The shape of meshwork and pore size is variable. A few specimens, whose outer shell is perforated by small pores,

show a less irregular or even regular structure with a hexagonal meshwork (Pl. 7, fig. 5). The one main spine is rodlike but shows traces of grooves near its base, and it tapers sharply toward the tip. This spine is much longer and thicker than the minor spines. There are between 14 and 25 minor spines; all are rodlike, thin, and long. The numerous by-spines are larger than those of other species and somewhat conical. Many are curved or tilted. The inner spines are a bit thicker than the radial beams, but all of them are rodlike. A six-rayed internal spicule is robust, and the median bar is very short.

**Remarks:** This species has an outer appearance that is quite different from that of *R. acuta*, however, they may be more closely related to one another than to any other species. The quite different external appearance is due to the presence or absence of by-spines and different meshwork structure which may reflect ecologic factors. A few specimens of *R. flamans* have a regular shell wall structure (Pl. 7, fig. 5) like the outer shell wall of *R. acuta*. Also, all their internal structural elements have the same characteristics (Table 3) excepting the inner shell wall structure; both species have the same robust six rays and a very short median bar which is constant at the species level and the number and shape of the inner spines and radial beams are the same.

**Material:** More than 50 specimens.

**Measurements (in  $\mu\text{m}$ ):** Outer shell diameter 90-115; outer shell thickness 2-3; outer shell pore diameter 5-20; inner shell diameter 48-50; inner shell pore diameter 7-12; maximum length of strongest spine 140; main spine base diameter 7.5-15; maximum length of minor spine 105; minor spine base diameter 5-12.5; median bar length 2-4.

***Radiobisphaera magnifenestra* Won n. sp.**

Plate 3, figure 20; Plate 5, figures 8, 12

**Derivation of name:** magnus (Lat.), large; fenestra (Lat.), opening.

**Holotype:** G7602

**Diagnosis:** Two spherical shells, an irregular and very coarsely latticed thin outer shell and a inner shell consisting of thick and coarse meshwork; numerous three-bladed outer spines, one of which is somewhat thicker and longer than the others; six three-bladed inner spines, numerous three-bladed or much rarer rodlike radial beams; a six-rayed internal spicule with a median bar.

**Description:** The outer shell is thin, and irregularly and very coarsely latticed, but partly hexagonal in structure. Generally, the meshwork of the coarse inner shell is thicker and less irregular than that of the outer shell, but in some specimens it is relatively regularly latticed. All the outer spines are long and three-bladed, and one of them is somewhat longer and thicker than the others. When the main spine is broken, it can be difficult to distinguish it from the others. The six rays of the internal spicule with a median bar extended to the six three-bladed inner spines. Most radial beams are three-bladed or, less commonly, rodlike.

**Material:** More than 50 specimens.

**Measurements (in  $\mu\text{m}$ ):** Outer shell diameter 100-125; outer shell pore diameter 7-13; inner shell diameter 40-50; inner shell pore diameter 7-11; maximum length of main spine 175; main

spine base diameter 14-20; maximum length of minor spine 125; minor spine base diameter 7-12; median bar length 8-9.

***Radiobisphaera multa* Won n. sp.**

Plate 3, figures 17-19

**Derivation of name:** multus (Lat.), numerous

**Holotype:** G11899

**Diagnosis:** Two shells with a densely latticed outer shell and a hexagonally latticed inner shell; one very thick main spine and numerous rodlike by-spines extended from radial beams and inner spines; rodlike six inner spines and numerous radial rodlike beams having uniform thickness; six-rayed internal spicule with a median bar.

**Description:** The outer shell is densely perforated by fairly small pores and somewhat irregularly latticed. The one main spine is straight or twisted and has three or more deep grooves. Its length is generally somewhat less than the shell diameter. The numerous by-spines equivalent to the minor spines of other species in this genus vary somewhat in number and length, but they are typically very thin, rodlike, and connected to the radial beams and inner spines between the two shells. The bases of the by-spines are grooved. The inner shell consists of a hexagonal meshwork that is slightly coarser than that of the outer shell. There is no difference in size and shape between the inner spines, which are the continuation of the six rays of the internal spicule, and the radial beams that arise from the surface of the inner shell.

**Remarks:** *Spongectactinella corynacantha* Nazarov and Ormiston 1983, also from the Gogo Formation, has an external appearance similar to that of *R. multa*. In addition, a few specimens bear no main spine and resemble *Spongectactinella* sp. 2 cf. *S. corynacantha* (Nazarov and Ormiston 1983, pl. 1, fig. 11), which differs from *S. corynacantha* only by the absence of the one main spine. In external appearance, *R. multa* differs from *S. corynacantha* by the length, number and shape of the minor spines, which are small and resemble to by-spines.

*S. corynacantha* is also similar to ?*R. multiaculeata stellaepolus* in external appearance. However, according to Nazarov and Ormiston's (1983) description, the internal spicule of *S. corynacantha* is thin, with a short median bar from which arise six to eight, possibly more, rodlike rays, and these rays typically branch distally (referring to apophyses) and join with the bases of the radial spines. Thus, *S. corynacantha* can not be compared with the two species. However, from the description and the illustration given by Nazarov and Ormiston, questions arise about the reality of the species *S. corynacantha*:

(a) The most incompatible point is the internal structure of *S. corynacantha*. According to their description and the hypothetical diagrammatic illustration of the internal structure of *S. corynacantha*, the rays of the internal spicule are furcated and the branches join with the bases of radial spines. However, from material now known, such an internal structure is present, neither in specimens of the present Gogo Formation fauna nor in any other Paleozoic entactiniids.

(b) In addition to the diversely expressed spine structure, Nazarov and Ormiston's description and the illustrated figures also show differences in the shell wall structure. They described the shell as spongy; however, according to their illustrations (pl. 1, figs. 1, 2, text-fig. 2A, 2B) of *S. corynacantha*, the wall struc-



ture of the specimens varies: latticed shell wall (pl. 1, figs. 1-2), and spongy tissue on a latticed layer (text-fig. 2B). A shell wall consisting of very fine meshwork can look like a very densely interwoven spongy tissue, and has been often misidentified as spongy shell. However, the shell walls of their specimens (pl. 1, figs. 1, 2) are not three-dimensionally constructed. Whatever Nazarov and Ormiston described *S. corynecantha*, in external appearance alone, the illustrated specimens (Nazarov and Ormiston 1983, pl. 1, fig. 1, 2) of *S. corynecantha* is typical of *Radiobisphaera* forms in Gogo faunas.

The subspecies ?*R. m. stellaepolus* is similar to *R. multa* n. sp. in its external appearance, but differs in having the three-bladed minor outer spines, the three-bladed inner spines between two shells, and fewer spines. The minor outer spines are also less numerous, longer, and thicker than those of *R. multa*. Where the minor spines are broken, it is sometimes not easy to distinguish between them without examination of internal structure.

**Material:** More than 100 specimens.

**Measurements (in  $\mu\text{m}$ ):** Outer shell diameter 150-200 (majority 185-200); outer shell thickness 8-12; outer shell pore diameter 2.5-7; inner shell diameter 70-80; inner shell thickness 5-4; inner shell pore diameter 7-8; major spine length 130-190; main spine diameter 25-45; median bar length 5-6.

***Radiobisphaera multiaculeata* Won n. sp.**

Plate 4, figures 1-12

*Helioentactinia perjucunda* NAZAROV and ORMISTON 1983. – AITCHISON 1993, pl. 1, fig. 12.

*Helioentactinia stellaepolus* AITCHISON 1993, pl. 5, fig. 13, (? pl. 7, fig. 17, not pl. 5, fig. 17)

*Helioentactinia aster* AITCHISON 1993, pl. 5, fig. 18 (not the holotype of pl. 7, fig. 18)

**Derivation of name:** multus (Lat.), numerous; aculeatus (Lat.), spiny.

**Holotype:** G11911

**Diagnosis:** Two spherical shells with a very densely latticed and smooth or minutely unevenly patterned to reticulated outer shell, an inner shell of hexagonal meshwork; numerous three-bladed spines, one of which is somewhat much stronger than the other spines; three-bladed inner spines and radial beams having slightly different or uniform thickness; a six-rayed internal spicule with a median bar.

**Remarks:** This species is abundant in this Gogo fauna. The basic structure of all the skeletal elements is the same, but the outer spines and outer shell wall structure are very varied. Thus, the external appearance is also varied. Some specimens have a smooth external shell wall (Pl. 4, figs. 7, 8). In other specimens, one to three (Pl. 4, figs. 1, 2) or more pores (Pl. 4, figs. 3, 4) are contained in a larger poreframe that stands slightly higher than the poreframes of the pores inside forming a unevenly patterned surface. In still others, the outer surface has a more coarsely patterned structure and appears to be reticulated (Pl. 4, figs. 5, 6). In some specimens having a smooth surface, traces of the reticulated structure can be seen at the base of spines (Pl. 4, fig. 7). The stage of development of the connections between the bases of spines and/or by-spines and neighboring poreframes determines the variation in the shell surface character. The outer spines of this species have different sizes. The spine size is related to that of the inner spines and radial beams. Where the inner spines and radial beams are thick, then all the outer spines

are also well developed and the difference between the one main spine and the other spines is small. In contrast, where the inner spines and radial beams are thin, except for the one main spine, all the other spines are weakly developed. The two end members of the species are quite different in their external appearances, but there are many intermediate forms (Pl. 4, figs. 3, 4, and Aitchison 1993, pl. 5, fig. 13).

***Radiobisphaera m. multiaculeata* Won n. ssp.**

Plate 4, figures 5-8, 11-12

**Holotype:** G11911

(?)*Helioentactinia perjucunda* NAZAROV and ORMISTON 1983. – AITCHISON 1993, pl. 1, fig. 12.

**Description:** The size of the outer shell varies. The shell is very finely perforated, and its surface texture ranges from smooth to finely or coarsely reticulated. Numerous three-bladed spines are well developed, and one of them is clearly longer and thicker. However, if the main spine is broken, it can be difficult to identify it from the others. The inner spines, which are the continuations of the six rays of the internal spicule, and radial beams arising from the surface of the inner shell are three-bladed and have the same appearance and thickness. The inner shell consists of a hexagonal meshwork that is much coarser than that of the outer shell. Within the inner shell, a six-rayed internal spicule with a median bar is located eccentrically.

**Remarks:** *R. m. multiaculeata* n. ssp. differs from ?*R. m. stellaepolus* by its well-developed minor spines. In the subspecies ?*R. m. stellaepolus*, the difference between main spine and minor spines is much greater than in *R. m. multiaculeata*.

