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Early Silurian (Llandoverian) radiolarians from the Ise area of the Hida "Gaien" Belt, central Japan

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Abstract. A moderately well-preserved Llandoverian (early Early Silurian) radiolarian fauna has been discovered from the Ise area of the Hida "Gaien" Belt, in Izumi Village, Fukui Prefecture, central Japan. This is the oldest known radiolarian fauna in Japan, and was recovered from calcareous nodules in the siliceous shale portion of a sedimentary sequence consisting of siliceous shale, alternating tuffaceous sandstone and shale, and tuffaceous sandstone. The fauna contains *Haplotaeniatum tegimentum, Syntagentactinia afflicta, S. excelsa, Oriundogutta* sp., *Inanihella* sp., *Auliela* sp., *Palaeoephippium*? sp., and *Orbiculopylorum* sp. This fauna is characterized by an abundance of species in the genera *Haplotaeniatum, Syntagentactinia* and *Oriundogutta*, and is comparable with the early to middle Llandoverian *Haplotaeniatum tegimentum* Assemblage and its equivalents in the southern Urals, Germany, and Nevada. Seventeen species of radiolarians belonging to 12 genera were systematically investigated.

Key words: Hida "Gaien" Belt, Ise area, Llandoverian, Radiolaria, Silurian

Introduction

An understanding of the biostratigraphy and taxonomy of Silurian and Devonian radiolarians has progressed remarkably in the past decade (e.g., Nazarov and Ormiston, 1993; Noble and Aitchison, 1995). Numerous late Early Silurian to Middle Devonian radiolarian studies have been published for Japan (e.g., Wakamatsu *et al.*, 1990; Furutani, 1990; Aitchison *et al.*, 1996; Umeda, 1998), Australia (e.g., Stratford and Aitchison, 1997; Aitchison *et al.*, 1999), the United States (Noble, 1994), the southern Urals (Amon *et al.*, 1995), westernmost China (Li, 1994), and Germany (Kiessling and Tragelehn, 1994). Based on these radiolarian biostratigraphic studies, we can estimate the age of radiolarian-bearing rocks of this interval.

Ordovician to early Early Silurian radiolarian biostratigraphy has been outlined by Nazarov and Popov (1980), Nazarov (1988), and Nazarov and Ormiston (1993). In addition to these studies, conducted in Kazakhstan and the southern Urals by Nazarov and his collaborators, a large number of Ordovician radiolarians have been reported from Spitsbergen (Fortey and Holdsworth, 1971), Newfoundland (Bergström, 1979; Renz, 1990a), the United States (Dunham and Murphy, 1976; Renz, 1990a, b; Kozur *et al.*, 1996), Australia (Webby and Blom, 1986; Goto *et al.*, 1992; Umeda *et al.*, 1992; Iwata *et al.*, 1995), Estonia (Nazarov and Nylvak, 1983), the Baltic region (erratic boulders) (Eisenack, 1971; Górka, 1994), China (Wang, 1993; Li, 1995), and Scotland (Aitchison,1998; Danelian and Clarkson, 1998). In contrast, besides Nazarov's works (Nazarov, 1998; Nazarov and Ormiston, 1993), only a few papers describing early Early Silurian (Llandoverian) radiolarians were published before the mid-1990s (Rüst, 1892; Stürmer, 1951, 1952, 1966; Goodbody, 1986). More recently, Llandoverian faunas have been described from the Cherry Spring Chert in Nevada (Noble *et al.*, 1997; Noble *et al.*, 1998), Dalarna, Sweden (Maletz and Reich, 1997), Cornwallis Island, Arctic Canada (MacDonald, 1998), and Germany (Noble *et al.*, 1998). These studies demonstrate that Llandoverian radiolarians have a high biostratigraphic potential. Early Silurian radiolarians, however, are still insufficiently known. Additional collecting is needed to establish a biostratigraphy and provide information on the faunal composition for this time period.

We are now studying the lithostratigraphy and radiolarian biostratigraphy of the Hida "Gaien" (=marginal) Belt in order to understand its tectonic and paleobiogeographic history (Kurihara and Sashida, 1998). We fortuitously discovered Llandoverian radiolarians in calcareous nodules from the siliceous shale part of the clastic and volcaniclastic sequence exposed in the Ise area of the westernmost part of the Hida "Gaien" Belt, in Izumi Village, Ohno County, Fukui Prefecture. This early Early Silurian radiolarian fauna is the oldest one known in Japan. In this paper, we discuss the age assignment of the radiolarian fauna and systematically describe 17 species which belong to 12 genera including

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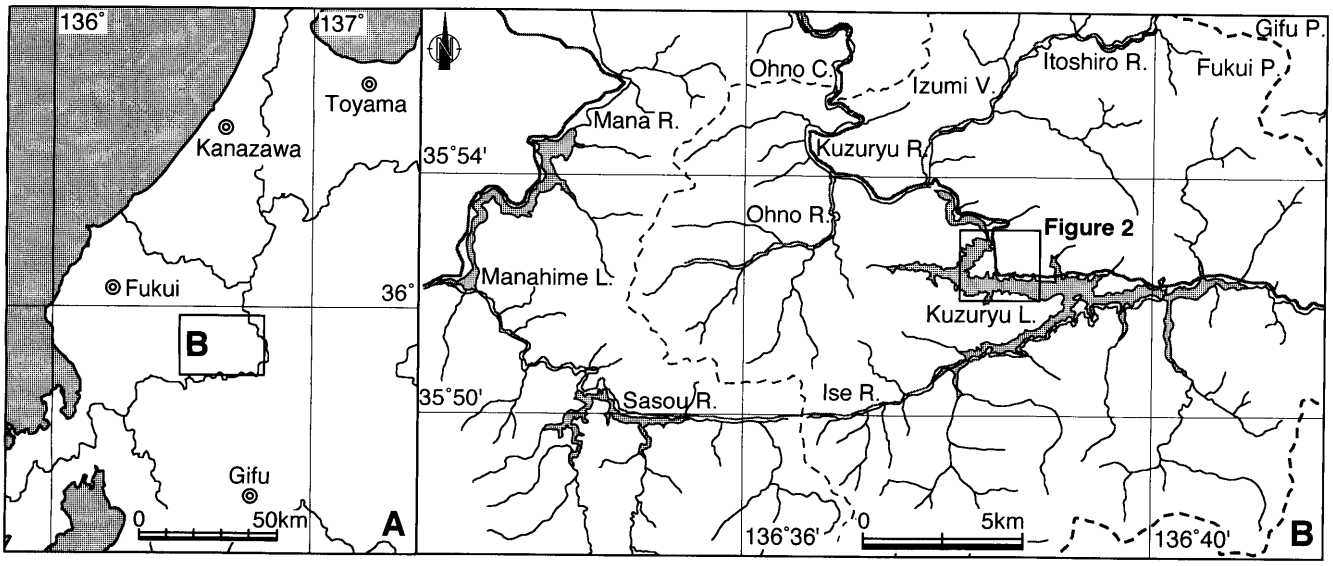


Figure 1. Index map showing the study area.

four undetermined genera.

Geologic setting

The Hida "Gaien" Belt, one of the most structurally complex areas in the Japanese geologic framework, occurs in a narrow area between the Hida and Mino Terranes. This belt is composed of weakly metamorphosed or unmetamorphosed Paleozoic and Mesozoic strata, including Ordovician to Devonian sediments, crystalline schists, and basic to ultrabasic rocks. Outcrops of these rocks can be found in the Omi-Renge, Fukuji, Moribu (Arakigawa), Naradani and Ise areas (e.g., Komatsu, 1990; Igo, 1990). The latter four of these five areas are covered by Middle Paleozoic strata and have been investigated by many workers (e.g., Tazawa *et al.*, 1997). Recent micropaleontological investigations of Ordovician strata show them to be fairly widely distributed in the Hitoegane district of the Fukuji area (Tsukada and Koike, 1996; Tsukada, 1997).

