

A diverse Upper Darriwilian radiolarian assemblage from the Shundy Formation of Kazakhstan: insights into late Middle Ordovician radiolarian biodiversity

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ABSTRACT – A diverse and well-preserved radiolarian assemblage was extracted from a carbonate sample of latest Darriwilian age from the Shundy Formation of the Aksuran Mountain (North Balkhash Region, Kazakhstan). The fauna is represented by 32 species or morphotypes which belong to nine genera, four families and two orders (Spumellaria and Entactinaria), including four new species described herein (*Syntagentactinia? angulata* n. sp. Pouille & Danelian, *Polyentactinia spinulenta* n. sp. Pouille & Danelian, *Haplotaeniatum circulus* n. sp. Pouille & Danelian and *H.? giganteum* n. sp. Pouille & Danelian). Representatives of the family Inaniguttidae are particularly abundant, representing c. 70% of the studied assemblage, especially genera *Triplococcus* and *Inanihella* that dominate the assemblage. Although the studied fauna contains both of the characteristic species and most of the genera of the previously defined *Haplentactinia juncta*–*Inanigutta unica* assemblage, differences in the assemblage structure are striking. The studied fauna also establishes that the two characteristic species of the *Inanihella bakanasensis*–*Triplococcus akzhala* assemblage are not restricted to the early–mid-Darriwilian, but their age range also extends to the latest Darriwilian..

KEYWORDS: Radiolaria, taxonomy, palaeobiodiversity, Darriwilian, Ordovician, Kazakhstan

INTRODUCTION

In spite of the major progress achieved recently in understanding the ‘Great Ordovician Biodiversification Event’ (Webby *et al.*, 2004; Servais *et al.*, 2010), our knowledge of the biodiversity and diversification dynamics of some biotic groups is still very fragmentary. This is particularly true for polycystine Radiolaria, a major component of the oceanic heterotrophic plankton in Early Palaeozoic marine ecosystems, from which only a few radiolarian assemblages have so far been recognized (Noble & Danelian, 2004; Maletz, 2007; Noble & Webby, 2009; Danelian *et al.*, 2013).

Middle Ordovician radiolarian faunas recovered from carbonate sequences in Kazakhstan are of major significance for advancing our understanding of Ordovician Radiolarian biodiversity. Middle Ordovician radiolarian assemblages are also known from siliceous sequences of Lower Palaeozoic orogenic belts (i.e. Scotland: Danelian & Clarkson, 1998; Danelian & Floyd, 2001; Kyrgyzstan: Danelian *et al.*, 2011; China: Buckman & Aitchison, 2001), but they are less well preserved, due to differences in taphonomic history and laboratory processing.

To date in Kazakhstan, three distinct Ordovician assemblages have been recognized from a restricted number of localities, dispersed around Lake Balkash (Nazarov, 1975, 1988; Nazarov *et al.*, 1977; Nazarov & Popov, 1980; Nazarov & Ormiston, 1993; Danelian & Popov, 2003), as follows (Fig. 1):

- The *Inanihella bakanasensis*–*Triplococcus akzhala* assemblage, described by Danelian & Popov (2003) from sample 8807-A of the Akhzal Formation. This assemblage was initially considered as Floian in age, but later it was also recovered from the lower Darriwilian of Argentina (Maletz *et al.*, 2009) and was considered as covering the upper Dapingian–lower Darriwilian interval (Maletz 2007, 2011).
- The *Proventocitum procerulum* assemblage was described by Nazarov & Popov (1980) from the middle Darriwilian of Kazakhstan (sample 19, coming from the Kurchilik Formation).

It was also recorded from Spitsbergen (Fortey & Holdsworth, 1971; Holdsworth, 1977; Maletz & Bruton, 2008) and Scotland (Aitchison, 1998). The *Proventocitum procerulum* assemblage was at first thought to range from late Floian to early Darriwilian (Nazarov & Popov, 1980; Danelian & Popov, 2003), but it is now referred to as Darriwilian in age (Maletz, 2007; Maletz & Bruton, 2008).

- The *Haplentactinia juncta*–*Inanigutta unica* assemblage was described by Nazarov & Popov (1980) from sample 553a, coming from the lower part of the Bestomak Formation (Chingiz Range). The radiolarian assemblage co-occurs with a diverse trilobite and brachiopod assemblage suggesting a latest Darriwilian–earliest Sandbian age (Nazarov & Popov, 1980). The radiolarian-bearing carbonate level is overlain in this section by black shales with graptolites of the *Nemagraptus gracilis* Biozone (lowermost Sandbian).

A new, diverse and rather well-preserved radiolarian assemblage from the uppermost Darriwilian in Kazakhstan is presented here. The radiolarian assemblage is dominated by members of the family Inaniguttidae, represented by five genera (*Triplococcus*, *Inanihella*, *Inanigutta*, *Inanibigutta* and *Kalimnasphaera*) and 14 species, which have been documented and discussed recently by Pouille *et al.* (2013), together with several co-occurring trilobites. This paper focuses essentially on the taxonomic study of the rest of the fauna that includes 18 species and morphotypes that belong to the families Haplentactiniidae, Polyentactinidae and Haplotaeniatidae, including four new species. It allows considerable improvement to our understanding of the radiolarian palaeobiodiversity during the late Darriwilian, a critical interval in the context of the Ordovician diversification (Servais *et al.*, 2008, 2010).

STRATIGRAPHIC SETTING AND AGE

The radiolarian-bearing sample was collected from locality 112, about 1100m WSW of the Aksuran Mountain (NW of Lake



Fig. 1. Schematic map indicating the location of Ordovician radiolarian-bearing samples from the Aksuran Mts, Kazakhstan discussed in this study (including sample 112). Boundaries limiting the main tectonic terranes present in the area are shown (modified after Danelian & Popov, 2003).

Balkhash) in the Atasu-Zhamshy Region (47°32'40.77"N, 73°2'47.34"E; Fig. 1). It was sampled from the middle part of the Shundy Formation, which consists of deep-water, black or dark grey bedded limestones intercalated with thin dark grey cherts, which probably accumulated at the base of a slope of a passive continental margin of a Lower Palaeozoic microplate. Details about its geological and stratigraphic setting are provided in Pouille et al. (2013).

Graptolites, identified by Tsai (in Apollonov et al., 1990) as *Hustedograptus* ex gr. *teretiusculus*, occurring in the same stratigraphic level as the radiolarian-bearing sample 112 suggest a

latest Darriwilian age. The trilobites (*Endymionia semielliptica*, *Nambeetella?* sp. and *Porterfieldia* sp. aff. *P. delicata*) found associated with the sample confirm this age (Pouille et al., 2013). Moreover, two radiolarian genera commonly present in sample 112 (*Syntagentactinia* and *Kalimnaspheara*) are known to first occur in the *Haplentactinia juncta*–*Inanigutta unica* assemblage which can be best correlated with the uppermost Darriwilian–lowermost Sandbian (see, for example, the discussion in Nazarov & Ormiston, 1993; Danelian & Popov, 2003; Maletz, 2011). Our assemblage also contains *Haplentactinia juncta*, one of the characteristic species of the *Haplentactinia juncta*–*Inanigutta unica* assemblage.

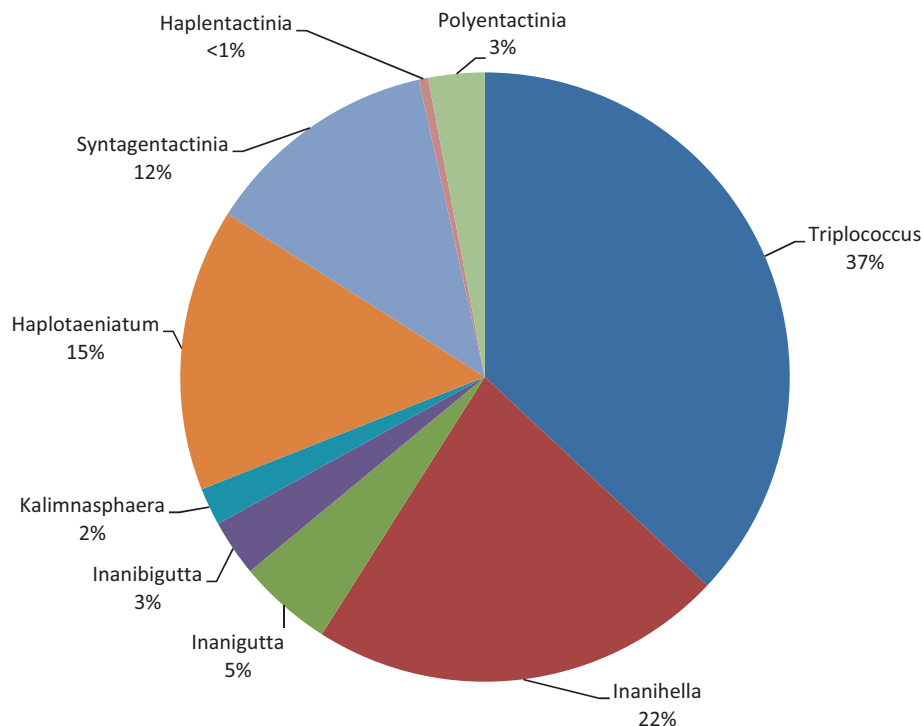


Fig. 2. Pie diagram showing the percentage relative abundance of radiolarian genera composing the assemblage of sample 112.

