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A New Siphonotretid Brachiopod from the Silurian of Central-Western New South Wales, Australia

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ABSTRACT. A new genus and species of Silurian siphonotretid brachiopod, *Orbaspina gelasinus* n.gen. and n.sp., is described from the late Llandovery (*amorphognathoides* Zone) to early Wenlock (*ranuliformis* Zone) Boree Creek Formation of central-western New South Wales, Australia. This represents the first confirmed report of a post-Ordovician siphonotretid from east Gondwana. Other supposed post-Ordovician siphonotretid occurrences are reviewed. Higher-level taxonomic relationships between the Siphonotretida and other linguliformean groups are discussed; based on present knowledge, the siphonotretids appear closest to the lingulellotretids or dysoristids.

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Siphonotretid brachiopods first appeared during the late Middle Cambrian with the oldest species, *Schizambon reticulatus* MacKinnon (in Shergold *et al*., 1976), occurring in the Mayaian stage of the Saian-Altai region in southwest Siberia (Aksarina & Pel'man, 1978). The siphonotretids slowly diversified throughout the Late Cambrian and Early Ordovician, reaching a peak diversity of 13 genera during the late Arenig as part of the great Ordovician diversification event (Bassett *et al*., 1999). Throughout the Middle and Late Ordovician, siphonotretid diversity steadily decreased and they were believed to have disappeared along with most of the Cambrian Evolutionary Fauna during the end-Ordovician extinction event; an event which saw a significant turnover in brachiopod communities worldwide (Harper & Rong, 1995; Rong & Harper, 1999; Bassett *et al*., 1999; Sheehan, 2001).

Until recently, the youngest accepted siphonotretid species was *Multispinula drummuckensis* Harper, from the upper Ashgill (upper Rawtheyan) South Threave Formation of southwest Scotland (Harper, 1984). Mergl (2000, 2001a,b) has recently documented fragmentary material from the Early Silurian to Early Devonian of the Barrandian of central Bohemia that he identified as belonging to four indeterminate siphonotretid species.

This paper describes a new genus of Silurian siphonotretid brachiopod, *Orbaspina* n.gen., with type species *Orbaspina gelasinus* n.gen. and n.sp., from the late Llandovery (*amorphognathoides* Zone) to early Wenlock (*ranuliformis* Zone) carbonate sequence of the Boree Creek Formation in central-western New South Wales, Australia (Valentine *et al*., 2003). *Orbaspina* n.gen. represents the first post-Ordovician siphonotretid brachiopod to be documented from east Gondwana.

Geology and stratigraphy of the Boree Creek Formation

The Boree Creek Formation, a sequence of impure limestones and sandstones, crops out extensively in central-western New South Wales. Sherwin (1971) divided the Boree Creek Formation in the type area at Cheesemans Creek into three lithological members (oldest to youngest):

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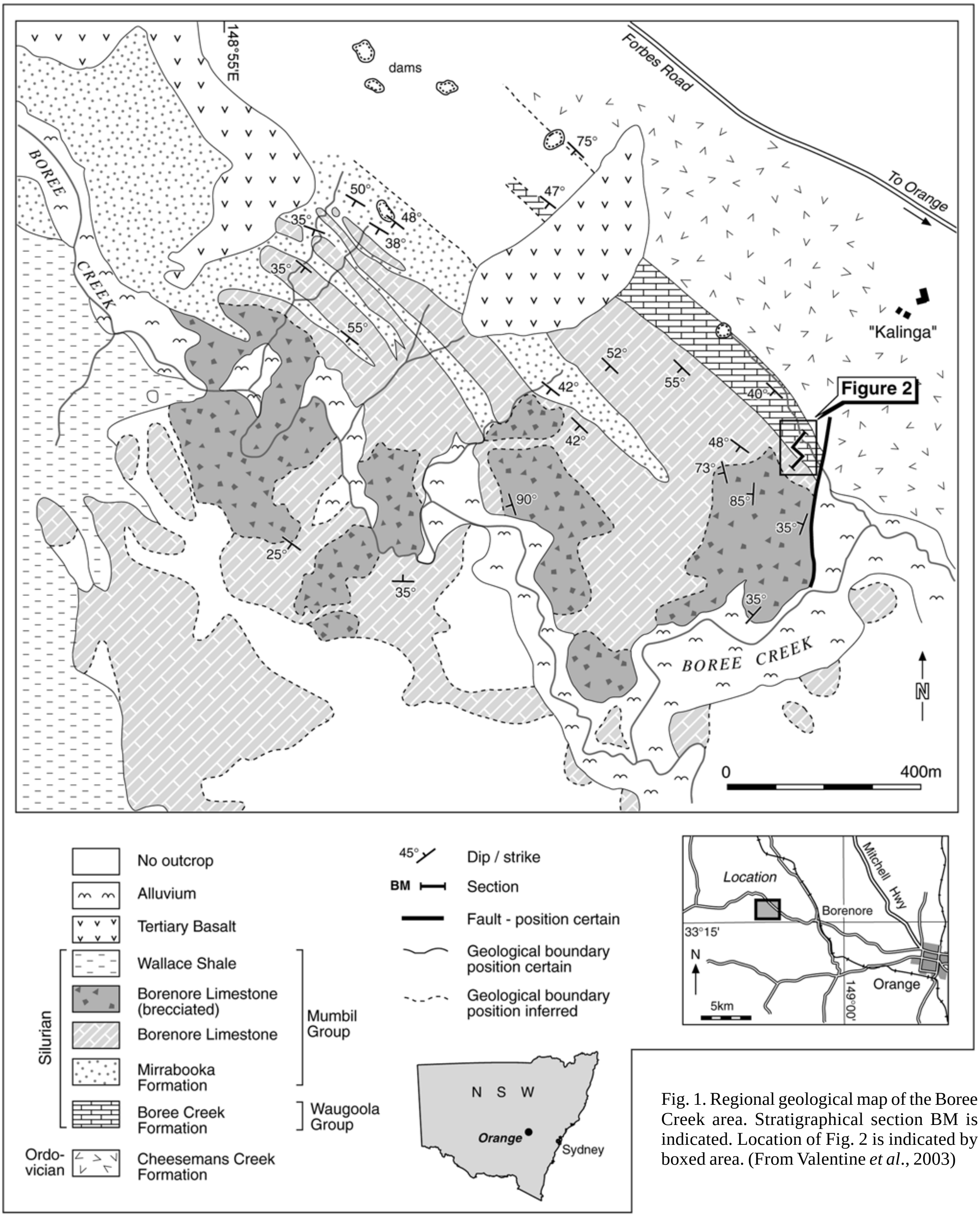

Fig. 1. Regional geological map of the Boree Creek area. Stratigraphical section BM is indicated. Location of Fig. 2 is indicated by boxed area. (From Valentine *et al*., 2003)

Limestone A, the tuffaceous trilobite beds and Limestone B. However, rapid lateral facies changes and lithological interfingering mean these units are only readily discernible in the type area (Pickett, 1982; Holloway & Lane, 1998). At the easternmost exposure of the Boree Creek Formation, where the BM section is located (Fig. 1), five distinct lithological units can been identified (Fig. 2). These include (from oldest to youngest): argillaceous and red limestones (equivalent to Sherwin's [1971] Limestone A), grey lensoidal limestone and sandstone (equivalent to Sherwin's [1971] tuffaceous trilobite beds), and Limestone B (Fig. 2). The lithology and faunal composition of each of these units has recently been described in detail by Valentine *et al*. (2003).

