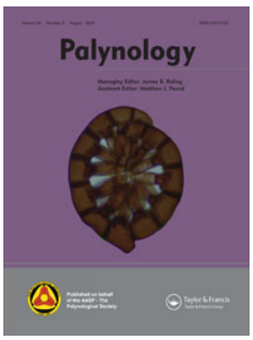

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Pellicle ultrastructure demonstrates that *Moyeria* is a fossil euglenid

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ABSTRACT

An earlier proposal of euglenid affinity for the acritarch *Moyeria* was based primarily on the pattern of bi-helical striate ornamentation as seen in scanning electron microscopy and light microscopy. Examination of specimens using transmission electron microscopy reveals that the 'striae' are actually integral components of the microfossil wall itself, corresponding to the pellicle strips of some euglenid species today. A Silurian specimen from Scotland preserves an articulated wall composed of thickened arches and thinner U-shaped interconnecting segments paralleling that seen in some modern photosynthetic euglenids. A second specimen from the *Moyeria* holotype section (Silurian of New York State) shows fused articulation, again compatible with some extant euglenids. This evidence is sufficient to transfer *Moyeria* out of the *Incertae sedis* group, Acritarcha, and into the Euglenida. This proposal helps establish the morphological basis for the recognition of euglenid microfossils and ultimately provides evidence of a lengthy fossil record of the eukaryotic supergroup Excavata.

KEYWORDS

acritarchs; *Euglena*; fossil algae and protists; *Moyeria*; Scotland; Silurian; USA

1. Introduction

In 1989, Jane Gray and Art Boucot posed the question, 'Is *Moyeria* a euglenid?', in an article that explored the arguments from morphology that supported the identification of the acritarch *Moyeria* Thusu 1973 as a fossil euglenid (Gray and Boucot 1989). *Moyeria* possesses a wall consisting of helically arranged, parallel striae that converge at two opposite apical poles, and this feature is also found in the pellicle of many extant euglenids. Gray and Boucot (1989) used scanning electron microscopy (SEM) to document prominent striae in two specimens from the Burvick Beds (Ludlow) in Sweden and another three specimens recovered from the Tuscarora Formation (Llandovery) in central Pennsylvania, USA. These specimens also clearly demonstrated apical whirl reduction, a character that is diagnostic of photosynthetic euglenids today (Leander and Farmer 2000; Leander 2004; Leander et al. 2007). But Gray and Boucot (1989) were somewhat cautious in proposing that *Moyeria* be identified systematically as a fossil euglenid, and never made any formal taxonomic recommendation. Subsequently, even though many authors have tacitly agreed with their conclusion, palynologists continue to refer to *Moyeria* as an acritarch, i.e. an organic-walled microfossil (OWM) of unknown systematic affinity.

Moyeria was originally described by Bindra Thusu from an outcrop of Wenlock age exposed along the south branch of Moyer Creek, about 8 km west of the town of Ilion, New York, USA (Thusu 1973). He formally designated one species, *Moyeria uticaensis*, but neglected to specify which of the four illustrated specimens was the holotype. Eisenack et al. (1976) considered *Moyeria uticaensis* to be a junior synonym of a striate acritarch originally described by Cramer (1971) as *Eupoikilofusa cabottii*. Miller and Eames (1982) transferred *E. cabottii* to *Moyeria* and emended the genus description to reflect the fact that the vesicle was not consistently fusiform in overall shape, thus falling outside the morphological description of *Eupoikilofusa*. Most authors, including Gray and Boucot (1989), subsequently referred to helically striate OWMs with variably globular shape found in Ordovician and Silurian rocks as *Moyeria cabottii*, retaining a genus name that was not validly published. Although this designation has not been the cause of any particular confusion, it is incorrect with respect to the rules of nomenclature (see Fensome et al. 1990 for a detailed explanation).

Thusu (1973, p. 142) specified the location coordinates of the holotype on the original strew slide, and we have located the original intended holotype specimen, which was illustrated in plate 2, figure 19 in Thusu (1973), and is confirmed as the holotype. We have also made an orthographic correction to the original species epithet, *uticaensis*, which now becomes *uticana*. This now validates the genus, *Moyeria*, and re-establishes *M. uticana* as its type species. We have also collected more material from the original section and have been able to further clarify the nature of *M. uticana* with respect to the more commonly used designation *M. cabottii*. These are two distinct species, as we detail below.