MATERIAL AND METHODS

Radiolarians were extracted from a black to dark grey micritic limestone sample after a standard treatment with 30% diluted acetic acid. Taxonomic study of this assemblage was made on the basis of SEM observation on over 450 specimens. This newly discovered assemblage is highly diverse, with a good state of preservation. All the types described here are housed in the public palaeontological collections of the Earth Sciences Department (SN5) of the University Lille 1 (France).

FAUNAL COMPOSITION

The identified radiolarian assemblage consists of four families (Inaniguttidae, Haplotaeniatidae, Haplentactiniidae and Polyentactiniidae), nine genera (*Inanihella*, *Triplococcus*, *Inanigutta*, *Inanibigutta*, *Kalimnaspheara*, *Haplotaeniatum*, *Syntagentactinia*, *Polyentactinia* and *Haplentactinia*) and 32 species or morphotypes. The radiolarians are dominated by inaniguttid species, which represent over two-thirds of the assemblage (69%; Fig. 2); they are represented by 5 genera (*Inanihella*, *Triplococcus*, *Inanigutta*, *Inanibigutta* and *Kalimnaspheara*) and 14 species. The rest is composed of *Haplotaeniatum* (15%), *Syntagentactinia* (13%), *Polyentactinia* (3%) and rare *Haplentactinia* (Fig. 2). The family Inaniguttidae is dominated by the genus *Triplococcus* that represents half of the Inaniguttidae (54%) and 37% of the whole assemblage (Fig. 2). Genus *Triplococcus* is represented in proportion of 89% by two species: *T. aksuranensis* (49%) and *T. akzhala* (40%) which are predominant, representing one-third (33%) of the assemblage. Genus *Inanihella* is dominated by 3 species (*I. hirta*, *I. bakanasensis* and *I. sp. B*) and represents 32% of the Inaniguttidae and 22% of the whole assemblage. The rest of the family Inaniguttidae is composed of *Inanibigutta* (8%), *Inanigutta* (4%) and *Kalimnaspheara* (2%).

The Haplotaeniatidae are composed, for a large part, of *H. sp.* cf. *H. tegimentum*, representing half of the *Haplotaeniatum* present in the sample (54%), *H. nobleae* (24%) and *H. circulus* (10%). The Haplentactiniidae are composed of 98% of representatives of the genus *Syntagentactinia*, dominated by *S.?* sp. cf. *S. excelsa* (47%). Genus *Haplentactinia* is represented by only one species: *H. juncta*, which represents 2% of the Haplentactiniidae. The family Polyentactiniidae is dominated (73%) by the species *P. spinulenta*.

SYSTEMATIC PALAEONTOLOGY (L. Pouille & T. Danelian)

Order Entactinaria Kozur & Mostler, 1982

Family Haplentactiniidae Nazarov in Nazarov & Popov (1980)

Genus Syntagentactinia Nazarov in Nazarov & Popov (1980)

Type species. *Syntagentactinia biocculosa* Nazarov in Nazarov & Popov (1980).

Syntagentactinia biocculosa Nazarov in Nazarov & Popov (1980)
(Pl. 1, figs 5–7)

1980 *Syntagentactinia biocculosa* Nazarov in Nazarov & Popov:
56; pl. 12, figs 1–3.

Material. Five specimens.

Description. Internal structure consists of a five- to six-rayed primary spicule incorporated in a small latticed inner shell. The primary rays of the initial spicule are prolonged outside into long rod-like spines (up to 200 µm). These primary spines can be straight or slightly curved on their proximal part. A small internal cavity with an irregular outline separates the inner shell from the outer shell. The outer shell structure consists of three to four spongy shell layers of irregular outline and that are closely interconnected by numerous

radial beams in a very complex three-dimensional arrangement. The different spongy layers of the shells are hardly distinct. The outer shell is mostly spherical (rarely sub-spherical) and displays a spongy external aspect. Inside the inner cavity, rare apophyses can branch from the primary rays to join the inner shell surface.

Dimensions (µm). Diameter of the outer shell: 232–277; of the inner shell: 76–98; length of primary spines: 120–220; thickness of the outer structure: 80–110.

Remarks. The skeleton structure and dimensions of *S. biocculosa* are very close to those of *S.?* sp. cf. *S. excelsa* Nazarov & Ormiston. However, it differs from it in possessing six long, robust rod-like spines, a less loose latticed inner shell and in having a less distinct inner cavity. It also differs from *S. pauca* Nazarov in possessing a thick multi-layered spongy outer shell and in its larger size. It also differs from *S. afflicta* Nazarov & Ormiston in the absence of internal half-closed shells, in the larger size of its inner shell (as compared with the material of Nazarov & Ormiston, 1993) and in its smaller size (for the material illustrated by Kurihara & Sashida, 2000).

Syntagentactinia? sp. cf. *S. excelsa* Nazarov & Ormiston, 1993
(Pl. 1, figs 1–4)

cf. 1993 *Syntagentactinia excelsa* Nazarov & Ormiston: 40; pl. 6, figs 13–14.

cf. 2000 *Syntagentactinia excelsa* Nazarov & Ormiston; Kurihara & Sashida: 153; figs 7.19, 7.20; 8.1–8.7.

Material. 29 specimens.

Description. The inner framework consists of a distinct spherical to subspherical loosely latticed inner sphere, centrally or slightly eccentrically located inside the internal cavity. The outer shell consists of a thick spherical spongy meshwork formed of three to four latticed shell layers closely interconnected in a three-dimensional way by many radial beams. In some cases it can be very difficult to distinguish the different shell layers, and the outer shell forms a very complex sponge-like ball. The inner shell is connected to the outer shells by a few beams. Primary spines are very thin, weakly developed and commonly not visible outside. The innermost structure is not preserved in our material.

Dimensions (µm). Diameter of the cortical shell: 231–283; of the inner shell: 76–97; Thickness of the outer shell: 45–75.

Remarks. This species differs from the other two Ordovician *Syntagentactinia* species described by Nazarov & Popov (1980) (*S. biocculosa* and *S. pauca*) in possessing a thick multi-layered spongy outer shell, in the absence of rod-like outer spines and in its larger size. Our specimens differ from *S. excelsa* as described by Nazarov & Ormiston (1993) only in their inner shell dimensions (40–42 µm in Nazarov & Ormiston's material),

but correspond relatively well to the dimensions given by Kurihara & Sashida (2000; 40–90 µm). The species differs from *S. afflicta* that co-occurs with *S. excelsa* in the absence of long, robust, rod-like spines and in its internal half-closed shells.

Syntagentactinia? sp. aff. *S. excelsa* Nazarov & Ormiston, 1993
(Pl. 1, figs 8–11)

aff. 1993 *Syntagentactinia excelsa* Nazarov & Ormiston: 40; pl. 6, figs 13–14.

aff. 2000 *Syntagentactinia excelsa* Nazarov & Ormiston; Kurihara & Sashida: 153; figs 7.19, 7.20; 8.1–8.7.

Material. 7 specimens.

Description. Spherical radiolarian with an outer shell structure formed of two (rarely three) spongy shell layers closely interconnected by many radial beams and arranged in a thick spongy three-dimensional way. The thickness of the spongy meshwork is variable. The internal framework consists of a large latticed inner shell with well-defined pores located inside a small hollow cavity. Inner shell is connected to the outer shells by short beams. Six primary rays protrude radially as very thin and short rod-like outer spines outside the outer shells. Thin secondary spines are present on the surface of the outer shell. The innermost framework is broken in every specimen but primary rays have been observed to protrude inside the inner shell.

Dimensions (µm). Diameter of the cortical shell: 260–330; of the inner shell: 100–120; thickness of the outer structure: 32–70.

Remarks. It differs from *S.?* sp. cf. *S. excelsa* and *S. biocculosa* in its larger size (see Table 1) and in possessing thin secondary spines on the surface of the outer shell. It differs from *S. pauca* in its thick spongy outer shell and its larger size.

Syntagentactinia? *angulata* n. sp. Pouille & Danelian
(Pl. 1, figs 12–14b)

Derivation of name. From the Latin word 'angulatus' meaning angular, bony.

