

Biostratigraphical and palaeobiogeographical implications of Lower Silurian Radiolaria from black cherts of the Armorican Massif (France)

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ABSTRACT – A moderately well-preserved radiolarian assemblage was recovered from organic-rich black chert in a Llandovery (Lower Silurian) sequence that crops out in southern Brittany (Chalonnès-sur-Loire section, Armorican Massif, France). The assemblage is composed of two families (Rotasphaeridae and Haplotaeniidae), four genera (?*Diparvapila*, *Secuicollacta*, *Orbiculopylorum*, *Haplotaeniatum*) and 13 species. Some were identified from whole specimens preserved in silica and extracted following dilute hydrofluoric acid processing, while others were recognized in thin-section preparations, as they are beautifully preserved as 'carbonized' microfossils. The age range suggested by conodonts and chitinozoans yielded after HF processing from one of the 27 studied samples is in good agreement with the previously published age based on graptolites. The recovered radiolarians are discussed, documented and compared with known Rhuddanian, Aeronian and lower Telychian assemblages in the literature. The stratigraphic ranges are extended for the species *Secuicollacta bipola*, *S. hexactinia*, *S. parvitesa*, *Orbiculopylorum granti* and *O. splendens* based on our new data. A significant number of radiolarians found in our samples occur in Llandovery sections from Alaska, Nevada, Arctic Canada and Sweden. These similarities are used to discuss the palaeodistribution of Lower Silurian Radiolaria and our observations support the hypothesis of a wide geographical distribution for these Palaeozoic species.

KEYWORDS: *Radiolaria*, *Silurian*, *biostratigraphy*, *plankton palaeobiogeography*, *Armorican Massif*

INTRODUCTION

Modern polycystine Radiolaria are widely distributed in all oceans. Their fossil record extends back to the Lower Cambrian (Pouille *et al.*, 2011; Korovnikov *et al.*, 2013) and provides a proxy to probe the biotic response of planktic heterotrophic micro-organisms to global environmental changes that took place during the Phanerozoic. In spite of their important potential, our present knowledge of Lower Palaeozoic radiolarian faunas is still fragmentary (Maletz, 2011), especially for the high palaeolatitudinal regions (Danielian *et al.*, 2013).

This holds also true for the Lower Silurian, as only few Llandovery radiolarian studies are published, such as the papers by Noble *et al.* (1997, 1998) for Nevada, MacDonald (1998, 2004, 2006a) for the Canadian Arctic, Won *et al.* (2002) for Alaska, Noble & Maletz (2000) and Umeda & Suzuki (2005) for Sweden, Noble *et al.* (1998) for Germany and Kurihara & Sashida (2000) for Japan. It is likely that Lower Silurian radiolarians were widely distributed and therefore they can be very useful for global biostratigraphic correlation (e.g. Noble & Aitchison, 2000 or MacDonald, 2006b). Noble & Aitchison (2000) tried to use the First Appearance Datum (FAD) and Last Appearance Datum (LAD) of several taxa in order to improve Lower Silurian radiolarian biozonation. However, significant parts of the Llandovery are still very poorly known due to the paucity of radiolarian records (i.e. the Rhuddanian and the Aeronian), not to mention the absence of radiolarian data from high latitudes.

We have recently extracted radiolarians from Lower Silurian organic-rich cherts that crop out in southern Brittany (France). In a preliminary account (Tetard *et al.*, 2014) we stressed mainly the geological, palaeogeographical and palaeoenvironmental setting of the studied sequence. The focus of this paper lies in the detailed

taxonomic discussion and documentation of the entire fauna recovered so far and its comparison with other Llandovery radiolarian assemblages known worldwide. The palaeogeographical position of the studied locality is advantageous because it was situated in middle to high palaeolatitudes and provides the opportunity to discuss the distribution of Lower Silurian radiolarian assemblages in the context of palaeogeographical position and of palaeoceanic circulation patterns.

GEOLOGICAL AND STRATIGRAPHIC SETTINGS

The Armorican Massif is composed of several Proterozoic and Lower Palaeozoic domains, deformed during the Variscan Orogeny and separated by major shear zones (Fig. 1a; Ballèvre *et al.*, 2009). Among these structures, the Ligerian domain is separated from the Central Armorican domain by the Northern South Armorican Shear Zone (SASZ) and limited to the south by a branch of the Southern SASZ. The studied section is located in the Ancenis unit of the Ligerian domain and composed of isolated Silurian sequences of 'phtanites' unreported in other domains (Piçarra *et al.*, 2002). Nowadays, these 'phtanites' are considered to be argillaceous black cherts, rich in silica and organic matter causing its black coloration (Dabard, 2000). This succession is likely to have been deposited over a distal slope along the northern continental margin of Gondwana (Piçarra *et al.*, 2009). For further details about the geological and palaeogeographical settings, the reader is referred to Tetard *et al.* (2014).

The outcrop of the studied 'Chalonnès-sur-Loire' section (Fig. 1; WGS84 coordinates: 47°20'44.29"N, 0°45'35.83"W) displays an isolated Silurian sequence of argillaceous and carbonaceous black chert, unknown from other areas of the

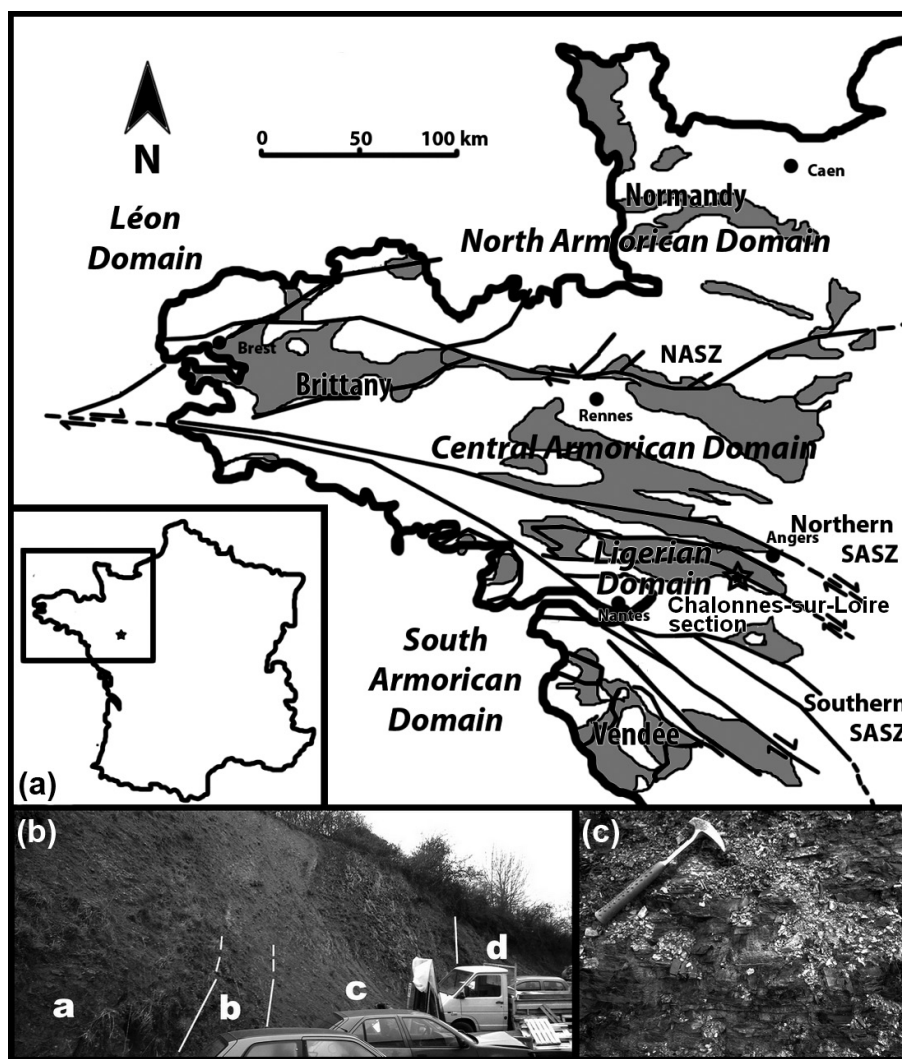


Fig. 1. (a) Distribution of Palaeozoic basement (grey areas), main tectonic features and location of the studied outcrop (star) of the Armorican Massif. (b) Photograph of the 'Chalonnès-sur-Loire' outcrop, displaying intervals 'a' (diamictite), 'b' (grey shale), 'c' (black chert and shale) and 'd' (deformed horizon). (c) Close-up picture of the 'phtanite' levels.