The Ise area, which extends from Izumi Village to Ohno City, Fukui Prefecture, is situated in the westernmost part of the Hida "Gaien" Belt. Its constituent rocks are exposed around Kuzuryu Lake and in the upper reaches of the Ise River to the Sasou-Mana River (Figure 1). The geology of this area has been studied by Kawai (1956), Kawai *et al.* (1957), Yamada (1967), and the Metal Agency of Japan (1980). Miyakawa and Yamada (1988) summarized the stratigraphy of the sedimentary rocks cropping out around Kuzuryu Lake, based on the studies of Yamada (1967) and Ohno *et al.* (1977). They subdivided these rocks into the following eight lithostratigraphic units, in ascending order: an unnamed Silurian unit, the Lower to Middle Devonian Kamianama Group, Middle Carboniferous Nagano Formation, Lower Permian Oboradani Formation, Middle Permian Nojiri Group and Magatoji Formation, post-Permian? Ohtani and Motodo Formations, and the Ashidani Group of unknown age. Among these lithostratigraphic units, the Nojiri Group, which is subdivided into the Oguradani Formation and overlying Konogidani Formation, crops out widely around Kuzuryu Lake. The other units, especially the Silurian and Devonian strata, complexly occur in narrow zones on the north side of Kuzuryu Lake and along the upper reaches of the Ise River.

Strata in this area contain rich Carboniferous and Permian fossils, including fusulinacians and corals in the Oboradani and Ohtani Formations, and brachiopods in the Oguradani Formation (e.g., Niko and Watanabe, 1987; Niko *et al.*, 1997; Tazawa and Matsumoto, 1998). The Devonian limestone of the Kamianama Group yields various kind of fossils (e.g., Hamada, 1959; Okazaki *et al.*, 1974; Kamiya and Niko, 1997) but no detailed paleontological study of them has been published. Recently, micropaleontological investigation by the present authors revealed the occurrence of Late Silurian to Middle Devonian radiolarians in the Kamianama Group (Kurihara and Sashida, 1998).

Lithology of the radiolarian-bearing rocks

The Early Silurian radiolarian-bearing calcareous nodules were collected from the siliceous shale portion of a sequence that consists of thin alternations of tuffaceous sandstone and shale, tuffaceous sandstone, and siliceous shale. The sequence crops out along a stream near the Kagero Tunnel, west of Nojiri, Izumi Village (Figure 2). Similar rocks are exposed in a roadcut east of the Anama Temple. These strata were previously assigned to the Konogidani Schalstein Formation (Ozaki *et al.*, 1954), the Tomedoro Schalstein "Member" [=Formation] (Kawai, 1956; Kawai *et al.*, 1957; Metal Agency of Japan, 1980), and the Permian Konogidani Formation (Yamada, 1967; Miyakawa and Yamada, 1988). Revision of the litho- and biostratigraphy in this area is needed (Kurihara, 1999).

In this stratigraphic section, the beds generally strike N25° to 35°W and dip 70° to 80°S (and sometimes almost verti-

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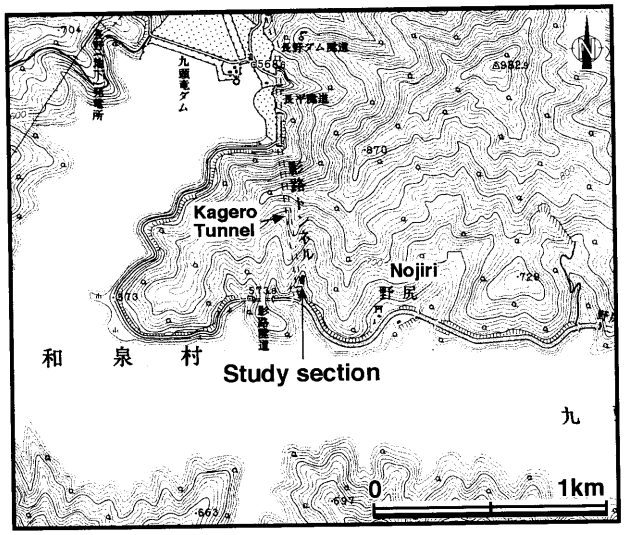


Figure 2. Locality map showing the location of the study section. Base map is after 1:25,000-scale topographic map of Japan, Quadrangle "Echizen-Asahi", Geographical Survey Institute of Japan.

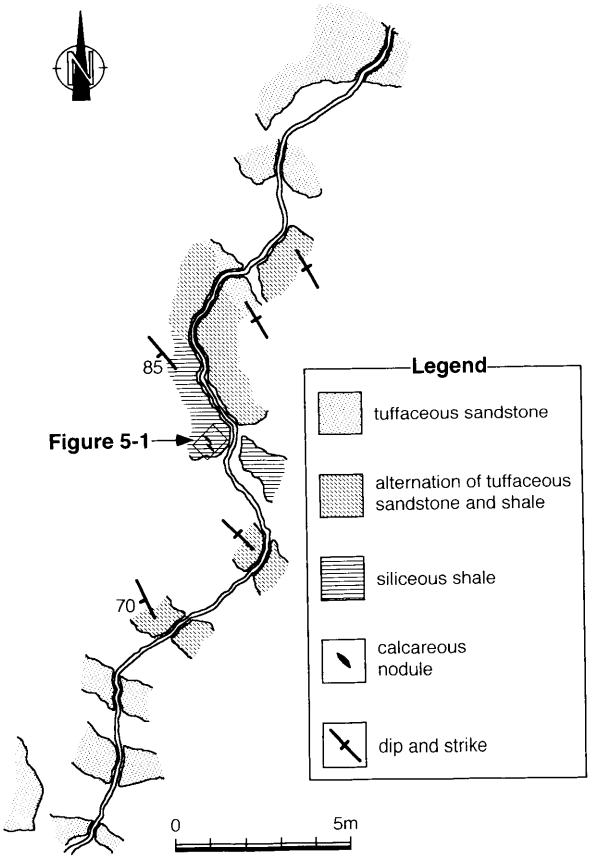


Figure 3. Route map along the study section.

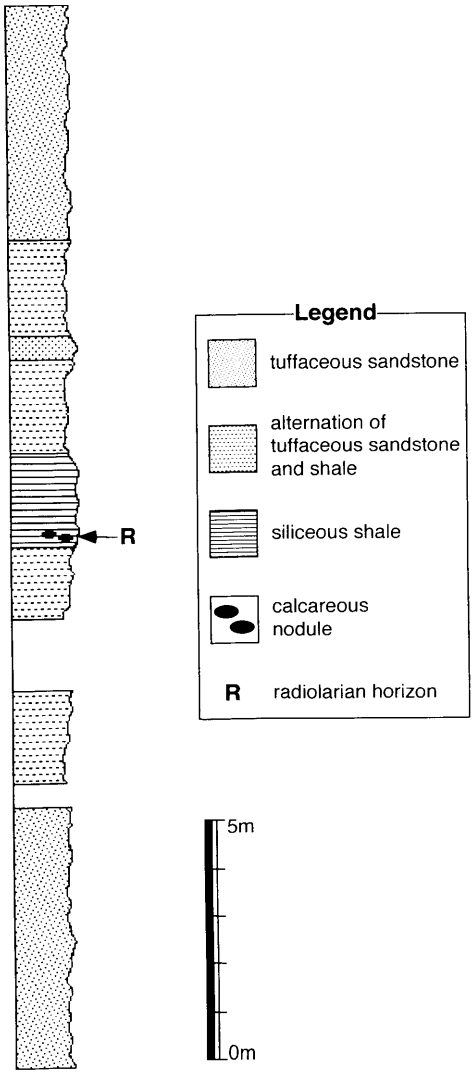


Figure 4. Column along the study section.

cally) (Figure 3). Although the stratigraphically highest structures were inaccessible in this section, we tentatively regard these rocks as a north-upward sequence, because sedimentary structures such as graded beddings indicating a north-upward orientation are observable at an outcrop east of the Anama Temple. The rock sequence of this section is as follows, in ascending order: tuffaceous sandstone (about 5.5 m); alternating tuffaceous sandstone and shale (about 4.5 m); siliceous shale (2 m); alternating tuffaceous sandstone and shale (4.5 m); and tuffaceous sandstone (5 m) (Figure 4). The tuffaceous sandstone is medium- to coarse-grained, massive and dark green to dark gray in color. The alternating tuffaceous sandstone and shale is thinly bedded and dark gray, gray, dark green, and black in color. Microscopic observation reveals that the sandstone layers are composed mainly of angular quartz fragments with a small amount of plagioclase and opaque minerals. The shale layers are partly similar to chert and contain very fine quartz grains in a muddy matrix with frequent thin lamina-

