

Radiolaria from the Telychian (Llandovery, Early Silurian) of Dalarna, Sweden

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ABSTRACT: A *Haplotaeniatum*-dominated radiolarian fauna has been discovered in Llandoveryan (Early Silurian) strata of the Scandinavian platform, Dalarna, Sweden. As one of six occurrences of this fauna world-wide, it supports the premise that many elements in the *Haplotaeniatum* Assemblage have a wide geographic distribution and will be of significance in building an Early Silurian radiolarian biostratigraphic scheme with global application. In addition to *Haplotaeniatum*, this fauna contains palaeosconidiid and secucollactine taxa that are known only from one other locality, the Cape Phillips Formation, Canadian Arctic. These taxa may prove to be fairly cosmopolitan and biostratigraphically useful as more data from other localities are collected. Two new genera, *Labyrinthosphaera* and *Gyrosphaera*, and three new species, *Labyrinthosphaera macdonaldi*, *Gyrosphaera siljanensis*, and *Gyrosphaera raneatela*, are described herein. *Labyrinthosphaera* has a multi-layered labyrinthine meshwork and with six or more tri-bladed spines. *Gyrosphaera* has a labyrinthine meshwork and displays spiraliform layering, similar to that described in *Haplotaeniatum*, indicating a close phylogenetic link between these two Llandoveryan taxa. Further data from additional localities is needed to determine the potential diachroneity of a global *Haplotaeniatum* acme zone, and to identify additional taxa whose first and last occurrences may be used as biostratigraphic datums for the Llandoveryan.

INTRODUCTION

Silurian radiolarian studies are in their formative stage, with the bulk of the descriptive literature having been published during the past 15 years. There are only a small number of published localities of Silurian radiolarians from around the world, including four from North America (i.e. Goodbody 1986; MacDonald 1997; Noble 1994; Noble et al. 1997), six from Asia (i.e. Nazarov and Ormiston 1984, 1993; Furutani 1990; Wakamatsu et al. 1990; Li 1991), three from Europe (i.e. Stürmer 1952; Gorka 1994; Briggs et al. 1996), and one from Australia (Aitchison 1990). Data for the Llandoveryan is particularly scant and includes data from the Ural Mountains and Kazakhstahn (Nazarov 1988; Nazarov and Ormiston 1993) Thuringia (Stürmer 1952; Noble et al. 1998), Nevada (Noble et al. 1997, 1998), and the Canadian Arctic (Holdsworth 1977; Goodbody 1982, 1986; Renz 1988; MacDonald 1997 1998). Despite the relatively scant amount of data accumulated, Silurian radiolarians show great promise for biostratigraphic application (Noble and Aitchison 1995). Advances in Silurian radiolarian biostratigraphy rely on the acquisition of well preserved and precisely dated assemblages that help document the range and distribution of potential marker taxa.

This paper describes a well-preserved assemblage from the *Spirograptus turriculatus* Zone of Dalarna, Sweden. The Dalarna fauna is significant for several reasons. First, radiolarian faunas of Llandoveryan age are scarcely known; the Dalarna fauna is one of six published Llandoveryan faunas in the world, and one of three known to be of Telychian age (late

Llandoveryan), providing valuable information as to the taxonomic make-up of Early Silurian radiolarian assemblages. Second, the preservation of this fauna is excellent, allowing for the observation of detailed internal structures in many of the taxa, which is necessary for taxonomic discrimination and phylogenetic linking. Thirdly, this paper provides the first documentation of a *Haplotaeniatum*-dominated radiolarian fauna from the Scandinavian platform. The *Haplotaeniatum tegimentum* Assemblage of Nazarov was first described from the Llandoveryan of the Urals and Kazakhstahn (Nazarov and Ormiston 1984; Nazarov 1988), and Thuringia (Stürmer 1952). *Haplotaeniatum*-dominated faunas subsequently have been described from the early Llandoveryan of Nevada, and provide increasing evidence that this assemblage may be of biostratigraphic significance on a global scale (Noble et al. 1997, 1998).

GEOLOGIC SETTING AND STRATIGRAPHY:

The fauna described herein was recovered from a calcareous concretion found in the lower part of the Kallholn Shale exposed in a 5.5m section at the Solberga quarry about 3km south of the village of Boda, on the eastern side of the Siljan Ring structure (text-fig. 1). The Siljan Ring is a meteorite impact structure in central Sweden that exposes a highly condensed section of Lower Ordovician - Silurian shelf carbonates and shales (Jaanusson 1982). In this succession two generations of stromatolite-bearing mudmounds are preserved with their flank deposits and onlapping shales bearing diverse shelly and graptolitic faunas of Early Silurian age. The graptolite-bearing

Kallholn Shale overlies the mudmounds at several localities (Wærn 1960; Jaanusson 1982) (text-fig. 2), and the lower part of the Kallholn Shale commonly contains large calcareous concretions with a well-preserved graptolite fauna (Hutt et al. 1970; Loydell 1991).

At the Solberga locality, the Kallholn Shale directly overlies the Boda Limestone (Maletz and Reich 1997, text-fig. 3). The greenish to brown and black shales include several light colored bentonite beds. Graptolites are common in the shales and the limestone concretions and belong to the upper part of the *Spirograptus turriculatus* Zone. A rich fauna of graptolites, sponge spicules, acritarchs, chitinozoans, and conodonts was found associated with the radiolarians (Maletz and Reich 1997). The graptolites are especially important, as they provide precise age control for the concretion. The radiolarians were briefly described and figured by Maletz and Reich (1997) together with a number of sponge spicules. The radiolarians were divided into three groups; one group with multiple rounded spines assigned to *Secuicollacta* Nazarov and Ormiston 1984; a second group of large forms with short fine spines, called *Spumellarida* indet. (*Haplotaeniatum cathenatum* Nazarov and Ormiston 1993 herein); and a third group with long tri-bladed spines identified as ?*Entactinia* (*Labyrinthosphaera* new genus herein). This paper provides a more detailed systematic treatment of this radiolarian fauna.

