The *Beothuka terranova* (Radiolaria) assemblage and its importance for the understanding of early Ordovician radiolarian evolution

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Abstract – The radiolarian *Beothuka terranova* occurs in the Arenigian *Didymograptellus bifidus* Biozone (uppermost Lower Ordovician) of Spitsbergen (Svalbard), associated with a diverse and well-preserved radiolarian fauna. The presence of typical Cambrian spicular radiolarians associated with derived spherical forms shows a gradational faunal change from the Cambrian to the Ordovician. The genus and species *Antygopora ordovicica* n. gen. et n. sp. is described.

Keywords: Ordovician, radiolarians, Spitsbergen, biostratigraphy, evolution.

1. Introduction

Lower Ordovician radiolarian assemblages are rare, and every new record yields important data and information for biostratigraphic correlation and interpretation. It is well known that radiolarians had a successful history already in the Cambrian, as diverse faunas have recently been described from Australia and western Newfoundland (Won & Below, 1999; Won & Iams, 2002), respectively. Similar faunas from Nevada (Kozur, Mostler & Repetski, 1996) are considered to be of lower Tremadocian age. Some taxa within these faunas were included in the Archaeospicularia (Dumitrica, Caridroit & De Wever, 2000), whereas the Archeoentactiniidae and Palaeospiculumidae (Won & Below, 1999) have uncertain relationships.

Aitchison, Flood & Malpas (1998) described distinctly different, supposedly lower Tremadocian radiolarians from the Little Port Complex of western Newfoundland, at the time a unique and the oldest known radiolarian assemblage. The fauna was recovered from red ribbon-bedded cherts found in tectonic contact with pillow lavas of an ophiolitic rock association dated radiometrically to 505 Ma. The age of the radiometrically dated rocks was used to infer the age of the radiolarian fauna as Tremadocian, based on the time scale of Harland et al. (1990). A biostratigraphic correlation was possible as the fauna was not associated with other fossils and was unique. The only biostratigraphically indicative datum was a possible specimen of the lower Ordovician conodont Cordylodus lindstroemi. The characteristic bipolar Beothuka terranova was the only named and described radiolarian of the fauna, whereas other faunal elements were illustrated, but left in open nomenclature. They include a second bipolar species as well as two different spherical forms, the detailed structure of which remains uncertain.

Younger Ordovician radiolarian faunas are referred to the Proventocitum procerulum fauna (Noble & Aitchison, 1995, 2000), thought to cover the whole Arenig time interval (Noble & Danelian, 2004). The fauna of this assemblage was described in some detail from Kazakhstan (Nazarov & Popov, 1980), Scotland (Aitchison, 1998) and Spitsbergen (Fortey & Holdsworth, 1971; Holdsworth, 1977). Danelian & Popov (2003) stated that the age of the fauna from Kazakhstan is Morrindunian (lower Arenigian), based on the co-occurrence with conodonts. Maletz & Bruton (2004) discussed a diverse middle Arenigian (late Castlemainian) radiolarian assemblage without Proventocitum procerulum from the Cow Head Group of western Newfoundland, associated with graptolites, indicating that these faunas are Castlemainian to lower Darriwilian. Proventocitum is not present in middle to upper Arenig, Chewtonian to Castlemainian faunas, suggesting that the Proventocitum fauna is considerably younger than previously thought and is most likely of lower to middle Darriwilian age. A gap in recorded radiolarian faunas of c. 20 Ma seems to be present in the lower Ordovician. The presence of a rich Beothuka *terranova* radiolarian assemblage in a graptolitiferous succession in Spitsbergen helps to fill this faunal gap.

2. The Lower Ordovician succession of Spitsbergen

The Lower to Middle Ordovician succession of Ny Friesland, northern Spitsbergen, has been described by



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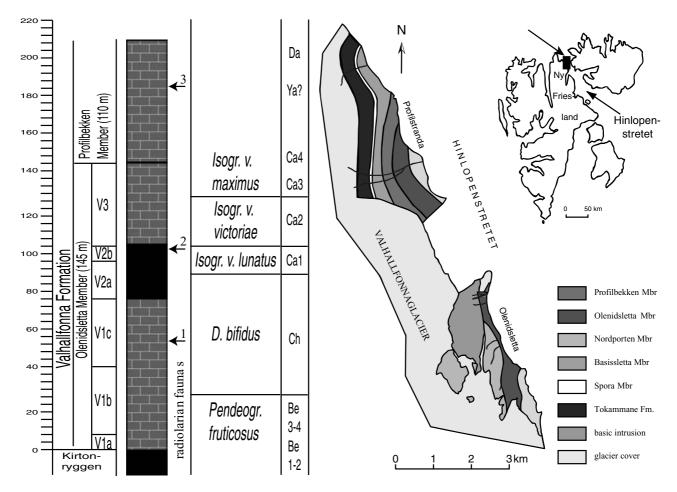