Specimens of *R. m. multiaculeata* are similar to those assigned to *Radiobisphaera perjucunda* (Nazarov and Ormiston 1983) by Aitchison. However, the specimen (Aitchison 1993, pl. 6, fig. 12) identified as *R. perjucunda* differs from the figured specimen, holotype, (Nazarov and Ormiston 1983, pl. 1, figs. 14, 15) of *R. perjucunda*. All the spines of the specimen figured by Aitchison are much stronger than those of specimen figured by Nazarov and Ormiston and their shape of both specimens are quite different. It is also questionable whether the spines of *R. perjucunda* illustrated by Aitchison are originally short and terminate abruptly. It looks as they are broken. In addition, the outer and inner shell wall structures of Aitchison's specimen are quite different from each other. In contrast, the mesh shape and size of inner and outer shell of *R. perjucunda* reported by Nazarov and Ormiston (1983) are the same. And according to Nazarov and Ormiston's description, the species has rodlike radial beams, whereas the specimen figured by Aitchison (1993, pl. 6, fig. 12) shows three-bladed radial beams.

This subspecies is also similar to *R. polyacanthina* (Foreman 1963). However, the former is distinguished from the latter by the shell wall structure and the number of spines. *R. polyacanthina* has an outer shell consisting of a hexagonally latticed meshwork and less numerous outer spines and radial beams than *R. m. multiaculeata*.

**Material:** More than 1,000 specimens.

**Measurements (in  $\mu\text{m}$ ):** Outer shell diameter 125-200; outer shell thickness 2-5; outer shell pore diameter 1-3.5; inner shell diameter 50-80; inner shell pore diameter 7-8; maximum length of strongest spine 250; strongest spine base diameter 25; maximum length of minor spine 25; maximum minor spine base diameter 13; median bar length 6-8.

? *Radiobisphaera m. stellaepolus* (Aitchison 1993)

Plate 4, figures 1-2, 9, 10

*Entactinosphaera* cf. *E. assidera* Nazarov 1975. – AITCHISON 1993, p. 115, pl. 6, figs. 2, 6.

*Helioentactinia aster* AITCHISON 1993, pl. 5, fig. 18 (but not the holotype of pl. 7, fig. 18).

*Helioentactinia stellaepolus* AITCHISON 1993, pl. 5, fig. 13, (? pl. 7, fig. 17, not pl. 5, fig. 17).

**Description:** The outer shell is densely and somewhat irregularly latticed. Two, three, or four pores of this shell are commonly grouped. The numerous outer spines consist of radially distributed minor spines and a main spine that is much longer and thicker than the others. The main spine has three or four grooves, but some of the grooves do not continue to the tip. The minor spines on the outer shell surface and inner spines and radial beams between two shells are three-bladed. Six inner spines, which are the continuations of the six rays of an internal spicule, are thicker than radial beams that arise from the outer surface of the inner shell. The inner shell consists of hexagonal meshes that are coarser than those of the outer shell. The six-rayed internal spicule with a median bar lies eccentrically in the inner shell.

**Remarks:** This subspecies is very similar to one illustrated paratype of *R. stellaepolus* (Aitchison 1993, pl. 5, fig. 13). According to Aitchison's diagnosis of *R. stellaepolus* (Aitchison 1993), most spines are rodlike with some longer three-bladed spines also developed. However, all spines of one illustrated paratype (Aitchison 1993, pl. 5, fig. 13) clearly are three-bladed and one of the spines is stronger. Moreover, one stronger and all the other spines of the holotype (Aitchison 1993, pl. 7, fig. 17) seem to be three-bladed; many of the outer spines are clearly three-bladed and even though a few spines of the holotype are not clearly shown in his figure, all the inner spines and radial beams are three-bladed. These three-bladed internal structures continue to the outer spines. The description of *R. stellaepolus*'s spines written by Aitchison agree only with one of his illustrated paratype (Aitchison 1993, pl. 5, fig. 17). Unlike the holotype, this paratype has several (six?) three-bladed main spines,

one of which is stronger, and rodlike minor spines like those of *R. variantia* n. sp. (See also remarks on *R. v. inaequalis* n. ssp.)

The shell wall structure of the three illustrated specimens (Aitchison 1993, pl. 5, figs. 13, 17, pl. 7, fig. 17) of *R. stellaepolus* is varied; the shell wall of the Holotype is thinner and its meshwork is less dense than the two paratype. The shell wall structures can be variable at a species level. Even though such shell wall structure in specimens of *R. multiaculeata* was not recovered in this fauna, if all the spines of Holotype are three-bladed, then, *R. stellaepolus* (Aitchison 1993) can be a subspecies of *R. multiaculeata*, ?*R. m. stellaepolus*.

The paratype (Aitchison 1993, pl. 5, fig. 18) of *R. aster* (Aitchison 1993) is characterized by a densely latticed outer shell, numerous three-bladed minor spines, and a strong main spine (broken in the figured specimen). The specimen strongly resembles the paratype of *R. stellaepolus* (Aitchison 1993, pl. 5, fig. 3), and ?*R. m. stellaepolus* in this paper.

The illustrated specimen of *Entactinosphaera* cf. *E. assidera* by Aitchison (1993, pl. 6, fig. 2) is similar to ?*R. m. stellaepolus*, and have the same basic structure as the species of *Radiobisphaera*. Not only the specimens identified as *Entactinosphaera* cf. *E. assidera* but also all two-shelled and latticed species having numerous radial spines in the Gogo Formation fauna have a six-rayed internal spicule. *Radiobisphaera* (former species of *Helioentactinia*, which consists of latticed two shells, including its type species) differs from *Bisphaera* (most species of former two-shelled *Entactinosphaera*) not by the presence of apophyses which it does not have but by the numerous radial beams between the two shells and the generally numerous outer spines which join to radial beams.

**Material:** More than 500 specimens

**Measurements (in  $\mu\text{m}$ ):** The numerical range or value in parentheses is for the common specimens: Outer shell diameter 115-180 (150-168); outer shell thickness 5-10 (7-10); outer shell pore diameter 1.5-6 (3); inner shell diameter 57-75 (70-75); inner shell thickness 2.5-4; inner shell pore diameter 5-7; major

# PLATE 1

A distance of 6mm on these photographs is equivalent to the length in mm indicated in parentheses.

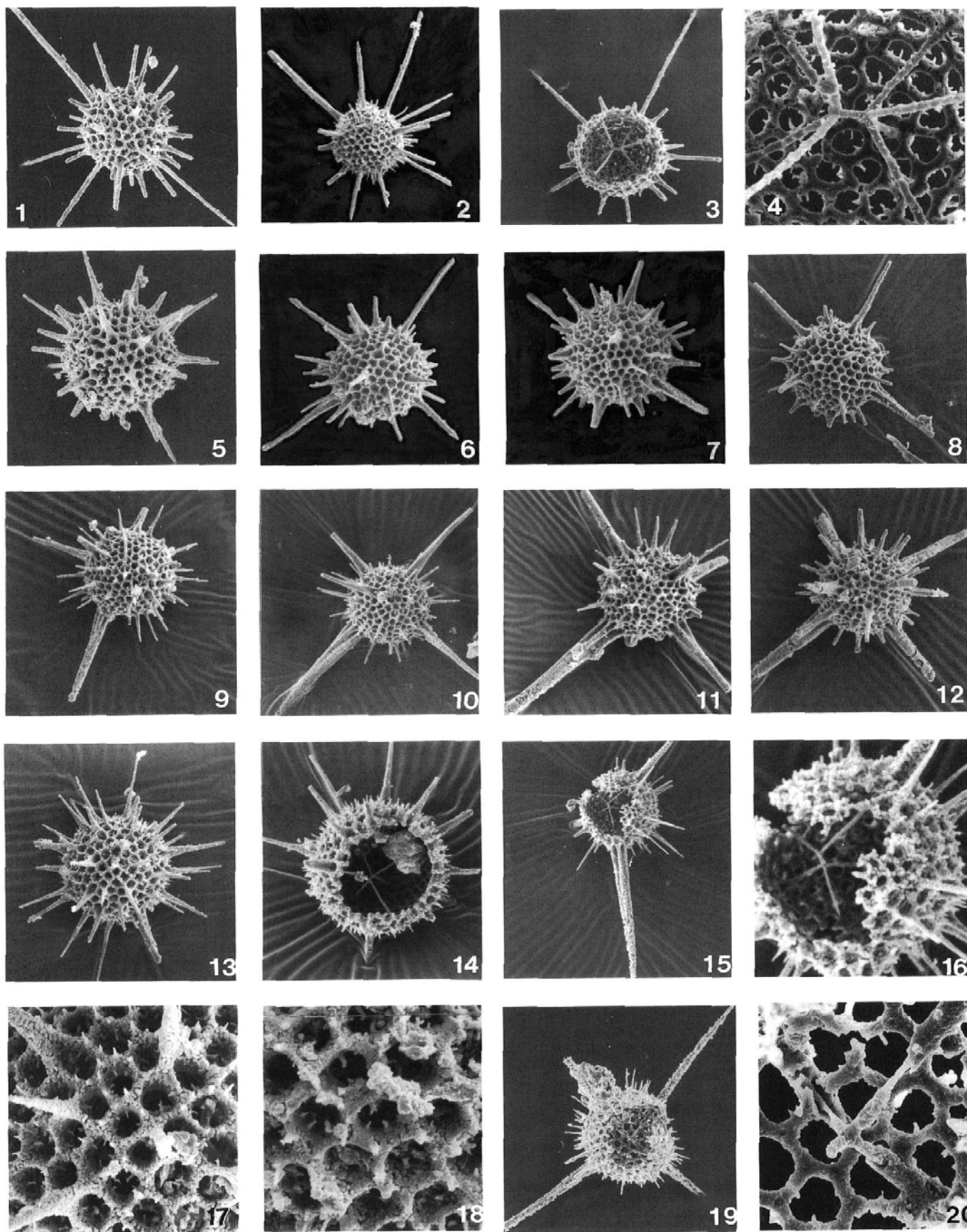
1-4, 18 *Entactinia octaradiata* n.sp. 1. Holotype: G12006 (41.4 $\mu\text{m}$ ). 2. G8401 (50 $\mu\text{m}$ ). 3. G9905 (40 $\mu\text{m}$ ). 4. Eight-rayed internal spicule of G9905 (10  $\mu\text{m}$ ). 18. Detail of surface structure showing microsepta of G8401 (10 $\mu\text{m}$ ).

