

Foraminifera from the Cambrian of Nova Scotia: The oldest multichambered foraminifera

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ABSTRACT: We report the occurrence of the oldest known multi-chambered trochospiral, planispiral and planispiral/uniserial foraminifera from the Lower to Middle Cambrian deposits in Nova Scotia (Canada). Morphologically, these forms closely resemble modern marsh foraminifera. If these are in fact similar or the same as present marsh foraminifera, their apparent lack of morphological evolution, and the agglutinated and complex multichambered nature of these foraminifera suggest that: 1) these organisms must have some unique characteristics favoring the development of a successful assemblage that appears to have survived to the present, 2) complex chamber arrangements started to develop before 500 Ma, and 3) either these forms are the ancestors to all multi-chambered foraminifera—including the calcareous foraminifera which are the dominant foraminiferal group today—or there was parallel evolution where these went undetected for 200 m.y. when the next occurrence of these chamber arrangements is reported.

Similar foraminifera have been found in Carboniferous and younger deposits where it is clear these were associated with ancient marshes. These fill some of the time gap between the Cambrian forms and modern marsh species.

INTRODUCTION

Both the age and the paleoenvironment of the rocks from which the foraminifera described below were found have been the subject of considerable debate for several decades, largely because Meguma Group or Supergroup (Pratt and Waldron 1991; Schenk 1995, 1997) in Nova Scotia is a 10,000m thick group of metasediments with very few identifiable fossils. Two deposits (text-fig. 1) that came to the attention of the authors, however, were examined for microfossils, which are described below.

The foraminifera described in this paper are the oldest multichambered forms ever reported, so a brief discussion of previously described early Paleozoic foraminifera is included.

Paleoenvironments of these rocks have been described solely on the basis of sedimentological characteristics prior to this study. For this reason, a discussion of the complexity of the stratigraphy of these rocks, and a summary of published geologic history, is included before discussion of the fauna itself to put the foraminiferal discovery into the proper perspective.

PREVIOUS WORK

Lower Paleozoic Foraminifera

The oldest previously reported foraminifera consist of extremely simple, tubular and spherical, agglutinated forms (*Platysolenites*, *Spirosolenites* and ?*Psammosphaera*) found worldwide near the Precambrian-Cambrian boundary (~545 my BP) (McIlroy et al. 1994). The primitive, unilocular, agglutinated genera *Psammosphaera* and *Saccammina*, reported by Cope and McIlroy (1998) from the Atdabanian Stage, were interpreted as dwellers of a shallow-sea environment.

Thirteen well preserved, agglutinated unilocular specimens of the genera *Ammodiscus*, *Glomospira*, and *Turritella* were re-

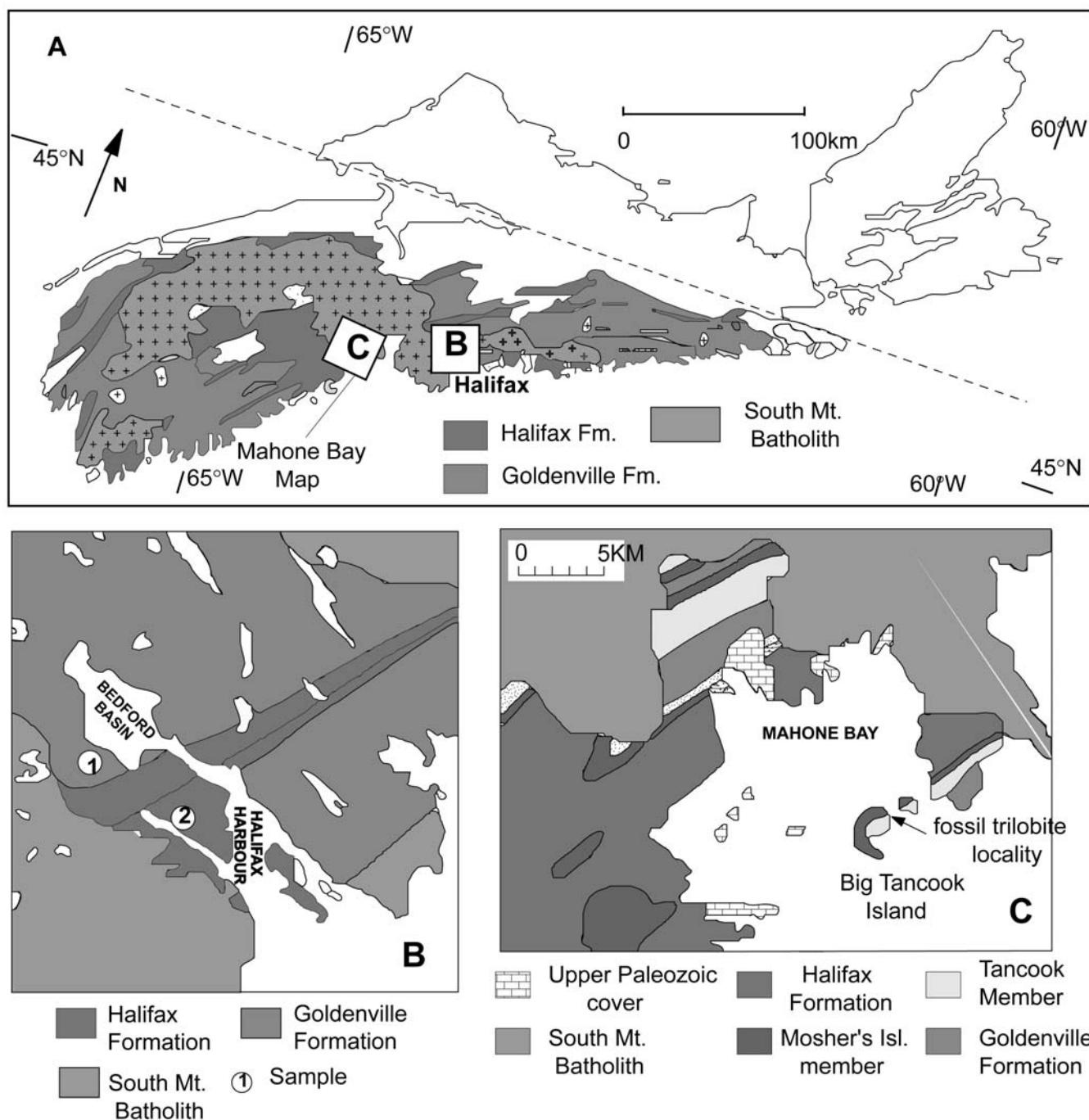
ported by Culver (1991, 1994) and Culver et al. (1996) from the Lower, possibly Middle Cambrian red and green siltstones of the Fougou Member of Nandoumari Formation of southeastern Senegal.

Thus far, no multichambered foraminifera have been reported from the Cambrian. Several slightly metamorphosed (marble) species of agglutinated foraminifera, both single and multichambered (*Saccammina*, *Tolypammina*, *Thurammina*, *Sorosphaera*, *Nephrossphaera*) and some indeterminate forms, apparently multichambered, were found in the Kuaffung Limestone of Poland (Skowronek and Steffahn, 2000) originally dated as Cambrian by Dahlgrün (1934). Based on several other lines of fossil evidence Skowronek and Steffahn (2000) placed the Kuaffung Limestone in the Ordovician-Silurian.

The oldest known, convincingly multichambered, uniserial agglutinated forms are from the Middle Ordovician Mifflin Formation of the Platteville Group of Illinois (~450Ma) (Gutschick 1986). The age of the first reputed calcareous form, *Saccaminopsis* (Sollas 1921), is enigmatic as it was originally reported as Late Ordovician (~440Ma) (Loeblich and Tappan 1964) but later changed to Devonian (~370Ma) (Loeblich and Tappan 1988).

Regional Geology and Previous Work in the Meguma Metasediments

In this paper, the stratigraphic nomenclature of Pratt and Waldron (1991) is used. The Meguma Group of southern Nova Scotia is suggested to be a thick succession of mostly deep-water siliclastic sedimentary rocks of uncertain age (Pratt and Waldron 1991). Fossils in the Meguma Group are very rare. A few finds in the Halifax Formation (upper part of the sequence) indicated Lower Ordovician ages, thus providing some chronological control (Smitheringale 1960; Crosby 1962; Cumming



TEXT-FIGURE 1

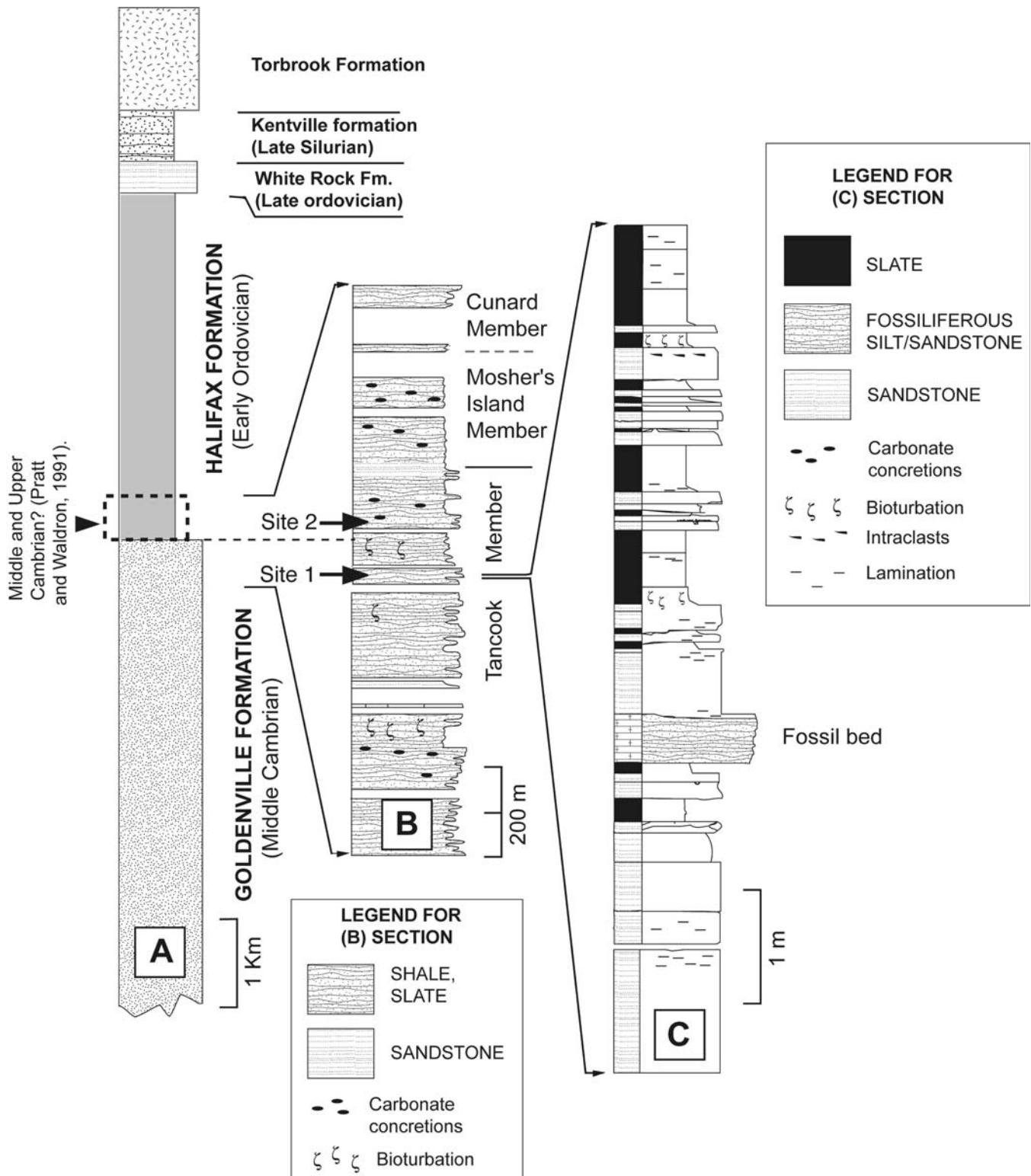
A) Regional geology map of Nova Scotia showing the distribution of the Meguma group. B) geographic positions of the two deposits discussed. Note the position of the granite batholith in relation to site 1. Site 2 was in a slightly higher stratigraphic position in the slate facies. C) Geographic position of the Pratt and Waldron's (1991) trilobite find in the Tancook Member of the Halifax Group.

