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The Radiolaria of the Herefordshire Konservat-Lagerstätte (Silurian), England

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ABSTRACT – Concretions of the Wenlock Series Herefordshire Konservat-Lagerstätte of the Welsh Borderland have yielded one of the few recorded Silurian radiolarian faunas world-wide and the only one known from the Silurian of Britain. The low diversity radiolarian fauna consists of new forms of Inaniguttidae (*Inanihella sagena* sp. nov. and *Inanihella* sp.), Haplentactiniidae (*Haplentactinia armista* sp. nov.) and a previously reported form of Secuicollactidae (*Secuicollacta hexatinia* (Won *et al*., 2002)). The fauna has affinities with Silurian radiolarian assemblages of the Urals, the Canadian Arctic and Alaska. Stratigraphically the Herefordshire fauna appears transitional between established Silurian radiolarian biozones. *J. Micropalaeontol*. **26**(1): 87–95, April 2007.

KEYWORDS: *Radiolaria, Konservat-Lagerstätte, Wenlock Series, Silurian, England*

INTRODUCTION

Radiolaria are Cambrian to Recent marine Protozoa represented in the stratigraphic record by their siliceous tests (Anderson, 1983). The group has importance in biostratigraphical and tectonic studies (e.g. Aitchison & Murchey, 1992; Noble & Aitchison, 2000). Radiolarian faunas from the Lower Palaeozoic are quite rare (e.g. see Noble & Aitchison, 1995, 2000) and relatively little studied. The discovery of radiolarians in the Silurian of Britain was based on material from concretions from Herefordshire in the Welsh Borderland, where the tests occur in association with a Konservat-Lagerstätte of Wenlock age (Briggs *et al*., 1996).

In addition to the normal shelly fauna the Herefordshire Konservat-Lagerstätte yields numerous small marine invertebrates with soft anatomy preserved in three dimensions. They include a stem group chelicerate (Orr *et al*., 2000a; Sutton *et al*., 2002), a vermiform aplacophoran-like mollusc (Sutton *et al*., 2001a, b, 2004), a polychaete worm (Sutton *et al*., 2001c), two myodocope ostracod species (Siveter *et al*., 2003, 2007), a phyllocarid (Briggs *et al*., 2004), a pycnogonid (Siveter *et al*., 2004), a barnacle (Briggs *et al*., 2005), a rhynchonelliformean brachiopod (Sutton *et al*., 2005a), a stem-group asteroid (Sutton *et al*., 2005b), a platyceratid gastropod (Sutton *et al*., 2006) and various undescribed sponges, orthoconic nautiloids, arthropods, echinoderms, graptolites and enigmatic forms of uncertain affinity. The fossils are exquisitely preserved as calcite infills within the concretions (Orr *et al*., 2000b). The morphology of each species is recovered and elucidated as a series of 'virtual fossils' using the methods developed by Sutton *et al*. (2001d, 2002). Acid digestion of thin-section off-cuts from the concretions has yielded a microfauna of mostly radiolarians, together with a few ostracod valves and conodont elements. Preservational aspects of the radiolarians, and the attendant implications for the taphonomy of the biota, have been addressed (Orr *et al*., 2002). This paper describes the radiolarian fauna and assesses its biostratigraphic and palaeozoogeographical significance.

METHODS AND MATERIAL

The radiolarian-bearing concretions are up to about 20 cm across, spherical to subspherical and composed mostly of calcium carbonate and clay minerals. The radiolarians are visible as randomly scattered specimens on the surfaces of concretions that have been broken using mechanical methods. Most of the radiolarians were recovered using about 4% acetic acid, followed by concentration in bromoform ($CHBr_3$) and then sieving with the 63 μm fraction collected and dry picked. The off-cuts from about 40 concretions were processed, yielding a few hundred poorly preserved to well-preserved tests in generally low abundances of 2–25 tests per 500 g sample.