Armorican Massif (Piçarra *et al.*, 2002). This succession was previously dated in detail by the presence of abundant graptolites throughout the sequence (Piçarra *et al.*, 2002). The section exhibits in its northeastern part a *c.* 30 m thick succession of uppermost Ordovician diamictite (interval 'a' on Figs 1 and 2), followed by *c.* 2 m thick grey shale (interval 'b'), accumulated respectively during the Hirnantian glaciation and the subsequent deglacial period. Then, *c.* 10 m of 'phtanite' (cm- to dm-thick black bedded chert rich in organic matter, interbedded with black shale containing pyrite) corresponding to the interval 'c' overlie conformably the grey siltstone and shale (Piçarra *et al.*, 2009). This interval represents the most complete Llandovery succession of the Ligerian domain, recording a continuous sedimentation during the Rhuddanian and the Aeronian, as testified by its graptolitic and chitinozoan content (Piçarra *et al.*, 2009). Interval 'd' corresponds to strata displaying deformed horizons, difficult to access (Piçarra *et al.*, 2002, 2009).

MATERIAL AND METHODS

Twenty-seven samples were collected at regular intervals (and depending on the accessibility of the outcrop) all along the 'c' interval of the studied sequence, corresponding to the interval of black chert and shale, from the base of the Rhuddanian to the upper Aeronian. Samples containing radiolarians were first selected under a polarizing microscope based on 30 µm-thick thin-section observations. Moreover, the mineralogy of some samples was confirmed by using RAMAN spectroscopy (Jobin Yvon, LabRam HR 800 UV).

Promising samples selected for laboratory processing were chemically treated as follows: samples were first washed, rinsed with distilled water, oven-dried, crushed into smaller fragments and then soaked in numbered plastic beakers containing diluted (4.8%) HF for 24 h. Then, the fragments were sieved with 63 µm and 630 µm sieves and rinsed. Fragments larger than 630 µm were soaked again in renewed 4.8% HF for 24 h, while the fraction

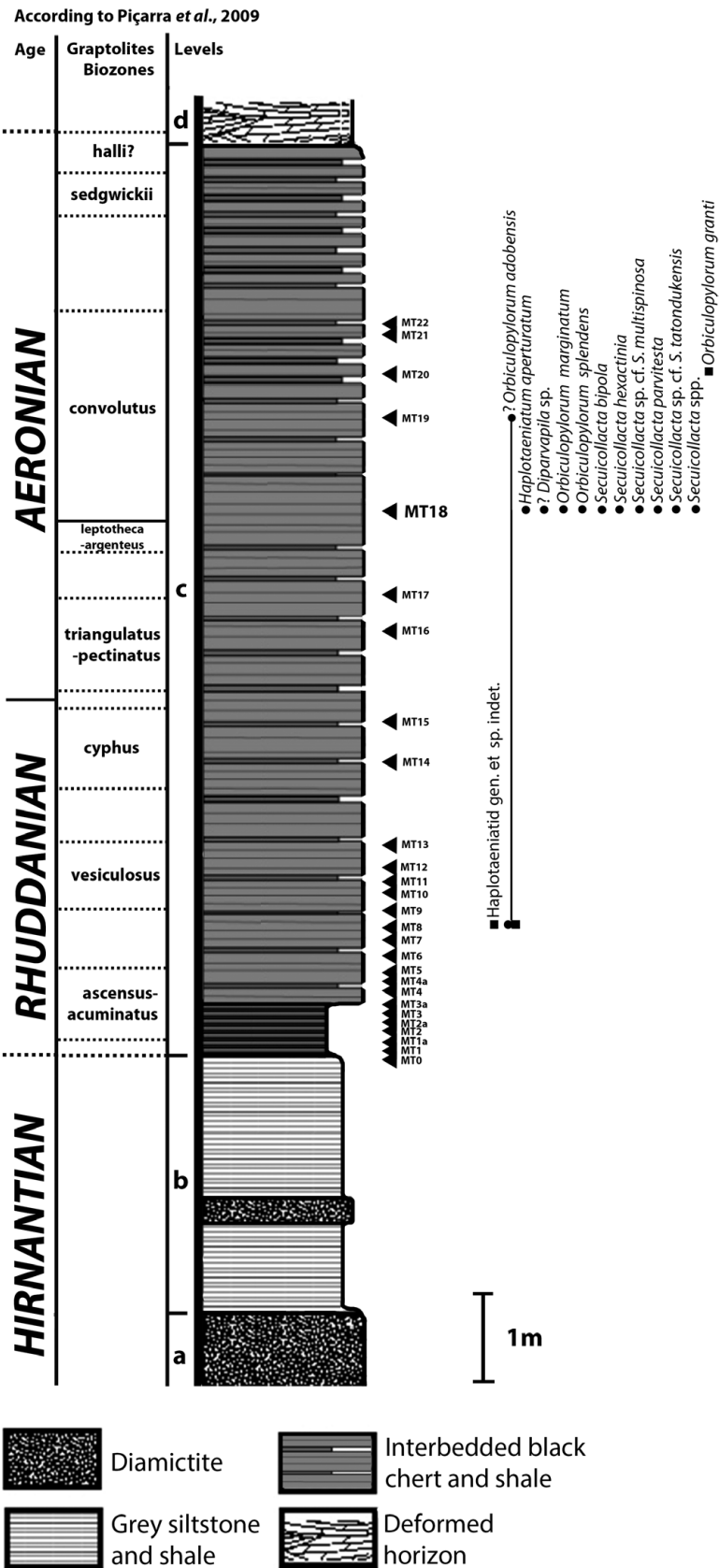


Fig. 2. Lithostratigraphy of the studied Chalonnès-sur-Loire outcrop, including the graptolite biozones identified by Piçarra *et al.* (2009) and the stratigraphic position of the radiolarian-bearing samples MT8, MT18, MT19 and MT20 (circles and squares represent SEM and thin section identifications, respectively).

comprised between 63 µm and 630 µm was filtered and dried for microscopic examination. This procedure was repeated six times. Residues were examined under a binocular microscope and radiolarians were picked, mounted on carbon stubs, metal coated, scanned and magnified with a scanning electron microscope (SEM; FEI, Quanta 200).

RESULTS

Petrography

In thin sections, we observed two different sedimentary textures; one exhibiting numerous chalcedonic spheres, 200–300 µm in diameter, which are probably very poorly preserved ‘radiolarian remains’, as mentioned by Piçarra *et al.* (2009), alternating with a second texture devoid of any spheres. These textures are interpreted to represent alternating radiolarian-rich and radiolarian-poor microfacies. However, both microfacies also exhibit thin laminations rich in quartz silt with a clayey matrix. Samples are also rich in organic matter (matrix as well as some radiolarians) and contain rhombic pyrite crystals. Occasionally, a chalcedonic sphere might contain well-preserved remains of Radiolaria (Tetard *et al.*, 2014, fig. 3.9) that can be identified in thin section (found in samples MT1, MT8, MT18, MT19, MT20). Those well-preserved radiolarians, as well as several others extracted and observed with a SEM (MT8, MT19) seem to be carbonized (RAMAN spectra), such as the Saxothuringian fauna reported by Noble *et al.* (1998).

Radiolarians

The best preserved radiolarians (Pls 1 and 2) come from the sample MT18 which corresponds to a jasper bed. In addition to radiolarians, some conodonts, chitinozoans and sponge spicules were also extracted and picked from the residue recovered from this sample MT18 (Pl. 2). Several radiolarians, although less well-preserved, were also recovered from other samples (e.g. c. 15 specimens from sample MT8, a few others from samples MT19 and MT20). Only the best specimens (i.e. around 150, 6 and 5, respectively, for samples MT18, MT19 and MT8) were mounted on carbon stubs for SEM observation. Regrettably only a fraction of them were identifiable (i.e. around 60 specimens from sample MT18, 2 specimens from MT8 and only one from MT19), a problem attributed to preservation. Some radiolarians were identified based on thin-section observations (samples MT8, MT18 and MT20; Pl. 3).

