

PORIFERA AND CHANCELLORIIDAE FROM THE MIDDLE CAMBRIAN OF THE GEORGINA BASIN, AUSTRALIA

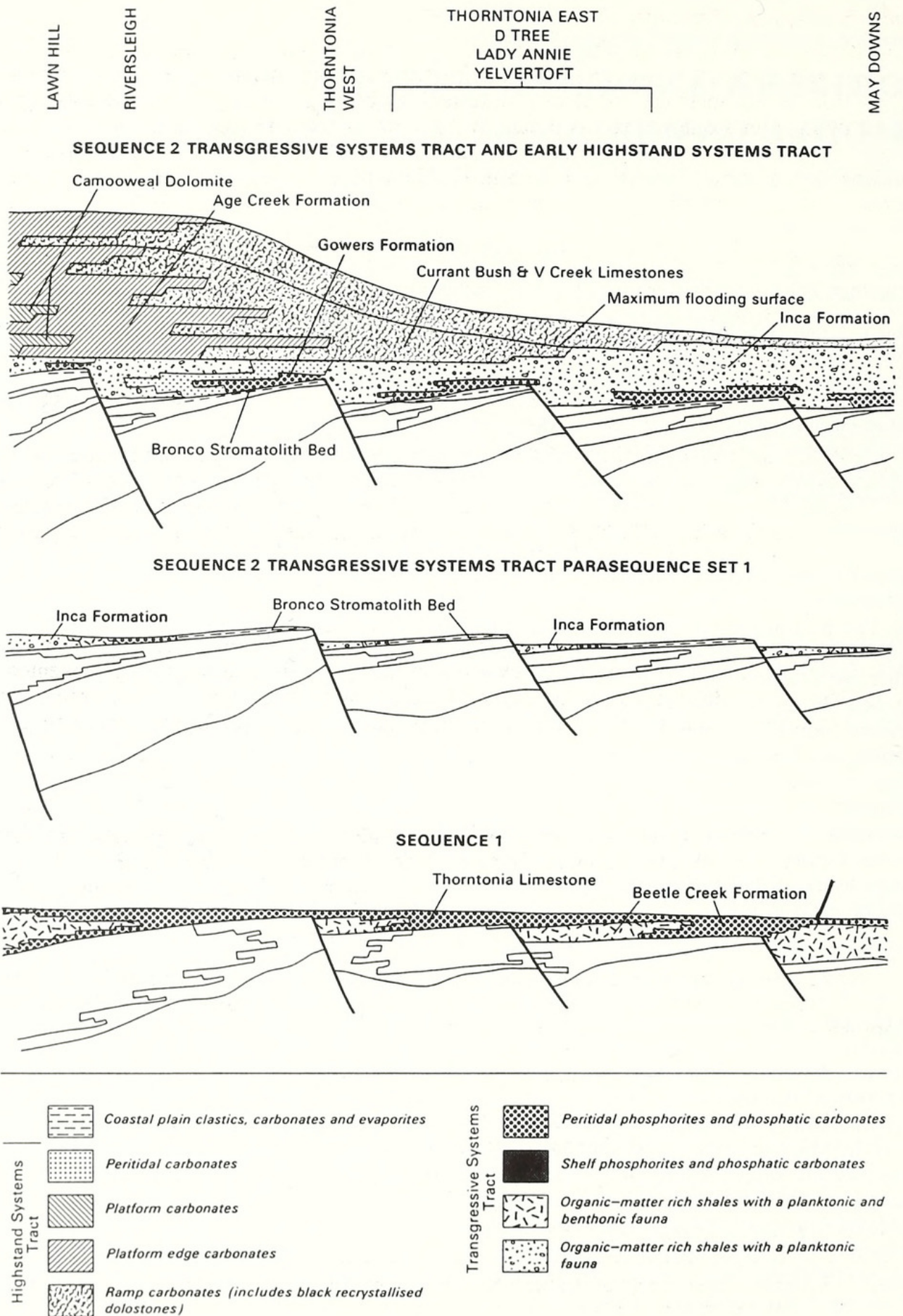
by DORTE MEHL

ABSTRACT. A rich assemblage of poriferan spicules and sclerites of the Chancelloriidae has been found in Mid Cambrian phosphatic sediments of the Georgina Basin. The hexactinellid spicules are especially diverse, and contain several new types. These include pulvinusactins (nom. nov.) and follipinules, strongly inflated triaxons which probably formed an armouring dermal layer in *Thoracospongia*, and cometiasters which may be the first Cambrian evidence of the Hexasterophora. Demosponge spicules, especially triaenes, are moderately diverse. Polyactine spicules with central canals are interpreted as proto-aster megascleres, which may have evolved into aster microscleres. Calcarean, heteractinellid spicules are also common. These features suggest an early Cambrian diversification of the Porifera. The systematic position of the Chancelloriidae is still controversial.

CAMBRIAN phosphatic sediments of the Georgina Basin are well known because of their well preserved fossils. Trilobites, brachiopods and molluscs were documented early (e.g. Öpik 1961, 1970). The phosphates are also rich in microfossils showing soft-body preservation (Müller and Hinz 1992). Sponge spicules have been mentioned only in passing, although they are common, together with *Chancelloria* sclerites, in residues of washed sediments from the eastern Georgina Basin. In 1986, a joint venture project was initiated between K. J. Müller (Bonn) and J. H. Shergold (Canberra), new fossil collections in the Georgina Basin were made by Below, Laurie, Shergold and Walossek, and they also sampled from all the main formations. Material was collected in three main areas: most came from Rogers Ridge, some from Ardmore Outlier, and the remainder from the Thornton area. Sediments were processed in 15 per cent. acetic acid and the residues were screened and washed. The assemblage includes the rich fauna of sponge spicules and chancelloriid sclerites described herein. The purpose of this publication is the documentation of the Porifera and Chancelloriidae found in the Georgina Basin, and a discussion of phylogenetic and systematic aspects of these groups.

STRATIGRAPHICAL AND PALAEOECOLOGICAL BACKGROUND

The Georgina Basin covers about 325 000 km² of central northern Australia and contains exposures of Cambro-Ordovician rocks deposited in a broad, shallow epicontinental sea. During the Mid Cambrian, a series of organic-rich muds, associated with phosphorites, was deposited. The stratigraphical framework of the Middle Cambrian has been provided by Öpik (1960, 1961), Smith (1972), Shergold and Druce (1980) and Shergold *et al.* (1985). Phosphogenesis persisted throughout most of the Mid Cambrian, and took place in the course of cyclic sedimentation related to upwelling during transgressions (Southgate and Shergold 1991). The stratigraphy and lithofacies have been described in detail by Shergold and Southgate (1986), so here only a short description of the formations is given, focusing on those in which sponge spicules and chancelloriian sclerites have been found. These are of early Mid Cambrian, Ordian to Undillan age. According to Southgate and Shergold (1991), the Mid Cambrian phosphorites of the Georgina Basin were deposited during two main transgressive episodes (Text-fig. 1).



TEXT-FIG. 1. For caption see opposite.

Thorntonia Limestone Formation

This was deposited throughout the eastern and northern part of the Georgina Basin, and is particularly well exposed at Rogers Ridge and in the Ardmore Outlier. The formation consists mainly of dolostone, limestone and chert with recurring phosphatic hardgrounds. The lower part of the Thorntonia Limestone represents a shallowing upward sequence. Oncolitic grainstones and stromatolitic algal boundstones indicate a shallow palaeoenvironment. Karst surfaces are recognized on top of the sequence. The Thorntonia Limestone contains a diverse fauna of mainly molluscs, trilobites, inarticulate brachiopods and sponge spicules. Age: Ordian.

Beetle Creek Formation

This formation comprises siliceous claystone, siltstone to sandstone, chert, thin-bedded limestone and phosphorite. This typically clastic formation is best developed in the Ardmore and Burke River outliers, where it is rich in fossils, mainly trilobites and molluscs, but also has produced a diverse assemblage of *Chancelloria* sclerites and sponge spicules. Age: Templetonian.

Inca Formation

This is a finely laminated siliceous shale with siltstone and chert layers and lenses of dark bituminous, dolomitic limestone. It is best developed in the Burke River Outlier. Fossil content is mainly planktic agnostid trilobites, sponge spicules and inarticulate brachiopods. The absence of benthic trilobite genera led Öpik (1970) to the conclusion that the sea floor was generally axoxic. Age: Upper Templetonian to Lower Undillan.

Gowers Formation

The formation consists of thin bedded mudstone to wackestone, commonly bituminous, with chert nodules and phosphate grains interrupted by series of hardgrounds with phosphatic cemented lag deposits. This unit, which crops out to the south and west of Thorntonia Station, represents a shallowing-upward sequence with emergent conditions at its top. Age: Upper Floran to Lower Undillan.

Devoncourt Limestone

This is a laminated and concretionary limestone, including black dolostones, probably deposited in deeper water (outer ramp environments). This unit is developed only in the Burke River Structural Belt and represents a highstand. Age: Upper Floran to Boomerangian, mainly Undillan.

MATERIALS AND METHODS

All the microfossils described here were examined by SEM. All specimens are housed at Australian Geological Survey Organisation, GPO Box 378, Canberra, Australia, where further litho-stratigraphical data are available.

SYSTEMATIC PALAEONTOLOGY

Phylum PORIFERA Grant, 1836

Class HEXACTINELLIDA Schmidt, 1870

Genus THORACOSPONGIA Mehl, 1996

Type species. *Thoracospongia follispiculata* Mehl, 1996.

TEXT-FIG. 1. Schematic development of stratigraphical sequences, transgressive systems 1 and 2, in the north-eastern part of the Georgina Basin (after Southgate and Shergold 1991).

Diagnosis. Pinules, most probably dermal spicules, with their pinular rays extremely inflated, associated with other strongly inflated triaxons called pulvinusactins.

Thoracospongia follispiculata Mehl, 1996

Plate 1, figures 2–4, 6–16; Text-figure 2

Material. Fourteen specimens: CPC 33671 (holotype), 33668 (a, b), 33670, 33673–33674, 34201–34203, 34205–34209.