The radiolarians recovered show an unusual preservation (Orr *et al*., 2002). Tests are preserved replicated in ankerite and clay minerals and occur either isolated or enclosed (*c*. 75% of the material) in spherical 'cocoons'. The cocoons are composed of quartz, kaolinite, pyrite or most commonly ankerite. The latter is a product of secondary dolomitization of the sparry calcite that was precipitated in the space originally occupied by the cytoplasm of the radiolarian (Orr *et al*., 2002).

The specimens were coated with gold prior to study using scanning electron microscopy. The figured material is deposited at the University Museum of Natural History, Oxford, nos. OUM C29536, C.29542, C.29594 to C.29598.

GEOLOGICAL SETTING

The radiolarian-bearing concretions occur randomly scattered within a fine-grained, weathered volcanic ash that has a maximum thickness of 1 m and is traceable laterally for approximately 40 m. The ash lies near the local base of several metres of calcareous shales. Palynological data obtained from processing the shales (G. Mullens, pers. comm., 2000), together with macrofossil evidence from local Wenlock strata, especially graptolites and brachiopods, infer a late Sheinwoodian to early Homerian (=approximately *Cyrtograptus ellesae* to *Cyrtograptus lundgreni* biozones), Wenlock Series age for the ash.

The ash and carbonate-rich muds accumulated on the outer margin of the eastern shelf of the Lower Palaeozoic Welsh depositional basin (see Bassett, 1974; Bassett *et al.*, 1992; Aldridge *et al.*, 2000), which was part of the microcontinent of Avalonia. In Wenlock times Avalonia lay at the southern margin of the remnant Iapetus Ocean in subtropical southerly latitudes, in proximity to the palaeocontinents of Laurentia and Baltica (Pickering & Smith, 1995; Fortey & Cocks, 2003). The calcareous shales yield the low diversity *Visbyella* brachiopod community (Hurst *et al.*, 1978), which is characteristic of sites near the outer limit of the shelly benthos during the Wenlock and probably reflects prevailing water depths of about 150–200 m (Brett *et al.*, 1993). Silurian radiolarian faunas world-wide, range from shallow shelf to abyssal oceanic settings.

STRATIGRAPHIC SIGNIFICANCE

The development of biostratigraphic schemes based on Silurian Radiolaria is still in its infancy. Silurian radiolarians are known from North America, Asia and Europe, in Llandovery to Přídolí strata, but described faunas are rare and their biostratigraphic potential has yet to be realized fully. Silurian radiolarians have been recorded from Germany (Stürmer, 1952; Noble *et al.*, 1998), the southern Urals part of Russia and Kazakhstan (Nazarov, 1975, 1988; Nazarov & Popov, 1980; Nazarov & Ormiston, 1984, 1993; Amon *et al.*, 1995), the Canadian Arctic (Goodbody, 1986; Renz, 1988; MacDonald, 1998, 1999, 2003, 2004, 2006a, b; Jones & Noble, 2006), Japan (Furutani, 1990; Wakamatsu *et al.*, 1990; Aitchison *et al.*, 1996; Umeda, 1997, 1998a, b, c; Kurihara & Sashida, 1998), Australia (Aitchison, 1991), Poland (Gorka, 1994), China (Li, 1994), Texas (Noble, 1994), Nevada (Noble *et al.*, 1997, 1998), Sweden (Maletz & Reich, 1997; Noble & Maletz, 2000; Umeda & Suzuki, 2005) and Alaska (Won *et al.*, 2002). Illustrations of the radiolarian faunas of purported Silurian age from southern France (Rüst, 1892) indicate they are more likely to be from Lower Carboniferous strata.

Radiolarian-bearing deposits of Wenlock age occur in the Canadian Arctic, with earlier studies describing the Palaeoscenidae and Ceratoikiscidae that dominate the faunas (Goodbody, 1986; Renz, 1988; MacDonald, 2003, 2004), whilst the secuicollactids and entactiniids are a minor component of these faunas and described in more recent work (MacDonald, 2003, 2006a; Jones & Noble, 2006). Some radiolarians described from China, Japan and the southern Urals and the early faunas from Texas (references as above) may also be of Wenlock age but, with the exception of samples from Japan for which SHRIMP data for pyroclastic zircons in radiolarian-bearing water-lain tuffs are available (Aitchison *et al.*, 1996), independent stratigraphic age control is not available.