DISCUSSION OF FAUNA

The most abundant species is *Haplotaeniatum cathenatum*, a large spherical form that comprises ~40% of the assemblage. *Secuicollactines* represent ~20% of the fauna, *Gyrosphaera* new genus ~20%, *Labyrinthosphaera* new genus ~15%, and palaeoscanidiids less than 5%. Of the *secuicollactines*, three genera were recognized; *Secuicollacta* Nazarov and Ormiston 1984, *Parvalanapila* MacDonald 1998, and *Diparvapila* MacDonald 1998. *Secuicollacta* is slightly more abundant than *Diparvapila*, and *Parvalanapila* is relatively rare. *Diparvapila* and *Parvalanapila*, recently described from the Canadian Arctic (MacDonald 1998), have not been recognized in the Urals or Kazakhstan, however, the *secuicollactine* spicule (see remarks under *Rotasphaeridae* and *Secuicollactinae* in Systematic Paleontology section) is internal in these two genera and may easily be missed, particularly in samples with less than exceptional preservation.

There is a striking similarity between the *secuicollactine* and palaeoscanidiid populations in this assemblage and that described from the Telychian (*Cyrtograptus sakmaricus* Zone) of the Cape Phillips Formation, Canadian Arctic (MacDonald 1997, 1998). Two species of palaeoscanidiids, three species of *Diparvapila*, and three species of *Secuicollacta* are recognized in the Dalarna sample. All of these species are present in the Cape Phillips Formation (Goodbody 1986; MacDonald 1998, 1999). The only difference is in their relative abundance, with the *secuicollactines*, particularly *Diparvapila* and *Parvalanapila*, forming a larger component of the Arctic fauna.

The degree of similarity of labyrinthine spumellarian genera (i.e., *Haplotaeniatum*, *Gyrosphaera*, and *Labyrinthosphaera*) between the Arctic and Dalarna faunas needs further investigation. *Gyrosphaera* and *Labyrinthosphaera* have been observed by the first author (PJN) in samples from the Cape Phillips Formation that are slightly younger (*Cyrtograptus sakmaricus* Zone), so it is quite possible that these taxa are present in the

older Telychian part of the section. The spiraliform coiling observed in *Gyrosphaera* suggests a close phylogenetic link with *Haplotaeniatum* and indicates that a clade of spiraliform labyrinthine radiolarians were prominent during the Llandoveryan. It is not currently known whether *Haplotaeniatum* is present in the Arctic. It will be important to determine its occurrence in order to assess the pervasiveness of *Haplotaeniatum*-dominated faunas, and to support any phylogenetic linking with *Gyrosphaera* and *Labyrinthosphaera*.

The Dalarna fauna provides several important pieces of information that contribute to Silurian radiolarian biostratigraphy. First, the close affinity with the Arctic Telychian fauna suggests that many of these species are geographically widespread, and one may predict that they will occur in other radiolarian-bearing Telychian rocks deposited in this general paleogeographic province, namely the equatorial seaway bridging the Laurentian, Siberian, and Baltoscandian continents. Second, no representatives of the family *Ceratoikiscidae* were found in the Dalarna sample. The nominal genus, *Ceratoikiscus* Holdsworth 1967, is presently known from strata of Wenlockian age (late Early Silurian) and younger (Holdsworth 1977; Goodbody 1986). Its first occurrence is considered an important datum for the Early Silurian. *Protoceratoikiscus* Goto et al. 1992 is a distinct taxon recognized in Middle - Late Ordovician rocks and has been proposed as a phylogenetic precursor to *Ceratoikiscus* (Goto et al. 1992). If these two genera belong to the same clade, it is reasonable to expect to find some *ceratoikiscids* in Llandoveryan strata; however, none have been found to date. Determining the stratigraphic ranges and phylogenetic relationships of these two *ceratoikiscids* will be important in determining their utility in biostratigraphy.

Thirdly, this study provides needed age control for the upper range of the *Haplotaeniatum* assemblage. Thus far, samples from Nevada, Thuringia, (Noble et al. 1998) and Sweden (herein) co-occur with graptolites and show that *Haplotaeniatum*-dominated assemblages may range at least as low as mid Rhuddanian (*Coronograptus cyphus* Zone) to as young as mid Telychian (*Streptograptus turriculatus* Zone). Nazarov and Ormiston (1984, 1993) suggest that the *Haplotaeniatum* assemblage may range as high as the middle Wenlockian based on the ages of graptolitic shale in the Sakmarsky Suite in the southern Urals and the Leviminsky zone in the polar Urals. However, the precise position of the last occurrence of *Haplotaeniatum* relative to graptolite collections in the Urals has not been published. We suggest that the upper range may be greatly over-extended because samples from North America that are demonstrably mid-Wenlockian have a profoundly different faunal composition than that of the *Haplotaeniatum* assemblage (Noble, in prep). If the *Haplotaeniatum* assemblage in the Urals does range into the Wenlockian, then its last occurrence is highly diachronous.

Further work is needed to determine the following: 1) the potential diachroneity of the last occurrence of *Haplotaeniatum*, particularly in the Urals; 2) the first occurrence of *Labyrinthosphaera*, a distinctive and easily recognizable taxon that may be a good datum in the late Llandoveryan; 3) the distribution of the *secuicollactine* taxa *Parvalanapila*, and *Diparvapila*; and 4) the distribution of distinct palaeoscanidiids, such as *P. echinatum*.

Systematic taxonomy

Type specimens have been assigned numbers from the University of California Berkeley Museum of Paleontology (UCMP) and will be stored there for future reference. Paratypes for a given species are mounted on a single slide and assigned one number by UCMP.

Class ACTINOPODA Calkins 1909
Subclass RADIOLARIA Müller 1858
Order POLYCYSTIDA Ehrenberg 1838
Suborder SPUMELLARIINA Ehrenberg 1875
Family HAPLENTACTINIIDAE Nazarov 1980
Subfamily HAPLACTINIINAE Nazarov 1980
Genus HAPLOTAENIATUM Nazarov and Ormiston 1993

Haplotaeniatum cathenatum Nazarov and Ormiston 1993
Plate 1, figures 13, 14, 16, 17

Haplotaeniatum cathenatum Nazarov and Ormiston 1993, p. 51, pl. 3, fig. 11.

Description: Large (280µm) spherical shell with multiple spiraliform or concentric layers, commonly with a pylome that penetrates the outermost three to four layers. Numerous short fine spines cover the cortical wall and extend inwards to inner-most cavity.

Remarks: This species is the most common taxon in the assemblage, comprising approximately 40%. The tight concentric/spiraliform layers are commonly the site for deposition of blobs of cristobalitic silica, which commonly obscure the delicate internal structure (Plate 1, fig. 14).

