

Acritarchs from the Hanford Brook Formation, New Brunswick, Canada: new biochronological constraints on the *Protolenus elegans* Zone and the Cambrian Series 2–3 transition

TEODORO PALACIOS*†, SÖREN JENSEN*, SANDRA M. BARR‡, CHRIS E. WHITE§ & RANDALL F. MILLER¶

*Área de Paleontología, Facultad de Ciencias, University of Extremadura, 06006 Badajoz, Spain

‡Department of Earth & Environmental Science, Acadia University, Wolfville, NS, B4P 2R6, Canada

§Nova Scotia Department of Natural Resources, Halifax, NS, B3J 2T9, Canada

¶New Brunswick Museum, 277 Douglas Avenue, Saint John, New Brunswick, E2K 1E5, Canada

(Received 17 April 2015; accepted 4 March 2016; first published online 27 April 2016)

Abstract – Diverse and well-preserved acritarchs are reported from the type section of the Cambrian Hanford Brook Formation at Hanford Brook, southern New Brunswick. This section fills an important gap in acritarch studies by providing the first detailed picture of changing acritarch associations close to the traditional lower–middle Cambrian boundary in Avalonia. Acritarchs from the St Martins Member, at the base of the succession, include *Skiagia ciliosa*, *Heliosphaeridium notatum*, *H. longum* and *Liepaina plana* and suggest attribution to Cambrian Stage 4. Acritarchs from the Somerset Street Member, in the middle of the formation, include *Eliasum llaniscum* and *Comasphaeridium silesiense*. This information adds new biochronological context to an ash bed in the Somerset Street Member previously dated as *c.* 510 Ma or 508 Ma, and to the endemic trilobites from the same member, including *Protolenus elegans*. It also places absolute ages on the basal range of stratigraphically important acritarchs. Both the acritarch assemblage and the radiometric age are consistent with a position very close to the traditional lower–middle Cambrian transition and likely within Cambrian Stage 5. Acritarchs from the Long Island Member, at the top of the succession, include additional taxa demonstrating assignment to Cambrian Stage 5. Both the Somerset Street and Long Island members probably correlate with the *Morocconus notabilis* Zone. The new acritarch species *Retisphaeridium striatum* Palacios is described. New data are presented on acritarchs from the upper part of the Hell's Mouth Formation, Wales, and correlation proposed with the Long Island Member.

Keywords: New Brunswick, Wales, acritarchs, middle Cambrian, Cambrian Series 3.

1. Introduction

The siliciclastic Hanford Brook Formation of southern New Brunswick has remained of international interest ever since George F. Matthew and his son William described the trilobite *Protolenus* and associated fauna from a section on Hanford Brook, some 40 km east of the city of Saint John (Matthew, 1892, 1895; Fig. 1). Protolenid trilobites were subsequently found elsewhere in Maritime Canada, various locations in present-day Europe and northern Africa, and found to consistently pre-date paradoxidids, trilobites widely considered to be middle Cambrian marker fossils (e.g. Cobbold, 1910; Richter & Richter, 1941; Schwarzbach, 1939) (lower Cambrian and middle Cambrian are here used in the sense of Lower Cambrian and Middle Cambrian, informal series that were used with more or less specific regional definitions and in a somewhat disparate sense in the various regions). Various, but often tentatively defined, *Protolenus* zones have been therefore considered terminal early Cambrian (e.g. Cowie, Rushton & Stubblefield, 1972; Sdzuy, 1972). This in-

terpretation has more recently come into question as the stratigraphical ranges of protolenids and paradoxidids overlap in both Morocco and Turkey (e.g. Geyer, 1990a; Dean & Özgül, 1994; Fletcher, 2003). Furthermore, most protolenid species have highly restricted geographic ranges, meaning that they have limited use in direct correlation. *Protolenus elegans*, for example, has not been found outside the Hanford Brook Formation.

Particularly relevant to current discussions on Cambrian stratigraphy, the Hanford Brook Formation contains one of the few dated ashes with a position close to the traditional lower–middle Cambrian transition, and to the as yet undefined Cambrian Series 2 to Cambrian Series 3 boundary (Peng, Babcock & Cooper, 2012). This ash bed, from the Somerset Street section in the city of Saint John (Fig. 1), originally reported as *c.* 511 Ma (Landing *et al.* 1998), was an important piece of evidence in establishing the current Cambrian time scale. The biochronological context of this ash bed is, however, not known with precision as the fauna of the Hanford Brook Formation consists of species not known elsewhere (trilobites; Westrop & Landing, 2000) or with relatively long stratigraphic ranges

†Author for correspondence: medrano@unex.es

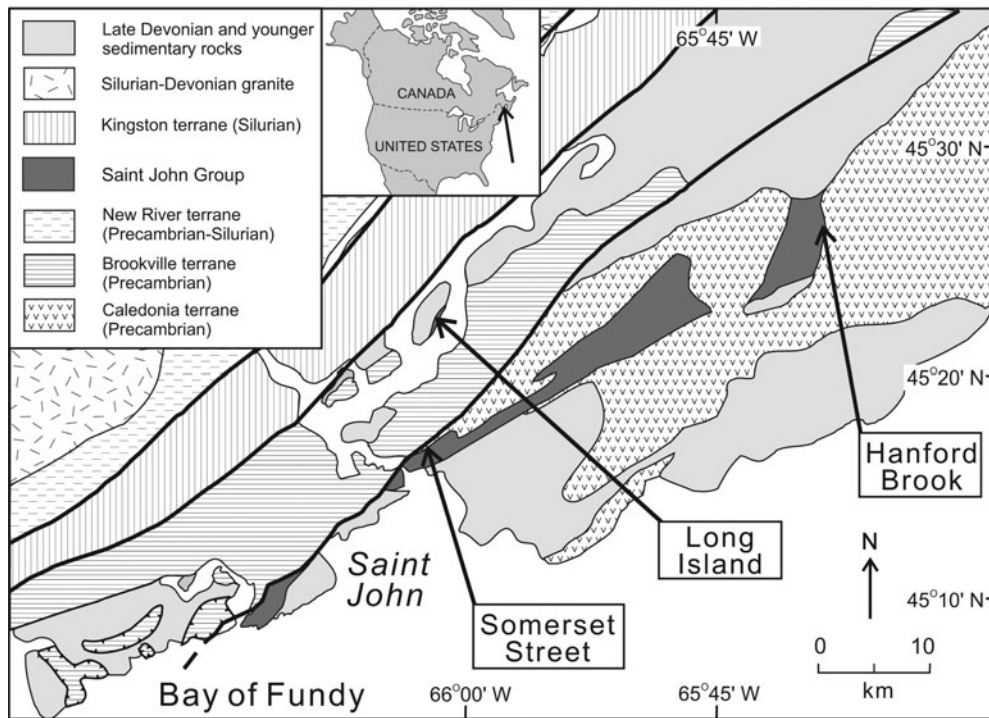


Figure 1. Location and geological setting for the Hanford Brook Formation in southern New Brunswick.

(brachiopods and bradorids; Siveter & Williams, 1997). Landing *et al.* (1998) suggested that the dated ash bed correlates with the late early Cambrian Toyonian Stage of Siberia (see Fig. 2). However, it has also been suggested that beds with *Protolenus elegans* correlate with the *Morocconus notabilis* Zone of Morocco (Geyer & Palmer, 1995; Geyer, Buschmann & Elicki, 2014), there traditionally considered middle Cambrian, and either uppermost Cambrian Series 2 or basal Cambrian Series 3 (Geyer, 2015; Fig. 2).

Here we provide new biochronological information on the Hanford Brook Formation based on the first study of acritarchs from this unit. Acritarchs have been widely used to provide biochronological age constraints on the traditional lower–middle Cambrian transition in the Acado-Baltic region and have been proposed as potential markers for the lower–middle Cambrian boundary there (e.g. Moczyłowska, 1999). Because Cambrian acritarchs show a high degree of cosmopolitanism (e.g. Molyneux *et al.* 2013), they have the potential to add insights into correlations where other fossil groups have more local distributions.

2. Geological setting and fauna

The Hanford Brook Formation is part of the Cambrian–Ordovician Saint John Group, a succession of mainly siliciclastic sedimentary rocks that crop out in fault-bounded slivers in and around Saint John, New Brunswick (Fig. 1; Tanoli & Pickerill, 1988). The thickest and best-preserved section of the Hanford Brook Formation is on Hanford Brook. The general lithological succession and fossil contents were first outlined by Matthew (e.g. 1890, 1895), who recognized this unit

	Siberia	Morocco	New Brunswick
Cambrian Series 3	O. i. middle Cambrian Amgan	<i>Pt. gibbus</i>	Forest Hills Formation
		<i>Kuonamkites</i>	
		<i>Oryctocara/Enixus ant.</i>	
Cambrian Series 2	O. g. lower Cambrian Botoman Toyonian	<i>Kymataspis arenosus</i>	Hanford Brook Formation
		<i>Ornamentaspis frequens</i>	
		<i>Morocconus notabilis</i>	
Cambrian Series 1	I. Cambrian	<i>Hupeolenus</i>	Long Island Member
		<i>Sectigena</i>	Somerset Street Mbr
			St Martins Member

Figure 2. Acritarch-based chronostratigraphic context of the Hanford Brook Formation with respect to the traditional lower–middle Cambrian transition as recognized in Siberia and Morocco, and the two possible candidate definitions for the base of Cambrian Series 2 on the first appearance of *Ovatoryctocara granulata* (O. g.) or *Oryctocephalus indicus* (O. i.). Correlation of Siberia and Morocco based on Geyer (2015).

as band b of division 1 of the (then) St John Group. The name Hanford Brook Formation originated from Hayes & Howell (1937), who recognized two members:

a lower *Beyrichonia* sandstone consisting of grey fine-grained sandstone, with glauconite, from which have been recovered brachiopods and bradorids but with no confirmed finds of trilobites, and an upper trilobite-bearing *Protolenus* shale dominated by siltstone and shale. Hayes & Howell (1937) remarked that this division is readily recognized only at Hanford Brook and that also here the transition is gradual. They also remarked on black sandstone that locally separates the Hanford Brook Formation from the underlying white quartz arenite of the Glen Falls Formation. The Hanford Brook Formation is overlain by dark shale of the Forest Hills Formation, yielding paradoxid trilobites, a unit that has been correlated with, and by some equated with, the Chamberlain's Brook Formation in Newfoundland.

In recent studies of the Hanford Brook Formation, Landing & Westrop (1996, 1998) and Westrop & Landing (2000) revised the lithostratigraphical terminology and introduced three members (facies associations), and new insights were offered on the sedimentology and depositional history. Their St Martins Member approximates to the *Beyrichonia* sandstone of Hayes & Howell (1937), with the addition of the basal black sandstone, the base of which they interpreted to represent a depositional hiatus from the underlying white quartzite. They interpreted the St Martins Member to represent nearshore deposition. The overlying dark grey mudstone and fine sandstone facies of the *Protolenus elegans*-bearing Somerset Street Member was interpreted by Landing & Westrop (1996) as dysaerobic sediments formed on a low-energy shelf. As originally conceived the top of this member consists of thick beds of massive quartz arenite, which they, in a later paper (Landing & Westrop, 1998), made the basal part of the Long Island Member, and which they interpreted to represent a depositional hiatus. The Long Island Member consists of mudstone and fine- to medium-grained grey sandstone, with hummocky cross-stratification and planar lamination. As already first observed by Matthew (1890) the sandstone beds are typically streaky owing to iron oxides.

A modern revision of the Hanford Brook trilobites is found in Westrop & Landing (2000), and the bradorids were critically reviewed by Siveter & Williams (1997). From the Somerset Street Member are known *Protolenus elegans*, *Protolenus? articephalus*, *Protagraulos priscus*, *Micmacca matthewi*, *Conomicmacca plana* and *Ellipsocephalus? galeatus*. These fossils are all known only from the Hanford Brook Formation, and several are known from scarce material only (see Westrop & Landing, 2000). Trilobites in the Long Island Member on Hanford Brook include *Kingaspidoidea cf. obliquoculatus* and, on Long Island, *Berabichia milleri* (Westrop & Landing, 2000). Because *Protolenus elegans* only occurs in a narrow portion of the strata that had been historically assigned to the *Protolenus* Zone, Westrop & Landing (2000) erected the *Protolenus elegans* Zone, with a more restricted stratigraphical range.

The Forest Hills Formation is dominated by grey mudstone with an impure limestone, close to the base. Trilobites in the basal part of the Forest Hills Formation, including *Eccaparadoxides etemnicus*, indicate correlation with the upper part of the Chamberlain's Brook Formation in Newfoundland, and the presence of a depositional break between the Hanford Brook and Forest Hills formations (e.g. Landing & Westrop, 1996).

3. Sections and sampling

The present study is largely based on detailed sampling through the Hanford Brook Formation at Hanford Brook (Fig. 1). Here the contact of the St Martins Member with the underlying Glen Falls Formation is not exposed. The Somerset Street Member is continuously exposed. We sampled the lower and upper parts of the Long Island Member, whereas the middle portion is covered. The lower part of the Forest Hills Formation was also sampled. The distribution of samples collected in 2012 is shown in Figure 3, which also indicates occurrences of selected acritarchs, and an interpretation of how our measured section compares to the members of Landing & Westrop (1998). The positions of acritarch samples are well constrained with respect to those of key levels yielding trilobites in earlier studies. Figure 4 includes complete information on acritarchs in each sample and also adds information from less systematic sampling in 2008 and 2009. The approximate positions of these samples relative to those of the 2012 samples are indicated.

Additional sampling of the Hanford Brook Formation was made within the area of the city of Saint John, on Somerset Street, and on Long Island (Fig. 1). The section on Somerset Street consists of a thin St Martins Member and the Somerset Street Member. Although the fine-grained material of the Hanford Brook Formation in this section is affected by metamorphism, the section is of importance as the location of the ash bed dated by Landing *et al.* (1998). Samples from coastal exposures on Long Island are within the Long Island Member.

