First discovery of Early Palaeozoic *Bathysiphon* (Foraminifera) – test structure and habitat of a 'living fossil'

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Abstract – The giant, agglutinated foraminiferan *Bathysiphon* Sars, previously Triassic–Recent, occurs in much older sedimentary rock (Early Ordovician, late early Tremadocian) of Avalonia. The genus extends back to *c*. 485 Ma based on its discovery in platform mudstone of the Chesley Drive Group in Cape Breton Island, Nova Scotia. Elongate (up to 60 mm), epibenthic *Bathysiphon* tubes occur in wave-rippled, green-grey mudstone with a low diversity, probably dysoxic fauna. The mudstone is coeval with and lithologically similar to the Shineton Formation in Shropshire and the Welsh Borderlands. Scanning microscopy of the *Bathysiphon* walls shows imbricated mica grains that parallel the long axis of the tests. The lumen has a mélange of packed sediment grains, some of which are spherical structures of siliciclastic mud studded with tetrahedral pyrite crystals. A felt-like, agglutinated test, a lumen packed with spherical structures (probable stercomata) and the domal ends of some specimens are consistent with modern *Bathysiphon*. This report is the first time that cytoplasmic activity and stercomata formation have been used to refer fossil protists to a modern group. *Bathysiphon* differs from the Cambrian foraminiferan *Platysolenites* Pander, which has an open lumen without stercomata, but support a comparable, sediment deposit-feeding niche. *Bathysiphon* is truly a 'living fossil', with a mode of test construction, cytoplasmic activity that formed stercomata and a niche unchanged for almost 500 million years. Foraminiferans have not been found prior to the Cambrian Period, and the Early Cambrian appearance of agglutinated foraminiferans is part of the radiation of Phanerozoic communities.

Keywords: *Bathysiphon*, Foraminifera, stercomata, Lower Ordovician, Tremadocian, Avalon, Nova Scotia, Cape Breton Island.

1. Introduction

The Cambrian Period and Cambrian Evolutionary Radiation were among the most important intervals in the history of life because they featured the appearance of all living skeletalized metazoan phyla (e.g. Landing, English & Keppie, 2010; Maloof *et al.* 2010). A number of protistan groups were also likely part of the Cambrian Evolutionary Radiation. For example, no unquestionable record exists of Foraminifera prior to the Cambrian Period, but with their appearance as fossils in the Cambrian, calcareous and agglutinated Foraminifera become the major Phanerozoic group of skeletalized protists. In this study, we greatly extend the stratigraphic range of the agglutinated foraminiferan *Bathysiphon* M. Sars (*in* G. O. Sars, 1872) back from the Mesozoic, and demonstrate that the test structure, habitat and cytoplasmic activity of this extant form were established by early Early Ordovician (late early Tremadocian) time, and were likely established in the Cambrian Period.

2. *Bathysiphon* and *Platysolenites*

The oldest organism traditionally referred to the Foraminifera is *Platysolenites* Pander, 1851: a form

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known from large (up to 10 cm long), very gently tapering, straight to gently curved, somewhat flexible, tube-like tests with an agglutinated wall and a hollow lumen. The initial part of the essentially rectilinear test has an amphora-shaped proloculus (McIlroy, Green & Brasier, 2001; Streng, Babcock & Hollingsworth, 2005). The subsequent part of the test may be hooked or spiralled (e.g. '*Spirosolenites*' Glaessner *in* Føyn & Glaessner, 1979) or more frequently relatively straight (Lipps & Rozanov, 1996; compare McIlroy, Green & Brasier, 2001, who regard *Spirosolenites* as a distinct ammodiscid-like foraminiferan genus). Horizontally embedded *Platysolenites* tests are frequently compacted and have weakly to strongly flattened cross-sections or are crushed and show a longitudinal fracture resulting from tensile forces (e.g. Lipps & Rozanov, 1996). This taphonomic history reflects the fact that the lumen was hollow (Loeblich & Tappan, 1987) and typically not filled with sediment prior to burial. Thus, the test was not strong enough to resist flattening or fracturing with sediment compaction. McIlroy, Green & Brasier (2001) also reported specimens in which the lumen is filled with structureless clay, presumably as a post-mortem infill.

The tests of *Platysolenites* could be the agglutinated tubes of a polychaete (Eichwald, 1860; Vachard, Pille & Gaillot, 2010, p. 211 and references therein).

However, most authors have accepted, with greater or lesser hesitation, the assignment of the type species *P. antiquissimus* Eichwald, 1860, from its topotype locality in the lowest Cambrian 'Blue Clay' of the eastern Baltic to the Foraminifera. The presence of agglutinated walls that seem to show a bimodal grain size or radial coarsening and also show the repair of longitudinal fractures outside the test wall (McIlroy, Green & Brasier, 2001) provide strong arguments that *Platysolenites* was a foraminiferan and not a metazoan.