Figure 1. Lithostratigraphy of the Vahallfonna Formation (based on Fortey & Bruton, 1973) with graptolite biostratigraphy revised from Cooper & Fortey (1982). 1 – *Beothuka terranova* radiolarian level. 2 – *Isograptus victoriae lunatus* Biozone radiolarians, not described herein. 3 – *Proventocitum procerulum* radiolarian fauna described by Fortey & Holdsworth (1971).

Fortey & Bruton (1973). Fortey (1974, 1975*a*,*b*, 1980) has described the trilobite faunas and Cooper & Fortey (1982) documented the graptolite record. The latter show that the Valhallfonna Formation ranges from the *Pendeograptus fruticosus* Biozone to the *Oncograptus* Biozone, and possibly higher. Cooper & Fortey (1982, p. 159) even suggested that the Valhallfonna Formation may range into the lower Llanvirnian.

The Lower to Middle Ordovician succession of the Valhallfonna Formation crops out in the coastal area north and south of the Buldrebreen arm of the Valhallfonna glacier in cliffs along the shore in northeastern Ny Friesland, Spitsbergen (Fig. 1). The Valhallfonna Formation is about 255 m thick. The lower member, the Olenidsletta Member, is 145 m thick, dominated in the lower part (0–75 m) by black limestones and shales, while in the middle part (75–102 m) this lithology alternates with grey, crystalline limestones. Black limestone and shales make up the main part of the upper 43 m. The overlying Profilbekken Member is 110 m thick with more variable lithologies, dominated by brown to black limestones. Fossils are common in the Valhallfonna Formation, with trilobites and graptolites being the most important faunal elements for the established biostratigraphy.

3. Spitsbergen radiolarians

Radiolarians from the Spitsbergen succession were first recognized by Fortey & Holdsworth (1971), who provided a preliminary account of what they considered were the oldest known radiolarian species. The fauna came from a level at 180-185 m above the base of the Valhallfonna Formation, in the Profilbekken Member (radiolarian fauna 3 in Fig. 1). Trilobites in the limestones are comparable with those from the Middle Table Head Formation (Fortey & Holdsworth, 1971, p. 36), and correlation with the upper Arenigian to lower Llanvirnian was suggested. Albani et al. (2001) and J. Maletz (unpub. Habilitation thesis, Ernst-Moritz-Arndt Univ., 1998) referred the Table Head Group to the upper Darriwilian (Da 3-4, late Middle Ordovician) based on their graptolite faunas. Holdsworth (1977) indicated the presence of further, considerably older radiolarian faunas in the Spitsbergen succession. Part of this material is described herein and comes from

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the Olenidsletta Member (levels 54.82 m and 102 m) of the Valhallfonna Formation (see Cooper & Fortey, 1982, fig. 1). These samples contain distinct faunas, even though a number of faunal elements are common to both levels.

The Beothuka terranova assemblage (radiolarian fauna 1 in Fig. 1) is tied to a precise graptolite biostratigraphy (Fig. 1). The fauna comes from a level in the lower part of the middle Arenigian (Chewtonian) Didymograptellus protobifidus Biozone of Cooper & Fortey (1982), now the Didymograptellus bifidus Biozone (see Williams & Stevens, 1988 for taxonomy of Didymograptellus species). It can be dated at approximately 475 Ma (Webby et al. 2004). The graptolite biostratigraphy of Spitsbergen is closely comparable to that of the Cow Head Group of western Newfoundland described by Williams & Stevens (1986, 1988) and the Australasian succession (Cas & VandenBerg, 1988; VandenBerg & Cooper, 1992). As these successions are used as a worldwide standard for the Lower Ordovician, a major mis-correlation is unlikely to alter the correlation of radiolarian and graptolite biozonations.