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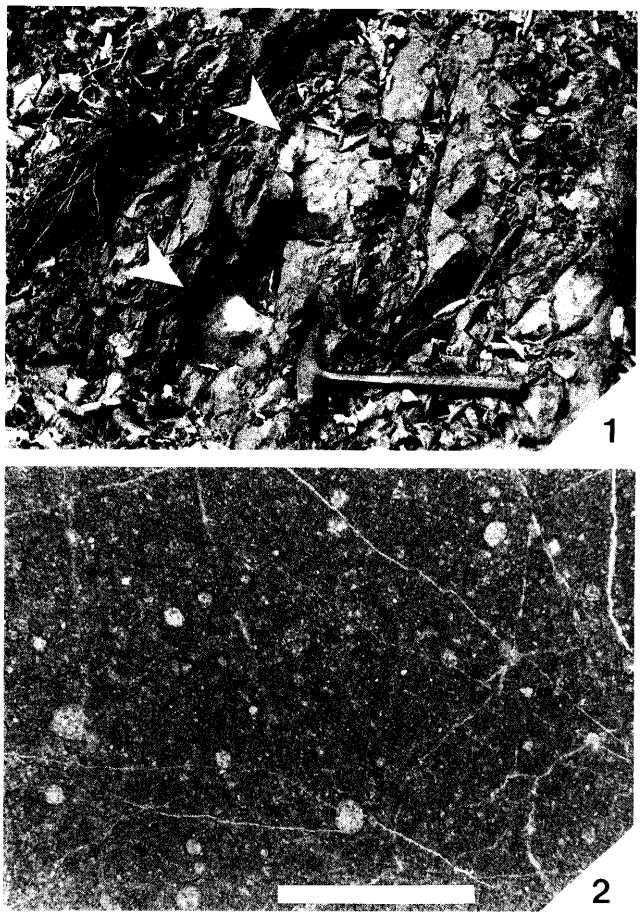


Figure 5. **1.** Photograph showing the occurrence of radiolarian-bearing calcareous nodules (white arrows) in the study section (see Figure 3 for locality). **2.** Photomicrograph of radiolarian-bearing calcareous nodule. Scale bar=1 mm.

tions of coarse quartz grains. The siliceous shale is dark gray and pale green in color and the thickness of each bed is 2 to 5 cm. In this exposure, the shale contains two calcareous nodules which are lenticular in shape and measure 15 cm and 6 cm in the major and minor axes, respectively (Figure 5.1). These nodules are hard, compact, dark gray in color and contain many radiolarian spheres. Radiolarian skeletons are scattered in a calcareous and muddy matrix, most are altered to calcite, and only their outlines formed of fine-grained quartz are preserved (Figure 5.2).

Method of extracting radiolarians

We collected calcareous nodules, siliceous shale, and the shaly part of the alternating tuffaceous sandstone and shale for radiolarian analysis. In order to extract radiolarians from the calcareous nodules, we soaked crushed rocks, each several centimeters in diameter, in a dilute acetic acid solution (5%) for 10 to 12 hours. For the siliceous rock samples, crushed rocks were soaked in a dilute hydrofluoric acid (HF) solution (5 to 10%) for about 24 hours. The samples were washed and sieved through 270# nylon mesh. Radiolarians picked from the dried residues were coated with gold in a vacuum evaporator and observed with a scanning electron microscope. Other specimens were sealed on a slide glass and observed with a transmitted light microscope.

Table 1. List of Llandoverian radiolarians from the calcareous nodule.

HAPLENTACTINIIDAE
Haplotaeniatum tegimentum Nazarov & Ormiston
Haplotaeniatum sp. A
Syntagentactinia afflicta Nazarov & Ormiston
Syntagentactinia excelsa Nazarov & Ormiston
Syntagentactinia ? sp.
INANIGUTTIDAE
Oriundogutta sp.
Oriundogutta ? sp.
Inanihella sp.
Inanihella ? sp.
Inaniguttidae gen. et sp. indet. sp. A
ANAKRUSIDAE
Auliela sp.
PALAEOSCENIDIIDAE
Palaeoephippium ? sp.
SPONGURIDAE
Sponguridae gen. et sp. indet. sp. A
PYLENTONEMIDAE
Cessipylorum ? sp.
INCERTAE SEDIS
Orbiculopylorum sp.
Spumellaria gen. et sp. indet. sp. A
Spumellaria gen. et sp. indet. sp. B
Spumellaria gen. et sp. indet.

Radiolarian fauna and age

Radiolarians were recovered only from the calcareous nodules, and were absent in the siliceous shale and the shaly part of the alternating tuffaceous sandstone and shale. The identified radiolarians consist of 18 species belonging to 13 genera (Table 1). Radiolarians extracted from the calcareous nodules are generally poorly preserved, and unidentified spumellarian fragments are also numerous. This fauna is characterized by abundant species of the families Haplentactiniidae and Inaniguttidae, in association with Anakrusidae, Palaeoscenidiidae, Sponguridae, and Pylentonemidae. *Haplotaeniatum* and *Syntagentactinia*, in the family Haplentactiniidae, are common and are characterized by large, spherical, spongy, or concentric-layered shells. The following Haplentactiniidae species are present:

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Haplotaeniatum tegimentum Nazarov and Ormiston, *Haplotaeniatum* sp. A, *Syntagentactinia afflicta* Nazarov and Ormiston, *Syntagentactinia excelsa* Nazarov and Ormiston, and *Syntagentactinia*? sp. Radiolarians of the family Inaniguttidae comprise the next most-dominant faunal component, including the following species: *Oriundogutta* sp., *Inanihella* sp., *Inanihella*? sp., and Inaniguttidae gen. et sp. indet. sp. A. Species in the families Palaeoscenidiidae and Sponguridae are less common, although *Palaeoephippium*? sp. and Sponguridae gen. et sp. indet. sp. A are present. The following species were allocated to the families Anakrusidae, Pylentonemidae, and to incertae sedis; *Auliela* sp., *Cessipylorum*? sp., and *Orbiculopylorum* sp.

Silurian radiolarian biostratigraphy was first rationalized by Nazarov (1988) and Nazarov and Ormiston (1993), who proposed two radiolarian assemblages: the Early Silurian *Haplotaeniatum tegimentum* Assemblage and the Late Silurian *Inanihella tarangulica-Secuicollacta cassa* Assemblage. The *H. tegimentum* Assemblage, described from a middle Llandoverian to Wenlockian siliceous rock sequence in the Sakmarsky Suite of the southern Urals, is characterized by *Haplotaeniatum labyrintheum* Nazarov and Ormiston, *H. cathenatum* Nazarov and Ormiston, *H. tegimentum* Nazarov and Ormiston, *Haplentactinia silurica* Nazarov and Ormiston, *Syntagentactinia excelsa* Nazarov and Ormiston, and *S. afflicta* Nazarov and Ormiston. As noted above, the present radiolarian fauna is characterized by species of *Haplotaeniatum* and *Syntagentactinia*, and therefore is referable to the *H. tegimentum* Assemblage of Nazarov (1988) and Nazarov and Ormiston (1993).

Noble *et al.* (1997) made a preliminary study of an early Llandoverian radiolarian fauna in the Cherry Spring Chert of Nevada. They extracted from sulfide nodules a well-preserved radiolarian fauna consisting of abundant, large pylomate sphaerellarians identified as *Cessipylorum* (?) sp. A and *Cessipylorum* (?) sp. B, some rotasphaerids such as *Rotasphaera* sp. and *Secuicollacta* spp., and *Oriundogutta* sp. In addition, Noble *et al.* (1998) noted that the Nevada fauna described by Noble *et al.* (1997) contains abundant species of *Haplotaeniatum*. From the Frankenwald and Thuringia, Germany, Noble *et al.* (1998) also reported *Secuicollacta* spp. from black, organic-rich chert, the age of which is constrained by co-occurring graptolites as early Rhuddanian to early Telychian (early to late Llandoverian). In the Main Valley, Germany, black chert gravel in Pleistocene river deposits contains well-preserved radiolarians, and was probably derived from the Frankenwald (Stürmer, 1951, 1952, 1966). Richter (1951) cited the age of this gravel as middle Rhuddanian to Aeronian (early to middle Llandoverian), and Noble *et al.* (1998) identified the following species in it: *Syntagentactinia*? sp., *Orbiculopylorum adobensis* Noble, Braun and McClellan, *Orbiculopylorum* sp., and *Haplotaeniatum* sp.