A number of reports have noted the resemblance of *Platysolenites* to modern *Bathysiphon* M. Sars *in* G. O. Sars (1872) (e.g. Loeblich & Tappan, 1964), and have even synonymized the two genera (e.g. Glaessner, 1978). Lipps (1992*a,b*) and Lipps & Rozanov (1996) emphasized the morphologic similarity between Recent specimens of the type species *B. filiformis* M. Sars *in* G. O. Sars (1872) and *Platysolenites* by noting that both genera have agglutinated, elongate tubes that were fragile, flexible and may have transverse rings. Lipps & Rozanov (1996) concluded that both genera are foraminiferans that are so similar morphologically that they noted a potential synonymy, which McIlroy, Green & Brasier (2001, p. 22) reported as an actual synonymization by Lipps & Rozanov (1996).

However, morphological differences exist between the two genera. McIlroy, Green & Brasier (2001) noted the absence of a proloculus in *Bathysiphon*, and proposed that *Bathysiphon* was derived from *Platysolenites* by the loss of the 'larval' proloculus. As a result, the apical ends of *Bathysiphon* tests are sharply pointed (e.g. Małecki, 1973; McIlroy, Green & Brasier, 2001).

A more important difference between the two genera was noted by Lipps & Rozanov (1996, p. 683), who noted that *Bathysiphon* differs 'from *Platysolenites* in commonly having its tube filled at one end with debris. The debris is sealed off from the rest of the test by a discoidal plug or by partitions'. The nature of this 'debris' is critical to the mode of tube construction, and this infill provides a character vital to the definition of *Bathysiphon* (Loeblich & Tappan, 1964, p. 186, 1987) that is not present in *Platysolenites*.

Bathysiphon was long reported to have a Triassic–Recent range (Loeblich & Tappan, 1987), a difference in stratigraphic range that might seem to emphasize its distinctiveness from the Cambrian *Platysolenites* (Lipps & Rozanov, 1996). However, we have now found undoubted specimens of *Bathysiphon* in the Lower Ordovician.

3. Geological setting

A poorly exposed, mudstone-dominated, Upper Cambrian–Lower Ordovician succession forms the axis of a NE-striking syncline that defines the McLeod Brook valley in southern Cape Breton Island, eastern Nova Scotia, Canada. Locality maps of the field area are in Bell & Gorenson (1938), Weeks (1947),

Hutchinson (1952) and Barr, White & McDonald (1992), and measured sections are in Landing & Fortey (2011). These rocks were divided by Hutchinson (1952) into chronostratigraphically, not lithologically, defined formations. These included an Upper Cambrian 'MacNeil Formation' and a Lower Ordovician 'MacLeod Brook Formation', which were said to differ in that calcareous nodules were present in the Upper Cambrian but not in the Lower Ordovician (Hutchinson, 1952, p. 29).

No lithologic difference was observed between these two 'formations' in the course of our field work in Cape Breton Island, and the supposedly nodule-free 'MacLeod Brook Formation' yielded abundant conodonts and chitinozoans from its calcareous nodules (Landing & Fortey, 2011). Thus, the entire 'MacNeil–MacLeod Brook' interval is now brought to the Chesley Drive Group (Landing, 1996; Landing & Fortey, 2011; Westrop, Adrain & Landing, 2011). The Chesley Drive Group is the youngest part of the terminal Ediacaran–Ordovician cover sequence of the Avalonian palaeocontinent in Nova Scotia (Landing, 1996).

Earlier work on the Lower Ordovician of Cape Breton Island included descriptions of low diversity benthic macrofaunas (i.e. trilobites, brachiopods, dendroid graptolites) (Matthew, 1903; Walcott, 1912; Bell & Gorenson, 1938; Hutchinson, 1952; Owens *et al*. 1982). More recent work included determination of a 483 ± 1 Ma U–Pb zircon age on a thin K-bentonite in the upper Tremadocian (Landing *et al*. 1997), and a description of the faunas (brachiopods, chitinozoans, conodonts, foraminiferans) and palaeoenvironments of the Lower Ordovician (Tremadocian) of McLeod Brook (Landing & Fortey, 2011).

The Tremadocian of McLeod Brook includes a lower dysoxic, green-grey mudstone with small calcareous nodules and wave-rippled surfaces and an upper anoxic/highly dysoxic black mudstone with methanogenic carbonate nodules (Landing & Fortey, 2011). These two lithologic divisions are strikingly similar to the upper lower Tremadocian Shineton Formation and upper Tremadocian Habberley Formation, respectively, in Shropshire and the Welsh Borderlands. The Shineton and Habberley formations reflect a progressive marine deepening through Tremadocian time, followed by a shallowing at the end of the Tremadocian (e.g. Fortey & Owens, 1991; Fortey *et al*. 2000). Such similarities in stratigraphic succession from coastal New England (Rhode Island, Massachusetts), to Maritime Canada (New Brunswick, northern mainland Nova Scotia, Cape Breton Island), eastern Newfoundland, and Wales and central England have been used as a basis to re-create the cool-water, siliciclastic platform of the terminal Cryogenian–Ordovician Avalonian continent (e.g. Landing, 1996, 2004, 2005).