1985). In the underlying Goldenville Formation, Pratt and Waldron (1991) discovered a trilobite-bearing bed, which yielded Middle Cambrian taxa of Acado-Baltic affinity (discussed in more detail later).

According to Williams and Hatcher (1982), the Meguma Group of southern Nova Scotia is one of the tectonostratigraphic subdivisions of the Appalachian Mountains. It is an allochthonous

terrane that was accreted onto eastern North America during the Acadian orogeny.

Traditionally, the Meguma Group has been subdivided into two formations. The lower one (Goldenville Formation) is dominated by thick-bedded to massive sandstone with interbedded shale later metamorphosed to slate (Phinney 1961; Schenk 1970; Harris and Schenk 1975; Waldron and Jensen 1985). The



TEXT-FIGURE 2

Stratigraphic column redrawn from Pratt and Waldron (1991) showing the stratigraphic position of the deposits discussed in this paper. A: Contact between Goldenville and Halifax Formations; B: enlargement of the contact zone showing the position of the Tancook Member; C: enlargement of the section of the Tancook Member containing the Middle Cambrian trilobites; notice how the trilobite deposit is in the identical stratigraphic position of site 1. Site 2 corresponds to the Mosher's Island Member of the Halifax Formation, placed by Schenk (1970, 1976, 1995, 1997) in Lower Ordovician; Pratt and Waldron (1991), however, believe it to be Cambrian; no accurate dating is possible without diagnostic fossils.

base of the Goldenville Formation has not been observed; estimates of its exposed thickness range up to 5600m (Taylor 1969). Schenk (1995, 1997) elevated the Meguma to Super-group rank.

The overlying Halifax Formation consists chiefly of slate, argillite, and siltstone, with subordinate thin-bedded sandstone interpreted as turbidites by Stow et al. (1984). Schenk (1970) recorded a thickness of 7 km, and thicknesses up to 10 km were estimated from structural cross sections by O'Brien (1986).

The Meguma Group was deformed and metamorphosed at about 400 Ma (e.g., Dallmeyer and Keppie 1987; Muecke et al. 1988) and intruded by granites at about 370 Ma (e.g., Clarke and Halliday 1980). Metamorphism is generally weak (chlorite grade) in the Mahone Bay area, but elsewhere it ranges up to sillimanite grade (Keppie and Muecke 1979).

The upper 870m of the Goldenville Formation were distinguished as the Tancook Member, characterized by thin to medium-bedded sandstone and slate. Slate dominates the upper 190m of this Member (Waldron 1987).

Previous Fossil Discoveries in the Meguma Group

Between 1200 and 2720m above the base of the Halifax Formation, the graptolite *Dictyonema flabelliforme* (s.l.) of Lower Ordovician (Tremadocian) age is found at several localities in southwestern Nova Scotia (Smitheringale 1960; Crosby 1962). Additional specimens of *Dictyonema* sp. and *Anisograptus* sp. were found by Cumming (1985) 2000-2450m above the base of the Formation in south-central Nova Scotia. Acritarchs recovered from the upper Halifax Formation at several localities are also of Tremadocian age (Keppie 1977).

The underlying Goldenville Formation was dated by K-Ar at 476 ± 19 and 496 ± 20 Ma (Wanless et al. 1972). A maximum age limit of 552 ± 5 Ma was provided by detrital titanite (Krogh and Keppie 1990) which confirms that the formation is placed somewhere between the lowermost Ordovician and the Middle Cambrian.

Trilobite Faunule

Pratt and Waldron (1991) described a trilobite faunule from the Tancook Member containing *Paradoxides* (s.l.), *Dorypyge*, *Agraulos*, and ellipsocephalids. The age Middle Cambrian indicated by these fossils is the first definitive age ever provided for these rocks.

Paradoxides (s.l.) ranges throughout the Middle Cambrian, as high as the *Lejopyge laevigata* Zone in one region of Sweden (Westergård 1953; Martinsson 1974) and equivalent to the "Piso sin Solenopleuropsidae" in one region of Spain (Sdzuy 1972). Ellipsocephalids range from upper Lower Cambrian through most of the Middle Cambrian region of Spain (Sdzuy 1972). *Agraulos* has been recorded only in the upper part of the Middle Cambrian region of Sweden, in the *Jincella brachymetopa* Zone, but occurs in older rocks elsewhere: in the Middle Cambrian region of Spain (Sdzuy 1972) and southern France (Courtessole 1973) and in the lower part of the Middle Cambrian of Bohemia (Snajdr 1958). *Dorypyge* is widespread in the Middle and upper Middle Cambrian of the Middle East, China, Spain, and Sweden and may also occur in older strata in Turkestan (Schränk 1977).

The Middle Cambrian age of this faunule is substantially older than any fossils in the Halifax Formation. This suggests that the remainder of the Goldenville Formation, below the bioclastic bed, may be as old as Lower Cambrian and that the overlying basal Halifax Formation may be a condensed sequence representing part of the Middle Cambrian and perhaps all of the Upper Cambrian. The condensed nature of the Halifax Formation is supported by its uniformly fine grain size, with comparatively rare sandstones (Pratt and Waldron 1991, fig. 2).

Geological Setting of Fossil Deposits in this Study

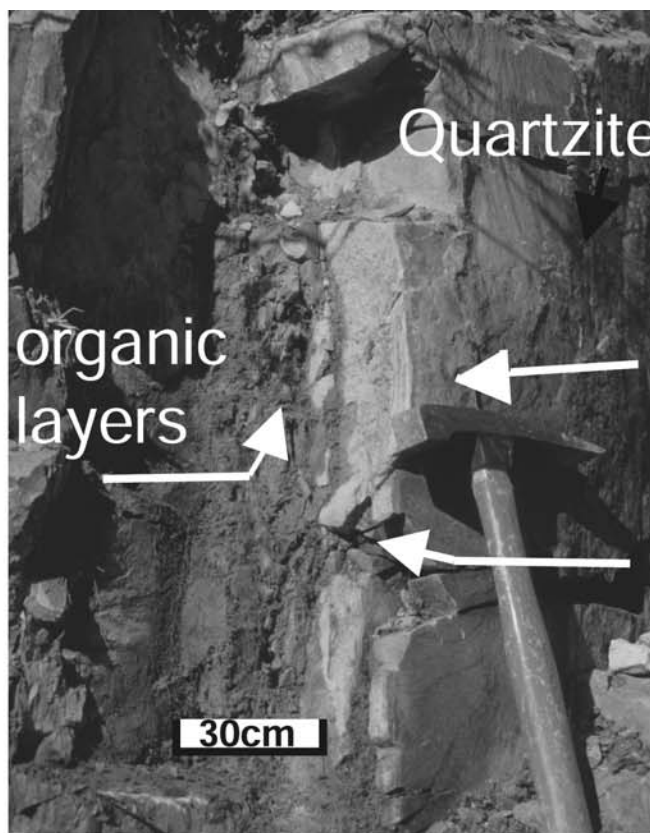
Because this entire sequence is largely metamorphosed, it had not been examined carefully by us for fossils; however, two areas found by amateur collectors were brought to the authors' attention. Samples were examined from the two deposits. One was a lens of seemingly unaltered sandy, organic sediments (site 1) and the other a very hard shale/slate where macrofossils had been found (M. Zentilli, pers. comm., 1995) that appeared