3.a. Faunal composition

The radiolarians from the Valhallfonna Formation were isolated from limestone samples prepared for chitinozoans by Bockelie (1980), but never analysed. All radiolarians described herein come from a level at 54.82 m in the Olenidsletta Member. The fauna includes Beothuka terranova, numerous spherical radiolarians and spicular forms, as well as remains of indeterminable radiolarians and a few sponge spicules of various types. The preservation of the radiolarians is quite variable. Numerous spheres that are present represent re-crystallized spherical radiolarians (Fig. 20), but it is impossible to identify them, as all structure has been eliminated. This type of preservation affects more than 50 % of all specimens. Other forms are fragmented, especially larger specimens of labyrinthine spherical radiolarians with long spines (Fig. 2i), but preservation of some forms is excellent and they show all details of their structure. Most specimens of Beothuka terranova and numerous other forms appear to be re-crystallized, involving a coarsening of their previously fine bars or lattice shells (Fig. 2h). A second sample from a level at 102 m above the base of the Olenidsletta Member (radiolarian fauna 2 in Fig. 1) has not yet been investigated in detail. It bears a similar but more diverse and better-preserved fauna from which Beothuka terranova is absent. The fauna also includes the common Antygopora ordovicica n. sp. (Fig. ;4a, d, h).

The main component of the fauna is *Antygopora* ordovicica n. sp. with about 35 % of all specimens. *Beothuka terranova* is represented by c. 17 % of the identifiable specimens. A similar number of specimens of *?Entactinia* sp. (c. 17.5 %) can be counted. Palaeo-

spiculumids (7-8 %) are a rare component of the fauna, while parechidninids are more common (*c*. 22 \%) but cannot be attributed to a certain species as they are highly fragmentary.

4. Systematic description

The material examined during this investigation is preserved in the collections of the Geological Museum (formerly Palaeontological Museum PMO), University of Oslo, Norway.

Subclass RADIOLARIA Müller, 1858 Order POLYCYSTINA Ehrenberg, 1838 Suborder Incertae sedis Family Incertae sedis Genus *Beothuka* Aitchison, Flood & Malpas, 1998

Type species. Beothuka terranova Aitchison, Flood & Malpas, 1998.

Beothuka terranova Aitchison, Flood & Malpas, 1998 Figure 2e, f

1998 Beothuka terranova sp. nov. Aitchison, Flood & Malpas, p. 417, fig. 1a-o.

Remarks. This species is fairly common in the sample, and most specimens are well preserved and complete. Broken specimens do not show any internal structure. The Spitsbergen material compares well in size, shape and skeletal development to the original description of the species from the Little Port Complex.

Genus Antygopora n. gen.

Type species. Antygopora ordovicica n. sp.

Origin of name. From the Greek antyx, -ygos for edge or rim and pora (pore), referring to the characteristic pore structure of the test.

Diagnosis. Spherical radiolarians with two cortical tests, formed by a typical thin layer pierced by round pores with elevated rims and ornamented on the surface with distinct connecting ridges forming a honeycomb pattern; internal spicule and spines apparently lacking.

Remarks. The genus appears to be the earliest radiolarian with a surface made of wide bandages forming a two-dimensional, thin-layered surface or test, not produced by round bars as is typical of younger Ordovician inaniguttids (Fig. 5f) and secuicollactids (Fig. 6c). This type of shell development can be compared with the rim growth described by Anderson & Swanberg (1981) and Thurow & Anderson (1986), which is known in Cretaceous to modern radiolarians and may point to the origin of these distinct patterns as early as in the early Ordovician.

Very similar forms have been found in the late Arenig *Isograptus victoriae maximodivergens* Biozone of western Newfoundland (Fig. 5a, b), indicating a wider distribution and usefulness for this genus. They are not