Family INCERTAE SEDIS

Gyrosphaera Noble and Maletz, n. gen.
Text-figure 3

Type species: *Gyrosphaera raneatela* new species

Diagnosis: Large spherical to subspherical shell composed of loose labyrinthine mesh forming three or more spiraled layers. Primary spines rod-shaped. Species vary in relative spine length, number of spines, and robustness of spines.

Description: Starting at the outside of the shell, layering can be traced in a spiral pattern internal to the center of the shell. Spiraling may appear to grade into crudely concentric layering. The primary spines do not appear to penetrate entirely to the center of the shell, but instead branch and diffuse into the innermost shell layer.

Remarks: Nazarov and Ormiston (1993) used the term spiraliform to describe similar layering in some taxa within the genus *Haplotaeniatum*. Spiraling in *Gyrosphaera* is subtle and easily missed due to the looseness of the labyrinthine meshwork. A slightly younger species of this genus has been observed by the first author (PJN) in latest Llandoveryian samples in the Canadian Arctic. The spiraliform layering is more apparent in the Arctic species. Due to the spiraliform nature of the shell and the penetration of primary spines to the central part of the shell, this genus is probably closely related to *Haplotaeniatum*; however no internal entactiniid spicule was observed. The family is currently classified as *incertae sedis*.

Range and Distribution: Telychian, so far as known; *Spirograptus turriculatus* Zone, Dalarna, Sweden, and *Cyrtograptus sakmaricus* Zone of the Canadian Arctic.

Etymology: Latin, *gyrus* - circular; whirl, *sphaera* - sphere

Gyrosphaera raneatela Noble and Maletz n. sp.
Plate 2, figures 1-3

Diagnosis: Large subspherical shell composed of a loose labyrinthine mesh that forms three to four spiraliform layers. Eight to eleven thin primary spines per hemisphere, with average length approximately one third shell diameter.

Description: Specimens vary in spine length and development of layering. Spines are usually straight, but may be slightly curved on occasion. A broken spine on one specimen is observed to be hollow.

Remarks: On average, *G. raneatela* has a slightly smaller shell diameter than *G. siljanensis* n. sp., and has thinner, shorter spines. It is easily distinguished from *Haplotaeniatum cathenatum* by having a looser meshwork, a subspherical outline, and a smaller average diameter.

Etymology: Latin, *aranea tela*, cobweb; spider's web

Range and distribution: *Spirograptus turriculatus* Zone, Dalarna, Sweden, as far as known.

Material: 33 specimens, 12 measured. Holotype: UCMP 39924, Paratypes: UCMP 39925

Measurements:

	shell diameter	spine length	width spine base	# spines per hemisphere
Min.	165µm	45µm	—	8
Max.	250µm	80µm	—	11
Avg.	200µm	71µm	10µm	9

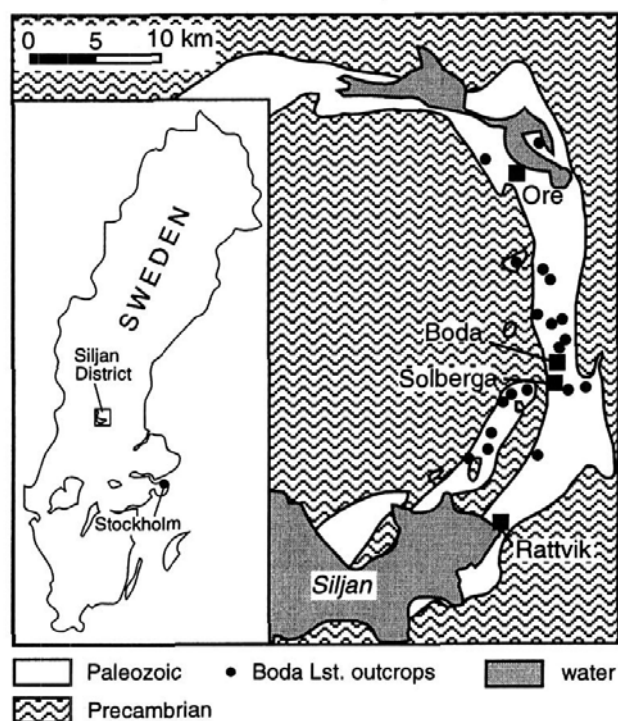
Gyrosphaera siljanensis Noble and Maletz n. sp.
Plate 2, figures 4, 5

Diagnosis: Large subspherical shell composed of a loose labyrinthine mesh that forms three to four spiraliform layers. Five to seven long thin primary spines per hemisphere, average length roughly equal to shell diameter.

Description: Specimens vary in their relative development of layers; some possessing a looser outer meshwork than others. This difference is interpreted to be a function of growth. Spine length, number of spines per hemisphere, and spine robustness varies slightly within the population examined. Defining characteristics are the loose labyrinthine nature of the shell, multiple layering, and relatively long and thin primary spines.

Remarks: *Gyrosphaera siljanensis* n. sp. can be distinguished from *G. raneatela* n. sp. by having longer slightly more robust primary spines, fewer spines per hemisphere, and a slightly larger average diameter. It can be readily distinguished from *Haplotaeniatum cathenatum* by having a looser more open meshwork, a more irregular outline, longer spines, and is about 25% smaller on average.

Etymology: Named after type locality in the Siljan District of Sweden.



TEXT-FIGURE 1
Map showing the Solberga locality in the Siljan District (After Jaanusson 1982).

Range and distribution: *Spirograptus turriculatus* Zone, Dalarna, Sweden, so far as known.

Material: 17 specimens, 8 measured. Holotype: UCMP 39922, Paratypes: UCMP 39923

Measurements:

	shell diameter	spine length	width spine base	# spines per hemisphere
Min.	160µm	90µm	—	5
Max.	260µm	260µm	—	7
Avg.	225µm	190µm	15µm	6

***Labyrinthosphaera* Noble and Maletz n. gen.**

Type Species: *Labyrinthosphaera macdonaldi* new species

Diagnosis: Multi-layered labyrinthine radiolarian with six to twelve long, tri-bladed primary spines; with or without secondary spines.

Description: Labyrinthine meshwork is similar in construction to that in *Gyrosphaera*, but is slightly denser. Layering appears to be concentric, however the tight packing and three-dimensional nature of the meshwork make it difficult to rule out spiraliform layering. Slight torsion is seen in the bladed spines on some specimens observed from latest Telychian samples from the Canadian Arctic, and to a lesser extent in the Dalarna specimens.

Remarks: *Labyrinthosphaera* can be distinguished from *Gyrosphaera* by the presence of tri-bladed spines, and by having a tighter labyrinthine meshwork.