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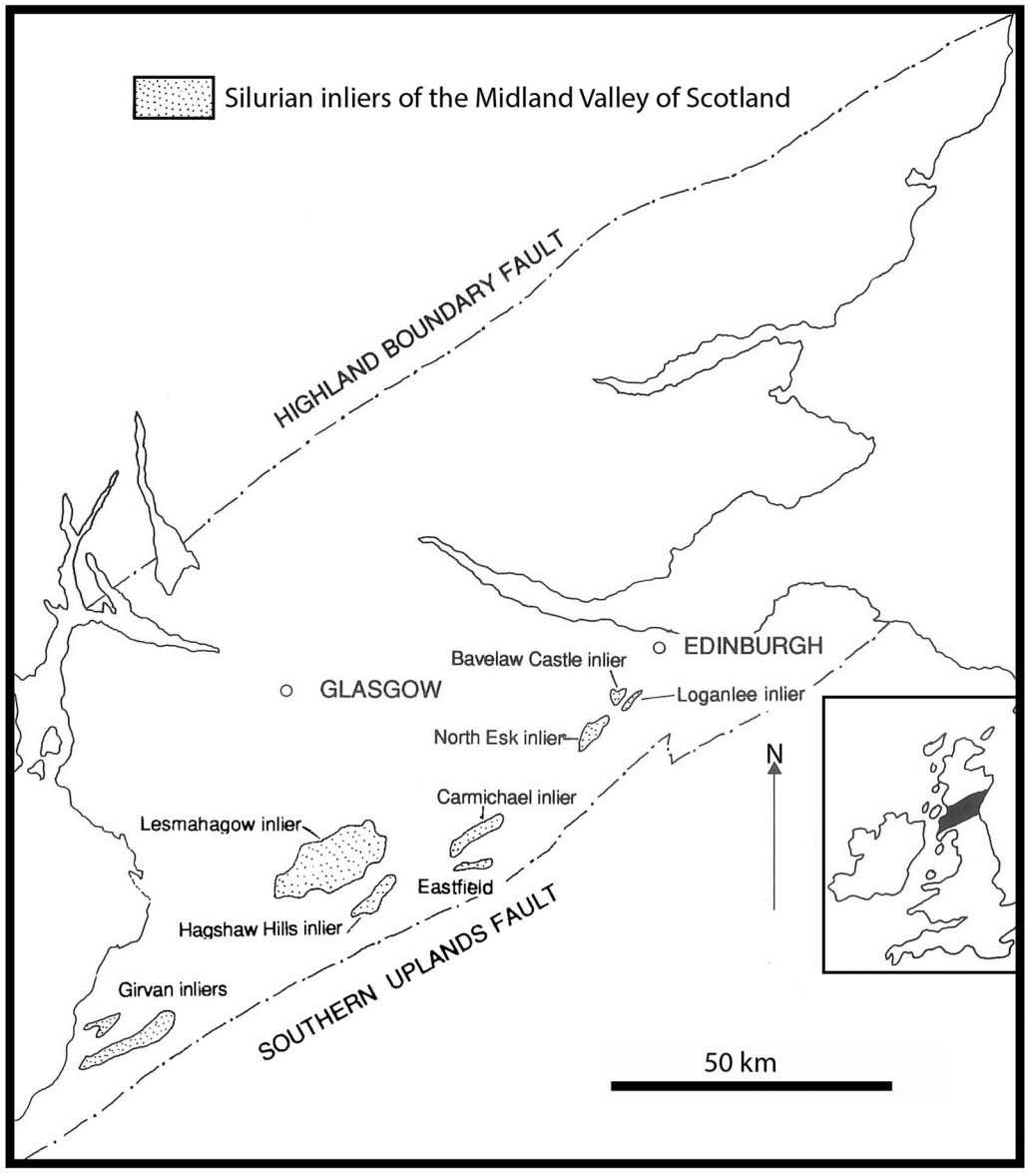

Figure 1. Location map for the Hagshaw Hills Inlier, Scotland (for more details see Wellman and Richardson 1993).

Extant euglenids do not possess a cell wall in the conventional sense; rather, their cells are enclosed by a proteinaceous pellicle which lies inside the cell membrane (Leedale 1964). The pellicle itself consists of a series of parallel strips that are interlocked to each other along their margins. The pellicle strips may be laterally fused, to form a rigid structure, or they may slide past each other allowing for euglenoid movement (Leander 2004; Leander et al. 2007, 2017). The strips, when isolated from each other in completely disrupted specimens and viewed by light microscopy (LM), have an optically thickened margin on one edge with a thinner flange on the opposite margin (Leedale 1967, fig. 8), although some strips may appear to be symmetrical, with two thickened edges. When viewed by transmission electron microscopy (TEM) in transverse sections, pellicle strips exhibit four main shapes as categorised by Leander and Farmer (2001): S shaped, M shaped, A shaped, and plateau shaped. When viewed by LM, it is apparent that the *Moyeria* wall is a series of regular strips, typically with a darker (dense) edge and a thinner tapering margin. Here we utilise the TEM to demonstrate that the 'striae' in *Moyeria* possess an ultrastructure that is fundamentally euglenoid in character. The articulated character of the *Moyeria* wall has now been documented in two independent Silurian specimens; one from the Hagshaw Hills of the Scottish Midlands and another from the *M. uticana* holotype section in New York State, USA.