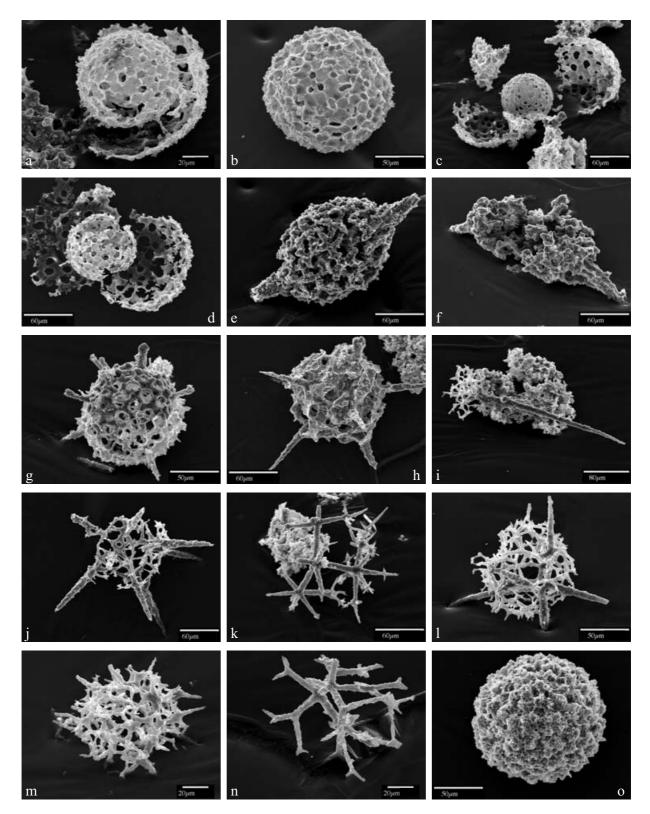


Figure 2. (a–d) *Antygopora ordovicica* n. gen. n. sp.: (a) PMO 205.718/13, holotype, showing two tests connected by few beams. (b) PMO 205.718/22, outer test with honeycomb surface structure. (c) PMO 205.718/44, specimen with broken outer sphere. (d) PMO 205.717/00, surface of inner sphere with several beams. (e, f) *Beothuka terranova* Aitchison, Flood & Malpas, 1998: (e) PMO 205.718/58, typical example. (f) PMO 205.718/129, broken specimen showing inside and grooved base of spine. (g) *Antygopora* (?) sp. PMO 205.718/73, specimen with one test bearing large pores with raised rims and about 10–12 spines. Indication of inner beams or spicule is visible on lower left side. (h, j) *Parechidnina* sp. B: (h) PMO 205.717/188, complete specimen with short spines. (j) PMO 205.717/08, juvenile form? (i) *Parechidnina* sp. A, PMO 205.718/25, long spine with labyrinthine mesh at base. (k) *Palaeospiculum* sp., PMO 205.718/28. (l) *?Entactinia* sp., PMO 205.718/190, showing ectopically placed spicule with six rays. (m) *?Parechidnina* sp., PMO 205.718/107, fragment. (n) *Ramuspiculum* sp., PMO 205.718/59. (o) PMO 205.717/43, re-crystallized sphere indet.



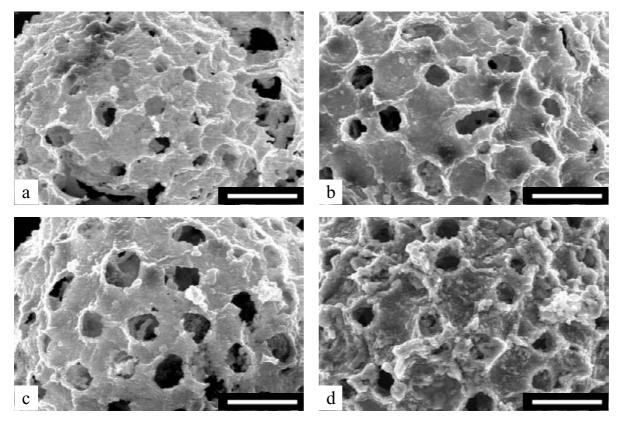


Figure 3. *Antygopora ordovicica* n. sp. surface details. (a) PMO 205.718/13, holotype, inner test, showing rims around pores and honeycomb structure. (b) PMO 205.718/22, outer test, showing strong rims and indications of honeycomb structure. (c) PMO 205.718/39, inner sphere with little indication of raised rims around pores, juvenile. (d) PMO 205.718/118, outer test, partially re-crystallized surface. Scale bar represents 20 μm.

known from younger Middle Ordovician faunas (see Danelian & Popov, 2003; Aitchison, 1998; Fortey & Holdsworth, 1971).

A form lacking the typical honeycomb surface structure of *Antygopora ordovicica* n. sp. has been included in the genus provisionally (Fig. 5d) as the distinct pore structure is prominent. The form was found in the Castlemainian of western Newfoundland and may indicate a considerable variability in this character in the genus.

Antygopora ordovicica n. gen. n. sp. Figures 2a–d, 3, 4, 5b, 6b

Type material. More than 40 specimens from a sample collected at a level 54.82 m above the base of the Valhallfonna Formation in the type section of the Olenidsletta Member, preserved on SEM stubs PMO 205.717, PMO 205.718.

Origin of name. From the presence of this species in the Ordovician.

Description. The thin inner sphere has a diameter of about 90–100 μ m. It is produced from wide and short bandages forming a relatively regular thin layer with rounded pores (Figs 3, 4). The distinct rims of the pores are slightly elevated in immature specimens (Fig. 4a, b,

d, e) and more strongly raised in mature ones (Fig. 4c, f), forming distinct surroundings of the circular pores. The typical layer of the test appears to be formed initially from bandages or ribbons (Fig. 4b, e). The bandages are about 6–9 μ m wide and about 1 μ m or less thick. The pores have a diameter of 8– 10 μ m and are usually round, but some forms with an elongated shape are also present (Fig. 2b) due to growth irregularities. The distribution of the pores is regular, but some may be closed in later ontogenetic stages so that the pores appear more irregular in spacing (Fig. 4i).