PLATE 1

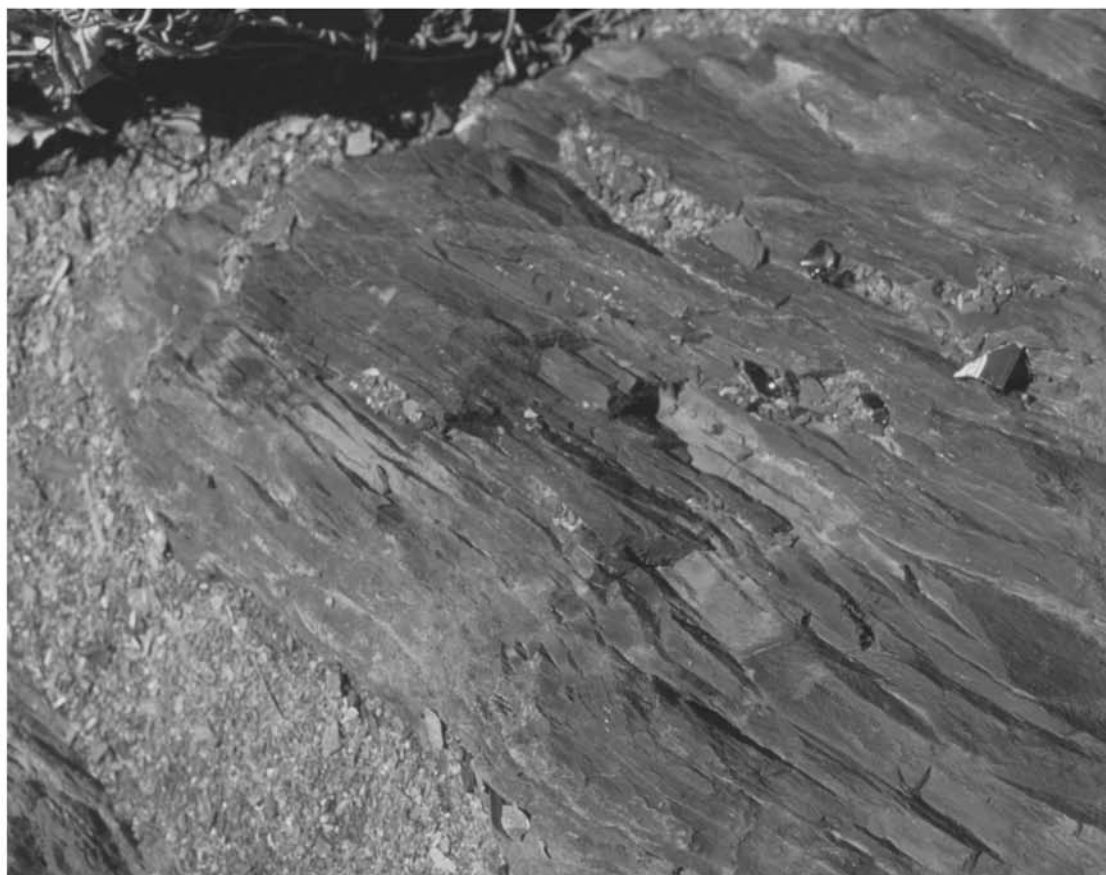
A Clayton Park lens (site 1) is shown encased in quartzite with an aureole of chert (contact zone in this photo). There are organic and light brown sand layers dipping the same direction as the quartzite, something that could not happen if these had been deposited after the quartzite. Unfortunately, this deposit no longer exists because, after being exposed by a road cut, it has been quickly weathered out due to its soft, easily degradable nature. Probably the reason why lenses such as this one have not been reported previously is that they weather out before being observed.

B Conrod's Park, Halifax (site 2). The rock at this site is the typical dark gray slate characterizing most of the Halifax Member of the Meguma Group. However, at this one locality, the slate seems to be more shale-like, which allowed the preservation of the bivalves of plate 2 and led to the sampling for foraminifera under the assumption that if shell fossils were preserved, foraminifera might also be preserved.

A



B



to be bivalves (site 2); these finds led to the belief that microfossils might also be found at these two locations (pl. 1).

Fossils from site 1 (text-figs. 1, 2; pl. 1, fig. A) were found in a lens of soft sediment embedded in metasediments (quartzite) of the Goldenville Formation. The lens became exposed in a recent road cut; it consists of unconsolidated, virtually unaltered sediment and is bedded parallel to the surrounding, nearly vertical quartzites, ruling out a recent emplacement. This is the only known lens in the Goldenville Formation with visible beds of clearly differentiated sand and organic layers. The lens was encased in a chert aureole, suggesting a contact metamorphic origin where fluids must have encased and solidified around it, protecting it from the regional metamorphism that occurred in the surrounding rocks. The sediments containing the microfossils consisted of unconsolidated yellow sandstone with dark bands of organic debris (pl. 1, fig. A). More photos are available for viewing on senior author's web site: <http://is.dal.ca/~es/staff/dbscott/scott.htm>.

It was suggested by some early reviewers of this paper that this lens could have been deposited after the original surrounding rock. This suggestion is difficult to accommodate without invoking a series of very strange circumstances. The lens is bedded parallel to the quartzite, thus a later infilling would imply: 1) the opening of a space between the metamorphic beds, 2) the horizontal position of the quartzite at the time of infilling, 3) the subsequent deposition of sediment in a lens parallel to the quartzite, and 4) the repositioning of the entire sequence to the present vertical angle. There is nothing to suggest these circumstances occurred.

Site 2 was within the Halifax Formation, a unit stratigraphically above site 1 (text-fig. 1; pl. 1, fig. B), but still within the Cambrian (Pratt and Waldron 1991; text-fig. 2B, pl. 1, fig. B). The rock at this site was the typical gray shale/slate of the Halifax Formation, which is usually devoid of any type of fossils. An unpublished find of fossils in this formation (pl. 2) attracted the attention of the authors. Art Boucot (Oregon State University), Lars Holmer at Uppsala University and John Peel (also from Uppsala) could not verify that these specimens were brachiopods since there was no shell material left. However they did all agree that these were shelled organisms with accretionary growing valves, concluding they could be either molluscs or brachiopods.

Despite the fact that the fossils have not been identified more accurately, their presence is important for a number of reasons: 1) they were the reason for sampling the hard shale of the Halifax Formation hitherto considered devoid of fossils; and 2) they were laying parallel to the bedding plane, were not disarticulated, and were not in a shell bed, suggesting an *in situ* placement (pl. 2D). The macrofossils are presently housed at the Nova Scotia Museum of Natural History.

METHODS

Processing and Examination

The unconsolidated sediment of site 1 was wet-sieved using various sieve sizes down to 63µm. The specimens were picked out of the dried residue using a dissecting microscope at 20-40x, and examined under SEM, and in thin sections of epoxy resin mounts under a transmitted-light, under a compound microscope. The best technique to reveal the multichambered nature of the specimens proved to be the mounting of grains

(125-212µm fraction) in epoxy resin, and subsequently grinding the mount to a 20µm thickness. Similar thin sections of Holocene palynological slides containing inner linings of agglutinated foraminifera are shown here also for comparison to the Cambrian forms (slide courtesy of E. Levac, Dalhousie University). The observation with SEM revealed the agglutinated nature of the tests, while that in transmitted light illustrated the morphological diversity and complexity of this fauna.

The sample from site 2 required more vigorous techniques to break down the hard shale, such as boiling the rock in water and using sodium hyposulfite (see Wightman et al. 1994). Several well preserved specimens were recovered from a small sample of this rock.

Illustration

Picked specimens from site 1 were illustrated with a scanning electron microscope (Bausch-Lomb Nannolab® at Department of Biology, Dalhousie) and filmed with Kodak® B/W plus X film (35mm). Thin sections and grain mounts were viewed and photographed with an Axiophot® transmitted light petrographic microscope with polarizer, using Fuji 64T® 35mm slide color film.

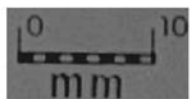
Specimens from site 2 were photographed using a Zeiss Aristophot® (reflected light) with Kodak® B/W plus X and Fuji 64T® slide color film (35mm). This equipment was at the Bedford Institute of Oceanography. SEM photos of specimens from this site were taken on an ElectroScan® e3 (now part of Phillips Electron Optics) and electronic versions were placed directly onto a CD. The presence of an EDAX system on the ESEM allowed us to determine a rough elemental composition of the site 2 fossils.

While illustrating the find, the limitations of the SEM in the study of poorly preserved micropaleontological material became apparent. While the transmitted light photographs show unmistakable foraminiferal structures, some of the SEM photographs of similar material show only the outline of what, *prima facie*, may or may not appear to be a foraminifer. However the SEM is able to see certain individual characteristics such as apertures, foramen, inner chambers and proloculi that are sometimes not visible with a light microscope; it also serves in illustrating the external texture that clearly shows these are agglutinated foraminifera.

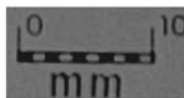
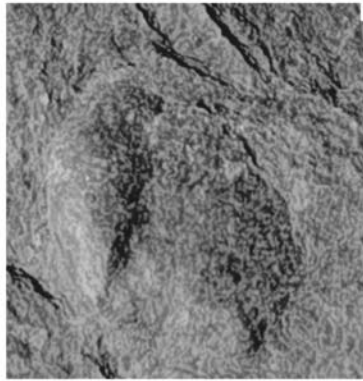
All photographs in this paper plus extra photos not published are available in color on the senior author's web site: <http://is.dal.ca/~es/staff/dbscott/scott.htm>

RESULTS

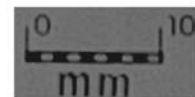
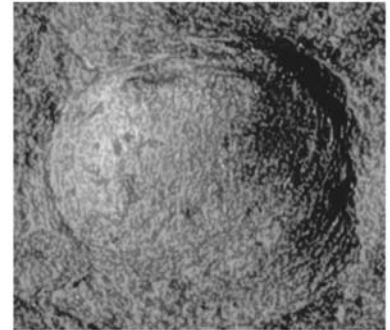
Before we illustrate the Cambrian material we include a plate of drawings and pictures of modern specimens. Plate 3 contains line drawings of modern species that are believed to be the most similar to the specimens found here. These are modified drawings of specimens from Scott et al. (2001). These drawings show the outlines of the species which can be compared to some of the photographs, in particular the grain mounts of Plate 4. Plate 3, fig. H is a photograph of *Trochammina macrescens* from a marsh surface sample to illustrate how even without compaction these specimens start to flatten out and develop cavities within the chambers. Plate 3, figs. I-J are transmitted light photographs of inner linings of agglutinated foraminifera from a Holocene palynological slide where the sediment was treated with a variety of acids, including HF, to dissolve the silica. Plate



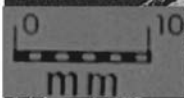
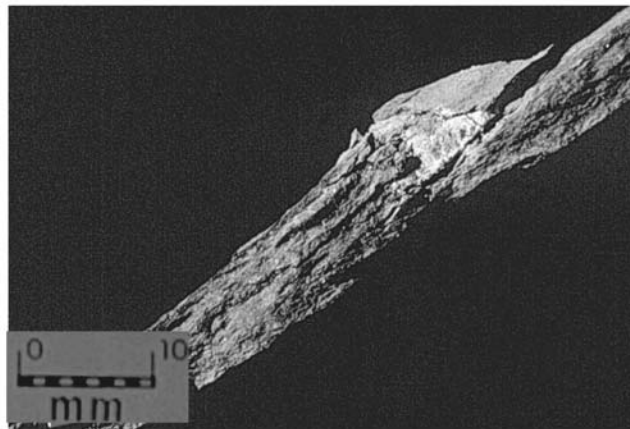
A



B



C



D

PLATE 2

Photos of bivalve fossils collected at site 2 by Armgard Zentilli and deposited at the Nova Scotia Natural History Museum.