In the lower Palaeozoic radiolarian biozonation proposed by Noble & Aitchison (2000), the base of the Silurian Long-spined inaniguttid Biozone 2 is defined by the Last Appearance Datum (LAD) of members of the Haplentactiniinae such as *Haplotaeniatum* Nazarov & Ormiston, 1993 as well as that of *Gyrosphaera* Noble & Maletz, 2000; forms which have multiple spiraliform or concentric shell layers (Fig. 1; note that the range of *Gyrosphaera* was drawn slightly too high in Noble & Aitchison, 2000, fig. 1, as its LAD should correspond with that of *Haplotaeniatum*). Such forms are common in late Llandovery (mid-Telychian *Spirograptus turriculatus* Biozone) faunas from Sweden but are absent from the Herefordshire fauna, possibly indicating that the LAD of such forms lies below the Sheinwoodian/Homerian stage boundary. The First Appearance Datum (FAD) of *Ceratoikiscum* Deflandre, 1953 defines the base of Long-spined inaniguttid Biozone 3 (Noble & Aitchison, 2000), in which the *Inanihella tarangulica* Nazarov & Ormiston, 1984 Group occurs. *Ceratoikiscum* is not present in the Herefordshire fauna but inanihellid specimens are relatively plentiful. This could be taken to indicate that the Herefordshire fauna contains radiolarians from a stratigraphic interval intermediate between the ranges of Long-spined inaniguttid Biozones 2 and 3 of Noble & Aitchison (2000). Alternatively, it is possible that the absence of *Ceratoikiscum* in the Herefordshire fauna is related to preservational factors. As ceratoikiscids are known from the Sheinwoodian of the Canadian Arctic (Renz, 1988), it is suggested that Noble & Aitchison (2000) may have drawn this boundary a little too high. The authors do not have series of samples that span a longer stratigraphic interval so are unable to clarify this issue further. It is noted that even where well-preserved material is available from sections of correlative age, such as the Cape Phillips Formation in the Canadian Arctic, recent work has not yet led to a unique and unambiguous interpretation of biozonation for this interval (MacDonald, 2006b, cf. Jones & Noble, 2006).

PALAEOZOOGEOGRAPHICAL AFFINITIES

The Herefordshire radiolarian fauna has only limited faunal ties with other regions. It has affinities at generic level with material described (Nazarov, 1988) from the upper part of the Sakmarskaya Suite (Wenlock?–Ludlow) of northwestern Mugodzhar in the southern Urals part of Kazakhstan. One rotaspherid species known from the late Aeronian to early Telychian, Llandovery Series of the Road River Formation, Tatonduk River area, east central Alaska (Won *et al.*, 2002) also occurs in the Herefordshire fauna.

SYSTEMATIC PALAEONTOLOGY

Class **Actinopoda** Calkins, 1909
Subclass **Radiolaria** Müller, 1858
Order **Polycystida**, Ehrenberg, 1838
Suborder **Spumellariina** Ehrenberg, 1875
Family **Inaniguttidae** Nazarov & Ormiston, 1984
(emend Noble, 1994)
Genus *Inanihella* Nazarov & Ormiston, 1984

Type species. *Helioentactinia*? *bakanasensis* Nazarov, 1975, Ordovician of central Kazakhstan.