The inner and outer spheres are connected by sparse beams $3-5 \mu m$ in thickness (Fig. 2a, d). The origin of these beams is uncertain. There is no indication that they continue as spines inside the inner sphere. There is also no indication that they continue outside and thus they are not called spines here, even though in immature specimens in which the outer test is not present, they might appear spine-like (Fig. 4b, g).

The surfaces of the bandages usually bear thin crests or ridges connecting the raised rims of the pores commonly forming the hexagonal pattern, characteristic of this species (Fig. 2a, b, 3). In mature specimens the surface might appear to be composed of deep depressions with conspicuous hexagonal pattern



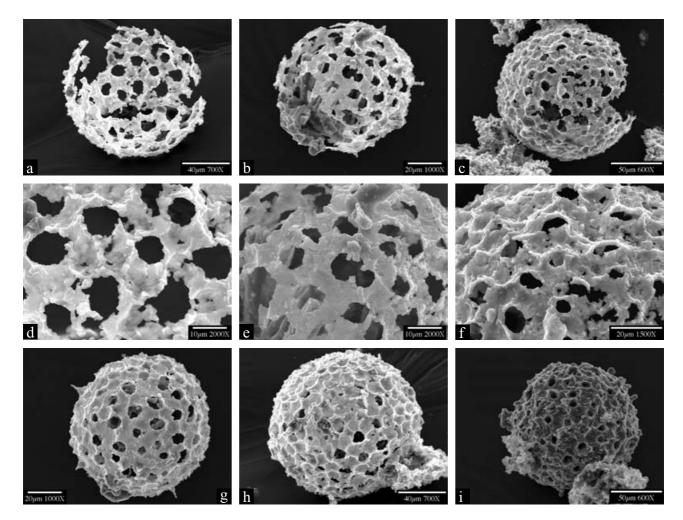


Figure 4. Ontogenetic change in *Antygopora ordovicica* n. sp. (a, d) PMO 205.715/177, juvenile with thin test and poorly developed elevated rims around pores. (b, e) PMO 205.717/12, slightly older form showing bandage-like surface of the test with vague indications of rims around pores and indications of beams originating from the side of bandages. (c, f) PMO 205.717/11, specimen with thicker test and pronounced rims, honeycomb structure visible. (g) PMO 205.717/74, specimen with poorly developed honeycomb structure and indication of widely spaced beams. (h) PMO 205.715/176, mature specimen with thick test. (i) PMO 205.718/118, specimen with thickened test and strongly developed surface structure and reduced width of pores. Specimens from sample 54.82 m, except (a, d, h) from sample 102 m.

and occasional pores (Fig. 4h). The development of the outer sphere is identical to the inner sphere and is therefore not described in detail here. The diameter of the outer sphere ranges between 125 and 140 μ m.

Remarks. The species is the most common radiolarian species in the sample. Considerable variation can be seen in the preservation of the shells, especially in wall thickness and the number of open pores, between immature and mature specimens, reflecting a distinct ontogenetic growth style (Fig. 4). Re-crystallization of specimens can result in much higher wall thickness (Fig. 4i).

Antygopora (?) sp. Fig. 2g

Material. One single, well-preserved specimen and a few fragments.

Description. Even though only one specimen is available, it is so distinct that a full description may be useful. The specimen has a sphere c. 105 μ m in diameter. The sphere is formed of wide bandages as in *Antygopora ordovicica* n. sp., but the raised rims of the pores are much more pronounced and reach a height of 5 μ m. The bars are only about 5 μ m wide, whereas the pores have a diameter of 8–10 μ m. There are numerous, short, blunt outer spines or more probably beams that might indicate the presence of a second sphere in complete specimens. There is evidence of inner spines or possibly an inner spicule (Fig. 2g).

Remarks. This morphotype differs from *A. ordovicica* n. sp. through the distinctly more prominent raised rims around the pores and the blunt spines. No connecting ridges or crests are visible on the surface of the specimen forming a hexagonal pattern.