Etymology: Latin, *labyrinthus* - maze, *sphaera* - sphere

Range and distribution: *M. turriculatus* Zone, Dalarna, Sweden, late Llandoveryan - mid Wenlockian of the Cape Phillips Formation, Canadian Arctic, so far as known.

***Labyrinthosphaera macdonaldi* Noble and Maletz n. sp.**

Plate 2, figures 6 - 11

Spumellarida indet., p. 1, figs. 5, 8 - 10, Maletz and Reich 1997.

Diagnosis: Spherical to subspherical shell consisting of two to three closely packed layers of loose labyrinthine mesh, long robust tri-bladed primary spines most commonly seven to eight in number, with or without secondary spines. Some secondary spines are tri-bladed, others are flat blades.

Description: Meshwork variably developed. On approximately two-thirds of the specimens, the delicate outer layer of meshwork is not present, leaving only remnant apophyses along spine bases, and giving an initial appearance that the test diameter is much smaller. On more poorly preserved material, apophyses may be absent and shells may appear smaller. Those specimens where the outermost layer is intact show variable development of secondary spines, some of which are tri-bladed and approximately 60% of the length and width of the primary spines. Other secondary spines are considerably thinner flat blades to rods. Primary spines are very robust, tri-bladed, and non tapering for most of the length, terminating in a blunt point.

Remarks: Outermost layer of meshwork is commonly not preserved, giving the shell an unfinished appearance.

Etymology: Named after Mr. Eugene MacDonald for his contributions to Silurian radiolarian taxonomy.

Range and distribution: *Spirograptus turriculatus* Zone, Dalarna, Sweden, so far as known.

Material: 31 specimens, 14 measured. Holotype: UCMP 39926, Paratypes: UCMP 39927

Measurements:

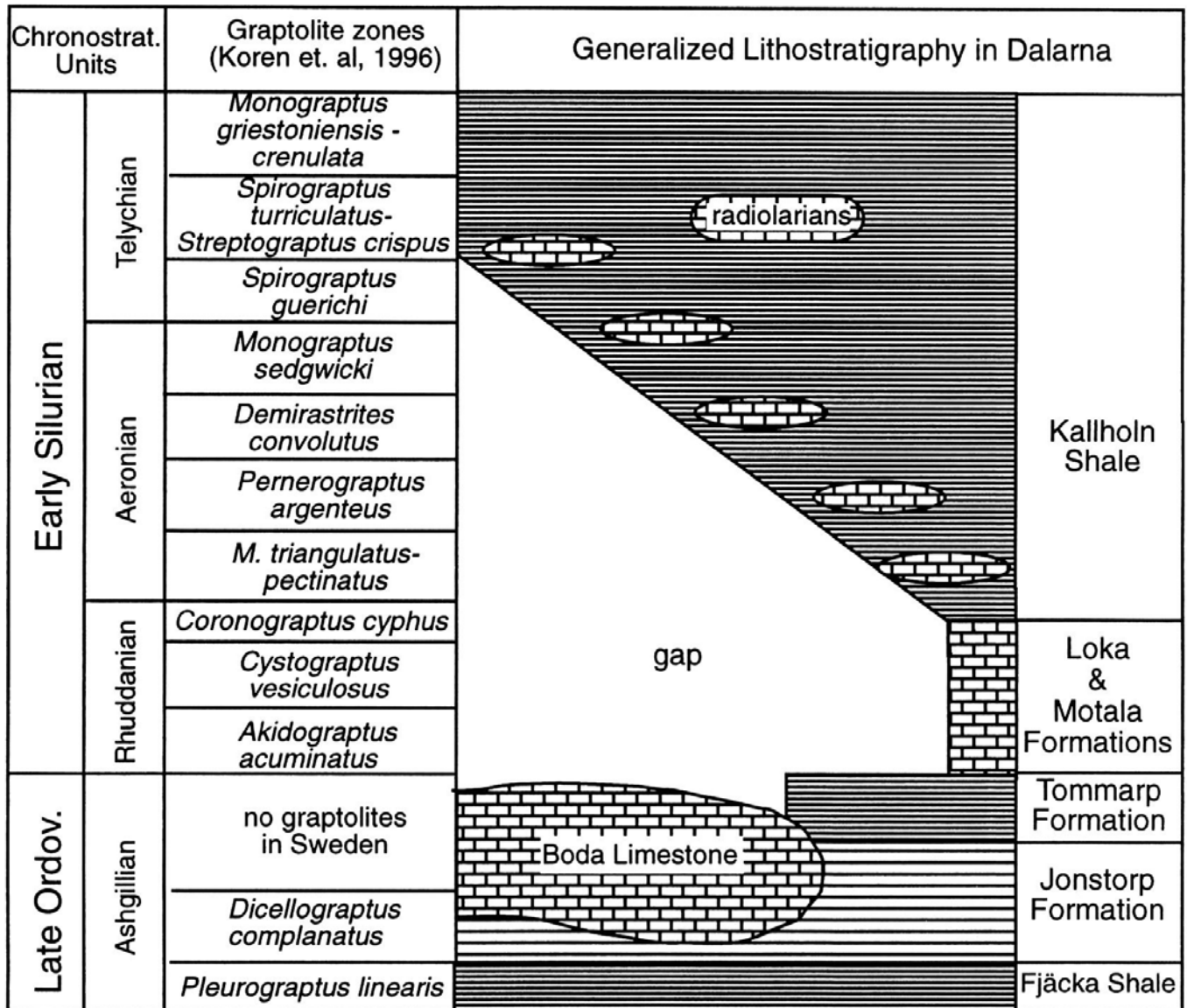
	shell diameter	max. spine length	width spine base	# spines
Min.	110µm	155µm	20µm	6
Max.	190µm	360µm	25µm	11
Avg.	150µm	210µm	24µm	8

Superfamily ROTASPHAERACEA Noble 1994

Family **Rotasphaeridae** Noble 1994

Emended Diagnosis: Test composed of a latticed shell formed by the coalescence of two or more rotasphaerid structures on either a single shell (cortical shell), or on the medullary shell in taxa with two shells. Each rotasphaerid structure consists of a primary spine more or less perpendicular to five or more rods which radiate from its base in a spoke-like fashion. The rods coalesce from individual rotasphaerid structures to form a coarse latticed network of large polygonal pore frames. Pore framework is further subdivided by the development of secondary rods that connect the primary rods together.