Diagnosis. A thick, dense and spongy outer shell, displaying a polygonal to quadrangular outline, bears six thick rod-like spines and encloses a much smaller latticed inner shell.

Holotype. Plate 1, figure 13 (USTL1142/048).

Paratype. Plate 1, figure 14 (USTL1142/058).

Material. 9 specimens.

Description. The internal framework consists of a six-rayed point-centred (?) spicule from which six primary rays originate. Apophyses branch from the primary rays at a distance of about 20–40 µm from

Explanation of Plate 1. Scanning electron micrographs of Entactinaria from sample 112 (Shundy Formation, North Balkhash Region, Kazakhstan). Scale bar 100 µm. **figs 1–4.** *Syntagentactinia?* sp. cf. *S. excelsa* Nazarov & Ormiston; **figs 5–7.** *Syntagentactinia biocculosa* Nazarov in Nazarov & Popov: **5**, specimen displaying broken internal spicule. **figs 8–11.** *Syntagentactinia?* sp. aff. *S. excelsa* Nazarov & Ormiston. **figs 12–14b.** *Syntagentactinia?* *angulata* Pouille & Danelian nov. sp.: **13**, holotype; **14a**, paratype; **14b**, magnified view of the paratype's internal structure displaying broken internal spicule and apophyses branching to form the innermost shell. **figs 15–18.** *Syntagentactinia?* sp. cf. *S. biocculosa* Nazarov in Nazarov & Popov. **fig. 19.** *Syntagentactinia?* sp. A.

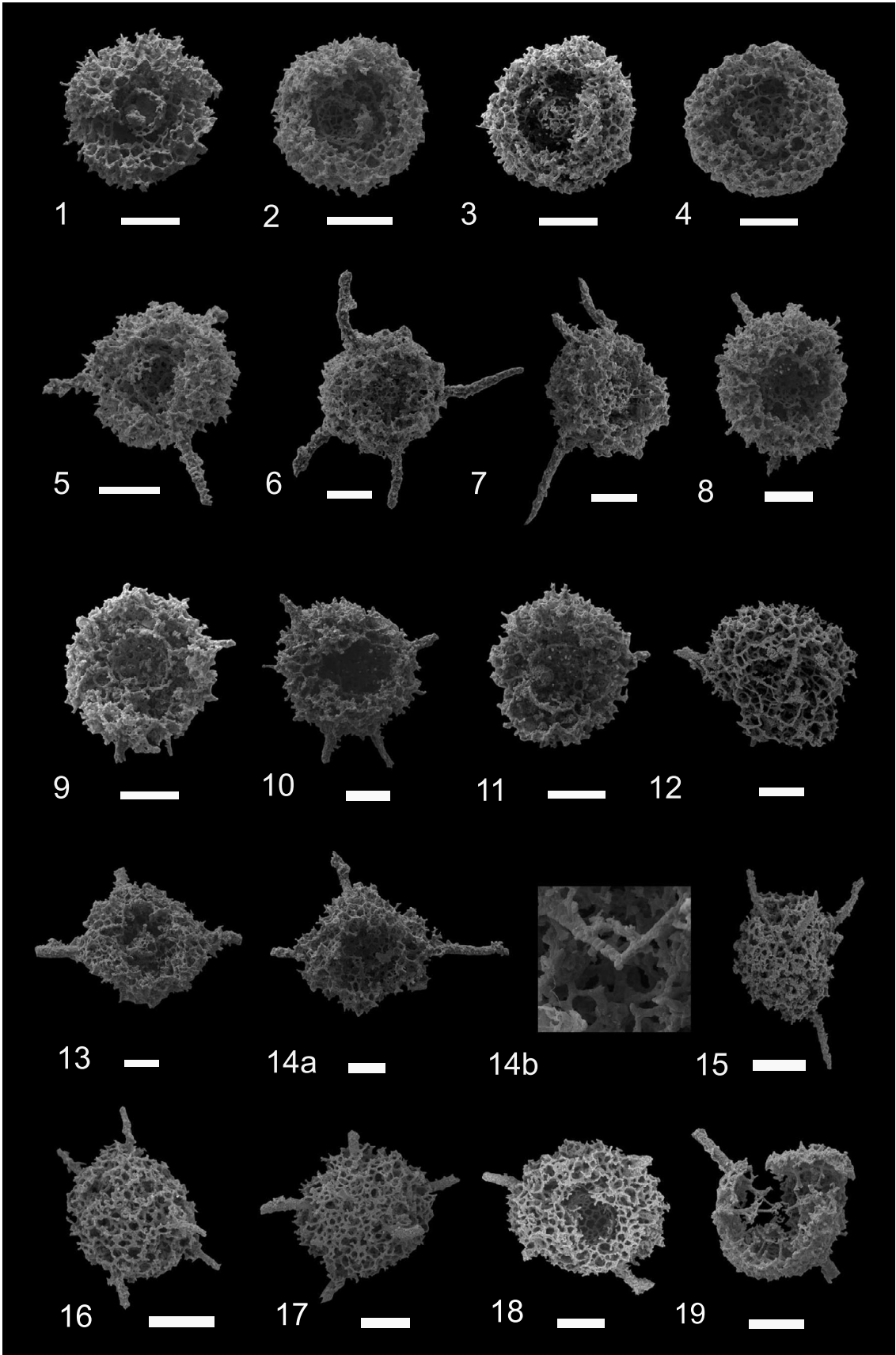


Table 1. Outer and inner shell diameter of *S.?* sp. aff. *S. excelsa* and related species.

(in μm)	<i>S.?</i> sp. aff. <i>S. excelsa</i>	<i>S.?</i> sp. cf. <i>S. excelsa</i>	<i>S. biocculosa</i>	<i>S. pauca</i>
outer shell \emptyset	260–330	231–283	175–277	110–160
inner shell \emptyset	100–120	76–97	35–98	50–82

Table 2. Outer shell diameter of *S.?* *angulata* and related species.

(in μm)	<i>S.?</i> <i>angulata</i>	<i>S. afflicta</i>	<i>S. excelsa</i>	<i>S. biocculosa</i>	<i>S. pauca</i>
outer shell \emptyset	346–400	240–310	234–277	175–225	110–160

the spicule centre to form a small irregularly latticed inner shell, which is unevenly porous and located inside a hollow cavity. The latter is very irregular in outline and clearly separates the inner and outer shells. The outer shell is formed of different groups of apophyses that branch from the primary rays to form a very thick, irregular and dense spongy meshwork (up to 130 μm thick). The outer shell displays a polygonal to quadrangular outline. Primary rays are disposed in the three rectangular axes and prolonged into thick rod-like outer spines.

Dimensions (μm). Diameter of the cortical shell: 346–400; of the inner shell: 64–85; length of primary spines: up to 200.

Remarks. Due to its small size, the inner shell surrounding the primary spicule can be mistaken for a microsphere on unbroken specimens. The primary spicule appears to be point-centred; however, it could also be interpreted as a broken bar-centred spicule, which explains the doubtful generic assignment. This species differs from other species of the genus *Syntagentactinia* in the polygonal to quadrangular outline of its outer shell, its wide inner cavity, its thick and complex three-dimensional non-layered meshwork and its much larger size (see Table 2).

Syntagentactinia? sp. cf. *S. biocculosa* Nazarov in Nazarov & Popov, 1980
(Pl. 1, figs 15–18)

cf. 1980 *Syntagentactinia biocculosa* Nazarov in Nazarov & Popov: 56; pl. 12, figs 1–3.

Material. 10 specimens.

Description. The spongy outer shell displays an ovoid shape with six primary spines. Two spines are located on the margin of one pole of the shell. The four other horn-like spines are situated on the opposite pole of the shell and are curved inwardly. The outer shell consists of a thick, multi-layered, three-dimensional meshwork. The inner framework consists of a latticed inner shell. The innermost part of the framework is unknown.

Dimensions (μm). Diameter of the outer shell: 190–318; diameter of the inner shell: 117–134; length of the outer spines: up to 150.

Remarks. It differs from other *Syntagentactinia* in its ovoid shape, the peculiar position of its primary spines and in the large size of its inner shell.

Syntagentactinia? sp. A
(Pl. 1, fig. 19)

Material. 1 specimen.

Description. This morphotype displays a primary spicule located inside a very small sphere surrounded by an inner and an outer shell. Six or more primary rays originate from the primary spicule aligned with thick rod-like external spines. Numerous beams connect the latticed inner shell with the outer shell. The outer framework consists of two latticed shell layers closely interconnected in a three-dimensional arrangement. The outermost shell layer displays a thick spongy aspect.

Dimensions (μm). Diameter of the innermost sphere: 33–38; of the inner shell: 91–98; of the outer shell: 229–238; length of the outer spines: up to 95; thickness of the outer shell wall: 33.