Description. This species is known only from isolated follipinules, which are pinules, 200–700 μm in diameter, with heavily inflated distal rays, covered by longitudinal ridges, and with outer rays being largely atrophied (Pl. 1, figs 8–13). Follipinules are normally associated with pulvinusactins, which are similarly swollen, normally four-rayed spicules, and it is assumed that the two types of spicule may have belonged originally to the same sponge. In a hypothetical reconstruction, Mehl (1996a) showed the possible spiculation of an armoured dermal layer consisting of heavily inflated follipinules and pulvinusactins.

The name *Pulvinusactin* is given to heavily inflated triaxons, mainly stauractins, 200–400 μm in diameter, with a pillow-like appearance (*pulvinus*, Lat. = pillow) (Mehl 1996a). This very common spicule type is basically triaxial, but rays are commonly atrophied to form pentactins (Pl. 1, fig. 3), mostly stauractins (Pl. 1, figs 2, 6, 14–15), tauactins (Pl. 1, figs 4, 7), or diactins (Pl. 1, fig. 16). Pulvinusactins are fairly abundant within the Georgina assemblage, and, like follipinules, may be interpreted functionally as spicules of a dermal cortex.

Remarks. Follipinule is the name for a special type of heavily inflated pinule (*follis*, Lat. = balloon) found commonly within the Georgina assemblage. Swelling of the distal ray sometimes extends to such a degree that the axial cross is completely buried and the paratangential rays are hardly visible, showing only as small spines protruding from the ball-shaped distal ray (Pl. 1, fig. 11). Thus, the proximal/paratangential rays might eventually be entirely buried, and the spicules would simply appear like spherical balls, which, especially in thin section, could easily be confused with demospongid sterrasters or radiolarians.

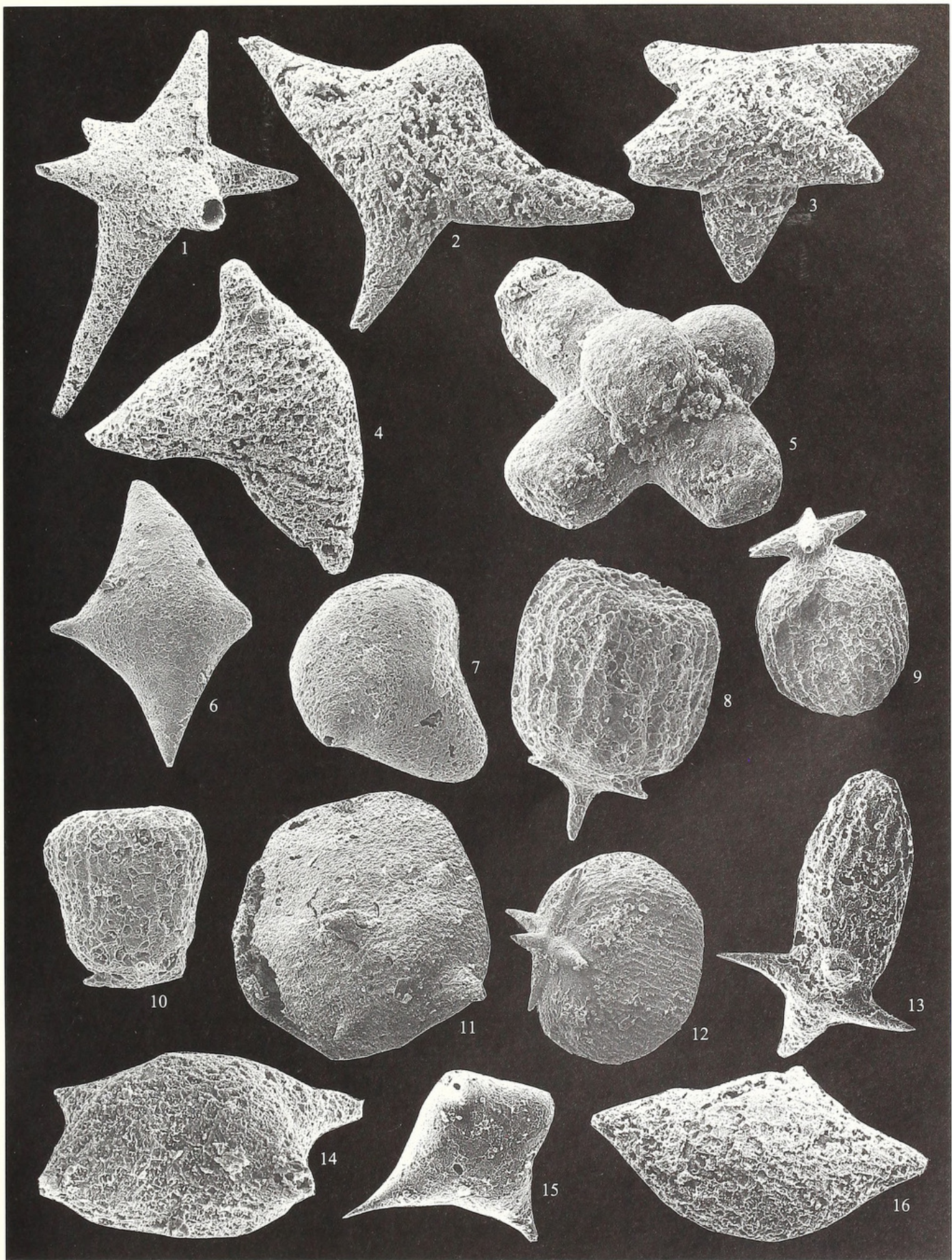
Archaeooides was introduced by Qian (1977) for smooth globular objects of uncertain phylogenetic association (for synonymy see Qian and Bengtson 1989). Within this assemblage, smooth spherical objects, c. 200–300 μm in diameter, are found associated with pinules. One must consider whether these spherical balls are poriferan spicules, either demospongid asters or hexactinellid follipinules. As described above, inflation of the pinulate rays beyond the axial crosses may eventually result in ball-shaped structures, which could easily be confused with asters. Smooth surfaces are sometimes found in follipinules, perhaps due to pre-depositional transport. The taxon *Archaeooides* is likely to cover various kinds of globular objects, such as radiolarians and sponge spicules.

Genus NABAVIELLA Mostler and Mosleh-Yazdi, 1976

Type species. *Nabaviella gracilis* Mostler and Mosleh-Yazdi, 1976.

EXPLANATION OF PLATE 1

Figs 1, 5. Regular hexactins. 1, CPC34200; Undillan; inflated hexactin with pointed rays; $\times 80$. 5, CPC34204; Templetonian; inflated stronglyl-hexactin; $\times 245$.
Figs 2–4, 6–13. *Thoracospongia follispiculata* Mehl, 1996. 2–4, Upper Floran–Lower Undillan. 2, CPC34201; pulvinusactin; $\times 205$. 3, CPC34202; inflated pentactin; $\times 160$. 4, CPC34203; inflated tauactin; $\times 150$. 6–7, pulvinusactins; ?Templetonian. 6 CPC33668a; $\times 90$. 7, CPC33668b; $\times 120$. 8–13, follipinules. 8–10, ?Templetonian. 8, CPC33671, holotype; $\times 155$. 9, CPC33674; $\times 120$. 10, CPC34205; $\times 125$. 11, CPC33673; Undillan; $\times 125$. 12–13, Templetonian. 12, CPC34206; $\times 145$. 13, CPC34207; $\times 95$. 14–15, pulvinusactins. 14, CPC33670; Upper Floran–Lower Undillan; $\times 200$. 15, CPC34208; Templetonian; $\times 90$. 16, CPC34209; Upper Floran–Lower Undillan; inflated diactin; $\times 180$.



MEHL, regular hexactins, *Thoracospongia*

Diagnosis. Clavulate monaxons with umbels of at least five spines. Sometimes the spicules show distal swellings.

Nabaviella? sp.

Plate 2, figures 3–4, 8–9, 11, 14

Material. CPC 33667, 34234, 34236, 34239.

Description. In this assemblage, the clavulate spicules are from *c.* 500 μm to a few mm in length. Their umbels are mostly with few (two to four) spines (Pl. 2, figs 3–4). However, those clavulate spicules with five or six spines (Pl. 2, figs 8–9, 11, 14) may be considered as true paraclavules and correspond to the species *Nabaviella umbelliformis* Dong and Knoll, 1996. One was found to have a small distal swelling (Pl. 2, fig. 9) similar to *Nabaviella gracilis* Mostler and Mosleh-Yazdi, 1976, and may be considered as a tylodisc (Mehl 1992). The latter were probably marginal spicules without anchoring function.