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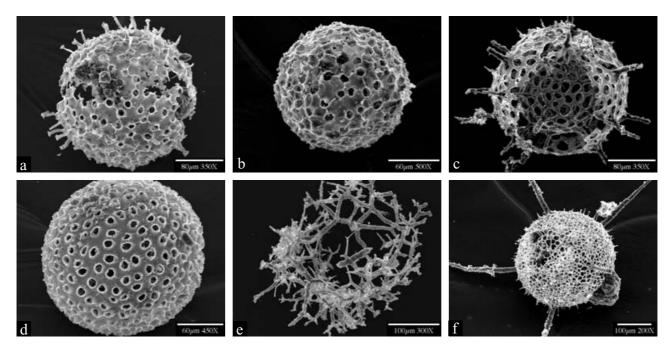


Figure 5. Radiolarians from the *Isograptus victoriae maximodivergens* Biozone of western Newfoundland. (a) *Antygopora* sp., JM 3.43, specimen with numerous blunt-ending beams indicating the presence of a second test and well-developed surface ornamentation. (b) *Antygopora ordovicica* n. sp., JM 3.68, typical mature specimen. (c) JM 6.19, spherical radiolarian indet. with numerous spines and beams. (d) *Antygopora* sp., JM 3.8, form without the typical honeycomb structure of *A. ordovicica*. (e) *?Parechidnina* sp., JM 5.59, specimen showing the bar-centred spicule and a loose three-dimensional mesh. (f) JM 1.5BB, spherical radiolarian indet. with long spines; internal and external beams are visible on the mesh of the outer shell.

?Entactinia sp. Fig. 21

Material. More than 20 specimens.

Description. The spicule is six-rayed with a c. 10 µm long median bar. The pointed rays are up to 80 µm long and 5–8 µm in diameter. The rays show a tetrahedral distribution. The sphere is constructed from apophyses on the spicule rays, which initially form a small hollow sphere of c. 60–70 µm in diameter. This is developed from thin (2–5 µm wide), irregularly branching bars forming meshes 10–15 µm wide. The meshes extend into a three-dimensional framework with a number of thin, external spines, not connected directly to the spicule. The test diameter is about 100 µm in the largest specimens. The spicule is included in the three-dimensional outer test in larger specimens and may be difficult to detect except for the protruding spines.

Remarks. *?Entactinia* sp. differs from the Cambrian to Lower Ordovician Archeoentactiniidae (Won & Below, 1999) in possessing a median bar-centred spicule. The true relationship of this form is unknown, as little is known about the origin and early evolution of the entactinids. A relationship to the Entactiniidae or Haplentactiniidae is possible, but wall structures in the Entactiniidae differ considerably from those of the species here described. Won (1997*a*,*b*) revised the Devonian Entactiniidae and also commented on some

early members. She also indicated that the relationship of the Haplentactiniidae to the Entactiniidae is uncertain.

Family PALAEOSPICULUMIDAE Won *in* Won & Below, 1999

Genus Palaeospiculum Won in Won & Below, 1999

Type species. Palaeospiculum burkensis Won *in* Won & Below, 1999.

Palaeospiculum sp. Fig. 2k

Remarks. This form is not common in the sample studied. Usually it is preserved as a small hexactine spicule with little distal branching. It rarely attains a size of more than 150 μ m. The rays are about 10 μ m in diameter and thin gradually towards their distal end. The branching occurs at distinct distances, mostly *c*. 50 μ m, where whorls of spines or spinules are produced. Distally, branching distances are more irregular.

The material looks similar to specimens of *Pa-laeospiculum greenpointensis* Won & Iams and *P. martinpointensis* Won & Iams. It clearly indicates the presence of typical late Cambrian faunal elements in the middle Arenig.

Genus Ramuspiculum Won & Iams, 2002

Type species. Ramuspiculum multiramosum Won & Iams, 2002.