Conodont faunas documented by Bischoff (1986) and Cockle (1999) suggest the Boree Creek Formation ranges in age from late Llandovery (*amorphognathoides* Zone) to early Wenlock (*ranuliformis* Zone). Simpson (1995) speculated that the argillaceous limestone might fall within the late Llandovery *celloni* conodont Zone, based on Männik & Aldridge's (1989) phylogeny of *Pterospathodus amorphognathoides* Walliser, and interpretation of the conodont distribution charts presented by Bischoff (1986, table 8). Through detailed sampling of the argillaceous limestone, Molloy & Simpson (2002) and Molloy (unpub. data), have recovered *P. amorphognathoides*-type Pa elements from samples BM-19.80, -19.70 and -14.70 and a Pb element from sample BM-19.80, suggesting the *amorphognathoides* zone extends down to at least sample BM-19.80 (Fig. 3). No evidence of *celloni* Zone conodont assemblages have been recovered (Molloy, unpub. data).

Talent *et al*. (1993) used isotopic data to document the likely presence of the Ireviken Extinction Event in the Boree Creek Formation, which Jeppsson (1997) confirmed using Bischoff's (1986, tables 7–9) conodont distribution charts. *Orbaspina gelasinus* n.gen. and n.sp. occurs as part of a moderately diverse linguliformean brachiopod assemblage documented through the Ireviken Event by Valentine *et al*. (2003); elements of which have been recovered from each unit of the Boree Creek Formation, except the sandstone unit. *Orbaspina gelasinus* n.gen. and n.sp. occurs only in the massive red and grey lensoidal limestones, from which 55 and 231 specimens have been recovered, respectively (Fig. 3). Specimens from the red limestone tend to be rather small and fragmentary, whereas those from the grey lensoidal limestone, most which occur in a 0.47 m thick sequence from sample BM13.80 to BM14.85, are larger and better preserved (Tables 1, 2).

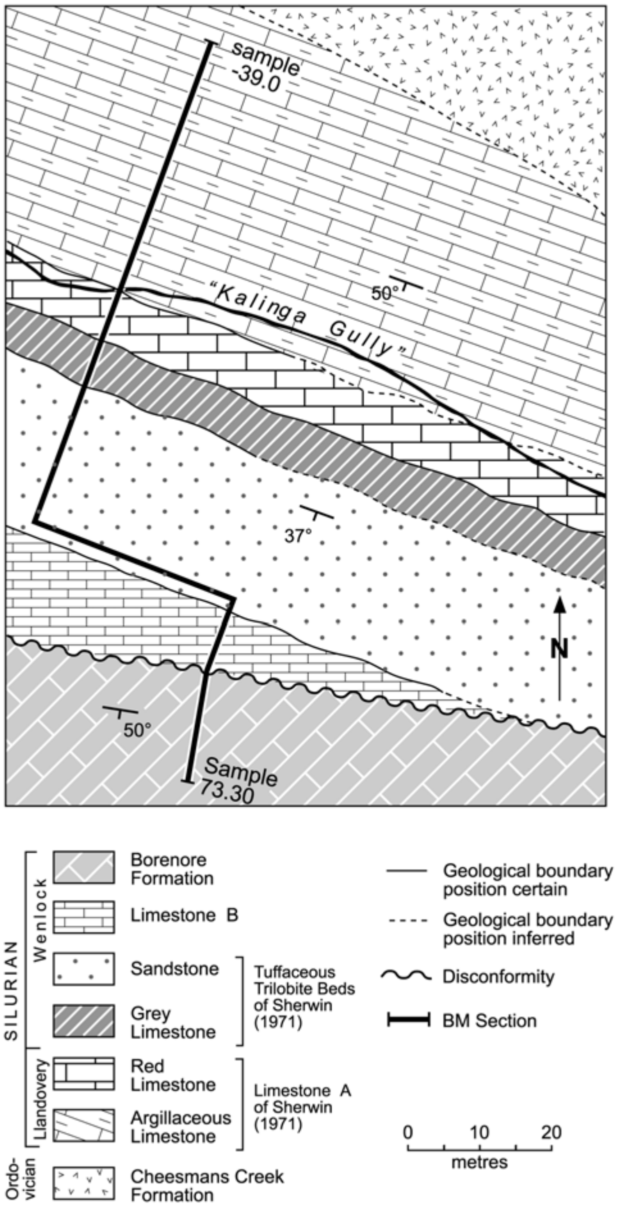

Fig. 2. Detailed geological map of the study area, showing location of the BM section. Note that section starts at sample BM-39.0 and ends at sample BM 73.30. (Modified after Valentine *et al*., 2003)

Post-Ordovician siphonotretid brachiopods

A number of supposed post-Ordovician siphonotretids have been documented from Europe, North America and Australia, particularly during the mid 1800s to early 1900s (e.g., Morris, 1849; Davidson, 1866; Hall & Clarke, 1892; Chapman, 1903, 1913). Following the introduction of the Ordovician System by Lapworth (1879), and its subsequent acceptance, most of these supposed post-Ordovician siphonotretids were reassigned to strata of Ordovician age. Taxa such as "*Siphonotreta*" *anglica* Morris, "*Siphonotreta*" *australis* Chapman, and "*Siphonotreta*" *plicatella* Chapman, recovered from genuine Silurian strata, have generally been dismissed or ignored.

"*Siphonotreta*" *anglica*, described by Morris (1849) from the Wenlock Limestone of Dudley, England, has been dated as Wenlock by Dorning (1983) based on acritarchs, chitinozoans and miospores. This species is unusual for a siphonotretid in that it has spines with regularly developed transverse grooves (giving them a beaded appearance) and a pitted post-larval shell (Morris, 1849; Davidson, 1866). The taxonomic assignment of this species was strongly refuted by Rowell (1962: 150) who noted "apart from the fact that the shell is spinose there is no evidence to support that the species is a *Siphonotreta*, or indeed that it is a member of the Siphonotretacea." Both Cocks (1978) and Holmer & Popov (2000) have also questioned the taxonomic assignment of this species. Only three specimens of "*Siphonotreta*" *anglica* are known to exist and a definitive assessment of this taxon must await detailed examination of the type material. However, it is worth noting the presence of a few weakly developed transverse grooves on the spines and a pitted post larval shell also occurs in *O. gelasinus* n.gen. and n.sp. (Figs. 5h–k, 6i, 7h).

Chapman (1903, 1910, 1914) also documented a possible post-Ordovician siphonotretid, "*Siphonotreta*" *australis*, from the Melbourne Formation cropping out in the Sewerage works in Domain Road, South Yarra, Melbourne, Australia. Rickards & Sandford (1998) have dated the Melbourne Formation at South Yarra as lower Ludlow in age based on graptolites. Syntype material of "*Siphonotreta*" *australis* examined by the authors (National Museum of Victoria Numbers 604 and 605) (Fig. 4), consist of internal moulds. No trace of spine bases or post-larval shell pitting, as described by Chapman (1903: 65), is evident on the