Remarks. The small sphere inside the inner shell can be distinguished from a microsphere only by the presence of primary rays protruding inside it. As the primary spicule is broken it is difficult to know the exact number of primary rays that originated from it. This morphotype differs from all other species of *Syntagentactinia* in its regular outline, the presence of a very small sphere surrounding the primary spicule and the presence of numerous beams connecting the inner with the outer shells. It also differs from all the species described in this paper in possessing a much thinner outer shell wall.

Genus *Haplentactinia* Foreman, 1963

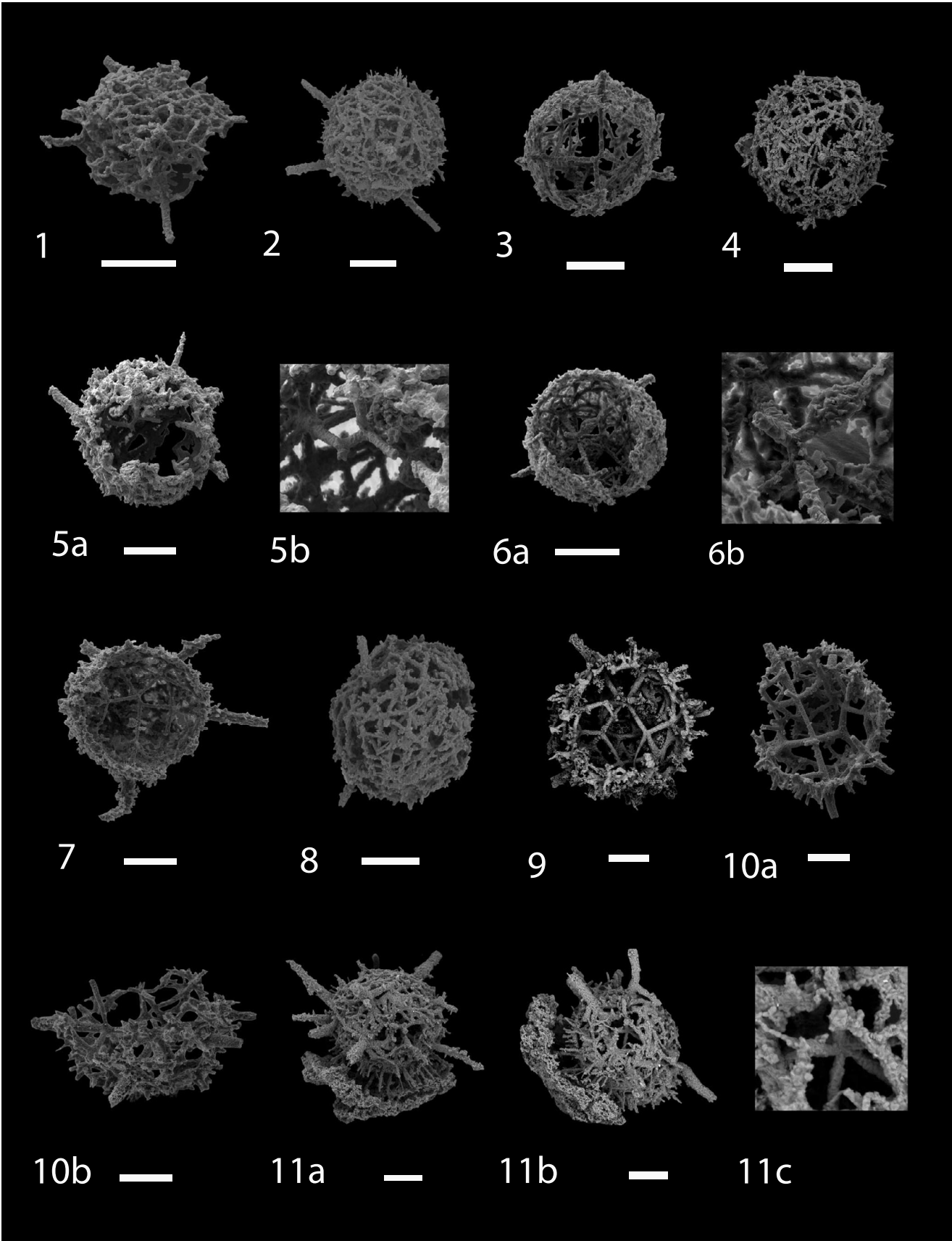
Type species. *Haplentactinia rhinophyusa* (Foreman, 1963).

Haplentactinia juncta Nazarov, 1975
(Pl. 2, fig. 1)

1975 *Haplentactinia juncta* Nazarov: 58; pl. 20, fig. 5, 6.

1980 *Haplentactinia juncta* Nazarov; Nazarov and Popov: 53; pl. 4, fig. 2; pl. 6, figs 3–5.

Explanation of Plate 2. Scanning electron micrographs of Entactinaria from sample 112 (Shundy Formation, North Balkhash Region, Kazakhstan). Scale bar 100 μm . **fig. 1.** *Haplentactinia juncta* Nazarov. **figs 2–8.** *Polyentactinia spinulenta* n. sp. Danelian & Pouille: 7, holotype; **5a, 6**, paratypes; **5b, 6b**, magnified view of paratypes displaying the primary spicule and the median bar. **fig. 9.** *Polyentactinia* sp. cf. *P. spinulenta* Danelian & Pouille. **figs 10a–b.** *Polyentactinia* sp. A. **figs 11a–c.** *Polyentactinia* sp. B: **11c**, magnified view of the internal spicule.



1988 *Haplentactinia juncta* Nazarov; Nazarov: pl. 10, fig. 4.

1994 *Haplentactinia* ? *juncta* Nazarov; Gorka: 174; pl. 2, figs E, F.

Material. 1 specimen.

Dimensions (µm). Diameter of the shell: 177–205; width of the meshes: 20–45, length of the spines (from median bar): up to 150 µm.

Remarks. This species differs from *H. armillata* in its wider and more loosely constructed mesh, smaller size (shell Ø: 320–400 µm in *H. armillata*) and absence of a bifurcated primary spine. It also differs from *H. infida* and *H. baltica* in its more rounded outline. In addition, *H. infida* differs from *H. juncta* in possessing one spine considerably larger than the others and in having apophyses on this spine located closer to the inner spicule, whereas other apophyses are at equal distance from it.

Family **Polyentactiniidae** Nazarov, 1975

Genus *Polyentactinia* Foreman, 1963

Type species. *Polyentactinia craticulata* Foreman 1963.

Polyentactinia spinulenta n. sp. Pouille & Danelian
(Pl. 2, figs 2–8)

Derivation of name. From the Latin word ‘spinulentus’ meaning thorny.

Diagnosis. A single spherical outer shell displaying a latticed meshwork of interwoven bars, bearing 6 rod-like outer spines, which originate from the primary rays of a short median bar located eccentrically in the internal part of the shell.

Holotype. Plate 2, figure 7 (USTL1140/008).

Paratypes. Plate 2, figure 5a (USTL1140/074); Plate 2, figure 6a (USTL1142/068).

Material. 11 specimens.

Description. Internal framework consists of a primary spicule formed of a short median bar (10–15 µm) from which six primary rays originate. The median bar is eccentrically located in the spherical skeleton and it may often appear point-centred depending on its orientation. The six primary rays continue outside the spherical shell as rod-like outer spines that can be straight or slightly curved. They bear a verticil of two perpendicular whorled rays that originate at the level of the cortical shell with which they are connected to the spherical skeleton. The shell is formed from a latticed meshwork with angular meshes formed from interwoven bars of various thicknesses. On well-preserved specimens numerous small simple or bifurcated spinules are present on the shell surface.

Dimensions (µm). Diameter of the shell: 227–305 (average, 262–284); length of primary spines: up to 120; length of the median bar: 10–15; thickness of the inner elements of the skeleton: up to 10.

Remarks. This species differs from *Astroentactinia* in the absence of characteristic pores and of any conical secondary spines on its

cortical shell. Its internal frame and its shell structure suggest an assignment to *Polyentactinia*. *P. spinulenta* differs from *P. offertata* Nazarov (an upper Darriwilian species described from the *Haplentactinia juncta*–*Inanigutta unica* assemblage) in possessing only 6 thin rod-like external spines and a shell formed from a meshwork of interwoven bars forming angular meshes and covered by small spinules, whereas *P. offertata* displays a porous latticed shell with more than 12 external spines. It differs from the Upper Ordovician species *P. ? estonica* Nazarov in possessing thinner, longer and less numerous outer spines and in its less massive shell structure. It differs from Silurian species *P. stelcki* and *?P. leeorum* in its larger size (c. 200 µm for *?P. leeorum*, 70–135 µm for *P. stelcki*), more angular mesh structure and the presence of interwoven bars.