5-7, 13, *Entactinia sexradiata* n. sp. 5. Holotype: G12004 (42.8 $\mu\text{m}$ ). 6. G7006 (37.2 $\mu\text{m}$ ). 7. G3606 (40 $\mu\text{m}$ ). 13. G3204 (40 $\mu\text{m}$ ). 14. Six-rayed internal spicule of G3603 (33.3 $\mu\text{m}$ ). 17. Detail of surface structure of G3204 (8 $\mu\text{m}$ ).

8 Intermediate specimen between *E. sexradiata* n. sp. and *E. mediforma* n. sp. The continuum of characteristics from multi-radiated forms to those having six main spines can be seen in figures. 5 to 12.

9-12, 15, *Entactinia mediforma* n. sp. 9. G7004 (43.4  $\mu\text{m}$ ). 10. Holotype: G3505 (50 $\mu\text{m}$ ). 11. G7002 (42 $\mu\text{m}$ ). 12. G7102 (43.4 $\mu\text{m}$ ). 15. G8903 (50 $\mu\text{m}$ ). 16. Six-rayed internal spicule of G8903 (17.4 $\mu\text{m}$ ).

19, 20 *Entactinia haeckeliana* n. sp. 19. G12009 (32.7 $\mu\text{m}$ ). 20. G12009 (4.6 $\mu\text{m}$ ); rays of the internal spicule are covered by tubes at the boundary between the internal spicule and the outer spines.



spine length 125-175 (125); major spine diameter at base 20-37 (30-37); median bar length 6-8.

***Radiobisphaera nazaroviana* Won n. sp.**

Plate 3, figures 14-16

*Derivation of name:* In honor of B. B. Nazarov

*Holotype:* G7604

*Diagnosis:* Two spherical shells, a hexagonally latticed extraordinarily thin outer shell and an irregularly latticed inner shell; six three-bladed main spines and rodlike very short by-spines; six three-bladed inner spines and numerous rodlike radial beams; a six-rayed internal spicule with a median bar.

*Description:* The spherical outer shell generally consists of a hexagonally latticed meshwork that is extremely thin and delicate and fragile. The inner shell is slightly thicker than the outer one, and its meshes are coarser and irregular. The six main spines are thick and three-bladed. They are approximately equal in length and thickness. The numerous thorns on the outer shell, which are commonly not preserved, are the continuations of the needle-like radial beams. The six three-bladed inner spines are very thick and connect to the six rays of an internal spicule with a median bar.

*Material:* More than 50 specimens

*Measurements (in  $\mu\text{m}$ ):* Outer shell diameter 100-115; outer shell pore diameter 6-8; inner shell diameter 45-50; inner shell pore size 5-17; main spine length 65-100; median bar length 5-6.

***Radiobisphaera variantia* Won n. sp.**

Plate 5, figures 1-7, 9-11.

*Helioentactinia stellaepolus* AITCHISON 1993, pl. 5, fig. 17, (not pl. 5, fig. 13, pl. 7, fig. 17).

(?)*Astroentactinia*? sp. aff. *A. crassata* Nazarov 1975. – NAZAROV et al. 1982, p. 170, fig. 5A

*Derivation of name:* variantia (Lat.), variety.

*Holotype:* G11956

*Diagnosis:* Two latticed spherical shells; outer shell finely latticed, smooth or slightly to strongly reticulated; inner shell coarsely and hexagonally to irregularly latticed; six three-bladed main spines present, one of which is slightly to much stronger than the other five, minor outer spines rodlike or three-bladed and weakly or strongly developed; inner spines extending from six rays of an internal spicule are three-bladed, whereas numerous radial beams are rodlike.

***Radiobisphaera v. variantia* Won n. ssp.**

Plate 5, figures 4-7, 11

*Holotype:* G11956

*Description:* The thin outer shell consists of a fine, irregular meshwork. Some of the poreframes join the base of by-spines and blades on spines to form a raised unevenly patterned structure. The meshwork of the inner shell is much coarser than that of the outer shell. There are commonly six three-bladed main outer spines, one of which is somewhat longer and thicker than the other five. Minor spines are varied in their length and shape. Some minor spines are rodlike, others are three-bladed. Generally, three-bladed minor spines are thicker and longer than the rodlike minor spines. Rarely, all the minor spines are three-bladed. In some specimens the main and some of the minor spines have almost the same shape and robustness; in these, the main and minor spine are difficult to distinguish from one another. However, all six main spines are connected with the six three-bladed inner spines, and the other rodlike radial beams arising from the outer surface of the inner shell join with the minor spines. The six three-bladed inner spines are connected to the six rays of an internal spicule that has a median bar.

*Remarks:* *R. v. variantia* n. ssp. has the same diagnostic characteristics as *R. v. inaequalis* n. ssp. except for the shell size and shell thickness and the degree of differences between the largest main spine and the other five. *R. v. inaequalis* has six main spines, one of which is stronger than the other five, while the difference between main and other spines in *R. v. variantia* is

## PLATE 2

A distance of 6mm on these photographs is equivalent to the length in mm indicated in parentheses.

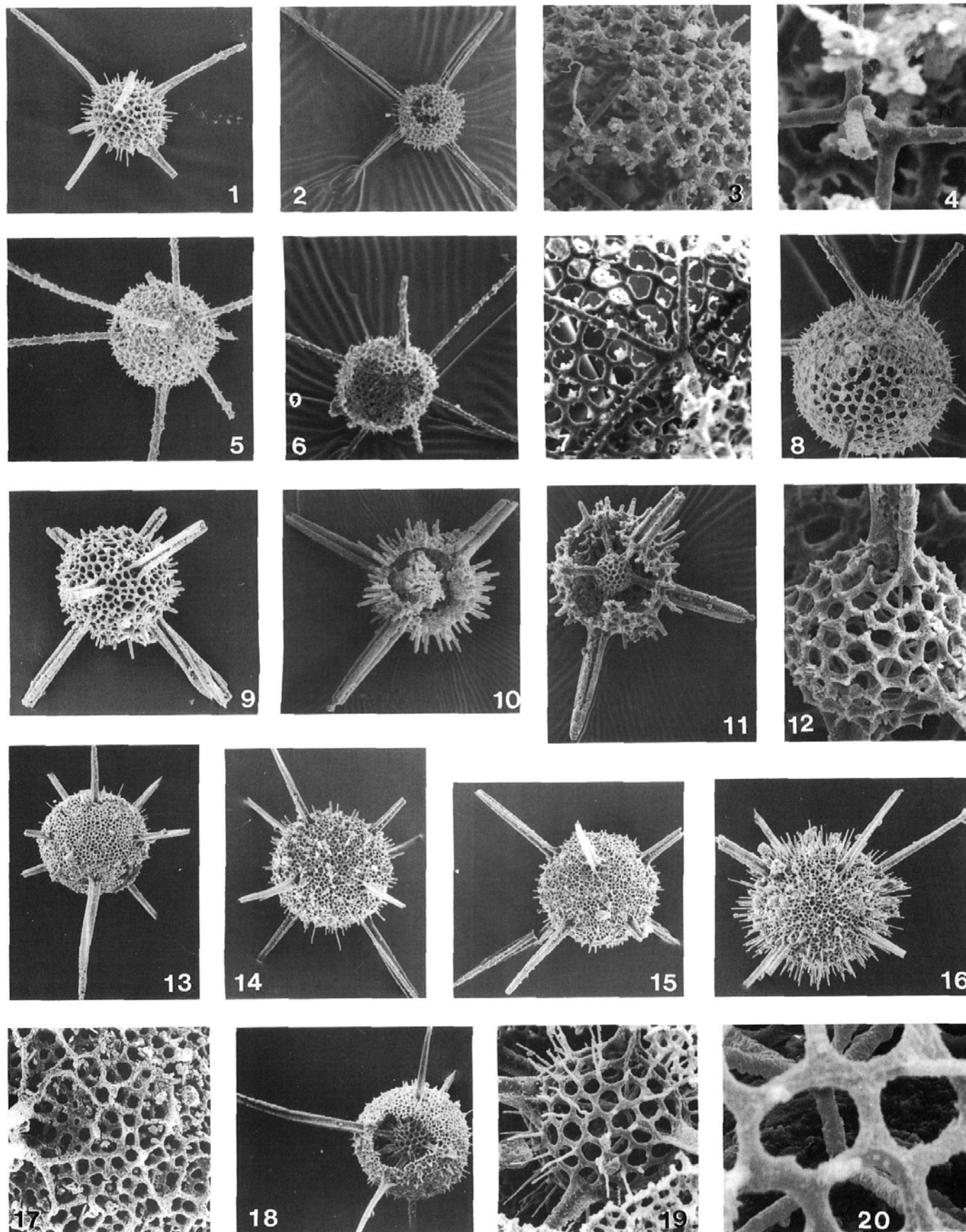
1-4 *Entactinia haeckeliana* n. sp. 1. Holotype: G12008 (36.7 $\mu\text{m}$ ). 2. G4506 (58.8 $\mu\text{m}$ ). 3. Detail of surface structure showing microsepta of G4506 (10.4 $\mu\text{m}$ ). 4. Six-rayed internal spicule of G4506 (4 $\mu\text{m}$ ); one-ray is broken.

5-8 *Entactinia hindeiana* n. sp. 5. Holotype: G11993 (37.5 $\mu\text{m}$ ); microthorns cover the spines. 6. G3605 (40 $\mu\text{m}$ ). 7. Eight-rayed internal spicule of G3605 (10 $\mu\text{m}$ ). 8. G11770 (24 $\mu\text{m}$ ); four rays of the internal spicule are developed along the shell wall.

9-12 *Bisphaera benigna* n. sp. 9. G1201 (75 $\mu\text{m}$ ); most of the by-spines are broken. 10. G7302 (76.9  $\mu\text{m}$ ); densely covered with by-spines. 11. Holotype: G7304 (55.5  $\mu\text{m}$ ). 12. G7304 (12.3  $\mu\text{m}$ ); six-rayed internal spicule, although one ray can not be seen in this view.