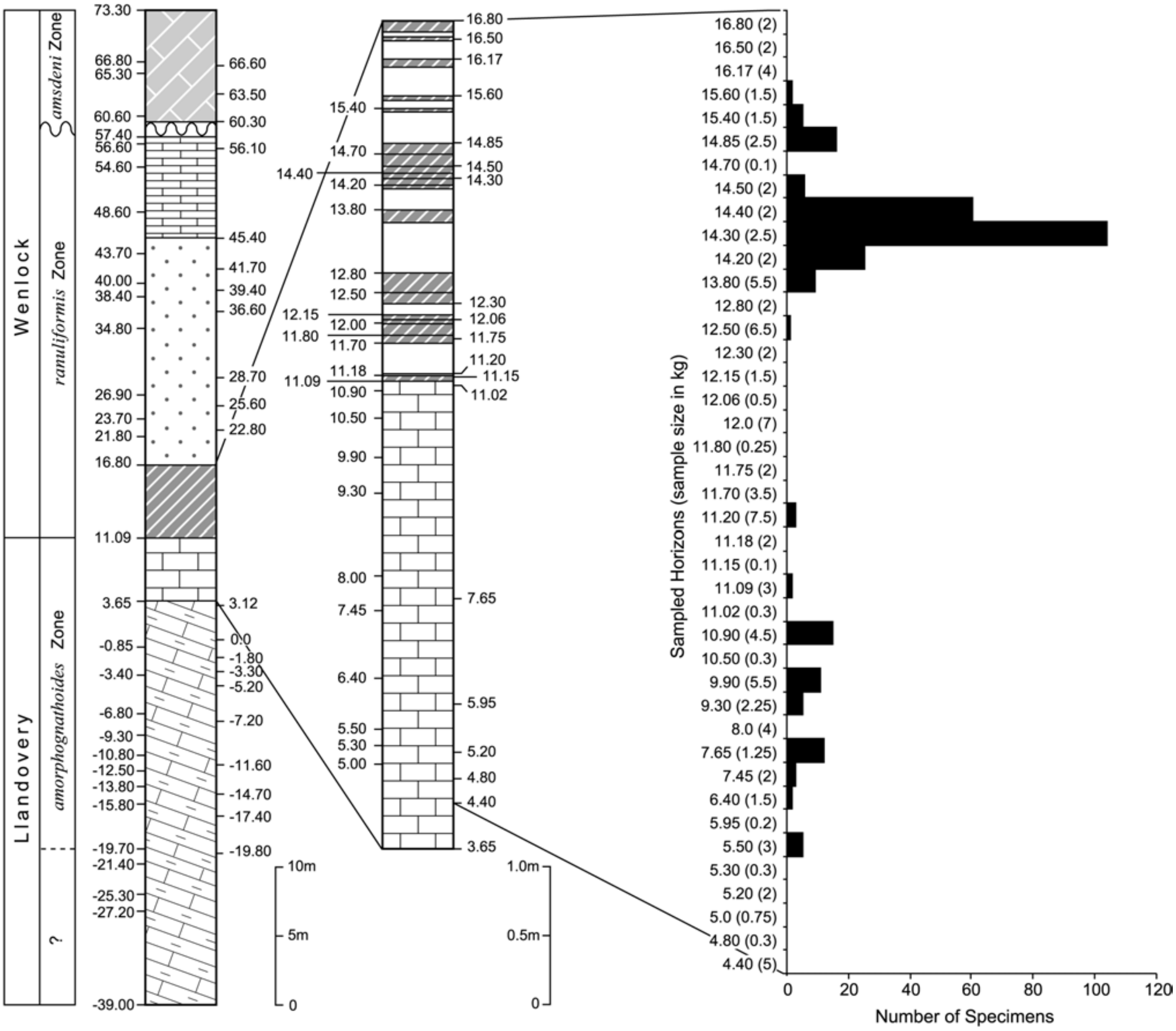

Fig. 3. Stratigraphic column of the BM section showing lithology and all sampled horizons. Lithological details of massive red and grey lensoidal limestones and sampled horizons for the 5.87 metres of section around the Llandovery-Wenlock boundary, from sample BM 3.65 to BM 16.80, is enlarged in the middle. Key to lithology as for Fig. 2; blank areas indicate no exposure. Modified after Valentine *et al*. (2003). Distribution and abundance of *Orbaspina gelasinus* n.gen. and n.sp. recovered from each sampled horizon in the massive red and grey lensoidal limestones is shown to the right. Sample size in kilograms for each horizon is given in brackets after each sample number.

specimens (Fig. 4). The lack of spines, large size of the specimens (specimen 604: width = 14 mm, length = 15 mm; specimen 605: width = 12 mm, length = 14 mm), well-developed, broad concentric rugae and apparent lack of a larval shell (Fig. 4) indicate the specimens are not siphonotretids. The material may well represent an indeterminate bivalve taxon. "*Siphonotreta*" *australis* can therefore be confidently rejected from the Siphonotretida.

Chapman (1913) described a second possible post-Ordovician siphonotretid, "*Siphonotreta*" *plicatella*, based on a single specimen recovered from the Yea Yean Formation of Victoria, Australia. Based on graptolite data, the Yea Yean Formation has been dated as middle to late Ludlow in age (Strusz *et al*., 1972). At the time of writing the holotype was unavailable for study. Chapman (1913: 100) described the exterior ornament as "consisting of concentric laminar folds and vertical striae; the latter probably representing remnants of short, spinose processes". There is no evidence of tubular hollow spines on the pedicle valve figured by Chapman (1913, pl. 10, figs. 1a–c). The fact that hollow spines are not actually preserved, and that a larval shell is not apparent, leads us to strongly question the siphonotretid affinity of this taxon.

More recently, Mergl (2000, 2001a,b) documented four indeterminate siphonotretids from the Barrandian of central Bohemia: Siphonotretine sp. from the Ludfordian Kopanina Formation of Řeporyje; Schizambonine sp. A from the Pragian Dvorce-Prokop Limestone of Klukovice; Schizambonine sp. B from the upper Dalejan Daleje-Třebotov Formation of Holyně; and Acanthambonine sp. from the Wenlock of the Motol Formation of Loděnice. These ages are based primarily on graptolite data presented

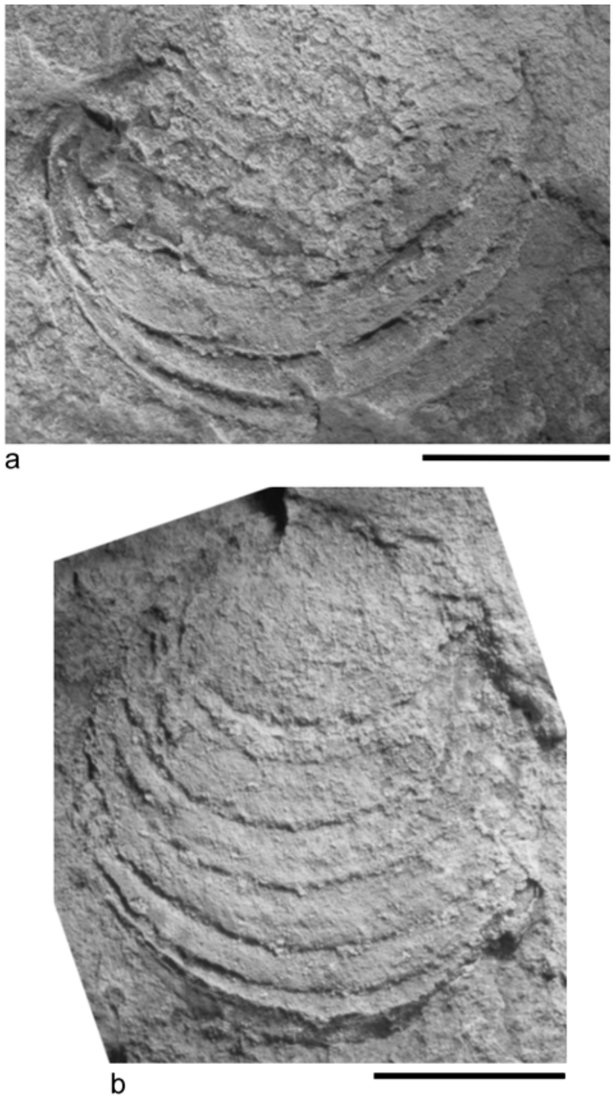

Fig. 4. "*Siphonotreta*" *australis*: *a*, syntype National Museum of Victoria Number 604, internal mould; *b*, syntype National Museum of Victoria Number 605, internal mould. Note the lack of spine bases and post-larval shell pitting contrary to the opinion of Chapman (1903). Scale bars = 5 mm.

in Mergl (2001b). Although rare, and based on fragmentary remains, the presence of tubular hollow spines (*sensu* Alvarez & Brunton, 2001), on each of these species is unmistakable, confirming siphonotretid affinities (Mergl, 2001a, fig. 35.3c–g; 2001b, pl. 36, figs. 6–16). Siphonotretine sp. and Schizambonine sp. A are both unusual in possessing a pitted post-larval shell, indicating both species may be related to *O. gelasinus* n.gen. and n.sp.