- | | |
|---|---|
| <p>A external imprint of photo B.</p> <p>B internal mold of the valve in photo A showing the crease, which may provide a clue for identification.</p> | <p>C internal mold from one valve; a hinge line is visible at the top of the specimen.</p> <p>D cross section with two articulated valves, suggesting they were in place when buried.</p> |
|---|---|

3, figs. I, K are trochospiral (pl. 4, figs. A, C, G) and plate 4, figure J is planispiral (see pl. 4, fig. C). If 600my of heating, compaction, folding, etc. is added to inner linings as in plate 3I-J, it is not hard to see how these might not look like the fossil foraminifera most workers are accustomed to observing.

The Cambrian taxa found at site 1 have been grouped tentatively and informally under the generic names of similar and commonly known, modern agglutinated, foraminiferal genera, including *Trochammina*, *Haplophragmoides*, and *Ammobaculites* (Scott and Medioli 1980) and one thecamoebian species, *Diffugia* (Medioli and Scott 1983). Comparing Cambrian specimens with modern genera may be premature, but it serves the purpose of placing them within a wide, easily identifiable category. Erecting new taxa based on relatively poorly preserved material would be unwarranted at this time without being able to distinguish all the physical traits that are needed to clearly describe genera. Only the best specimens have been illustrated, but the samples at this site were rich in organic fragments, many of which were fragments of the organic linings of foraminiferal specimens. These "linings" are very similar to what is observed even in modern marsh sediments for similar morphologies. Some pollen preparations of marsh sediments (pl. 3), after the sediment has been treated with HF to remove the silica, contain inner linings that would appear similar to these (F.McCarthy, Brock University, Canada, and E. Levac, pers. comm. 1998, 2002, respectively).

At site 2 one type (*Trochammina*) was clearly observed, but other fragments, which could not be identified, may represent different forms. The specimens were almost crystalline in appearance under the dissecting microscope but the EDAX system associated with the ESEM pictures verified that these were carbon based, not metallic.

The specimens have been illustrated with different techniques to highlight the different, relevant features listed in the following sections. First the grain mounts from site 1 (pl. 4) are shown to illustrate the multichambered nature of these forms; second the SEM photos from six specimens from site 1 are shown to illustrate individual characteristics (pls. 5, 6). Features such as: apertures (pl. 5, figs. C-E, pl. 6, figs. I-K), foramen (pl. 5, figs. F-H), umbilical areas (pl. 5, figs. A, B, pl. 6, figs. D, E) and, in one case, a proloculus (pl. 6, figs. F-H) are indicated; some of the specimens from site 2 are shown using the SLM, reflected light, SEM, and transmitted light micrographs (pl. 7). No grain mounts of the material from site 2 were prepared to avoid sacrificing the best specimens, two of which are housed at the Smithsonian Institution in Washington, D.C. (museum numbers USNM # 510790 and USNM # 510791 in plates 7 caption), while others have been deposited at the Nova Scotia Museum (Halifax) of Natural History and the National Museum of Natural History in Ottawa, Ontario.

DISCUSSION

Chronostratigraphy

The trilobites found by Pratt and Waldron (1991) are solid evidence that those deposits are at least as old as Middle Cambrian. Since deposits studied in this paper are stratigraphically equivalent, they are also Middle Cambrian. If the foraminifera themselves were reworked, they can only be older. The deposit at site 1 is certainly unusual but it can be argued that it is the same age as the rock encasing it, and this deposit contains the highest diversity fauna of the two sites.

Foraminiferal Morphology and Implications for Evolution of Early Foraminifera

The first problem that arises with specimens this old is the fundamental question whether or not they are physically or organically produced. For the specimens here we have shown that they are organic material, both by the physical destruction of some of the specimens of site 1 with H₂O₂ to prove they were not mineralic and the EDAX measurements of the specimens of site 2 that demonstrated they were carbon based. The next problem then is to determine what they might be. There are few fossils of this age that remotely resemble the fossils reported here and anything this old becomes problematic in terms of microfossils since there are so few comparative specimens. One organism that appears superficially similar to coiled foraminifera is the green algae, *Botryococcus*. These algae are known throughout the geologic record from the Pre-Cambrian to present (Batten and Grenfell 1996). The only confusion that could arise with the specimens discussed here would be with the thin sections in plate 4 where only the organic inner linings are visible. However, the size of *Botryococcus* is a maximum of 30 microns and the size of even one chamber in the specimens of plate 4 are more than 100 microns. The specimens in plates 5 and 6 are the same as those in the thin sections except they are photographed with SEM, clearly showing these specimens are agglutinated, unlike *Botryococcus*. Some of the features in plates 5 and 6 illustrate typical foraminiferal traits. In plate 6, figures F-H there is a distinct proloculus which is the oldest proloculus ever reported; plate 5, figures F-H illustrate distinct foramen, another characteristic of foraminifera; plate 5, figures I, J show distinct chambers also characteristic of multi-chambered foraminifera; distinct primary and secondary apertures are illustrated in plates 5, figures C-E, plate 6, figures I-K, and plate 7, figures K, L. None of these can be linked to any functional morphology, which is usually the case for foraminifera, but all these features are distinctive of modern foraminifera and might have their origins in these early Cambrian forms. Comparing the Cambrian specimens with the drawings and photographs of Holocene specimens in plate 3 suggests that not only are these Cambrian fossils foraminifera, but that they are almost indistinguishable from modern forms.

Another question that has arisen is the nature of agglutination of these specimens. In the SEM photographs there are not the distinct grains often associated with agglutinated species. However, typical marsh species, to which these specimens compare the most closely, have very fine agglutination (see pl. 3H, the modern species, *Trochammina macrescens*) which is so thin that the chambers collapse. In many cases, even in modern samples, only the pseudochitinous inner lining will remain, much like the linings shown in plate 4. The cement is assumed to be organic since marsh specimens left unrefrigerated will deteriorate from bacterial action (Scott et al. 2001).

Some individual animal taxa are known to have persisted without detectable evolution throughout the Phanerozoic (e.g., the brachiopod *Lingula*), and the foraminifera reported by Culver (1991, 1994) are genera that are still present today in shallow water and deep-water environments. It is not without precedent therefore, that genera might survive from the Cambrian to the present. The difference in this group of specimens is that they are multi-chambered and have chamber arrangements (trochospiral, planispiral and planispiral to uniserial) that do not occur in the previously reported fossil record until 200m.y. later (e.g. Thibadeau 1994; Tibert 1996; Tibert and Scott 1999; Wightman et al. 1993, 1994).

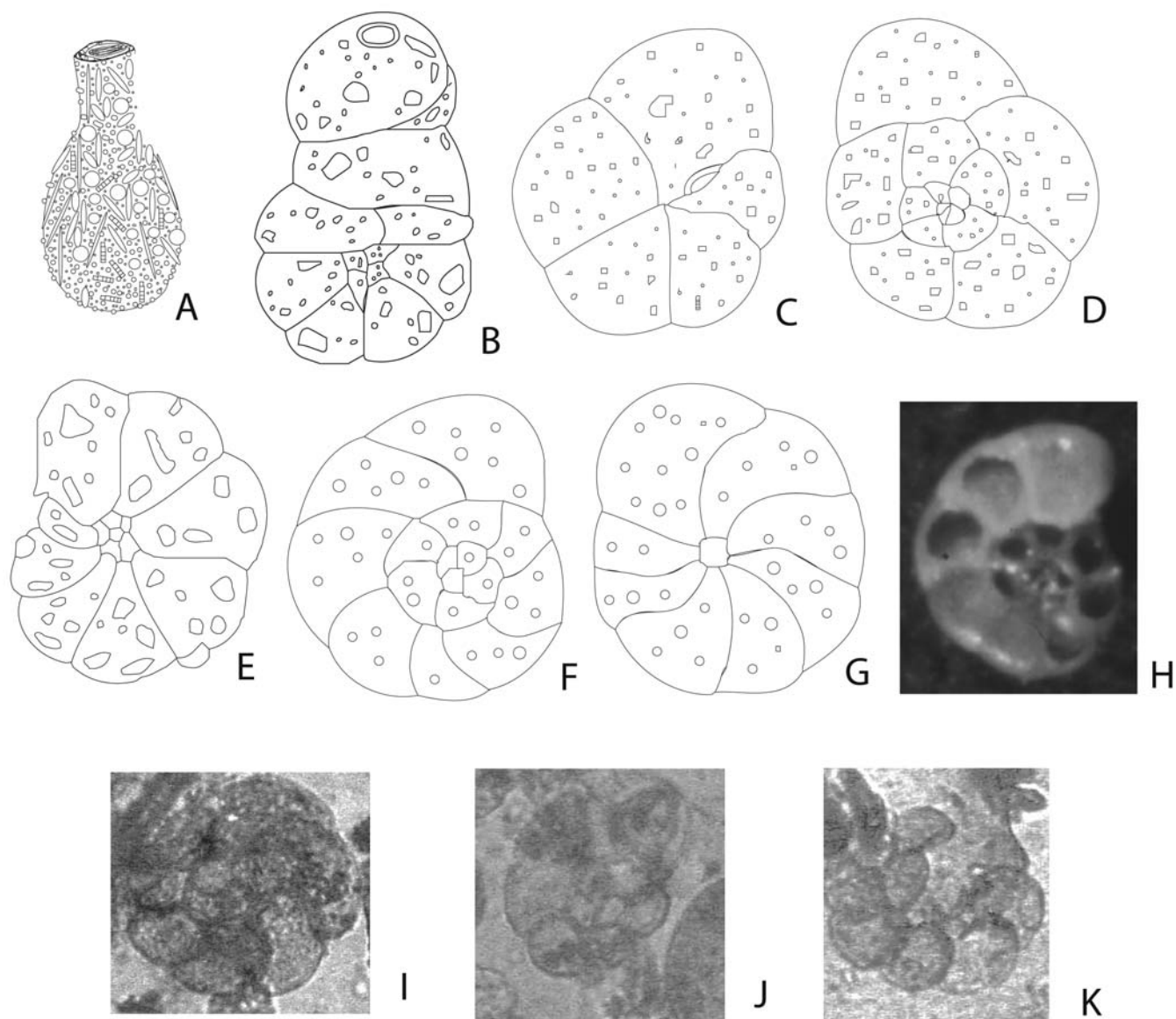


PLATE 3

Line drawings of the most common types of recent foraminifera that are suggested to be most similar to the Cambrian specimens.
All figures redrawn from Scott et al. 2001.