The recovered assemblage is composed of archaeospicularian Radiolaria belonging to the family Rotasphaeridae (*Secuicollacta bipola* Won *et al.*, 2002, *S. hexactinia* Won *et al.*, 2002, *S. sp. cf. S. multispinosa* Won *et al.*, 2002, *S. parvitesa* Won *et al.*, 2002, *S. sp. cf. S. tatondukensis* Won *et al.*, 2002, *Secuicollacta* spp. and ?*Diparvapila* sp.) and to the spumellarian family Haplotaeniidae (*Haplotaeniatum aperturatum* Noble *et al.*, 1998, *Orbiculopylorum marginatum* Noble *et al.*, 1998 and *O. splendens* Noble *et al.*, 1998) for sample MT18. Among the radiolarians recovered from samples MT8, MT19 and MT20, only spumellarian haplotaeniids were identified. More particularly, a few specimens of ?*O. adobensis* Noble *et al.*, 1998 were identified in samples MT8 and MT19, and one specimen was identified as *Orbiculopylorum granti* MacDonald, 2006, in sample MT20. The occurrence of identified taxa is summarized in Figure 2.

Conodonts and chitinozoans

Four species of chitinozoans were recovered from sample MT18 (*Conochitina* ?*edjelensis* Taugourdeau, 1963, *Conochitina* ?*iklaensis* Nestor 1980, *Cyathochitina* ?*campanulaeformis* Eisenack, 1931 and *Spinachitina* ?*maennili* Nestor, 1980), as well as two species of conodonts (*Distomodus staurognathoides* Walliser, 1964, *Walliserodus curvatus* Branson & Branson, 1947) and sponge spicules (Pl. 2). The species identification of the chitinozoans is doubtful due to a poor preservation. The taxon ranges of these different species of conodonts (Kleffner, 1987; Zhang & Barnes, 2002; Hints *et al.*, 2006) and chitinozoans (Loydell *et al.*, 2003, 2010; Ghavidel-syooki, 2006; Ghavidel-syooki & Vecoli, 2007; Butcher, 2009; Nestor, 2012) is provided in Figure 3.

SYSTEMATIC PALAEONTOLOGY

Subclass **Radiolaria** Müller, 1858

Superorder **Polycystina** Ehrenberg, 1838; emend. Riedel, 1967

Order **Archaeospicularia** Dumitrica, Caridroit & De Wever, 2000

Family **Rotasphaeridae** Noble, 1994; emend. Noble & Maletz, 2000

Remarks. While for Dumitrica *et al.* (2000), the family Rotasphaeridae is a junior synonym of Secuicollactidae, we follow here the opinion of Jones & Noble (2006) and treat Secuicollactidae as the junior synonym of Rotasphaeridae because the former was introduced into the literature only informally.

Genus *Diparvapila* MacDonald, 1998

Type species. *Diparvapila hicoeki* MacDonald, 1998.

?*Diparvapila* sp.
(Pl. 1, fig. 1)

Material. One specimen.

Dimensions (in µm). Cortical shell diameter: 116; medullary shell diameter: 61; primary spine length: at least 48–50.

Remarks. The specimen is poorly preserved; however, a medullary shell is observed, which may indicate that this is a specimen of *Diparvapila*. Its medullary shell is a bit larger than that reported for *D. larseni* MacDonald, 1998, although the conical shape and size of spines are comparable. However, only two primary spines are preserved, probably not intact; the others seem to be broken; pores are not visible, thus preventing species-level identification.

Genus *Secuicollacta* Nazarov & Ormiston, 1984; emend. MacDonald, 1998

Type species. *Secuicollacta cassa* Nazarov & Ormiston, 1984.

Remarks. Won *et al.* established the genus *Parasecuicollacta* in 2002 based on a lumpy surface with ragged elements and short and conical primary spines, while *Secuicollacta* exhibits a smooth surface and clearly visible primary and secondary rods. We follow

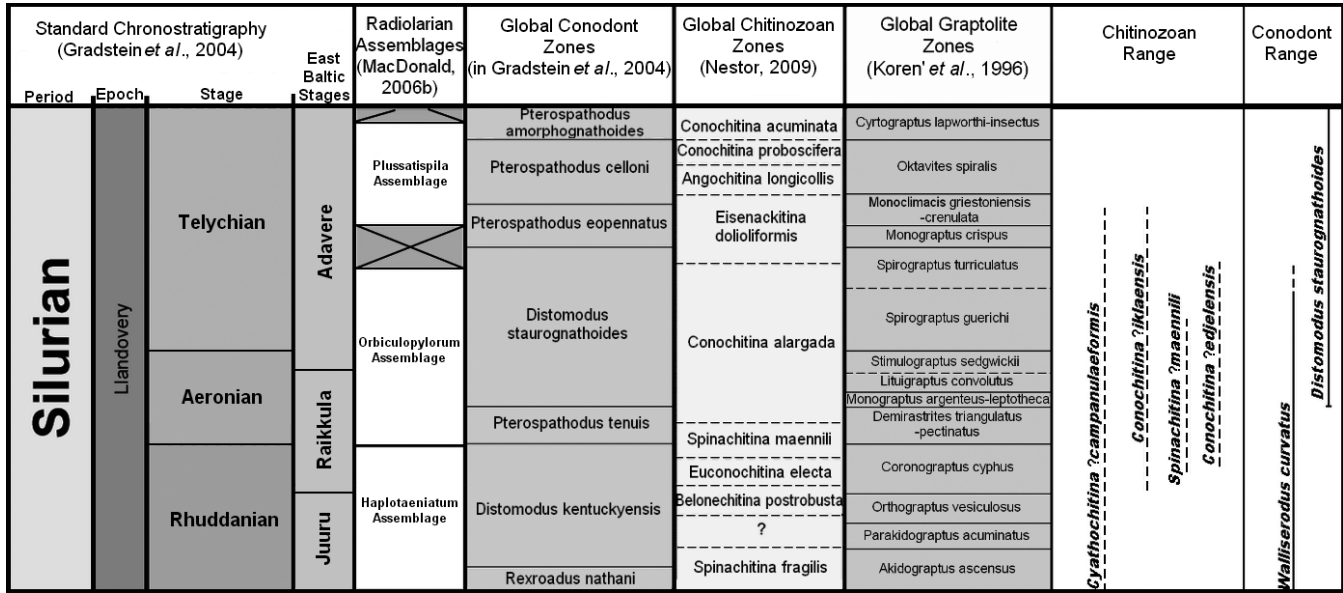


Fig. 3. Correlation chart of Early Silurian standard and east Baltic stratigraphic scales and radiolarian, conodont, chitinozoan and graptolite zonations. This figure also displays the range of the recovered conodonts and chitinozoans.

here the opinion of Jones & Noble (2006) and consider *Parasecuicollacta* as a junior synonym of *Secuicollacta*.

Secuicollacta bipola (Won, Blodgett & Nestor, 2002)
(Pl. 1, figs 2?, 3)

2002 *Parasecuicollacta bipola* Won, Blodgett & Nestor: 953; figs 3.1–3.6, 3.14–3.17.

2014 *Secuicollacta bipola* (Won, Blodgett & Nestor, 2002); Tetard et al.: fig. 3.1.

Material. Four specimens.

Dimensions (in µm). Shell diameter: 95–111; primary spines length: up to 52–60.

Occurrence. Middle Aeronian (sample MT18), Chalonnes-sur-Loire section, France (this study); lower Telychian, Road River Formation, Tatonduk River area, east-central Alaska (Won et al., 2002); lower to upper Telychian, Cape Phillips Formation, Cornwallis Island Nunavut, Canadian Arctic (MacDonald, 2006b).

Remarks. Some of our specimens exhibit only one major spine, the other one being probably broken, as mentioned by Won et al. (2002). These specimens (e.g. Pl. 1, fig. 2) are tentatively identified as *Secuicollacta bipola*, because of their poor preservation.