13-20 *Bisphaera dissimilicortex* n. sp. 13-16, 18: variable shell wall structure. 13. G11916 (48 $\mu\text{m}$ ). 14. Holotype: G11919 (40 $\mu\text{m}$ ). 15. G11917 (44.5 $\mu\text{m}$ ). 16. G12928 (50 $\mu\text{m}$ ). 17. G11917 (12 $\mu\text{m}$ ); reticulated microscopic surface structure. 8. G11927 (39 $\mu\text{m}$ ). 19. G11927 (12.2 $\mu\text{m}$ ). 20. Eight-rayed internal spicule; one ray which is connected to the rear spine of the two spines directed toward the bottom of G11927 (3 $\mu\text{m}$ ) (fig. 18) is concealed.





not so great and even some minor spines are nearly as well developed as the main spines. In addition, many of the minor spines of *R. v. variantia* are three-bladed and well developed, while those of *R. v. inaequalis* are generally weak and many of them are rodlike. The many intermediate forms are difficult to classify. However, each end member is distinctly different.

This subspecies is similar to a specimen of *Astroentactinia*? sp. aff. *A. crassata* Nazarov 1975 from Gogo Formation, illustrated by Nazarov et. al (1982, fig. 5A). They assigned the species questionably to *Astroentactinia* because the internal structure of the species is not clear. As they described if an inner shell is present, it possibly represents a species of *Radiobisphaera* (former *Helioentactinia*). The presence of two kinds of three-bladed and rodlike spines of their specimen suggests that the species may belong to *R. v. variantia*.

**Material:** More than 100 specimens.

**Measurements (in  $\mu\text{m}$ ):** Outer shell diameter 100-135; outer shell thickness 2.5-6; outer shell pore diameter 2.54; inner shell diameter 40-50; inner shell pore diameter 6-10; maximum length of largest spine 185; maximum diameter of the five weaker main spines base 15; maximum length of rodlike spine 80; median bar length unmeasurable.

***Radiobisphaera v. inaequalis* Won n. ssp.**

Plate 5, figures 1, 2, 9, 10

*Helioentactinia stellaepolus* AITCHISON 1993, pl. 5, fig. 17, (not pl. 5, fig. 13, pl. 7, fig. 17).

**Derivation of name:** *inaequalis* (Lat.), unequal.

**Holotype:** G11934

**Description:** The somewhat irregularly latticed outer shell is finely perforated. The shell surface is slightly or strongly and variously unevenly patterned. In many specimens, one to three pores are contained within a large poreframe; in other speci-

mens two to six pores are grouped within a frame that stands a bit higher than that of those inside and forms a minutely unevenly patterned surface. In still others, the patterned structure appears more strongly as a reticulated pattern. The inner shell consists of a regular to subregular meshwork that is much coarser than that of the outer shell. The largest main spine is constant in its thickness for the greater part of its length and gradually tapers near the tip. It is clearly stronger than the other five three-bladed main spines. Numerous weak outer minor spines are generally rodlike, but they are rarely three-bladed. The six main three-bladed spines extend from the six three-bladed inner spines, which join with the six rays of an internal spicule. The other rodlike radial beams between the two shells arise from the outer surface of the inner shell and are connected to the minor spines on the outer shell surface.

**Remarks:** The diagnosis of the *Helioentactinia stellaepolus* Aitchison 1993 and of *R. v. inaequalis* are the same except for details of the inner shell structure. *R. stellaepolus* (Aitchison 1993) seems to be heterogeneous; Aitchison's specimens (pl. 5, fig. 13, and pl. 7, fig. 17) have one strong spine and numerous three-bladed minor spines, while in one figured specimen (Aitchison, 1993, pl. 5, fig. 17), many of the spines are rodlike and some of the longer ones are three-bladed, and one distinctly robust spine is present. *R. v. inaequalis* has an external appearance similar to that of Aitchison's specimen (1993, pl. 5, fig. 17).

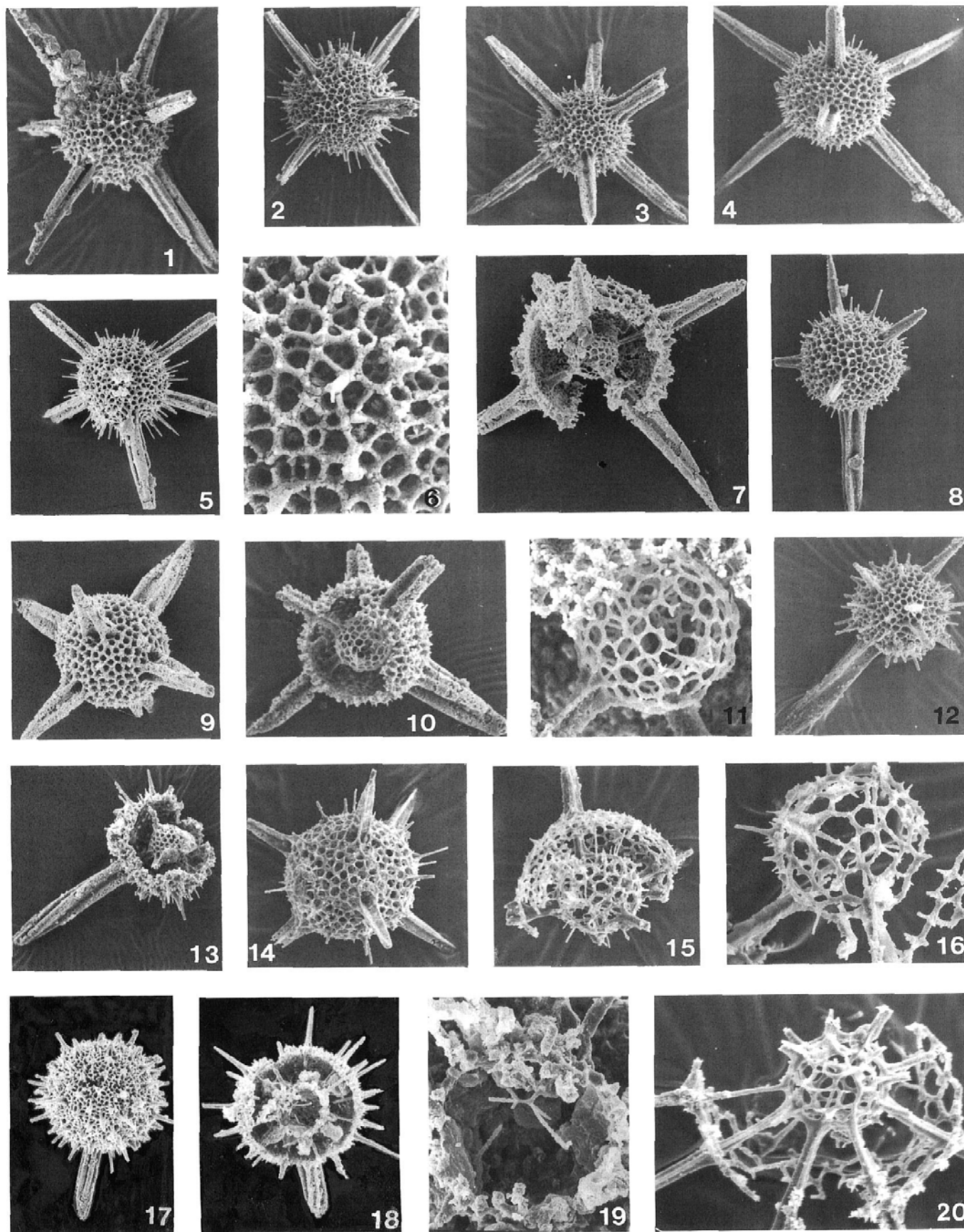
**Material:** More than 50 specimens.

**Measurements (in  $\mu\text{m}$ ):** Outer shell diameter 138-148 (rarely as low as 120); outer shell thickness 7-9; outer shell pore diameter 2-3.5; inner shell diameter 50; inner shell pore diameter 7.5-10; maximum length of main spine 150; main spine diameter at base 20-23; maximum length of minor spine 125; maximum diameter of minor spine base 13; rodlike spine length maximum 118; rodlike spine base diameter 7-9; median bar length unmeasurable.

### PLATE 3

A distance of 6mm on these photographs is equivalent to the length in  $\mu\text{m}$  indicated in parentheses.

- |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <p>1-8 <i>Bisphaera cribrisimilis</i> n. sp. These figures show the gradation in shell wall characteristics.</p> <p>1,2,6,7 <i>Bisphaera c. cribrisimilis</i> n. ssp. 1. Holotype: G7106 (45.4<math>\mu\text{m}</math>). 2. G7401 (50<math>\mu\text{m}</math>). 6. Surface structure of G7401 (10<math>\mu\text{m}</math>). 7. G11945 (40<math>\mu\text{m}</math>).</p> <p>3 G7407 (40<math>\mu\text{m}</math>); intermediate meshwork structure between <i>B. c. cribrisimilis</i> and <i>B. c. crassa</i>.</p> <p>4,5,8 <i>Bisphaera c. crassa</i> n. ssp. 4. G9806 (35.7<math>\mu\text{m}</math>). 5. Holotype: G11938 (52.6<math>\mu\text{m}</math>). 8. G9807 (37.3<math>\mu\text{m}</math>).</p> <p>9-11 <i>Bisphaera solidispinosa</i> n. sp. 9. Holotype: G11931 (34.9<math>\mu\text{m}</math>). 10. G7306 (28.5<math>\mu\text{m}</math>). 11. G7306 (10<math>\mu\text{m}</math>); six-rayed internal spicule, one ray is broken.</p> | <p>12,13 <i>Bisphaera uniprocera</i> n. sp. 12. Holotype: G3401 (40<math>\mu\text{m}</math>). 13. G7206 (40<math>\mu\text{m}</math>); minor spines are very poorly developed.</p> <p>14-16 <i>Radiobisphaera nazaroviana</i> n. sp. 14. Holotype: G7604 (25<math>\mu\text{m}</math>). 15. G7504 (20<math>\mu\text{m}</math>). 16. G9206 (10.6<math>\mu\text{m}</math>); the six-rayed internal spicule.</p> <p>17-19 <i>Radiobisphaera multa</i> n. sp. 17. Holotype: G11899 (52.2<math>\mu\text{m}</math>). 18. G11897 (44.5<math>\mu\text{m}</math>); all the inner spines and radial beams are similar and rodlike. 19. A six-rayed internal spicule of G11897 (12<math>\mu\text{m}</math>).</p> <p>20 <i>Radiobisphaera magnifenestra</i> n. sp. 20. G2905 (13.3<math>\mu\text{m}</math>); the meshwork of outer and inner shells is very coarse.</p> |
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Genus *Meschedea* Won 1983

Type species: *Meschedea pyramispinosa* Won 1983

**Emended Diagnosis:** Spherical skeleton with multi-layered outer shell and a latticed inner shell, the outermost part of the outer shell sometimes covered by thin spongy tissue; six or more outer spines, six inner spines, numerous radial beams between shells, and a six-rayed internal spicule with a median bar; no apophyses.