- A *Diffugia bacillifera*, thecamoebian, as in plate 4E;
- B *Ammobaculites dilatatus*, planispiral; as in plate 4B;
- C *Trochammina inflata*, trochospiral, ventral side;
- D *T. inflata*, dorsal side; as in plate 4 A, C;
- E *Haplophragmoides manilaensis*, planispiral, as in plate 4D;
- F *Trochammina ochracea*, trochospiral, dorsal;
- G *T. ochracea*, ventral;
- H light photograph of a specimen of *Trochammina macrescens* (x50) from a surface sample — notice

- even in this non-fossil specimen chambers collapse and specimens flatten out without any compaction;
- I transmitted light photograph of a Holocene inner lining of a trochamminid specimen from a palynological slide preparation taken from a core in the Gulf of St. Lawrence, Canada (slide preparation courtesy of E. Levac, Dalhousie University);
- J photograph from the same slide as I of a planispiral innerlining;
- K photograph from the same slide as I of a broken trochamminid (all magnifications for photographs I-K are x100).

There are relatively few verified finds of Cambrian foraminifera to compare with and no reports of anything similar to what is reported here. One problem may be that when micro-paleontologists have found organic deposits in fossil settings they have traditionally assumed they were freshwater deposits and ignored them; palynologists, of course, have looked at these but have usually destroyed the mineralic components of the deposit with acids and have not observed what foraminifera (or thecamoebians) may have been present, although some have reported organic linings that were probably foraminifera or thecamoebians (e.g. pl. 3, figs. I-K, and F, McCarthy, Brock University, P. Ogden and E. Levac, Dalhousie University., per. comm. 1995 and 1980 and 2002 respectively). Another problem in the specific deposits discussed here is that unless one has seen how even modern marsh foraminifera collapse their chambers after death (see pl. 3, fig. H), these foraminifera might have been overlooked; this was initially the case for the foraminifera found in the Carboniferous deposits of Nova Scotia (Thibaut 1994; Tibert 1996; Tibert and Scott 1999; Wightman et al. 1993, 1994).

Porter and Knoll (2000) report Pre-Cambrian thecamoebians from the Grand Canyon (USA.). These fossils were in freshwater deposits of roughly 750 Ma and it appears that also these forms are almost indistinguishable from some present day species, just as in the specimen shown here in plate 4, figure E is very similar to the present day *Diffugia*. Hence it appears that at least part of the assemblage illustrated here might have had its origins in the Pre-Cambrian.

Few multi-species groups, as observed in site 1, have been reported to be in existence – they appear to be morphologically similar to present day marsh foraminifera and occur in sediment that could have been intertidal in terms of some sedimentological characteristics. The morphological similarities of these foraminifera with those reported from Lower Carboniferous marsh deposits of Nova Scotia (Thibaut 1994; Tibert 1996; Tibert and Scott 1999; Wightman et al. 1993, 1994) as well as scattered occurrences of Mesozoic salt marsh foraminifera (e.g. Wall 1976), partially fills the large chronological gap of 500 Ma between the Cambrian and modern salt marsh species.

Paleo-environmental Assessment

Modern intertidal marsh foraminiferal communities have one of the highest levels of productivity among benthic foraminiferal populations (Scott and Medioli 1980). The occurrence of an entire foraminiferal assemblage with relatively high abundances

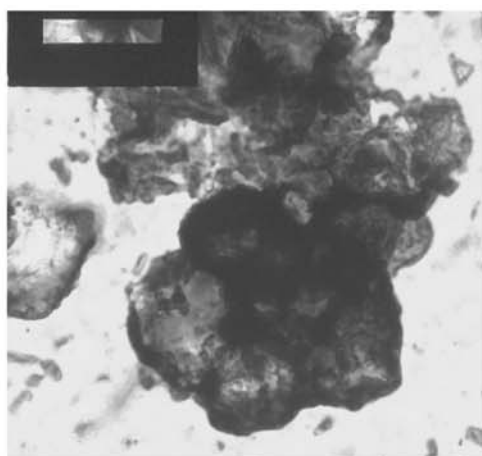
(several 100 in 20cc of sediment) in the Cambrian, similar to that of present day marshes, is interesting from the standpoint of not only morphological considerations but also community structure in the sense that these were already abundant and have continued to be abundant in marshes to the present with the same apparent lack of competition. However, were these organisms as restricted in the Cambrian as they are now? Presently salt marshes are areas where the abundances are high and the diversity is low with only 8-10 truly endemic species of marsh foraminifera occurring worldwide (Scott and Medioli 1980). However, if other primitive life forms such as stromatolites are considered, those organisms dominated the early life but are now restricted to hypersaline or alkaline environments by competitive pressures (Walter et al. 1992). Is it possible that this could be the case for these primitive marsh-like forms that may have dominated the world's oceans in the Cambrian only to be replaced by more advanced forms soon after the "Cambrian" explosion? Unfortunately there are comparatively few deep-water sequences such as the Meguma Supergroup and that one is mostly metamorphic and with few fossils of any kind positively identified. Hence, it is not surprising that these forms have not been reported previously from very old deposits. If the present day situation is considered, there is a very small percentage of the marine environment that is intertidal and much of that is not preserved. Preservation of these environments does not occur in great abundance until the Carboniferous, which coincidentally was the earliest reported occurrences of these forms prior to this paper.

The paleoenvironment, as interpreted from the sedimentology, was suggested to be distal turbidites (Stow et al. 1984). Certainly, in the absence of any fossil remains and the metamorphic alteration of the rocks, this was an acceptable interpretation. However, the foraminifera and other fossils reported here, suggested to be *in situ*, may suggest a different paleoenvironment if in fact these foraminifera retained the same environmental range as they have now. In the deposit from site 2, the bivalves were certainly not deposited by a turbidity current. They are lying parallel to the bedding plane, in articulated position, not in a shell layer, and encased in shale; a hydraulic regime incapable of transporting a bivalve shell suggests an *in situ* life position. For site 1 there is a mixture of well developed sand layers and organic layers that is similar to a present day shallow lagoon/estuarine environment. Admittedly the site 1 deposit, in particular, is not a widespread type of phenomena in the Meguma Group. This may be because these lenses are not well preserved once exposed to surface processes; the photo of site 1

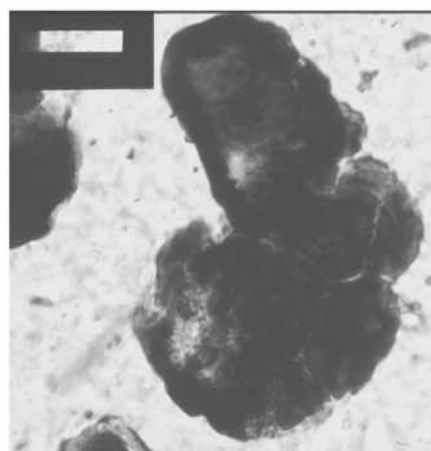
PLATE 4

Transmitted light photographs are of grain mounts of specimens from site 1.

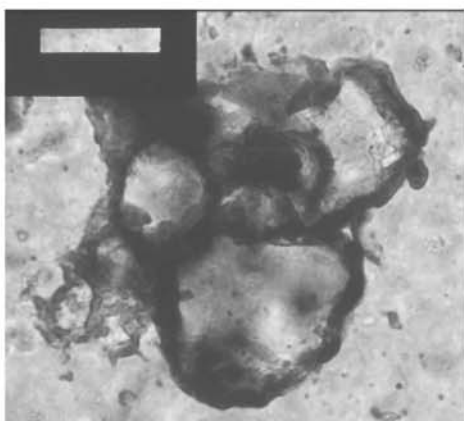
- | | |
|---|---|
| <p>A "<i>Trochammina</i>-like" specimen, scale bar = 60µm;</p> <p>B "<i>Ammobaculites</i>-like" specimen, scale bar = 150µm;</p> <p>C "<i>Trochammina</i>-like" specimen, scale bar = 60µm;</p> <p>D "<i>Haplophragmoides</i> -like" specimen, scale bar = 300µm;</p> | <p>E thecamoebian-like specimen similar to the modern <i>Diffugia bacillifera</i>, scale bar = 60µm;</p> <p>F "<i>Ammobaculites</i>-like" specimen, scale bar = 60µm;</p> <p>G "<i>Trochammina</i>-like" specimen, scale bar = 60µm;</p> <p>H another coiled but incomplete form, scale bar = 60µm.</p> |
|---|---|