The Avalon palaeocontinent is now a terrane in the coastal NE Appalachians, SE Ireland (Wexford terrane), southern Britain and parts of western Europe (e.g. Brabant massif of central Belgium and anticlinoria to the east in Belgium and Germany). The Avalon

Figure 1. *Bathysiphon* specimens from the upper Chesley Drive Group (lower Lower Ordovician, upper lower Tremadocian), Cape Breton Island; all hypotypes from sample McL-1-7.0 (Landing & Fortey, 2011). (a) *Bathysiphon* sp., wave-oriented specimens NBMG 15190 and NBMG 15191, upper and lower, respectively, on mudstone bedding surface with numerous valves of *Eurytreta sabrinae* (Callaway, 1877) (scale bar 1 mm); (b) locally exfoliated specimen showing stercomata fill (visible at higher magnification) at upper right side of figure (scale bar 5 mm).

terrane resulted from collisions of the Early Palaeozoic Avalon continent with Laurentia ('ancestral North America') and the Baltica palaeocontinent during the Middle Palaeozoic Caledonian–Acadian orogeny (e.g. Landing, 1996, 2005).

4. Localities and age

Specimens of *Bathysiphon* (identification discussed in Section 5 below) were found only in the green-grey mudstone-dominated interval that forms the upper lower Tremadocian in the MacLeod Brook valley. The foraminiferans were found at two sections (localities McL-1 and McL-2) along MacLeod Brook. These two cut banks are downstream from where the Bourinot Road (a dirt track) crosses McLeod Brook (see Weeks, 1947 and Hutchinson, 1952 for detailed maps). A few, largely disarticulated specimens of the trilobites *Asaphellus homfrayi* (Salter, 1866) and *Conophrys salopiensis* (Callaway, 1877) occur at McL-1 and McL-2 (Hutchinson, 1952; Landing & Fortey, 2011) and establish a late early Tremadocian age. By the Webby *et al*. (2004) time scale, these localities have an age of *c*. 485 Ma.

Locality McL-1, a low cliff section (strike N 5° E, dip 70° E) on the north side of the brook and *c*. 315 m downstream from the ford, is Hutchinson's (1952) locality 18618 that he described as a fifth of a mile (*c*. 325 m) downstream from the Bourinot Road

crossing. *Bathysiphon* (28 specimens collected) occurs on a wave-rippled surface with abundant, disarticulated valves of the phosphatic brachiopod *Eurytreta sabrinae* (Callaway, 1877) (Fig. 1a). This surface is 7.0 m above the base of the section (Landing & Fortey, 2011, table 1).

Locality McL-2 (strike N 30° E, vertical dip) is *c*. 75 m further downstream from McL-1 and on the northwest bank of the brook. McL-2 is Hutchinson's (1952) locality 18657, and is a quarter of a mile (*c*. 402 m) downstream from the ford. Two *Bathysiphon* specimens were recovered 5.7 m above the base of the section.

5. Are these *Bathysiphon* specimens?

5.a. Scanning electron microscopy and external and internal morphology

Several surfaces at localities McL-1 and McL-2 have conspicuous, very elongate (up to 60 mm), essentially non-tapering, whitish-grey, rod-like structures that are about 1.0 mm in diameter. These rod-like structures are generally straight, although several specimens show a very gentle curvature.