Noble *et al.* (1997) pointed out the following characters of the Nevada fauna: (1) the species belonging to the family Inaniguttidae of the Wenlockian to Ludlowian, which have long and robust spines, are different from inaniguttids of the Nevada fauna. (2) Wenlockian to Ludlowian rotasphaerids commonly have six rods per spine unit and highly diversified spines such as grooved or bladed ones. In contrast, rotasphaerid species in the Nevada fauna have five rods per spine unit and rod-shaped spines. (3) The Nevada fauna does not contain species in the families Palaeoscenidiidae and Ceratoikiscidae, which are notable taxa in Wenlockian faunas (Goodbody, 1986; Renz, 1988). Rotasphaerids have never been found in the present fauna, although their absence may be due in part to preservational bias, as these taxa are small and delicate. The morphological characters of the inaniguttids and the absence of ceratoikiscids are consistent with the work of Noble *et al.* (1997). The Nevada fauna also contains species of *Syntagentactinia* and *Haplotaeniatum*. In addition, large spherical radiolarians with the concentric and loosely spongy layers of the German fauna (Stürmer, 1951, 1952, 1966; Noble *et al.*, 1998) are very similar to the species of *Syntagentactinia* and *Haplotaeniatum* in the present fauna. Although *Orbiculopylorum* is rare, the present fauna is similar in its taxonomic composition to those in Nevada and Germany.

Nazarov and Ormiston (1993) inferred the age of the *H. tegimentum* Assemblage to be middle Llandoverian to Wenlockian by showing that this assemblage occurs in a siliceous shale sequence that contains *Monograptus triangulatus* to *M. testis* zone graptolites. Noble *et al.* (1998) noted that the age of the *H. tegimentum* Assemblage is Rhuddanian (early Llandoverian) to early Homerian (late Wenlockian) and that the lower range of this assemblage is consistent with the age of the Nevada and German faunas. However, they questioned the upper range of this assemblage, because the early to middle Llandoverian radiolarian fauna is markedly different from the late Llandoverian fauna. The late Llandoverian faunas reported by Maletz and Reich (1997) and MacDonald (1998) lack large spongy spumellarians such as *Haplotaeniatum* and are characterized by the abundance of various taxa of rotasphaerids and entactiniids. According to Noble *et al.* (1998), the fauna from the middle Telychian (upper Llandoverian) of Dalarna, Sweden contains *Haplotaeniatum* species but otherwise differs from the Nevada fauna in faunal composition. Therefore, as pointed out by Noble *et al.* (1998), the upper range of the *H. tegimentum* Assemblage does not extend above the Telychian, and possibly not above the Rhuddanian to Aeronian (early to middle Llandoverian).

We cannot determine the precise age of the present fauna, but we assign it to the early to middle Llandoverian, based on its similarity to the *H. tegimentum* Assemblage and to the Nevada and German faunas, as mentioned above.

Systematic paleontology

All specimens described in this paper are deposited in the Institute of Geoscience, University of Tsukuba (IGUT).

Order Polycystina Ehrenberg, 1838, emend. Riedel, 1967b
Suborder Spumellaria Ehrenberg, 1875
Family Haplentactiniidae Nazarov in Nazarov and Popov, 1980
Subfamily Haplentactiniinae Nazarov in Nazarov and Popov, 1980
Genus ***Haplotaeniatum*** Nazarov and Ormiston, 1993

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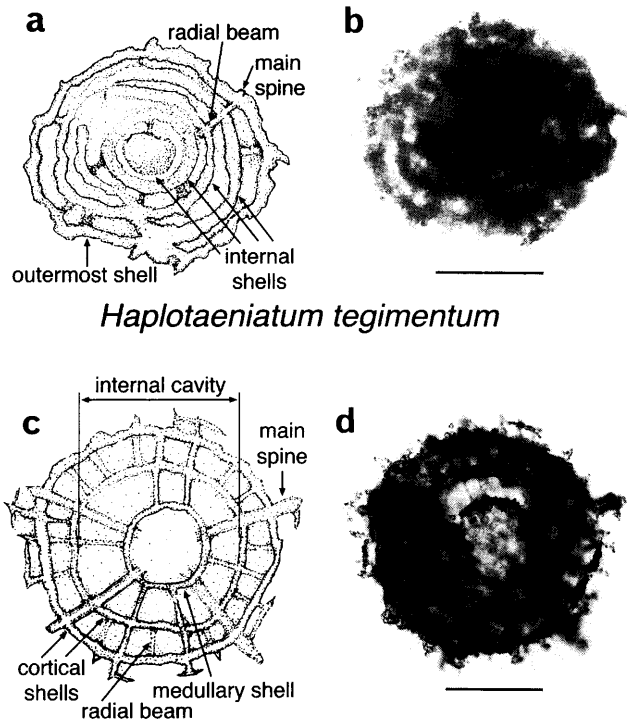


Figure 6. Schematic diagrams of skeletal structures and light transmission microphotographs of *Haplotaeniatum tegimentum* Nazarov and Ormiston (**a, b**) and *Syntagentactinia excelsa* Nazarov and Ormiston (**c, d**). Scale bars=100 μm.

Type species.—*Haplotaeniatum labyrintheum* Nazarov and Ormiston, 1993.

Remarks.— Nazarov and Ormiston (1993) stated that the internal shells of this genus are interpreted as having formed by apophyses developed on the main spines. They also illustrated the schematic internal structure of this genus (Nazarov and Ormiston, 1993, text-figure 8b) and emphasized an important role of the main spines on skeletal structure as the characteristic of the family Haplentactiniidae. However, no specimen has the entactiniid-like internal structure formed by the main spines and extremely eccentrically positioned innermost shell among the photos presented by Nazarov and Ormiston (1993, pl. 3, figs. 9–16). Therefore, the generic diagnosis concerning the main spine by Nazarov and Ormiston (1993) is unconvincing, and the suprageneric classification of the genus *Haplotaeniatum* is problematic. We are not able to make an emendation for this genus owing to our poorly preserved material. However, the generic diagnosis and suprageneric classification of this genus will need to be revised on the basis of well-preserved material. In this paper, we follow the diagnosis presented by Nazarov and Ormiston (1993).

Haplotaeniatum tegimentum Nazarov and Ormiston, 1993

Figure 7.1–7.13

Haplotaeniatum tegimentum Nazarov, 1988, p. 188, pl. 11, fig. 7 (nomen nudum); Nazarov and Ormiston, 1993, p.42, pl.3, figs. 14–16.

Description.—The external appearance of the shell is spherical, irregular spherical, or slightly elliptical. The outermost shell has many oval to irregularly rounded pores. In some specimens, a pylome-like oversized pore is present on the outermost shell surface (Figure 7.9–7.13). The inside of the outermost shell has an irregular spongy meshwork. The internal shells are spherical to subspherical, three to four in number, and concentrically arranged (Figure 6a, b). The innermost shell is often eccentrically positioned. Pores of the internal shells are circular to oval and differ in size. A small number of short, conical spines arise from the surface of the outermost shell. Under a transmitted light microscope, a radial beam (probably the main spine) penetrating the concentric internal shells and extending to the outermost shell is present (Figure 6a, b), but its detailed morphology is unclear owing to poor preservation. Short radial beams randomly arise from the outer surface of the internal shell. These beams connect the internal and outermost shells.

Measurements.—Based on 13 specimens, in μm. Diameter of the outermost shell, 230–270, average, 250.

Remarks.—More than twenty specimens of this species were examined. According to the generic diagnosis of Nazarov and Ormiston (1993), this genus is characterized by having several concentric or spiral forms for the internal shells. A distinct spiral form was not observed in the present specimens, because the complex connections of the radial beams prevented us from appraising the inner structure of the shell. As shown in Figure 6a and 6b, several concentric internal shells are present. This species is distinguished from *Haplotaeniatum labyrintheum* Nazarov and Ormiston by having short, conical spines. *Haplotaeniatum cathenatum* Nazarov and Ormiston, which is characterized by having a large pylome, is similar to this species, especially to the above-described pylomate form. However, it is difficult to compare this species with *H. cathenatum*, because only one broken specimen of the latter species was illustrated by Nazarov (1988) and Nazarov and Ormiston (1993). *Haplotaeniatum? aperturatum* Noble, Braun and McClellan differs from the present species by having an irregular, spongy ball-like external shape and lacking a distinct internal shell.

Range and occurrence.—Middle to late Llandoverian, southern Urals, southern Bashkiria and Northwestern Mugodzhar; Silurian, Cabriere, France; Llandoverian, Ise area in the Hida "Gaien" Belt.

Haplotaeniatum sp. A

Figure 7.14–7.16

Description.—The shell is subspherical or slightly elliptical. The outermost shell has more than ten large circular to oval pores per hemisphere. The outermost shell bears no spines, but has small conical protuberances at the junction of intervening bars. The internal shell consisting of a loose lattice is subspherical, with large oval pores on its surface. Radial beams arise from the surface of the internal shell and connect the internal and cortical shells. These beams are

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usually unbranched, but rarely bifurcate.