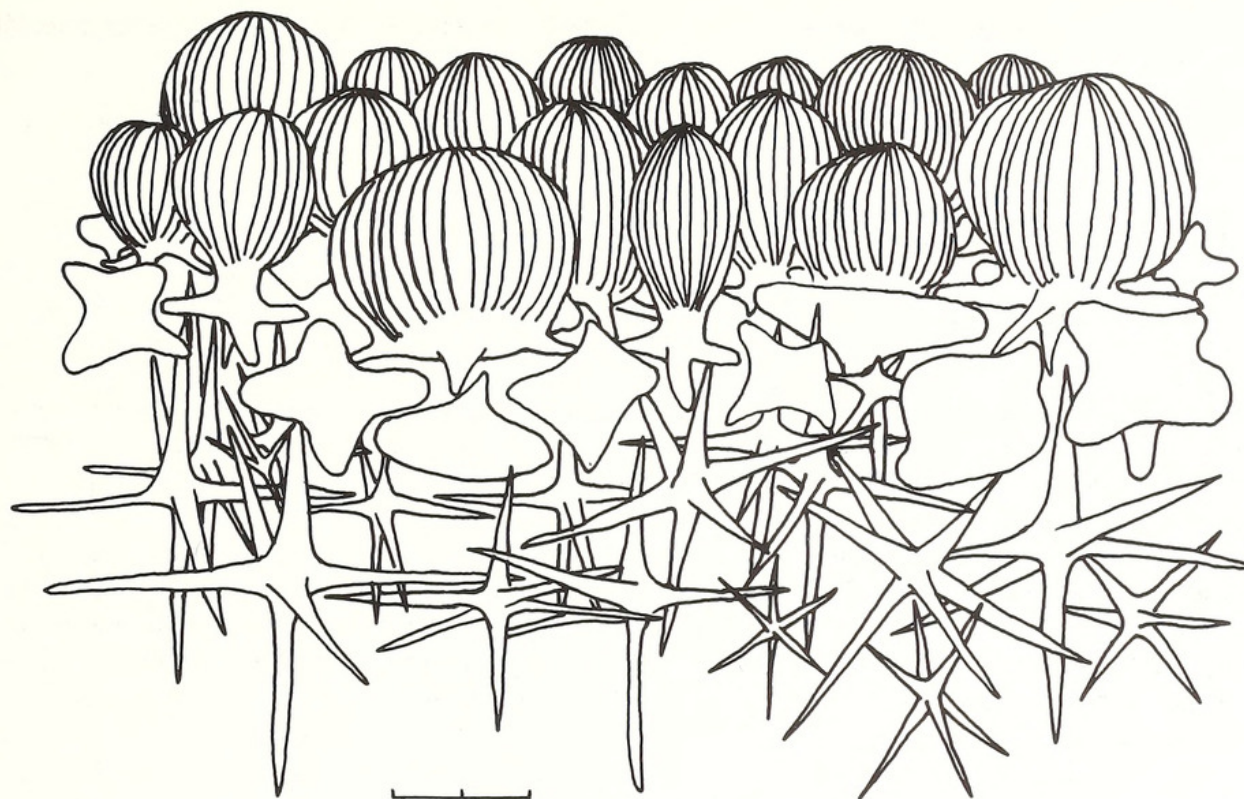
Remarks. Paraclavules or tylodiscs may also in some cases be root-tuft anchoring spicules. Morphologically they are monactins with one clavulate end, known as an ‘umbel’, with four to six spines. Dong and Knoll (1996) classified *Nabaviella* as genus *incertae sedis*, but these spicules are definitely from hexactinellids, which are the only sponges known to possess clavules. Clavulate spicule types are difficult to distinguish when their locations within the sponge body are not known. In recent hexactinellids, clavules are normally marginal spicules associated with dermal or gastral membranes. Anchoring spicules are parts of root tufts in lyssacine hexactinellid sponges, protruding from the basal regions of the sponge body. In some cases, they are extremely large spicules (in some Recent amphidiscophoran hexactinellids, e.g. *Monorhaphis* and *Hyalonema*, they can be more than 1 m long). Functions of common clavulate spicules in Early Palaeozoic sponges remain unknown, because they are rarely found *in situ*. Paraclavules were documented in a dermal position in Devonian dictyosponges (Hall and Clarke 1899). However, such spicules are normally only found isolated in Palaeozoic sediments. Some authors (e.g. Finks 1970) have assumed closer phylogenetic relationships or even homology between paraclavules, clavules, and amphidiscs.

Although similar in appearance, amphidiscs and clavules are two basically different types of spicules, as proven by the different locations of the rudimentary crosses of their central axial canals. In sceptrules (scopules and clavules) the axial cross is located within the inflated terminal end. These spicules, thus, can be considered to be true monactins. Amphidiscs have been documented to possess an axial cross in the middle of the shaft between the two terminal umbels; they are diactine spicules (Mehl 1992). Amphidiscs and clavules, thus, have different evolutionary histories, as documented by their phylogenetic relationships. Amphidiscs are a constituent character of the Amphidiscophora. True amphidiscs appear in the upper Silurian (Mostler 1986a). ‘Hemidiscs’ with one umbellate and one tylote end documented by Mostler and Mosleh-Yazdi (1986) from the Upper Cambrian, called tylodiscs by Mehl (1992), most probably evolved independently of amphidiscs and their reduced equivalents, hemidiscs. Clavules in the sense of sceptrules (Mehl 1992) are a constituent character of the Clavularia, Hexasterophora. The fossil record of scopules which are definitely sceptrules begins in the lower Ordovician (Kozur *et al.* 1997a). The nature of most Early Palaeozoic monactins with umbels normally called clavules (e.g. Bengtson 1968) is uncertain though, and an assemblage of spicules from various hexactinellid taxa may have been included in this term. In order to avoid confusion with the definite sceptrules of Mesozoic and Recent hexactinellids, the name paraclavule seems appropriate for Palaeozoic forms.

Subphylum HEXASTEROPHORA Schulze, 1887

Genus FLOSCULUS Dong and Knoll, 1996

Type species. *Flosculus gracilis* Dong and Knoll, 1996.



TEXT-FIG. 2. Hypothetical reconstruction of *Thoracospongia follispiculata*; for explanation see text. Scale bar represents 200 μm .

Diagnosis. Hexactine spicules with stout primary rays, some of which are split into numerous secondary rays.

Kometia gracilis (Dong and Knoll, 1996)

Plate 2, figures 1–2, 5

Material. Three specimens: CPC 33675, 34228, 34231.

Description. This name given for triaxons 400–800 μm in diameter with short, pointed, principal rays of which one or two split into 30–50 delicate secondary rays, 350–500 μm long. They are often gently curved and slightly barbed at their distal ends. When broken, it can be seen that the secondary rays are hollow, so each of them originally contained an extension of the axial filament.

Remarks. The genus *Flosculus* was erected by Dong and Knoll (1996) for Late Cambrian spicules from China and attributed to the Hexactinellida *incertae sedis*. However, hexactins in which all six rays are split into several secondary rays are called hexasters. This spicule type is a constituent character of the hexactinellid taxon, Hexasterophora, the sister group of the Amphidiscophora. In the most simple type, the oxyhexaster, the earliest record of which is from the lower Ordovician (Mostler 1986a), each of the six rays has simply two secondary, pointed rays. The more advanced discohexaster, known from the Mesozoic to the Recent, is characterized by small swellings or discs at the end of each terminal ray. The Middle Cambrian hexaster-like spicules described here have only one or two of the six hexactine rays split into numerous secondary rays. It is thus not entirely certain that these spicules are true hexasters. If this can be proven, e.g. by other Cambrian transitional forms, it will extend the palaeontological record of the Hexasterophora from lower Ordovician to the Middle Cambrian. A similar spicule fragment, maybe the same ?hexaster-type, was documented from Late Cambrian sediments of Argentina (Heredia *et al.* 1987).

A very interesting hexactinellid spicule assemblage from the upper Ordovician of New South Wales has been documented by Webby and Trotter (1993). Spicules similar to those described here

from the Georgina Basin were figured and described, and *Kometia cruciformis* Webby and Trotter, 1993 was erected. Those hexasters possess six principal rays, one of which is split into a large number of barbed secondary rays. Their overall shape and size-range is almost identical to those of the Georgina specimens, and for this group of hexasters the name *kometiaster* may be given. However, the Ordovician hexasters, though most probably belonging to the same group as the Cambrian ones, differ in some respects: there are fewer secondary rays (only *c.* 15–25), and their terminal ends are more distinctly barbed and somewhat inflated. Kometiasters are the oldest ?hexaster spicules known. Thus, it is very probably that the major hexactinellid group, Hexasterophora, can be traced back to the Middle Cambrian.

OTHER HEXACTINELLID SPICULES

Regular hexactins

Plate 1, figures 1, 5

Material. Two specimens: CPC 34200, 34204

Description. Hexactins are regular triaxons with six rays at right angles (Pl. 1, fig. 1). They represent the original spicule symmetry of the Hexactinellida (Mehl 1991), but those hexactinellid spicules derived from hexactins, such as pinules, hexasters, pentactins, stauractins, tauactins and diactins, are by far the most common spicule types in this assemblage. Their sizes are highly variable, from about 100 μm to several mm in diameter. Some inflated hexactins are characterized by long rays that terminate in a point (Pl. 1, fig. 1). Similar 'blown-up' hexactins with inflated rays have been documented from the Late Cambrian La Cruz Formation of Argentina (Heredia *et al.* 1987). Others show inflated rays with rounded ends of approximately equal length (Pl. 1, fig. 5). Transitions to other triaxone spicules with less than six rays are indicated by various degrees of reduction of one or several rays.

Regular pinules and their monactine and diactine derivatives

Plate 2, figures 7, 10; Plate 3, figure 18

Material. Three specimens: CPC 34227, 34233, 34235.

Description. These are triaxons, variable in size from *c.* 0.5–1 mm, and with spined, distal rays. The spines are commonly in an alternating arrangement, which gives a pine-tree like appearance (Pl. 3, fig. 18). Observations of Recent Hexactinellida indicate that the pinules are peripheral (dermal or gastral) spicules whose spined, distal ray often protrudes beyond the outer membrane of the sponge wall. Their proximal rays are often reduced, so these spicules are pinular pentactins. In long, slender pinules (Pl. 2, fig. 10) paratangential rays may be reduced, resulting in a variously spiny diactins (called uncinates) or monactins (Pl. 2, fig. 7).

Remarks. In modern Hexactinellida, pinular spicules are of widespread occurrence within many taxa of both Amphidiscophora and Hexasterophora. Consequently, such spicules must be

EXPLANATION OF PLATE 2

Figs 1–2, 5. *Kometia gracilis* (Dong and Knoll, 1996); ?Upper Templetonian; ?hexasters. 1, CPC33675; $\times 105$. 2, CPC34228; $\times 130$. 5, CPC34231; $\times 83$.

Figs 3–4, 8–9, 11, 14. *Nabaviella?* sp. 3–4, 11, 14, clavules. 3–4, ?Upper Templetonian; possible anchoring spicules. 3, CPC34229; $\times 70$. 4, CPC34230; $\times 75$. 11, CPC34236; Templetonian; $\times 50$. 14, CPC34239; Upper Floran–Lower Undillan; $\times 58$. 8, CPC34234; ?Upper Templetonian; paraclavule; $\times 78$. 9, CPC33667; ?Upper Templetonian; tylodisc; $\times 180$.

Fig. 7. Monactin, 'uncinate' with atrophied proximal rays; CPC34233; ?Upper Templetonian; $\times 100$.

Fig. 10. Pinular hexactin, with prolonged distal ray; CPC34235; ?Upper Templetonian; $\times 170$.