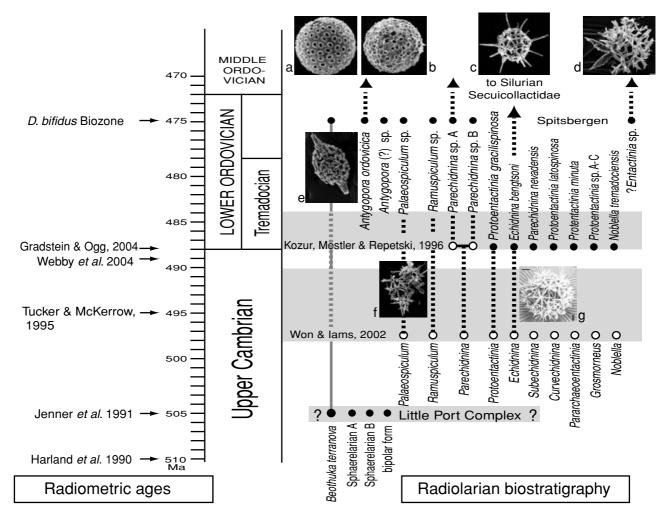


Figure 6. Upper Cambrian to lower Ordovician radiolarian faunas and time scale. For the highly diverse Cambrian faunas of Won & Iams (2002) only the genus names are given for easier comparison. Grey underlain areas show uncertainties in biostratigraphic ranges. Dotted lines indicate known ranges of genera. Specimens: (a) *Antygopora* sp., JM 3/60, western Newfoundland, *Isograptus victoriae maximodivergens* Biozone. (b) *Antygopora ordovicica* n. sp., JM 3/68, western Newfoundland, *Isograptus victoriae maximodivergens* Biozone. (c) *Secuicollacta* sp. Llandovery, Dalarna, Sweden. (d) Entactinid species indet., PMO 205.716/44, Spitsbergen, 102 m level. (e) *Beothuka terranova*, PMO 205.718/58, Spitsbergen. (f) *Palaeospiculum* sp. PMO 205.715/55, Spitsbergen, 102 m level. (g) *Subechidnina florea*, western Newfoundland (Won & Iams, 2002).

Ramuspiculum sp. Figure 2n

Remarks. Very few specimens have been found that belong to *Ramuspiculum*. They are all small, with a point-centred hexagonal spicule and irregular distal branchings. The maximum size of the forms is about 100 μ m.

Genus Parechidnina Kozur, Mostler & Repetski, 1996

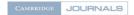
Type species. Parechidnina nevadensis Kozur, Mostler & Repetski, 1996.

Parechidnina specimens Figure 2h-j, ?m

Remarks. Numerous fragments of labyrinthine forms are present in the material. However, complete specimens have not been discovered. The material

may be separated into two main groups showing closest relationships to the upper Cambrian to lower Ordovician (Tremadocian) genus *Parechidnina* Kozur, Mostler & Repetski. A group of long-spined forms (*Parechidnina* sp. A) is represented by a few specimens (Fig. 2i). The material consists of slender spines, up to 250 μ m long and at maximum 10 μ m wide, which taper gradually towards their distal ends. Remains of a three-dimensional mesh are present at the proximal end of the spines. The number of spines and size of the test are unknown.

The second group (*Parechidnina* sp. B) contains forms with robust and short spines, usually not more than 110 μ m long and 10 μ m wide (Fig. 2h, j). They taper both proximally and distally. More complete fragments show that the spines do not meet in the centre of the radiolarian. The spines are connected by round bars, straight or slightly curved, *c*. 4–5 μ m in



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diameter, forming a coarse three-dimensional mesh. A few fairly complete specimens show a less dense mesh that appears to develop into a spherical shape with an empty interior (Fig. 2j). Other complete specimens are strongly re-crystallized and do not show internal details at all (Fig. 2h). The material shows structural relationships to *Parechidnina* (see Won & Iams, 2002), especially in the development of the three-dimensional mesh formed from thin radial spines or bars and curved connecting bars, and is therefore included in the genus.

5. The age of the *Beothuka terranova* radiolarian assemblages

A radiolarian assemblage including Beothuka terranova was first described from the Little Port Complex of western Newfoundland (Aitchison, Flood & Malpas, 1998). The material was isolated from cherts associated with pillow basalts in a tectonic mélange and interpreted as an ophiolitic succession in the Humber Arm allochthon (Williams, 1973, 1975). The igneous rocks of the Little Port Complex yielded U/Pb zircon ages of 508 ± 8 Ma (Mattinson, 1975) and 505 ± 3 Ma (Jenner et al. 1991; Cawood & Suhr, 1992). These ages were used to determine the age of the Beothuka terranova assemblage as the only fossils found in the complex, except for a possible specimen of the conodont Cordylodus lindstroemi. Aitchison, Flood & Malpas (1998) inferred a basal Ordovician (Tremadocian) age for the faunas, based on the time scale of Harland et al. (1990), even though they mentioned that newer evidence pointed to an age of 495 Ma for the base of the Ordovician (Tucker & McKerrow, 1995). Thus, the fauna could have been correlated with the Late Cambrian. Unfortunately the radiolarian assemblage was the only one of this composition known and an independent biostratigraphic determination was not possible at the time. As new radiometric dating positions the Cambrian/Ordovician boundary at c. 488 Ma (Gradstein & Ogg, 2004), the inferred Tremadocian age of the Little Port Complex Beothuka fauna may be questioned. The chronostratigraphic correlation of the radiometric date with the time scale of Gradstein, Ogg & Smith (2005) would now indicate its age to be Middle Cambrian. The presence of the fauna in a tectonic mélange instead of in a rock succession, however, may shed doubt on the age of the fauna based on a radiometric dating.