Systematic palaeontology

Type and figured paratypic material is lodged in the palaeontological collections of the Australian Museum (AMF).

Phylum Brachiopoda Duméril, 1806

Discussion. The higher level classification used herein follows that of Holmer & Popov (2000).

Subphylum Linguliformea Williams, Carlson, Brunton, Holmer & Popov, 1996

Class Lingulata Goryanskij & Popov, 1985

Order Siphonotretida Kuhn, 1949

Discussion. Under Beecher's (1891) brachiopod classification scheme, the siphonotretids were placed in the order Neotremata, erected for the so-called "more advanced" inarticulates which had the pedicle opening confined to the ventral valve (Beecher, 1891; Carlson, 2001). Prior to this, higher-level brachiopod taxonomy had followed a wide variety of classification schemes that saw the siphonotretids associated with a number groups including the obolids (e.g., Morris, 1849; Gagel, 1890) and the discinids (e.g., Davidson, 1866). Beecher's (1891) classification scheme, or variations thereof, remained in vogue for over a century before being supplanted by Rowell (1965) for the first edition of the *Treatise on Invertebrate Paleontology* and Goryanskij (in Sarytcheva, 1960) in the *Osnovy Paleontologii*.

Following Rowell (1962), Williams (1962) and Wright (1963), Rowell (1965: H287-H288) classified the siphonotretids as a superfamily of the Acrotretida, stating that the "structure of the dorsal posterior margin, particularly that of early genera, suggests that the acrotretaceans may have provided the ancestral stock." This "traditional" view of siphonotretid classification was maintained by numerous workers (e.g., Krause & Rowell, 1975; Aksarina & Pel'man, 1978; Havlíček, 1982; Williams & Curry, 1985; Mergl, 1995). Phylogenetic analysis of the relationships between higher-level brachiopod taxa undertaken by Rowell (1981), Carlson (1991) and Popov *et al*. (1993) supported this view.

Under Goryanskij's (in Sarytcheva, 1960) classification scheme, the siphonotretids were placed in their own order, the Siphonotretida, a scheme also followed by numerous workers (Goryanskij, 1969; Popov & Nõlvak, 1987; Holmer, 1989; Popov & Holmer, 1994; Robson & Pratt, 2001). The cladistic analyses of higher level brachiopod relationships undertaken by Holmer & Popov (1994), Holmer *et al*. (1995), Williams *et al*. (1996), Holmer & Popov (2000), revising the earlier work of Rowell (1981), Carlson (1991) and Popov *et al*. (1993), supported Goryanskij's (in Sarytcheva, 1960) view that the siphonotretids were a distinct, monophyletic group united by the presence of tubular hollow spines.

Acrotretid affinities can also be rejected on several additional counts. Siphonotretids lack the small pitted larval shell characteristic of all acrotretids (Biernat & Williams, 1970; Williams & Curry, 1991; Holmer & Popov, 2000), instead having a larger and smooth larval shell (Holmer & Popov, 2000).

Acrotretid shells are composed of 1 µm thick horizontal laminae connected by numerous round columellae, about 3 µm in diameter, aligned perpendicular to the laminae. The laminae and columellae are composed of needle-shaped apatite crystallites about 170 nm wide and 1 µm long (Poulsen, 1971; Ushatinskaya *et al.*, 1988; Holmer, 1989; Ushatinskaya, 1990). In contrast, the shell structure of siphonotretids consists of up to 15, 1 µm thick horizontal laminae composed of microgranular apatite measuring up to 500 nm across. Biernat & Williams (1970) and Ushatinskaya *et al.* (1988) considered each of the narrow spaces between the lamina to have been filled with organic material during life. Ushatinskaya *et al.* (1988: 45) remark that "this structure most closely resembles the lingulid shell structure, but an important difference is the development, at the surface of the siphonotretid valves, of hollow spines…"

Both the acrotretids and siphonotretids possess a foramen located wholly within the ventral valve, a possible uniting feature. However, a similar type of foramen has also been described in the lingulid family Lingulellotretidae (Koneva & Popov, 1983). The foramen of most siphonotretids becomes enlarged through resorption forming an elongate, triangular pedicle track. While such a feature is known in members of the acrotretid family Curticiidae (Rowell & Bell, 1961), it has also been documented from the lingulid family Dysoristidae (Popov & Ushatinskaya, 1992).

Muscle scars and mantle canal systems are poorly defined in most siphonotretid genera, and this is generally attributed to poor mineralization of the innermost shell layer (Holmer & Popov, 1994, 2000). Features of the muscle system have been described to varying degrees for *Schizambon* (Rowell, 1962, 1977; Chuang, 1971), *Siphonotreta, Siphonobolus* and *Celdobolus* (Havlíček, 1982). Chuang (1971) and Rowell (1977) both attempted (through very different interpretations) to reconstruct the muscle system of *Schizambon* on the assumption that it resembled the muscle system of a discinid. However, Havlíček (1982) has shown that the siphonotretid muscle system is also comparable with many early Palaeozoic lingulids, an arrangement accepted by Holmer & Popov (2000). The siphonotretid mantle canal system has been best described by Havlíček (1982) for *Celdobolus* and *Siphonobolus*, and by Rowell (1962) for *Schizambon*. Despite still being poorly known, the mantle canal systems of these genera appear most like those of early Palaeozoic lingulids (Holmer & Popov, 2000).

Unfortunately, the earliest history of the siphonotretids is poorly represented in the fossil record. The oldest known species, *Schizambon reticulatus* from the Mayaian of the Saian-Altai region of southwest Siberia (Aksarina & Pel'man, 1978) and the late Idamean of the Bowers Group of Northern Victoria Land, Antarctica (MacKinnon in Shergold *et al.*, 1976) already possesses an ornament of hollow spines and an elongate pedicle track formed through resorption. The other known Cambrian siphonotretid genera, *Gorchakovia* and *Helmersenia*, also possess these features.

Based on the evidence presented above, Rowell's (1962, 1965) assessment that the siphonotretids were most closely related to the acrotretids cannot be sustained. Despite many features of the siphonotretids still being poorly understood, they appear most similar to the lingulellotretids or dysoristids from which they are most likely to be descended (Holmer & Popov, 2000).

Superfamily Siphonotretoidea Kutorga, 1848

Family Siphonotretidae Kutorga, 1848

Genera included. *Siphonotreta* de Verneuil, 1845; *Acanthambonia* Cooper, 1956; *Alichovia* Goryanskij, 1969; *Celdobolus* Havlíček, 1982; *Cyrbasiotreta* Williams & Curry, 1985; *Eosiphonotreta* Havlíček, 1982; *Gorchakovia* Popov & Khazanovitch (in Popov *et al.*, 1989); *Helmersenia* Pander (in von Helmersen, 1861); *Karnotreta* Williams & Curry, 1985; *Mesotreta* Kutorga, 1848; *Multispinula* Rowell, 1962; *Nushbiella* Popov (in Kolobova & Popov, 1986); ?*Quasithambonia* Bednarczyk & Biernat, 1978; *Schizambon* Walcott, 1884; *Siphonobolus* Havlíček, 1982; *Siphonotretella* Popov & Holmer, 1994; *Orbaspina* n.gen., described herein.