Remarks: Noble (1994) erected the Rotasphaeridae to formalize Holdsworth's (1977) informal group, the rotasphaerids, and



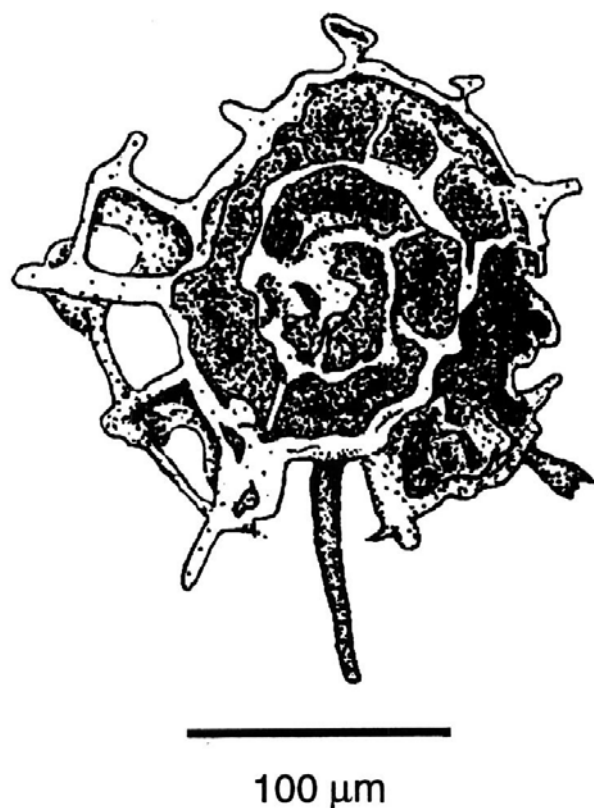
TEXT-FIGURE 2

Generalized biostratigraphy and lithostratigraphy of the Upper Ordovician - Lower Silurian succession in Dalarna (After Maletz and Reich 1997).

considered it phylogenetically separate from the Haplentactiniidae. This diagnosis is now expanded to include the definition of Secuicollactinae Nazarov and Ormiston 1984 as emended by MacDonald (1997). Rotasphaerid structures include both an ectopically placed spicule (*sensu* Nazarov and Ormiston 1984) present in the secuicollactines (text-fig. 4A) and primary spine units (*sensu* Noble 1994) present in both secuicollactine and nonsecuicollactine rotasphaerids (text-fig. 4A, B). The rotasphaerid structures may be found on a single latticed shell, as in *Secuicollacta* Nazarov and Ormiston 1984 and *Rotasphaera* Noble 1994, or on the medullary shell, as in *Diparvapila* MacDonald 1997.

Interpretation of the ectopic spicule as a rotasphaerid structure is pivotal to the emendment herein. In the case of *Secuicollacta*, the similarity between the ectopic spicule and other rotasphaerid structures is so great that the spicule has been

missed by most workers in both moderately preserved and well preserved material (Holdsworth 1977; Wakamatsu et al. 1990; Renz, 1990; Noble 1994; Amon and Braun 1994). MacDonald (1997) disagrees that the secuicollactine spicule is a rotasphaerid structure. The secuicollactine spicule is much more pronounced in *Diparvapila* and *Parvalanapila*, perhaps because they possess only one primary spine unit at the antapical end, and the spicule is very robust. MacDonald (1997) considered these two genera non-rotasphaerids. We disagree. After examining the internal structure of *Diparvapila*, we believe that the medullary shell is sufficiently similar to the single shelled rotasphaerids to warrant its inclusion within the Rotasphaeridae. Furthermore, we believe that all Secuicollactinae, particularly *Secuicollacta*, bear greater morphologic affinity to nonsecuicollactine rotasphaerids than to the family they were originally assigned, Haplentactiniidae Nazarov 1980. Haplentactiniids, as typified by the genus *Haplentactinia* Foreman



TEXT-FIGURE 3

Sketch made by camera lucida of *Gyrosphaera* new genus showing spiralfirm coiling.

1963, have an eccentric point-centered entactiniid spicule that typically has 4 or 6 rays that extend to form the primary spines. We believe that the inclusion of taxa with a non-entactiniid spicule within the Haplentactinidae overextends the family and recommend a revision to remove forms with an ectopic spicule. MacDonald (1998) acknowledges that there are problems in classifying the Secuicollactinae within the Haplentactinidae, citing the spine structure as his chief reason. Haplentactiniids have simple rod-shaped spines, whereas some secuicollactines have a more complex bladed spine structure. In addition, the rays of the spicule extend to form the primary spines in *Diparvavila* and *Parvalanapila* (as with *Haplentactinia*), but not in *Secuicollacta*. The primary spines of *Secuicollacta* arise from the primary spine units, whereas the rays of the ectopic spicule form basal spines that are only minor projections. For all of these reasons, we believe the Secuicollactinae are more appropriately placed within the Rotasphaeridae.

Subfamily **Secuicollactinae** Nazarov and Ormiston 1984, emend. MacDonald 1998

Remarks: This subfamily was originally erected by Nazarov and Ormiston (1984) as a means of placing their newly described genus, *Secuicollacta*, within the spicular Haplentactinidae. The distinct and uniting feature in *Secuicollacta* is an ectopic spicule that bears some resemblance to the spicule on *Pentactinocarpus* Dumitrica (1978). As discussed previously, the ectopic secuicollactine spicule was described as a rotasphaerid structure by Holdsworth, who recognized "most

commonly, perhaps invariably, more than one radiation point [i.e. rotasphaerid structure] is present" in specimens he assigned to the informal group, the rotasphaerids. Complications arose in adhering to Nazarov's taxonomy because the photos of *Secuicollacta* showing a unique spicule were equivocal. Additional Silurian material recovered during the late 1980's included taxa assigned to *Secuicollacta* that had several rotasphaerid structures, with no single ectopic spicule apparent (Furutani et al. 1990; Wakamatsu et al. 1990; Noble 1994). Unfortunately, Nazarov passed away in 1989 and clarification of his observations was not possible. In conversations intended to clarify the relationship between the rotasphaerids and *Secuicollacta*, Holdsworth stated that he believed *Secuicollacta* and his rotasphaerids were the same and that Nazarov's ectopic spicule appeared to be one of several rotasphaerid structures (personal communication to P. Noble, April, 1990). Noble (1994) erected the genus *Rotasphaera* to formalize Holdsworth's rotasphaerids and to classify specimens from west Texas and Japan. She also revised *Secuicollacta* to fit within the Rotasphaeridae.