Remarks. In addition to the specimens assigned herein to *Inanihella* at least two other, previously figured specimens

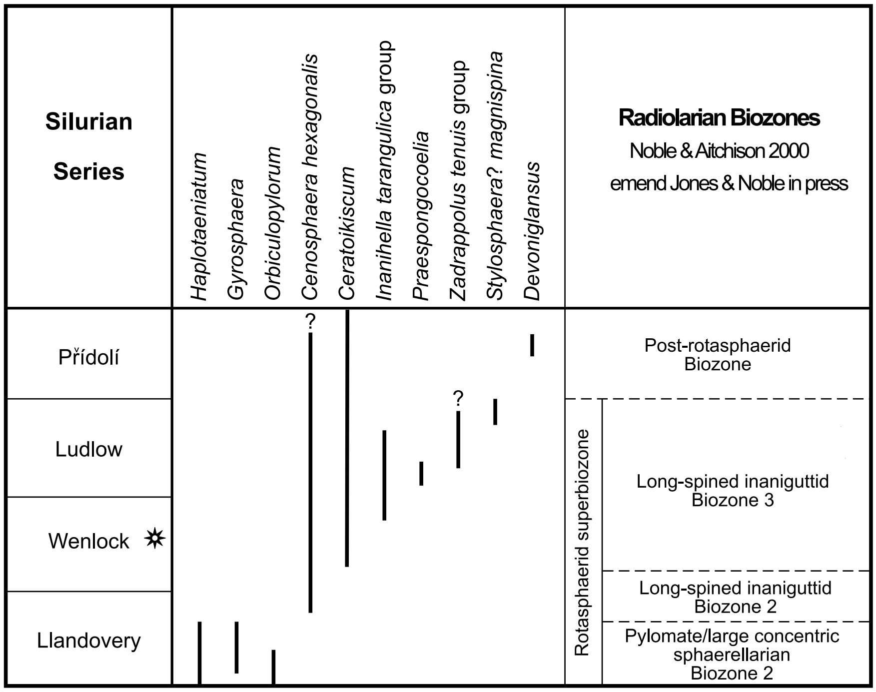


Fig. 1. Stratigraphic occurrence of key Silurian radiolarian taxa and the radiolarian biozones of Noble & Aitchison (2000), as revised by Jones & Noble (in press). The icon denotes the stratigraphic position of the radiolarian fauna of the Herefordshire Konservat-Lagerstätte.

from the Herefordshire Konservat-Lagerstätte may also be congeneric (Orr *et al.*, 2002: pl. 1, fig. 9, OUM C.29537; pl. 2, figs 1, 4, OUM C.29538). These specimens are mostly hidden within 'cocoons' and more detailed identification is not possible.

Inanihella sagena sp. nov.
(Pl. 1, figs 1–7)

2002 unnamed spumellarian specimens (OUM C.29502, C.29534, C.29535, C.29536) Orr *et al.*: pl. 1, figs 1–8.

Derivation of name. Latin, *sagena*, a fish-net; alluding to the porous shells.

Diagnosis. Large *Inanihella* species, >200µm diameter, with two cortical shells, secondary spines and relatively few main spines.

Holotype. University Museum of Natural History, Oxford, OUM C.29594; Plate 1, figs 1–4. Late Sheinwoodian to early Homerian, Wenlock Series, Herefordshire.