Discussion. Walcott (1912) included the Obolellidae, comprising the genera *Obolella*, *Botsfordia, Schizopholis* and *Quebecia*, in the superfamily Siphonotretacea regarding these taxa as "primitive" siphonotretids. Despite comprising a mixed assemblage of calcareous and phosphatic taxa this group remained essentially unchallenged until the reviews of Goryanskij (in Sarytcheva, 1960) and Rowell (1962, 1965). Each of these genera lack hollow spines, except for *Schizopholis*, which belongs to the Acrothelidae, a group characterized by the presence of hollow spines developed on the larval shell of both valves. Schindewolf (1955) rejected Walcott's (1912) taxonomic assignment for *Schizopholis*, reassigning the genus to a new family and superfamily, Schizopholididae and Schizopholidacea, respectively. Holmer & Popov (2000) have since synonymized Schizopholidacea with Acrothelidae. Rowell (1962: 146) synonymized *Quebecia* with *Yorkia*, believing it to show "all the essential characters of *Yorkia*." Goryanskij (in Sarytcheva, 1960) also included the calcareous obolids within the Siphonotretida, but these were regarded by Rowell (1962) to constitute a separate superfamily on the basis of their calcitic shell structure. *Botsfordia* was reassigned by Schindewolf (1955) to a new family, Botsfordiidae.

In addition to *Siphonotreta* and *Schizambon*, Walcott (1908, 1912) assigned a second group of calcareous and phosphatic taxa consisting of *Dearbornia*, *Trematobolus* and *Keyserlingia*, to the Siphonotretidae. Walcott (1912: 80) described *Dearbornia clarki* Walcott as "one of the simple or rudimentary forms of the Siphonotretidae". Bell (1941: 219) reassigned *D. clarki* to *Acrothele* on the basis of its organophosphatic shell composition and "a morphology congeneric with *Acrothele*." *Trematobolus*, while superficially resembling *Schizambon*, lacks hollow spines and has a calcareous composition that led Rowell (1962) to reassign this genus to the Obolellidae. *Keyserlingia* now resides within the acrotretid family Ceratretidae (Holmer & Popov, 2000).

As discussed by Brock (1998), Walcott (1897, 1912) also assigned the yorkiids to the Siphonotretidae. However, the calcareous shell composition, rudimentary articulation structures and lack of hollow spines in the yorkiids led Rowell (1962) to relocate them into a new family, the Yorkiidae, within the Obolelloidea. As their placement here was also uncomfortable, Rowell (1965) relocated them a second time to the Kutorginoidea, a classification that has since been accepted by most other workers (see Brock, 1998: 611).

Cooper (1956) assigned *Acanthambonia*, residing within a new subfamily, Acanthamboniinae, to the obolids. Despite being a somewhat uncomfortable placement, it was followed by Wright (1963), Rowell (1965), Cocks (1978) and Williams & Curry (1985). Goryanskij (1969), while maintaining Cooper's (1956) taxonomic placement of *Acanthambonia*, questioned this assignment and highlighted a number of common features shared between *Acanthambonia* and *Helmersenia* (including tubular hollow spines). This led Havlíček (1982) and subsequent workers (e.g., Popov & Nõlvak, 1987; Holmer, 1989; Schallreuter, 1999) to reassign Acanthamboniinae to the siphonotretids.

Rowell (1962, 1965), Havlíček (1982) and Harper *et al*. (1993) placed *Dysoristus* and *Ferrobolus* within the Siphonotretidae. However, the lack of hollow spines, baculate shell structure and pitted larval shell microornament in both genera (Popov & Ushatinskaya, 1992; Popov & Holmer, 1994), indicates their affinities lie more closely with the Lingulida (Holmer & Popov, 2000), particularly the zhanatellids (Popov & Holmer, 1994).

The poorly known genus *Craniotreta*, from the Middle Cambrian west Taurus Mountains of Turkey, was described by Termier & Monod (1978) as a siphonotretid. However, the acrotretid-like shell structure, apical process, muscle scars and lack of hollow spines indicate the affinities of *Craniotreta* do not lie with the siphonotretids. Holmer & Popov (2000) have speculated that *Craniotreta* may be synonymous with the acrotretid *Linnarssonia*.

Orbaspina n.gen.

Type species. *Orbaspina gelasinus* n.gen. and n.sp., Llandovery to Wenlock, central-western New South Wales, Australia.

Diagnosis. A siphonotretid with large, keyhole-shaped pedicle foramen extending forward through resorption to form an elongate, broadly triangular, pedicle track; pedicle track covered posteriorly by a concave plate and anteriorly by short "listrum-like" plate; tubular hollow spines of uniform size arranged in concentric rows close to valve margin; post larval shell bearing numerous subcircular dimples loosely arranged in concentric rows.

Etymology. *Orba* L., orphan, refers to the occurrence of this taxon after the supposed demise of the siphonotretids during the end-Ordovician extinction event; *spina* L., thorny, in reference to the post-larval shell ornament of tubular hollow spines.

Remarks. Features considered to be of generic significance among the siphonotretids include the nature of the pedicle foramen and tube, the pseudointerarea of both valves and the presence of tubular hollow spines (Holmer & Popov, 2000). Based on these features, *Orbaspina* n.gen. appears closest morphologically to those genera grouped together by Havlíček (1982) and Popov & Holmer (1994) in the subfamily Schizamboninae. The most characteristic feature of these siphonotretids is the large pedicle foramen that extends forward through resorption, forming an elongate triangular pedicle track that may be covered posteriorly by a plate. However, the dimpled post-larval shell of *Orbaspina* n.gen. is unknown in any previously described Cambrian or Ordovician siphonotretid. This feature is present on a number of post-Ordovician siphonotretids including, "*Siphonotreta*" *anglica* Morris (1849), and Siphonotretine sp. and Schizambonine sp. A Mergl (2001a,b). The short "listrum-like" plate anteriorly covering the pedicle track of *O. gelasinus* n.gen. and n.sp. (Fig. 6g) has not been previously documented among the siphonotretids.

Orbaspina gelasinus n.sp.

Figs. 5–7

"New genus A" Valentine, Brock & Molloy (2003): pl. 3, figs. 18–29.

Type material. HOLOTYPE: AMF120610 (Fig. 5a–g): dorsal valve from sample BM 14.85, *ranuliformis* Zone, Boree Creek Formation (Fig. 3). Figured PARATYPES: AMF122212 (Fig. 5h–k): dorsal valve from sample BM 14.85, *ranuliformis* Zone, Boree Creek Formation (Fig. 3); AMF120612 (Fig. 6a–d): ventral valve from sample BM 14.30, *ranuliformis* Zone, Boree Creek Formation (Fig. 3); AMF120613 (Fig. 6e, f): ventral valve from sample BM 14.30, *ranuliformis* Zone (Fig. 3); AMF122213 (Fig. 6g): ventral valve from sample BM 13.80, *ranuliformis* Zone (Fig. 3); AMF122214 (Fig. 6h): ventral valve from sample BM 9.90, *amorphognathoides* Zone (Fig. 3); AMF122215 (Fig. 6i): fragment from sample BM 9.30, *amorphognathoides* Zone (Fig. 3); AMF122216 (Fig. 7a–d): fragment from sample BM 13.80, *ranuliformis* Zone (Fig. 3); AMF122217 (Fig. 7e, f): fragment from sample BM 14.30, *ranuliformis* Zone (Fig. 3); AMF122218 (Fig. 7g): dorsal valve fragment from sample BM 11.20, *ranuliformis* Zone (Fig. 3); AMF122220 (Fig. 7i,j): dorsal valve fragment from sample BM 14.40, *ranuliformis* Zone (Fig. 3). Unfigured PARATYPES: 34 ventral valves, 101 dorsal valves and 140 fragments (Fig. 3).

Type locality and horizon. Massive red and grey lensoidal limestones at "Kalinga", along the BM section (samples BM 5.50 to BM 15.60) (Fig. 3) through the Boree Creek Formation, central-western New South Wales, Australia (Fig. 1).

Age. Early Silurian: late Llandovery (*amorphognathoides* Zone) to early Wenlock (*ranuliformis* Zone) (Bischoff, 1986; Cockle, 1999; Molloy, unpub. data).

Etymology. *Gelasinus* L., dimpled, in reference to the dimpled post-larval shell ornament.