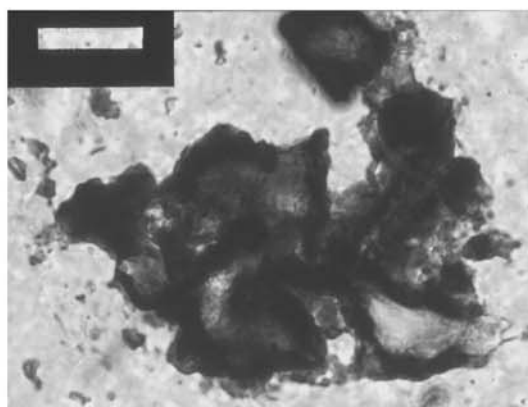
A



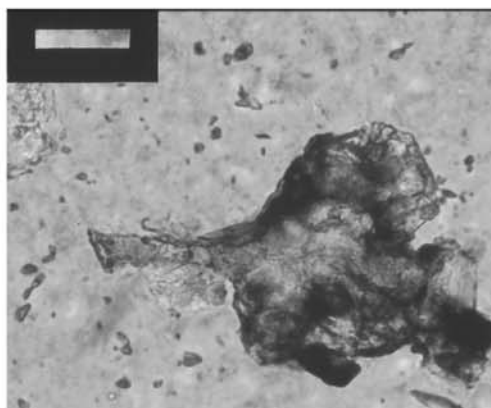
B



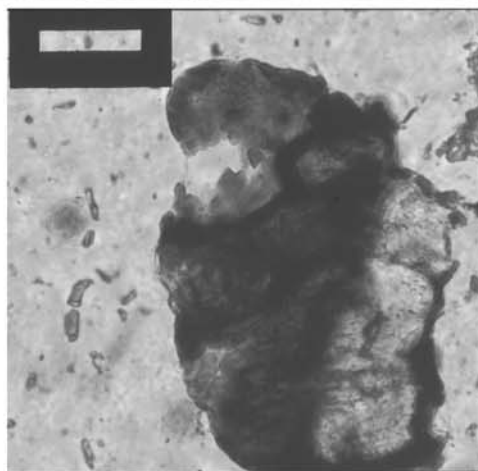
C



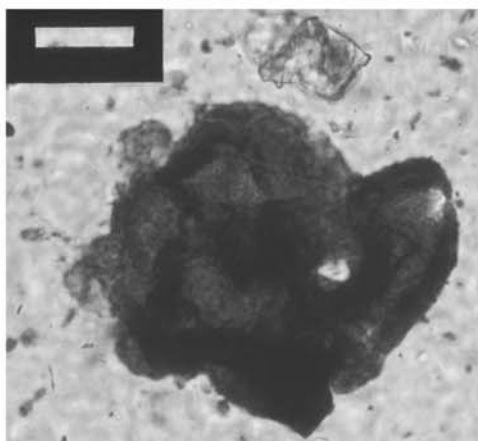
D



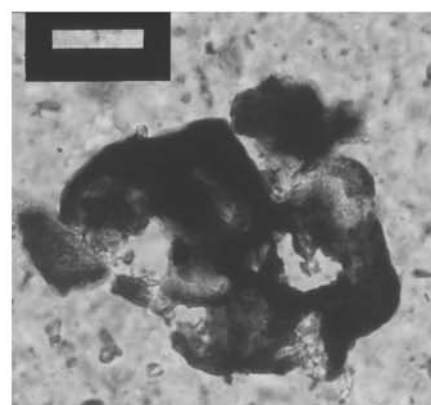
E



F



G



H

is now the only record of the lens which, in few years, has been eroded out of the much harder surrounding quartzite. For site 2, the mono-specific character of foraminifera, the occurrence of the bivalves, and the black shale could be hemi-pelagic muds between distal turbidite layers, consistent with previous interpretations of the Halifax Formation (Stow et al. 1984). Also modern deep sea foraminifera, that are agglutinated, are similar to these, especially *Trochammina ochracea* (pl. 3, figs. f, g), and that would not be inconsistent with this deposit being deep water hemipelagic. Whether or not these fossils are *in situ* or not is one question but in any case, the fossils themselves cannot be younger than Middle Cambrian.

Scientific Significance

All the basic multichambered arrangements observed in today's foraminifera are present in these Cambrian forms, and, assuming that such structures did not develop instantaneously, this leads to the inevitable conclusion that multichambered structures must have been in existence long before Middle Cambrian. This agrees with the findings of McLroy et al. (1994) who noted that by the end of the Lower Cambrian Atdabanian stage, foraminifera were well diversified and had already developed many major adaptations in agglutinated design, except the multichambered one. It appears from these data that in fact the multi-chambered arrangement had evolved by that time.

Another question posed by this find concerns the possibility that these marsh-like forms are ancestors of all subsequent multichambered foraminifera. Given the sparse fossil record for this time period we may never know the answer to this question but it appears that either: 1) there was parallel evolution of these morphologies and that these morphologies developed independently in calcareous foraminifera or, 2) it is possible that the trochospiral, planispiral and planispiral-to-uniserial chamber arrangements in later foraminifera may have come from these early agglutinated forms. Whatever the answers are to the above questions of environmental and ancestral affinities, these Cambrian foraminifera may still represent the dawn of foraminiferal life, or genuine "living fossils", linking some of the oldest species of the group to the modern advanced forms dominating the world's oceans today.

CONCLUSIONS

1) The foraminifera reported here are Cambrian or older.

2) These foraminifera are approximately 50 million years older and far more diverse than the previously reported earliest multichambered finds.

3) These foraminifera appear to be morphologically similar to modern day marsh foraminifera.

4) It is unlikely that the diverse morphologies reported for foraminifera in the Devonian and later (trochospiral, planispiral, planispiral to uni-serial) evolved independently from the same morphologies illustrated for the Cambrian fauna shown here. Hence these species could be the precursors for most of the diverse morphologies now exhibited by calcareous and agglutinated foraminifera alike.

5) The group of foraminifera found here might be one of the oldest assemblages of fossils still present as "living fossils"; it is impossible, however, to determine if they were restricted to an intertidal environment in the Cambrian as at present.

6) It is also possible that these forms are reworked in the Meguma Group is a turbidite, but the fossils themselves can only be older in that case.

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Colin Corkum of Halifax, Nova Scotia brought the presence of site 1 deposits to the attention of the senior author. Marcos Zentilli informed us of the bivalves found by his wife, Armgard, which led to our sampling of site 2; Darren Drake of the Nova Scotia Natural History Museum retrieved those fossils from the museum. Steve Culver (East Carolina University) supplied many of the early Cambrian references; he also reviewed a several early versions of this paper, which was extremely helpful. We also thank Jere Lipps (University of California) and many anonymous reviewers for helpful suggestions to the present paper. Milton Graves, Marcos Zentilli, Sandy Grist, Mike Collins, Elisabeth Levac and Don Fox (all from Dalhousie University), Jere Lipps, Arthur Boucot (Oregon State University), Lars Holmer, and John Peel (Uppsala University) helped the authors with many aspects of this work. Gordon Brown, Chloe Younger, Findlay Muir and Dan Abriel (Dalhousie University), and Frank Thomas (Bedford Institute of Oceanography) helped with many of the technical aspects (processing, photography, grain mounts). Bruce Hayward (University of Auckland) and Martin Buzas (Smithsonian Institution) reviewed the final draft. Funding for photography was from an NSERC research grant to Scott.

PLATE 5

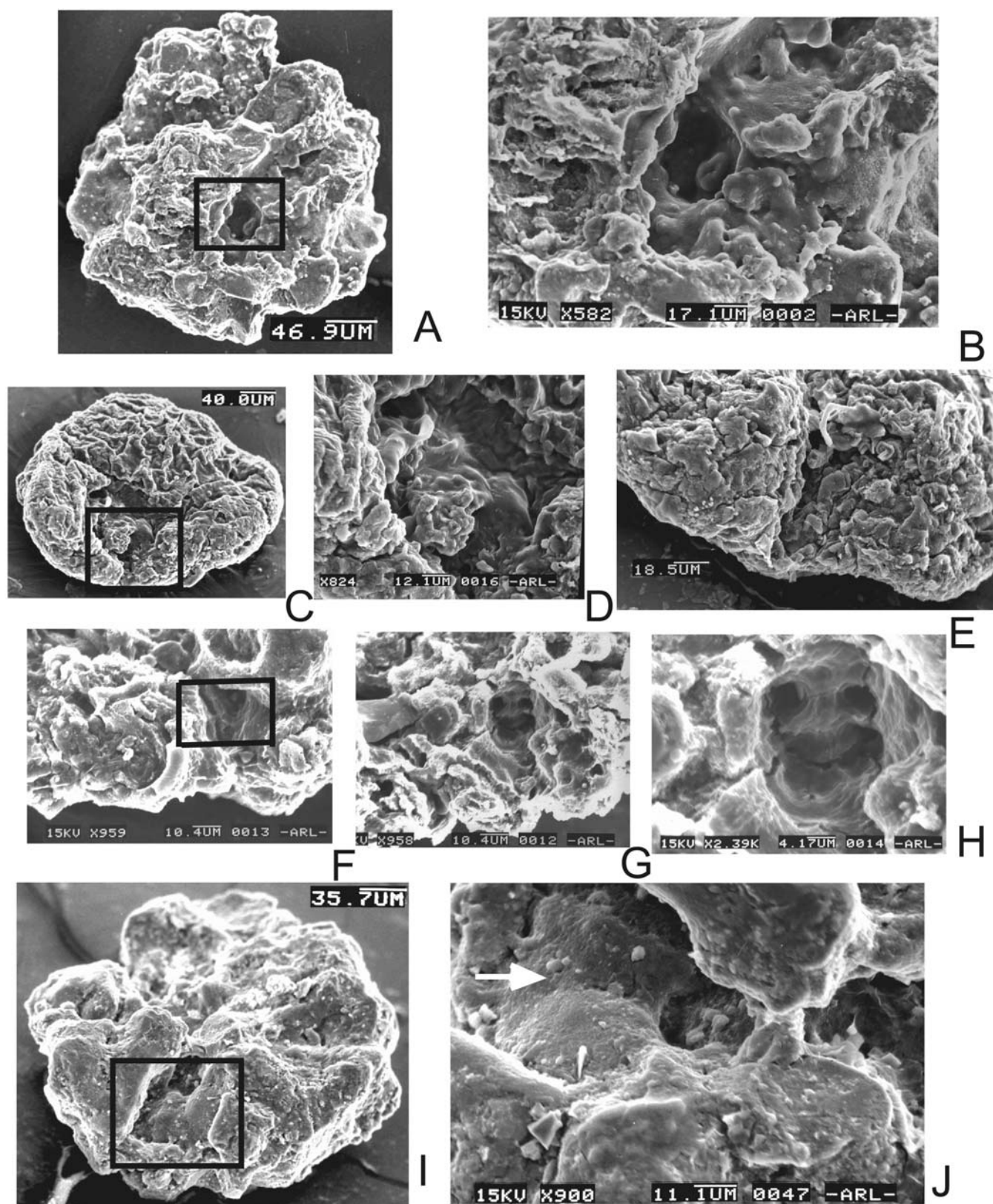
SEM photographs of specimens from site 1; scale bars are on each photograph.

A,B ventral view of a trochamminid showing the inner part of the whorl in fig. B (box in fig. A is enlarged in fig. B);

C-E C, D, Another trochamminid showing ventral side (box in fig. C is enlarged in fig. D); E, dorsal view of same trochamminid specimen showing another aperture-like structure;

F-H Edge view of a trochamminid with chamber partly missing exposing the inner part of chamber (box in figure F progressively enlarged in figures G and H) showing the foramen on one septum;

I,J Dorsal view of a trochamminid again with part of outer whorl missing (box in fig. I enlarged in fig. J) exposing inner chambers and sutures (arrow).