Secuicollacta hexactinia (Won, Blodgett & Nestor, 2002)
(Pl. 1, figs 4–8)

1998 *Secuicollacta* spp. Noble, Braun & McClellan: fig. 6.7 (only).

2002 *Parasecuicollacta hexactinia* Won, Blodgett & Nestor: 955; figs 3.7–3.11, 3.13.

2007 *Secuicollacta hexactinia* (Won, Blodgett & Nestor); Siveter et al.: pl. 2, fig. 6.

2014 *Secuicollacta hexactinia* (Won, Blodgett & Nestor); Tetard et al.: fig. 3.2.

Material. Thirteen specimens.

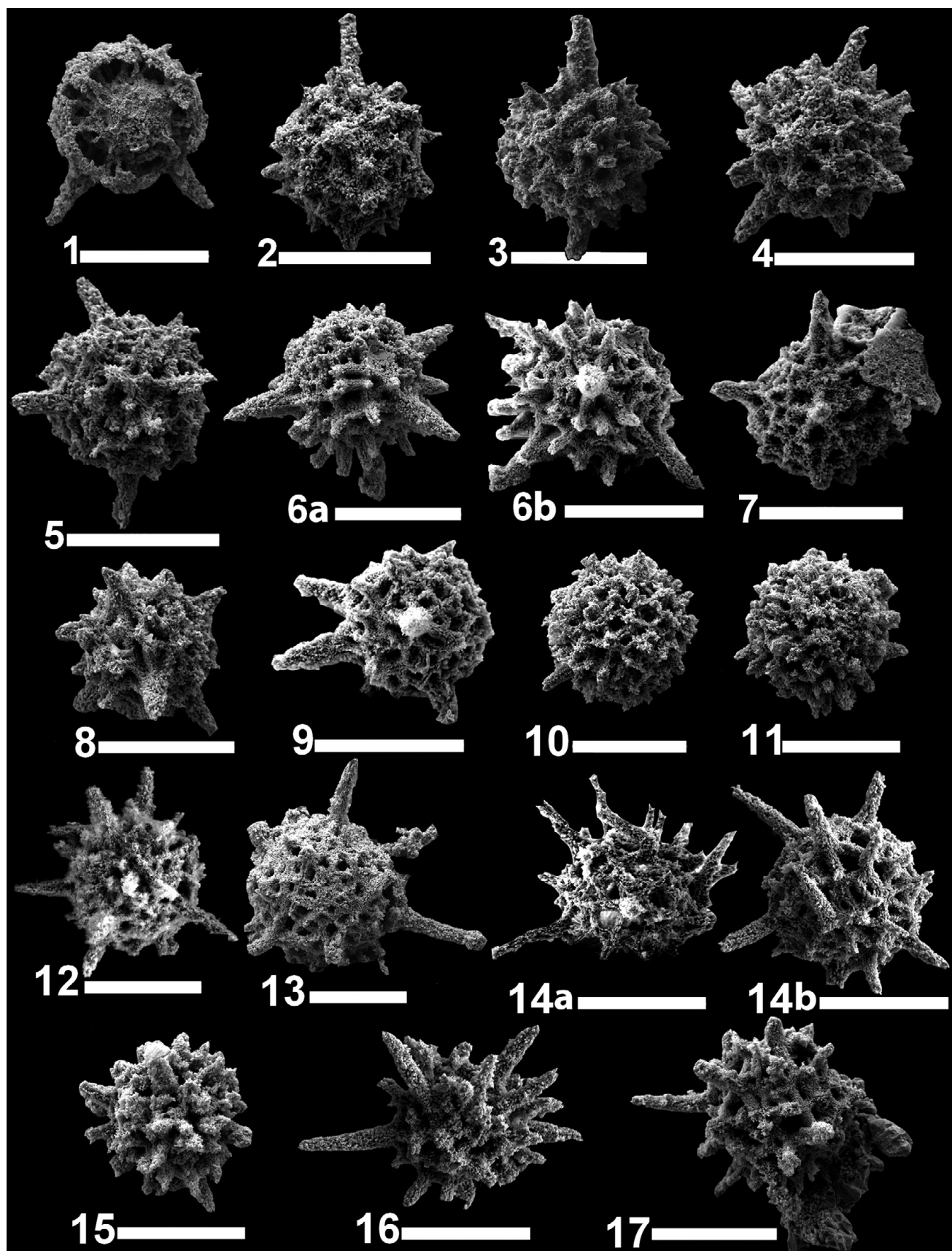
Dimensions (in µm). Shell diameter: 100–129; primary spines length: up to 40–65.

Occurrence. Middle Aeronian (sample MT18), Chalonnes-sur-Loire section, France (this study); lower Telychian, Road River Formation, Tatonduk River area, east-central Alaska (Won et al., 2002); upper Sheinwoodian to lower Homerian, Wenlock Series of Herefordshire, England (Siveter et al., 2007).

Remarks. This species is easily distinguishable thanks to the octahedral arrangement of the primary spines. Won et al. (2002) indicate this species may be synonymous with *S. teli* MacDonald, 1998 which also has a similar spine arrangement, but since no SEM images showing external details were included by MacDonald, the species are left separate. The presence of by-spines and the number, shape and arrangement of principal spines are in good agreement with the description of both species. *Secuicollacta glabiosa* MacDonald, 1998 differs by the lack of by-spines, a more bladed surface and sometimes more than 6 spines (MacDonald, 1998).

Secuicollacta sp. cf. *S. multispinosa* (Won, Blodgett & Nestor, 2002)
(Pl. 1, figs 9–11)

cf. 2002 *Parasecuicollacta multispinosa* Won, Blodgett & Nestor: 955; figs 4.4–4.9.



2014 *Secuicollacta multispinosa* (Won, Blodgett & Nestor, 2002); Tetard *et al.*: fig. 3.3.

Material. Ten specimens.

Dimensions (in μm). Shell diameter: 99–131; primary spines length: up to 58.

Remarks. This species is very similar to *S. hexactinia*, but differs in having more than six primary spines, generally shorter and without any peculiar arrangement. Our specimens display a relatively small and thick spherical shell with a coarse latticed meshwork, without primary spine or with very short ones on some specimens. The identification is doubtful due to poor preservation. This species also shows primary units without primary spine or very small ones (a primary unit with five primary rods is visible in Pl. 1, fig. 10).

Secuicollacta parvitesta Won, Blodgett & Nestor, 2002
(Pl. 1, figs 12–13)

2002 *Secuicollacta parvitesta* Won, Blodgett & Nestor: 949; figs 2.5–2.14, 2.18?, 2.19–2.21.

2006 *Secuicollacta parvitesta* Won, Blodgett & Nestor, 2002; Jones & Noble: 300; pl. 1, fig. 7.

2014 *Secuicollacta parvitesta* Won, Blodgett & Nestor, 2002; Tetard *et al.*: fig. 3.4–3.5.

Material. Six specimens.

Dimensions (in μm). Shell diameter: 118–160; primary spines length: up to 48–91.

Occurrence. Middle Aeronian (sample MT18), Chalonnes-sur-Loire section, France (this study); lower Telychian, Road River Formation, Tatonduk River area, east-central Alaska (Won *et al.*, 2002); upper Sheinwoodian, Cape Phillips Formation, Nunavut, Arctic Canada (Jones & Noble, 2006).

Remarks. Won *et al.* (2002) established two morphotypes for this species. The first one exhibits a smaller shell, more numerous by-spines, fewer and larger pores, while the second one has a denser meshwork. Our specimens exhibit a size difference and may represent examples of both morphotypes; however, poor preservation precludes such detailed discrimination. According to Won *et al.* (2002), this species is very similar to *S. alaskensis* Won *et al.*, 2002 which shows a thinner shell wall with a finer structure and shorter spines, and to *S. tatondukensis* exhibiting a less delicate meshwork and larger pores.

Secuicollacta sp. cf. *S. tatondukensis*
Won, Blodgett & Nestor, 2002
(Pl. 1, fig. 14)

cf. 2002 *Secuicollacta tatondukensis* Won, Blodgett & Nestor: 951; figs 1.14–1.20, 2.1–2.4, 6.5a, b.