Measurements.—Based on three specimens, in μm. Diameter of the outermost shell, 230–270, average, 260.

Remarks.—This form is easily distinguished from other species of *Haplotaeniatum* by having large circular to oval pores and the loose lattice to its internal shell. This species is similar to specimens of *Haplotaeniatum primordialis*? (Rüst, 1892) described by Nazarov and Ormiston (1993). According to Nazarov and Ormiston (1993), the latter species is characterized by its smaller dimensions (194 to 208 μm) and a smaller number of internal shells. The present species differs from *H. primordialis*? (Rüst, 1892) by having a large diameter to the outermost shell.

Range and occurrence.—Llandoverian, Ise area in the Hida "Gaien" Belt.

Genus ***Syntagentactinia*** Nazarov in Nazarov and Popov, 1980

Type species.—*Syntagentactinia biocculosa* Nazarov in Nazarov and Popov, 1980.

Syntagentactinia afflicta Nazarov and Ormiston, 1993

Figure 7.17, 7.18

Syntagentactinia afflicta Nazarov, 1988, pl. 11 fig. 6 (nomen nudum); Nazarov and Ormiston, 1993, p. 40, pl. 5, figs. 12, 13; Noble, Braun and McClellan, 1998, p. 723, fig. 5-2.

Description.—The shell of this species is composed of concentric cortical shells and a small medullary shell situated in the internal cavity. The cortical shells are spherical and two or three in number with long, robust, rod-shaped main spines. The main spines are commonly four in number and continuous into the medullary shell. In the interior of the medullary shell, however, the structure and emanation of the main spines are unclear. The diameter of the inner cortical shell is about two-thirds that of the outermost cortical shell. The surfaces of the outermost and inner cortical shells are irregularly perforated with oval to subangular pores. Many thin, radial beams connecting the outermost and inner cortical shells arise from the surface of the inner cortical shells. Due to being connected by many radial beams, the outermost and inner cortical shells form very complex sponge-like layers. Since only the broken medullary shell is preserved in our specimens, the detailed structure of the medullary shell is unclear. Based on observation with a transmitted light microscope, the diameter of the medullary shell is about one-third to one-fifth that of the outermost cortical shell.

Measurements.—Based on two specimens, in μm. Diameter of the outermost cortical shell, 280–300, average, 290; diameter of the inner cortical shell, 160–200, average, 180.

Remarks.—This species is easily distinguished from *Syntagentactinia excelsa* Nazarov and Ormiston by having long, robust main spines. Nazarov in Nazarov and Popov (1980) described *Syntagentactinia biocculosa* Nazarov and *Syntagentactinia pauca* Nazarov from the Middle Ordovician strata of eastern Kazakhstan. Nazarov's figures in Nazarov and Popov (1980) of these Ordovician species are transmitted light photomicrographs, so it is difficult to compare Silurian species with Ordovician species in detail. Nazarov and Ormiston (1993), however, mentioned that *S. afflicta* is distinguished from Ordovician species by the clearly expressed internal half-closed shells and the development in the majority of specimens of two to four rather than six main spines.

Range and occurrence.—Early Llandoverian, northern Adobe Range, Nevada; middle to late Llandoverian, southern Urals, southern Bashkiria and Northern Mugodzhar; Llandoverian, Ise area in the Hida "Gaien" Belt.

Syntagentactinia excelsa Nazarov and Ormiston, 1993

Figures 7.19, 7.20; 8.1–8.7

Syntagentactinia excelsa Nazarov and Ormiston, 1993, p. 40, pl. 6, figs. 13, 14.

Description.—The external appearance of the cortical shell is spherical, subspherical, or elliptical, with thin rod-like main spines. The main spines are directly continuous into the internal portion of the shell (Figure 6c, d). The cortical shell is composed of two or three layers with irregular, three-dimensional meshwork. The surface of the cortical shell is irregularly porous and has small spines. The medullary shell, consisting of a spherical to irregularly shaped loose lattice, is placed in the internal cavity and has a diameter about 30 % that of the cortical shell diameter. The medullary and cortical shells are connected by short radial beams arising randomly from the surface of the medullary shell.

Measurements.—Based on five specimens, in μm. Diameter of the cortical shell, 200–270, average, 250; diameter of the medullary shell, 40–90, average, 70.

Remarks.—This species is distinguished from other species of this genus by having thin, weakly developed main spines. Some specimens of this species have a smaller cortical shell than that of *Syntagentactinia afflicta* described above. Although Nazarov and Ormiston (1993) suggested that this species has a peculiar eccentric position of the medullary shell, this characteristic is not clearly shown in their illustrated specimen (Nazarov and Ormiston, 1993, pl. 4, fig. 13). The shell constitution of this species is similar to that of *Syntagentactinia*? sp. illustrated by Noble *et al.* (1998) from chert gravel of the Main Valley, Germany. However, *Syntagentactinia*? sp. of Nobel *et al.* (1998) has a large diameter of the cortical shell, up to 700 μm. *Syntagentactinia* sp. A of Noble *et al.* (1998) is similar to the present species, but differs from *S. excelsa* by having a distinctly latticed medullary shell.

Range and occurrence.—Middle to late Llandoverian, southern Urals, southern Bashkiria and Northwestern Mugodzhar; Llandoverian, Ise area in the Hida "Gaien" Belt.

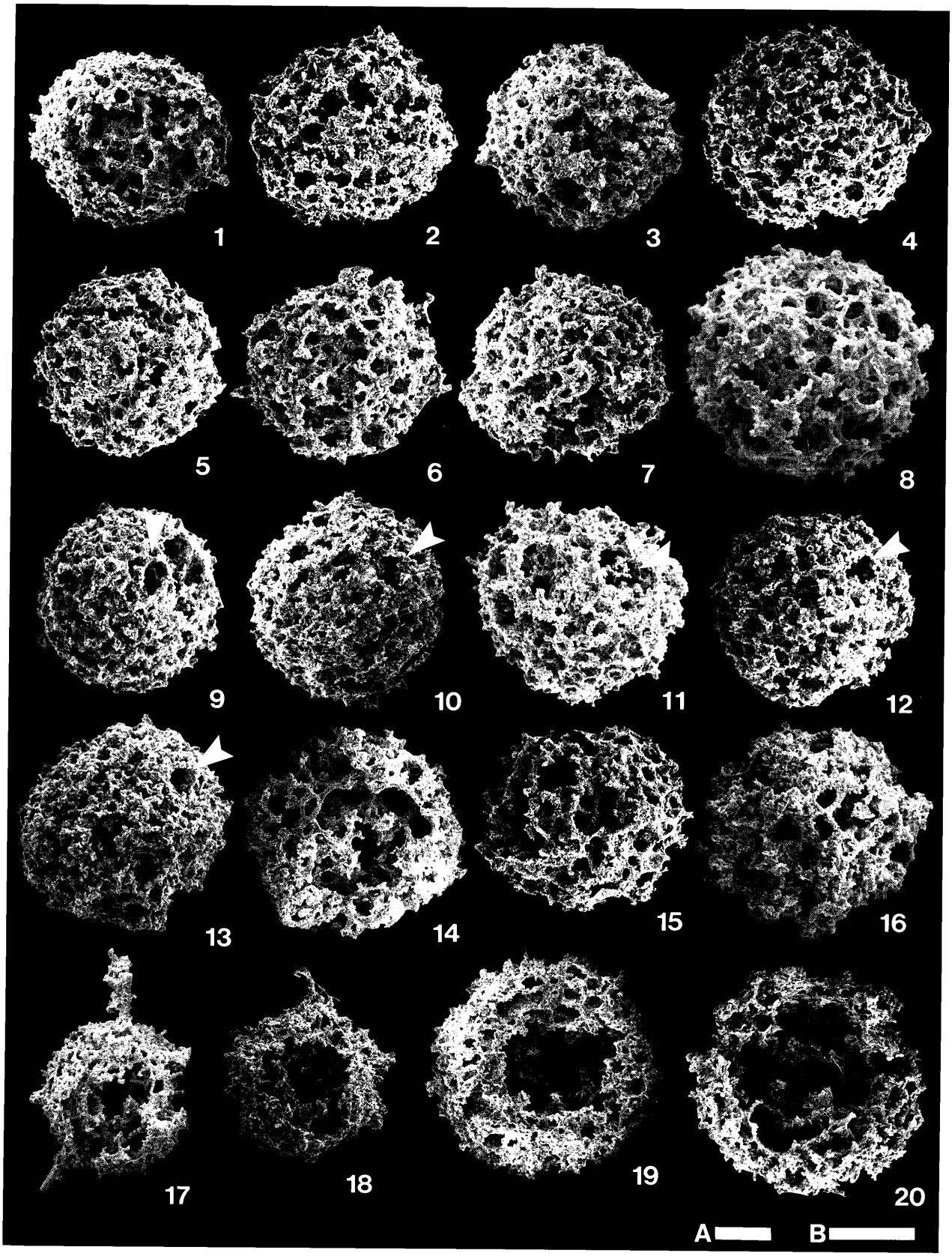
Syntagentactinia? sp.