Careful taxonomic work by MacDonald (1998) on the Cape Phillips material shows that Noble's revision of *Secuicollacta* was premature. MacDonald shows that specimens of *Secuicollacta* have one main spicule and additional rotasphaerid structures (primary spine units). For these reasons, he re-assigned *Secuicollacta* and two new genera, *Parvalanapila* and *Diparvavila*, to the Secuicollactinae, and restored part of Nazarov's original diagnosis of *Secuicollacta*. MacDonald retained the genus *Rotasphaera* and left it within the Rotasphaeridae because he found a few specimens in which no single ectopic spicule could be identified.

After examining well preserved material from the locality of Nazarov's *S. cassa* collections and examining material from the Ordovician - Early Silurian of the Arctic, Sweden, and North America, it is apparent to the first author (PJN) that there is a main spicular structure in many specimens of *Secuicollacta*. It should be noted that the ectopic spicule is not identifiable in all specimens in even the best preserved material, possibly due to reabsorption of spines and bars during shell development. For this reason, taxa assigned to the genus *Rotasphaera*, may well be members of *Secuicollacta* whose spicule is obscured by later growth, resorption, or poor preservation. In less well preserved material, the spicule is often impossible to recognize, and may appear as one of numerous rotasphaerid structures.

The present recommendation is to follow MacDonald's revision of the genus *Secuicollacta*, and place the subfamily Secuicollactinae within the family Rotasphaeridae on the basis of the shared rotasphaerid structures. The distinction between Secuicollactinae and other members of the Rotasphaeridae is the presence of an ectopic spicule in the Secuicollactinae. Members of the subfamily Secuicollactinae include *Secuicollacta*, *Parvalanapila*, and *Diparvavila*. *Rotasphaera* is not assigned to a subfamily within the Rotasphaeridae. Future examination of well preserved material containing *Rotasphaera* and *Secuicollacta* will be necessary to determine whether these two genera should be combined.

Genus **SECUICOLLACTA** Nazarov and Ormiston 1984, emend. MacDonald 1998

Secuicollacta malevola MacDonald 1998
Plate 1, figure 6

Secuicollacta malevola MacDonald 1998, p. 588, figs. 3.1 - 3.3; p. 598, figs. 6.1, 6.2.

Remarks: This species is fairly common in this assemblage. In some specimens, an ectopic secuicollactine spicule can be recognized, with the basal rays forming basal spines (text-fig. 4). However, primary rods radiating from the base of the primary spine in other rotasphaerid structures also extend into basal spines, making the recognition of the main ectopic spicule difficult.

Secuicollacta vallipuellae MacDonald 1998
Plate 1, figures 7, 8

Secuicollacta vallipuellae MacDonald 1998, p. 588, figs. 3.6 - 3.10, p. 600, figs. 7.11, 7.2.

Remarks: Specimens assigned to this species are fairly spinose and exhibit hollow spines. They are very common in the Dalarna assemblage.

Secuicollacta glaebosea MacDonald 1998
Plate 1, figures 9

Secuicollacta glaebosea MacDonald 1998, p. 590, figs. 4.7-4.9, p. 600, figs. 7.4, 7.8.

Remarks: This species is more robust and compact than other species of *Secuicollacta* in the assemblage.

Genus *Diparvapila* Macdonald 1998

Remarks: Identification of this genus was made by examination with transmitted light microscopy. As noted by MacDonald (1998), the general orientation and curve of exterior basal spines in some specimens reflects the position of the inner spicule. In other specimens, the external basal spines may be straight. In this material, recognition of a slight curvature in the exterior basal spines was helpful in isolating specimens through reflected light microscopy during initial picking.

Diparvapila larseni MacDonald 1998
Plate 1, figures 3, 4

Diparvapila larseni MacDonald 1998, p. 596, figs. 5.1, 5.2, p. 601, figs. 8.4, 8.5.

Remarks: This species represents a small component of the fauna. Fourteen specimens were picked.

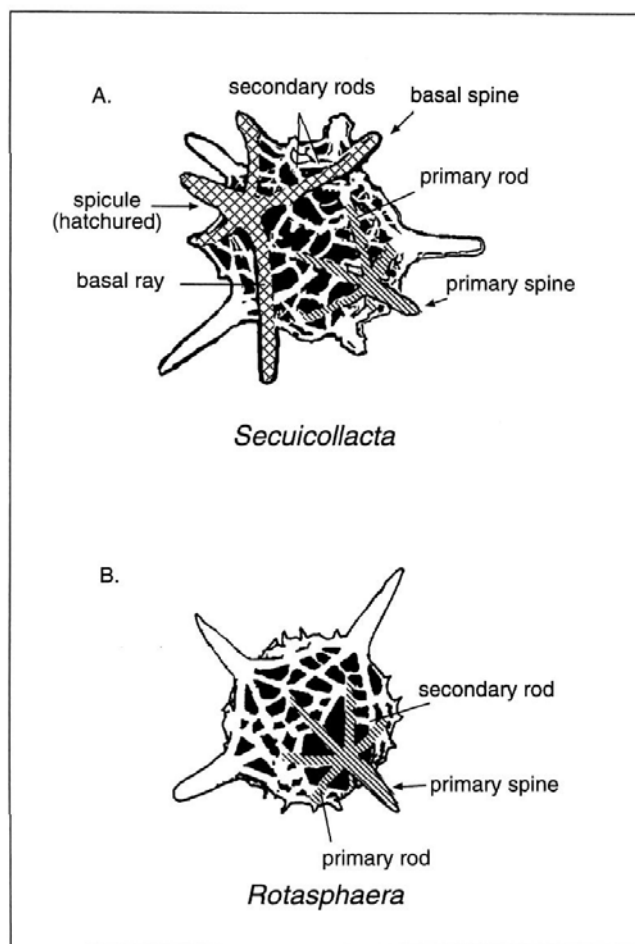
Diparvapila hickocki MacDonald 1998.
Plate 1, figure 5

Diparvapila hickocki MacDonald 1998, p. 590, figs. 4.6, 4.10-4.12, p. 601, figs. 8.9-8.11.

Remarks: As noted in the remarks under the original description, *D. hickocki* differs from *D. larseni* by having a more delicate shell with smaller pores and a regular pore arrangement. In addition, specimens we assign to this genus differ from those assigned to *D. larseni* by having slightly longer spines.