Material. Two specimens.

Dimensions (in μm). Shell diameter: 116–122; primary spines length: up to 64–72.

Remarks. Our specimens are similar to *S. tatondukensis* but with uncertainty due to poor preservation. They are also similar to *S. parvitesta* Morphotype 1, but differ in having more major spines, fewer by-spines and larger pores.

Secuicollacta spp.
(Pl. 1, figs 15–17)

Material. Three specimens.

Description. Our specimens show a small spherical shell. Spines are numerous and large, making the meshwork barely visible, but it seems to be composed of straight rods. Primary units are recognizable; major spines appear to be the primary spines of primary units. These spines are larger and longer than by-spine-like spines.

Dimensions (in μm). Shell diameter: 92–108; primary spines length: up to 62–71.

Remarks. Our specimens exhibit numerous outer spines which appear to be broken, and typical large and straight primary rods. Plate 1, figure 17, is similar to *Secuicollacta* sp. in Won *et al.* (2002) in having straight primary rods. This specimen is also similar to *S. parvitesta*, but differs in having more numerous and shorter outer spines, and a meshwork consisting principally of straight primary rods.

Order **Spumellaria** Ehrenberg, 1875; emend. Riedel, 1967
Family **Haplotaeniidae** Won, Blodgett & Nestor, 2002; emend. Maletz, 2011

Genus *Haplotaeniatum* Nazarov & Ormiston, 1993

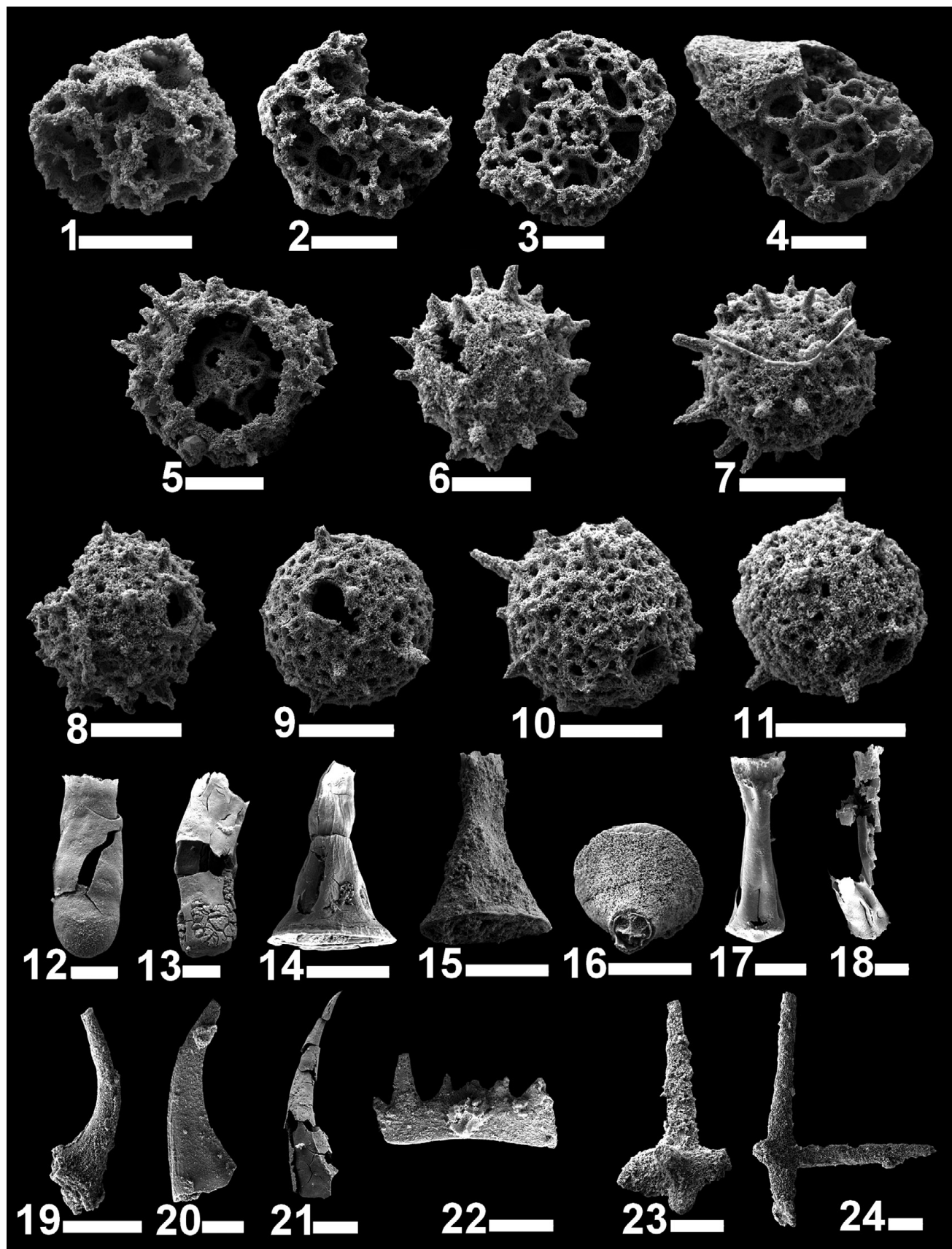
Type species. *Haplotaeniatum labyrinthum* Nazarov & Ormiston, 1993.

Remarks. This genus is characterized by a large spherical skeleton, containing a spirally arranged meshwork throughout most of the shell that consists of a succession of whorls and thus exhibits a three-dimensional spongy structure.

Haplotaeniatum aperturatum Noble, Braun & McClellan, 1998
(Pl. 2, fig. 1)

1998 *Haplotaeniatum?* *aperturatum* Noble, Braun & McClellan: 721; fig. 4.6.

Explanation of Plate 1. **fig. 1.** *Diparvapila* sp. (MT18). **fig. 2.** *Secuicollacta bipola* Won *et al.*, 2002 (MT18). **fig. 3.** *Secuicollacta bipola* Won *et al.*, 2002 (MT18). **figs 4–8.** *Secuicollacta hexactinia* Won *et al.*, 2002 (MT18). **figs 9–11.** *Secuicollacta* sp. cf. *S. multispinosa* Won *et al.*, 2002 (MT18). **fig. 12–13.** *Secuicollacta parvitesta* Won *et al.*, 2002 (MT18). **fig. 14.** *Secuicollacta* sp. cf. *S. tatondukensis* Won *et al.*, 2002 (MT18). **figs 15–17.** *Secuicollacta* spp. (MT18). Scale bar 100 μm .



- 2002 *Haplotaeniatum aperturatum* Noble, Braun & McClellan; Won *et al.*: 961; figs 5.11–5.13.
 2005 *Haplotaeniatum aperturatum* Noble, Braun & McClellan; Umeda & Suzuki: 91; pl. 2 figs 3, 4.
 2014 *Haplotaeniatum aperturatum* Noble, Braun & McClellan; Tetard *et al.*: fig. 3.6.

Material. One specimen.

Occurrence. Upper Rhuddanian, Garden Pass, Northern Adobe Range, Nevada (Noble *et al.*, 1998); middle Aeronian, Kallholn Formation, Siljan district, Sweden (Umeda & Suzuki, 2005); middle Aeronian (sample MT18), Chalonnes-sur-Loire section, France (this study); lower Telychian, Road River Formation, Tatonduk River area, east-central Alaska (Won *et al.*, 2002).

Genus *Orbiculopylorum* Noble, Braun & McClellan, 1998

Type species. *Orbiculopylorum marginatum* Noble, Braun & McClellan, 1998.

?*Orbiculopylorum adobensis* Noble, Braun & McClellan, 1998 (Pl. 2, figs 2–4; Pl. 3, figs 1–2)

?1997 *Cessipylorum?* sp. B Noble, Ketner & McClellan: 220; pl. 1, figs 9–10.

?1998 *Orbiculopylorum adobensis* Noble, Braun & McClellan: 721; fig. 4.3, fig. 6.5.

?2005 *Orbiculopylorum adobensis* Noble, Braun & McClellan; Umeda & Suzuki: 91; pl. 2 fig. 5.

Material. Five specimens.