**Remarks:** One of the diagnostic characteristics of this genus is its two-layered outer shell. The specimens of *M. crassicornis* n. sp., and *M. pyramispinosa* Won 1983, and *M. hirusta* Won 1983 make up a series of shell wall structures. The outer shell wall of *M. hirusta* has two very closely connected shells. *M. pyramispinosa* has a tightly connected two-layered outer shell. The outer shell of *M. crassicornis* is two-layered with thin spongy tissue on the surface. A few specimens of *M. crassicornis* have an outer shell that is faintly multi-layered spongy tissue. In general, the outer shell wall structure of this genus has characteristics intermediate between those of the compact spongy tissue or multi-layered spongy shell of *Plenoentactinia* n. gen. and the multi-shelled, latticed shell wall of *Entactinosphaera* Foreman 1963 (type species of *Entactinosphaera*, species that were earlier assigned to *Belowea* Won 1983 and *Provisocyntra* Nazarov 1981). The structure of this genus shows characteristics intermediate between the Entactiniinae and Retentactiniinae, but the component species of this genus generally have a few more characteristics in common with Entactiniinae than with the Retentactiniinae. This genus is tentatively placed under subfamily Entactiniinae.

In external appearance, some specimens (e.g., Won, 1983, pl. 4, fig. 7) of *M. pyramispinosa* Won 1983 and *M. hirusta* Won 1983 seems to have a thin spongy tissue on the outer layer, which may not be preserved due to diagenetic or preparation processes. The thin outermost spongy tissue of *M. multicortex* is likewise not always preserved.

*Meschedea crassicornis* Won n. sp.

Plate 5, figures 17-20; Plate 7, figures 1-3

**Derivation of name:** crassus (Lat.), thick; cortex (Lat.), cortex.

**Holotype:** G5705

**Diagnosis:** Spherical skeleton with a two-layered outer shell which is covered by thin spongy tissue, and coarsely latticed inner shell; six three-bladed outer spines, six three-bladed and numerous rodlike inner spines; a six-rayed internal spicule with a median bar.

**Description:** The outer shell is generally two layered, and the outer layer is covered by thin, spongy tissue. If the spongy layer is not preserved, the hexagonally to polygonally latticed outer shell can be observed (Pl. 5, fig. 18). The two layers, which have approximately the same thickness, are very closely connected to one another. The outer layer is rarely indistinctly developed. A few specimens have an outer shell that is not two layered, but consists of faintly multi-layered spongy tissue on a basal layer (Pl. 7, fig. 3). The inner shell is irregularly and coarsely latticed. Six outer spines are short and three-bladed and are the continuations of six three-bladed thick inner spines extending to the six rays of an internal spicule with a median bar. Numerous thin radial beams are present between inner and outer shell. No apophyses are developed on the rays or on the inner spines. In some specimens by-spines are developed on the outermost shell surface.

**Remarks:** At first glance, the specimens of the described species seem to be small forms of *Plenoentactinia concreta* n. sp., and a few specimens have a multi-layered spongy tissue like that in *P. concreta* but differing in having a distinct inner shell. *M. crassicornis* is very similar to *M. pyramispinosa* Won 1983, but it has an outer shell consisting of thinner layers and a smaller irregular, coarsely latticed inner shell.

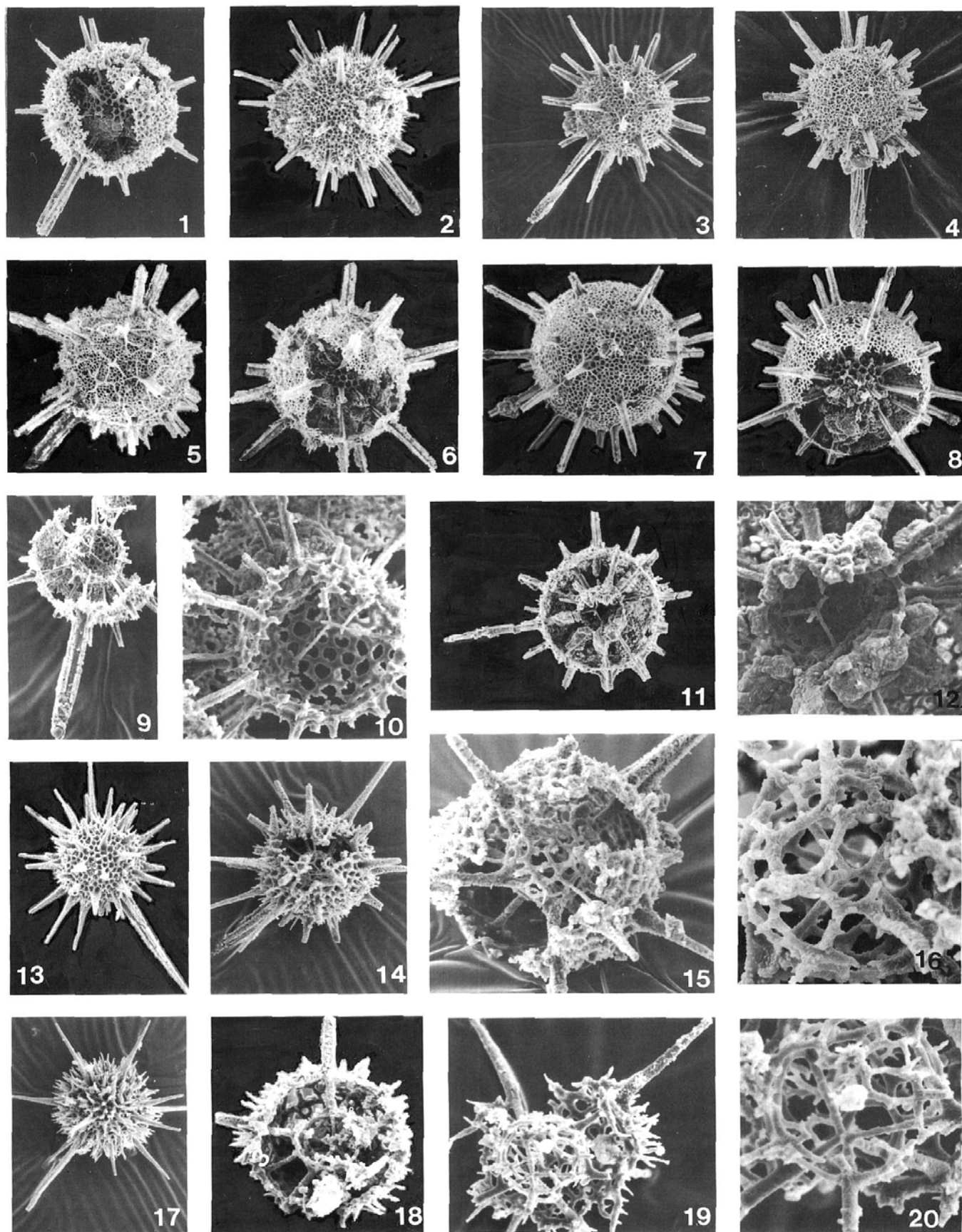
**Material:** More than 50 specimens.

#### PLATE 4

A distance of 6mm on these photographs is equivalent to the length in  $\mu\text{m}$  indicated in parentheses.

- 1-12 *Radiobisphaera multiaculeata* n. sp. The gradation in spine development and diverse shell wall structure is shown in these figures.
- 1,2,9,10 ?*Radiobisphaera m. stellaepolus* (Aitchison 1993). 1. Holotype: G11950 (40 $\mu\text{m}$ ). 2. G11902 (46.2 $\mu\text{m}$ ). 9. G7802 (30.3 $\mu\text{m}$ ). 10. The six-rayed internal spicule structure of G7802 (12.3 $\mu\text{m}$ ); all the radial beams and inner spines have the same shape and three-bladed.
- 3,4 Intermediate between *R. m. multiaculeata* and ?*R. m. stellaepolus*. 3. G7708 (40 $\mu\text{m}$ ). 4. G11906 (54.5 $\mu\text{m}$ ).
- 5-8,11,12 *Radiobisphaera m. multiaculeata* n. ssp. 5. Holotype: G11911 (40  $\mu\text{m}$ ). 6. Internal structure of G11911 (40 $\mu\text{m}$ ). 7. G11909 (40 $\mu\text{m}$ ). 8. Internal structure of G11909 (38 $\mu\text{m}$ ). 11. G11914 (46.2 $\mu\text{m}$ ); internal spicule structure; all the radial beams and inner spines are similar and three-bladed. 12. G11914 (18.5 $\mu\text{m}$ ).
- 13-16 *Radiobisphaera acuta* n. sp. 13. Holotype: G3103 (40 $\mu\text{m}$ ). 14. G3004 (33.3 $\mu\text{m}$ ). 15. G8901 (14.2 $\mu\text{m}$ ). 16. G8901 (5.8 $\mu\text{m}$ ); median bar is very short.
- 17-20 *Radiobisphaera flamans* n. sp. 17. Holotype: G3007 (40 $\mu\text{m}$ ). 18. G3101, the outer shell is very irregular (19.3 $\mu\text{m}$ ). 19. G920 (14 $\mu\text{m}$ ). 20. G9204 (5.8 $\mu\text{m}$ ); because of the view angle, the very short median bar of the six-rayed internal spicule is not visible





**Measurements (in  $\mu\text{m}$ ):** Outermost shell diameter 100-120; basal layer diameter 70-80; outer shell pore diameter 6-7.5; inner shell diameter 45-50; inner shell pore diameter 6-10; spine length 10-25, median bar length 5.

Family Incertae sedis

Genus *Apophysactinia* Won n. gen.

Type species: *Apophysactinia trispinula* n. sp.

**Derivation of name:** apophysis (Gr.), apophysis; actina (Gr.), spine.

**Diagnosis:** With or without(?) a spherical shell, six rays arising from an median microbar, each ray having three apophyses at one or two levels. The apophyses can be elements of mesh forming a very loosely constructed shell or lie free on spines. Microthorns present along the rays and apophyses.