Diagnosis. As for genus by monotypy.

Description. Ventral valve incompletely known, planar to weakly convex, ?subcircular in outline. Lateral margins evenly curved; posterior margin weakly angular. Maximum width at, or slightly anterior of, valve midlength. In lateral profile, valve highest around midlength. Larval shell subrectangular, smooth, averaging 65 µm in width and 30 µm in length, separated from post-larval shell by distinct change in elevation. Foramen keyhole-shaped, ?centrally located at anterior end of elongate triangular to subtriangular pedicle track. Pedicle track covered posteriorly by concave plate bearing numerous, closely spaced growth lamellae and anteriorly by very short, flat "listrum-like" plate. Post-larval shell ornament with low rounded concentric ridges, becoming stronger towards margins, spaced at intervals averaging 25 µm. Tubular hollow spines sparsely developed along tops of concentric ridges, projecting at low angle from valve surface, becoming more numerous towards valve margins.

Ventral valve interior with long, posteriorly convex, ridge-like pseudointerarea following line of posterior margin. Pseudointerarea extending up to 88% valve width. Propareas long, narrowly triangular, separated from central portion of pseudointerarea by long, anteriorly divergent,

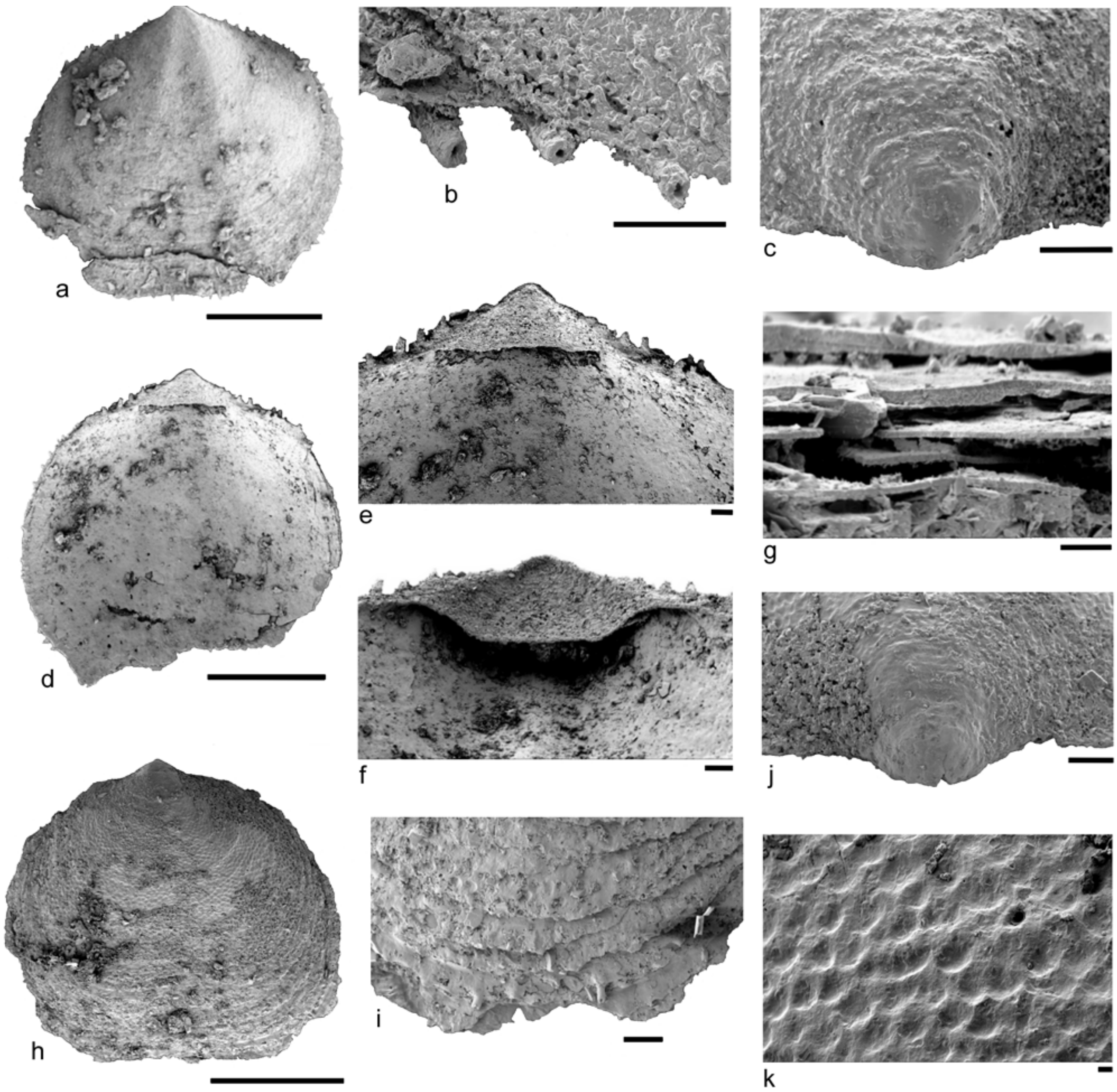

Fig. 5. *Orbaspina gelasinus* n.gen. and n.sp.: *a–g*, holotype AMF120610, dorsal valve from sample BM 14.85, external view (*a*), detail of spines along posterior margin (*b*), detail of larval shell (*c*), internal view (*d*), detail of pseudointerarea in plan view (*e*), and anterior view (*f*), detail of shell lamina along broken section of anterior margin (*g*); *h–k* paratype AMF122212, dorsal valve from sample BM 14.85: external view (*h*), detail of anterior margin showing frill-like nature of growth lamellae (*i*), deatil of larval shell (*j*), detail of post-larval shell dimpling (*k*). Scale bars = 1 mm (*a, d, h*); 100 µm (*b, c, e, f, j, i*); 10 µm (*g, k*).

uniformly narrow grooves that "articulate" with raised portion of propareas on dorsal valve pseudointerarea. Central portion of pseudointerarea strongly arcuate, lacking median plate. Transmedian and umbonal muscle scars subcircular, posterocentrally located. Other muscle scars not observed. Inner surface of plate covering pedicle track bearing shallow median groove that terminates at posterior margin of foramen around valve midlength. Foramen bounded anteriorly and laterally by low ridge. No pedicle tube observed. Vascular system not observed.

Dorsal valve convex, subcircular in outline with evenly rounded lateral margins and gently curved anterior and posterior margins. Maximum width at, or slightly anterior of, valve midlength. In lateral profile, valve highest at midlength, flattening anteriorly. Sulcate in anterior view, particularly in larger specimens. Larval shell smooth, subcircular to subrectangular, averaging 140 µm in length and 200 µm in width. Larval shell separated from post-larval shell by change in elevation and onset of post-larval shell ornament. Post-larval shell ornament of irregular concentric growth lamellae becoming better developed, occasionally frill-like, towards margins. Lamellae spaced at intervals of 50 to 250 µm, averaging 115 µm. Post-larval shell bearing numerous subcircular dimples loosely arranged in concentric rows, ranging from 20 to 40 µm, averaging 30 µm, in diameter. Short tubular hollow spines of uniform size, averaging 175 µm in length, projecting at low angle from valve surface. Spines developed on

Table 1. Average dimensions and ratios of ventral valves of *Orbaspina gelasinus* n.gen. and n.sp. Note that due to the incomplete nature of ventral valves recovered, it was not possible to obtain accurate measurements of length. The most complete ventral valve recovered (Fig. 6g) measures 2.34 mm in length. See text below for abbreviations.