Figs 12–13. Tauactins. 12, CPC34237; Templetonian; $\times 115$. 13, CPC34238; ?Upper Templetonian; $\times 60$.



MEHL, Cambrian spicules

considered to be either a primitive type of spicule or one that developed several times convergently within the Hexactinellida; both may be true. Various different shapes of pinules exist: most common is the classical, tree-like pinule with a densely spined distal ray (Pl. 3, fig. 18).

Many fossil and some recent hexactinellids, e.g. *Heterochone calyx* (Schulze, 1887), possess pinules with inflated distal rays. However, extremely inflated spicules, such as in the follipinules of *Thoracospongia*, seem to be a feature particular to Palaeozoic sponges. The Permian *Stioderma* (Finks 1960) was armoured by a dense surface layer of hexactins with swollen, ball-shaped distal and paratangential rays. Rigby (1975) figured pentactine pinules from the Cambrian of Texas and reconstructed these spicules with swollen rays as dermalia. Mostler and Mosleh-Yazdi (1976) described similar spicules from the Upper Cambrian of Iran and, based on them, erected the new genus and species *Rigbyella ruttneri*. The inflated hexactins documented by these authors are characterized by one main ray with a terminally split end. They do not show elongate ridges on their outer surfaces, such as are common in the Georgina Basin specimens.

Platy, spider-like pentactins

Plate 3, figures 6, 9–11

Material. Eight specimens: CPC 34215–34221, 34226.

Description. These abundant spicules are fairly large, up to 1 mm in diameter, bilaterally symmetrical with five unequal rays at oblique angles, which all lie more-or-less in one somewhat concave-convex level. One ray is short, flattened and plate-like; some show a fine tuberculation (Pl. 3, figs 6, 9–11). The remaining rays protrude symmetrically on each side of the inflated one. They are positioned at angles of *c.* 70–75° to neighbouring rays. Angles between rays on either side of the symmetry plane range between *c.* 90° and almost 170°.

Remarks. In spite of their irregular appearance, these spicules resemble some pentactins, whose rays have been modified into angles different from 90°, as is often the case, especially in Cambrian spicules. In this case the symmetrical rays are interpreted as paratangentialia, and the short inflated ray would then be the fifth, normally vertical, one, which has been strongly modified in shape and is totally bent out of a right angle. The common ornamentation of the inflated ray of these spicules indicates that they may be phylogenetically derived from pinulate pentactins, in which the distal ray is often inflated and shorter than the paratangential ones. Morphologically transitional forms between almost regular pentactins and 'spiderpentactins' have been observed. Similar pentactins have been documented from the Upper Cambrian by Heredia *et al.* (1987, fig. 6) and by Bengtson (1986, fig. 9).

EXPLANATION OF PLATE 3

Figs 1–5. Stauractins. 1, CPC34210; ?Upper Templetonian; aberrant stauractin with all four rays turned in one direction; $\times 50$. 2, CPC34211; Undillan; platy stauractin; $\times 85$. 3–5, Upper Floran–Lower Undillan; platy stauractins. 3, CPC34212; $\times 40$. 4, CPC34213; $\times 83$. 5, CPC34214; $\times 32$.
Figs 6–12, 17–18. Pentactins. 6, 9–11, platy, spider-like pentactins. 6, 9–10, Upper Floran–Lower Undillan. 6, CPC34215; $\times 125$. 9, CPC34218; $\times 58$. 10, CPC34219; $\times 75$. 11, CPC34220; ?Upper Templetonian; $\times 110$. 7, CPC34216; Templetonian; almost regular pentactin; $\times 88$. 8, CPC34217; Upper Floran–Lower Undillan; $\times 125$. 12, 17, ?Upper Templetonian. 12, CPC34221; small, two-dimensional pentactin; $\times 165$. 17, CPC34226; two-dimensional pentactin; $\times 145$. 18, CPC34227; Templetonian; pentactine pinule; $\times 113$.
Figs 13–16. Polyactins, possibly triaenes with reduced rhabds. 13–14, 16, ?Upper Templetonian. 13, CPC34222; $\times 165$. 14, CPC34223; $\times 140$. 16, CPC34225; $\times 145$. 15, CPC34224; Upper Floran–Lower Undillan; $\times 140$.



MEHL, stauractins, pentactins, polyactins

Stauractins

Plate 3, figures 1–5

Material. Five specimens: CPC 34210–34214.

Description. These are four-rayed spicules, present in great quantities within the Georgina Basin assemblage. The four rays are normally in a regular arrangement at right angles, but sometimes they seem to be 'compressed' with their rays at different angles (Pl. 3, fig. 1). Because all spicules are well-preserved, such 'deformation' is not likely to be due to post-depositional processes. Stauractins mostly range between 0.5–1 mm, but they are highly variable in both shape and size.

Platy stauractins. These represent a new spicule type. They are platy and flattened in their central area and, thus, appears almost shield-like (Pl. 3, figs 2–5). These platy stauractins are very common within the Georgina Basin assemblage, but have not been reported from elsewhere. Interpretation of these peculiar stauractins with regard to their position within the sponge body thus poses a problem, although they are most likely to be dermal.

Tauactins

Plate 2, figures 12–13

Material. Two specimens: CPC 34237–34238.

Description. T-shaped triactine spicules with only three rays at right angles occur (Pl. 2, figs 12–13) but are not very common within this assemblage. Similar tauactins were documented only from the Upper Cambrian of Queensland by Bengtson (1986, fig. 9L). Tauactins are of widespread occurrence in Recent lyssacine Hexactinellida, where they are normally mesenchymal rather than peripheral spicules, but their fossil record is poor, especially from the Lower Palaeozoic.

EARLY PALAEOZOIC RADIATION OF THE HEXACTINELLIDA

The oldest known well preserved body fossils of sponges are the earliest Cambrian hexactinellids from Hunan Province, China (Steiner *et al.* 1993). The sponges described by Chen *et al.* (1990) from the Lower Cambrian of Chenjiang, Yunnan Province as *Quadrolaminiella* were classified as demosponges, but should be attributed to the Hexactinellida, family Dictyospongidae Hall, 1884 (see also Hall and Clarke 1898). Because of the comparably high diversity of these Early Cambrian Hexactinellida and because of the occurrence of isolated spicules in the Late Proterozoic Shibatan Member in Hubei Province, Steiner *et al.* (1993) predicted the occurrence of hexactinellid sponges in the Upper Precambrian. The documentation of the sponge genus *Palaeophragmodictya* attributed to the Hexactinellida, family Dictyospongidae, from the Ediacara fauna, South Australia (Gehling and Rigby 1996), is a confirmation of this hypothesis, provided that the genus belongs in the Hexactinellida. However, according to my observations of type specimens, spicules cannot be identified with certainty in the Ediacara material. The reticulate pattern characterizing these fossils may be impressions of soft tissue only, e.g. collagen (which is probably the preservation state of all the Ediacara fossils). In fact, *Palaeophragmodictya* might well represent the first documentation so far of the hypothetical, aspicular, primitive sponges postulated by Reitner and Mehl (1996).

Triaxone hexactinellid spicules have been documented from the Upper Proterozoic of the Yangtze Platform, South China (Steiner *et al.* 1993). The monophylum Hexactinellida comprises the sister groups Amphidiscophora and Hexasterophora which can be traced back to the Lower Palaeozoic (Mehl 1996a). The oldest oxyhexasters, from the upper Ordovician, and amphidiscs, from the upper Silurian, were reported by Mostler (1986a), Mostler and Mosleh-Yazdi (1976) documented monaxone spicules with one clavulate and one swollen, barbed end, from the Upper Cambrian and based on these *Nabaviella elegans* was erected. These spicules, first classified by the authors as cancelloriides, then re-interpreted by Mostler (1986) as hemidiscs, are very large (c. 0.6–3.2 mm). They have only slight similarity to true hemidiscs, the oldest of which are known from

the Upper Carboniferous (Kling and Reif 1969) and most probably are reduced amphidiscs. Thus, it is uncertain whether the Amphidiscophora and Hexasterophora originated in the Cambrian. However, diverse assemblages of hexactinellid spicules, especially kometiasters, found in the Middle Cambrian of the Georgina Basin argue for a major radiation within the Hexactinellida that probably took place in the Early Cambrian.

Heavy silicification is a very common characteristic of Early Palaeozoic hexactinellid spicules; protection against predators or water turbulence may have been the reason for this defensive armouring. Similarly, massive surface spiculation of Cambrian hexactinellids might be interpreted as a defensive strategy against predators, such as *Aysheaia* that supposedly fed on sponges (Whittington 1978). Another possibility for such spiculation is the development of a dermal cortex for stabilization under conditions of variably high water-energy. A similar strategy is followed by the demosponges, e.g. the Geodidae, known from the Lower Cambrian to Recent (Reitner and Mehl 1995), with their massive cortex layers consisting of sterrasters. *Stioderma*, with its massive dermal pinular spicules, is the only similar hexactinellid sponge found among representatives of the Demospongiae and Calcarea in the shallow-water Pennsylvanian shelf facies in Texas (Finks 1960). Documentation of the Hexasterophora from the Lower Palaeozoic has been questioned by Wiedenmayer (1994), who claimed that some of the upper Ordovician to Permian hexasters described by Mostler (1986a) were pseudohexasters, in reality mesotrienes, attributable to the Demospongiae. The main argument for this re-interpretation is that some of Mostler's hexasters show secondary rays, each with an extension of the axial canal, but in hexactinellid spicules, according to Wiedenmayer (1994), axial canals should not continue into any of the distal rays. However, this 'rule' has been negated, because Liassic hexasters with axial canals continuing through the secondary rays have been documented (Mostler 1989, pls 1–2). Isolated amphidiscs are known from the upper Silurian, and entirely preserved amphidiscophoran sponges with amphidiscs and hemidiscs *in situ* were found in Late Carboniferous phosphorites from Uruguay by Kling and Reif (1969). In view of this strong evidence, there is little doubt that the Hexactinellida constitute an ancient and conservative group, whose major taxa reach back far into the Lower Palaeozoic.