Dimensions (in μm). Outermost shell diameter: 225–326.

Remarks. This species was first assigned to the genus *Orbiculopylorum* by Noble *et al.* (1998) based on a less dense meshwork interstitial to the medullary and cortical areas. It was reassigned to the genus *Haplotaeniatum* by Won *et al.* (2002) because the separation between cortical and medullary areas is not as clear in this species as it is in other species of *Orbiculopylorum*. However, the species identified as *H. adobensis* by Won *et al.* (2002) was synonymized with *H. fissura* by MacDonald (2006a) and considered distinct from *O. adobensis*. Our specimens are assigned to ?*O. adobensis* based on the features listed above, but doubts remain because we were not able to observe the pylome.

Orbiculopylorum granti MacDonald, 2006 (Pl. 3, fig. 4)

2006a *Orbiculopylorum granti* MacDonald: 29; figs 2.3, 2.5, 2.8, 6.1, 6.2, 6.5, 6.6.

Material. One specimen.

Dimensions (in μm). Principal cortical shell diameter: 305 ('secondary' cortical shell diameter: 415); inner meshwork diameter: 135.

Occurrence. Uppermost Rhuddanian, lower Aeronian, Cape Phillips Formation, Cornwallis Island Nunavut, Canadian Arctic (MacDonald, 2006a); middle Aeronian (sample MT20), Chalonnes-sur-Loire section, France (this study).

Orbiculopylorum marginatum Noble, Braun & McClellan, 1998 (Pl. 2, figs 5–8)

1997 *Cessipylorum?* sp. A Noble, Ketner & McClellan: 220; pl. 1, figs 11, 12.

1998 *Orbiculopylorum marginatum* Noble, Braun & McClellan: 719; fig. 4.1.

2002 *Orbiculopylorum marginatum* Noble, Braun & McClellan; Won *et al.*: 952; figs 5.18–5.20.

2005 *Orbiculopylorum marginatum* Noble, Braun & McClellan; Umeda & Suzuki: 91; pl. 2 figs 6, 7.

2014 *Orbiculopylorum marginatum* Noble, Braun & McClellan; Tetard *et al.*: fig. 3.7.

Material. Fifteen specimens.

Dimensions (in μm). Cortical shell diameter: 166–236; medullary shell diameter: 82–99.

Occurrence. Upper Rhuddanian, Garden Pass, Northern Adobe Range, Nevada (Noble *et al.*, 1998); middle Aeronian, Kallholn Formation, Siljan district, Sweden (Umeda & Suzuki, 2005); middle Aeronian (sample MT18), Chalonnes-sur-Loire section, France (this study); lower Telychian, Road River Formation, Tatonduk River area, east-central Alaska (Won *et al.*, 2002).

Orbiculopylorum splendens Noble, Braun & McClellan, 1998 (Pl. 2, figs 9–11)

1998 *Orbiculopylorum splendens* Noble, Braun & McClellan: 720; fig. 4.2.

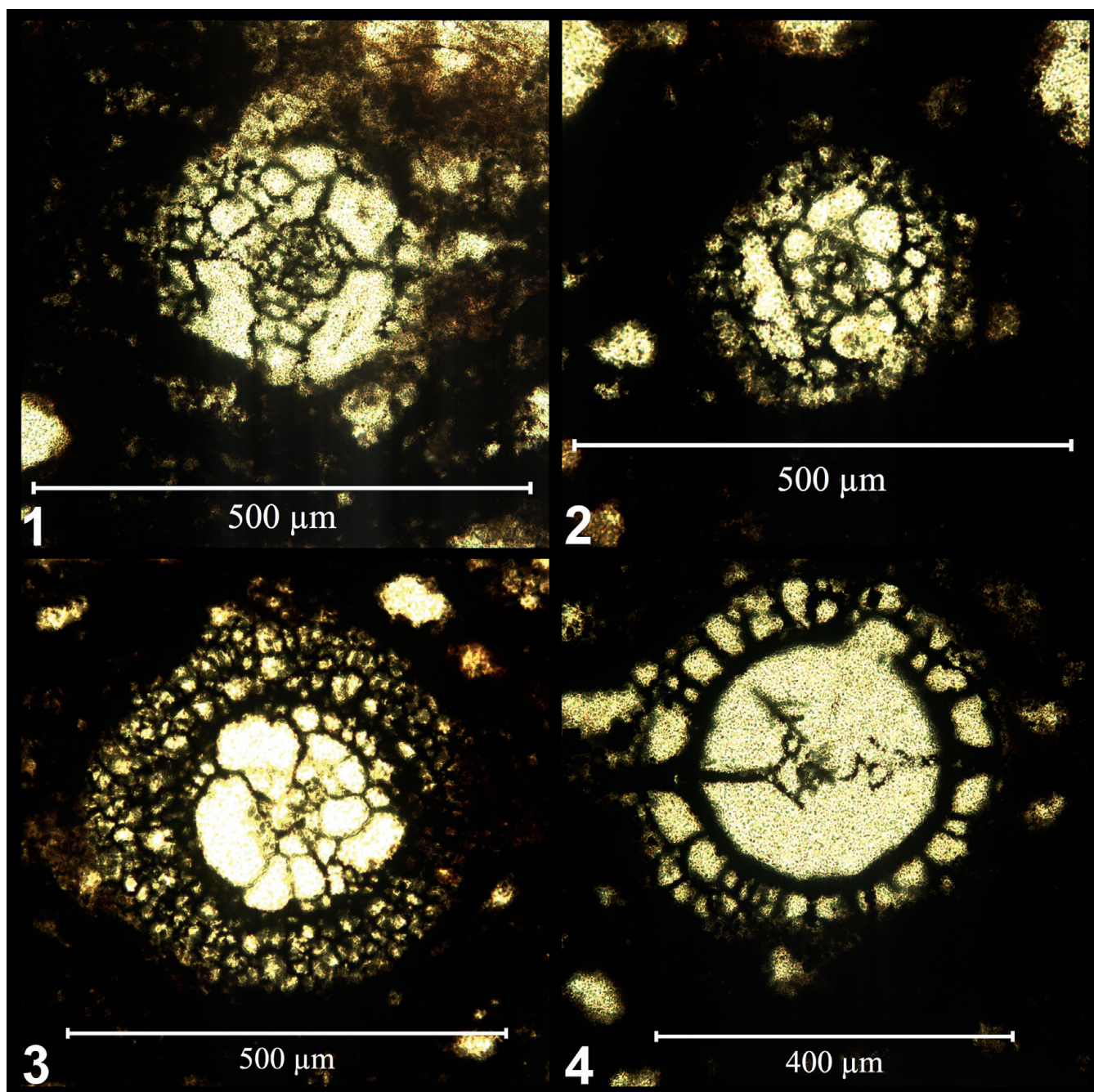
2014 *Orbiculopylorum splendens* Noble, Braun & McClellan; Tetard *et al.*: fig. 3.8.

Material. Eight specimens.

Dimensions (in μm). Cortical shell diameter: 170–193.

Occurrence. Upper Rhuddanian, Northern Adobe Range, Nevada (Noble *et al.*, 1998); middle Aeronian (sample MT18), Chalonnes-sur-Loire section, France (this study).

Explanation of Plate 2. **fig. 1.** *Haplotaeniatum aperturatum* Noble *et al.*, 1998 (MT18). **figs 2–4.** ?*Orbiculopylorum adobensis* Noble *et al.*, 1998: 3, 4 (MT8); 2 (MT19). **figs 5–8.** *Orbiculopylorum marginatum* Noble *et al.*, 1998 (MT18). **figs 9–11.** *Orbiculopylorum splendens* Noble *et al.*, 1998 (MT18). **fig. 12.** *Conochitina ?iklaensis* Nestor, 1980 (MT18). **fig. 13.** *Conochitina ?edjelensis* Taugourdeau, 1963 (MT18). **figs 14–16.** *Cyathochitina ?campanulaeformis* Eisenack, 1931 (MT18). **figs 17–18.** *Spinachitina ?maennili* Nestor, 1980 (MT18). **fig. 19.** *Distomodus staurogathoides* Walliser, 1964 (MT18). **figs 20–21.** *Walliserodus curvatus* Branson & Branson, 1947 (MT18). **fig. 22.** Conodont S-element. **figs 23–24.** Hexactinellid megascleres *incertae sedis* (MT18). Scale bar 50 μm for figs 12–13, 17–18; 100 μm for the rest.