**Remarks:** Except for the specimens of *Apophysactinia testacea* n. sp., the other species of *Apophysactinia* show no clear trace of a spherical shell. The relation between *A. testacea* and the two other species, *A. trispinula* n. sp. and *A. duplospinula* n. sp., might be the same as that between *Palaescenidium* Deflandre 1953 and *Tlecerina* Furutani 1983. However, the presence of a spherical shell cannot be completely excluded. The thin elements forming the shell wall in *A. testacea* are extremely delicate and are generally not detectable. Where the difference between fine and thick elements in a specimen is pronounced, the fine ones are more commonly eliminated than in the specimen consisting entirely of fine, delicate elements. The main skeletons of *A. duplospinula* n. sp. and *A. trispinula* n. sp. are more robust than that of *A. testacea*. Whether the shell wall was originally present or not, the species have the same basic structure.

The species of *Apophysactinia* are somewhat similar to some species of *Palaeohippium* Goodbody 1986, specifically *P. tricone* Goodbody 1986. *Apophysactinia* is characterized by

apophyses arising from the rays, whereas the rays of *Palaeohippium* are bi- to trifurcated at their tips.

*Apophysactinia duplospinula* Won n. sp.

Plate 6, figures 15, 16, 20

**Derivation of name:** duplus (Lat.), double; spinula (Lat.), spinule

**Holotype:** G5808

**Diagnosis:** Skeleton consisting of two sets of three rays connected by a median microbar. Distally, three apophyses arising from each ray at two levels lying very close to one another. One or two(?) rays can have only one set of apophyses.

**Description:** Two sets of three rodlike rays are connected by an almost unmeasurably short median microbar; they do not radiate from a single point. The rays are constant in their thickness and taper only at the tips. The length of the six rays is approximately equal. Three straight apophyses arise from each ray at two levels. However, the apophyses can be developed on one or two (?) rays at only one level. The apophyses can be very long or very short. The longer the apophyses, the greater the distance from where the second set of apophyses arise to the tip of the spine. In a given specimen, both long and short apophyses can be present. Microthorns are well developed along the middle portion of each ray.

**Remarks:** This species is distinguished from *A. trispinula* n. sp. by its small size and two sets of three apophyses on most spines.

**Material:** Twenty-two specimens

**Measurements (in  $\mu\text{m}$ ):** Total ray length 250-450, ray length from where the second apophyses arise to the tip of ray (=outer spine length) 32-350; apophyses length 35-250; ray length from where the first apophyses arise to the origin of rays 175-205;

## PLATE 5

A distance of 6mm on these photographs is equivalent to the length in  $\mu\text{m}$  indicated in parentheses.

1-7,9-11 *Radiobisphaera variantia* n. sp. The relation between *R. v. inaequalis* n. ssp. and *R. v. variantia* is suggested by the gradual change of five weaker main spines and by-spines.

1,2,9,10 *Radiobisphaera v. inaequalis* n. ssp. 1. Holotype: G11934 (46.2 $\mu\text{m}$ ). 2. G7806 (38.1 $\mu\text{m}$ ). 9. G.7603, radial beams are rodlike, and inner spines are three-bladed (10.2 $\mu\text{m}$ ). 10. G7707 (30.7 $\mu\text{m}$ ); the meshwork structure of the inner shell is intermediate between that of *R. v. inaequalis* n. ssp. and *R. v. variantia* n. ssp.

3 Spine structure intermediate between *R. v. variantia* and *R. v. inaequalis*.

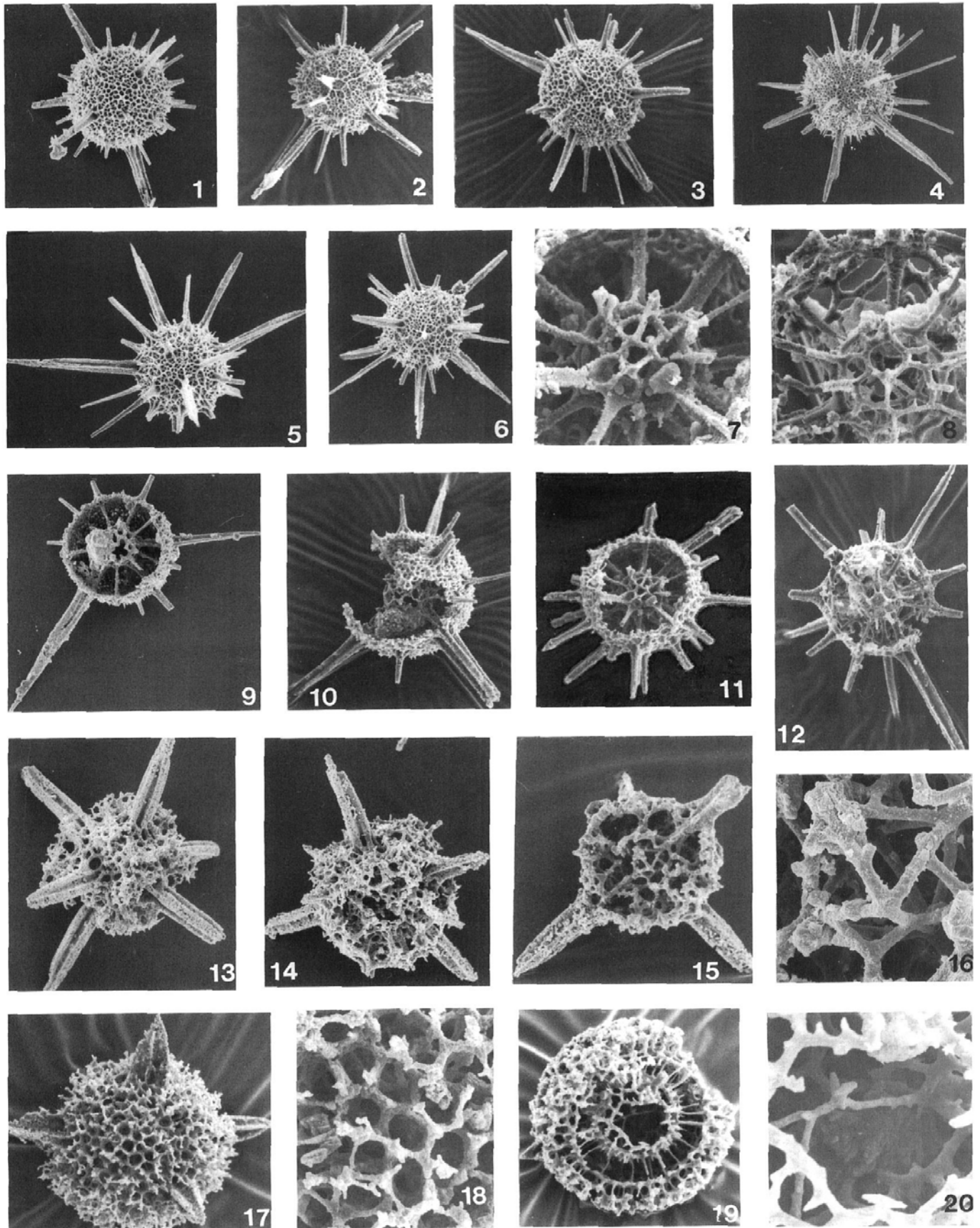
4-7,11 *Radiobisphaera v. variantia* n. ssp. 4. G11957 (44.4 $\mu\text{m}$ ). 5. Holotype: G11956 (40 $\mu\text{m}$ ). 6. G11954

(46.1 $\mu\text{m}$ ). 7. G8803 (12.5 $\mu\text{m}$ ); inner spines are three-bladed, and radial beams are rodlike. 11. G8003 (33.3 $\mu\text{m}$ ); the meshwork of the inner shell is irregular.

8,12 *Radiobisphaera magnifenestra* n. sp. 8. Holotype: G7602, the internal spicule is six rayed, and the meshwork of the outer shell is very coarse and irregular (10.3 $\mu\text{m}$ ). 12 Holotype: G7602, (27.7 $\mu\text{m}$ ).

13-16 *Intracarpus octaedron* n. sp. 13. Holotype: G12002 (50.4 $\mu\text{m}$ ). 14. G12003 (46.2 $\mu\text{m}$ ); note the layered shell structure. 15. G12001 (33.3 $\mu\text{m}$ ). 16. Octaedron internal framework of G12001 (6.3 $\mu\text{m}$ ).

17-20 *Meschedea crassicortex* n. sp. 17. Holotype: G5705 (16.5 $\mu\text{m}$ ). 18. The regularly latticed shell wall structure under spongy tissue of G5705 (5 $\mu\text{m}$ ). 19. G5701 (15.3 $\mu\text{m}$ ). 20. The six-rayed internal spicule of G5701 (4 $\mu\text{m}$ ).





length between first set and second set of apophyses 12-25; ray thickness 10-12; median bar length 0.5-1.5.

*Apophysactinia testacea* Won n. sp.

Plate 6, figures 9-12, 18, 19

*Derivation of name:* testaceus (Lat.), having a shell

*Holotype:* G9108

*Diagnosis:* Skeleton of six rays with a median microbar. Straight, long apophyses arising from each ray at one or more levels. Apophyses forming a base for a the very large, loose, irregularly constructed shell.

*Description:* The test consists of a spherical shell and six rays. The shell is very open and loose, consisting of very thin and long bars which are irregularly three-dimensionally woven. From each ray arise three or four bars at from one to a maximum of three levels. The first and second set of these bars correspond to apophyses, but the third set shows no difference from other meshwork bars. The ray length from the center to the first set of apophyses is constant, while that between the first and second set of apophyses varies. The first set of apophyses is longest and generally well preserved even in broken specimens. The length and thickness of the six rays are almost the same. The thickness of the ray is almost constant or gradually becomes slightly thicker and then thinner and tapers to the distal part. The six rays are connected with an extremely short median microbar. However, in a few specimen, they are connected by a relative long median bar (Pl. 6, fig. 18).

*Material:* More than 50 specimens.

*Measurements (in  $\mu\text{m}$ ):* Approximate shell diameter 550-600; maximum total ray length 570 (maximum outer spine length

from where the apophyses arise to the tip 260; ray length from median bar to where the apophyses arise 112-150 (majority 120-125)); ray thickness 4-5; maximum length of apophyses 190; median bar length 1-3.5 (two specimens, 6 and 15).

*Apophysactinia trispinula* Won n. sp.

Plate 6, figures 13, 14, 17

*Derivation of name:* tri (Lat.), three; spinula (Lat.), spinule.

*Holotype:* G6004

*Diagnosis:* Six-rayed skeleton with a median microbar; distally, three apophyses arising from each ray at one level.

*Description:* Six rays are connected with a median microbar which is extremely short or unmeasurable. The thickness and length of the rays are the same from origin to where the apophyses arise. On the middle part of the rays, but more toward the proximal part, there are numerous microthorns that can also be observed on the apophyses and on the distal parts of each ray.