Subphylum PINACOPHORA Mehl and Reitner, *in* Reitner, 1992

Diagnosis. This taxon was erected for the adelphotaxon of the Hexactinellida and comprises the sister groups Demospongiae and Calcarea. The main constituent character of the Pinacophora is the constant presence of pinacocytes in adult sponges. These are specialized flattened cells, differentiated into endo- and exopinacocytes, which are restricted to the inner and outer surfaces, respectively. Parts of the pinacocytes are specialized into porocytes, which line the pores to channels and in many cases make these pores contractile. Representatives of the Demospongiae and Calcarea in the fossil record are identified mainly by the mineralogy and symmetry of their spicules.

Class DEMOSPONGIAE Sollas, 1875

Diagnosis. This group is characterized by siliceous spicules, basically tetractins and monactins.

Tetractins

Plate 4, figures 1, 4–11

Material. Nine specimens: CPC 34240, 34243–34250.

Description. Basically regular orthotriaenes have three rays of equal length and distances of about 120° and a fourth longer ray, called the rhabd, at right angles to the other three. Regular orthotriaenes with long rhabds, although not common, are found (Pl. 4, figs 5, 11). Dichotriaenes with atrophied rhabds also occur (Pl. 4, fig. 6), as well as irregular triactins with variable angles between the rays and often with the rhabds partly or completely reduced (Pl. 4, figs 1, 4, 7–10).

Remarks. The tetractin represents the regular four-rayed calthrops symmetry, which is considered a plesiomorphic spicule within the Demospongiae (Mehl and Reitner 1991). Both orthotriaenes and calthropses have been found earlier in core samples from the Middle Cambrian of the Georgina Basin (van Kempen 1990). Since the presence of tetractins is an ancient, plesiomorphic character of the Demospongiae, in itself it does not contribute to the phylogenetic reconstruction of relationships within the Demospongiae. As stated by van Soest (1987, 1991), 'Tetractinomorpha' *sensu* Levi (1953) is not a monophyletic group. For this reason, Reitner (1992) introduced the taxon Aster-Tetractinellida for all tetractin-bearing demosponges with aster microscleres. Aster-Tetractinellida corresponds largely to *Astrophora* Sollas, 1888.

Demospongid diactins

Plate 4, figure 3

Material. CPC 34242.

Description. These are mainly oxeas and strongyles. In the Georgina Basin assemblage they are locally slightly acanthose (Pl. 4, fig. 3), they are of various sizes, mostly between 400 μm and 800 μm . Their phylogenetic attribution is uncertain, because various diactins are widespread within the Demospongiae.

Order SIGMATOPHORA Sollas, 1888

Diagnosis. Demospongiae with sigmata as microscleres.

Sigmata

Plate 4, figure 2

Material. CPC 34241.

Description. Only a single sigmatose spicule has been found (Pl. 4, fig. 2). This spicule is basically a diactin with both ends curved to point toward each other. It is a typical C-shaped sigma, except for its very large size (320 μm).

Remarks. Compared with most recent sigmata (*c.* 10–50 μm), this Middle Cambrian spicule is very large, which suggests that the sigma-microscleres might have evolved from Protosigma megascleres that were originally curved/bent oxeas.

Morphogroup DESMA-BEARING DEMOSPONGIAE = 'LITHISTIDA' Schmidt, 1870

Family ANTHASPIDELLIDAE Miller, 1889

Diagnosis. Demosponges with dendroclones arranged in ladder-like trabs, often with coring monaxons in the fusions between trabs.

EXPLANATION OF PLATE 4

Figs 1, 4–11. Tetractins: triaenes and probable triaene-derived polyactins. 1, CPC34240; Upper Floran–Lower Undillan; polyactin; $\times 80$. 4, CPC34243; Upper Floran–Lower Undillan?; triaene? with reduced rhabd; $\times 70$. 5, CPC34244; Templetonian; orthotriaene with curved rays; $\times 61$. 6, CPC34245; Templetonian; trichotriaene; $\times 95$.

Fig. 2. Oxea: sigmatose spicule; CPC34241; ?Upper Templetonian; proto-sigma?; $\times 200$.

Fig. 3. Acanthose oxea: demospongid diactin; CPC34242; Upper Floran–Lower Undillan; $\times 125$.

Figs 12–15. *Rankenella mors* (Gatehouse, 1968); ?Upper Templetonian. 12, CPC34251; $\times 135$. 13, CPC34252; $\times 125$. 14, CPC34253; $\times 140$. 15, CPC34254; two dendroclones still fused; $\times 83$.



MEHL, tetractins, oxeas, *Rankenella*

Genus RANKENELLA Kruse, 1983

Type species. Arborella mors Gatehouse, 1968.

Rankenella mors (Gatehouse, 1968)

Plate 4, figures 12–15

Material. Four specimens: CPC 34251–34254.

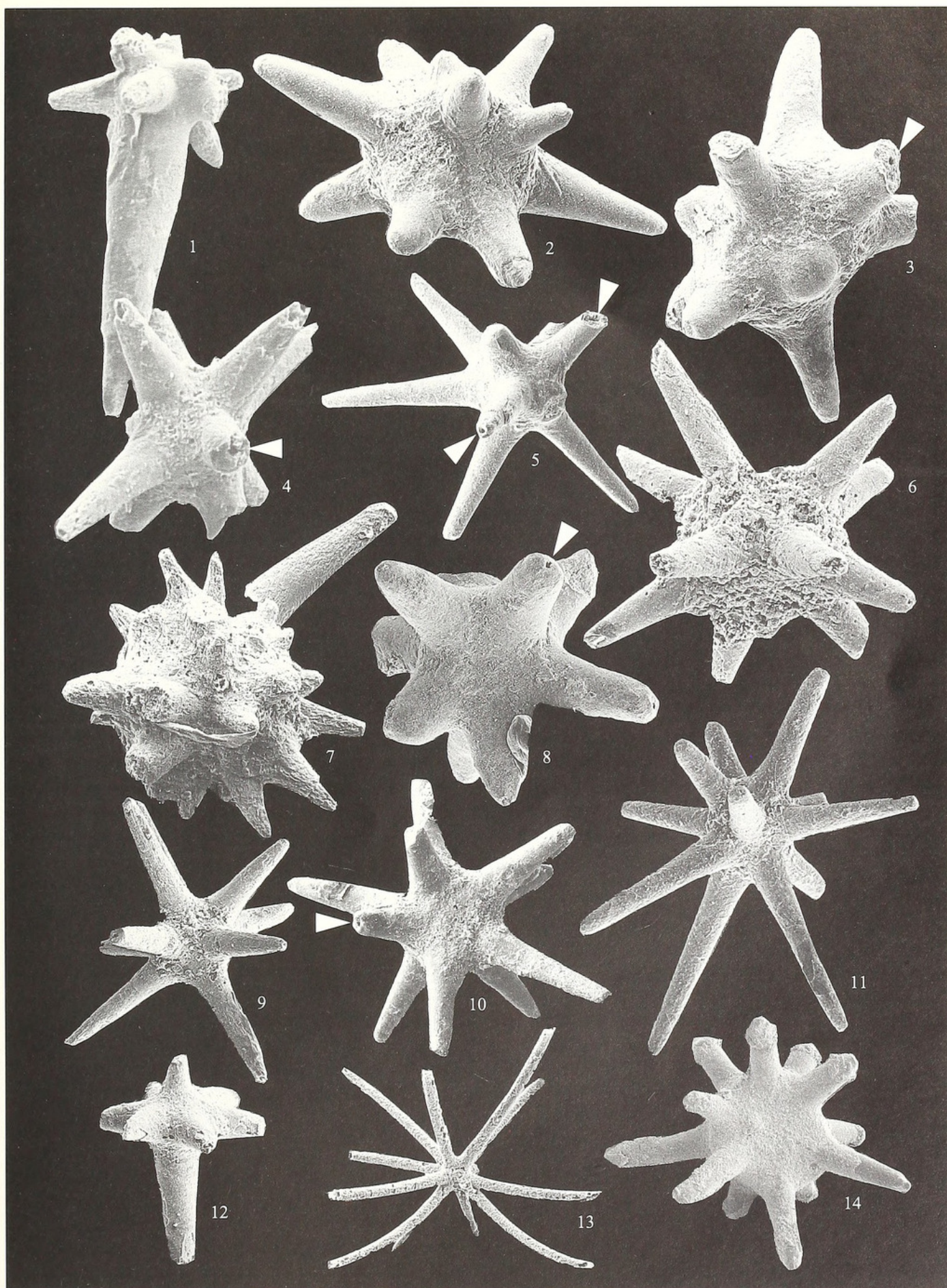
Description. Tubular, often branching sponges with deep oscula; encrusting forms also occur, normally with a distinctive dermal layer and many round oscula. The skeletal architecture is anthaspidellid (van Kempen 1978, 1983). Dendroclones in ladder-like series forming radial trabs between inner and outer surface. No coring monaxons have been observed within the fusions between dendroclones. Irregular spicules known as desmas are not common within the Georgina Basin assemblages. In the Georgina Basin, *Rankenella mors* is known from isolated dendroclones as well as silicified, entirely preserved sponge fossils. The regular dendroclones, 200–400 μm long, show relatively long articulated cladomes and brachyomes at opposite ends of the smooth shafts. Two or three spicules are occasionally found still fused together by their articulated, root-like ends (Pl. 4, fig. 15).

Remarks. This type of isolated spicule from the Georgina Basin was originally described as *Arborella mors* Gatehouse, 1968. Later, entire sponge fossils were found by Kruse (1983) in Australia in the Mid Cambrian Ranken Limestone. These sponges were determined as representatives of the Anthaspidellidae with the typical spiculation of regular ladder-like trabs of dendroclones. The simple dendroclones of these sponges were recognized as identical with those documented by Gatehouse as *A. mors* on the basis of isolated spicules, and this species was assigned to a new genus *Rankenella* by Kruse (1983). Kruse (1996, fig. 3c) figured an encrusting specimen with a silicious covering sheet and round elevated oscula. According to my observations of this specimen, it seems definite that the covering sheet, which can be observed on other specimens as well, is not the result of secondary silicification only, but is a true dermal layer.