Most *Polyentactinia* species are described from the Devonian to Permian interval. As concerns the Devonian species, *P. spinulenta* is easily distinguished from *P. kossistekensis*, *P. rudihispida* and *P. propinga* by its internal structure and number of primary spines (7–8 rays for *P. kossistekensis*; 7–10 rays for *P. propinga* and *P. rudihispida*). *P. circumretia* differs from *P. spinulenta* by having a 6- to 7-rayed point-centred spicule centrally located and bi- or trifurcated outer spines. *P. spinulenta* differs from *P. polygonia*, *P. craticulata* and *P. leptosphaera* in its larger size (90–180 µm in *P. polygonia*; 115–150 µm in *P. craticulata*; 160–240 µm in *P. leptosphaera*). The shell structure of *P. spinulenta* also differs from *P. invenusta* and *P. tenera*, which display a thin and delicate shell structure constructed in a three-dimensional way as thick spongy tissue.

Polyentactinia. sp. cf. *P. spinulenta* Pouille & Danelian
(Pl. 2, fig. 9)

Material. 2 specimens.

Description. Internal framework consists of an initial spicule formed of a very short median bar (about 8 µm) eccentrically located that may appear point-centred depending on orientation. Five primary rays emerge from the median bar and turn into thick rod-like outer spines outside the shell surface. Two primary rays are longer than the others and bear at their distal ends two long perpendicular whorled rays connected to the outer shell meshwork. Some of them may emerge from the shell surface as secondary spines. Simple apophyses can be present at the distal end of these whorled rays and be merged with the bars of the shell meshwork. The shell is formed of a loose meshwork of thick straight and curved bars interwoven in a disorderly manner or fused. Numerous simple or bi- to trifurcated spinules are present on the shell surface.

Dimensions (µm). Diameter of the shell: 330–365; length of the median bar: c. 8; thickness of the inner elements of the skeleton: up to 20.

Remarks. This species differs from *P. spinulenta* in having much thicker primary rays, a thicker skeleton structure, larger dimension and in the presence of numerous spinules on the shell surface. It also differs from *P. spinulenta* in possessing whorled rays on only two primary spines and in having only five primary spines and a much shorter median bar.

Polyentactinia sp. A
(Pl. 2, figs 10a–10b)

Material. 1 specimen.

Description. Internal framework consists of an initial spicule formed of a long median bar (about 60 µm), eccentrically located, from which five (six?) primary rays originate. The primary rays are prolonged into thick rod-like straight outer spines. Two to three perpendicular whorled rays originate at the distal parts of each primary rays and fuse with the spherical skeleton. Some of them emerge from the shell surface as rod-like secondary spines. Apophyses branch from the primary spines to form an irregular spherical loose meshwork consisting of thick straight and curved bars interwoven in a disorderly manner or fused. Numerous simple or bi- to trifurcated spinules are present on the shell surface.

Dimensions (µm). Diameter of the shell: 325–365; length of the median bar: about 60; thickness of the inner elements of the skeleton: up to 20.

Remarks. This specimen differs from *P. sp. cf. P. spinulenta* in possessing up to three whorled rays on the primary spines and also in the larger size of the median bar.

Polyentactinia sp. B
(Pl. 2, figs 11a–11c)

Material. 1 specimen.

Description. The outer shell displays an ovoid outline and is characterized by an intergrowth of strongly fused bars. The skeleton is very compact and made of thick elements. Eight to ten thick rod-like outer spines emerge from the shell surface and can bear small simple apophyses. Numerous thin and long spinules are present on one side of the shell surface. The internal framework is hidden except for a six-rayed point centred spicule visible from a wide opening.

Dimensions (µm). Diameter of the shell: 282–335; length of the outer spines: up to 122.

Remarks. Internal framework remains uncertain as the inner structure of the shell is not entirely visible. The six-rayed point-centred spicule may be considered as the initial skeleton but none of the thick rod-like outer spine seems to be connected with the rays of this spicule. Therefore, a more detailed study of the inner-frame is needed to understand the internal structure. *Polyentactinia* sp. B outer shell structure clearly differs from all other *Polyentactinia* species in its characteristic intergrowth of strongly fused bars and the more developed long spinules covering the shell surface. This skeletal structure of *Polyentactinia* sp. B displays some affinities with the Silurian genus *Palaeohippium* but it differs from it by not showing a saddle-shaped internal spicule with apical and basal hemispheres.

Order **Spumellaria** Ehrenberg, 1875

Family **Haplotaeniidae** (Won *et al.*, 2002)

Genus *Haplotaeniatum* Nazarov & Ormiston, 1993,
emend. Won *et al.*, 2002, emend. Jones & Noble, 2006

Type species. *Haplotaeniatum labyrinthum* Nazarov & Ormiston, 1993

Haplotaeniatum circulus n. sp. Pouille & Danelian
(Pl. 3, figs 1–2b)

Derivation of name. From the Latin word ‘circulus’ meaning circle.

Diagnosis. Large spherical spongy outer shell, bearing long and massive rod-like spines, encapsulates 5–6 pseudospongy internal shells displaying a slightly spiraliform arrangement and a small latticed microsphere from which primary spines originate.

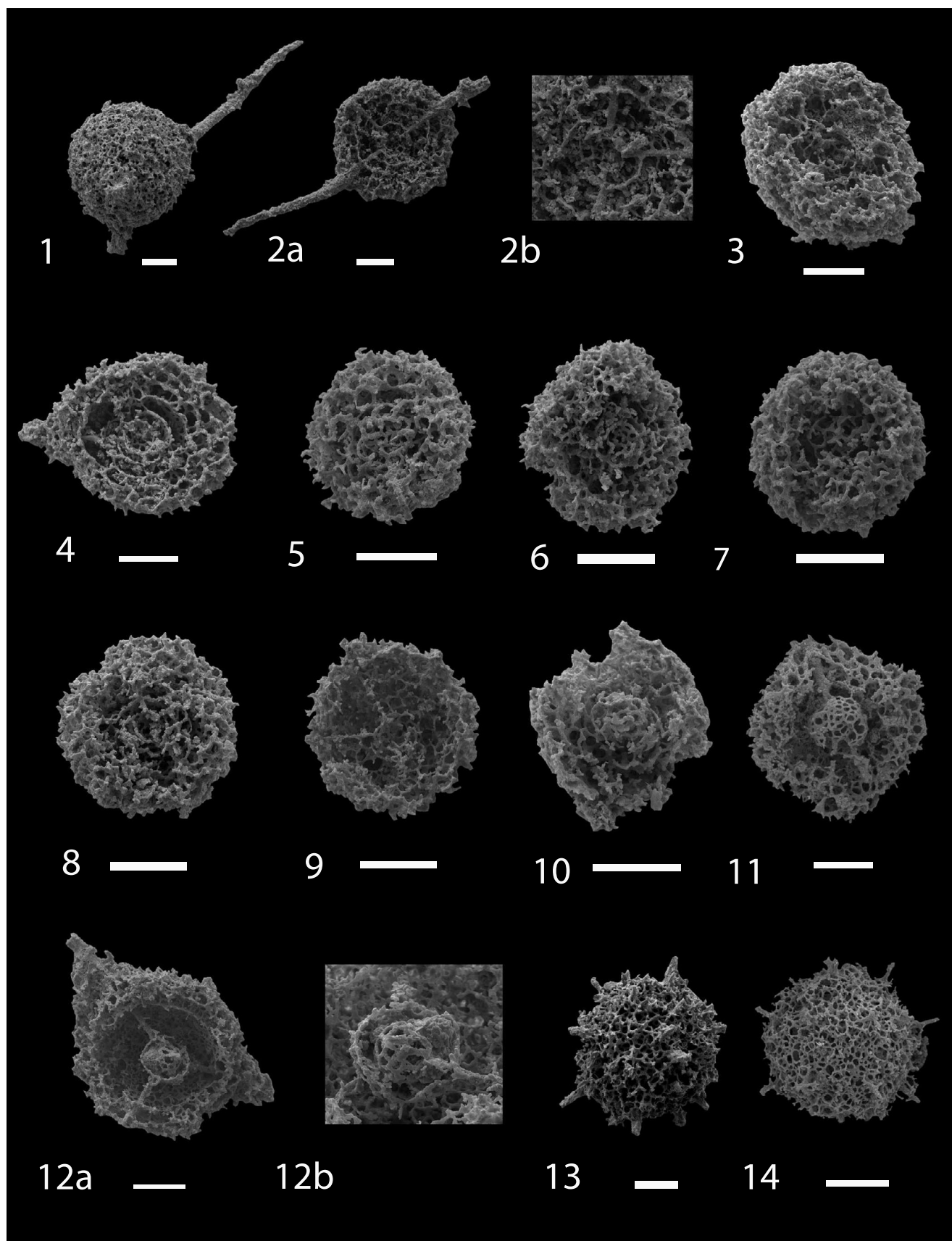
Holotype. Plate 3, figure 2 (USTL1142/061).