These rod-like structures are bounded by a medium grey border that is significantly darker that the greenish grey colour of the rock (Fig. 1a). Scanning electron microscopy (SEM) of the central rod-like structures showed that they are composed of a uniformly
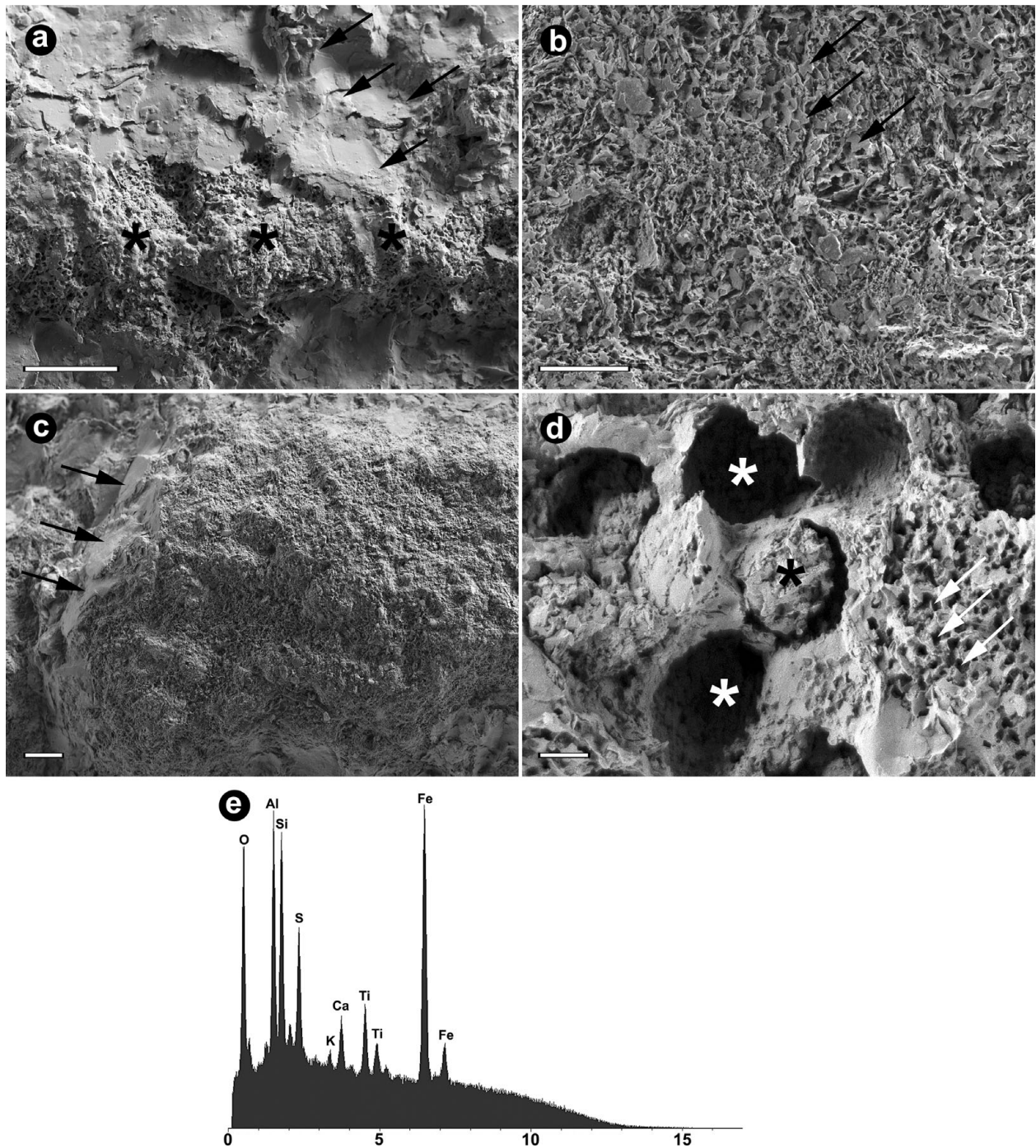
Figure 2. Well-preserved specimens of lower Lower Ordovician (upper lower Tremadocian) *Bathysiphon*, sample McL-1-7.0 from Cape Breton Island, Nova Scotia, viewed by SEM. (a) Overview of a tangentially-fractured specimen shows imbricated, flake-like, micaceous grains comprising the test wall (black arrows) and finer matrix filling the test lumen (black stars) (scale bar 5 μm); (b) more centrally, the lumen matrix is seen as a mélange of fine, often flake-like grains (e.g. black arrows) (scale bar 5 μm); (c) terminal portion of NBMG 15747 appears capped (black arrows) with imbricated micaceous grains (scale bar 25 μm); (d) stercomata-like spheroids (black star) and complementary depressions (white stars) that apparently result from the loss of these structures during specimen handling, are seen embedded in the lumen matrix (scale bar 3 μm); (e) X-ray spectrum of the stercomata-like spheroid marked by black star in (d) reveals peaks characteristic of aluminium silicate-based minerals and pyrite; this spectrum is comparable to and representative of 100 X-ray analyses done on 15 stercomata-like aggregates from the Early Ordovician specimens.

fine-grained material (Fig. 1b). Higher resolution SEM shows that the darker grey border marginal to the 'rods' is composed of fine-grained siliciclastic sediments that show a felt-like fabric of imbricated, relatively flat, micrometre-scale mica grains aligned roughly parallel to the axis of the 'rods' (Fig. 2a). The terminal portion