REFERENCES

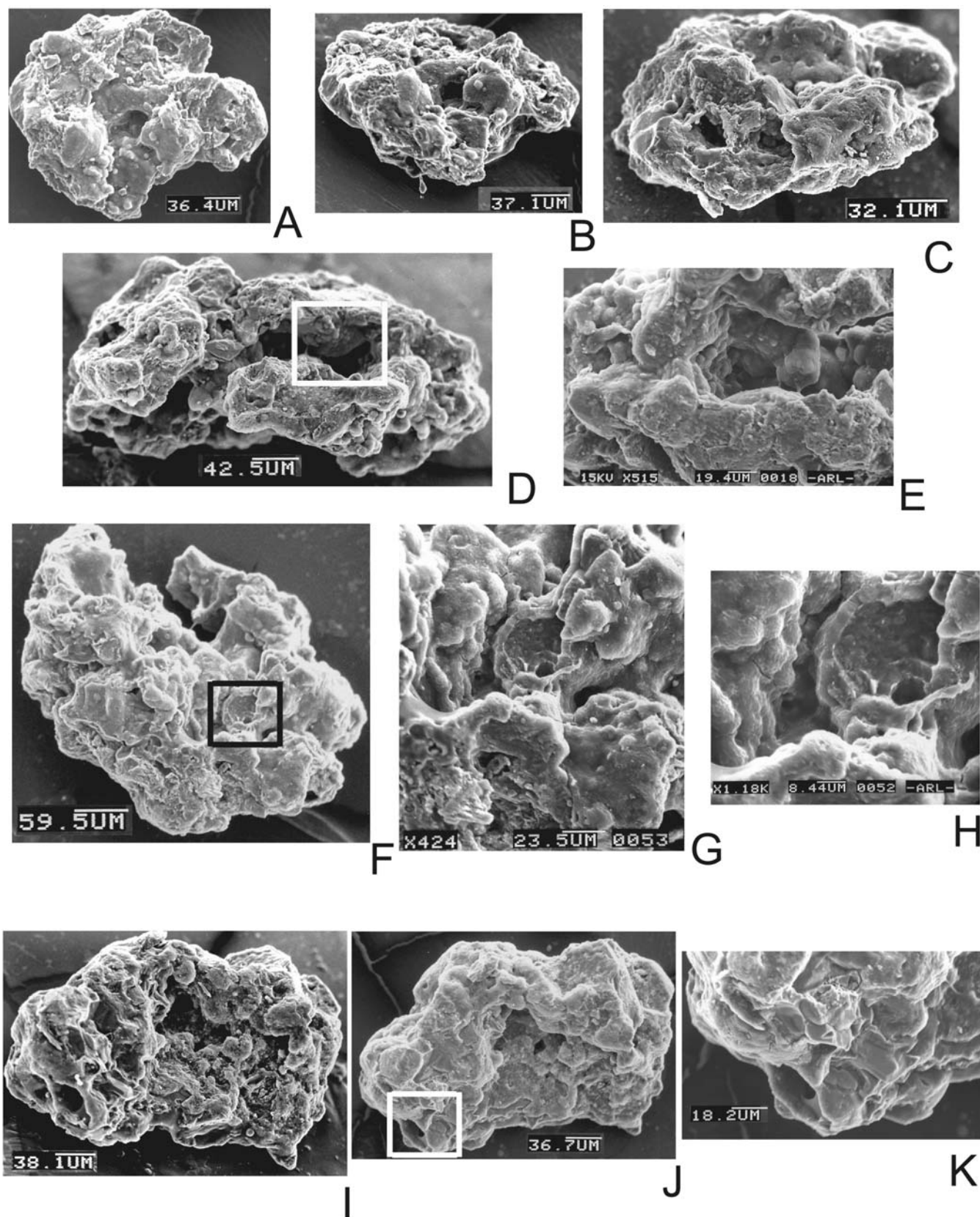
- BATTEN, D. J. and GRENFELL, H. R., 1996. Green and blue-green algae 7D-*Botryococcus*. In: Jansonius, J. and McGregor, D.C. Eds. *Palynology: Principles and Applications: American Association of Stratigraphic Palynologists Foundation*, 1: 205-214.
- CLARKE, D. B., and HALLIDAY, A. N., 1980. Strontium isotope geology of the South Mountain batholith, Nova Scotia. *Geochimica et Cosmochimica Acta*, 44:1045-1058.
- COPE, J. C. W., and MCILROY, D., 1998. On the occurrence of the foraminiferans in the lower Cambrian of the Llangynog Inlier, South Wales. *Geological Magazine*, 135: 227-229.
- COURTESOLE, R., 1973. Le Cambrien Moyen de la Montagne Noire: biostratigraphie. Laboratoire de Geologie CEARN, Faculté des Sciences de Toulouse, Toulouse, 248 p.
- CROSBY, D. G., 1962. Wolfville map-area, Nova Scotia. Geological Survey of Canada, Memoir 325, 67 p.
- CULVER, S. J., 1991. Early Cambrian foraminifera from West Africa. *Science*, 254: 689-691.
- , 1994. Early Cambrian foraminifera from the southeastern Taoudeni Basin, West Africa. *Journal of Foraminiferal Research*, 24:191-202.
- CULVER, S. J., REPETSKI, J. E., POJETA, J., Jr., and HUNT, D., 1996. Early and middle (?) Cambrian metazoan and protistan fossils from West Africa. *Journal of Paleontology*, 70: 1-6.
- CUMMING, L. M., 1985. A Halifax slate graptolite locality, Nova Scotia. Geological Survey of Canada, Current Research, part A., Paper 85-1A: 215-221.
- DAHLGRÜN, F., 1934. Zur Altersdeutung des Vordevons im westsudetischen Schiefergebirge: *Zeitschrift für Deutsch Geologie Gesellschaften*, 86: 385-393.
- DALLMEYER, R. D., and KEPPIE, J. D., 1987. Polyphase late Paleozoic tectonothermal evolution of the southwest Meguma Terrane, Nova Scotia: Evidence from $^{40}\text{Ar}/^{39}\text{Ar}$ mineral ages. *Canadian Journal of Earth Sciences*, 24: 1242-1254.
- GUTSCHICK, R. C., 1986. Middle Ordovician agglutinated foraminifera including *Reophax* from the Mifflin Formation, Platteville Group of Illinois. *Journal of Paleontology*, 60: 233-248.
- HARRIS, I. M., and SCHENK, P. E., 1975. The Meguma Group. *Maritime Sediments*, 11: 25-46.
- KEPPIE, J. D., 1977. Tectonics of southern Nova Scotia. Nova Scotia Department of Mines, Paper 77- 1, 34p.
- KEPPIE, J. D., and MUECKE, G. K., 1979. Metamorphic map of Nova Scotia. Nova Scotia Department of Mines, Map, scale 1: 1,000,000.
- KROGH, T. E., and KEPPIE, J. D., 1990. Age of detrital zircon and titanite in the Meguma Group, southern Nova Scotia, Canada: Clues to the origin of the Meguma Terrane. *Tectonophysics*, 177: 307-323.
- LOEBLICH, A. R. JR., and TAPPAN, H., 1964. Sarcodina (chiefly "thecamoebians" and foraminiferida). In: Moore, R. C. et al., Eds. *Treatise on Invertebrate Paleontology*, part C, Protista 2, v. 1, 2, Geological Society of America and University of Kansas Press, 900p.
- , 1988, *Foraminiferal Genera and their Classification*. New York: Van Nostrand Reinhold Co., v. 1, 2, p. 1-970.
- MARTINSSON, A., 1974. The Cambrian of Norden. In: Holland C. H., Ed. *Cambrian of the British Isles, Norden, and Spitsbergen*. London: John Wiley & Sons, 185-283.
- MCILROY, D., GREEN, O. R., and BRASIER, M. D., 1994. The world's oldest foraminiferans. *Microscopy Analysis*, 147:13-15.
- MEDIOLI, F. S., and SCOTT, D. B., 1983. Testate arcellaceans of eastern Canada. Cushman Foundation for Foraminiferal Research, Special Publication No. 21, 63 p.
- MUECKE, G.K., ELIAS, P., and REYNOLDS, P.H., 1988. Hercynian/Alleghenian overprinting of an Acadian Terrane: $^{40}\text{Ar}/^{39}\text{Ar}$ studies in the Meguma Zone, Nova Scotia, Canada. *Chemical Geology*, 73:153- 167.
- O'BRIEN, B. H., 1986. Preliminary report on the geology of the Mahone Bay area, Nova Scotia. Geological Survey of Canada, Current Research, Part A, Paper 86-1A: 439-444.
- PHINNEY, W. C., 1961. Possible turbidity current deposit in Nova Scotia. *Geological Society of America Bulletin*, 72: 1453-1454.
- PORTER, S. M., and KNOLL, A. H., 2000. Testate amoebae in the Neoproterozoic Era: Evidence from vase-shaped microfossils in the Chuar Group, Grand Canyon. *Journal of Paleobiology*, 26: 360-388.
- PRATT, B. R., and WALDRON, J. W. F., 1991. A Middle Cambrian trilobite faunule from the Meguma group of Nova Scotia. *Canadian Journal of Earth Sciences*, 28: 1843-1853.
- SCHENK, P. E., 1970. Regional variation of the flysch-like Meguma Group (lower Paleozoic) of Nova Scotia, compared to recent sedimentation off the Scotian Shelf. In: Lajoie, J., Ed. *Flysch sedimentology in North America*, Geological Association of Canada, Special Paper no. 7: 127- 153.
- , 1976. A regional synthesis (of Nova Scotia geology). *Maritime Sediments*, 12: 17-24.

PLATE 6

SEM photographs of specimens from site 1; scale bars are on each photograph.

- A-C "*Haplophragmoides*-like" specimen in side view (fig. A) and tilted views (figs. B, C) showing the raised rim around the umbilicus;
- D,E "*Haplophragmoides*-like" specimen showing the planispiral structure, the box in fig. D is enlarged in fig. E giving a sense of the spiral inside the umbilicus;

- F-H "*Haplophragmoides*-like" broken specimen showing the inside of the inner whorl and revealing the proloculus (box in fig. F, enlarged in figs. G, H);
- I-K "*Ammobaculites*-like" specimen, fig. I showing the agglutinated nature of these specimens and figs. J, K showing an aperture (box in fig. J enlarged in fig. K).