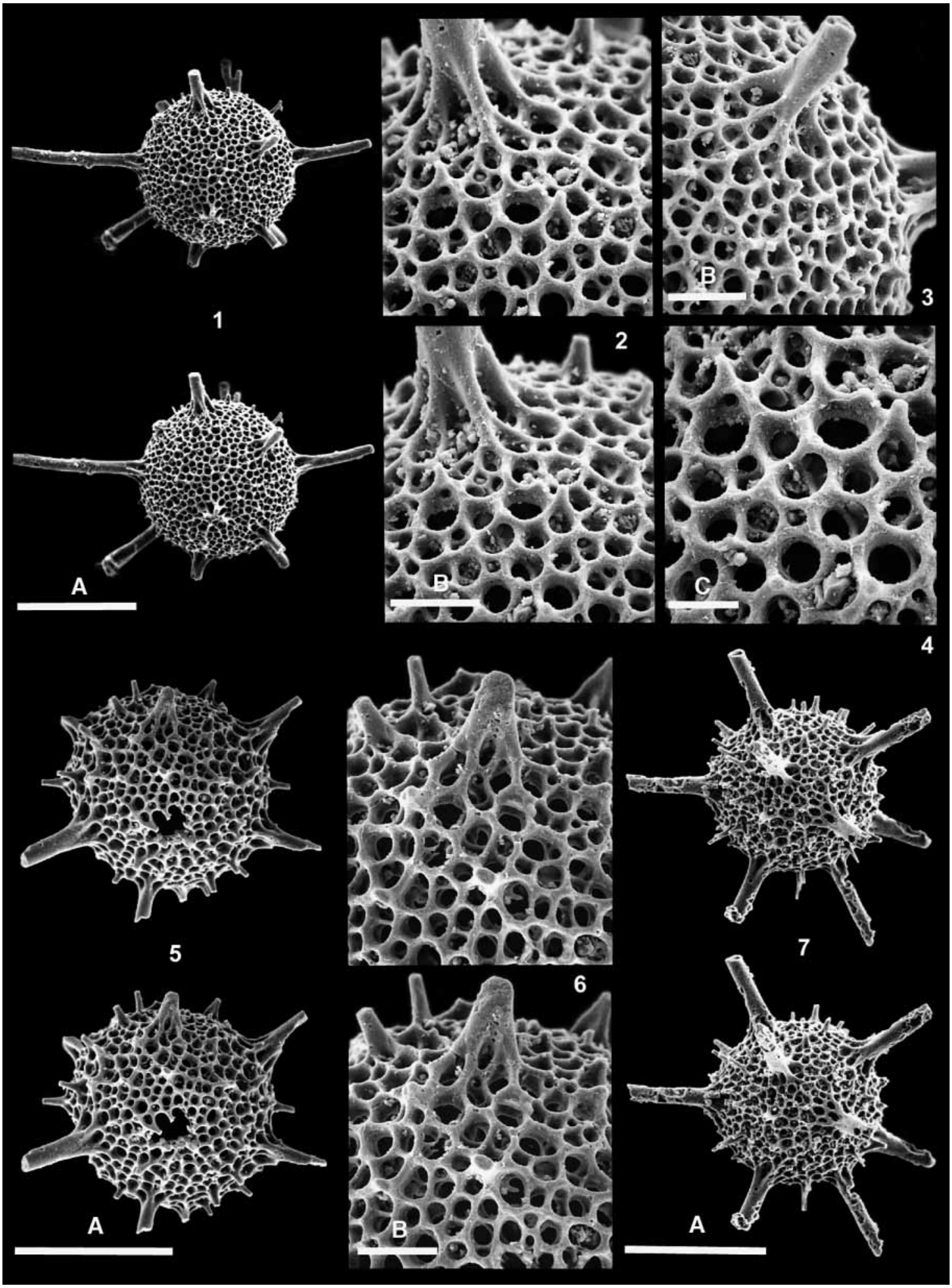
Material. At least ten specimens.

Description. The two cortical shells are concentric, irregularly porous and close together (see Pl. 1, fig. 6 where a finer inner cortical shell can be seen <50 µm below the pores of the outer cortical shell on specimen OUM C. 29595). They are interconnected by numerous small rods that do not extend beyond the shells. Numerous (6–20) long, rod-like cylindrical, non-tapering main spines are connected with solid rays of the internal framework to the inner cortical shell. They are buttressed at the outer-most cortical shell and their diameter is considerably less towards the medullary shell. Numerous secondary spines emanate from nodes between pores on the outer-most cortical shell.

Distribution. Known only from the type locality.

Remarks. *I. sagena* is similar to several inanihellids described from the upper part of the Sakmarskaya Suite (Wenlock?–Ludlow) of northwestern Mugodzhar, southern Urals, Kazakhstan (Nazarov, 1988; described in English in Nazarov & Ormiston, 1993) in having two irregularly porous cortical shells. However, *I. sagena* differs in having considerably fewer main spines than *Inanihella permeata* Nazarov & Ormiston, 1993, *I. leniuncula* Nazarov & Ormiston, 1993 and *I. macrocantha* (Rüst, 1892) of Nazarov (1988) and it also has secondary spines.