of one specimen appears to be 'capped', and the tube possibly repaired, by these grains (Fig. 2c). Although *Bathysiphon* test walls can be composed of almost any type of detrital grain, ranging from quartz and feldspar fragments to sponge spicules, the Cape Breton specimens resemble, for example, modern specimens
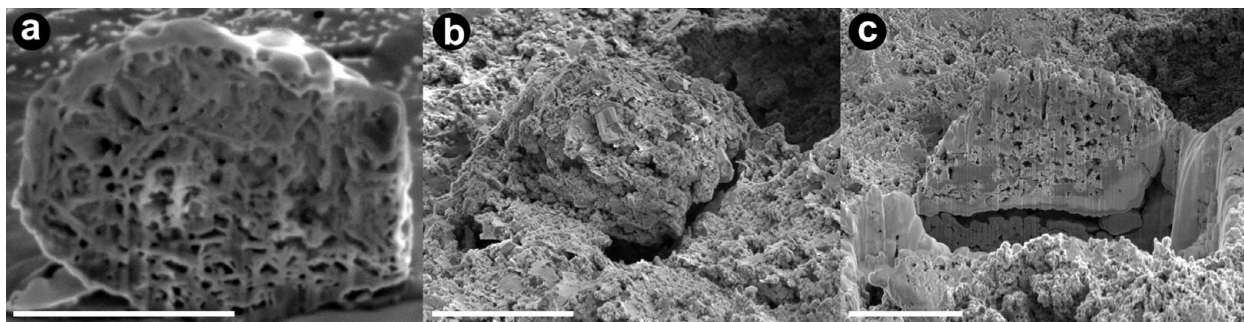
Figure 3. FIB-milled stercomata viewed by SEM. (a) an aldehyde-fixed, critical-point-dried and Pt-coated modern *Bathysiphon* (scale bar 2 μm); (b) spheroidal structure (putative stercome) from a Cape Breton fossil specimen (NBMG 15748) before and (c) after cutting (scale bars are 5 μm). Interior aspects of cut specimens appear porous and 'moth-eaten' because of the spaces between intersecting grains within the aggregates; similar 'curtaining' artefacts (longitudinal streaks) result from the composite nature of these grains.

of *B. argenteus* Heron-Allen & Earland, 1913 that are known to selectively pick up mica flakes to construct their test (Cole & Valentine, 2006).

The central 'rods' of the remains are composed of a tightly packed mélange of grains (Fig. 2a–d). These grains include a background of small siliceous sediment particles which, in some specimens, are punctuated with relatively uniformly sized, spherical structures that are studded with small, protruding tetrahedral crystals of pyrite (Fig. 2d). These spherical structures, often with the form of oblate or ellipsoid spheroids, have an aspect ratio of 0.76, with their long axis ranging from 6.5 μm to 13 μm (mean = 9.2 μm; n = 106). Each spheroid consists of an aggregate of siliceous, flake-like sediment grains and pyrite microcrystals. Qualitative X-ray microanalysis of the sediment at approximately 100 points in 15 of the spherical grains was completed. This X-ray analysis shows similarity across all of the grains with peaks for aluminium silicate and minor peaks for potassium, magnesium and titanium, as well as the iron and sulphur of pyrite (Fig. 2e).

These spherical structures seem comparable in size and composition to stercomata, which are essentially cytoplasmic waste pellets that reflect sediment-eating by agglutinated Foraminifera (e.g. Cartwright, Gooday & Jones, 1989) and modern xenophytophore protozoans (e.g. Antcliffe, Gooday & Brasier, 2011, p. 1164). In support of this assessment, similar X-ray spectra (but lacking the iron and sulphur peaks of pyrite) were obtained from stercomata of modern specimens of *Bathysiphon capillare* (data not shown; Gooday, Pond & Bowser, 2002).

As a further comparison, we applied focused ion-beam (FIB) milling coupled with SEM (see Fliegel *et al.* 2010) to cut and examine the interior structure of stercomata from modern *B. capillare* and the spheroids found in MacLeod Brook fossils. Comparison of their interior aspects revealed remarkably similar porous, 'moth-eaten' appearances (Fig. 3). Both the modern stercomata and the Ordovician spheroids are clearly dominantly aggregates of siliceous flakes, with scattered, unweathered pyrite tetrahedrons in the Ordovician specimens.

5.b. Taxonomy

Our scanning microscopy analysis of the MacLeod Brook fossils is fully compatible with their interpretation as the tests of a giant agglutinated foraminiferan – specifically the tests of *Bathysiphon*. Direct comparisons can be made with Gooday, Pond & Bowser's (2002) field and scanning microscopy examinations of the modern species *B. capillare* de Folin, 1886, and with Gooday's (1988) review of a number of Recent species from the bathyal northeastern Atlantic Ocean.

The surface texture of the tube walls of *Bathysiphon* are highly variable, and range from smooth to rough, depending on the type and coarseness of sediment used to build the walls and the arrangement of the grains (e.g. Małecki, 1973; Gooday, 1988). The test walls of Recent *Bathysiphon capillare*, *B. flavidus* de Folin, 1886 and *B. rufus* de Folin, 1886 are composed of imbricated plate-like minerals that make the test surface shiny (Gooday, 1988; Gooday, Pond & Bowser, 2002, fig. 1A, B). Unfortunately, the MacLeod Brook specimens are tightly bound to their grey-green mudstone matrix, and the specimens typically do not break out of the rock to expose the surface of the agglutinated test. Rather, the specimens fracture through the agglutinated test wall, which rarely presents a positive relief relative to the fracture surface. However, high magnification scanning microscopy shows that the test walls are composed of a felt-like layering of flat silicate grains as in *B. capillare* and some other modern *Bathysiphon* species (Fig. 2a).