Samples of shale and mudstone of about 50 grams were collected and treated with palynological preparation techniques as outlined in Vidal (1988). Palynological slides containing figured and type material are deposited in the collections of the New Brunswick Museum (NBMG), Saint John, New Brunswick, with numbers 15578–15597, except material from the Hell's Mouth Formation, Wales, which is deposited in the collections of Área de Paleontología of the Universidad de Extremadura, Badajoz. Accession numbers are referred to in the figure captions, which also provide sample numbers and England finder coordinates.

4. Distribution of acritarchs

Most acritarchs from the Hanford Brook Formation are readily identifiable as well-characterized species

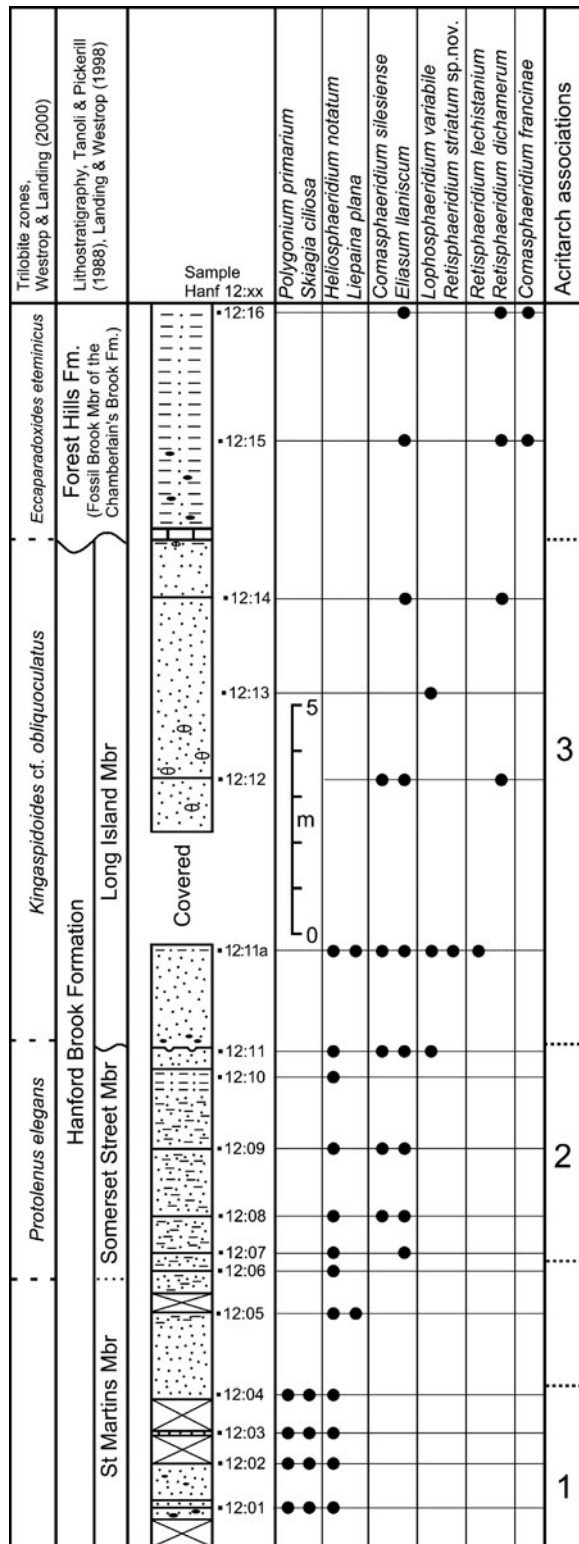


Figure 3. Distribution of the more representative acritarchs in the Hanford Brook Formation and lower part of the Forest Hills Formation on the basis of sampling conducted in 2012. Full species list is provided in Figure 4.

(Figs 5–12). In the systematic palaeontology (Section 8 below) remarks are provided on the identification of *Retisphaeridium* Staplin, Jansonius & Pocock (1965), *Retisphaeridium lechistanium* Jachowicz-Zdanowska (2013) and *Lophosphaeridium variabile*

Volkova (1974), and the new species *Retisphaeridium striatum* Palacios sp. nov., is described.

4.a. Hanford Brook Formation, Hanford Brook section

In this section acritarchs are well preserved and the near complete outcrop has enabled a clear palynological characterization of the section. Three distinctive associations of acritarchs are recognized (Fig. 3). The preservation of acritarchs in the St Martins and Long Island members is generally superior to that of the Somerset Street Member, in which acritarch vesicles are affected by the growth of cubic or framboidal pyrite. This is consistent with more strongly reducing conditions during deposition of the Somerset Street Member. The occurrence in sample Hanf 12:11 of the problematic organic-walled microfossil *Octoedryxium truncatum* Rudavskaya, 1973 is possible direct evidence for sulphate-reducing bacteria (cf. Stanevich, 2003).

Association 1, found in much of the St Martins Member, includes diverse and well-preserved acritarchs of the diagnostic species *Skiagia ciliosa* (Volkova) Downie, 1982 (Fig. 5a–c), *S. orbiculare* (Volkova) Downie, 1982, *Polygonium primum* (Jankauskas) Sarjeant & Stancliffe, 1994 (Fig. 5e, f), *P. varium* (Volkova) Moczyłowska, 1991 (Fig. 6h), *Heliosphaeridium notatum* (Volkova) Moczyłowska, 1991 (Fig. 6b), *Comasphaeridium strigosum* (Jankauskas) Downie, 1982 (Fig. 9a), *Heliosphaeridium longum* (Moczyłowska) Moczyłowska, 1991 (Fig. 6c), *H. dissimilare* (Volkova) Moczyłowska, 1991 (Fig. 6a), *Granomarginata squamacea* Volkova, 1968, *Solisphaeridium implicatum* (Fridrichsone) Moczyłowska, 1998, *Globosphaeridium cerinum* (Volkova) Moczyłowska, 1991, and scarce *Liepaina plana* Jankauskas & Volkova in Volkova et al. 1979 (Fig. 6i) and *Skiagia insigne* (Fridrichsone) Downie, 1982 (Fig. 5d).

Association 2, found through the Somerset Street Member, is characterized by the appearance of *Comasphaeridium silesiense* Moczyłowska, 1998 (Fig. 9b, d), undoubted *Eliasum llaniscum* Fombella, 1977 (Fig. 7d), *Lophosphaeridium variabile* Volkova, 1974 (Fig. 7a, b), *Multiplicisphaeridium dactylum* Vidal in Moczyłowska & Vidal, 1988 (Fig. 6e, f) and *Heliosphaeridium* sp. A (Fig. 6d). These are associated with species present in the previous association such as *Heliosphaeridium notatum* and *H. longum*. Besides the first appearance of several taxa, of note is the disappearance of *Polygonium primum* and *Skiagia* species, and a short interval in the upper part of the St Martins Member characterized by a low diversity and abundant non-diagnostic *Leiosphaeridia* spp.

Association 3, coinciding with the Long Island Member, is marked by the appearance of *Celtiberium* sp. (Fig. 6g), *Comasphaeridium maximum* Palacios, 2015 (Fig. 8b), *C. longispinosum* Hagenfeldt, 1989 (Fig. 9c), *Retisphaeridium dichamerum* Staplin, Jansonius & Pocock, 1965, *R. lechistanium* Jachowicz-Zdanowska, 2013 (Fig. 12a–d) and *Retisphaeridium*

		<i>Comasphaeridium strigosum</i>	<i>Globosphaeridium cerinum</i>	<i>Lophosphaeridium tentativum</i>	<i>Heliosphaeridium dissimilare</i>	<i>Polygonium varium</i>	<i>Polygonium primarium</i>	<i>Skiagia ciliosa</i>	<i>Skiagia orbiculare</i>	<i>Skiagia insigne</i>	<i>Solisphaeridium implicatum</i>	<i>Heliosphaeridium notatum</i>	<i>Liepaina plana</i>	<i>Heliosphaeridium longum</i>	<i>Comasphaeridium silesiense</i>	<i>Eliasum ilaniscum</i>	<i>Heliosphaeridium sp. A</i>	<i>Lophosphaeridium variabile</i>	<i>Multiplicisphaeridium dactilum</i>	<i>aff. Sagatum priscum</i>	<i>Celtiberium sp. A</i>	<i>Retisphaeridium striatum sp. nov.</i>	<i>Retisphaeridium lechistanium</i>	<i>Retisphaeridium dichamerum</i>	<i>Comasphaeridium maximum</i>	<i>Comasphaeridium longispinosum</i>	<i>Comasphaeridium francinae</i>			
Hanford Brook Fm.	Forest Hills Fm.	Hanf12-18																												
		Hanf12-16																												
		Hanf12-15																												
	Long Island Mbr	Hanf12-14																												
		Hanf09-10																												
		Hanf12-13																												
		Hanf12-12																												
		Hanf12-11a																												
		Hanf12-11																												
	Somerset Street Mbr	Hanf12-10																												
		Hanf12-9																												
		Hanf08-16																												
		Hanf08-15																												
		Hanf09-7																												
		Hanf12-8																												
		Hanf12-7																												
		Hanf09-6																												
		Hanf09-5																												
		Hanf12-6																												
	St. Martins Mbr	Hanf12-5																												
		Hanf12-4																												
		Hanf12-3																												
		Hanf12-2																												
		Hanf08-14																												
		Hanf09-3																												
		Hanf12-1																												
	Hanf09-1																													

Figure 4. (Colour online) Plot of acritarchs found in samples of the Hanford Brook Formation and lower part of the Forest Hills Formation collected in 2008, 2009 and 2012. Sample 09:1 approximates level of sample 12:1. Samples 09:3 and 08:14 approximate level of 12:4. Sample 09:5 approximates level of sample 12:7. Samples 08:15 and 09:6 approximate level of sample 12:8. Samples 08:16 and 09:7 approximate level of sample 12:9.

striatum Palacios sp. nov (Fig. 11a). This assemblage also includes abundant and well-preserved *Liepaina plana* (acme) (Fig. 6j) and aff. *Sagatum priscum* (Kiry-anov & Volkova) Vavrdová & Bek, 2001 (Fig. 8a).

4.b. Hanford Brook Formation, other sections

Acritarchs are scarce and poorly preserved in the Hanford Brook Formation in the Somerset Street section. *Skiagia* cf. *ciliosa* was identified close to the St Martins Member – Somerset Street Member transition,

and in samples some metres above the dated ash bed were found *Heliosphaeridium longum* and *H. notatum*. Samples from the Long Island Member on Long Island include *Retisphaeridium striatum* (Fig. 11b) and *R. lechistanium*, also found in this member on Hanford Brook.

4.c. Forest Hills Formation, Hanford Brook section

In samples from the Forest Hills Formation appear abundant *Comasphaeridium francinae*

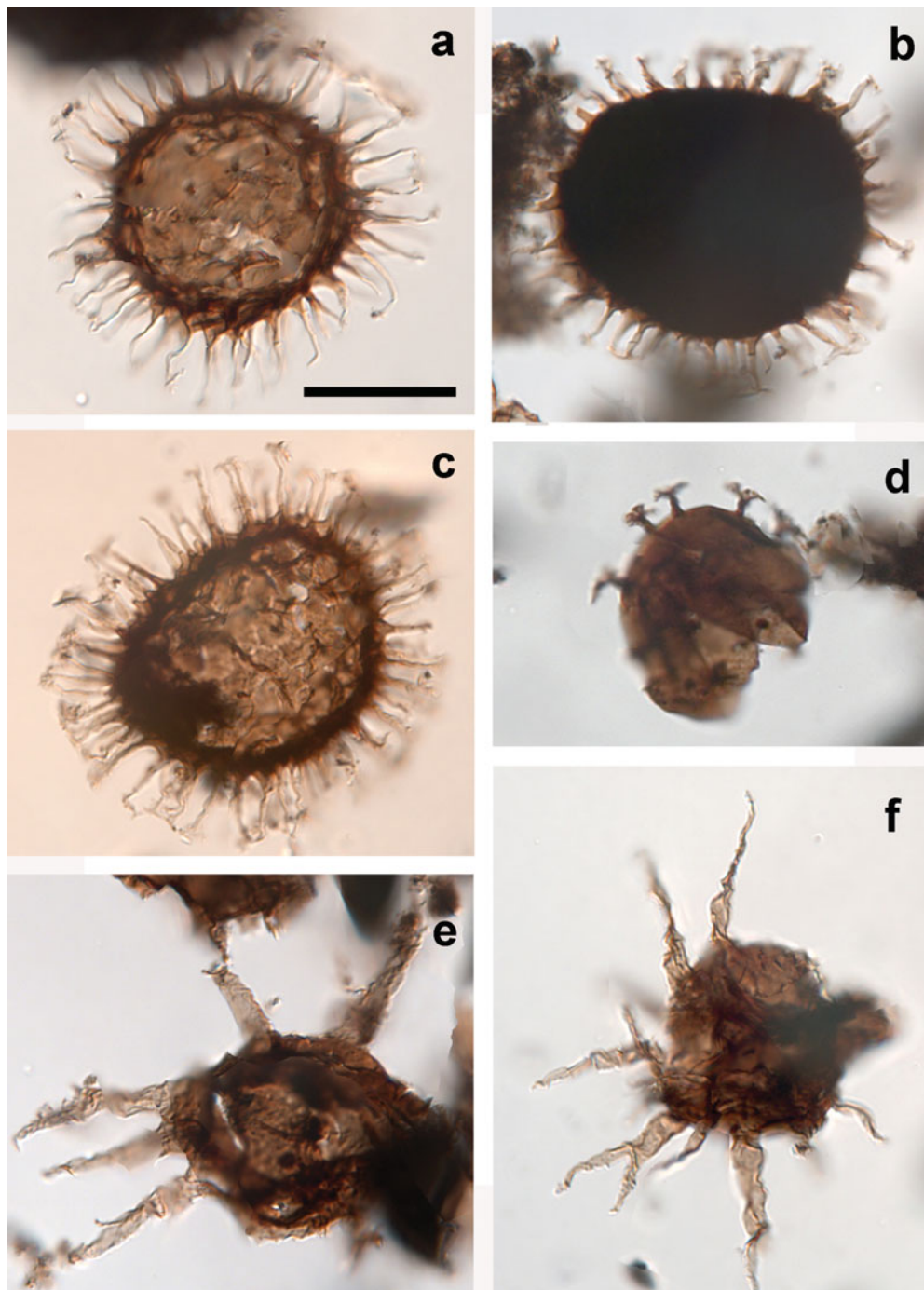


Figure 5. (Colour online) Acritarchs from the St Martins Member, Hanford Brook Formation, Hanford Brook. Scale bar is equivalent to 20 μm . (a–c) *Skiagia ciliosa* (Volkova) Downie, 1982. (a) Hanf 12:1, NBMG15584:001, V-31-1. (b) Hanf 12:3, NBMG15586:001, B-15-4 specimen with internal endocyst. (c) Hanf 12:3, NBMG15585:001, E-20-2. (d) *Skiagia insigne* (Fridrichsone) Downie, 1982, Hanf 08:14, NBMG15578:001, H-31-1. (e, f) *Polygonium primarium* (Jankauskas) Sarjeant & Stancliffe, 1994. (e) Hanf 09:1, NBMG15581:001, N-48-4. (f) Hanf 12:4, NBMG15587:001, F-31.