The anthaspidellid *Rankenella* is the earliest desma-bearing sponge so far described. Because the taxon 'Lithistida' is definitely not monophyletic (Gruber 1993), and no definite microscleres are known from *Rankenella* (or the Anthaspidellidae), it cannot be decided definitely whether this group belongs to the Astrophora or to the Sigmatophora. However, regular vertical and horizontal tracts of oxeas ('isodictyal architecture'), like those characteristic of the Anthaspidellidae, are known from some non-desma-bearing representatives of the Haplosclerida, Sigmatophora (Reitner and Kohring 1990). This skeletal architecture, which is probably symplesiomorphic within Haplosclerida, gives rise to the hypothesis that the Anthaspidellida may be a stem lineage representative of the Sigmatophora.

EXPLANATION OF PLATE 5

Figs 1–14. Polyactins, most of which show central canals (arrows), probably demospongiaen mesotriaenes and protoasters; Templetonian. 1–2, mesotriaenes. 1, CPC34255; $\times 168$. 2, CPC34256; $\times 175$. 3–11, protooxyasters. 3, CPC34257; $\times 165$. 4, CPC34258; $\times 168$. 5, CPC34359; $\times 125$. 6, CPC34260; $\times 170$. 7, CPC34261; $\times 160$. 8, CPC34262; $\times 240$. 9, CPC34263; $\times 110$. 10, CPC34264; $\times 125$. 11, CPC34265; $\times 120$. 12, CPC34266; octactine?; $\times 125$. 13, CPC34267; Upper Templetonian; problematical polyactin-radiolarian spicule; $\times 80$. 14, CPC34268; polyactin, similar to large strongylacanthaster; $\times 98$.



MEHL, polyactins

Order ASTROPHORA Sollas, 1888

Diagnosis. Demospongiae with aster.

Oxyasters

Plate 5, figures 1–11, 14

Material. Eleven specimens: CPC 34256–34265, 34268.

Description. These are fairly large (250–600 μm) spherical spicules with ten to 20 rays that radiate from the inflated centre (Pl. 5, figs 1–11, 14). Normally, these rays are of approximately equal length (c. 75–250 μm), but in some specimen a few rays are reduced, and in others one or two rays reach almost double length (Pl. 5, figs 1–5, 7, 12). Basal ray diameter is 40–50 μm , but one specimen (Pl. 5, fig. 13) has considerably thinner rays, and it is questionable whether it is a sponge spicule at all. Generally, these polyactins show radial symmetry. Some of them, however, show a somewhat bilateral-symmetrical shape (Pl. 5, figs 9, 12). When broken, most of the spicule rays show central canals (Pl. 5, arrows).

Remarks. Most of the polyactine spicules from the Georgina assemblage possess ten to 12 radial rays and thus show morphological similarity with those of some later Palaeozoic Heteractinellida, e.g. the Mississippian *Asteractinella*. Some of the polyactins show a bilateral-symmetrical arrangement of eight rays, six of which radiate in one level, with the remaining two pointing away at right angles (CPC 34266; Pl. 5, fig. 12). This pattern corresponds to the diagnosis of the Octactinellida, as given by Hinde (1887–1912). Octactinellida is a sub-taxon of Heteractinellida (e.g. Rigby 1983), and some of the spicules with bilateral symmetry that do not show axial canals might be heteractine polyactins. However, in most of the polyactins, the axial canals continue into the rays; these are not massive, like spicules of the Calcarea, but are definitely demospongiaen.

Most of the spherical spicules with few and relatively long, radiating rays look almost identical to oxyasters. A few polyactins show rounded or even spined ends to their rays (Pl. 5, fig. 14) and are similar to the asters of some recent demosponges, e.g. the strongylacanthasters of *Geodia* or acanthose euasters of *Timea*. Although much larger in size, the Cambrian polyactins show great morphological affinity with the oxyasters of some Recent tetractinellids. For these reasons, most of the polyactins from the Georgina Basin may be considered as true demospongid aster spicules. However, Recent oxyasters are normally ten to 15 times smaller than these Cambrian polyactins. This suggests that the Recent aster microscleres may be derived from Palaeozoic protoaster megascleres. Reif (1968, figs 10–12) figured similar polyactins from the upper Ordovician of Scandinavia, which he referred to as 'Aster-formige Megasklere' (aster-shaped megasclere). It is also possible that these Cambrian polyactins may be special mesotriaenes. Interesting analogues are the spherical polyactins from the Upper Triassic published as *Costamorphia zlambachensis* by Mostler (1986b, p. 345, pl. 4). The size range and overall morphology of these spicules, which also show central canals in all rays, is very similar to those from the Georgina Basin. However, in the Triassic spicules two rays are generally longer than the other ones, and Mostler (1986b) called the long rays 'Pseudorhabde' and interpreted his spicules as mesotriaenes. In many of the Georgina Basin polyactins the same phenomenon can be observed, and it cannot be discounted that these spicules are also derived mesotriaenes.

Thus, it must be considered whether the aster microscleres might have evolved from mesotriaene megascleres. This hypothesis is supported by the fact that the oxyaster seems to be a plesiomorphic form, probably very close to the original proto-aster (Reitner 1992, fig. 13a).

THE EARLY EVOLUTIONARY HISTORY OF THE DEMOSPONGIAE

Astrophora and Sigmatophora

These are the two major groups within the Demospongiae. They correspond only partly to the taxa 'Tetractinomorpha' and 'Ceractinomorpha' as defined by Lévi (1953), which have been shown to be polyphyletic (van Soest 1987, 1991). According to phylogenetic-systematic analyses of Recent

sponges, Aster-Tetractinellida and Sigmatophora are sister taxa. The presence of aster-microscleres is the constituent character of the Astrophora, and that of sigma-microscleres is a main autapomorphy of the Sigmatophora. Because of its distribution within this group, the oxyaster is considered as a phylogenetically early and original type of aster-microsclere, close to the hypothetical protoaster (Reitner 1992). So far, the Lower Cambrian oxyasters from Shanxi, China, (Zhang and Pratt 1994) are the earliest recorded oxyaster-type spicules.

Sigmata and asters. Sigmataose microscleres are a constituent character of the monophylum Sigmatophora. Middle Cambrian sigmata, as documented here and by Kruse (1990, pl. 24, fig. J), are the earliest reported. Thus, the existence of both main demospongid groups in the Middle Cambrian has been demonstrated. The sigma-microscleres may have evolved from Proto-sigma-megascleres that were originally curved/bent oxea. Similarly, the oxyasters in this assemblage are very large, more like average megascleres. These spicules would be 'megascleres' according to the common size-based classification of sponge spicules. However, the hypothesis that aster and sigma microscleres evolved from corresponding megascleres seems to be discordant with the fact that in Recent demosponges, mega- and microscleres are developed in different somatic layers by distinctly different types of sclerocytes. Demospongid megascleres are secreted by megasclerocytes, which originate ontogenetically from the large archaeocytes with nucleolate nuclei. They seem to be non-homologous with microscleres, which are secreted by smaller microsclerocytes with anucleolate nuclei (Simpson 1984). Consequently, I would expect the two spicule-types to have evolved independently within the Demospongiae rather than in the Hexactinellida, whose 'microscleres' have been documented to be reduced megascleres (Mehl 1992). It is possible, however, that sigmata and asters evolved independently of other spicules, but initially as larger spicules. Certain aster microscleres, e.g. sterrasters of Recent representatives of the Geodidae, are much larger than some size-reduced megascleres, such as microstrongyles or microcalthropses. According to the present stage of palaeontological knowledge, it seems likely that the microscleres evolved from megasclere prototypes: Sigmata from oxeas and asters from polyactine mesotriaenes.

Rankenella mors (Gatehouse, 1968) is by far the earliest representative of the 'lithistid' Anthaspidellidae. Desmata are of very widespread distribution and thus seem to be a plesiomorphic spicule-type within the Demospongiae. The taxon 'Lithistida', based on the presence of desmata megascleres, has proven to be polyphyletic, since it comprises representatives of various demospongid groups (Gruber 1993). Anthaspidellidae constitutes a well established monophylum characterized by the autapomorphic skeletal architecture of dendroclone desmas in ladder-like tracts fixed at radiating bundles of monaxons. They are the oldest desma bearing demosponges in the fossil record. Within these sponges, the desmas form skeletal strands by fusion of their cladomes and may be cored by monaxone spicules, such as styles and oxeas (van Kempen and ten Kate 1980; van Kempen 1983, 1989).

Class CALCAREA Bowerbank, 1864

Diagnosis. Pinacophoran sponges with calcitic spicules of basically triradiate symmetry, without axial canals.

Order HETERACTINELLIDAE Hinde, 1888

Diagnosis. Palaeozoic Calcarea with polyactine spicules.

Genus EIFFELIA Walcott, 1920

Type species. *Eiffelia globosa* Walcott, 1920.

Diagnosis. Calcarea with planiradiate, mostly six-rayed spicules.

Eiffelia sp.

Plate 6, figures 1–3, 7–9, 11–12

Material. Seven specimens: CPC 34269–34271, 34275–34277, 34281.

Description. *Eiffelia globosa* is known from the Burgess Shale as small globular sponges with deep oscula and a skeleton of normally hexiradiate, sometimes slightly concavo-convex spicules with six rays in one plane, radiating from a flattened centre. The diameter of the *Eiffelia* spicules in the Australian assemblage is highly variable, from c. 300 μm to almost 2 mm. The spicule surfaces are smooth, and the rays normally have rounded ends. All of the six rays diverge at angles of 50–70° (average 60°). As in all Heteractinellida (and Calcarea), the spicules of *Eiffelia* have no central canals. In most specimens the rays are of more-or-less equal length, and although some spicules have one or two rays greatly prolonged, whereas others are largely reduced (Pl. 6, fig. 7), they probably all belong to the genus *Eiffelia*.

Remarks. Entire specimens of *Eiffelia globosa* in body preservation from the Burgess Shale were studied by Rigby (1986), who found in these sponges up to four orders of six-rayed spicules. This may explain the remarkable variation in shape and size between the spicules attributed to *Eiffelia*. But, the possibility of more than one species within the isolated spicule assemblage from the Georgina Basin cannot be excluded.

Genus CANINSTRUMELLA Rigby, 1986

Type species. *Caninstrumella alternata* Rigby, 1986.