As in modern *Bathysiphon capillare*, the lumens of the agglutinated tests from the Lower Ordovician are packed with an association of sediment grains and apparent stercomata. As stercomata are pellets of waste material that reflect sediment ingestion, both the presence of the stercomata and a probable detritivore niche are consistent with assignment of these elongate tests to *Bathysiphon* (e.g. Gooday, Pond & Bowser, 2000). The presence of the well-developed, fine-grained pyrite in the stercomata may be explained by the fact that the lumen of the *Bathysiphon* test is occupied by cytoplasm. If the Ordovician specimens were buried alive and died in the sediment (discussed in Section 6.c below), the decay of the cytoplasm and any

other organic material would promote the synthesis of pyrite in the enclosed chamber of the stercomata-filled lumen (e.g. Landing, Geyer & Bartowski, 2002).

A very few specimens from the Tremadocian of Cape Breton Island have rounded, domal ends that are also composed of a felt-like layer of platy minerals (Fig. 2c). This feature is also consistent with assignment of the Ordovician forms to *Bathysiphon*. Gooday (1988) showed that five of six modern *Bathysiphon* species that he re-described either had domal apertural ends or domed internal partitions composed of agglutinated sediment.

A number of *Bathysiphon* species have been named. However, distinguishing taxa in forms with few but individually variable characters (i.e. diameter, length, apical angle, relative curvature, presence or absence of transverse ridges) is difficult to justify. Thus, the oldest known *Bathysiphon* specimens described herein from the Lower Ordovician are left in open nomenclature as *Bathysiphon* sp.

6. Habitat of Ordovician *Bathysiphon* from Cape Breton Island

6.a. Ambient energy of *Bathysiphon*–brachiopod assemblages

Localities McL-1 and McL-2 have a similar lithology and fossils. The greenish grey mudstone has thin-bedded, fine-grained quartz arenite lenses in small ripples (< 5 mm high) with the bifurcating crests of wave ripples. Their low height and the fine-grained sand composition reflect low energy levels at the sediment–water interface, so gentle that long specimens (up to 60 mm) of the roughly N–S-oriented, fragile, agglutinated foraminiferan *Bathysiphon* are preserved and not fragmented. Disarticulated phosphatic brachiopod shells (visceral side generally down) are associated (Fig. 1a). The roughly N–S orientation of the *Bathysiphon* tubes on the rippled surfaces suggests an E–W sense of wave progression, in terms of modern coordinates. The length and mere presence of the fragile *Bathysiphon* specimens suggest that these remains are essentially *in situ*, and were not significantly transported (see *Bathysiphon* 'shell beds' of Miller, 2008).

6.b. Bottom-water oxygenation

Bathysiphon ranges from well oxygenated to dysoxic conditions on modern sea floors (Gooday, Pond & Bowser, 2002). The sparse, shallow burrowing of the laminated McLeod Brook mudstones, with burrows limited to shallow, small *Planolites* Nicholson, 1873 (Landing & Fortey, 2011), is consistent with relatively low oxygen conditions (e.g. Sageman, Wignall & Kauffman, 1991). Benthic skeletalized organisms, which characteristically require higher levels of oxygenation, are limited to a few horizons with abundant, disarticulated, phosphatic brachiopod valves (*Schizam-*

bon? *priscus* (Matthew, 1901), *Eurytreta sabrinae* (Callaway, 1877), *Linguella nicholsoni* Callaway, 1877) and a few, largely disarticulated specimens of the trilobites *Asaphellus homfrayi* (Salter, 1866) and *Conophrys salopiensis* (Callaway, 1877) (Hutchinson, 1952, table 1).

6.c. Autecology and taphonomy of Ordovician *Bathysiphon*

An interpretation of the habitat of the Ordovician *Bathysiphon*–brachiopod associations requires a few considerations. *Bathysiphon* has a highly variable autecology in the Mesozoic–Recent. Individuals may have a more or less horizontal orientation within the sediment (e.g. Gooday, Pond & Bowser, 2002) that is parallel to bottom currents (Saja, Pfefferkorn & Phillips, 2009). However, live specimens can be vertical and project above the sediment–water interface (Miller, 1987, 2008). The genus is typically considered a deep marine form (e.g. Gooday, Pond & Bowser, 2002; Miller, 2005), but occurs in marginal marine/lagoonal habitats in the Mesozoic (Johnson, Kulver & Kamola, 2005).