- , 1995. Chapter 3, Meguma Zone. In: Williams, H., Ed, Geology of the Appalachian-Caledonian Orogen in Canada and Greenland. Geological Survey of Canada, Geology of Canada, no. 6: 261-277.
- , 1997. Sequence stratigraphy and provenance on Gondwana's margin: the Meguma Zone (Cambrian to Devonian) of Nova Scotia, Canada. Geological Society of America Bulletin, 109: 395-409.
- SCHRANK, E., 1977. Kambrische Trilobiten der China-Kollektion v. Richthofen 4 und letzter Teil: Mittelkambrische Fauna von Wulopu. Zeitschrift für Geologische Wissenschaften (Berlin), 5: 141-165.
- SCOTT, D. B. and MEDIOLI, F. S., 1980. Quantitative studies of marsh foraminiferal distributions in Nova Scotia: Their implications for the study of sea-level changes. Cushman Foundation for Foraminiferal Research, Special Publication no. 17, 63p.
- SCOTT, D. B., MEDIOLI, F. S. and SCHAFER, C. T., 2001. Monitoring of Coastal Environments using Foraminifera and Thecamoebian Indicators. Cambridge University Press, 176p.
- SDZUY, K., 1972. Das Kambrium der acadobaltischen Faunenprovinz. Zentralblatt für Geologie und Paläontologie, 2: 1-91.
- SKOWRONEK, A., and STEFFAHN J., 2000. The age of the Cuffing Limestone (W Sedates, Poland) -a revision due to new discovery of microfossils. Neues Jahrbuch für Geologies und Paleontologie, Monatshefte, 2: 65-82.
- SMITHERINGALE, W. C., 1960. Geology of Nictaux-Torbrook map-area, Annapolis and Kings counties, Nova Scotia. Geological Survey of Canada, Paper 60-13, 32 p.
- SNAJDR, M., 1958. Trilobiti českého středního kambria [The trilobites of the Middle Cambrian of Bohemia]. Rozpravy Ustředního ústavu geologického, no. 24, 280 p.
- SOLLAS, W. J., 1921. On *Saccammina carteri* Brady, and the minute structure of the foraminiferal shell. Quarterly Journal of the Geological Society of London, 77: 193-212.
- STOW, D. A. V., ALAM, M., and PIPER, D. J. W., 1984. Sedimentology of the Halifax Formation, Nova Scotia: Lower Palaeozoic fine-grained turbidites. In: Piper, D.J.W., and Stow, D.A.V., Eds. Fine grained sediments: Deep-water processes and facies: Geological Society of London, Special Publication no. 15: 127-144.
- TAYLOR, F.C., 1969. Geology of the Annapolis-St. Mary's Bay map-area, Nova Scotia (21 A, 21 B east half). Geological Survey of Canada, Memoir 358, 65 p.
- THIBAUDEAU, S., 1994. Agglutinated brackish water foraminifera and arcellaceans from the upper Carboniferous, coal-bearing strata of the Sydney Basin, Nova Scotia: Taxonomic descriptions, assemblages, and environments of deposition: unpublished MS thesis, Dalhousie University, 252 p.
- TIBERT, N. E., 1996. A paleoecological interpretation for the ostracodes and agglutinated foraminifera from the earliest Carboniferous marginal marine Horton Bluff Formation (Blue Beach Member), Nova Scotia, Canada: unpublished MS. thesis, Dalhousie University, 300 p.
- TIBERT, N. E., and SCOTT, D. B., 1999. Ostracodes and agglutinated foraminifera as indicators of paleoenvironmental change in an Early Carboniferous brackish bay, Atlantic Canada. Palaeos, 14: 246-260.
- WALDRON, J. W. F., 1987. Sedimentology of the Goldenville-Halifax transition in the Tancook Island area, South Shore, Nova Scotia. Geological Survey of Canada, Open File 1535, 1 p. 4 sheets, 3 appendices.
- WALDRON, J. W. F., and JENSEN, L. R., 1985. Sedimentology of the Goldenville Formation, Eastern Shore, Nova Scotia. Geological Survey of Canada, Paper 85-15, 31 p.
- WALL, J. H., 1976. Marginal marine foraminifera from the Late Cretaceous Bearpaw-Horseshoe Canyon transition, southern Alberta, Canada. Journal of Foraminiferal Research, 6:193-201.

PLATE 7

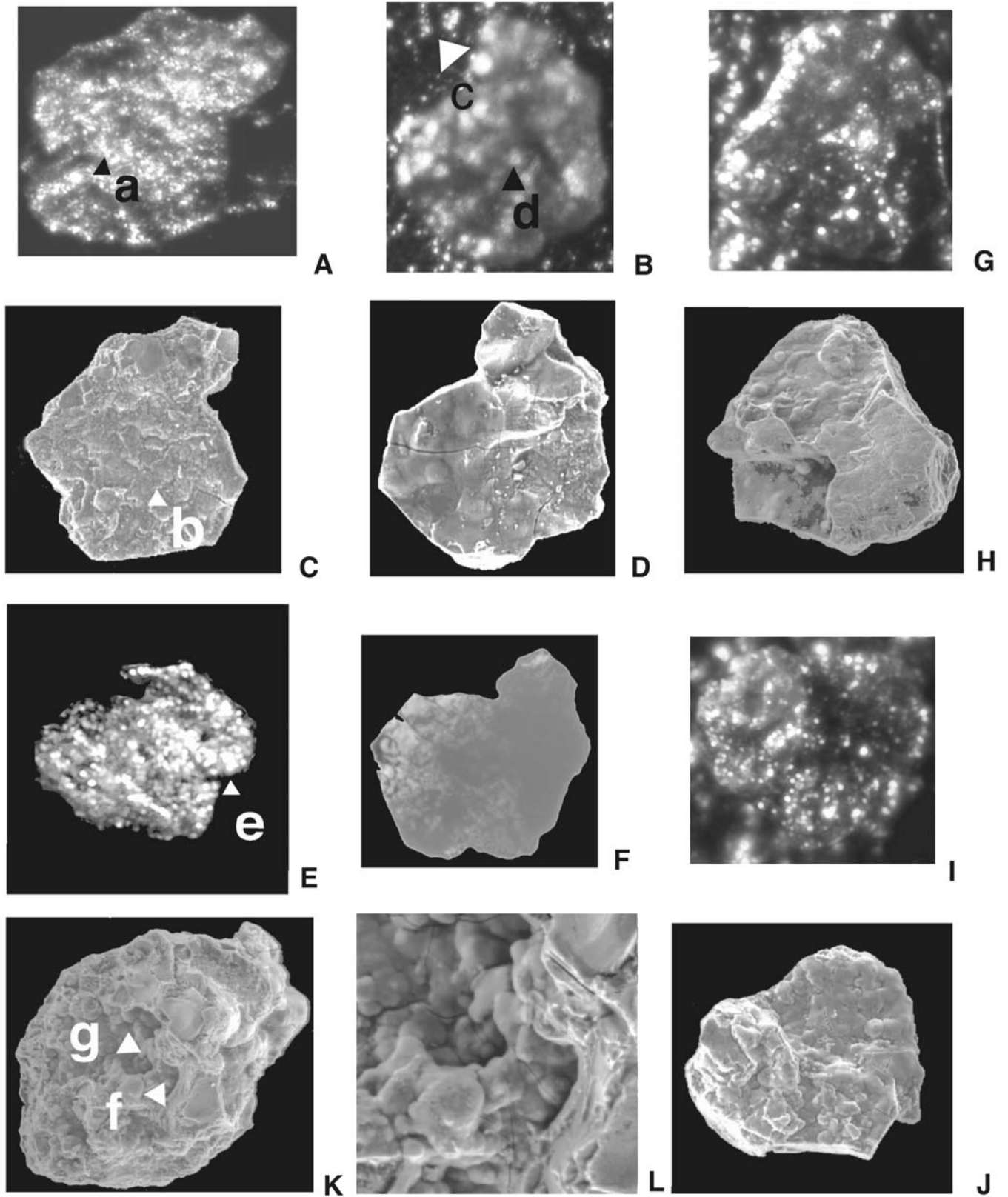
Various types of photographic techniques for specimens of site 2; all magnifications from A to J are $\times 640$.

Figure A-F (Specimen 1) (trochamminid), USNM # 510790.

- | | |
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| <p>A SLM ventral view, arrow a indicates inner umbilical area;</p> <p>B reflected light dorsal view, arrow d indicates the inner whorl, arrow c indicates the last chamber;</p> <p>C SEM ventral view, arrow b indicates the same position as arrow a in fig. A;</p> | <p>D SEM dorsal view;</p> <p>E reflected light slanted view of the last chamber (arrow e);</p> <p>F transmitted light dorsal or ventral view with faint shadows of chambers.</p> |
|--|--|

Figures G-J (specimen 2) (trochamminid), USNM # 510791).

- | | |
|---|--|
| <p>G reflected light dorsal view;</p> <p>H SEM dorsal view;</p> <p>I reflected light ventral view;</p> <p>J SEM ventral view;</p> | <p>K SEM ventral view ($\times 480$) of specimen showing apertures (arrows g and f);</p> <p>L Same specimen as figure K ($\times 1310$), enlarged to show the rim around the aperture (arrow f).</p> |
|---|--|



- WALTER, M. R., GROTZINGER, J. P., and SCHOPF, J. W., 1992, Proterozoic stromatolites. In: Schopf, J.W. and Klein, C., Eds. The Proterozoic Biosphere. New York: Cambridge University Press, 253-260.
- WANLESS, R. K., STEVENS, R. D., LACHANCE, G. R., and DELABIO R. N., 1972. Age determinations and geological studies, K-Ar isotopic ages. Geological Survey of Canada, Paper 71-2, 96p.
- WESTERGÅRD, A. H., 1953. Non-agnostidean trilobites of the Middle Cambrian of Sweden, III. Sveriges Geologiska Undersökning, Series C, no. 46, 42 p.
- WIGHTMAN, W. G., SCOTT, D. B., MEDIOLI, F. S., and GIBLING, M.R., 1993. Carboniferous marsh foraminifera from coal-bearing strata at the Sydney Basin, Nova Scotia: a new tool for identifying paralic coal-forming environments. *Geology*, 21: 631-634.
- WIGHTMAN, W. G., SCOTT, D. B., MEDIOLI, F. S., and GIBLING, M.R., 1994. Agglutinated foraminifera and thecamoebians from the late Carboniferous Sydney coalfield, Nova Scotia: paleoecology, paleoenvironments, and paleogeographical implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 106:187-202.
- WILLIAMS, H., and HATCHER, R. D., 1982. Suspect terranes and accretionary history of the Appalachian orogen. *Geology*, 10: 530-536.

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