Explanation of Plate 3. figs 1–2. *?Orbiculopylorum adobensis* Noble *et al.*, 1998 (MT8). **fig. 3.** Haplotaeniid gen. et sp. indet. (MT8). **fig. 4.** *Orbiculopylorum granti* MacDonald, 2006 (MT20).

Remarks. This species differs from *O. marginatum* in possessing less numerous and larger spines on its cortical shell (*c.* 8 per hemisphere, but *c.* 15 in *O. marginatum*). Intermediate forms can be found.

Haplotaeniid gen. et sp. indet.
(Pl. 3, fig. 3)

Material. One specimen.

Dimensions (in µm). Cortical shell diameter: 450.

Remarks. Observed only in thin section, this specimen is characterized by a very loose inner meshwork, while the outer part is, on the contrary, very dense.

DISCUSSION

Integrated biostratigraphy and Radiolarian age ranges

The studied sequence at Chalonnes-sur-Loire was previously dated by abundant graptolites collected and identified by Piçarra *et al.* (2009). Based on their biostratigraphical assignment

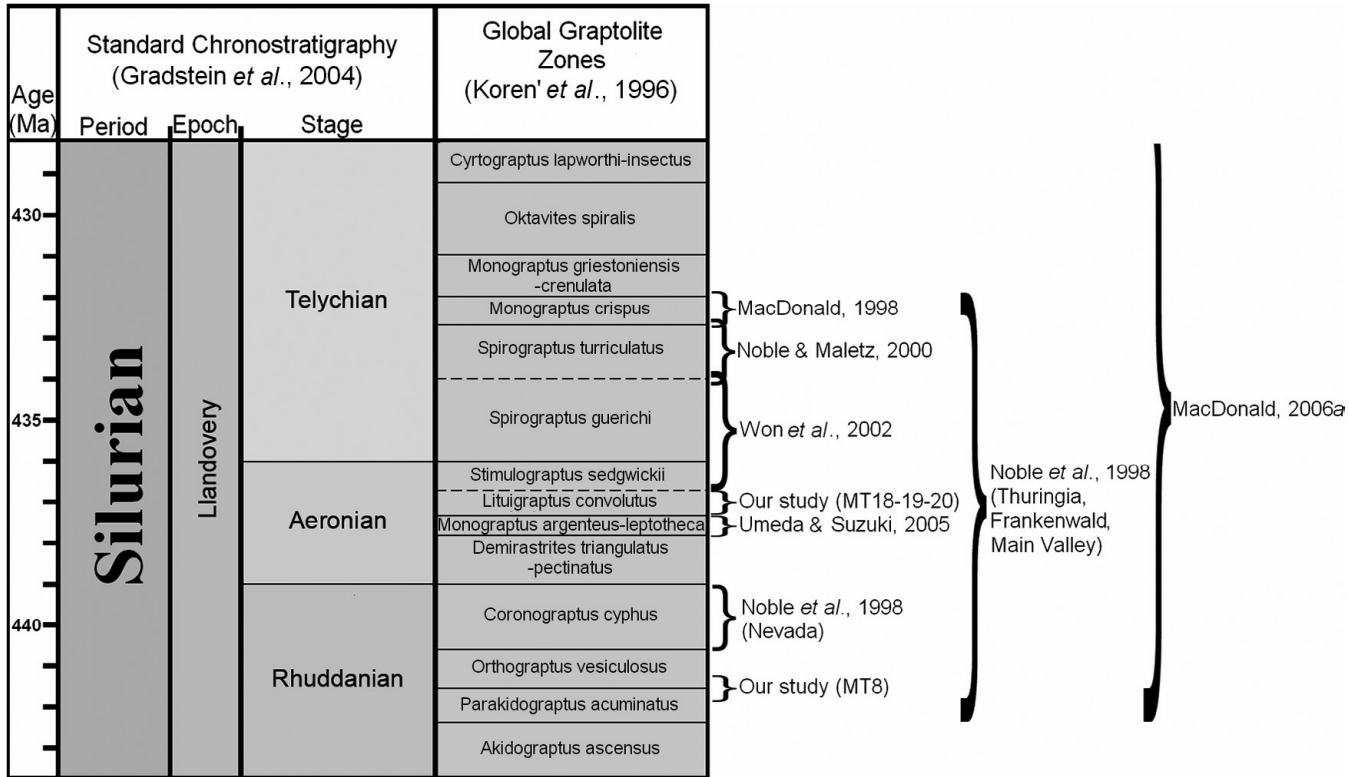


Fig. 4. Chronostratigraphic assignment of all known Llandovery radiolarian faunas in the literature including those discussed in our study.

(compare with their fig. 3), samples MT18, MT19 and MT20 can be assigned to the middle Aeronian (*Lituigraptus convolutus* graptolite biozone); in the same way, our sample MT8 can be assigned to the lower Rhuddanian (see Fig. 2). The common age range of conodonts and chitinozoans recovered from sample MT18 is in good agreement with the more accurate age provided by graptolites (see Fig. 3).

Silurian radiolarian biostratigraphy has made significant progress over the last 20 years, with the Llandovery being initially characterized by a single zone (Nazarov & Ormiston, 1993), but subdivided later into three (MacDonald, 2006b; see Fig. 3). Sample MT18 contains numerous *Orbiculopylorum* specimens and it may be assigned to the *Orbiculopylorum* assemblage of MacDonald's biozonation (2006b), which is an informal taxon range zone whose base and top are respectively defined by the first and last occurrence of the genus *Orbiculopylorum*. In the Arctic sections studied by MacDonald (2006a, 2006b), the *Orbiculopylorum* assemblage was recovered from the lowermost Aeronian *Campograptus curtus* through mid-Telychian *Spirograptus turriculatus* Arctic graptolite zones. *Orbiculopylorum* was not found in material older than Aeronian in the Arctic (MacDonald 2006b).

Based on their occurrences in our section, the stratigraphic range of several secuicollactid and haplotaeniid species can be extended. Thus, for species *Secuicollacta bipola*, *S. hexactinia* and *S. parvitesa*, for which the oldest previously known level was the lower Telychian (Won et al., 2002), their age range can be now extended down to the middle Aeronian. Concerning the haplotaeniid species *Orbiculopylorum granti*, known previously

from the lower Aeronian (MacDonald, 2006a), its age range is now extended up to the middle Aeronian. The same holds true for species *O. splendens*, previously known only from the upper Rhuddanian (Noble et al., 1998).

Similarity to coeval radiolarian assemblages

Figure 4 shows the age calibration of all known Llandovery radiolarian assemblages. Those described by Noble & Maletz (2000) and MacDonald (1998, 2004) will not be considered in the following discussion, as their age is younger than the age of our fauna. The assemblage described by MacDonald (2006a) will not be considered either because it deals only with the family Haplotaeniidae and not with the entire assemblage, and because the highly dissimilar preservation between well-preserved limestone and moderately preserved chert samples makes it difficult to make any meaningful comparisons of taxonomic composition.