Jachowicz-Zdanowska, 2013, a characteristic acritarch first described in open nomenclature by Martin in Martin & Dean (1984) from Newfoundland. There its first appearance is from the upper part of the Chamberlain's Brook Formation, below a level that contains *Badulesia* aff. *B. tenera*, *Ecceparadoxides etemincus* and *Hartella terranovica* (Martin & Dean, 1988, fig. 3), included in the AO-1 acritarch Zone (equivalent to the *Hartella* Zone). This zone also includes scarce *Eliasum llaniscum*

and *Retisphaeridium dichamerum*, and the zone is also characterized by the absence of *Cristallinium cambriense* (Slaviková) Vanguetaine, 1978. Other occurrences of *C. francinae* are in the Nant-y-big Formation, NW Wales, in levels of the *Tomagnostus fissus* Zone (lower Drumian, recorded as Acritarch gen. et sp. nov. Martin in Martin & Dean, 1984; Young *et al.* 1994), where it occurs with *R. dichamerum*, *C. cambriense* and *Heliosphaeridium? llynense* Martin. A similar assemblage, but without *Cristallinium*

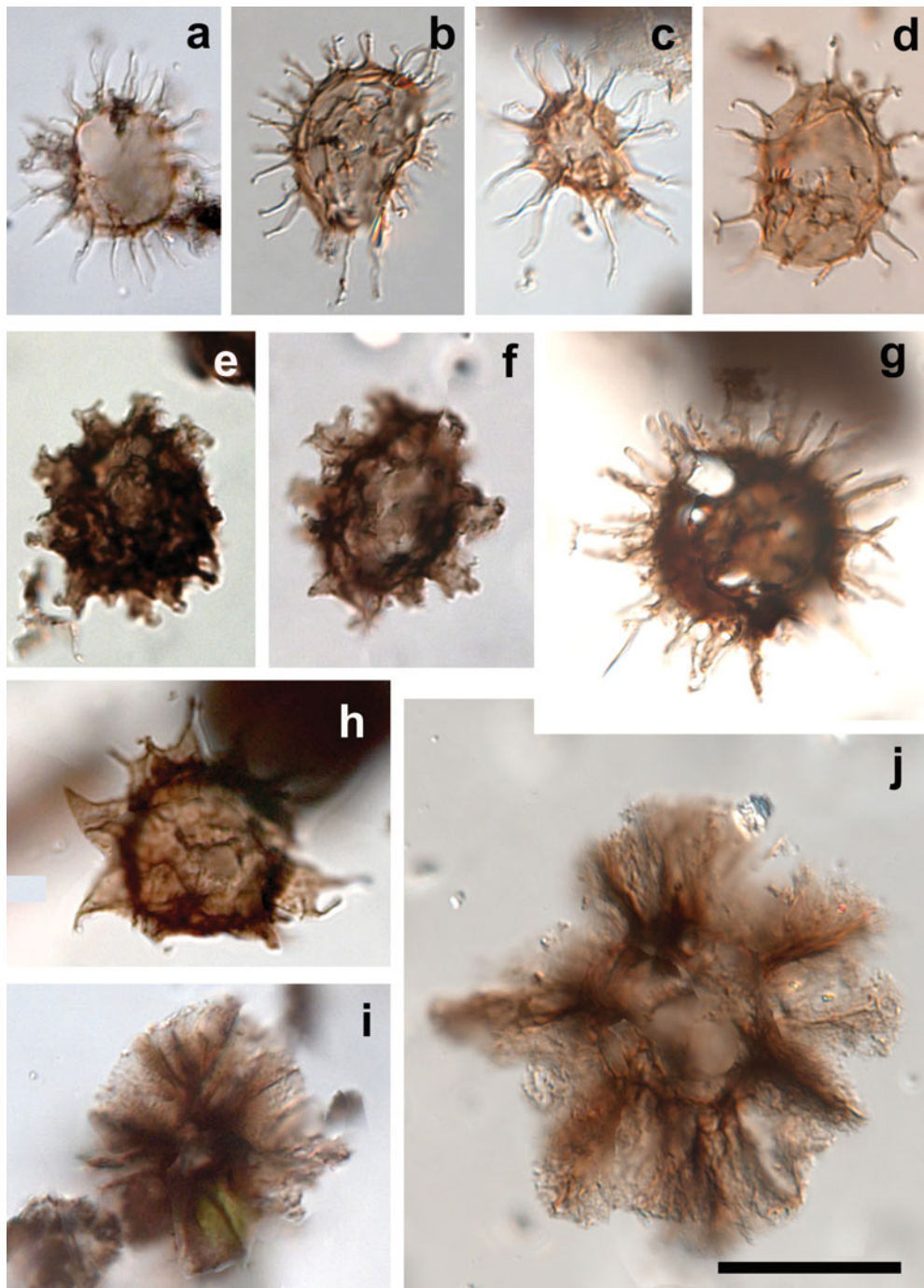


Figure 6. (Colour online) Acritarchs from Hanford Brook Formation at Hanford Brook. St Martins Member (a, b, i), Somerset Street Member (c–f, h) and Long Island Member (g, j). Scale bar is equivalent to 20 μm . (a) *Heliosphaeridium dissimulare* (Volkova) Moczydłowska, 1991, Hanf 08:14, NBMG15578:002, D-47-1. (b) *Heliosphaeridium notatum* (Volkova) Moczydłowska, 1991, Hanf 12:1, NBMG15584:002, B-41-2. (c) *Heliosphaeridium longum* (Moczydłowska) Moczydłowska, 1991, Hanf 08:15, NBMG15579:001, E-38-3-4 (d) *Heliosphaeridium* sp. A, Hanf 12:8, NBMG15588:001, L-49-3. (e, f) *Multiplicisphaeridium dactylum* Vidal in Moczydłowska & Vidal, 1988. (e) Hanf 08:16, NBMG15580:001. (f) Hanf 08:16, NBMG15580:002, B-28-1-2. (g). *Celtiberium* sp., Hanf 12:11a, NBMG15592:001, C-39. (h) *Polygonium varium* (Volkova), Sarjeant & Stancliffe, 1994, Hanf 08:16, NBMG15580:003, T-30-2. (i, j). *Liepaina plana* Jankauskas & Volkova in Volkova *et al.* 1979. (i) Specimen of small dimensions, Hanf 08:14, NBMG15578:003, D-38-1. (j) Hanf 12:11a, NBMG15592:002, C-20-4.

cambriense, occurs in the Dugald Formation in Nova Scotia (Palacios *et al.* 2012). Jachowicz-Zdanowska (2013) described *Comasphaeridium francinae* from the Sosnowiec Formation in Silesia, Poland, in her BAMA VIII acritarch assemblage Zone, from levels that correlate with the *Paradoxides paradoxissimus*

Zone. On the Iberian Peninsula it appears in the Oville Formation, northern Spain, in the IMC1 and lower part of the IMC2 acritarch zones, in levels assigned to the Upper Leonian – Lower Caesaraugustian (*P. asturianus*–*Badulesia tenera* zones). In southern Spain it appears in volcanosedimentary beds of the upper

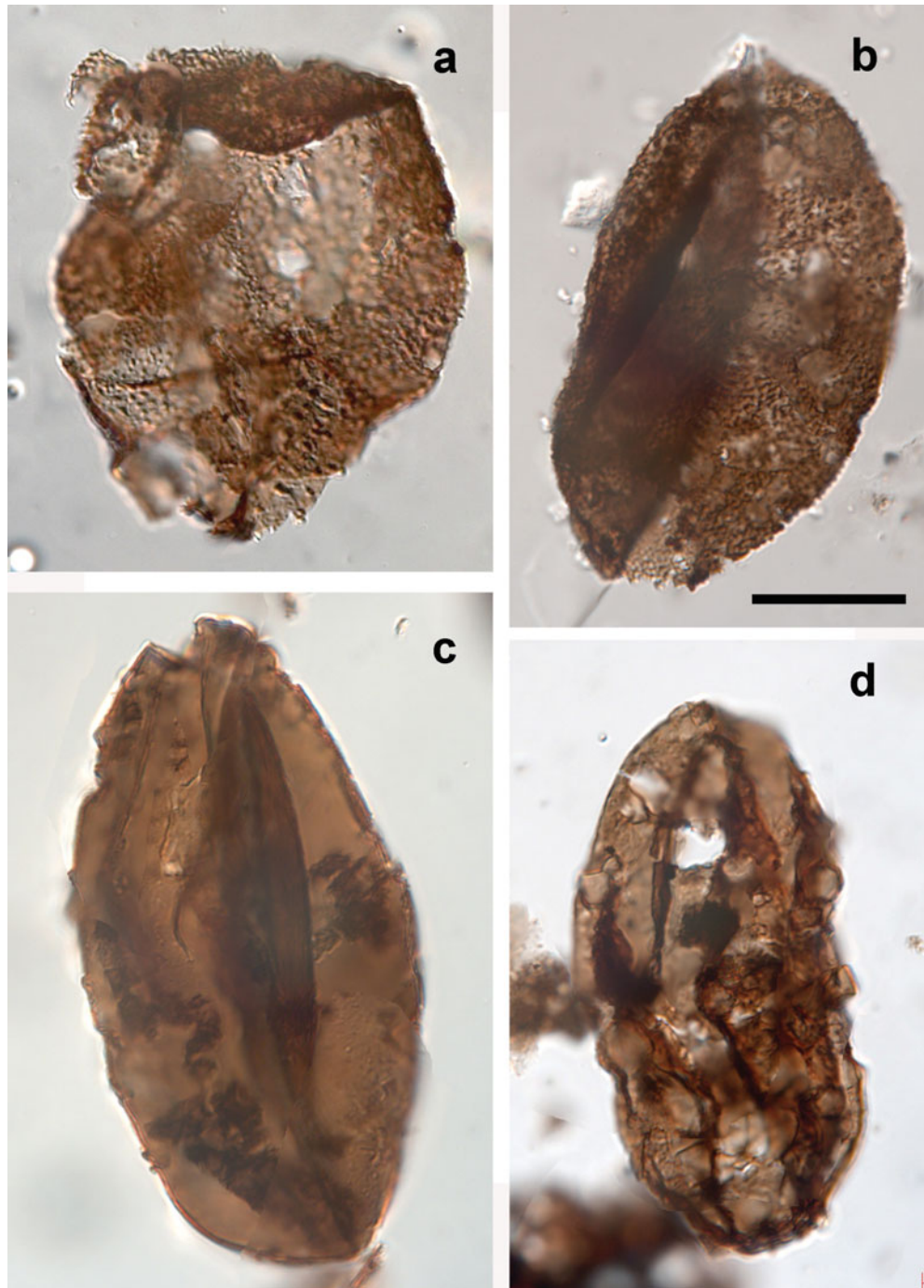


Figure 7. (Colour online) Acritarchs from the Hanford Brook Formation at Hanford Brook. (a, c, d) Somerset Street Member, (b) Long Island Member. Scale bar is equivalent to 20 μm . (a, b) *Lophosphaeridium variabile* Volkova, 1974. (a) Hanf 08:16, NBMG15580:004, G-24. (b) Hanf 12:11a, NBMG15593:001, Z-47-3. (c, d) *Eliasum llaniscum* Fombella, 1977, or (c) a flattened leiosphaerid? (c) Hanf 12:9, NBMG15589:001, G-42-4. (d) Hanf 12:8, NBMG15588:002, F-34-4.

part of the Vallehondo Formation, top of the IMC1 acritarch Zone, in levels that overlie an occurrence of *Parasolenopleura* sp. and *Paradoxides* sp. (Palacios, Jensen & Apalategui, 2006; Palacios, 2014).