*Remarks:* It is uncertain whether the shell wall of this species is not preserved or never existed. The outer shell of this species might be broken, leaving only strong six rays and apophyses. The spherical shell of *A. testacea* n. sp. is very commonly not preserved, leaving mainly the first bars that correspond to the first set of apophyses. Thus, the specimens of *A. testacea* lacking a shell and those of *A. trispinula* have the same structure. These species are distinguished from each other by the different length ratios among structural elements, including the strength of the six rays. The six rays of this species are always more robust than those of *A. testacea*.

## PLATE 6

A distance of 6mm on these photographs is equivalent to the length in  $\mu\text{m}$  indicated in parentheses.

1,2 *Magentactinia fragilis* n. sp. 1. Holotype: G2801 (55.5 $\mu\text{m}$ ). 2. The six-rayed internal spicule of G2801 (10 $\mu\text{m}$ ); one ray near the center of this view is broken.

3-5 *Magnisphaera gigantea* n. sp. 3. The eight-rayed internal spicule structure and irregularly latticed inner shell structure of G11972 (7.1 $\mu\text{m}$ ). 4. Holotype: G11972 (100 $\mu\text{m}$ ). 5. G2805 (86.2 $\mu\text{m}$ ).

6 *Magnisphaera aitchisoniana* n. sp. Holotype: G2806 (68.9 mm); two sets of apophyses arise on spines.

7 A variant specimen of *M. gigantea* n. sp. G2804 (83.3 $\mu\text{m}$ ); bars arise from a spine at two levels, and one of them is not connected with other neighboring bars to form meshwork but protrudes like a spine.

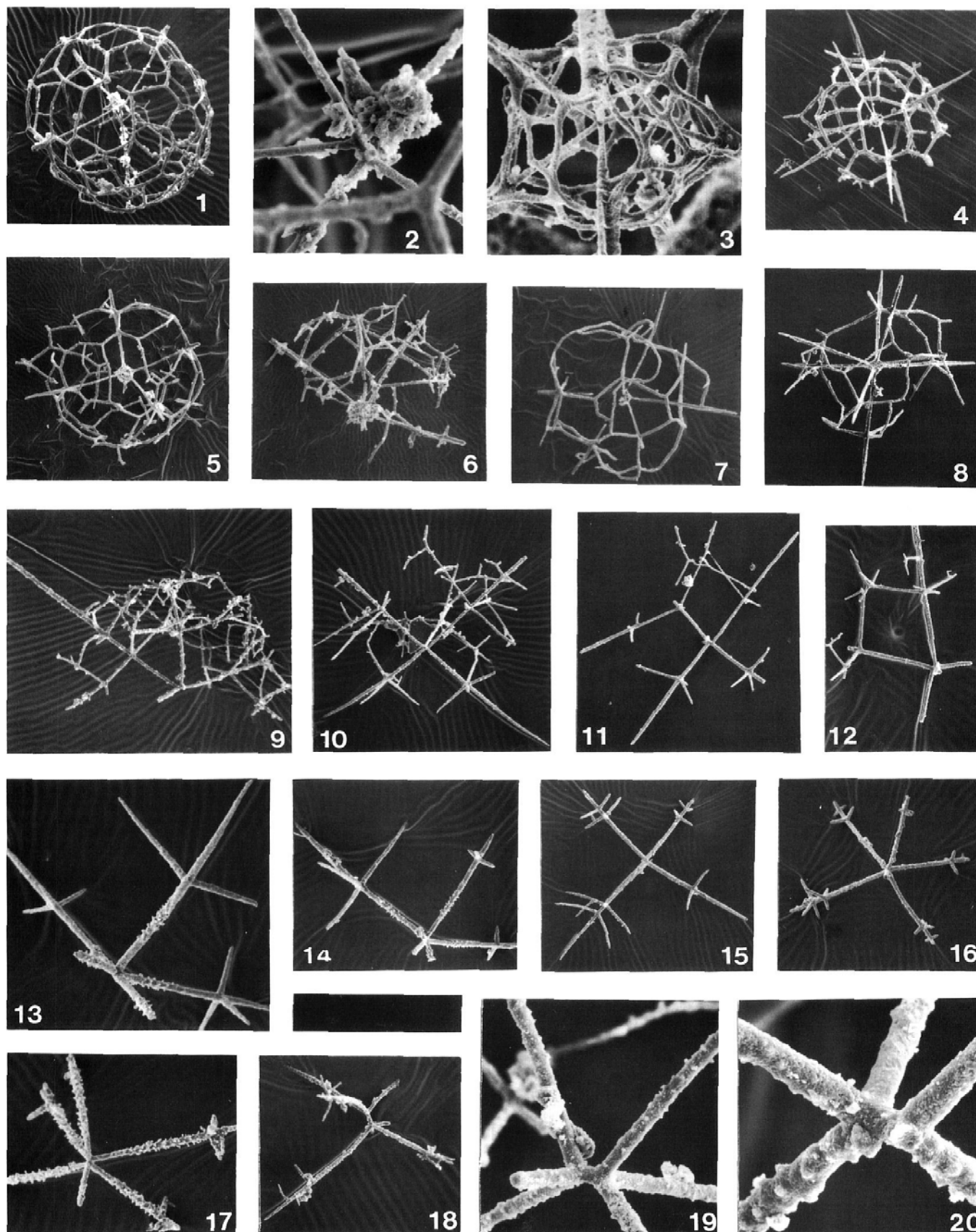
8 *Magnisphaera imperfecta* n. sp. Holotype: G9401 (11.1 $\mu\text{m}$ ).

9-12 *Apophysactinia testacea* n. sp. 9. G5805 (66.6 $\mu\text{m}$ ); partly preserved meshwork of a spherical shell is connected to apophyses which arise at two levels on rays. 10. Holotype: G9108 (66.6 $\mu\text{m}$ ); very little of the meshwork of this shell is preserved. The basic skeletal structure is the same as that of *A. trispinula* n. sp. 11. G9306 (71.4 $\mu\text{m}$ ); three apophyses on rays. 12. G5907 (53.3 $\mu\text{m}$ ); rays are thickly developed like those of *A. trispinula*. 18. G5908 (53.3 $\mu\text{m}$ ); a variant form with a median bar. 19. G9208 (10 $\mu\text{m}$ ); a median microbar.

13, 14, 17 *Apophysactinia trispinula* n. sp. 13. Holotype: G6004 (50 $\mu\text{m}$ ); on two rays, one of three apophyses lies upon the ray and is not visible. 14. G5903 (66.7 $\mu\text{m}$ ). 17. G6003 (45.3 $\mu\text{m}$ ); a variant form of *A. trispinula*.

15, 16, 20 *Apophysactinia duplospinula* n. sp. 15. Holotype: G5808 (88.8 $\mu\text{m}$ ), two rays of a six-rayed spicule are broken. 16. G6002 (66.6 $\mu\text{m}$ ); a variant form of *A. duplospinula* n. sp. has short apophyses. 20. Median microbar of G6002 (5.5 $\mu\text{m}$ ).





*Palaeohippium tricornis* Goodbody 1986 and *A. duplospinula* n. sp. differ from this species in the trifurcated rays and by the two sets of apophyses, respectively.

**Material:** More than 50 specimens.

**Measurements (in  $\mu\text{m}$ ):** Total ray length 350-525; ray length from where the apophyses arise to the tip of ray (=outer spine length) 150-325; ray length from where the apophyses arise to the origin of rays 200-210; ray thickness 10-12; apophyses length 75-300; median bar length 0.5-1.5.

Genus ***Intracarpus* Won n. gen.**

**Derivation of name:** intra (Lat.), inside; corpus (Lat.), body.

**Type species:** *Intracarpus octaedron* n. sp.

**Diagnosis:** A spherical to polygonal spongy shell with an internal polyhedral framework, no apophyses present.

**Remarks:** The described genus differs from the other genera of the family Entactiniidae in its lack of an internal spicule structure. Because of the unusual polyhedral internal framework, its systematic position is uncertain.

***Intracarpus octaedron* Won n. sp.**

Plate 5, figures 13-16

**Derivation of name:** octaedron (Gr.), octahedron.

**Holotype:** G12002

**Diagnosis:** An isometric to spherical shell with two to four indistinctly layered spongy shell layers and six outer spines. The octahedral internal structure consisting of straight bars.

**Description:** The spongy skeleton is subspherical to isometric and has three to five indistinct layers including the internal framework. Generally, the elements forming the spongy shell thicken gradually toward the outside. The layers are three-dimensionally constructed, and each spongy layer is connected by straight connecting bars whose distal ends are furcated. The inner skeleton consists of twelve straight bars, each of which forms part of the edge of an octahedral frame. The internal spicule of an inner skeleton was not observed. The six outer spines have three pronounced grooves and join to the six corners of the octahedron.

**Remarks:** This species has a similar external appearance to taxa belonging to Retentactiniinae which are characterized by a spongy shell with apophyses. However, the spongy shell of *I. octaedron* has no apophyses. The species has also no internal spicule but has an octahedral internal framework. No other comparable species have been described. Thus, the familial assignment of this species is uncertain.

**Material:** More than 50 specimens.

**Measurements (in  $\mu\text{m}$ ):** Shell diameter 125-262 (smallest form: 75); spine length 75-130 (smallest form: 38); spine thickness at base 23-50 (smallest form: 15); maximum length of straight bar forming octaedron (smallest and large form) 22-24.

Genus ***Magentactinia* Won n. gen.**

**Type species:** *Magentactinia fragilis* n. sp.

**Derivation of name:** Magnus (Lat.), large.

**Diagnosis:** The very large single spherical shell having a very open, large-pored framework and a six-rayed internal spicule with a median bar. Sometimes secondary struts subdividing each mesh opening present. Three meshwork bars arising on each spine thicker than those making up the remainder of the shell.

**Remarks:** *Magentactinia* differs from *Magnisphaera* n. gen. and *Entactinia* Foreman 1963 by the lack of an inner shell and by the extraordinarily large shell size and extremely open meshes, respectively. Specimens of *Entactinia suave* Nazarov 1977 (in Krueck and Nazarov 1977) and *Polyentactinia* aff. *suave* (Nazarov, 1988, p. 87, fig. 27 v) belong to this genus.

***Magentactinia fragilis* Won n. sp.**

Plate 6, figures 1, 2

**Derivation of name:** fragilis (Gr.), fragile.

**Holotype:** G2801

**Diagnosis:** A very large shell consisting of an irregular, polygonal, very coarsely latticed meshwork; six short outer spines extending from the six rays of an internal spicule with a short median bar; without apophyses, but the three meshwork bars arising from each of the spines thicker than those elsewhere.