The Alaskan assemblage (Fig. 5a) described by Won et al. (2002) shares 10 of its 17 species in common with the assemblage described by Noble et al. (1997, 1998) from Nevada, which contains 19 species (see Won et al. [2002] for a detailed comparison). Our assemblage shares at least 5 (and possibly 8) species in common with the Alaskan fauna (*Secuicollacta bipola*, *S. hexactinia*, *S. parvitesa*, *Haplotaeniatum aperturatum*, *Orbiculopylorum marginatum*, *Secuicollacta* sp. cf. *S. multispinosa*, *Secuicollacta* sp. cf. *S. tatondukensis* and ?*O. adobensis*). The Armorican assemblage also shares several species with the Nevada fauna described by Noble et al. (1998), such as several secuicollactids (i.e. *Secuicollacta hexactinia* and *S. multispinosa*) and haplotaeniids such as *Haplotaeniatum aperturatum*, *Orbiculopylorum*

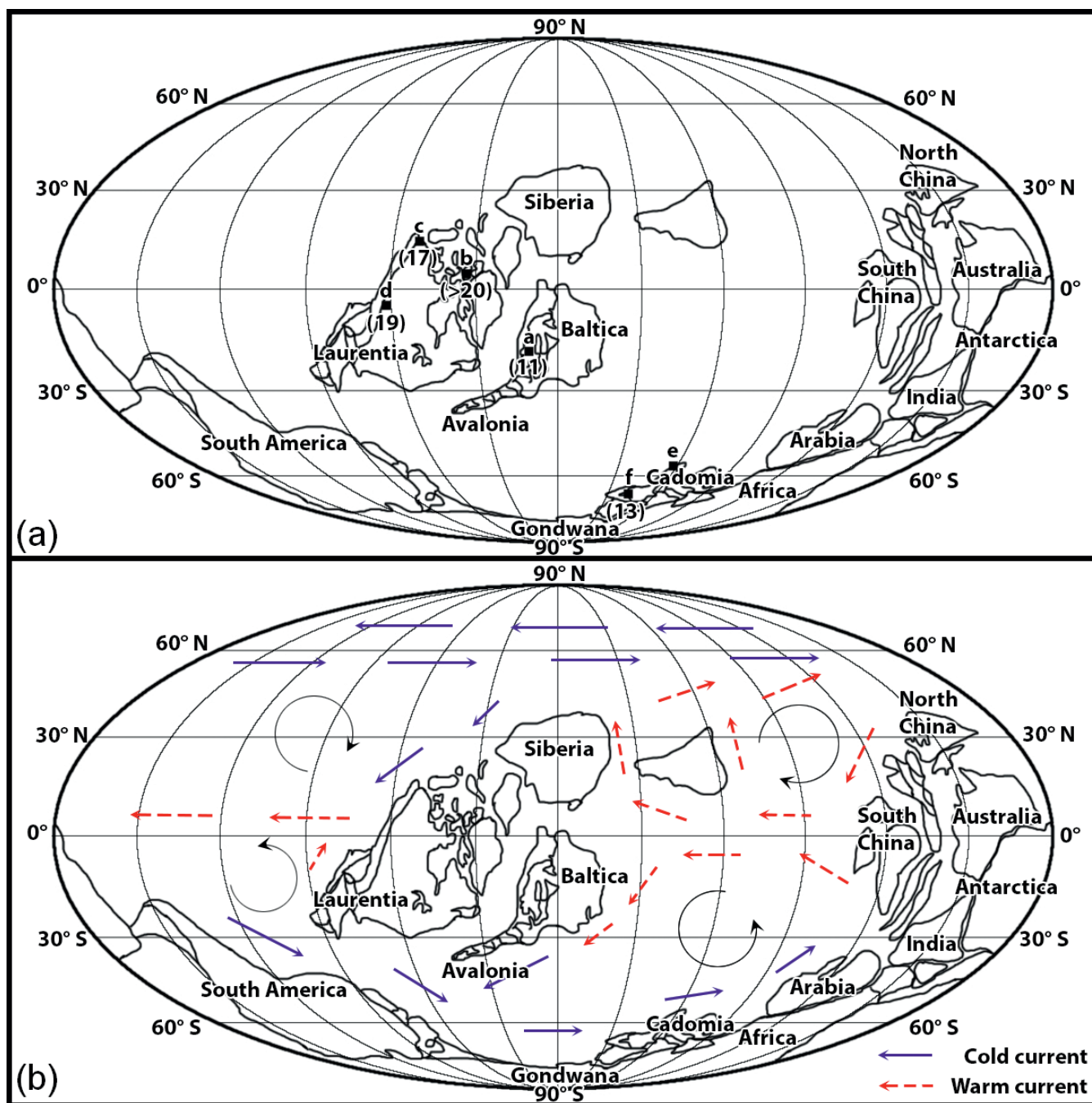


Fig. 5. (a) Palaeogeographical distribution of nearly all known Llandovery radiolarian localities. **a** – Dalarna, Sweden (Umeda & Suzuki, 2005). **b** – Arctic Canada (MacDonald, 1998, 2004, 2006a). **c** – Alaska (Won *et al.*, 2002). **d** – Nevada (Noble *et al.*, 1997, 1998). **e** – Thuringia (Noble *et al.*, 1998). **f** – Armorican Massif (Tetard *et al.*, 2014). Numbers in brackets indicate the diversity of recorded species. (b) Global oceanic circulation during the lower Silurian (after Ziegler *et al.*, 1977; Armstrong *et al.*, 2009; Servais *et al.*, 2014).

adobensis, *O. marginatum*, *O. splendens* and possibly *O. granti*. The Swedish fauna described by Umeda & Suzuki (2005) contains three species (*Haplotaeniatum aperturatum*, *Orbiculopylorym adobensis* and *O. marginatum*) which are also present in the assemblages listed above.

Palaeogeographical distribution and palaeoceanographic scenarios

As discussed above, our assemblage from the Armorican Massif shares many common species with assemblages known from palaeogeographically widely dispersed areas in the lower Silurian,

such as the Alaskan assemblage of Won *et al.* (2002), the Nevadan faunas of Noble *et al.* (1997, 1998) and the Swedish assemblage of Umeda & Suzuki (2005). Several hypotheses detailed hereafter can possibly explain this global pattern of distribution for the Silurian and they may be responsible for the relative similarities between the equatorial and peripolar assemblages.

The incursion of tropical radiolarians into polar areas is not rare in modern oceans (Bjørklund *et al.*, 2012), some of them being brought into high latitudes by regular pulses of warm water masses originated from the tropical realm. Figure 5b illustrates a schematic map of global oceanic circulation during the Silurian, reconstructed after Ziegler *et al.* (1977), Armstrong *et al.* (2009) and Servais *et al.* (2014). It displays warm currents circulating towards the south, with western, central and eastern components. The western component is part of a west-Laurentia gyre that drives warm water away from Laurentia and drags plankton along southern Africa into high latitudes, whereas the central and eastern components circulate along the Baltica and Avalonia land masses, within the east Baltica gyre. Thus, planktic populations living in these currents could have been shifted from an equatorial into an austral position and be deposited into the Armorican and Thuringian basins.

Another important factor to take into account is the possible discrepancy between biocoenosis (living assemblage), thanatocoenosis (death assemblage) and taphocoenosis (fossil assemblage) (De Wever *et al.*, 1994). Indeed, these planktic micro-organisms are considerably dependent on the oceanic currents (Bjørklund *et al.*, 2012) and thus skeletons of radiolarians could be possibly transported over long distances even after their death. However, it is usually accepted that the lateral transport of radiolarian shells along long distances is limited. Indeed, the principal transport component is considered to be the sinking through aggregates and fecal pellets (De Wever *et al.*, 1994; Lazarus, 2005). Thus the transport of micro-organisms is very restricted and the presence of foreign taxa in unusual latitudes (e.g. cold-water radiolarians into low latitudes, or reverse) probably shows the tolerance of this species (Lazarus, 2005).

CONCLUSION

The 'Chalonnès-sur-Loire' section consists essentially of Llandovery (Rhuddanian to Aeronian) black chert alternating with black shale that is rich in organic matter and pyrite and was deposited in an outer offshore environment, probably along a continental slope located on an intermediate-high latitudinal Gondwanan margin. This outcrop produced numerous graptolites and radiolarians, and an assemblage consisting of 13 species is described herein. Based on the composition of our assemblage in the best preserved sample (MT18), the upper part of the section was assigned to the *Orbiculopylorum* assemblage, which ranges from the base of the Aeronian to lower Telychian in the Arctic where it was originally defined. In the 'Chalonnès-sur-Loire' section, the *Orbiculopylorum* assemblage is definitively recognized in the middle Aeronian *Lituigraptus convolutus* graptolite zone, but may extend lower into the middle Rhuddanian, depending on whether specimens identified as *?Orbiculopylorum adobensis* are, in fact, this species. Comparison with other known lower Silurian assemblages, known essentially from tropical regions, reveals many similarities with our assemblage, which argues for

a wide biogeographical dispersal of lower Silurian radiolarian plankton.

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