A comparison of recently described Middle and Upper Cambrian (Won & Below, 1999; Won & Iams, 2002; Dong, Knoll & Lipps, 1997) and Tremadocian, Lower Ordovician (Kozur, Mostler & Repetski, 1996) radiolarians with the *Beothuka* assemblage can now be made and gives further evidence of a different age for the *Beothuka terranova* assemblage of western Newfoundland (Fig. 6). The Spitsbergen *Beothuka terranova* assemblage includes a number of taxa (*Parechidnina* sp., *Palaeospiculum* sp., *Ramuspiculum* sp.) found already in upper Cambrian to Tremadocian faunas, but also faunal elements, relating to younger Arenigian faunas (*?Entactinia* sp., *Antygopora* spp.). The *Beothuka terranova* assemblage from the Little Port Complex bears spherical radiolarians that may be related to *Antygopora* as well as other spined spherical forms, but none of the Late Cambrian palaeospic-ulumids and echidninids. It shows that the *Beothuka terranova* assemblage is quite different from these Cambrian to early Ordovician assemblages. It is most likely that the *Beothuka terranova* assemblage in the Little Port Complex is not of the age reflected in the radiometric dating of the succession and, based on palaeontological evidence, should be re-assigned to the Arenigian.

6. Evolution of early Ordovician radiolarian faunas

Upper Cambrian radiolarians are best known from the Cow Head Group of western Newfoundland (Won & Iams, 2002). They include spicular forms referred to the Archeoentactiniidae (Pararcheoentactinia), Palaeospiculumidae (Palaeospiculum, Ramuspiculum), Protoentactiniidae (Protoentactinia) and Echidninidae (Echidnina, Curvechidnina, Subechidnina) and the genera Paraechidnina and Grossmorneus with uncertain relationships. The recognized genera are shown in the range chart (Fig. 6). Little is known about their exact biostratigraphic ranges as few samples have been investigated by Won & Iams (2002). The Echidninidae and Protoentactiniidae were also found in the Tremadocian of Nevada (Kozur, Mostler & Repetski, 1996), whereas in the Beothuka assemblage of Spitsbergen the Palaeospiculumidae are represented by a single species of Palaeospiculum and Ramuspiculum, associated with common Parechidnina specimens. The comparison of the spherical forms from the Little Port Complex with the Spitsbergen fauna is difficult due to the poor preservation, but they may indicate an Arenigian age also.

The upper Cambrian Cow Head Group fauna of Won & Iams (2002) is connected by a number of faunal elements with mid-Arenigian radiolarian faunas of Spitsbergen, and the Tremadocian fauna of Kozur, Mostler & Repetski (1996) bridges these. Noble & Danelian (2004) discussed a complete faunal turnover in the early Ordovician, somewhere in the late Tremadoc, as known faunas did not show any common faunal elements between Cambrian and Ordovician faunas. They observed that several new body plans appeared suddenly in the Arenig, including the proventocitids and inaniguttids. However, a change in diversity was not observed associated with this turnover. They also noted a considerable gap in our knowledge of Lower Ordovician radiolarian faunas that may have contributed to the assumption of a total faunal turnover.

The upper Castlemainian radiolarian fauna from western Newfoundland (Maletz & Bruton, 2004) bears *Antygopora ordovicia* n. sp. (Fig. 5b) and a related form



without the typical honeycomb structure (Fig. 5d), indicating the distinctiveness of the Arenigian radiolarian faunas.

The middle Arenigian Beothuka fauna of Spitsbergen suggests that the radiolarian faunal turnover is actually a progressive replacement of faunal elements and a number of important upper Cambrian genera, especially of the Palaeospiculumidae, and the parechininids survive for a fairly long time into the Arenigian. The supposed phylogenetic relationship of the Cambrian Echidninidae and the Silurian Secuicollactidae, forming the Archaeospicularia of Dumitrica, Caridroit & De Wever (2000), would also indicate that intermediate forms should be present in the Lower Ordovician, even though they have not been recorded. A closer relationship of lower Palaeozoic radiolarians and a stepwise turnover can be therefore expected. Detailed structural investigation of the Arenigian radiolarian assemblages of western Newfoundland will certainly add further to the understanding of early Palaeozoic radiolarian evolution.

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