5. Biochronological implications of the acritarch distribution

The distribution of the three acritarch associations described here each broadly corresponds with a member of the Hanford Brook Formation and with a

faunal zone. Westrop & Landing (2000) suggested that some of the differences in fauna through the Hanford Brook Formation are related to differences in depositional setting. The distribution of organic-walled microfossils in general is not considered to be strongly affected by environmental conditions, except for low-diversity assemblages dominated by leiosphaerids in stressed shallow-water or deep-water basinal settings. We therefore find it likely that the observed changes in acritarch associations largely reflect evolutionary events/turnover. The succession of acritarchs through

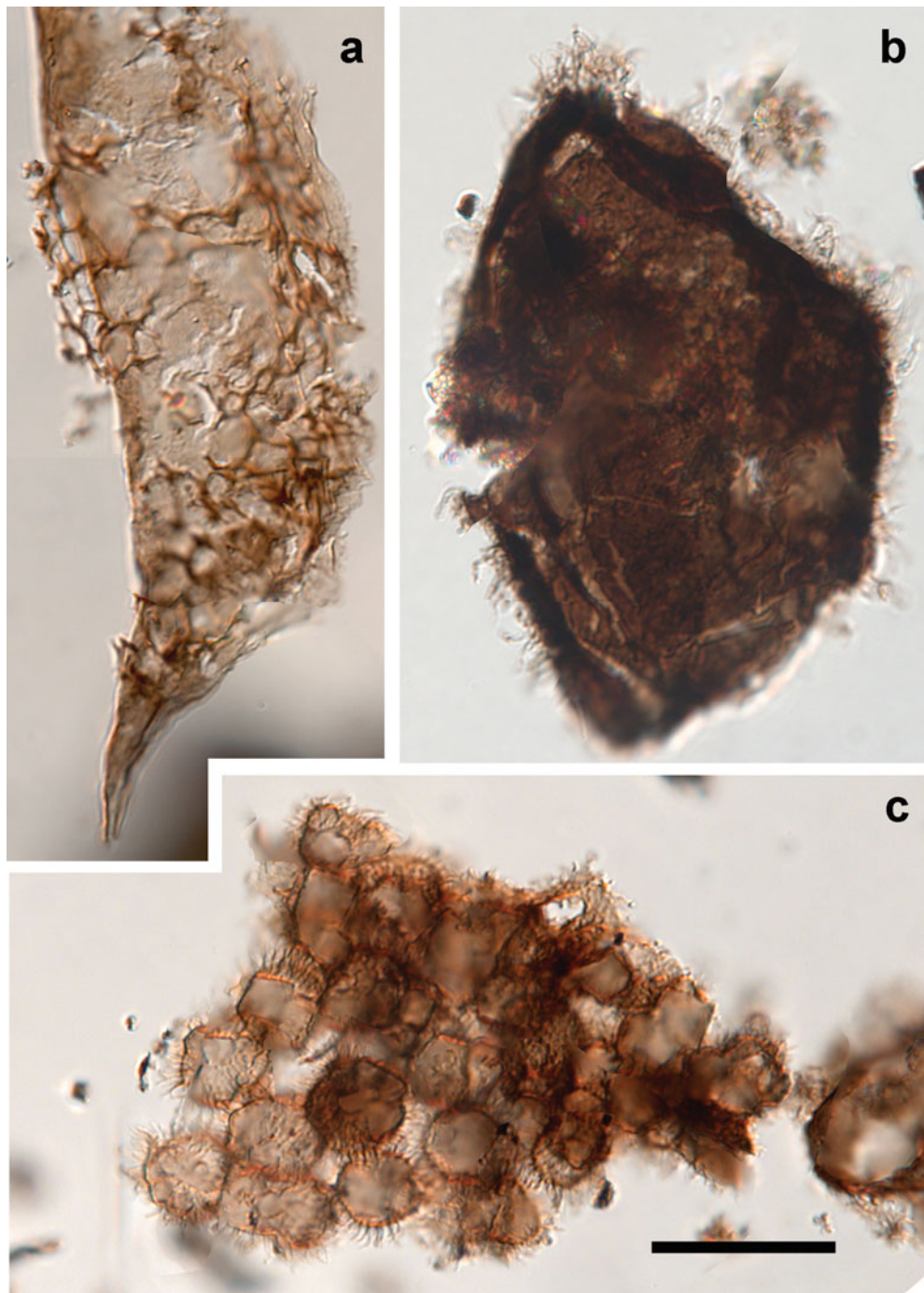


Figure 8. (Colour online) Acritarchs from the Hanford Brook Formation at Hanford Brook. (a, c) Somerset Street Member, (b) Long Island Member. Scale bar is equivalent to 20 μm . (a) aff. *Sagatum priscum* (Kirjanov & Volkova) Vavrdová & Bek, 2001, Hanf 12:11, NBMG15590:001, F-48-2. (b) *Comasphaeridium maximum* Palacios, 2015, Hanf 12:12, NBMG15594:001, N-38-1. (c) *Asteridium lanatum* (Volkova) Moczydłowska, 1991, cluster of up to 30 specimens, Hanf 09:5, NBMG15582:001, Y-48-3.

the section of the Hanford Brook Formation at Hanford Brook therefore offers the opportunity to contrast the succession of acritarchs through a section that is likely to be close to, or span, the lower–middle Cambrian transition and the base of Cambrian Series 3. The succession of acritarchs across the traditional lower–middle Cambrian transition has been studied in particular detail in Baltica (e.g. Volkova *et al.* 1979, 1983; Moczydłowska, 1991, 1999) and in Spain (e.g. Palacios, 2015). The Hanford Brook Formation contains a range of acritarch species also found in those areas,

making it possible to put its macrofossils and dated ash bed in an improved biochronological framework. In turn, this allows numerical ages to be placed on acritarch associations.

Association 1, with *Heliosphaeridium notatum*, *H longum* and rare *Liepaina plana*, is indicative of the *Volkovia–Liepaina* Zone of Moczydłowska (1991). This zone has been considered to be latest early Cambrian in age and to correspond to the *Protolenus* Zone as recognized in Baltica (Moczydłowska, 1991). Moczydłowska (1991) established the

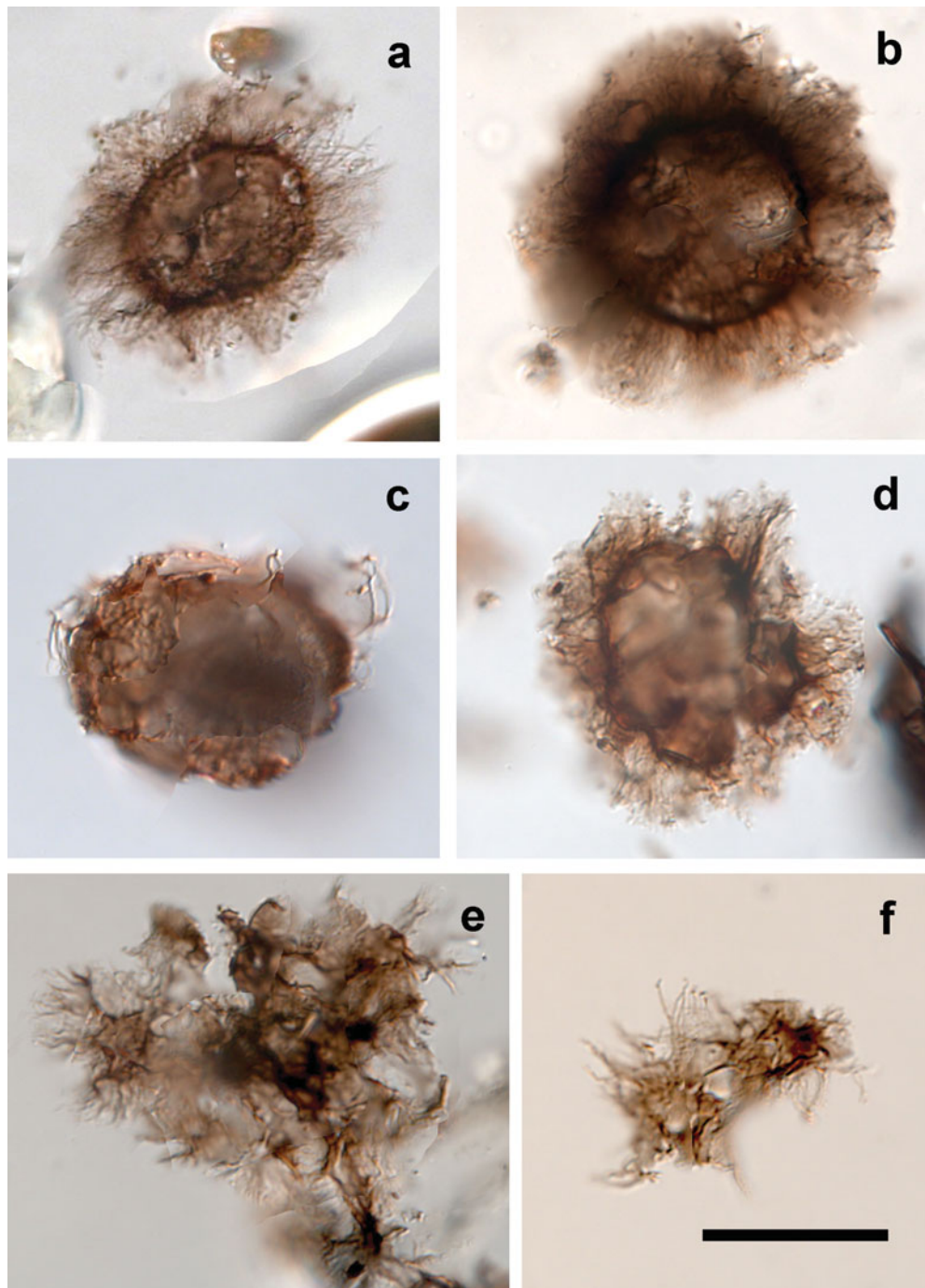


Figure 9. (Colour online) Acritarchs from the Hanford Brook (a–d) and Forest Hills (e, f) formations at Hanford Brook. (a, d) Somerset Street Member, (b, c) Long Island Members. Scale bar is equivalent to 20 μm . (a) *Comasphaeridium strigosum* (Jankauskas) Downie, 1982, Hanf 08:16, NBMG15580:005, T-33-2. (b, d) *Comasphaeridium silesiense* Moczydłowska, 1998. (b) Hanf 12:11a, NBMG15593:002, J-39. (d) Hanf 12:8, NBMG15588:003, D-38-3 (c) *Comasphaeridium longispinosum* Hagenfeldt, 1989, Hanf 09:10, NBMG15583:001, Z-42. (e, f) *Comasphaeridium francinae* Jachowicz-Zdanowska, 2013. (e) Hanf 12:15, NBMG15595:001, Q-19-4. (f) Hanf 12:16, NBMG15596:001, B-25-1.

Volkovia–Liepaina Zone in eastern Poland on the basis of the first appearance of *V. dentifera* and *L. plana*, although both are scarce and consequently recognition of this acritarch zone is difficult, as Moczydłowska (1991) indicated. *Liepaina plana* is reported from the middle Cambrian in Baltica (Kibartai Horizon, Volkova *et al.* 1979, 1983, and the *Acadoparadoxides oelandicus* Beds in south-central Sweden and western Finland (Hagenfeldt, 1989). Żylińska & Szczepanik (2009) re-

ported *Liepaina plana* from the Cambrian Series 3 Kobierniki Beds of the Holy Cross Mountains. In the Oville Formation, northern Spain, it appears in levels that include Upper Leonian trilobites (*Paradoxides asturianus* and *Tonkinella* aff. *breviceps*, Palacios, 2015). In the Hanford Brook Formation, *Liepaina plana* is abundant in the Long Island Member, where it occurs with acritarchs diagnostic of Cambrian Series 3 (see below). Occurrences of *L. plana* in the lower Cambrian

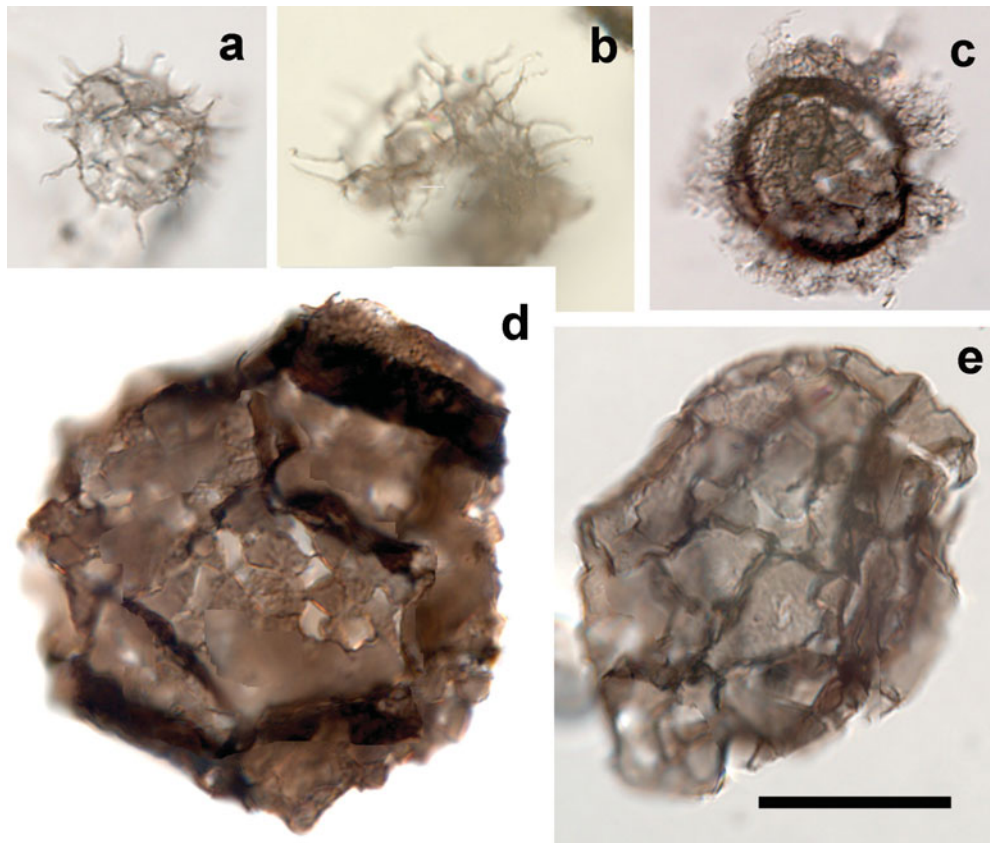


Figure 10. (Colour online) Acritarchs from the Hell's Mouth Formation, St Tudwal's Peninsula, Wales. Scale bar is equivalent to 20 μm . (a) *Heliosphaeridium notatum* (Volkova) Moczydłowska, 1991, TUD-2, UexWal 001:001, B-31-2-4 (b) *Heliosphaeridium* sp. A, TUD-2, UexWal 001:002, V-17-4 (c) *Comasphaeridium silesiense* Moczydłowska, 1998, TUD-2, UexWal 001:003, K-17-2-4. (d) *Retisphaeridium lechistanium* Jachowicz-Zdanowska, 2013, TUD-2, UexWal 002:001, B-43-4. (e) *Retisphaeridium dichamerum* Staplin, Jansonius & Pocock, 1965, TUD-2, UexWal 001:004, B-39.

are scarce. Moczydłowska & Vidal (1986) referred to, but did not illustrate, the occurrence of *L. plana* with *Skiagia ciliosa* from the Holmia C Zone of Norway. Żylińska & Szczepanik (2009) reported small specimens as *Liepainia* sp. from the Cambrian Series 2 of Poland, considering that these differ from specimens typical for the Cambrian Series 3. A similar situation is found in the St Martins Member of the Hanford Brook Formation with rare (three) specimens, although this well-preserved material can be assigned to *Liepainia plana* (Fig. 6i). Two additional species characteristic of the *Volkovia*–*Liepainia* Zone are *Heliosphaeridium notatum* and *H. longum* (Moczydłowska, 1991, fig. 5). *H. notatum* is a common species with a wide distribution in beds equivalent to the *Protolenus* Zone and lowermost middle Cambrian of Baltica, Avalonia and Gondwana (Moczydłowska, 1991, 1998; Palacios & Moczydłowska, 1998; Palacios, Jensen & Apalategui, 2006; Palacios, 2008; Palacios *et al.* 2012).