Diagnosis. Conical to basket-like sponges with skeletons of four- to six-, mostly five-rayed planiradiate spicules with short buttons on their convex, ?upper surfaces.

Caninstrumella? sp.

Plate 6, figures 6, 10

Material. Three specimens: CPC 34274, 34278–34279.

Description. Polyactine spicules, with five or six equally spaced rays and one to seven vertical rays, which are largely atrophied and appear as buttons (Pl. 6, figs 6, 10). Diameter normally varies between 300–600 μm . They are not very common.

Remarks. In a study of the sponges from the Burgess Shale, Rigby (1986) erected the genus *Caninstrumella* for heteractinids with four to six tangential rays and the proximal and distal rays reduced to short buttons. The polyactins from the Georgina Basin are highly variable: they generally have nodes on the convex side only, but sometimes possess as many as seven elevated nodes: one central one with the others equally distributed on the central plate in the central axis of

EXPLANATION OF PLATE 6

Figs 1–3, 7–9, 12. *Eiffelia* sp.: heteractinide hexiradiate spicules. 1–3, 7–8, 12, Templetonian. 1, CPC34269; $\times 56$. 2, CPC34270; $\times 113$. 3, CPC34271; $\times 68$. 7, CPC34275; $\times 40$. 8, CPC34276; $\times 55$. 11, CPC34279; $\times 63$. 12, CPC34280; $\times 130$.

Figs 4–5. Undetermined triaene or heteractinellid(?) spicules; Templetonian. 4, CPC34272; $\times 68$. 5, CPC34273; $\times 85$.

Figs 6, 10. *Caninstrumella?* sp. spicules. 6, CPC34274; Upper Floran–Lower Undillan; $\times 83$. 10, CPC34278; Templetonian; $\times 155$.



MEHL, Cambrian spicules

each ray. In spite of these differences, these spicules may still be attributable to *Caninstrumella*, since no elevated nodes are seen on the spicules of any of the type specimens of *Eiffelia* (pers. obs.). The pyritic preservation of the Burgess Shale specimens may have obscured such fine structures. Further complete Cambrian Heteractinellida preserved differently might help complete the reconstruction of this genus.

Undetermined triaene or heteractinellid (?) spicules

Material. Two specimens: CPC 34272–34273.

Description. These spicules are more-or-less planiradiate with six to eight pointed rays. They are not uncommon in the Georgina assemblage (Pl. 6, figs 4–5). It is uncertain whether these are heteractinellid spicules or mesotriaenes with reduced rhabds.

ON THE SYSTEMATICS OF THE HETERACTINELLIDAE

This group was originally classified as belonging to the Hexactinellida by Hinde (1888). Heteractinellida was placed in Calcarea by Rietschel (1968) on account of their monocrystalline calcitic spicules and absence of central canals in their spicules. This placement was followed by later spongiologists (e.g. Rigby 1991; Reitner 1992). Reitner and Mehl (1996) considered the Heteractinellida in this sense to be a stem-group member of the Calcarea-taxon. The earliest known representatives of this group are from the Middle Cambrian. *Eiffelia globosa* and *Caninstrumella alternata*, both from the Burgess Shale, possess planiradiate spicules very similar to those found in the Georgina Basin. *Jawonya gurumal* Kruse, 1987 from the Middle Cambrian of north Australia, the oldest heteractinellid sponge so far documented, has highly variable polyactine spicules. This indicates that the original heteractinellid spicules showed little symmetry, and the regular six-rayed, planiradial shape of *Eiffelia* spicules is a derived feature within the Heteractinellidae. *Eiffelia* is monospecific. The type species is *Eiffelia globosa* Walcott, 1920, the lectotype of which was designated by Rigby (1986). This and the reference specimens, and also the holotype of *Jawonya gurumal* have been recently re-studied by me. Some confusion still exists with regard to the Octactinellidae within the Heteractinellida. In his original description, Walcott (1920, p. 324, text-fig. 10) figured a six-rayed, composite cancelloriid sclerite and described this with 'a central hexagonal disc' as characteristic of his octactinellid species *Eiffelia globosa*. Sdzuy (1969, p. 132, pl. 14, figs 31–35; pl. 15, figs 1–3) classified *Eiffelia* within the Cancelloriidae and figured definitely cancelloriid sclerites as '*Eiffelia? hispanica* n. sp.' However, re-examination of the type specimens of *Eiffelia globosa* (U.S. Nat. Mus. cat. nos 66521–66523; Walcott 1920, pl. 86, figs 1, 1a–b) definitely excludes the presence of central discs or any composite spicules in *Eiffelia*, which has massive six-rayed, planiradial spicules only.

The Georgina collection also contains polyactin spicules that show no particular symmetry. They have variable numbers of pointed rays, generally of different lengths, radiating from the centre. No central canals have been observed within these spicules. Most of them are probably heteractinellid sponge spicules, but so far they cannot be attributed definitely to any particular group. Very irregular polyactins with similar ray-numbers are present in the dermal layer of the Middle Cambrian heteractinellid sponge *Jawonya gurumal* Kruse, 1987, from north Australia. Presumably, some of the irregular polyactins from the Georgina Basin belong to the same or some closely related species. Several authors (e.g. Rigby and Dixon 1979) have documented massive, irregular polyactins from Early Palaeozoic strata.

MICROFOSSILS OF UNCERTAIN SYSTEMATIC POSITION

Pseudo-poriferan spicules, probably Radiolaria

Plate 5, figure 13

Material. Two specimens: CPC 34232, 34267.

Description. Rather small (about 250–350 μm ; only one exception found with 475 μm), thin-rayed polyactins with sometimes slightly curved, often hollow rays (Pl. 5, fig. 13) or they may be planiradiate. These fossils cannot be attributed definitely to any heteractinellid, demospongid or hexactinellid group, although some of them appear to show triaxial symmetry of the curved rays (Pl. 2, fig. 6). It is almost certain that most of these are not poriferan spicules. In some cases, such spicules are fused into a loose framework of a spherical ball, about 1 mm in diameter. Similar spherical frameworks of spicules from the Upper Cambrian were published as sponges by Bengtson (1986). However, according to new data by Kozur *et al.* (1997b) these spicules belong to large radiolaria, probably the oldest with mineralized skeletons.

CHANCELLORIIDAE Walcott, 1920

Genus CHANCELLORIA Walcott, 1920

Type species. *Chancelloria eros* Walcott, 1920.

Diagnosis. The completely preserved fossils, rarely found, are sessile, thin-walled, conical and with skeletons of polyactine, composite sclerites.

Chancelloria eros Walcott, 1920

Plate 7, figures 1, 3, 7–8, 12, 14–15

Material. Seven specimens: CPC 34281, 34383, 34287–34288, 34292, 34294–34295.

Description. The holotype, from the Burgess Shale, is a poorly preserved, pyritized specimen, characterized by (6–8 + 1) and rare (4 + 0) sclerites. Within the Georgina Basin collection, only isolated chancelloriide sclerites have been found. The (7 + 1) type is the most common type. It has a flat base with a comparably large central disc and wide, circular basal pores (Pl. 7, figs 6–8, 15). Total diameters of the sclerites are 0.7–1.0 mm. From the polygonal central disc the marginal rays radiate in a flat angle from 0 to *c.* 20°, exceptionally up to 45°. The length of marginal rays is variable, even between individual rays of the same sclerite, generally ranging between 200–400 μm . The central ray is normally somewhat longer.

Remarks. According to Bengtson *et al.* (1990), the chancelloriide scleritomes from the Burgess Shale, which Walcott (1920) included into the type species *Ch. eros*, are from several different species. The lectotype designated by Goryanskij (1973), figured by Walcott (1920, pl. 86, fig. 2; pl. 88, fig. 1f), has been re-studied by me. The (incomplete) scleritome is composed of rather large, 1–2 mm in total diameter, sclerites that are mainly (6–7 + 1). Individual rays are *c.* 1–1.6 mm long. Most chancelloriides in the Australian collection are only *c.* 0.7–1.0 mm in total diameter and thus are fairly small, compared with those reported by other authors (e.g. Walcott 1920; Rigby 1978). However, two or three size-ranges of sclerites are present within a chancelloriide scleritome. Also, sclerites become successively larger from the base upwards towards the ontogenetically younger part of the scleritome (Rigby 1978 and pers. obs. of new complete chancelloriides from the Wheeler Shale). Individual rays 1–2 mm long with polygonal basal outlines also occur within this assemblage. They obviously represent originally joined composites of larger, broken chancelloriide sclerites.

Chancelloria racemifundis Bengtson, in Bengtson *et al.*, 1990

Plate 7, figures 2, 6, 13

Material. Three specimens: CPC34282, 34286, 34293.

Description. The sclerites are generally rather small, 300–800 μm in diameter, with a highly variable number of long slender rays, (3–7 + 0) and (5–11 + 1) according to Bengtson (in Bengtson *et al.* 1990). Protruding ridges

and nodular deposits surround the basal foramina, and the entire circular base is rather small and bordered by a distinct ridge.

Chancelloria cf. *pentacta* Rigby, 1978

Plate 7, figure 10

Material. CPC 34290.

Description. The sclerites have the composition (5+1), (4+1) or (6+1). They are c. 0.8–1.0 mm in total diameter with rays 300–500 μ m long. The polygonal outline of the basal disc, from which the rays curve away at steep angles of c. 60°, measures only 100–200 μ m in diameter.

Remarks. It is uncertain whether these chancelloriide sclerites actually belong to the species *C. pentacta*. The type specimens of *C. pentacta*, as documented by Rigby (1978) from the Mid Cambrian Wheeler Shale, have generally larger sclerites with slightly more slender rays.

Chancelloria sp.

Plate 7, figure 9

Material. CPC 34289.

Description. A new type of sclerite (Pl. 7, fig. 9) with three to five marginal rays that bend away sharply, almost 90° from the base, is not very common within this assemblage. The basal pores are bordered by clearly elevated spines protruding above the basal surface. The thin outer wall is often in phosphatic preservation.

Genus *ARCHIASTERELLA* Sdzuy, 1969

Type species. *Archiasterella pentactina* Sdzuy, 1969.