Diparvapila sp. A.
Plate 1, figure 1

Diparvapila sp. A MacDonald, 1998, p. 596, fig. 5.3, p. 602, figs. 9.4, 9.5



TEXT-FIGURE 4

A. Schematic diagram of *Secuicollacta* showing skeletal elements. The secuicollactine spicule is hatched and one of the primary spine units is striped. B. Schematic diagram of *Rotasphaera* showing skeletal elements as defined by Noble (1994). One of the primary spine units is striped.

Remarks: Specimens assigned to this species are most easily recognized by the tapered bladed spines. Rare; only 4 specimens picked.

Genus *PARVALANAPILA* MacDonald 1998

Parvalanapila ? sp.
Plate 1, figure 2

Remarks: Several specimens were tentatively assigned to this genus because their cortical shell appeared thicker than those specimens assigned to *Diparvapila*. In transmitted light, these specimens show what appears to be a single thick cortical shell composed of a latticed sphere on which the spicule sits. Additional layers of labyrinthine material cover the spicule to form a thicker cortical shell. While focusing through one or two specimens, a slight separation between the latticed inner shell and the labyrinthine covering is seen, suggesting that there may be two shells and these specimens may be more appropriately assigned to *Diparvapila*. They are a rare component of the assemblage.

Family PALAEOSCENIDIIDAE Riedel 1967
Genus PALAEOEPPHIUM Goodbody 1986

Palaeoepphium echinatum Goodbody 1986
Plate 1, figures 10, 11

Palaeoepphium echinatum GOODBODY 1986, p. 151, pl. 6, figs. 9-11, p. 7, figs. 1-3.

Remarks: Basal rays extend prominently from the connecting median bar to their distal termination. An array of spinules extends off ray each to form a loosely enveloping shell. Nine specimens were picked.

Insolitignum dissimile (Goodbody 1986)
Plate 1, figure 12

Palaeoepphium dissimile GOODBODY 1986, p. 141, pl. 3, figs. 10-12

Insolitignum dissimile MACDONALD 1999, p. 2053, pl. 1, figs. 2, 3, pl. 2, fig. 1.

Remarks: This taxon is fairly common. It appears as a naked spicule with incipient spinules and node-like projections running up the basal rays. The distinct feature in this species is one short basal ray that is angled differently than the other basal rays (Plate 1, fig. 12). MacDonald (in press) recognizes this species in the Canadian Arctic and considers the asymmetry of the fourth ray to be sufficient for placement in a new genus.

ACKNOWLEDGMENTS

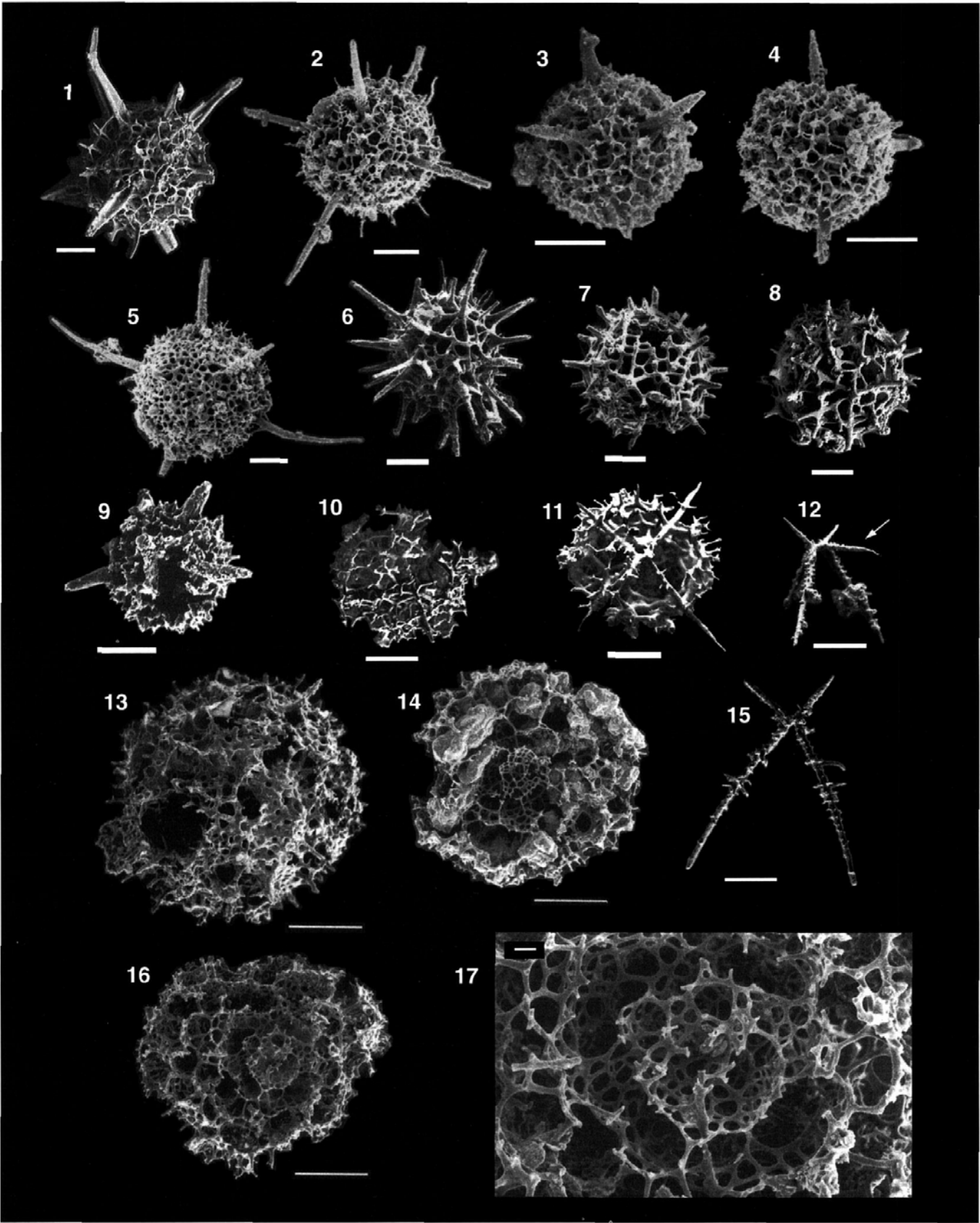
PJN would like to thank A. Braun, E. Amon, and A. Lenz for providing comparative material from the Tarangul Mountains and from the Canadian Arctic. We thank B. Carter and F. Mekik for comments that helped improve this manuscript. H. Gorka and E. MacDonald are thanked for their reviews.