Nazarov (1988) regarded some of his material as conspecific with *Acanthosphaera macrocantha* Rüst, 1892 from France. However, the French taxon has well-developed pores and appears to have a single cortical shell, whereas the material from Kazakhstan is irregularly porous and has a double cortical shell. The entire assemblage described from supposedly Silurian rocks of Cabrière in France exhibits greater similarity to Lower Carboniferous rather than Silurian forms, and it seems likely that the material that Nazarov (1988) assigned to *I. macrocantha* is a different species. Indeed, Noble (1994) reassigned this taxon to *Oriundogutta* Nazarov, 1988.



Explanation of Plate 1.

All of the specimens (University Museum of Natural History, Oxford) are from the Wenlock Series, Silurian, Herefordshire, England. Figs 1, 2, 5–7 are stereo-pairs. **figs 1–7.** *Inanihella sagena* sp. nov.: **1–4,** holotype, OUM C.29594 – **1,** complete specimen, × 75, **2–4,** details of lattice and spines, × 300, × 280, × 510; **5–6,** OUM C. 29595 – **5,** complete specimen, × 100, **6,** details of lattice and spines, × 250; **7,** OUM C.29536, complete specimen, × 90. Scales: A, 250 μm; B, 50 μm; C, 25 μm.

Inanihella sp.
(Pl. 2, figs 1–5)

2002 unnamed spumellarian specimens (OUM C.29540, OUM C.29541, OUM C.29542) Orr *et al*.: pl. 2, figs 5–8.

Material. About ten specimens

Description. Large, robust, porous inner cortical shell, >250 µm diameter, separated from an additional gossamer outer cortical shell by approximately 50 µm. The outer cortical shell is extremely fragile and may be openly latticed. The shells are concentric and are interconnected by numerous small rods that do not extend beyond the shells. About six long, rod-like cylindrical, non-tapering main spines are buttressed onto the innermost cortical shell. The outer cortical shell lies beyond the buttresses. Thin solid rays emanating from the main spines continue inside the internal framework.

Distribution. Known only from the Herefordshire Konservat-Lagerstätte.

Remarks. Description of this form is limited by the fragmentary preservation of the specimens. Vestiges of several extremely fragile gossamer outer cortical shells, in addition to those noted in the description, are observable in several specimens within surrounding spherical 'cocoons' (Pl. 2, figs 2, 3, 5), but it has proved impossible to isolate such tests intact. Full details of the original structure remain unknown.

Order **Entactinaria**, Kozur & Mostler, 1982
Family **Haplentactiniidae** Nazarov *in* Nazarov & Popov, 1980
Subfamily **Haplentactiniinae** Nazarov *in* Nazarov & Popov, 1980
Genus *Haplentactinia* Foreman, 1963

Type species. *Haplentactinia rhinophyusa* Foreman, 1963, Upper Devonian Huron Shale, Ohio.

Haplentactinia armista sp. nov.
(Pl. 2, fig. 7)

Derivation of name. Latin *arma*, weapons, and suffix *ista*, signifying an agent; alluding to the appearance of the spines.

Diagnosis. *Haplentactinia* with small, spherical, pseudo-spongy cortical shell. Six massive, rod-like cylindrical and gradually tapering main spines that meet at a point-centred spicule; no secondary spines. No medullary shell visible.

Holotype. University Museum of Natural History, Oxford, OUM C.29598; Plate 2, fig. 7. Late Sheinwoodian to early Homerian, Wenlock Series, Herefordshire.

Material. About ten specimens.

Description. Specimens have a well-developed spherical pseudo-spongy cortical shell approximately 90 µm in diameter. Six massive rod-like spines are well developed and taper gently. The maximum length of these spines and the nature of their distal terminations were not observed on specimens, all of which are broken. Main spines meet at a point-centred spicule. No secondary spines were observed on any specimen.

Distribution. Known only from the type locality.