As discussed in Section 6.a above, the orientation of the Ordovician specimens and occurrence with disarticulated, but not fragmented, phosphatic brachiopod valves in wave-ripple troughs (Landing & Fortey, 2011) suggest an *in situ*, quite shallow-water occurrence by comparison with Recent *Bathysiphon* species. The wave-determined orientation indicates that the Ordovician *Bathysiphon* individuals lived at the sediment–water interface, although it is possible that they were subsequently buried and lived at a shallow depth within the sediment. The presence of a test with a cap-like end composed of imbricated mica grains suggests repair of a test potentially broken by wave activity (Fig. 2c). Gooday (1988) noted a similar domed end of the tube in Recent *Bathysiphon* tubes, which may also represent tube repair.

As large *Bathysiphon* individuals are essentially immobile (Gooday, Pond & Bowser, 2002), further burial, perhaps by wave-deposited sediment, would kill these large individuals by stranding them in sediment below the interface with oxygenated sediment. As evidence of dysoxic water at the sediment–water interface exists at localities McL-1 and McL-2 (discussed in Section 6.b above), the pO_2 level probably fell quickly in these platform sediments. Burial and death with the decay of cytoplasm of the *Bathysiphon* individuals may have been responsible for formation of pyrite tetrahedrons in the stercomata (discussed in Section 5.b above).

Although a relatively small number of *Bathysiphon* specimens (30) were collected from Cape Breton Island (Landing & Fortey, 2011, table 1), our SEM examination of a number of broken tests shows that they range from having the lumen filled with a fine-grained matrix (Fig. 2a, b), to a mixture of matrix and stercomata, to spheroidal stercomata (Fig. 2d) that show the presence of pyrite (Fig. 2e). This range of lumen fills suggests that the Cape Breton Island *Bathysiphon*

specimens range from buried dead individuals (lumens emptied and then filled with fine matrix) to buried living individuals (with lumens filled with stercomata and pyrite growth in the stercomata).

7. Discussion

The stratigraphic range of the agglutinated, giant foraminiferan *Bathysiphon* is now extended well down from the Triassic and, is essentially comparable to, but the converse of, finding living specimens of groups once thought long extinct (e.g. *Nautilus* and coelacanths). The discovery of Lower Ordovician *Bathysiphon* specimens in shallow-water, siliciclastic platform specimens from the Avalon palaeocontinent in Cape Breton Island show that characteristic morphologic and cytoplasmic features of the genus were established at least by late early Tremadocian time (*c*. 485 Ma). These features include an agglutinated, very long, essentially untapered test with a wall composed of a felt-like layering of flat siliciclastic grains and a lumen that may be packed with sediment grains and stercomata formed by cytoplasmic activity. The presence of stercomata demonstrates that the consumption of sediment, probably along with other micro-organic debris and micro-organisms, has been important in the autecology of the genus since Early Ordovician time. The stercomata that fill the lumen of these tube-like Ordovician specimens emphasize their assignment to *Bathysiphon*.

Perhaps more importantly, the stercomata show that cytoplasmic activity that is responsible for stercomata formation in foraminiferans and *Gromia* Dujardin, 1835, a member of a possible sister group (Adl *et al*. 2005; Gooday & Bowser, 2005), was well established at least by early Early Ordovician time, and can be used as a taxonomic character to recognize these protistans. However, stercomata, along with the absence of a proloculus, further suggest that there is no phylogenetic relationship to *Platysolenites*, which has an empty lumen and a proloculus.

Bathysiphon in the early Early Ordovician is younger than the oldest undoubted foraminiferans, which are agglutinated, and include the early Early Cambrian *Platysolenites* and late Early Cambrian specimens from west Africa (Culver, 1991, 1994). Scott, Medioli & Braund (2006) reported younger agglutinated foraminiferans from the Middle Cambrian part of the Meguma Group in south-coastal Nova Scotia, and compared them to modern marsh foraminiferans. We regard the identifications of these Nova Scotia specimens as Middle Cambrian foraminiferans as highly dubious. Indeed, Scott, Medioli & Braund's (2006) Site 1 specimens were recovered from a thin lens of soft sediment, and their organic material dissolved under the action of hydrogen peroxide. The available evidence suggests that the Site 1 specimens are relatively modern agglutinated foraminiferans that occur in a shallow fissure fill packed with Pleistocene or Holocene sediment. The organic material of the specimens from Site 1 has not been turned to graphite in this chlorite-grade facies, and this sole known occurrence of 'marsh foraminiferans' in continental slope facies is problematical (see Keppie & Muecke (1979) and Stow, Alam & Piper (1984) for Meguma Group metamorphism and sedimentology). The illustrated material from Scott, Medioli & Braund's (2006, pls 2, 7) Site 6 shows 'bivalves' that are certainly not identifiable as bivalves, and 'foraminiferans' that look like the porous sediment grains that commonly result from chemical disaggregation of siliciclastic rocks.