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Plate 1

- 1 *Diparvapila* sp. A. MacDonald 1998. Scale bar = 50µm.
- 2 *Parvalanapila* ? sp. Scale bar = 50µm.
- 3,4 *Diparvapila larseni* MacDonald 1998. Scale bar = 50µm.
- 5 *Diparvapila hicoeki* MacDonald 1998. Scale bar = 50µm.
- 6 *Secuicollacta malevola* MacDonald 1998. Scale bar = 50µm.
- 7,8 *Secuicollacta vallipuellae* MacDonald 1998. Scale bar = 50µm.
- 9 *Secuicollacta glaebosea* MacDonald 1998. Scale bar = 50µm.
- 10,11 *Palaeoepphium echinatum* Goodbody 1986. Scale bar = 50µm. 10; view from side, 11; dorsal view.
- 12 *Insolitignum dissimile* (Goodbody 1986). Arrow points to asymmetrical basal ray. Scale bar = 50µm.
- 15 ? *Insolitignum dissimile* Goodbody 1986. Broken specimen. Scale bar = 50µm.
- 13,14, 16,17 *Haplotaeniatum cathanatum* Nazarov and Ormiston 1993. 13, Whole specimen showing pylome. Scale bar = 100µm. 14, Cross section showing overgrowths of cristoballitic silica that commonly obscure wall structure. Scale bar = 100µm. 16, Cross section showing subtle spiraliform layering. 17, Enlargement of Figure 16 showing spiraliform layering. Note that spiraling is not perfect, but the edge of each layer can be traced in an outwardly spiraling pattern. Note thin rods that protrude inward to the center of the sphere (broken) and may have formed an entactiniid spicule. No complete spicule was observed and any specimens. Scale bar = 10µm.



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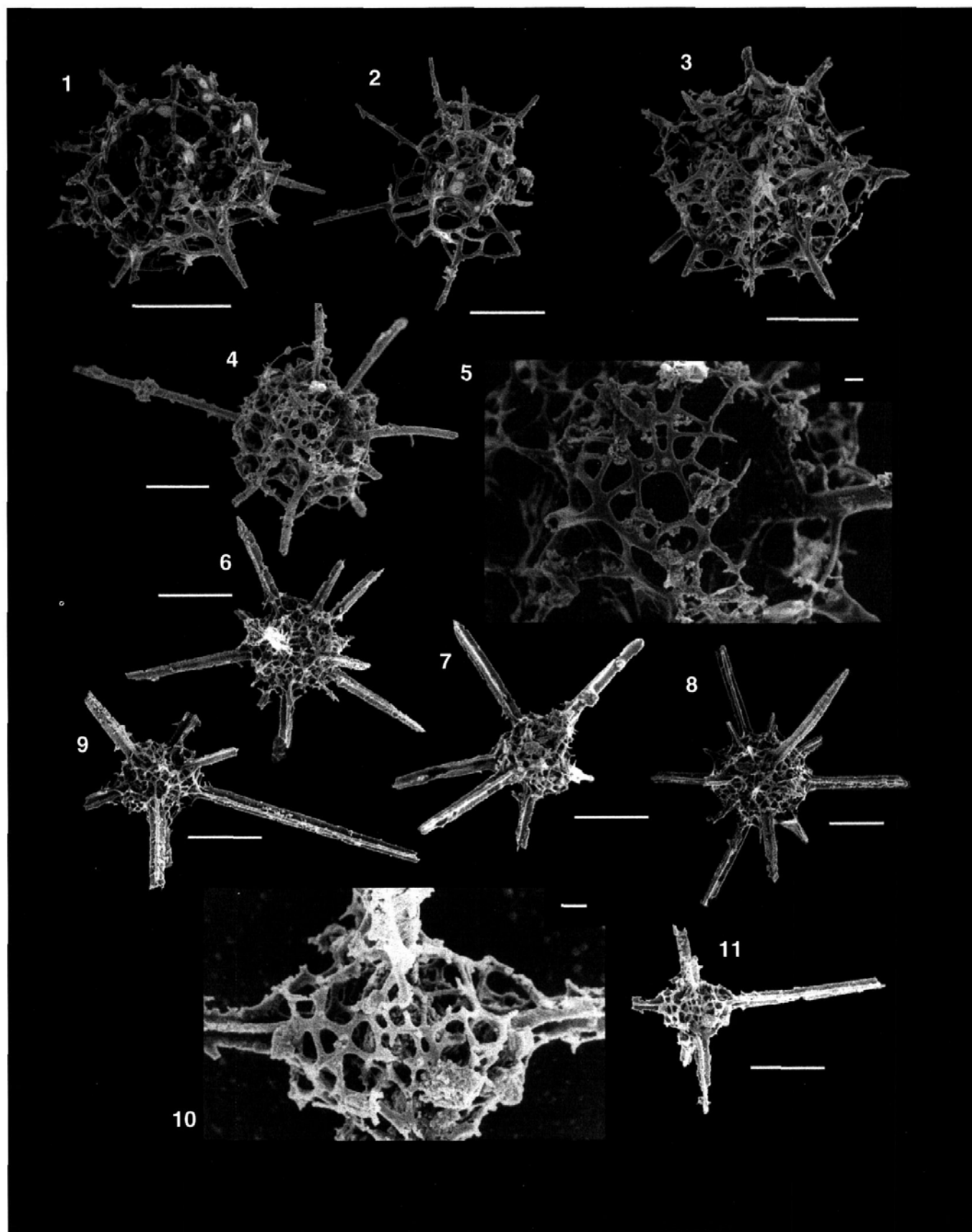
Manuscript received March 23, 1999

Revised manuscript accepted January 13, 2000

Plate 2

- 1-3 *Gyrosphaera raneatela* n. sp. Scale bar = 100µm. 1 and 2, paratypes, broken specimens showing loose packing of layers. Subtle spiraliform layering is seen in 1. 3, holotype.
- 4,5 *Gyrosphaera siljanensis* n. sp. 4, Holotype. Scale bar = 100µm. 5, enlargement of Holotype. Scale bar = 10µm.

- 6-11 *Labyrinthosphaera macdonaldi* n. sp. 8, Holotype. Note smaller tri-bladed secondary spines Scale bar = 100µm. 8, 7, 9, 11, Paratypes. Scale bar = 100µm. 10, Enlargement of 11 showing labyrinthine meshwork. Scale bar = 10µm.



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