Among the species of Association 2, *Comasphaeridium silesiense* has been considered diagnostic of the middle Cambrian or Cambrian Series 3 (Moczydłowska, 1998, 1999; Palacios, 2008; Jachowicz-Zdanowska, 2013). One problematic aspect of this species is the possible confusion with the lower Cambrian *Comasphaeridium strigosum*, although in *C. strigosum* the processes are separated at the distal

tips (Moczydłowska, 2011) whereas in *C. silesiense* they are fused and densely arranged (Moczydłowska, 1998). *Eliasum llaniscum* is characterized by a vesicle divided into spindle-shaped areas or plates, although care has to be taken to avoid confusion with flattened specimens of *Leiosphaeridia* (Palacios, 2015). The lower stratigraphic range is mostly given as uppermost lower Cambrian – middle Cambrian (e.g. Molyneux, Le Hérisse & Wicander, 1996) or middle Cambrian (e.g. Moczydłowska, 1999). Moczydłowska (1998) identified as *Eliasum llaniscum* specimens described by Volkova *et al.* (1979, pl. 16:6–8) from the Rausve horizon, but noted that the age of this occurrence is in question. Additionally, we note this material likely is flattened *Leiosphaeridia* sp. *Lophosphaeridium variable* is characteristic of the middle Cambrian, with occurrences in the *Acadoparadoxides oelandicus* Superzone in the Baltic area (Volkova, 1974; Volkova *et al.* 1979, 1983; Hagenfeldt, 1989), and the Sosnowiec Formation, Poland, in the *Acadoparadoxides oelandicus* Superzone (Moczydłowska, 1998). In Newfoundland it has been reported as *Eliasum? hutchinsonii* (see synonymy in Section 8) from the basal Manuels River Formation, within the *Paradoxides hicksii* Zone (Martin & Dean, 1984). *Heliosphaeridium* sp. A. is a problematic form that has been reported as *Multiplisphaeridium martae* Cramer & Díez, 1972 in Silesia

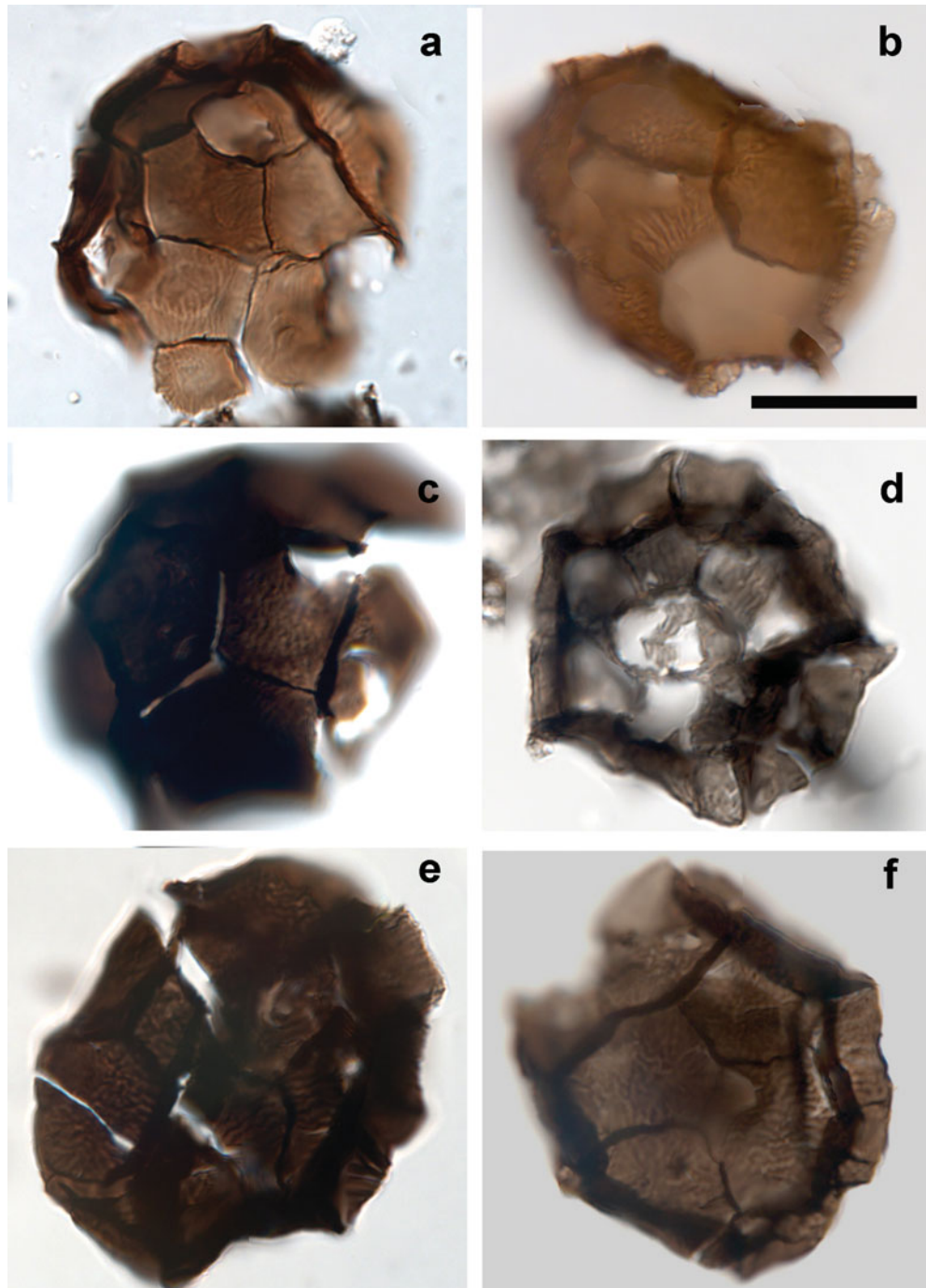


Figure 11. (Colour online) *Retisphaeridium striatum* Palacios sp. nov., from the Long Island Member, Hanford Brook Formation (a, b) and Hell's Mouth Formation, St Tudwal's Peninsula, Wales (c–f). Scale bar is equivalent to 20 μm . (a) Holotype, showing the clear plate division and circular pylome, Hanford Brook, Hanf 12:11a, NBMG15592:005, Z-38-1 (b) Long Island, Li 09:5, NBMG15597:001, U-41-2-4. (c) Specimen showing the clear plate division, TUD-2, UexWal 002:003, A-15-4. (d) Degraded specimen showing circular pylome, TUD-2, UexWal 002:004, F-46-4. (e) TUD-2, UexWal 002:005, K-23-3. (f) TUD-2, UexWal 002:006, L-27-4.

(Moczyłowska, 1998; Jachowicz-Zdanowska, 2013) and in southern Spain from the IMC 1 Zone (Palacios, Jensen & Apalategui, 2006; Palacios, 2014), where it is found with *E. llaniscum* and *C. silesiense*. The specimens assigned to *M. martae* likely constitute a new species with diagnostic characters of the genus *Heliosphaeridium*, with heteromorphic simple and bifurcate processes. In *Multiplicisphaeridium martae*, the processes are columnar, heteromorphic and manate, with rounded distal terminations as described in

the type material from the Oville Formation (Cramer & Díez, 1972, fig 2). *Multiplicisphaeridium dactylum*, which is rare in this association, has been reported from southern Sweden, where it is found with *Tubulosphaera perfecta* Palacios in Palacios & Moczyłowska, 1998, *Celtiberium geminum* Fombella, 1977 (attributed to *Celtiberium* sp., see above) and *E. llaniscum* in glauconitic sandstone in levels assigned to the *Eccaparadoxides insularis* Zone (Eklund, 1990; Palacios & Moczyłowska, 1998).

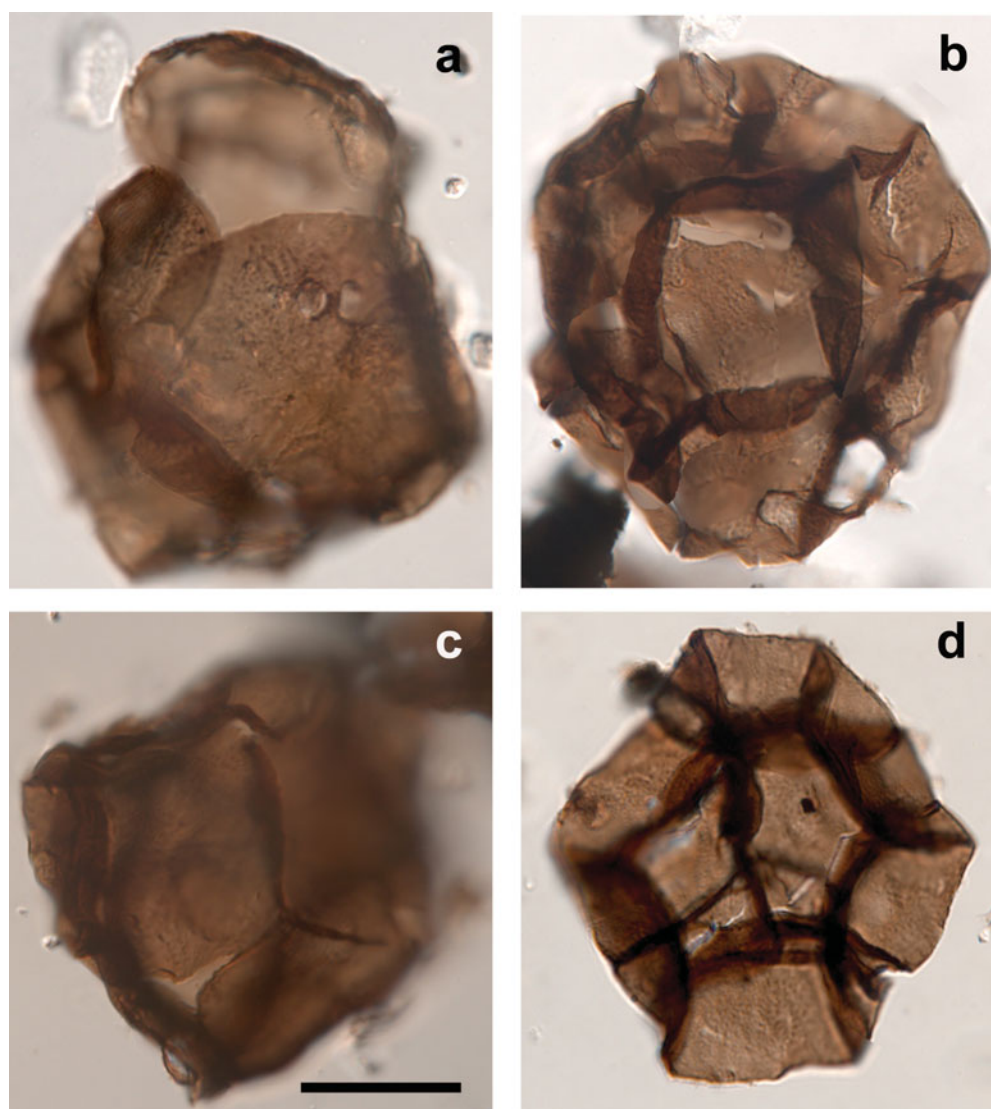


Figure 12. (Colour online) *Retisphaeridium lechistanium* Jachowicz-Zdanowska, 2013, from the Long Island Member, Hanford Brook Formation, Hanford Brook. Scale bar is equivalent to 20 μm . (a) Specimen showing plate division, Hanf 12:11a, NBMG15593:004, X-31 (b) Flattened specimen showing circular pylome, Hanf 12:11a, NBMG15593:005, S-25-2-4. (c) Specimen showing incipient plate division, Hanf 12:11a, NBMG15592:006, H-25. (d) Flattened specimen showing polygonal outline, Hanf 12:11a, NBMG15593:006, Z-38-1.

Association 3, from the Long Island Member, includes *Celtiberium*, *Comasphaeridium maximum*, *Comasphaeridium longispinosum*, *Retisphaeridium dichamerum*, *Retisphaeridium lechistanium* and *Retisphaeridium striatum*, all of which have first appearance datums in this assemblage. This assemblage also includes abundant and well-preserved *Liepaina plana* and aff. *Sagatum priscum*. *Comasphaeridium longispinosum* has been reported from the middle Cambrian or Cambrian Series 3 of Sweden (*Acadoparadoxides oelandicus* Superzone, Hagenfeldt, 1989), Silesia, Poland (Moczydłowska, 1998; Jachowicz-Zdanowska, 2013), Nant-y-big Formation, Wales (*P. paradoxissimus* Zone; Young *et al.* 1994), southeastern Turkey (*Pardailhania* to *Solenopleuropsis* Zone, Dean *et al.* 1997), the Oville Formation, northern Spain, Upper Leonian – Lower Caesaraugustian (*Badulesia*

Zone), IMC1–IMC2 acritarch zones (Palacios, 2015), and southern Spain (IMC1 Zone, Palacios, 2014). *Comasphaeridium maximum* has been reported from the Oville Formation, where it occurs in the IMC2–IMC4 acritarch zones, bracketed between the *Badulesia* and *Solenopleuropsis* zones (Palacios, 2015). *Celtiberium* sp. corresponds to a specimen illustrated as *Celtiberium geminum* from Sweden (glauconitic sandstone, Eklund, 1990), but which is significantly different from genuine *Celtiberium geminum* (Fombella, 1977, pl. 1:10–11; Palacios, 2015, pl. 3:7). *Retisphaeridium lechistanium* (see Section 8) has been reported from the Cambrian Series 3 of Silesia, Poland (*P. paradoxissimus* Zone, Jachowicz-Zdanowska 2013). A sample from the Eskasoni Formation of the Bourinot Belt, Nova Scotia, yielded *Eliasum llaniscum*, *Retisphaeridium dichamerum*, *Heliosphaeridium notatum*, aff. *Sagatum*

priscum and *Skiagia* sp, and was considered most likely attributable to basal Cambrian Stage 5 (Palacios *et al.* 2012).