Material. 6 specimens.

Description. *Haplotaeniatum* formed of five to six irregularly circular pseudospongy latticed shells arranged in a slightly spiraliform fashion. Internal framework consists of a small, centrally located, latticed microsphere. Four visible primary rays originate from the microsphere. They are prolonged into long, massive rod-like spines (up to 350 µm or more) outside the shell. Apophyses branch from the primary spines to form the different latticed shells surrounding the microsphere. A few apophyses can be irregularly placed giving the shell a spiraliform arrangement. The shells are connected together by thin beams, irregularly placed, forming a ‘cellular-wall’. The shell layer forms numerous half-loops at the points where it is connected to the radial beams. The outermost shell is formed of a three-dimensional spongy meshwork which originates from two to three groups of apophyses branching from the primary spines. The outer shell displays a spherical shape. No secondary spines are present.

Dimensions (µm). Diameter of the outer shell: 290–354; of the microsphere: 40–52; length of primary spines: up to 368; thickness of the cortical shell wall: 42–48.

Remarks. This species differs from the Late Ordovician species of the genus *Haplotaeniatum* in its shell structure formed of four to five irregularly circular pseudospongy shells, its perfectly spherical shape and its large size (outer shell Ø: 104–170 µm in *H. spinatum*; c. 145 µm in *H. fenestratum*; 115–291(?) µm in *H. prolatum*; 180–230 µm in *H. ovatum*). Externally, *H. circulus* may appear similar to *H. ovatum* when the latter displays a circular outline. However, *H. circulus* can still be easily distinguished from it by the presence of long thick rod-like outer spines and the absence of a pylome. *H. circulus* shows closer affinities with Lower Silurian species. It shares a similar shell structure with *H. labyrinthum* in the presence of three to five spiraliform shells united by means of transverse cross-beams. Both species share approximately the same size (outer shell Ø: 336–354 µm in *H. circulus*; 296–354 µm in *H. labyrinthum*, microsphere Ø: 40–52 µm in *H. circulus*; 38–43 µm in *H. labyrinthum*) but *H. circulus* still differs from *H. labyrinthum* in having a centrally positioned microsphere, a thinner meshwork and very thin cross beams. *H. circulus* also differs from



H. labyrinthum in the length of its primary spines (up to 368 µm in *H. circulus*; up to 100 µm in *H. labyrinthum*). However, this difference is certainly preservational as *H. labyrinthum*'s spine length *sensu* MacDonald (2006) reaches 480 µm. *H. circulus* also displays structural similarities with *H. cathenatum* which possess four to five intermediate shells of an isometric form between the microsphere and outer shell. Our species differs from *H. cathenatum*, however, in having a more spherical shape, well-developed massive primary spines (spine length up to 368 µm in *H. circulus*; up to 80 µm in *H. cathenatum*) and in the absence of a pylome.

H. circulus also differs from *H. primordialis*? and *H. tegimentum* in its larger size, which is 194–208 µm in *H. primordialis*? and 240–264 µm in *H. tegimentum*, and in its well-developed outer spines (up to 40 µm in *H. primordialis*?; up to 20 µm in *H. tegimentum*). It also differs from *H. tegimentum* in the absence of half-closed shells and conical external spines and in possessing a centrally located microsphere.

Haplotaeniatum sp. cf. *H. circulus* Pouille & Danelian
(Pl. 3, figs 3–4)

Material. 9 specimens.

Description. Shell consisting of a centrally located microsphere surrounded by four to five shells arranged in a spiraliform fashion. Shell layers are interconnected by small and irregularly placed beams. They display a cellular outline, forming numerous half-loops at the point where they are linked to the beams. The outermost shell is egg-shaped and formed of a thin spongy meshwork. At least two primary spines were observed to originate from the microsphere. Outer spines are thick and covered with spongy accretions that accentuate the ellipsoidal shape. No secondary spines are present.

Dimensions (µm). Diameter of the outer shell: 240–358; of the microsphere: 50–55.

Remarks. In its shell structure this morphotype resembles *H. circulus*. However, it differs from it in its more accentuated spiraliform construction, in its ellipsoidal shape and its weakly developed primary spines. It also resembles *H. labyrinthum*, but it differs from it in possessing very thin radial beams, weakly developed primary spines, a larger, centrally located, microsphere (Ø: 38–43 µm in *H. labyrinthum*) and more distinct layering.

Haplotaeniatum sp. cf. *H. tegimentum* (Nazarov in Nazarov & Ormiston, 1993)
(Pl. 3, figs 5–10)

cf. 1993 *Haplotaeniatum tegimentum* Nazarov in Nazarov & Ormiston: 42; pl. 3, figs 14–16.

cf. 2000 *Haplotaeniatum tegimentum* (Nazarov in Nazarov & Ormiston); Kurihara & Sashida: 152; pl. 7, figs 1–13.

cf. 2004 *Haplotaeniatum tegimentum* (Nazarov in Nazarov & Ormiston); Kurihara: pl. 1, figs 1–2.

Material. 33 specimens.

Description. The internal framework consists of a microsphere surrounded by a complex meshwork of several latticed layers formed from curved to curled bars developed in a spiraliform way. The curled bars give rise to numerous small half-closed loops around the microsphere. No internal cavity appears to be individualized. The microsphere, which is not easily distinct, is, in general, centrally located. Rare beams are present. Three to four primary rays originate from this microsphere but they are rarely developed externally. The outer shell consists of a thick spongy, three-dimensional shell of variable thickness. It displays a spherical to subspherical outline.

Dimensions (µm). Diameter of the outer shell: 220–280; of the microsphere: 26–38.

Remarks. Morphologically this species is very similar to *H. tegimentum* illustrated by Kurihara (2004), from which it differs in its centrally located microsphere and in the absence of any external spines. It differs from the co-occurring *H. circulus* and *Haplotaeniatum* sp. cf. *H. circulus* in its less distinct and less numerous internal shell layers, its thickest spongy outer shell and its denser layering structure formed of numerous small half-closed loops around the microsphere. It also differs in its smaller outer shell and smaller microsphere.

This taxon differs from the Upper Ordovician species of the genus *Haplotaeniatum* in its internal shell structure, its dense and thick three-dimensional spongy outer spherical shell and its large size (outer shell Ø: 104–170 µm in *H. spinatum*; c. 145 µm in *H. fenestratum*; 115–291(?) µm in *H. prolatum*; 180–230 µm in *H. ovatum*). It is easily distinguished from *H. ovatum* by its more discernable internal layering and the absence of a pylome. It differs from *H. labyrinthum* and *H. cathenatum* in its smaller size (outer shell Ø: 296–354 µm in *H. labyrinthum*; 308–394 µm in *H. cathenatum*), in possessing fewer internal shell layers that are more densely constructed, forming numerous half-closed loops of a very small size around the microsphere and a thick spongy three-dimensional outer shell. It also differs from *H. labyrinthum* in possessing a centrally located microsphere, lacking rod-like external spines and a cellular wall, and from *H. cathenatum* in lacking a pylome and thin secondary spines. It differs from *H. primordialis*? in its larger size (outer shell Ø: 194–208 µm in *H. primordialis*?) and its denser internal shell structure. It differs from *H. fissura* in possessing a thick spongy outer shell with no distinct pores and the absence of a distinct gap between the microsphere and outer layers of the shell, the absence of a pylome and the weak development of primary spines. It differs from *H. aperturatum* and *H. adobensis* in lacking large pores on the outer shell surface, in having a more distinct internal spiraliform structure and lacking a pylome.

Explanation of Plate 3. Scanning electron micrographs of Spumellaria from sample 112 (Shundy Formation, North Balkhash Region, Kazakhstan). Scale bar 100 µm. **figs 1–2b.** *Haplotaeniatum circulus* n. sp. Danelian & Pouille: **2a**, holotype; **2b**, magnified view of holotype displaying the microsphere and inner shell. **figs 3–4.** *Haplotaeniatum* sp. cf. *H. circulus* Pouille & Danelian. **figs 5–10.** *Haplotaeniatum* sp. cf. *H. tegimentum* (Nazarov in Nazarov & Ormiston). **fig. 11.** *Haplotaeniatum*? sp. A. **figs 12a–b.** *Haplotaeniatum*? *giganteum* n. sp. Pouille & Danelian: **12a**, holotype; **12b**, magnified view of holotype displaying the microsphere and inner shell. **fig. 13.** *Haplotaeniatum* sp. B. **fig. 14.** *Haplotaeniatum* sp. C.