Figure 8.8

Remarks.—Only one poorly preserved specimen was obtained. The shell of this species is composed of an irregu-

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larly fine spongy layer having three thick main spines. This spongy layer may be a product of the state of preservation. This species is similar to *Syntagentactinia*? sp. of Noble *et al.* (1998), except that it has a rather small shell diameter. Although its detailed shell structure has not yet been examined, we tentatively include this form in *Syntagentactinia*.

Range and occurrence.—Llandoverian, Ise area in the Hida "Gaien" Belt.

Family Inaniguttidae Nazarov and Ormiston, 1984, emend. Noble, 1994

Genus ***Oriundogutta*** Nazarov, 1988

Type species.—*Astroentactinia ramificans* Nazarov, 1975.

Oriundogutta sp.

Figure 8.9–8.15

?*Oriundogutta* sp. Noble, Ketner and McClellan, 1997, pl. 1, figs. 7, 8.

Description.— The thick, spherical cortical shell is single and latticed with 10 to 15 external spines per hemisphere. The external spines are short, conical to rod-like and taper distally. Five to six main spines arising from the surface of the medullary shell in each hemisphere are long and have one or two short by-spines. The pores of the latticed shell are circular, and oval to irregularly circular in shape. Thick and broad pore frames are pentagonal or hexagonal in shape. The medullary shell is small, latticed and polyhedral to spherical in shape. The pores of the medullary shell are circular to oval and larger than those of the cortical shell. The pore frames of the medullary shell are thinner than those of the cortical shell. SEM and transmitted light microscopic observations show the absence of an internal spicule in the interior of the medullary shell.

Measurements.— Based on five specimens, in μm. Diameter of the cortical shell, 150–300, average, 210; diameter of the medullary shell, 60–110, average, 90.

Remarks.—More than twenty specimens of this species were examined and they bear diagnostic characters of the *Oriundogutta*: one porous, thick cortical shell, a polyhedral to spherical medullary shell, and more than eight external spines. It is distinguished from other species of this genus by having short, conical to rod-like external spines and a smaller number of these spines. ?*Oriundogutta* sp., reported by Noble *et al.* (1997) from the lower Llandoverian of Nevada, is exceedingly similar to this species in external shape.

Range and occurrence.—Early Llandoverian, northern Adobe Range, Nevada; Llandoverian, Ise area in the Hida "Gaien" Belt.

Oriundogutta? sp.

Figure 8.16–8.20

Remarks.—The cortical shell of this species is spherical and has three to four sturdy, rod-like main spines per hemisphere. Some of the examined specimens have several thin, needle-like spines. The external shell features of *Oriundogutta*? sp. are similar to those of *Oriundogutta ramificans* (Nazarov), except that the former's main spines are smaller in number. This species is distinguished from *Oriundogutta* sp. by having a finely perforated cortical shell and thin pore frames. The internal shell structure cannot be observed, so the generic position of this species is tentative.

Range and occurrence.—Llandoverian, Ise area in the Hida "Gaien" Belt.

Genus ***Inanihella*** Nazarov and Ormiston, 1984, emend. Noble, 1994

Type species.—*Helioentactinia bakanasensis* Nazarov, 1975.

Inanihella sp.

Figure 9.1–9.4

Description.—The shell of this species is composed of two latticed cortical shells with more than four main spines per hemisphere. The inner cortical shell is spherical and has circular to oval pores with pentagonal to hexagonal pore frames. The outer cortical shell is delicate and irregularly perforated. Several short, needle-like spines arise from the surface of the outer cortical shell. The inner and outer cortical shells are connected by many thin radial beams. Based on observations with a transmitted light microscope, the internal shell is single, and probably latticed, but its detailed structure has not been observed. The main spines are thin, rod-like and taper gently toward the distal end.

Measurements.— Based on four specimens, in μm. Diameter of inner cortical shell, 190–220, average, 200; diameter of outer cortical shell, 260–300, average, 280; maximum length of spine, 70.

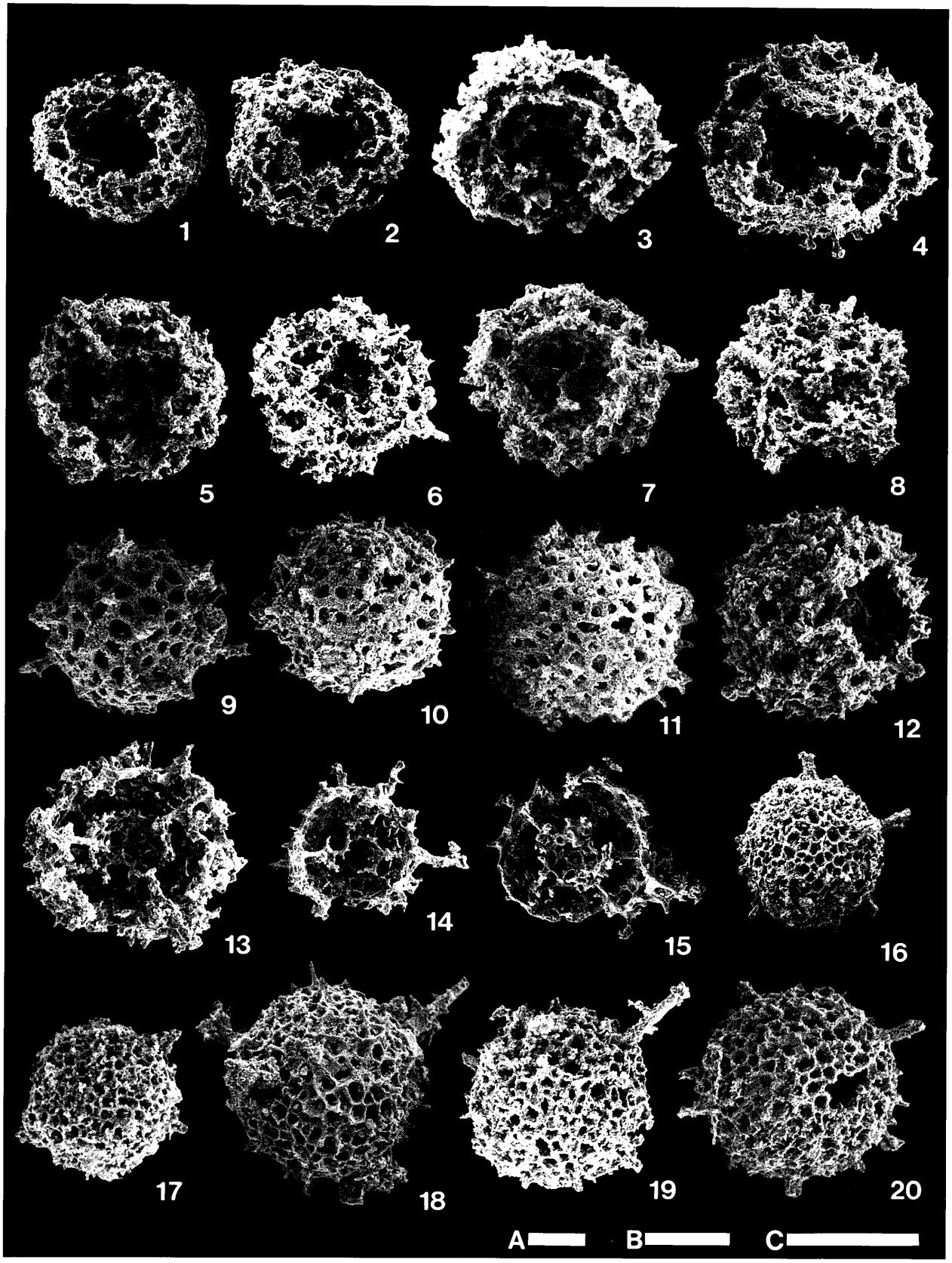
Remarks.—This species is characterized by the presence of two cortical shells, yet no specimens were found that perfectly preserve the delicate outer cortical shell. The present form has a spine morphology similar to *Inanihella bakanasensis* (Nazarov) reported from the Middle Ordovician of Kazakhstan by Nazarov (1975).