Acritarchs do not provide data for an evaluation of the duration of a possible Somerset Street Member to Long Island Member hiatus, but in any case would be consistent with Westrop & Landing's (2000) suggestion that it is of minor duration.

6. Interregional correlation

6.a. Correlation with Newfoundland

Species-based macrofossil correlation between the Hanford Brook Formation and Avalonian successions in Newfoundland is not possible, but correlation has generally been made with the Brigus Formation. Near the top of the Redlands Cove Member, Cape St Mary's Peninsula, are found the protolenids *Orodes howleyi*, *Protolenus mckillopi*, *Catadoxides harveyi* and *Latoucheia* sp. (Fletcher, 2006). *Ovatoryctocara granulata*, an important form for the ongoing discussion of the Cambrian Series 2–3 transition, occurs near the top of the Brigus Formation within beds attributed to the *Morocconus notabilis* Zone (Fletcher 2003, 2006). The only information on acritarchs from the Brigus Formation in Newfoundland is Martin & Dean's (1983) report from Manuels River, Conception Bay, in grey-green shales of the *Catadoxides magnificus* Zone, some 6 m below middle Cambrian beds. The relationship of this zone to the general trilobite zonation is uncertain, and it has been considered both younger (e.g. Geyer & Palmer, 1995) and older (Landing & Westrop, 1998) than the *Orodes* Zone. Acritarchs, of low diversity and lacking any processes-bearing forms, include *Peramorphia manuelsenensis* Martin in Martin & Dean, 1983, *Retisphaeridium dichamerum* and *Grano-marginata squamacea*. From the same location Martin & Dean (1983) recorded acritarchs from the lower part of the Chamberlain's Brook Formation (*Paradoxides bennettii* Zone). The main addition compared to the acritarch assemblage of the Brigus Formation is *Eliasmus llaniscum*.

Landing & Westrop (1996) and Westrop & Landing (2000) suggested that the *Protolenus*-bearing part of the Hanford Brook Formation correlates in time with lower parts of the Brigus Formation of the *Callavia* Zone. Accordingly, Landing & Westrop (1998, fig. 20) tentatively attributed the Hanford Brook Formation to their latest early Cambrian depositional sequences 4A and 4B in Newfoundland represented respectively by the St Mary's (*Callavia* Zone) and Jigging Cove members of the Brigus Formation. The acritarch associations from the Somerset Street and Long Island members both suggest that these units are younger than previously thought. In terms of the depositional sequences of Landing & Westrop (1998), the Somerset Street Member would be at least as high as sequence 4B, with the Long Island Formation corresponding to one of the basal middle Cambrian sequences, meaning a short

duration for the hiatus between the Hanford Brook and Forest Hills formations.

6.b. Correlation with Morocco

An important lower–middle Cambrian transition succession is found in Morocco, with a trilobite-based zonation (Fig. 2) that has also in part been implemented in Avalonia. In the zonation of Geyer (1990a), the first middle Cambrian Zone in Morocco, the *Hupeolenus* Zone, is characterized by the appearance of species of the protolenid *Hupeolenus*. The second zone is defined on the range of the eodiscid *Morocconus notabilis* (previously *Cephalopyge notabilis*: see Geyer & Landing, 2004 for a discussion of this zone). The lower part of this zone contains species of the protolenid *Hamatolenus*. In Morocco, species of *Protolenus* are restricted to the *Morocconus notabilis* Zone. The level of first appearance of *Ovatoryctocara granulata* likely correlates to the middle portion of the *Morocconus notabilis* Zone (Elicki & Geyer, 2013). There are no macrofossils that allow direct correlation of the Hanford Brook Formation with the Moroccan succession. Early reports of varieties of *Protolenus elegans* from Morocco (e.g. Neltner & Poctey, 1950) were later revised and assigned to other protolenid genera (e.g. Geyer, 1990b). However, Geyer & Malinky (1997) noted that of the species of *Protolenus* described from Morocco, *Protolenus densigranulatus* and *P. interscriptus*, more closely resemble *Protolenus elegans* than do any other protolenid. This would suggest that the *Protolenus elegans* Zone in the Hanford Brook Formation can be correlated with the *Morocconus notabilis* Zone, as suggested by Geyer, Buschmann & Elicki (2014). Some additional evidence in this direction is presented below (Section 6.c) from Wales. On the other hand, *Kingaspidooides cf. obliquoculatus* from the Long Island Formation compares to *Kingaspidooides obliquoculatus* Geyer, from the *Hupeolenus* Zone of the Asrir Formation of Morocco. The only published study of Moroccan middle Cambrian acritarchs (Vanguetaine & van Looy, 1983) comes from a section that does not allow for comparison with the trilobite zonation. T.P. sampled for acritarchs in rocks of the *Morocconus notabilis* Zone in two sections of the Jbel Wawrmast Formation in the Anti-Atlas region of Morocco (see Devaere, Clausen & Álvaro, 2014 for section details). Here the Tatelt Member is attributed to the upper part of the *Hupeolenus* Zone and the lower part of the *Morocconus notabilis* Zone. Fauna of the *Morocconus notabilis* Zone is found in the succeeding Brèche à Micmacca and Tarhoucht members. At the type section for the Jbel Wawrmast Formation at Ourika Wawrmast, seven samples from the Tatelt Member and four samples from the Tarhoucht Member were all negative. At the Assemame quarry five samples from the Brèche à Micmacca and one sample from the Tarhoucht Member were all negative. All processed samples were devoid of organic material, also in the Assemame quarry where ongoing excavation essentially eliminates the possibility of

recent weathering. The Moroccan Cambrian Series 2–3 transition remains to be characterized with acritarchs.

6.c. Correlation with England and Wales

In England and Wales part of the comparable time interval has been referred to as the Protolenid–Strenuellid Zone (Cowie, Rushton & Stubblefield, 1972). Cobbold (1910, 1921) correlated a fauna from carbonates in the Comley area, Shropshire, with the *Protolenus* fauna of Matthew. The succession here is condensed and thought to contain many hiatuses, but is richly fossiliferous and of additional importance in containing dated ash beds. Protolenids have been reported from a 15 cm thick phosphatic limestone, known as bed Ac5 of the Comley Limestone, and also as the *Protolenus* Limestone (e.g. Rushton, 1974). From this unit has been reported the protolenids *Latoucheia latouchei* and *Cobboldites comleyensis*, as well as bradorids (Siveter, Waloszek & Williams, 2003). Harvey *et al.* (2011) reported a date of 509.10 ± 0.77 Ma from an ash bed in the Upper Comley Sandstone, tentatively assigned to the *Eoparadoxides harlani* Zone. There exists no published information on acritarchs from this succession, which represent shallow-water deposition within the Welsh basin, but acritarchs relevant to the present study have been reported from Hell's Mouth Formation on the St Tudwal's Peninsula in distal parts of the Welsh basin.

Young *et al.* (1994) reported a diverse acritarch assemblage from the Hell's Mouth Formation, St Tudwal's Peninsula, Wales, including *Retisphaeridium dichamerum*, *Peramorphia manuellsensis*, *Cymatiosphaera ovillensis* Cramer & Díez (probably synonymous with *Retisphaeridium lechistanium*), *Eliasum llaniscum* and *Comasphaeridium* sp. (very similar to *C. silesiense*) that they considered uppermost lower Cambrian. *Peramorphia manuellsensis*, an acritarch otherwise only described from the Brigus Formation of Newfoundland, was recorded from a level some 66 m below the top of the formation. This material came from a section at Trwyn y Ffosle. Trilobites have been found at the nearby section at Trwyn Carreg-y-Tir, with *Leptochilodiscus* (formerly *Kerberodiscus*) *succinctus*, *Serrodiscus ctenoa* and the protolenid *Hamatolenus douglasi* found 16.5 m below the top of the formation (Bassett, Owens & Rushton, 1976). Rushton & Molyneux (2011) tentatively correlated the trilobite-bearing beds near the top of the Hell's Mouth Formation at Trwyn Carreg-y-Tir with the *Morocconus notabilis* Zone of eastern Newfoundland. Here we provide new information on acritarchs in a sample from the trilobite locality at Trwyn Carreg-y-Tir, which include *Retisphaeridium striatum* (Fig. 11c–f), *R. dichamerum* (Fig. 10e), *R. lechistanium* (Fig. 10d) and *Comasphaeridium silesiense* (Fig. 10c). This association compares closely to that of the Long Island Member in New Brunswick, with particular note of the occurrence of *Retisphaeridium striatum*. Accepting Rushton & Molyneux's (2011) correlation of the

upper part of the Hell's Mouth Formation with the *Morocconus notabilis* Zone, the commonality in acritarch associations supports the interpretation that at least the Long Island Member can be correlated with the *Morocconus notabilis* Zone.

7. Discussion

The present study documenting the succession of acritarch associations through some 20 m of section in the Hanford Brook Formation provides one of the most complete records of these fossils across the lower–middle Cambrian transition anywhere, and the most detailed to date from Avalonia. The assemblage of acritarchs in the St Martins Member is best considered terminal Cambrian Stage 4, with diverse *Skiagia*, and with *Heliosphaeridium longum* and *H. notatum*. This assemblage may broadly correspond to the *Volkovia dentifera*–*Liepainia plana* acritarch Zone in Baltica, although as discussed above the recognition of that zone is problematic. Because of its abundance and wide distribution, *H. notatum* may be the species best suited to characterize the uppermost part of the lower Cambrian (and potentially Cambrian Series 2). Association 2 of the Somerset Street Member contains several species that have been previously considered indicative of the middle Cambrian, such as *Eliasum llaniscum*, *Lophosphaeridium variabile* and *Comasphaeridium silesiense* (Volkova, 1974; Moczyłowska, 1998, 1999). Under the assumption of no substantial age difference between the *Protolenus elegans* Zone in the sections on Somerset Street and Hanford Brook, the dated ash bed is middle Cambrian on the basis of acritarchs. Originally reported as 511 ± 1 Ma (Landing *et al.* 1998), it was later reported as 510 ± 1 Ma (Bowring & Schmitz, 2003, fig. 3) and 508.05 ± 2.75 Ma (Schmitz, 2012). This is within error of the 509.10 ± 0.77 Ma date from an ash bed in the Upper Comley Sandstone, England, that Harvey *et al.* (2011) considered to provide a minimum age for the boundary between Cambrian Series 2 and 3. The combined acritarch and geochronological evidence show that *Protolenus elegans* is close to the Cambrian Stage 4–5 transition and more likely Cambrian Stage 5. Our study also supports earlier suggestions that *Eliasum llaniscum* and *Comasphaeridium silesiense* are useful middle Cambrian marker fossils (Moczyłowska, 1999). Association 3 from the Long Island Member includes a number of species indicative of the middle Cambrian.

The available acritarch studies suggest that the traditional lower–middle Cambrian transition is marked by a clear change in acritarchs, well reflected in the Hanford Brook Formation, including: the appearance of large acritarchs (*Eliasum llaniscum*, *Lophosphaeridium variabile*, *Comasphaeridium maximum*) and important evolutionary innovations that are maintained through the middle Cambrian and Furongian with morphological characteristics similar to those of dinoflagellates (division into plates, with

vesicle of ‘placoid acritarchs’, represented by *Eliasum*, *Retisphaeridium*, *Cristallinium*, *Vulcanisphaera* and *Timofeevia*). This innovation of ‘plate structured forms’, was already identified by Potter (1974). Both tendencies are well seen in associations 2 and 3 of the Hanford Brook Formation. Acritarch associations 2 and 3 may both correspond to the *Morocconus notabilis* Zone (Fig. 2), although additional acritarch data from sections with macrofossils are needed.

One of the favoured candidates for defining the base of the not-yet-defined Cambrian Series 3 is the first appearance of the oryctocephalid trilobite *Ovatoryctocara granulata*, likely to approximate the lower–middle Cambrian transition as traditionally used in Europe and Siberia (e.g. Peng, Babcock & Cooper, 2012; Gozalo *et al.* 2013; Fig. 2). A candidate type section for the base of Cambrian Series 2 defined on *Ovatoryctocara granulata* is in the Kaili Formation of China, where acritarchs have been reported by Yang & Yin (2001) and Yin *et al.* (2009, 2010). Two acritarch assemblages have been identified from the potential Cambrian Series 2–Series 3 transition in the Wuliu–Zengjiayan section of the Kaili Formation, south China (Yin *et al.* 2010). The lower *Leiomarginata simplex*–*Fimbriaglomerella membranacea* assemblage contains morphologically simple forms and long-ranging forms. A second *Cristallinium cambriensis*–*Heliosphaeridium nodosum*–*Globosphaeridium cerinum* assemblage commences slightly below the first appearance of *Oryctocephalus indicus*, providing a potential tight correlation point between trilobites and acritarchs. The report of *Cristallinium cambriensis* and *Cristallinium dubium* at this level is, however, lower than that from other known occurrences, and typical transitional taxa such as *Eliasum llaniscum* and *Comasphaeridium silesiense* are missing. Kaili Formation acritarchs have also been reported from sections at Balang (Yang & Yin, 2001). Figured material of *Cristallinium* is not convincing. These incongruous aspects of the acritarch record in the Chinese sections with respect to that of the Acado-Baltic region need to be clarified before it allows for a fuller evaluation of global acritarch-based correlation of these levels.