	W	LI	ML	WI	FP	WP	LI/WI	WI/W
	Red Limestone							
N	1	5	8	5	5	7	5	
mean	1.29	0.17	0.05	0.84	0.57	0.45	23%	
SD		0.05	0.02	0.39	0.08	0.07	0.1	
minimum		0.1	0.03	0.38	0.45	0.35	13%	
maximum		0.23	0.7	1.4	0.67	0.54	26%	
	Grey Limestone							
N	6	9	20	11	18	12	9	3
mean	1.69	0.27	0.05	1.27	0.78	0.59	23%	72%
SD	0.36	0.06	0.02	0.3	0.18	0.23	0.05	0.13
minimum	1.3	0.18	0.01	0.85	0.45	0.4	18%	64%
maximum	2.05	0.38	0.09	1.8	1.1	1	35%	88%

lamellae, sparsely in older portions of valve, becoming more numerous and arranged in rows toward margins, including posterior margin. Spines bearing occasional, faintly developed, transverse grooves.

Dorsal valve interior with large triangular, orthocline to anacline, shelf-like pseudointerarea, extending up to 85% valve width. Median plate triangular, concave, flat-bottomed, bearing numerous, closely spaced growth lamellae. Propareas narrowly subtriangular, raised above pseudointerarea with rounded crests, also bearing numerous growth lamellae. Some specimens with two hollow spines projecting from underneath pseudointerarea into body cavity. Outside lateral and transmedian muscle scars located immediately anterior of pseudointerarea, weakly impressed, elongately suboval, extending to approximately 25% valve length. Muscle scars separated by very low, broadly rounded, indistinct median ridge, widening anteriorly, reflecting external sulcus. Median ridge occasionally forming a very short, but distinct ridge at posterior end of muscle field. Central muscle scars indistinct, located around valve midlength. Remaining muscle scars not observed. Vascular system not observed. Numerous holes, occasionally with a very low, narrow ridge around them, connect spines with valve interior, particularly around margins.

Measurements. Following the morphological measurements for organophosphatic brachiopods used by Popov & Holmer (1994: 35), the average dimensions and ratios of *Orbaspina gelasinus* n.gen. and n.sp. are given in Tables 1 and 2. All dimensions given are in millimetres. Abbreviations used are as follows: FP, point of origin of pedicle foramen from posterior margin; L, length; LI, maximum length of pseudointerarea; ML, median length of pseudointerarea; N, number of specimens measured; SD, standard deviation; W, width; WI, maximum width of pseudointerarea; WP, maximum width of pedicle track.

Discussion. Tubular hollow spines are the one diagnostic feature of the Siphonotretida uniting them as a monophyletic clade (Holmer & Popov, 2000). Although not numerous, particularly on the ventral valve, tubular hollow spines are clearly discernible on both valves of *O. gelasinus* n.gen. and n.sp. (Figs. 5a,b,h,i, 6a,b,i, 7a–f). The hollow internal spines projecting from underneath the pseudointerarea of the dorsal valve in some specimens (Fig. 7i,j) has not previously been observed in other siphonotretids. As they would have presumably been surrounded by soft tissue throughout life, their function remains unknown. Although not unique to the siphonotretids, all siphonotretids

Table 2. Average dimensions and ratios of dorsal valves of *Orbaspina gelasinus* n.gen. and n.sp.

	L	W	LI	ML	WI	L/W	LI/WI	LI/L	ML/L	WI/W
holotype	2.67	2.87	0.57	0.29	2.02	93%	28%	21%	11%	70%
	Red Limestone									
N	3	6	7	23	6	3	4	3	3	2
mean	0.89	1.32	0.32	0.28	0.96	87%	44%	34%	18%	57%
SD	0.22	0.38	0.13	0.15	0.37	0.05	0.35	0.14	0.06	0.34
minimum	0.74	0.86	0.15	0.1	0.46	83%	21%	19%	14%	34%
maximum	1.14	1.8	0.45	0.7	1.5	93%	96%	45%	25%	81%
	Grey Limestone									
N	14	16	16	61	15	12	15	10	13	22
mean	2.27	2.83	0.78	0.44	1.88	93%	36%	32%	18%	66%
SD	0.51	0.48	0.44	0.11	0.49	0.15	0.06	0.16	0.06	0.12
minimum	0.9	2.23	0.4	0.22	1.14	75%	27%	17%	10%	46%
maximum	3.04	4.02	2.23	0.8	2.83	121%	47%	73%	33%	85%

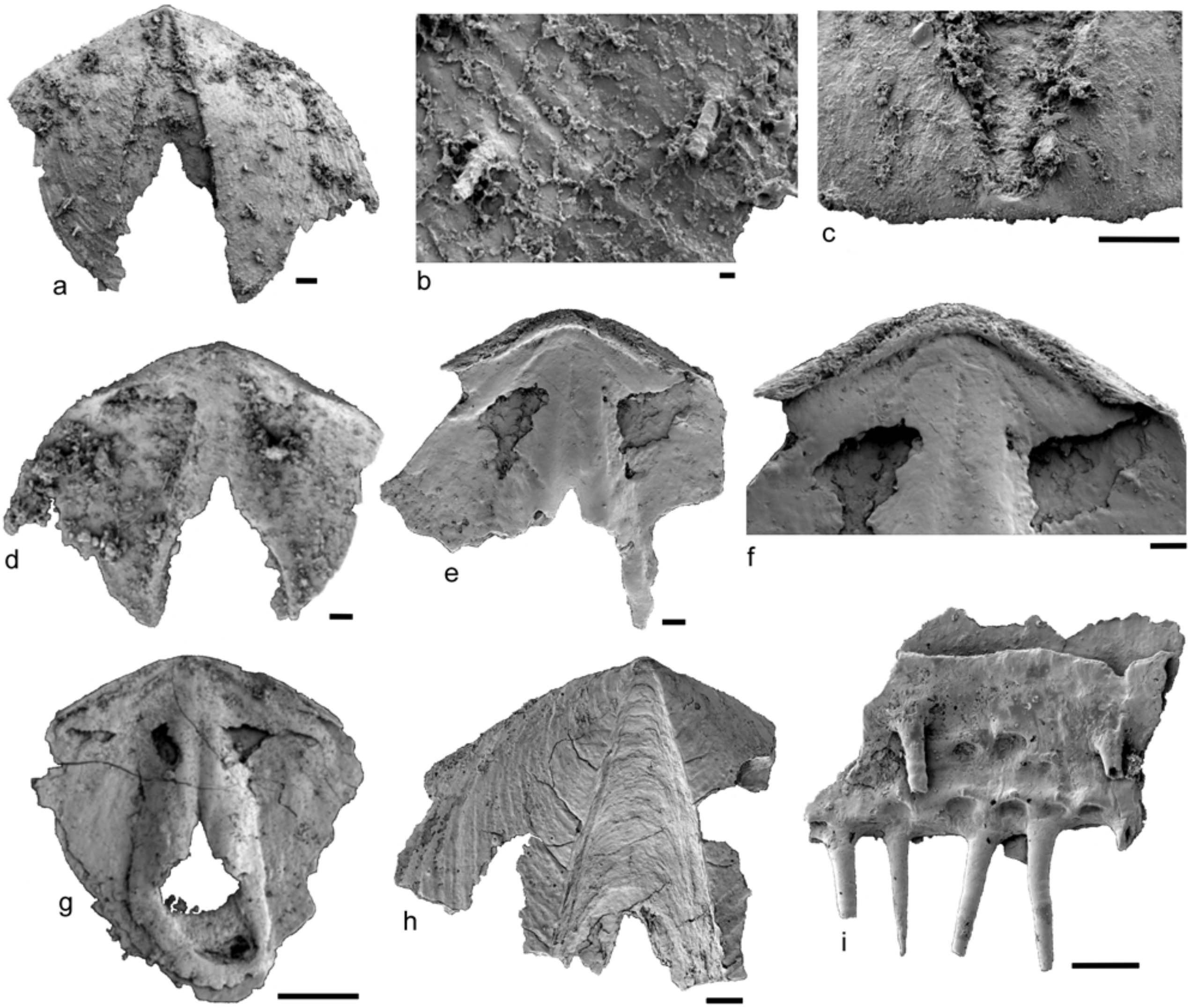

Fig. 6. *Orbaspina gelasinus* n.gen. and n.sp.: *a–d*, paratype AMF120612, ventral valve from sample BM 14.30, external view (*a*), detail of spines on anterior slope (*b*), detail of larval shell (*c*), internal view (*d*); *e, f*, paratype AMF120613, ventral valve from sample BM 14.30, internal view (*e*), detail of pseudointerarea (*f*); *g*, paratype AMF122213, ventral valve from sample BM 13.80, internal view, note the "listrum-like" plate covering the anterior portion of the pedicle track as indicated by arrow; *h*, paratype AMF122214, ventral valve from sample BM 9.90, external view showing common state of presentation of recovered ventral valves; *i*, paratype AMF122215, fragment from sample BM 9.30, external view. Scale bars = 500 µm (*g*); 100 µm (*a, c–f, h, i*); 10 µm (*b*).