Range and occurrence.—Llandoverian, Ise area in the Hida "Gaien" Belt.

Figure 7. 1–13. *Haplotaeniatum tegimentum* Nazarov and Ormiston, 1: IGUT-TK 863, 2: IGUT-TK 816, 3: IGUT-TK 874, 4: IGUT-TK 894, 5: IGUT-TK 782, 6: IGUT-TK 858, 7: IGUT-TK 875, 8: IGUT-TK 958, 9: IGUT-TK 860, 10: IGUT-TK 783, 11: IGUT-TK 794, 12: IGUT-TK 884, 13: IGUT-TK 776. White arrows of 9 to 13 indicate a pylome-like oversized pore. **14–16.** *Haplotaeniatum* sp. A, 14: IGUT-TK 866, 15: IGUT-TK 873, 16: IGUT-TK 801. **17, 18.** *Syntagentactinia afflicta* Nazarov and Ormiston, 17: IGUT-TK 897, 18: IGUT-TK 824. **19, 20.** *Syntagentactinia excelsa* Nazarov and Ormiston, 19: IGUT-TK 817, 20: IGUT-TK 747. Scale bars A and B each equal 100μm; A applies to 15, 17, 18, B to 1–14, 16, 19, 20.

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***Inanihella*? sp.**

Figure 9.5–9.7

Remarks.—The basic skeleton of this species is composed of a porous inner cortical shell with traces of delicate outer cortical shell. The internal shell structure has not yet been observed. Three or four rod-like main spines are present on the inner cortical shell per hemisphere. Many short conical spines arise from the junction of the pore frame of the inner cortical shell. The inner cortical shell and main spines of this species are very similar to those of the *Inanihella* sp. described above. Although only traces of the delicate outer cortical shell are present, we tentatively include this form in *Inanihella*.

Range and occurrence.—Llandoverian, Ise area in the Hida "Gaien" Belt.

Inaniguttidae gen. et sp. indet. sp. A

Figure 9.8, 9.9

Remarks.—Several poorly preserved specimens were examined. This species is characterized by a large, spherical cortical shell with an oversized pore. This pylome-like pore is circular in shape and has no lip on its surrounding pore frame. The external shell morphology is somewhat similar to the *Oriundogutta* sp. herein. We tentatively include this species in the family Inaniguttidae. A larger sample of this species is needed in order to determine its generic position.

Range and occurrence.—Llandoverian, Ise area in the Hida "Gaien" Belt.

Family Anakrusidae Nazarov, 1977
Genus ***Auliela*** Nazarov, 1977

Type species.—*Auliela aspersa* Nazarov, 1977.

Auliela sp.

Figure 9.10

Description.—The shell is spherical, with more than one hundred spines arising from the hemisphere. The spines are straight, cylindrical and taper gently toward the distal end. Most of these spines are short or broken, owing to poor preservation, but some attain 60 μm in length. There are no pores on the shell surface. The internal structure is unknown.

Measurements.—Based on one specimen, in μm. Diameter of shell, 300; maximum length of spine, 60.

Remarks.—Only one specimen of this species was examined. Our specimen has a spherical shell with numerous cylindrical spines. This character and the external shape indicate assignment to the genus *Auliela*. *Auliela aspersa* Nazarov, the type species of this genus, described from the Middle Ordovician of eastern Kazakhstan by Nazarov (1977), is similar to the present species. The spines of *A. aspersa* Nazarov are described as being hollow, but the present specimen has mostly solid spines. This difference may be attributed to the development of secondary deposits of silica and poor preservation. This species, however, differs from *A. aspersa* Nazarov in having a rather smaller shell and shorter spines. *Auliela taplowensis* Webby and Blom, described from the Upper Ordovician of eastern Australia by Webby and Blom (1986), differs from this species by having longer spines and a smaller shell diameter.

Range and occurrence.—Llandoverian, Ise area in the Hida "Gaien" Belt.

Family Palaeoscenidiidae Riedel, 1967a, emend.
Holdsworth, 1977; Goodbody, 1982;
Furutani, 1983; Goodbody, 1986
Genus ***Palaeoephippium*** Goodbody, 1986

Type species.—*Palaeoephippium bifurcum* Goodbody, 1986.

***Palaeoephippium*? sp.**

Figure 9.11–9.13

Remarks.—Completely preserved specimens of this species have not yet been obtained. The basic skeleton of this species probably consists of a six-rayed form. The spines arising from each ends of a short medium bar are rod-like, gently tapered toward the distal end. Among these spines, three (probably four) spines have two or three rather thin secondary spines at the midpoint of their length, and the other spines lack the branched spines. *Palaeoephippium tricorne* Goodbody, described from the Cape Phillips Formation of the Canadian Arctic Archipelago by Goodbody (1986), has indistinguishable apical and basal spines and is similar to this species. Furthermore, this species has a resemblance to *Haplentactinia arrhinia* Foreman, 1963 in having a six-rayed basic spicule. However, the former species differs from the latter by having branches arising at one level along some spines and lacking an irregularly latticed shell. In this paper, we tentatively assign this species to the genus *Palaeoephippium*, considering its similarity to *P. tricorne*.

Range and occurrence.—Llandoverian, Ise area in the Hida "Gaien" Belt.