8. Systematic palaeontology

Group ACRITARCHA Evitt, 1963 (*incertae sedis*)
Genus *Retisphaeridium* Staplin, Jansonius & Pocock, 1965

Type species. *Retisphaeridium dichamerum* Staplin, Jansonius & Pocock, by original designation.

Remarks. *Retisphaeridium* and *Cymatiosphaera* are frequently confused because ‘The collapse of the body produces a roughly reticulate pattern of folds, simulating polygonal fields’ (Downie, 1982). The diagnostic features of *Retisphaeridium* are most evident in those specimens that are least deformed, and consist of clear

evidence of polygonal plates limited by sutures along which they rupture into plates (Staplin, Jansonius & Pocock, 1965, pl. 19: 1, 2; Downie, 1982, fig. 11p; Martin & Dean, 1983, pl. 43.2, fig. 9; Palacios, 2015, pl. 2:1). Following this criterion, the presence of a vesicle divided into equal-sized polygonal plates, and in some case the presence of a circular pylome, described for the first time in *R. striatum*, are considered the most diagnostic features of *Retisphaeridium*. These characters are shared with *Cristallinium* in which plate sutures additionally are ornamented and some species, such as *C. cambriense* possess a circular pylome (Moczyłowska *et al.* 2011, fig. 3d; Palacios 2015, pl. 2:3). The similarity of *Retisphaeridium* and *Cristallinium* (Downie, 1982, p. 279) might justify their inclusion in a common genus. However, this would require an extensive review of the two genera, which is beyond the scope of this paper. Here, forms with sutures without ornamentation are included in *Retisphaeridium*.

Retisphaeridium striatum Palacios sp. nov.
(Fig. 11a–f)

Holotype. Hanf 12:11a, specimen NBMG15592:005, from sample Hanf 12:11a, England finder coordinates Z-38-1, Fig. 11 a.

Type locality and stratum. Hanford Brook, southern New Brunswick, Canada. Hanford Brook Formation (shale and mudstone of the Long Island Member).

Etymology. From the Latin *striatum*, from the striate surface ornamentation.

Diagnosis. Vesicle polygonal in outline, thick walled with striate surface. Vesicle divided into polygonal plates (mainly pentagonal) that rupture readily along the plate sutures. Excystment by circular pylome.

Dimensions. Based on 47 well-preserved specimens. Vesicle width 37–59 μm (mean 45 μm); 42 μm in holotype. Number of plates in visible area 7–10 (mean 8); 10 in holotype. Pylome (observed in 11 specimens) width 12–19 μm ; 13 μm in holotype. Ratio between pylome diameter and vesicle is 0.29–0.36; 0.30 in holotype.

Discussion and comparison. *Retisphaeridium dichamerum* and *Cristallinium cambriense* are similar in size and in the number of plates and in both has been observed a circular pylome (Palacios, 2015 and unpub. obs.). *R. dichamerum* lacks ornamentation and *C. cambriense* has a granular ornamentation and sutures ornamented with small denticles.

Stratigraphic occurrence. The best-preserved material, although rare, come from Hanford Brook and Long Island, New Brunswick, Canada in the Long Island Member, Hanford Brook Formation. More abundant, but less well-preserved, material from the St Tudwal’s Peninsula, Wales, in the Hell’s Mouth Formation.

Retisphaeridium lechistanium
 Jachowicz-Zdanowska, 2013
 Figs 10d, 12a–d

1994 *Cymatiosphaera ovillensis* Cramer & Díez (1972), Martin in Young *et al.*, pl. 10j, q.

2013 *Retisphaeridium lechistanium* Jachowicz-Zdanowska sp. nov., Jachowicz-Zdanowska, pl. 34: 1–6.

Description. Vesicle polygonal in outline, thick walled with microgranulate ornamentation. The vesicle is divided into large polygonal plates that rupture readily along the plate sutures. The suture zones of the plates are frequently folded in flattened specimens.

Dimension. Based on 13 well-preserved specimens. Vesicle width 51–66 µm (mean 58 µm). Number of plates in visible area 4–8 (mean 6).

Remarks. The dimensions and number of plates in the present material correspond to that of *R. lechistanium* and although the vesicle surface was considered smooth in the original diagnosis, material illustrated by Jachowicz-Zdanowska (2013, pl. 34) shows a microgranular surface. Figured specimens of *Cristallinium ovillensis* in Young *et al.* (1994) are here considered to be flattened specimens of *R. lechistanium*.

Stratigraphic occurrence. Present record in Hanford Brook Formation (Long Island Member), New Brunswick, Canada. Hell's Mouth and Ceriad formations in Wales equivalent to *Protolenus*–*P. paradoxissimus* Zone (this paper and Young *et al.* 1994). Sosnowiec Formation, Silesia, Poland, equivalent to *Paradoxides paradoxissimus* Zone.

Genus *Lophosphaeridium* Timofeev, 1959, ex Downie, 1963, emended Lister, 1970

Type species. *Lophosphaeridium rarum* Timofeev, Russia, 'Glauconic beds', Lower Ordovician.

Lophosphaeridium variabile Volkova, 1974
 Fig. 7a, b

1974 *Lophosphaeridium variabile* Volkova sp. nov., Volkova, pl. 28:4–5.

1979 *Lophosphaeridium variabile* Volkova, 1974, Volkova *et al.*, pl. 16:9–12.

1984 *Eliasum? hutchinsonii* Martin in Martin & Dean, pl. 57:2, figs 1–5, 7, 9.

1989 *Lophosphaeridium variabile* Volkova, 1974, Hagenfeldt, pl. 2:8.

Description. Spherical vesicle, circular in outline and ellipsoidal in flattened specimens. The vesicle surface is granulate with granulae of different sizes. One specimen has a possible circular pylome.

Dimensions. Diameter of vesicle 52–101 µm (mean 68 µm), granulae 2.5–0.3 µm, based on 11 well-preserved specimens.

Remarks. The present specimens are similar to the type material of *Lophosphaeridium variabile* described by Volkova (1974), in both vesicle size and shape, and in tubercle dimensions. *Eliasum? hutchinsonii* is synonymous with *L. variabile* because it shows the same dimensions and type of ornamentation.

Stratigraphic occurrence. Baltica, *Acadoparadoxides oelandicus* Zone (Volkova, 1974; Volkova *et al.* 1979, 1983; Hagenfeldt, 1989). Newfoundland, Canada, Manuels River Formation, *Paradoxides hicksii* Zone, Martin & Dean (1984). Present record New Brunswick, Canada, Somerset Street and Long Island members, Hanford Brook Formation.

Acknowledgements. TP and SJ acknowledge funding from the Spanish Ministry of Science and Innovation through grants CGL-2008-0473 and CGL 2012–37237, both co-financed by Fondo Europeo de Desarrollo Regional (FEDER). Fieldwork and travel costs for TP and SJ were defrayed partially by two Matthew Grants from the New Brunswick Museum, which are gratefully acknowledged. SB acknowledges support for her work in New Brunswick over the years from the New Brunswick Department of Energy and Mines and from the Natural Sciences and Engineering Research Council of Canada. This paper benefited from the reviews of Stewart Molyneux and Małgorzata Moczyłowska.

References

- BASSETT, M. F., OWENS, R. M. & RUSHTON, A. W. A. 1976. Lower Cambrian fossils from the Hell's Mouth Grits, St Tudwal's Peninsula, North Wales. *Journal of the Geological Society, London* **132**, 623–44.
- BOWRING, S. A. & SCHMITZ, M. D. 2003. High-precision U–Pb zircon geochronology and the stratigraphic record. In *Zircon: Experiments, Isotopes, and Trace Elemental Investigation* (eds J. M. Hanchar & P. W. O. Hoskin), pp. 305–26. Reviews in Mineralogy and Geochemistry 53.
- COBBOLD, E. S. 1910. On some small trilobites from the Cambrian rocks of Comley Shropshire. *Quarterly Journal of the Geological Society of London* **66**, 19–51.
- COBBOLD, E. S. 1921. The Cambrian horizons of Comley (Shropshire) and their brachiopoda, pteropoda, gastropoda etc. *Quarterly Journal of the Geological Society of London* **76**, 325–86.
- COWIE, J. W., RUSHTON, A. W. A. & STUBBLEFIELD, C. J. 1972. A correlation of Cambrian rocks in the British Isles. *Geological Society Special Report* **2**, 1–42.
- CRAMER, F. H. & DíEZ, M. DEL C. R. 1972. Acritarchs from the upper Middle Cambrian Oville Formation of León, northwestern Spain. *Revista Española de Micropaleontología, número extraordinario 30, Aniversario E. N. Adaro*, 39–50.
- DEAN, W. T., MARTIN, F., MONOD, O., GUNAY, Y., KOZLU, H. & BOZDOGAN, N. 1997. Precambrian? and Cambrian stratigraphy of the Penbegli-Tut inlier, southeastern Turkey. *Geological Magazine* **134**, 37–53.
- DEAN, W. T. & ÖZGÜL, N. 1994. Cambrian rocks and faunas, Hudai area, Taurus Mountains, southwestern Turkey.

- Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* **64**, 5–20.
- DEVAERE, L. CLAUSEN, S. & ÁLVARO, J. J. (eds) 2014. *Stratigraphic Overview of the Ediacaran and Cambrian from the Anti-Atlas, Morocco*. University Lille 1.
- DOWNIE, C. 1982. Lower Cambrian acritarchs from Scotland, Norway, Greenland and Canada. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **72**, 257–85.
- DOWNIE, C. 1963. 'Hystrichospheres' (acritarchs) and spores of the Wenlock Shales (Silurian) of Wenlock, England. *Palaeontology* **6**, 625–52.
- ELICKI, O. & GEYER, G. 2013. The Cambrian trilobites of Jordan – taxonomy, systematics, and stratigraphic significance. *Acta Geologica Polonica* **63**, 1–56.
- EKLUND, K. 1990. Lower Cambrian acritarch stratigraphy of the Bårstad 2 core, Östergötland, Sweden. *Geologiska Föreningens i Stockholm Förhandlingar* **112**, 19–44.
- EVITT, W. R. 1963. A discussion and proposals concerning fossil dinoflagellates, hystrichospheres, and acritarchs I. *Proceedings of the National Academy of Sciences of the United States of America* **49**, 158–64.
- FLETCHER, T. P. 2003. *Ovatoryctocara granulata*: the key to a global Cambrian stage boundary and the correlation of the olenellid, redlichiid and paradoxiid realms. *Special Papers in Palaeontology* **70**, 73–102.
- FLETCHER, T. P. 2006. *Bedrock Geology of the Cape St. Mary's Peninsula, Southwest Avalon Peninsula, Newfoundland (includes parts of NTS map sheets 1M/1, 1N/4, 1L/16 and 1K/13)*. St. John's: Government of Newfoundland and Labrador, Geological Survey, Department of Natural Resources, Report 06-02, 117 pp.
- FOMBELLA, M. A. 1977. Acritarcos de edad Cámbrico medio-inferior de la Provincia de León, España. *Revista Española de Micropaleontología* **9**, 115–24.
- GEYER, G. 1990a. Revised Lower to lower Middle Cambrian biostratigraphy of Morocco. *Newsletters on Stratigraphy* **22**, 53–70.
- GEYER, G. 1990b. Die Marokkanischen Ellipsocephalidae (Trilobita: Redlichida). *Beringeria* **3**, 1–363.
- GEYER, G. 2015. Exotic trilobites from the Lower–Middle Cambrian boundary interval in Morocco and their bearing on the Cambrian Series 3 lower boundary. *Paläontologische Zeitschrift* **89**, 749–81.
- GEYER, G., BUSCHMANN, B. & ELICKI, O. 2014. A new lowermost middle Cambrian (Series 3, Stage 5) faunule from Saxony (Germany) and its bearing on the tectonostratigraphic history of the Saxothuringian domain. *Paläontologische Zeitschrift* **88**, 239–52.
- GEYER, G. & LANDING, E. 2004. A unified Lower – Middle Cambrian chronostratigraphy for West Gondwana. *Acta Geologica Polonica* **54**, 179–218.
- GEYER, G. & MALINKY, J. M. 1997. Middle Cambrian fossils from Tizi n'Tichka, the High Atlas, Morocco; Part 1, Introduction and trilobites. *Journal of Paleontology* **71**, 620–37.
- GEYER, G. & PALMER, A. R. 1995. Neltneriidae and Holmiidae (Trilobita) from Morocco and the problem of Early Cambrian intercontinental correlation. *Journal of Paleontology* **69**, 459–74.
- GOZALO, R., DIES ALVAREZ, M. E., GAMEZ VINTANED, J. A., ZHURAVLEV, A. YU., BAULUZ, B., SUBIAS, I., CHIRIVELLA MARTORELL, J. B., MAYORAL, E., GURSKY, H. J., ANDRES, J. A. & LIÑÁN, E. 2013. Proposal of a reference section and point for the Cambrian Series 2–3 boundary in the Mediterranean subprovince in Murero (NE Spain) and its intercontinental correlation. *Geological Journal* **48**, 142–55.
- HAGENFELDT, S. E. 1989. Middle Cambrian acritarchs from the Baltic depression and south-central Sweden: taxonomy and biostratigraphy. *Stockholm Contributions in Geology* **41**, 177–250.
- HARVEY, T. H. P., WILLIAMS, M., CONDON, D. J., WILBY, P. R., SIVETER, D. J., RUSHTON, A. W. A., LENG, M. J. & GABBOTT, S. E. 2011. A refined chronology for the Cambrian succession of southern Britain. *Journal of the Geological Society, London* **168**, 705–16.
- HAYES, A. O. & HOWELL, B. F. 1937. *Geology of Saint John, New Brunswick*. Geological Society of America Special Papers no. 5, 146 pp.
- JACHOWICZ-ZDANOWSKA, M. 2013. Cambrian phytoplankton of the Brunovistulicum – taxonomy and biostratigraphy. *Polish Geological Institute Special Papers* **28**, 1–150.
- LANDING, E. & WESTROP, S. R. 1996. Upper Lower Cambrian depositional sequence in Avalonian New Brunswick. *Canadian Journal of Earth Sciences* **33**, 404–17.
- LANDING, E. & WESTROP, S. R. 1998. Cambrian faunal sequence and depositional history of Avalonian Newfoundland and New Brunswick: Field Workshop. In *Avalon 97 – The Cambrian Standard* (eds E. Landing & S. R. Westrop), pp. 5–75. New York State Museum Bulletin 492.
- LANDING, E., BOWRING, S. A., DAVIDEK, K. L., WESTROP, S. R., GEYER, G. & HELDMAIER, W. 1998. Duration of the Early Cambrian: U–Pb ages of volcanic ashes from Avalon and Gondwana. *Canadian Journal of Earth Sciences* **35**, 329–38.
- LISTER, T. R. 1970. *The Acritarchs and Chitinozoa from the Wenlock and Ludlow Series of the Ludlow and Millichope Areas, Shropshire*. Monograph of the Palaeontographical Society no. 124 (issue 528), 100 pp.
- MARTIN, F. & DEAN, W. T. 1983. Late Early Cambrian and Early Middle Cambrian acritarchs from Manuels River, eastern Newfoundland. In *Current Research, Part B. Geological Survey of Canada, Paper 83-1B*, 353–63.
- MARTIN, F. & DEAN, W. T. 1984. Middle Cambrian acritarchs from the Chamberlains Brook and Manuels River Formations at Randon Island, eastern Newfoundland. In *Current Research, Part A. Geological Survey of Canada, Paper 84-1A*, 429–40.
- MARTIN, F. & DEAN, W. T. 1988. Middle and Upper Cambrian acritarch and trilobite Zonation at Manuels River and Randon Island, eastern Newfoundland. *Geological Survey of Canada Bulletin* **381**, 1–91.
- MATTHEW, G. F. 1890. On Cambrian organisms in Acadia. *Transactions of the Royal Society of Canada* **7** (4), 135–62.
- MATTHEW, G. F. 1892. *Protolenus*—a new genus of Cambrian trilobites. *Bulletin of the Natural History Society of New Brunswick* **10**, 34–7.
- MATTHEW, G. F. 1895. The *Protolenus* Fauna. *Transactions of the New York Academy of Sciences* **14**, 101–53.
- MOCZYDŁOWSKA, M. 1991. Acritarch biostratigraphy of the Lower Cambrian and Precambrian–Cambrian boundary in southeastern Poland. *Fossils and Strata* **29**, 1–127.
- MOCZYDŁOWSKA, M. 1998. Cambrian acritarchs from Upper Silesia, Poland – biochronology and tectonic implications. *Fossils and Strata* **46**, 1–121.
- MOCZYDŁOWSKA, M. 1999. The Lower–Middle Cambrian boundary recognized by acritarchs in Baltica and at the margin of Gondwana. *Bollettino della Società Paleontologia Italiana* **38**, 207–25.
- MOCZYDŁOWSKA, M. 2011. The Early Cambrian phytoplankton radiation: acritarch evidence from the Lükati Formation, Estonia. *Palynology* **35**, 103–45.

