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., 2006) and a few ostracod valves (Sutton et al., 2000a; Sutton 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 o-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 (CHBr₃) and then sieving with the 63 µm fraction collected and dry picked. The o-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 more 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 Shinwoodian 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 *Vishyella* brachiopod community (Hurst et al., 1978), which is characteristic of sites near the outer limit of the shelly benthos during the Wenlok 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 Pridoli 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), 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 secucolactids 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 Haploactiniinae such as *Haplotactiniatum* 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 *Haplotactiniatum*). 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 Shinwoodian/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 inanihilid 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 Shinwoodian 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 Mugodzhair 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 PALAEOONTOLOGY**

Class *Actinopoda* Calkins, 1909

Subclass *Radiolaria* Müller, 1858

Order *Polyceystida*, Ehrenberg, 1838

Suborder *Spumellaria*ina Ehrenberg, 1875

Family *Inanihelliidae* Nazarov & Ormiston, 1984

(emend Noble, 1994)

Genus *Inanihella* Nazarov & Ormiston, 1984

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

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


**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 Sakmarshay 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.
Silurian Radiolaria of England

_Inanihella sp._

(Pl. 2, figs 1–5)


**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 Silurian Konservat-Lagerstätte, 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 Sakmarkskaya Suite of the southern Urals in that the apophyses that join to form the cortical shell are notably less coarse (thinner).

Order _Archaeospicularia_ Dumitrice, Caridroit & DeWever, 2000
Superfamily _Secuicollactacea_ Nazarov & Ormiston, 1984
(synonym: _Rotasphaeracea_ Noble, 1994)
Family _Secuicollactidae_ Nazarov & Ormiston, 1984


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, *Parvalanapilia fleischerorum* MacDonald, 1998 has a denser labyrinthe 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), *Haplenactinidae* (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.

**ACKNOWLEDGEMENTS**

This research was funded by the Leverhulme Trust (F/08581/E), the Natural Environment Research Council (GR3/12053) and English Nature. The authors thank Derek Briggs (Yale University) and Eugene MacDonald (St Francis Xavier University) and Paula Noble (University of Nevada) for comments on the manuscript; A. Swift, R. Branson and W. Thornton (University of Leicester) and S. Ziabrev (formerly of The University of Hong Kong) for technical help; T. Hall, J. Sinclair and R. Fenn for general assistance; and the University of Leicester (David J. S.; study leave).

**REFERENCES**


Manuscript received 13 August 2005

Manuscript accepted 21 January 2007
Silurian Radiolaria of England