Family Sponguridae Haeckel, 1887, emend.
Pessagno, 1973

Sponguridae gen. et sp. indet. sp. A

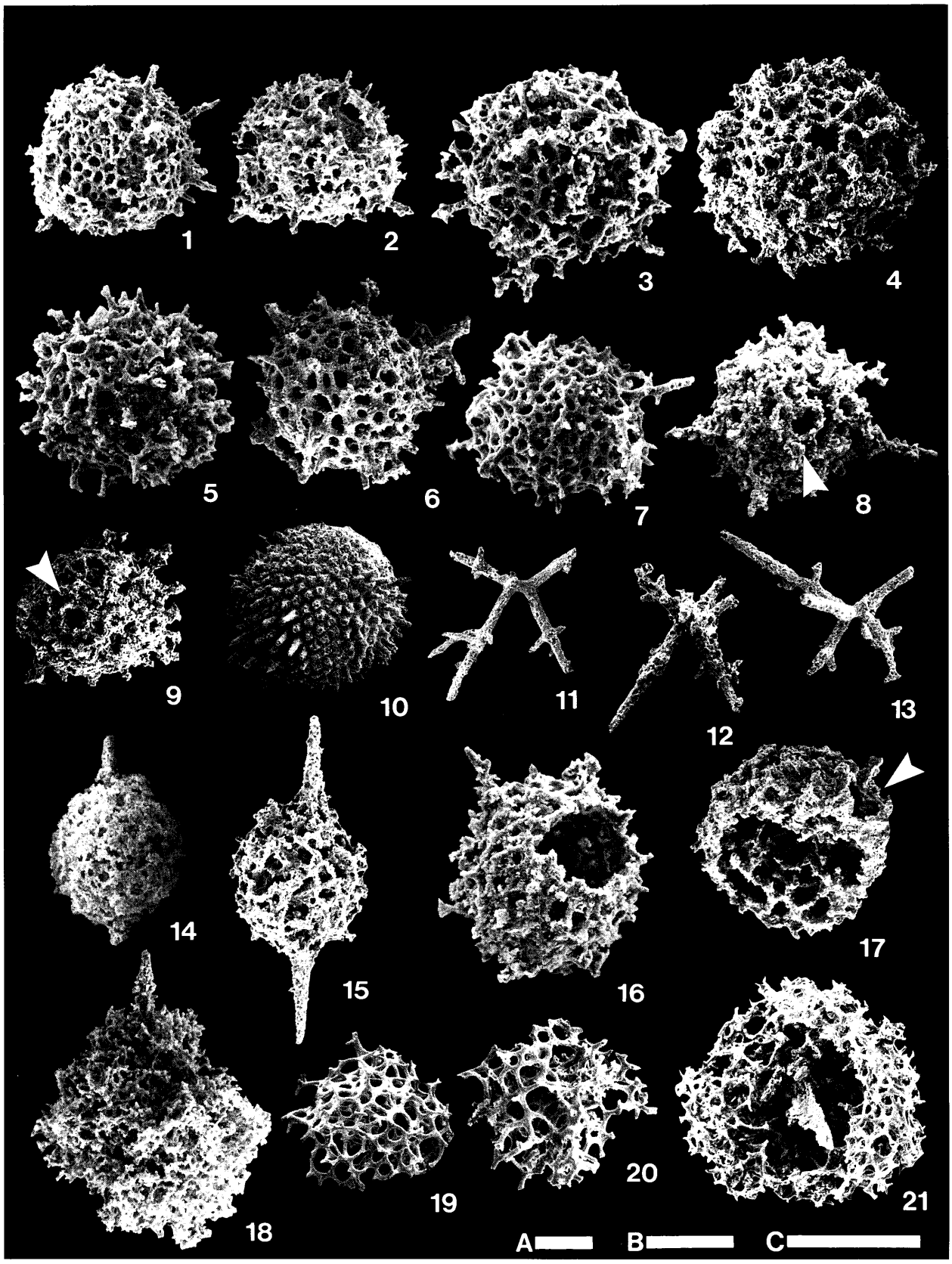
Figure 9.14, 9.15

Description.—The shell is elliptical, with two polar main

Figure 8. **1–7.** *Syntagentactinia excelsa* Nazarov and Ormiston, 1: IGUT-TK 723, 2: IGUT-TK 836, 3: IGUT-TK 961, 4: IGUT-TK 864, 5: IGUT-TK 724, 6: IGUT-TK 822, 7: IGUT-TK 766. **8.** *Syntagentactinia*? sp., IGUT-TK 899. **9–15.** *Oriundogutta* sp., 9: IGUT-TK 859, 10: IGUT-TK 895, 11: IGUT-TK 819, 12: IGUT-TK 879, 13: IGUT-TK 901, 14: IGUT-TK 761, 15: IGUT-TK 850. **16–20.** *Oriundogutta* ? sp., 16: IGUT-TK 892, 17: IGUT-TK 931, 18: IGUT-TK 845, 19: IGUT-TK 865, 20: IGUT-TK 919. Scale bars A, B and C each equal 100μm; A applies to 1, 8, 16, 17, B to 2–7, 9–11, 13–15, 18–20, C to 12.

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spines. These spines are rod-like, strongly tapered, and identical in length and thickness. The proximal portions of the spines are weakly bladed. The surface of the outer shell has many circular to polygonal pores of irregular size. The interior of the shell consists of a loose, irregular spongy meshwork. The distinctly layered internal structure was not observed.

Measurements.—Based on one specimen, in μm. Length of major axis of shell, 190; length of minor axis of shell, 150; length of spines, 100.

Remarks.—Several poorly preserved specimens of this species were examined. Although the internal structure of the multiple concentric spongy layers is unknown, this form is characterized by an elliptical spongy shell and polar main spines, and is included in the family Sponguridae. Noble (1994) has recognized Late Silurian genera (*Pseudospongoprunum* Wakamatsu, Sugiyama and Furutani, 1990, and *Devoniglansus* Wakamatsu, Sugiyama and Furutani, 1990) of the family Sponguridae. The species assigned to *Pseudospongoprunum* by Noble (1994) are especially characterized by a subspherical to elliptical spongy shell with polar main spines, and they are similar to the present species. This unidentified species, however, differs from all species of *Pseudospongoprunum* by having a loose spongy meshwork and equal lengths to the polar main spines. The exact identification of this species is postponed until sufficient specimens have been examined.

Range and occurrence.—Llandoverian, Ise area in the Hida "Gaien" Belt.

Family Pylentonemidae? Deflandre, 1963
Genus ***Cessipylorum*** Nazarov in Afanas'eva, 1986

Type species.—*Pylentonema insueta* Nazarov in Nazarov, Popov and Apollonov, 1975.

Remarks.—Nazarov and Ormiston (1993) tentatively placed the genera *Cessipylorum* and *Aciferopylorum* Nazarov and Ormiston, 1993 in the family Pylentonemidae Deflandre. We tentatively follow that placement.

Cessipylorum? sp.

Figure 9.16

Remarks.—Only one specimen was examined. The cortical shell is subspherical and irregularly porous, and bears a large circular aperture. The pore frame around the aperture is slightly turned up and has small conical spines. The presence of a medullary shell and an inner structure is unclear. The other species in *Cessipylorum*, such as *Cessipylorum apertum* (Nazarov), have long, robust main spines, but this species has only a few thin and short spines. The generic placement of this species is tentative.

Range and occurrence.—Llandoverian, Ise area in the Hida "Gaien" Belt.

Family Incertae sedis
Genus ***Orbiculopylorum*** Noble, Braun and McClellan, 1998

Type species.—*Orbiculopylorum marginatum* Noble, Braun and McClellan, 1998.

Orbiculopylorum sp.

Figure 9.17

Remarks.—The illustrated specimen is distinguished by a prominent pylome on the cortical shell. The cortical shell is thick and probably perforated. However, the detailed structure of the cortical shell cannot be observed, owing to poor preservation. The pylome is circular and flanged. The medullary shell consists of a loose lattice and is irregularly spherical and centrally located. This species is similar to *Orbiculopylorum adobensis* Noble, Braun and McClellan, described from the Cherry Spring Chert of Nevada by Noble *et al.* (1998). However, the former species differs from the latter by having a less compact medullary shell.

Range and occurrence.—Llandoverian, Ise area in the Hida "Gaien" Belt.

Spumellaria gen. et sp. indet. sp. A

Figure 9.19, 9.20

Labyrinthine spumellarian Noble, Ketner and McClellan, 1997, pl. 1, fig. 14.

Description.—The shell consists of a spongy, three-dimensional meshwork and is irregularly spherical. The spongy meshwork is loose, delicate and has no regular structure or layering. The exterior meshwork seems to be looser than that in the interior. The pores framed by the looped, loose, spongy meshwork are circular to elliptical and vary in size. On the external surface of the shell, short subconical to cylindrical spines arise from the pore frame and usually bifurcate, or rarely trifurcate, at their distal end.

Measurements.—Based on two specimens, in μm. Diameter of shell, 120-170, average, 145.

Remarks.—This species is characterized by an irregular spongy shell without layering. A form referable to this species has been reported by Noble *et al.* (1997) as Labyrinthine spumellarian. *Haplotaeniatum fenestratum* Goto, Umeda and Ishiga, described from the Upper

Figure 9. **1–4.** *Inanihella* sp., 1: IGUT-TK 973, 2: IGUT-TK 976, 3: IGUT-TK 986, 4: IGUT-TK 893. **5–7.** *Inanihella*? sp., 5: IGUT-TK 975, 6: IGUT-TK 855, 7: IGUT-TK 937. **8, 9.** Inaniguttidae gen. et sp. indet. sp. A, 8: IGUT-TK 956, 9: IGUT-TK 808. White arrows of 8 and 9 indicate an oversized pore. **10.** *Auliela* sp., IGUT-TK 732. **11–13.** *Palaeoephippium*? sp., 11: IGUT-TK 843, 12: IGUT-TK 737, 13: IGUT-TK 842. **14, 15.** Sponguridae gen. et sp. indet. sp. A, 14: IGUT-TK 940, 15: IGUT-TK 827. **16.** *Cessipylorum*? sp., IGUT-TK 922. **17.** *Orbiculopylorum* sp., IGUT-TK 743. White arrow of 17 indicates a pylome. **18.** Spumellaria gen. et sp. indet., IGUT-TK 972. **19, 20.** Spumellaria gen. et sp. indet. sp. A, 19: IGUT-TK 725, 20: IGUT-TK 851. **21.** Spumellaria gen. et sp. indet. sp. B, IGUT-TK 868. Scale bars A, B and C each equal 100μm; A applies to 1, 2, 8, 10, 14, 18, B to 3–7, 9, 11–13, 15–17, 19, 21, C to 20.

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Ordovician of eastern Australia by Goto *et al.* (1992), is similar to this species in the basic construction of its spongy shell. However, *H. fenestratum* lacks certain diagnostic characteristics of *Haplotaeniatum*, such as concentric layers or a spiral form. The taxonomic placement of this species will depend on finding additional specimens.

Range and occurrence.—Early Llandoverian, northern Adobe Range, Nevada; Llandoverian, Ise area in the Hida "Gaien" Belt.

Spumellaria gen. et sp. indet. sp. B

Figure 9.21

Remarks.—Several broken specimens were obtained. The illustrated specimen has a spherical shell consisting of a spongy, three-dimensional meshwork. The spongy meshwork structure of this species is similar to that of Spumellaria gen. et sp. indet. sp. A, described above, but differs from the latter by having an internal cavity.

Range and occurrence.—Llandoverian, Ise area in the Hida "Gaien" Belt.

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