The Cape Breton *Bathysiphon* specimens are the oldest undoubted representatives of the genus, although the genus likely extends into older strata. Winchester-Seeto & McIlroy (2006) tentatively referred two acid-isolated test linings from the lowest Cambrian (Lontova Formation) in St Petersburg, Russia, to *Bathysiphon*? However, the basis for not referring these linings to associated *Platysolenites* is not persuasive (i.e. there are impressions of larger agglutinated grains on the linings than those used by *Platysolenites* and the tubes have a very small diameter (*c*.52–62 μm)). Indeed, *Bathysiphon* tests incorporate a wide size range of materials that range from clay or small mica flakes (Cole & Valentine, 2006; this study) to sponge spicules (e.g. Małecki, 1973). Similarly, the lumens of the Cape Breton specimens, as an example, reach 600 μm, and emphasize that the lumen is very narrow only in the apical parts of the *Bathysiphon* test.

Purported much older foraminiferans are known from the upper Ediacaran of the South China platform (Hua *et al*. 2010) and Uruguay (Gaucher & Sprechmann, 1999). The Chinese forms are amphora-shaped and have a bulbous apical end, constricted collar and an open aperture with an overhanging lip in some specimens. The Uruguayan *Tithanotheca* Gaucher & Sprechmann is very similar. The Uruguayan and Chinese forms resemble organic-walled, late Cryogenian 'vase-shaped microfossils' from the Great Basin of the United States that have been compared with testate amoebae (e.g. Porter, Meisterfeld & Knoll, 2003 and sources therein). The primary differences are the larger size of the Chinese specimens and their reported mineralized walls. The agglutinated test of *Tithanotheca* is comparable to that in some testate amoebae. We consider the foraminiferan assignment of the Chinese and Uruguayan specimens to be dubious. Indeed, thin-sections do not show any pores through the walls of the Chinese forms, which are common to many foraminiferans (see Hua *et al*. 2010, fig. 6). Similarly, Hua *et al*. (2010) note that their 'foraminiferans' have either calcareous, siliceous or agglutinated tests, but their illustrations do not prove that these wall compositions were primary. Their figure 6a–c shows primarily imperforate, organic-walled tests in two specimens, with a lenticular, thin layer of apparent prismatic calcite limited to the lower right side of one specimen (Hua *et al*. 2010, fig. 6b, c). This thin, lensing calcareous 'layer' may be alternatively interpreted as a local development of shelter spar during

early diagenesis. Similarly, SEM views of three types of external and internal siliceous laminae in the Chinese specimens show layers that are questionably primary, and do not seem to have been secreted by the vase-shaped organisms. These laminae (Hua *et al.* 2010, p. 1761, fig. 7a–d) often show moulds resulting from the dissolution of agglutinated grains or an intergrowth with 'radially oriented acicular calcite crystals of diagenetic origin'. The texture and composition of the siliceous laminae most resemble those of a porcellanite, and suggest initial calcareous cementation followed by silicification on an organic wall of a large testate amoebae.

Far older (*c.* 715 Ma) possible foraminiferans are reported from cap carbonates on Sturtian glacial deposits in northern Namibia. These fossils comprise composite (agglutinated and organic) tubes that are 'flexible' (Bosak *et al.* 2011, p. 68), an unexpected mode of preservation as the remains come from an area that underwent anchizonal metamorphism in the Damaran orogeny (e.g. Clauer & Kröner, 1979) and the carbonaceous material seemingly should be brittle d_{2-3} graphite (e.g. Landis, 1971). Bosak *et al.* (2011) compared the Namibian remains with agglutinated monothalamous foraminiferans. However, the *c.* 200 Ma interval that separates the Namibian remains from distinctive Early Cambrian foraminiferans such as *Platysolenites* seemingly makes an assignment of the Namibian forms to the Foraminifera tenuous.

8. Conclusions

An uncomfortable discrepancy exists between the middle Proterozoic age provided by molecular clocks for the origin of the Foraminifera (e.g. Pawlowski *et al.* 2003), their absence in the Ediacaran (e.g. Antcliffe, Gooday & Brasier, 2011) and the younger, *c.* 520 Ma, age provided by the oldest persuasive foraminiferan from the Baltic and Avalon continents (i.e. *Platysolenites*) and the somewhat younger west African forms (Culver, 1991, 1994). Perhaps more important for the origin of more complex Phanerozoic (and Recent) ecosystems is that the early evolution of agglutinated foraminiferans seems to have been part of the origin and diversification of modern (i.e. Phanerozoic) skeletalized taxa during the Cambrian Evolutionary Radiation (e.g. Landing & Westrop, 2004). *Platysolenites* was part of this initial diversification of the Foraminifera. The appearance of agglutinated foraminiferans in Early Cambrian time suggests that skeletalized protists, as well as skeletalized metazoans, were part of the progressive 'modernization' of marine communities and ecosystems during the Early Cambrian. The fact that the earliest record of *Bathysiphon* now extends back into early Early Ordovician time suggests that this 'living fossil' has occupied the same niche and constructed its test in the same manner perhaps as other agglutinated Foraminifera since Cambrian time.

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