Haplotaeniatum? giganteum n. sp. Pouille & Danelian
(Pl. 3, figs 12a–12b)

Derivation of name. From the Latin word ‘giganteus’ meaning gigantic, huge.

Diagnosis. A large, spherical and spongy three-layered outer shell surrounds a much smaller inner latticed shell which encapsulates a microsphere. Six rod-like spines originate from the microsphere; they are covered proximally by numerous branching apophyses that join the outer shell.

Holotype. Plate 3, figure 12 (USTL1172/085).

Material. 5 specimens.

Description. Internal framework consists of a centrally located, latticed microsphere with uneven pores of variable size. This microsphere is encapsulated in a subspherical to oval inner latticed shell. Six primary rays originate in the microsphere and prolong outside the shell into thick rod-like spines. The inner shell is clearly separated from the outer shell by a large empty cavity. Small and simple apophyses, irregularly placed, can branch from the primary rays between the inner and outer shells. Some apophyses can join the inner shell surface. The outer framework consists of three thinly latticed oval shell layers closely interconnected by numerous short beams in the form of a three-layered wall arrangement. The outer shell surface displays a spongy aspect. Outer spines are covered at their proximal part with numerous apophyses branching to join the outer shell surface which contribute to give the shell a strong ellipsoidal shape.

Dimensions (µm). Diameter of the outermost shell: 336–470; of the inner shell: 90–100; of the microsphere: 55–59; of the inner cavity separating outer and inner shells: 55–74; thickness of the outer structure: 50–62; width of microsphere: 5–18.

Remarks. The internal part of *H.? giganteum* has been observed on only two specimens. This species is here assigned to the genus *Haplotaeniatum* based on its internal framework consisting of a microsphere. However, this is currently uncertain because it also displays some morphological affinities to the genus *Syntagentactinia* and it does not display any spiraliform arrangement as in *Haplotaeniatum*. On the contrary, it is formed of concentric shells, with internal and outer shells separated by a wide empty internal cavity, as in *Syntagentactinia*. In their emendation of the genus *Haplotaeniatum*, Won *et al.* (2002) included specimens that are definitely separated into outer and inner parts, but Jones & Noble (2006) removed from it the forms possessing distinct inner and outer areas. Some *Syntagentactinia* possess a very small innermost sphere surrounding the primary spicule that can be mistaken for a microsphere (see *S.? angulata* Pouille & Danelian n. sp. and *Syntagentactinia?* sp. A). However, as no primary rays have been observed to protrude inside the microsphere, as it stands this species is assigned to the genus *Haplotaeniatum*.

Haplotaeniatum? sp. A
(Pl. 3, fig. 11)

Material. 1 specimen.

Description. Internal framework consists of a centrally located latticed microsphere from which six (?) primary rays originate. The microsphere is surrounded by a spherical inner latticed shell. The inner shell is clearly separated from the outer shell by a small empty cavity. Very thin and tiny beams emerge from the surface of the inner shell to connect the outer shell. The primary rays give rise to thick rod-like outer spines. Three to four groups of apophyses branch from the primary spines to form a thick three-dimensional indistinctly layered spongy meshwork.

Dimensions (µm). Diameter of the outermost shell: 319–325; of the inner shell: 99–100; of the microsphere: 53–54; of the inner cavity separating outer and inner shells: 28–41; thickness of the outer structure: 40–83.

Remarks. This morphotype is formed of concentric shells, with the internal and outer shells separated by an empty internal cavity, as in *Syntagentactinia*. As no primary rays have been observed to protrude inside the microsphere, this species is tentatively assigned to the genus *Haplotaeniatum*. It differs from *H.? giganteum* n. sp. Pouille & Danelian in its smaller size but also in possessing a smaller inner cavity of an irregular outline and a thick three-dimensional, indistinctly layered, spongy outer meshwork.

Haplotaeniatum sp. B
(Pl. 3, fig. 13)

Material. 2 specimens.

Description. This specimen displays a dense three-dimensional mesh of bars which are interwoven in a disorderly manner to form a spherical shell. About 20 thick and short outer spines are irregularly placed on the shell surface. The outer shell displays a subspherical irregular outline. Inner structure is unknown.

Dimensions (µm). Diameter of the outer shell: 313–320; thickness of the base of the outer spines: 20 to 25.

Remarks. This species differs from other species of the genus *Haplotaeniatum* in the presence of numerous outer spines. A high number of outer spines is encountered most often in *Oriundogutta* which can possess from 8 to 20 external horns. However, *Oriundogutta* is distinguished by possessing a two-dimensional porous outer shell, whereas our morphotype displays a thick three-dimensional disorderly interwoven meshwork.

Haplotaeniatum sp. C
(Pl. 3, fig. 14)

Material. 1 specimen.

Description. This specimen displays a roughly spherical test formed of a dense three-dimensional mesh of fine bars. It consists of several three-dimensionally interwoven latticed layers which give the shell a spongy appearance. There are about 20 thin short outer spines present. Apophyses may branch from the proximal

A radiolarian assemblage from the Shundy Formation, Kazakhstan

part of the outer spines and merge into the outer shell meshwork. Internal structure is unknown.

Dimensions (µm). Diameter of the outer shell: 238–255; thickness of the base of the outer spines: 5 to 7.

Remarks. This species differs from *Haplotaeniatum* sp. B in having a thinner and more delicate meshwork and thinner outer spines (thickness of the base of the outer spines: 20–25 µm in *Haplotaeniatum* sp. B) and also in its smaller size (outer shell Ø: 313–320 µm in *Haplotaeniatum* sp. B).

DISCUSSION

Before our study, 30 radiolarian species and morphotypes were known from the upper Darriwilian–lowermost Sandbian *Haplentactinia juncta*–*Inanigutta unica* assemblage described by Nazarov & Popov (1980). The new assemblage described in this paper presents an entirely new fauna, comprising 32 species and morphotypes (Fig. 3) recorded for the first time in the latest Darriwilian H. teretisculus graptolite zone.

The radiolarian assemblage found in our sample (112) may be correlated with Nazarov's assemblage from sample 553a, as they share six genera (*Syntagentactinia*, *Kalimnasphaera*, *Polyentactinia*, *Inanihella*, *Inanibigutta* and *Haplentactinia*) and one characteristic species (*Haplentactinia juncta*). However, in spite of their more-or-less similar age, their high diversity and the number of common genera, the species composition of the two assemblages is very different (see Fig. 3). Indeed, despite their high diversity (9 genera and 32 species/morphotypes in sample 112; 10 genera and 30 species/morphotypes in sample 553a), the two assemblages share only 2 species (*Haplentactinia juncta* and *Syntagentactinia biocculosa*) and two closely related morphotypes (*Kalimnasphaera aperta* and *Kalimnasphaera* sp. aff. *K. aperta*, *Inanihella* *bakanasensis* and *Inanihella* sp. cf. *I. bakanasensis*).

Additionally, in spite of the high diversity of inaniguttids in sample 553a, our assemblage contains two genera (*Haplotaeniatum* and *Triplococcus*) which appear to be absent from the *Haplentactinia juncta*–*Inanigutta unica* assemblage. Moreover, these two taxa are very abundant in the 112 assemblage as they represent 52% of the total number of specimens present in the studied fauna. On the other hand the 112 assemblage lacks the genera *Oriundogutta*, *Bissylentactinia* and *Ceratoikiscum*?, which are present in the 553a assemblage.

This difference in assemblage structure may be due to the different age of the samples, as the radiolarians studied by Nazarov (in Nazarov & Popov, 1980) from sample 553a appear to be slightly younger than our assemblage, as sample 553a was collected just below beds that contain the gracilis graptolites. Alternatively, the striking difference between the two assemblages may be due to palaeoenvironmental/palaeoceanographic or biofacies differences.