- MOCZYDŁOWSKA, M., LANDING, E., ZANG, W. & PALACIOS, T., 2011. Proterozoic phytoplankton and timing of Chlorophyte algae origins. *Palaeontology* **54**, 721–33.
- MOCZYDŁOWSKA, M. & VIDAL, G. 1986. Lower Cambrian acritarch zonation in southern Scandinavia and south-eastern Poland. *Geologiska Föreningens i Stockholm Förhandlingar* **108**, 201–23.
- MOCZYDŁOWSKA, M. & VIDAL, G. 1988. Early Cambrian acritarchs from Scandinavia and Poland. *Palynology* **12**, 1–10.
- MOLYNEUX, S. G., DELABROYE, A., WICANDER, R. & SERVAIS, T. 2013. Biogeography of early to mid Palaeozoic (Cambrian–Devonian) marine phytoplankton. In *Early Palaeozoic Biogeography and Palaeogeography* (eds D. A. T. Harper & T. Servais), pp. 365–97. Geological Society of London, Memoir no. 38.
- MOLYNEUX, S. G., LE HÉRISSE, A. & WICANDER, R. 1996. Paleozoic phytoplankton. In *Palynology: Principles and Applications* (eds J. Jansonius, & D. C. McGregor), pp. 493–529. College Station, Texas: American Association of Stratigraphic Palynologists Foundation.
- NELTNER, L. & POCTEY, N. 1950. Quelques faunes géorgiennes du Maroc. *Notes et Mémoires du Service Géologique, Maroc* **74**, 53–83.
- PALACIOS, T. 2008. Middle Cambrian acritarch zones in the Oville Formation and their correlation with trilobite zones in the Cantabrian Mountains, Northern Spain. In *Advances in Trilobite Research* (eds I. Rábano, R. Gozalo & D. García Bellido), pp. 289–95. Cuadernos del Museo Geominero no. 9.
- PALACIOS, T. 2014. A pilot proposal of a Middle Cambrian (Series 3) acritarch biozonation in northwestern Gondwana. In *Stratigraphic Overview of the Ediacaran and Cambrian from the Anti-Atlas, Morocco* (eds L. Devaere, S. Clausen & J. J. Álvaro), pp. 27–8. University Lille 1.
- PALACIOS, T. 2015. Acritarch assemblages from the Oville and Barrios Formations, northern Spain: a pilot proposal of a middle Cambrian (Series 3) acritarch biozonation in northwestern Gondwana. *Review of Palaeobotany and Palynology* **219**, 71–105.
- PALACIOS, T., JENSEN, S., APALATEGUI, O. 2006. Biostratigrafía de acritarcos en el Cámbrico Inferior y Medio del margen septentrional de Gondwana (Área de Zafra, Suroeste de la Península Ibérica). In *22 Jornadas de la Sociedad Española de Paleontología, Libro de Resúmenes* (ed. E. Fernández-Martínez), pp. 156–61.
- PALACIOS, T., JENSEN, S., WHITE, C. E. & BARR, S. M. 2012. Cambrian acritarchs from the Bourinot belt, Cape Breton Island, Nova Scotia: age and stratigraphic implications. *Canadian Journal of Earth Sciences* **49**, 289–307.
- PALACIOS, T. & MOCZYDŁOWSKA, M. 1998. Acritarch biostratigraphy of the Lower–Middle Cambrian boundary in the Iberian Chains, province of Soria, northeastern Spain. *Revista Española de Paleontología, Numero Extraordinario, Homenaje al Prof. Gonzalo Vidal*, 65–82.
- PENG, S., BABCOCK, L. E. & COOPER, R. A. 2012. The Cambrian. In *The Geologic Time Scale 2012* (eds F. M. Gradstein, J. G. Ogg, M. Schmitz & G. Ogg), pp. 437–88. Amsterdam: Elsevier.
- POTTER, T. L. 1974. British Cambrian acritarchs – a preliminary report. *Review of Palaeobotany and Palynology* **18**, 61–2.
- RICHTER, R. & RICHTER, E. 1941. Die Fauna des Unterkambriums von Cala in Andalusien. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **455**, 1–90.
- RUDAVSKAYA, V. A. 1973. Akritarkhi pograničnikh otlozhenij rifeya i kembriya yuga vostočnoj Sibiri. In *Mikrofosilii Drevnejshikh Otlozhenij* (eds T. F. Vozzhennikova & B. V. Timofeev), pp. 17–21. Moscow: Nauka.
- RUSHTON, A. W. A. 1974. The Cambrian of Wales and England. In *Cambrian of the British Isles, Norden, and Spitsbergen* (ed. C. H. Holland), pp. 43–121. London: Wiley.
- RUSHTON, A. W. A. & MOLYNEUX, S. G. 2011. Welsh Basin. In *A Revised Correlation of the Cambrian Rocks in the British Isles* (eds A. W. A. Rushton, P. M. Brück, S. G. Molyneux, M. Williams & N. H. Woodcock), pp. 21–7. Geological Society of London, Special Report no. 25.
- SARJEANT, W. A. S. & STANCLIFFE, R. P. W. 1994. The *Micrhystridium* and *Veryhachium* complexes (Acritarcha: Acanthomorphytae and Polygonomorphytae): a taxonomic reconsideration. *Micropalaeontology* **40**, 1–77.
- SCHMITZ, M. D. 2012. Radiometric ages used in GTS 2012. In *The Geologic Time Scale 2012* (eds F. M. Gradstein, J. G. Ogg, M. Schmitz & G. Ogg), pp. 1045–77. Amsterdam: Elsevier.
- SCHWARZBACH, M. 1939. Die oberlausitzer *Protolenus*-fauna. Weiter funde aus dem schlesischen Kambrium und ihre allgemeine bedeutung. *Jahrbuch der Preussischen Geologischen Landes-Anstalt Berlin* **59** (for 1938), 769–85.
- SDZUY, K. 1972. Das Kambrium der acadobaltischen Faunenprovinz. Gegenwärtiger Kenntnisstand und Probleme. *Zentralblatt für Geologie und Paläontologie, Teil II* **1972**, 1–91.
- SIVETER, D. J., WALOSZEK, D. & WILLIAMS, M. 2003. An early Cambrian phosphatocopid crustacean with three-dimensionally preserved soft parts from Shropshire, England. *Special Papers in Palaeontology* **70**, 9–30.
- SIVETER, D. J. & WILLIAMS, M. 1997. Cambrian bradoriid and phosphatocopid arthropods of North America. *Special Papers in Palaeontology* **57**, 1–69.
- STANEVICH, A. M. 2003. Relics of marine bacterial coenoses from Neoproterozoic Formations of the south margin of Siberian Platform. In *Instruments, Methods, and Mission for Astrobiology 6* (eds R. B. Hoover, A. Yu. Rozanov & J. H. Lipps), pp. 28–37. Proceedings of SPIE 4939.
- STAPLIN, F. L., JANSONIUS, J. & POCKOCK, S. A. J. 1965. Evaluation of some acritarchous hystrichosphere genera. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **123**, 167–201.
- TANOLI, S. K. & PICKERILL, R. K. 1988. Lithostratigraphy of the Cambrian–Lower Ordovician Saint John Group, southern New Brunswick. *Canadian Journal of Earth Sciences* **25**, 669–90.
- TIMOFEEV, B. V. 1959. *Drevnejshaya Flora Pribaltiki*. Leningrad: Trudy VNIGRI 129, 320 pp.
- VANGUESTAINE, M. 1978. Criteres palynostratigraphiques conduisant a la reconnaissance d'un pli couche revinien dans le sondage de Grand-Halleux. *Annales de la société géologique de Belgique* **100**, 249–76.
- VANGUESTAINE, M. & VAN LOOY, J. 1983. Acritarches du Cambrien moyen de la Vallee de Tacheddirt (Haut-Atlas, Maroc) dans le cadre d'une nouvelle zonation de Cambrien. *Annales de la société géologique de Belgique* **106**, 69–85.
- VAVRDOVÁ, M. & BEK, J. 2001. Further palynomorphs of Early Cambrian age from clastic sediments underlying the Moravian Devonian (borehole Němčičky-3). *Bulletin of the Czech Geological Survey* **76**, 113–26.
- VIDAL, G. 1988. A palynological preparation method. *Palynology* **12**, 215–20.

- VOLKOVA, N. A. 1968. Akritarkhi dokembrijskikh i nizhekembrijskikh otlozhenij Estonii . In *Problematiki Pogranichnykh Sloev Rifeja i Kembriya Russkoj Platformy, Urala i Kazakhstana* (N. A. Volkova, Z. A. Zhuravleva, V. E. Zabrodin & B. Sh. Klinger), pp. 8–36. Moscow: Nauka.
- VOLKOVA, N. A. 1974. Akritarkhi iz pogranichnykh sloev nizhnego-srednego kembriya zapadnoj Latvii. In *Biostratigrafiya i Paleontologiya Nizhnego Kembriya Evropy i Srednoj Azii* (eds I. T. Zhuravleva & A. Yu. Rozanov), pp. 194–8. Moscow: Nauka.
- VOLKOVA, N. A., KIRJANOV, V. V., PISKUN, L. V., PASHKYAVICHENE, L. T. & JANKAUSKAS, T. V. 1979. Rastitel'nye mikrofosilii. In *Paleontologiya Verkhne-dokembrijskikh i Kembrijskikh Otlozhenij Vostochno-Evropejskoj Platformy* (eds B. M. Keller & A. Yu. Rozanov), pp. 4–38. Moscow: Nauka.
- VOLKOVA, N. A., KIRJANOV, V. V., PISKUN, L. V., PASKEVICIENE, L. T. & JANKAUSKAS, T. V. 1983. Plant microfossils. In *Upper Precambrian and Cambrian Palaeontology of the East-European Platform* (eds A. Urbanek & A. Yu. Rozanov), pp. 7–46. Warszawa: Wydawnictwa Geologiczne.
- WESTROP, S. R. & LANDING, E. 2000. Lower Cambrian (Branchian) trilobites and biostratigraphy of the Hanford Brook Formation, southern New Brunswick. *Journal of Paleontology* **74**, 858–78.
- YANG, R. & YIN, L. 2001. Acritarch assemblages from the Early–Middle Cambrian Kaili Formation of east Guizhou province and biostratigraphic implication. *Acta Micropalaeontologica Sinica* **18**, 55–69.
- YIN, L., YANG, R., PENG, J. & KONG, F. 2009. New data regarding acritarch biostratigraphy from the Early–Middle Cambrian Kaili Formation in Chuandong, Guizhou Province, China. *Progress in Natural Science* **19**, 107–14.
- YIN, L., ZHAO, Y., YANG, R. & PENG, J. 2010. Acritarchs from the Early–Middle Cambrian Kaili Formation in the Wuliu–Zengjiaya section, eastern Guizhou Province, China. *Acta Palaeontologica Sinica* **49**, 164–73.
- YOUNG, T., MARTIN, F., DEAN, W. T. & RUSHTON, A. W. A. 1994. Cambrian stratigraphy of St Tudwal's Peninsula, Gwynedd, northwest Wales. *Geological Magazine* **131**, 335–60.
- ZYLINSKA, A. & SZCZEPANIK, Z. 2009. Trilobite and acritarch assemblages from the Lower – Middle Cambrian boundary interval in the Holy Cross Mountains (Poland). *Acta Geologica Polonica* **59**, 413–58.