Diagnosis. Sclerites in the configuration (3–6+0) with their rays radiating at steep angles from the central plate.

Archiasterella sp.

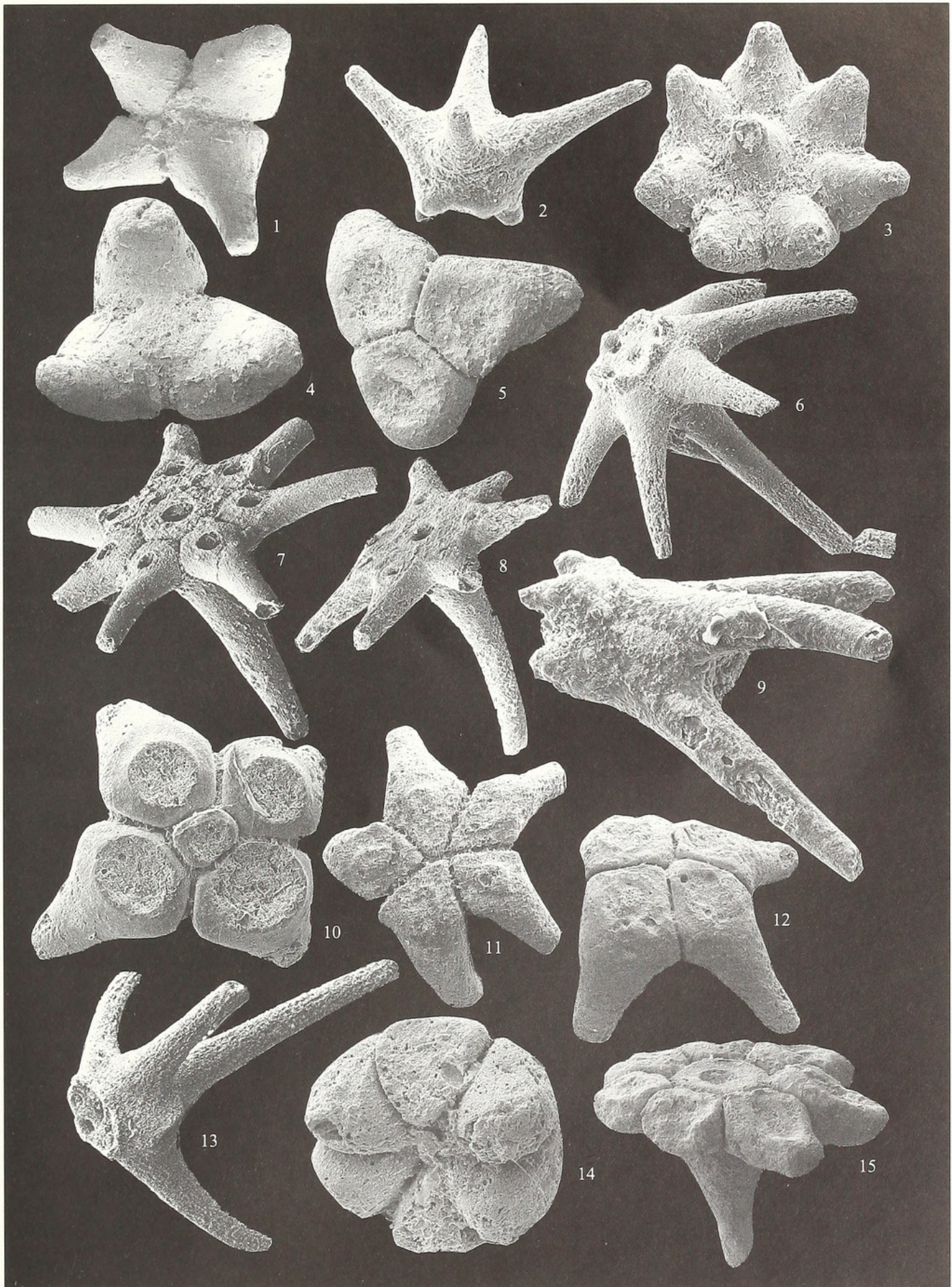
Plate 7, figure 11

Material. CPC 34291.

Description. This sclerite has steeply projecting marginal rays, but no central ray. Composition (5+0) is the most common type, according to Bengtson *et al.* (1990). One of the rays may be almost vertical to the base, whereas the others project at slightly more gentle angles.

EXPLANATION OF PLATE 7

- Figs 1, 3, 7–8, 12, 14–15. *Chancelloria eros* Walcott, 1920. 1, 3, 12, 14–15, Ordian. 1, CPC34281; $\times 42$. 3, CPC34283; $\times 42$. 12, CPC34292; $\times 41$. 14, CPC34294; $\times 160$. 15, CPC34295; $\times 50$. 7–8, Templetonian. 7, CPC34287; $\times 70$. 8, CPC34288; $\times 75$.
 Figs 2, 6, 13. *Chancelloria racemifundis* Bengtson, in Bengtson *et al.*, 1990; Templetonian. 2, CPC34282; $\times 120$. 6, CPC34286; $\times 100$. 13, CPC34293; $\times 105$.
 Figs 4–5. *Allonia erromenosa* Jiang, in Luo *et al.*, 1982; CPC34284; Ordian. 4, $\times 44$. 5, $\times 39$.
 Fig. 9. *Chancelloria* sp.; Templetonian; $\times 105$.
 Fig. 10. *Chancelloria* cf. *pentacta* Rigby, 1978; CPC34290; Ordian; $\times 75$.
 Fig. 11. *Archiasterella* sp.; CPC34291; Ordian; $\times 31$.



MEHL, *Chancelloria*, *Allonia*, *Archiasterella*

Genus ALLONNIA Doré and Reid, 1965

Type species. *Allonnia triporata* Doré and Reid, 1965.

Diagnosis. Sclerites with few, stout rays.

Allonnia erromenosa Jiang, in Luo *et al.*, 1982

Plate 7, figures 4–5

Material. Two specimens: CPC 34284–34285.

Description. Sclerites fairly large, *c.* 1 mm in diameter, with stout rays, normally in the configuration (3 + 0), but (4 + 0) also occurs. The rays bend away sharply (at 60–80°) from the wide, plane base which has large pores. A central ray is missing, but the base may be somewhat swollen in the central region.

SYSTEMATIC POSITION OF THE CHANCELLORIIDAE

Natural assemblages of cancelloriide sclerites are not common. The Burgess Shale material contains a few fairly complete specimens, which Walcott (1920) interpreted as sponges and described as a new genus *Chancelloria*. For a long time, the original classification of these sessile, sclerite-bearing Chancelloriidae as sponges was not questioned in the literature. On the contrary, Sdzuy (1969) classified the heteractinide genus *Eiffelia* within the Chancelloriidae, which he considered as the stem-group of all Porifera. For this reason, many authors (e.g. Mostler and Mosleh-Yazdi 1976) have attributed the cancelloriids to the Heteractinellida. Goryanskij (1973) was the first to argue for the necessity of excluding the Chancelloriidae from the Porifera. Bengtson and Missarzhevsky (1981) concluded, on account of the hollow, composite nature of cancelloriide sclerites, that it is impossible for them to be homologous with poriferan spicules. Consequently, they interpreted the sclerites as belonging to an exoskeleton and proposed the new class Coeloscleritophora to include the Chancelloriidae and, in their view, closely related families. Bengtson and Missarzhevsky (1981) considered the Coeloscleritophora, although of uncertain systematic position within the Metazoa, to be most probably a monophyletic group, which currently comprises the following taxa: Wiwaxiidae, Siphonuchitidae and Chancelloriidae. However, the microstructure of cancelloriide sclerites is very different from those of the supposedly closely related *Wiwaxia*, and their homology is more than doubtful. The interpretation of the Chancelloriidae as Coeloscleritophora has been accepted also by most spongiologists (e.g. Rigby 1986).

New evidence (Butterfield and Nicholas 1996) of well-preserved cancelloriide sclerites, from which organic walls were dissolved with HF, appears to give reason to doubt the interpretation by Bengtson and Missarzhevsky (1981). The Chancelloriidae are known so far from the relatively complete scleritomes of the Mid Cambrian Burgess Shale (Walcott 1920; Rigby 1986) and Wheeler Shale (Rigby 1978). New, promising, complete and well-preserved cancelloriides from the Wheeler Shale are currently being studied by me. The results of preliminary studies of these specimens and the Georgina assemblage have been published (Mehl 1996b), but more detailed descriptions will probably provide new evidence on this enigmatic fossil group. Few sclerites from the Georgina Basin are found with their outer walls still present in a phosphatic preservation. These sclerite walls are composed of fibrous needles in a regular radial orientation. Most probably, these were originally crystals of aragonite, which have been diagenetically altered by heavy phosphatization (Mehl 1996b). This interpretation corresponds with the results of James and Klappa (1983) and Bengtson *et al.* (1990), who suggested that the cancelloriide sclerites were originally aragonitic. Although spicules have evolved convergently several times within the Porifera (Mehl and Reitner 1991; Reitner and Mehl 1996), no poriferan spicules of aragonitic mineralogy are known. Sponge spicules consist of either calcite or opaline silica. The calcitic spicules are monocrystalline, they are formed by an extracellular mode of secretion, and thus are massive without axial filaments or central canals

(Ledger and Jones 1977). Siliceous spicules, in contrast, are secreted intracellularly by sclerocytes and contain a thin axial filament in a central canal.

The cancelloriide composite type of sclerites, with large internal cavities and with inner and outer walls consisting of aragonitic needles, does not correspond with any known mode of spicule formation within the Porifera. Thus, Cancelloriide sclerites are not homologous with any known sponge spicules. However, many sponges do possess the ability to secrete CaCO_3 extracellularly, in addition to their spicules. Also, other types of skeletons are known, e.g. some horny sponges agglutinate sand grains between spongin fibres in their organic skeletons. According to Butterfield and Nicholas (1996), the organic walls of cancelloriide sclerites show remarkable similarity to the spongin spiculoids produced by some modern dendroceratid sponges. However, my observations of the massive spicules in different *Darwinella* species has so far provided no confirmation of a poriferan affinity of the Cancelloriidae.

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