Remarks. *H. armista* differs from *H. silurica* Nazarov & Ormiston, 1993 from the Lower Silurian Sakmarskaya Suite of the southern Urals in that the apophyses that join to form the cortical shell are notably less coarse (thinner).

Order **Archaeospicularia** Dumitrica, Caridroit & DeWever, 2000
Superfamily **Secuicollactacea** Nazarov & Ormiston, 1984
(synonym: **Rotasphaeracea** Noble, 1994)
Family **Secuicollactidae** Nazarov & Ormiston, 1984
(synonym: Family **Rotasphaeridae** Noble, 1994;
emend Noble & Maletz, 2000; Won *et al*., 2002)

Discussion. See Dumitrica *et al*. (2000), Noble & Maletz (2000) and Won *et al*. (2002) for discussion of higher-level taxonomic assignments within the Order Archaeospicularia.

Genus *Secuicollacta* Nazarov & Ormiston, 1984
(emend MacDonald, 1998)
(synonym: Genus *Parasecuicollacta* Won, Blodgett & Nestor, 2002 (see Jones & Noble, 2006))

Type species. *Secuicollacta cassa* Nazarov & Ormiston, 1984, Silurian Wenlock–Ludlow series, Tarangul River, northern Mugodzhar, southern Urals, Kazakhstan.

Secuicollacta hexactinia (Won, Blodgett & Nestor, 2002)
(Pl. 2, fig. 6)

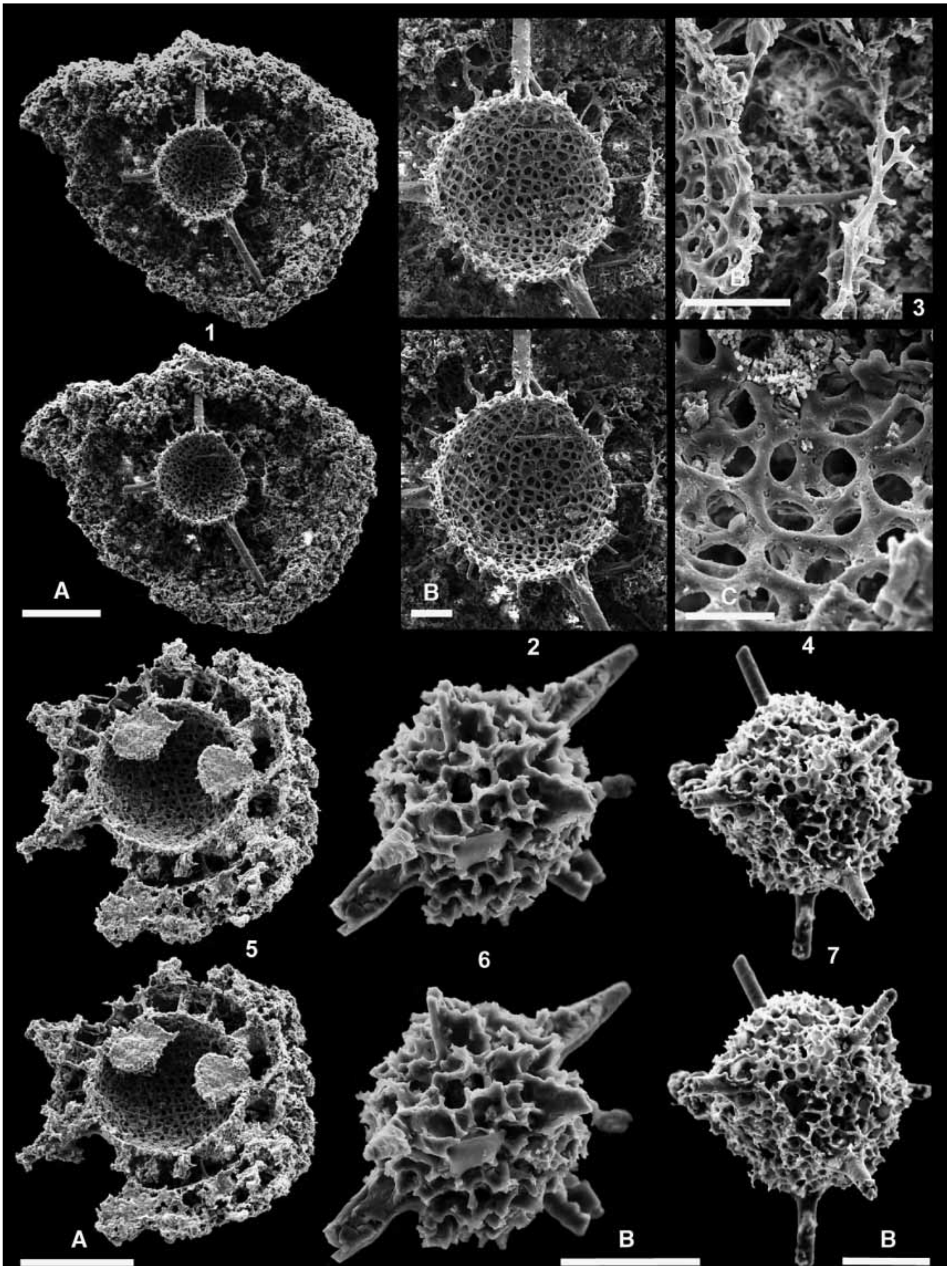
2002 *Parasecuicollacta hexactinia* Won *et al*.: 955, fig. 3: 7–11.