**Description:** The thin and delicate spherical shell is very open and consists of a pentagonal to hexagonal meshwork. Mesh openings are very large, and the bars forming the mesh are very thin and long. The mesh opening diameter is more than ten times larger than the bar diameter. The six rodlike outer spines are very short with a blunt point. The internal spicule with a median bar is very thin and six rayed. Apophyses are not present, but three meshwork bars arising from the spines are thicker than those that link the rest of the meshwork and may correspond to apophyses.

**Remarks:** Except for the absence of the inner shell, the characteristics of this species are the same as those of *Magnisphaera gigantea* n. sp. This species has the same diagnostic characteristics of *Entactinia suave* Nazarov 1977 (in Krueck and Nazarov, 1977), but it differs in having an irregular framework.

**Material:** One specimen.

**Measurements (in  $\mu\text{m}$ ):** Shell diameter 335; median bar length 5.

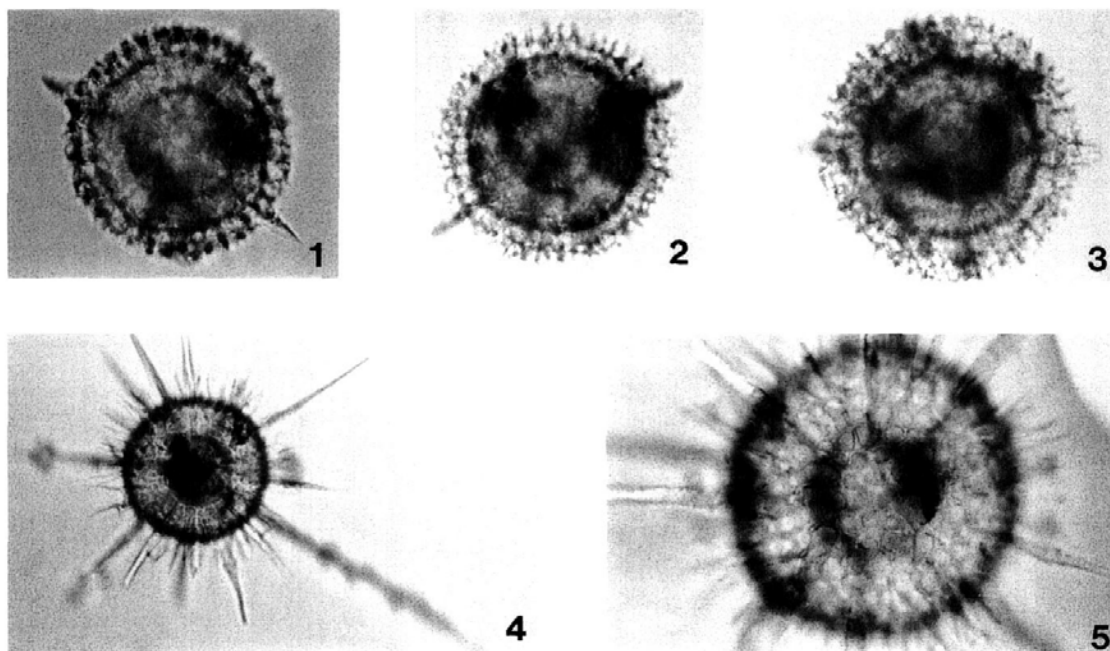
Genus ***Magnisphaera* Won n. gen.**

**Type species:** *Magnisphaera gigantea* n. sp.

**Derivation of name:** magnus (Lat.), large.

**Diagnosis:** A very large skeleton with two shells; the outer shell consisting of a polygonal (four- to eight-sided) or irregular lattice that is extremely loose, completely two-dimensional, partly or wholly three-dimensional, or incompletely latticed; straight or drooping bars forming meshwork; an irregularly latticed inner shell; the eight-rayed internal spicule with a median bar, no inner apophyses, with or without outer apophyses.

**Remarks:** This genus shows a wide variability. All the variation in structural elements appears gradational, and it is not easy to classify every specimen. Some have a completely latticed outer shell wall without apophyses. Others have an incompletely latticed shell because some meshwork bars are not connected to neighboring bars but protrude outward like a spine.



## PLATE 7

1-3 *Meschedea crassicortex* n. sp. 1. G 13-6 (330x). 2. G 11-2 (300x); a very thin spongy tissue on the second layer of the outer shell is visible. 3. G. 11-24, (330x); a

variant form of *Meschedea crassicortex* has an outer shell of thick faintly layered spongy tissue.

4,5 *Radiobisphaera flamans* n. sp. 4. G 6-25 (220x). 5. G 18-41 (440x); focused on shell wall structure, showing regular latticed shell wall structure.

Still others are partly or completely three-dimensionally constructed with apophyses on one to several rays. End members in the range of structure in the genus are clearly related through the many intermediate forms.

Some specimens of this genus have the same basic structure as that of two-shelled, latticed entactiniids. However, the new genus is characterized by an unusually large shell size and an extremely loosely constructed shell wall. Some species even have a meshwork which has drooping bars and/or is incompletely latticed.

Due to its unclear relation to other taxa, the familial position of this new genus is left open.

Well-preserved, complete specimens of *Magnisphaera* are rare because of their extremely loose and delicate meshwork. Fragments of similar very coarsely latticed shells were collected from several Carboniferous faunas. Some of these were described as *Lithocannosphaeropsis taylori* by Ormiston and

Lane (1976), but it is uncertain whether this species has an inner shell. The genus *Lithocannosphaeropsis* was erected by Deflandre (1960) without any description or diagnosis. The type species, *Lithocannosphaeropsis fallax* Deflandre 1960 also lacked a formal description, but according to his illustration, the species is small, and its detailed shell structure is not clear.

***Magnisphaera aitchisoniana* Won n. sp.**

Plate 6, figure 6

*Derivation of name:* After the name of J. C. Aitchison.

*Holotype:* G2806

*Diagnosis:* Two shells; extremely large outer shell interwoven coarse, loosely, and partially or wholly three-dimensionally; inner shell with irregularly latticed meshwork. Apophyses on one to several inner spines at one or more levels; an eight-rayed internal spicule with a median bar.

**Description:** The outer shell is constructed by thin bars which are connected to straight apophyses on one to a maximum of six inner spines. The apophyses can arise at one or more levels on the inner spines. In some specimens, only one inner spine bears apophyses, and here the shell wall structure is three-dimensional only where the apophyses arise. Eight outer and eight inner spines are three-bladed. An eight-rayed internal spicule with a median bar is located eccentrically in the irregularly latticed inner shell. Inner apophyses are not present.

**Remarks:** Some specimens are similar to the intermediate form (Pl. 6, fig. 7) which belong to *Magnisphaera* (See remarks on *M. gigantea* n. sp.)

**Materials:** Six specimens.

**Measurements (in  $\mu\text{m}$ ):** Shell diameter 400-420; maximum spine length 80; inner shell diameter 60; median bar length ?.

***Magnisphaera gigantea* Won n. sp.**

Plate 6, figures 3-5

**Derivation of name:** giganteus (Lat.), very large.

**Holotype:** G11972

**Diagnosis:** A two-shelled skeleton, very large outer shell consisting of an irregular, extremely coarse, loosely latticed that is two-dimensionally woven; the bars forming the meshwork can be straight or drooping; a small, subspherical, very irregularly latticed inner shell. Eight outer and eight inner three-bladed spines present, and an eight-rayed internal spicule with a median bar.

**Description:** The spherical outer shell is very large, extremely coarse, and loosely latticed. It consists of very thin, long bars which vary in thickness and can be straight or drooping. Each mesh opening is somewhat different in its shape and size. The mesh opening diameter is ten to twenty times wider than the width of the bar forming the meshwork. The mesh shapes can be irregular tetragons, pentagons, hexagons, or octagons. Secondary struts are rare; the very large pores subdivided into smaller pores by the struts. Many specimens have no by-spines. In a few specimens paired by-spines arise from some of the junctions of the meshwork bars or at various places on the bars. The eight three-bladed external spines are connected to the eight three-bladed inner spines. The subspherical, very irregularly latticed inner shell is much smaller than the outer shell and consists of two-dimensionally latticed meshwork. The eight-rayed internal spicule with a median bar is located eccentrically in the inner shell. Outer and inner apophyses are not present.

**Remarks:** This species differs from *M. aitchisonia* by the two-dimensionally latticed shell structure. A few specimens of *Magnisphaera* (Pl. 6, fig. 7) show characteristics intermediate between *M. gigantea* n. sp., *M. imperfecta* n. sp., and *M. aitchisoniana* n. sp. In their general features, they are similar to *M. gigantea*. However, they have protruding meshwork bars that resemble the spines and their meshwork is not uniformly latticed and the shell is not completely closed as in *M. imperfecta*, and some bars arise at two levels on one spine, and one of the bars resembles an apophysis, as in *M. aitchisoniana*.

**Material:** Eighteen specimens.

**Measurements (in  $\mu\text{m}$ ):** Shell diameter 385-480; pore diameter 50-100; mesh bar diameter 5-12; spine length 70-160; inner shell diameter 50-55; median bar length 8-9.

***Magnisphaera imperfecta* Won n. sp.**

Plate 6, figure 8

**Derivation of name:** imperfectus (Lat.), incomplect

**Holotype:** G9401

**Diagnosis:** A two-shelled skeleton with a roughly spherical outer shell consisting of an extremely loose meshwork that is incompletely latticed and with an irregularly latticed inner shell, some meshwork bars protrude outward like spines, eight outer spines, and an eight-rayed internal spicule with a median bar.

**Description:** Three bars arise on each spine, and they are connected though intervening bars to bars on neighboring spines to form the meshwork. However, one of these bars on some rays is not connected to the other elements, but is directed outward like a spine. Thus, the meshwork is not uniformly connected and the shell is not completely closed. The eight outer spines are three-bladed. The very small inner shell is irregularly latticed. An eight-rayed internal spicule with a median bar lies within the inner shell.

**Remarks:** This species differ from *M. gigantea* n. sp. in having an incompletely closed shell and in having protruding meshwork bars that are similar to spines.

**Material:** Two specimens.

**Measurements (in  $\mu\text{m}$ ):** Shell diameter 380-450; pore diameter 100-200; mesh bar diameter 5-8; spine length 70-100; inner shell diameter 50-55; median bar length 8-9.

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