possesses a smooth, unpitted larval shell (Holmer & Popov, 2000), a feature also present in *O. gelasinus* n.gen. and n.sp. (Figs. 5a,j, 6c). The shell structure of *O. gelasinus* n.gen. and n.sp. is consistent with that described by Biernat & Williams (1970) and Ushatinskaya *et al*. (1988) for other siphonotretids (Fig. 5g).

Recently, Mergl (2001a,b) documented four indeterminate post-Ordovician siphonotretids from central Bohemia, two of which were described as possessing a pitted post larval shell. Siphonotretine sp., represented by a single fragment from the Ludlow Kopanina Formation of Řeporyje, has deep, regular, closely spaced pits, somewhat similar to the pitting found on acrotretid larval shells. The spines of this species are also more numerous and erect than in *O. gelasinus* n.gen. and n.sp. The second taxon, Schizambonine sp. A, is represented by a dorsal valve fragment recovered from the Pragian Dvorce-Prokop Limestone of Klukovice. It possesses minute, scattered spines, somewhat similar to those observed on the pedicle valve of *O. gelasinus* n.gen. and n.sp. The post-larval shell pitting, however, is finer and more regular than the dimpling observed in *O. gelasinus* n.gen. and n.sp. Little is known about the internal features of these two species.

"*Siphonotreta*" *anglica* (Morris), from the Wenlock Coalbrookdale Formation of Dudley, England, was

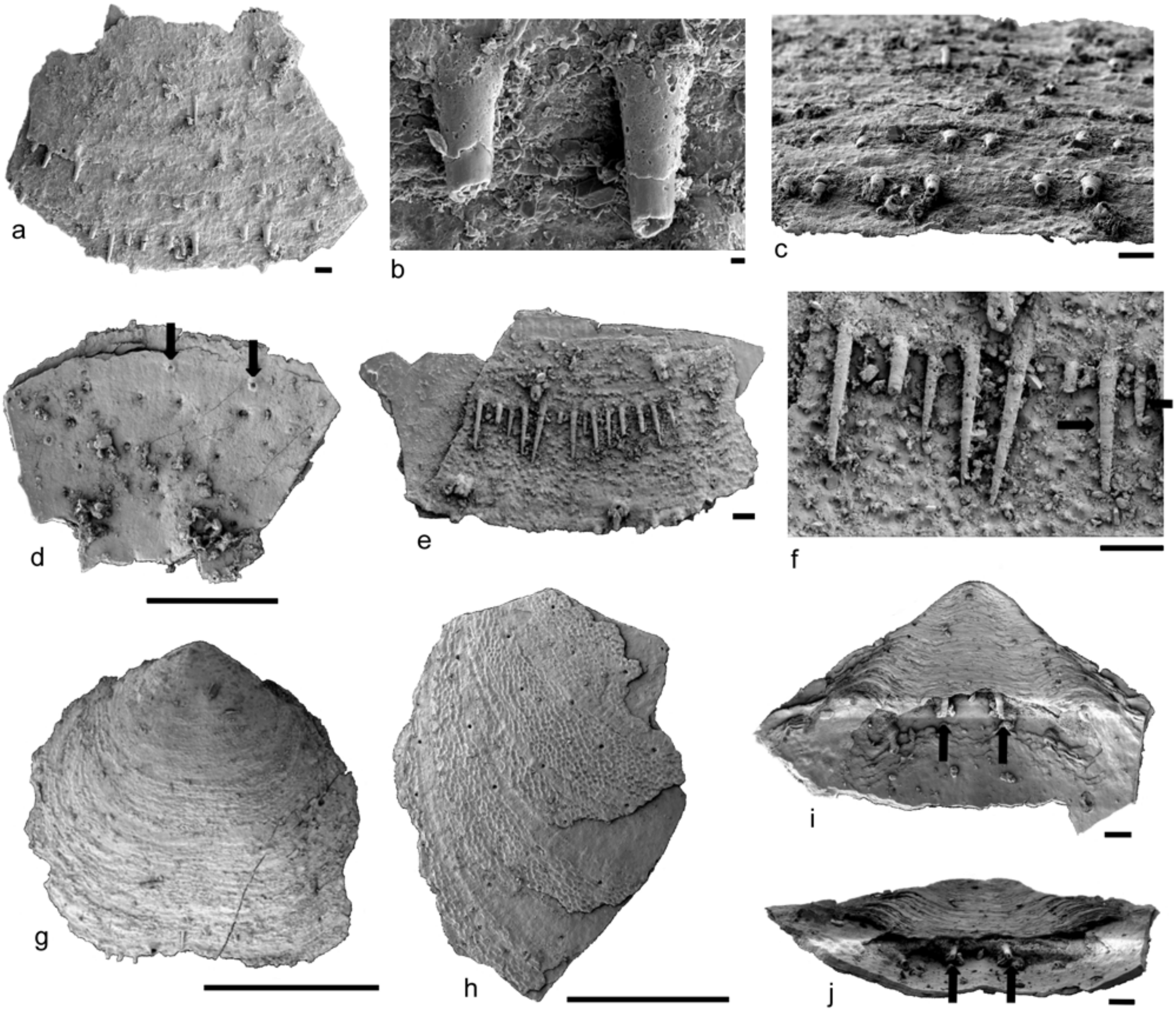

Fig. 7. *Orbaspina gelasinus* n.gen. and n.sp.; *a–d*, paratype AMF122216, fragment from sample BM 13.80, external view (*a*), detail of spines (*b*), anterior view (*c*), interior view with spine openings on internal surface indicated by arrows (*d*); *e*, *f*, paratype AMF122217, fragment from sample BM 14.30, external view (*e*), detail of spines with weak transverse grooves on spines indicated by arrows (*f*); *g*, paratype AMF122218, dorsal valve from sample BM 15.40, external view; *h*, paratype AMF122219, dorsal valve fragment from sample BM 11.20, external view showing well developed post-larval shell dimpling; *i*, *j*, paratype AMF122220, fragment of dorsal valve pseudointerarea from sample BM 14.40, with two spines projecting from underneath the pseudointerea as indicated by arrows, in plan (*i*) and anterior views (*j*). Scale bars = 1 mm (*a, d, g, h*); 100 µm (*c, e, f, i, j*); 10 µm (*b*).

described by Morris (1849: 321) as possessing spines which were "…regularly and transversely sulcated or centrated, giving the spines a beaded or jointed appearance"; a feature also noted by Davidson (1866). Some spines of *O. gelasinus* n.gen. and n.sp. bear the occasional, faintly developed, transverse groove (Fig. 7f), whereas no trace of similar grooving can be observed on any of the spines in Mergl's (2001a,b) material. "*Siphonotreta*" *anglica* also has more numerous spines and a more regular post-larval shell pitting than *O. gelasinus* n.gen. and n.sp. A comparison of internal features is not possible as these have not been described in "*Siphonotreta*" *anglica*.

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