Material. Five specimens.

Description. Single, very small spherical shell approximately 50–60 µm diameter. Six short main spines approximately half the diameter of the shell and strongly tapering. Two spines are polar and better developed that the others which are arranged equatorially. The shell is irregularly reticulated and ragged.

Distribution. Known from the Road River Formation, late Aeronian to early Telychian, Llandovery Series, Tatonduk River area, east central Alaska, as well as the late Sheinwoodian to early Homerian, Wenlock Series of Herefordshire.

Remarks. The Herefordshire specimens have a dense ragged lattice and are closely similar to *S. hexactinia* (Won *et al*., 2002). Although the two largest spines are polar and similar to those observed in *S. bipola* (Won *et al*., 2002), the presence of four additional spines suggests assignment to *S. hexactinia*. The presence of an ectopically placed spicule and primary units is



Explanation of Plate 2.

All of the specimens (University Museum of Natural History, Oxford) are from the Wenlock Series, Silurian, Herefordshire, England. Figs 1, 2, 5–7 are stereo-pairs. **figs 1–5.** *Inanihella* sp.: **1–4,** OUM C. 29596 – **1,** broken specimen in a 'cocoon', × 50; **2–4,** details of lattice and spines, × 100, × 300, × 550; **5,** OUM C.29542, broken specimen in a 'cocoon', × 75. **fig 6.** *Secuicollacta hexactinia*. Complete specimen, OUM C. 29597, × 450. **fig 7.** *Haplentactinia armista* sp. nov. Holotype, complete specimen, OUM C. 29598, × 275. Scales: A, 250 μm; B, 50 μm; C, 25 μm.

consistent with the diagnosis of *Secuicollacta*. Although outwardly similar, *Parvalanapila fleischerorum* MacDonald, 1998 has a denser labyrinthine wall structure. The presence of equatorially arranged spines distinguishes the external morphology from that of *Secuicollacta glaebosa* MacDonald, 1998.

CONCLUSIONS

The Wenlock Series Herefordshire Konservat-Lagerstätte has yielded the only radiolarian fauna known from the Silurian of Britain and one of the few Wenlock radiolarian faunas known world-wide. As with most other documented Silurian radiolarian material the Herefordshire fauna is from near-shelf/shelf sediments. The low diversity fauna consists of Inaniguttidae (one new and one congeneric species), Haplentactiniidae (one new species) and Secuicollactidae (one species). It has limited affinities with Silurian radiolarian assemblages of the southern Urals, Canadian Arctic and Alaska. Stratigraphically, the Herefordshire fauna appears transitional between established Silurian radiolarian Long-spined inaniguttid biozones 2 and 3.

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