Our assemblage can be also correlated with the *Inanihella bakanasensis*–*Triplococcus akzhala* assemblage reported by Danelian & Popov (2003) and Maletz *et al.* (2009), as it contains both of the characteristic species. It is worth remembering that it is also dominated by species of the genera *Triplococcus* and *Inanihella*, which comprise 59% of the entire fauna. However, Danelian & Popov's (2003) and Maletz *et al.*'s (2009) assemblages are much less diverse (only 3 species described in samples P10 and A17 of

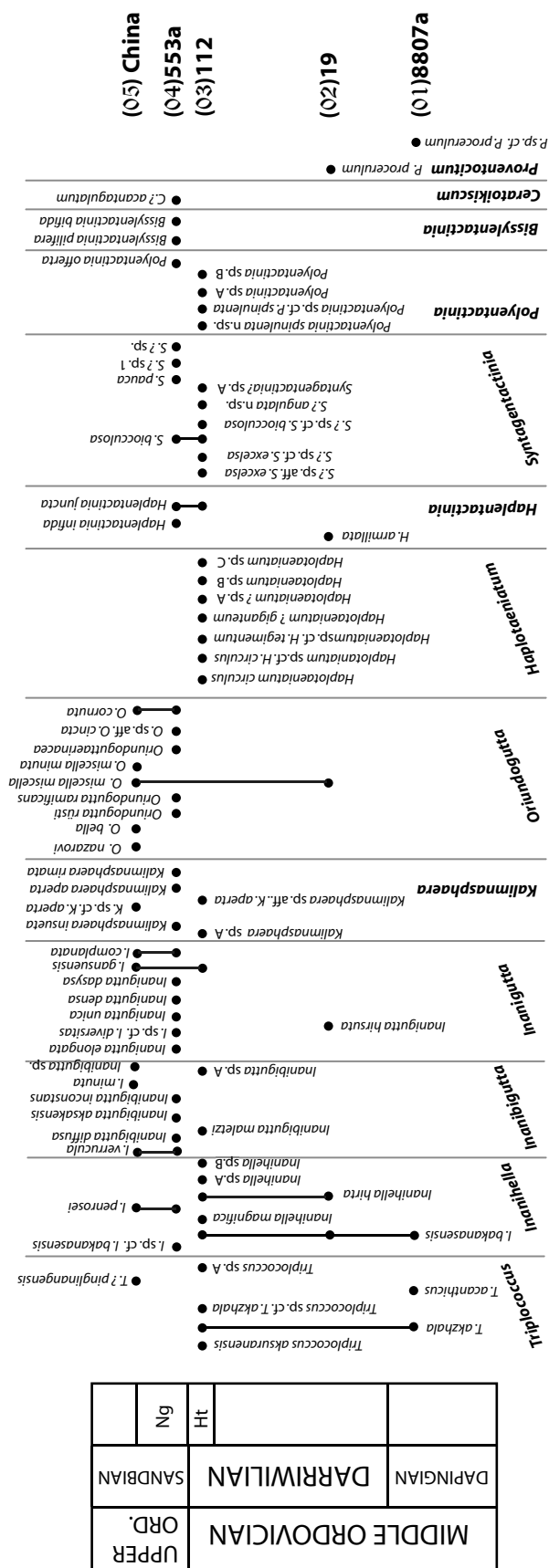


Fig. 3. Middle–Upper Ordovician radiolarian samples from Kazakhstan and China, biostratigraphy and correlation with graptolite zones. Faunal assemblages from Kazakhstan: 01 – sample 8807a. *Inanihella bakanasensis*–*Triplococcus akzhala* assemblage (Danelian & Popov, 2003); 02 – sample 19. *Proventocium procerulum* assemblage (Nazarov & Popov, 1980); 03 – sample 112 assemblage described in this paper; 04 – sample 553a. *Haplentactinia juncta*–*Inanigutta unica* assemblage (Nazarov, 1975; Nazarov & Popov, 1980); 05 – assemblage from China (Wang, 1993). Ng, Nemagraptus gracilis graptolite zone; Ht, Hustedograptus teretisculus graptolite zone.

Maletz *et al.* (2009) and 4 species from sample 8807 as studied by Danelian & Popov, 2003). Our assemblage, therefore, confirms that the two characteristic species of the *Inanihella bakanasensis*–*Triplococcus akzhala* assemblage are not restricted to the early–mid-Darriwilian but also extend into the latest Darriwilian. Therefore, only the *Proventocitum procerulum* assemblage can be used to define the upper Dapingian–mid-Darriwilian interval.

The uppermost Darriwilian is characterized by the *Haplentactinia juncta*–*Inanigutta unica* assemblage. In the light of our new radiolarian assemblage from the *Hustedograptus teretisculus* Biozone, the uppermost Darriwilian can now be better defined by the co-occurrence of the genera *Syntagentactinia*, *Kalimnasphaera*, *Inanibigutta*, *Protoceratoikiscum*, which first occur from the *Hustedograptus teretisculus* Biozone, and the genera *Triplococcus* and *Polyentactinia*. It is also characterized by the absence of the genus *Proventocitum*. It displays the following characteristic species: *Haplentactinia juncta*, *Inanigutta unica*, *Triplococcus aksuranensis*, *Kalimnasphaera aperta* and *Syntagentactinia biocculosa*.

This study considerably improves our knowledge of radiolarian species occurring in the upper Darriwilian and provides a much better view of the radiolarian palaeobiodiversity during this critical interval from which well-studied planktonic groups (acritarchs, graptolites or chitinozoans) are known to reach their maximum diversity (Servais *et al.*, 2008, 2010).

CONCLUSION

The description of an entirely new assemblage composed of 32 species and morphotypes, including six new species (four described here and two in Pouille *et al.*, 2013) from the Shundy Formation of the Aksuran Mountain, enables us to improve our understanding of the palaeobiodiversity of upper Darriwilian Radiolaria. It also allows us to better define the age range and community structure of Middle Ordovician radiolarian assemblages, including the age range of previously recognized assemblages.

ACKNOWLEDGEMENTS

Lauren Pouille and Taniel Danelian acknowledge support from the University Lille 1 and the CNRS. Leonid Popov acknowledges logistical support from the National Museum of Wales. Philippe Recourt helped with the SEM. Constructive remarks by the two reviewers, Paulian Dumitrica and Jorg Maletz, and the handling editor, Claire Allen, improved the initial manuscript.

Manuscript received 15 April 2014

Manuscript accepted 15 April 2014

Scientific editing by Claire Allen.

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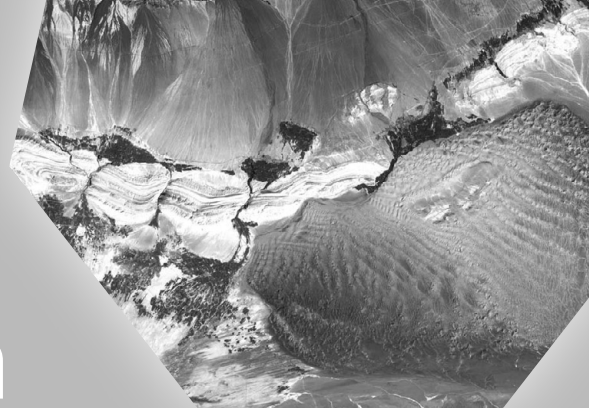
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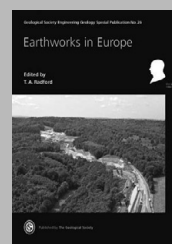
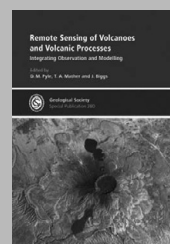
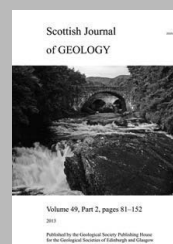
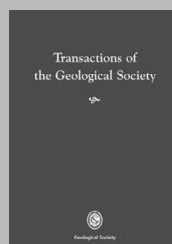
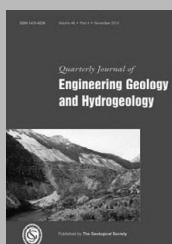
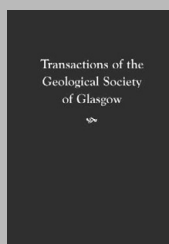
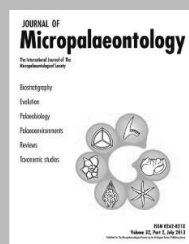
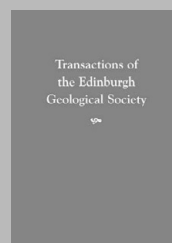
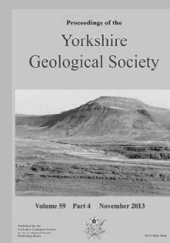
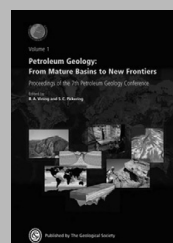
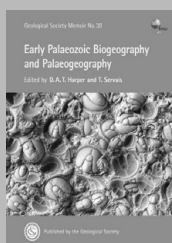
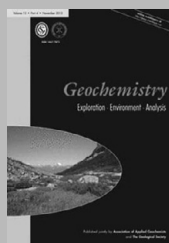
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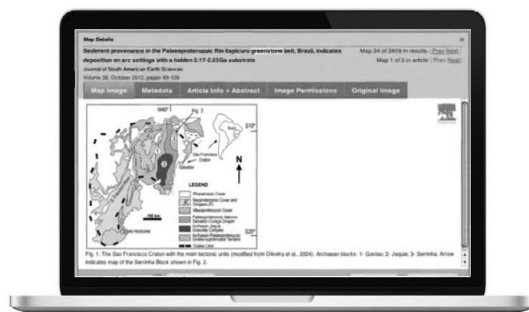
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