2. Material and methods

Specimens of *Moyeria* were isolated from fresh rock collected in the field by CHW (Fish Bed Formation; Figure 1) and by PKS (the Ilion Shale Member of the Lockport Formation and the Joslin Hill Member of the Herkimer Formation; Figures 2 and 3). Rock samples were cleaned and crushed and 40 g was demineralised using standard palynological hydrochloric acid (HCl)-hydrofluoric acid (HF)-HCl acid maceration techniques. The residue was sieved through a 20-μm mesh. A heavy liquid (zinc bromide) separation was then undertaken to remove any remaining

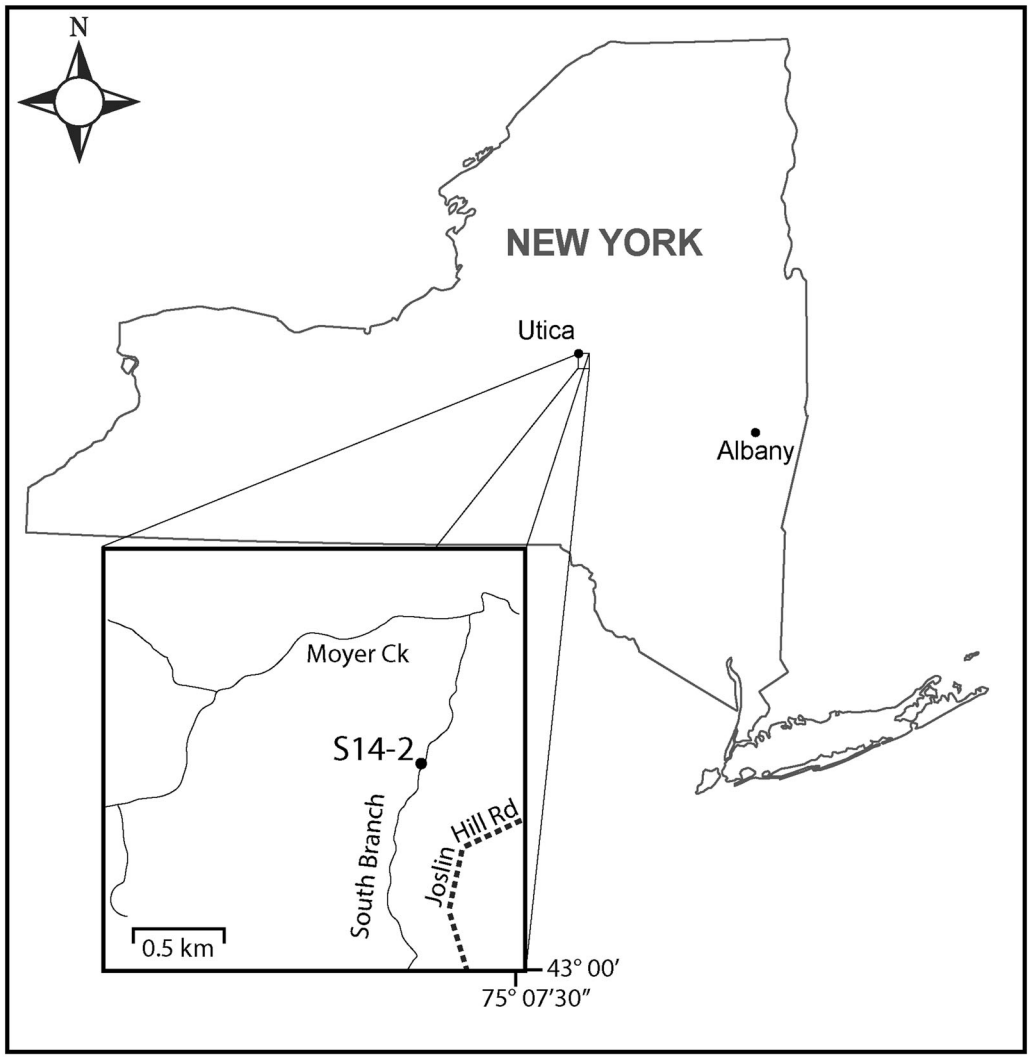

Figure 2. Location map for the section along the south branch of Moyer Creek, New York State, located in the SE quadrant of the Utica East USGS Quadrangle. Sample S14-2 is located at 43°0.5835′N 75°7.8618′W. Source: Authors.

Figure 3. Photograph of sample S14-2 at its collection site. Hammer is 30.5 cm in length.

undissolved minerals, followed by further sieving using a 20-μm mesh. Some of the organic residue was mounted on glass slides using epoxy resin for LM analysis. The remaining residue was examined under a dissecting microscope and individual specimens picked for TEM analysis. Picked specimens were embedded in a small agar block and then embedded in epoxy resin using standard preparatory techniques. Sections were cut using an ultramicrotome and imaged using a JOEL 2010 transmitting electron microscope operating at 80 kV.

3. Results

3.1. The Hagshaw Hills specimen

Specimens of *Moyeria* (Plates 1, 2) were isolated from the Upper Silurian (427 Ma) non-marine deposits of the Fish Bed Formation of the Hagshaw Hills inlier, Scotland. The Hagshaw Hills inlier is one of a series of Silurian inliers located along the southern margin of the Midland Valley of Scotland (Figure 1). The stratigraphical sequence in the inlier represents a marine to freshwater transition, and the Fish Bed Formation consists predominantly of siltstones

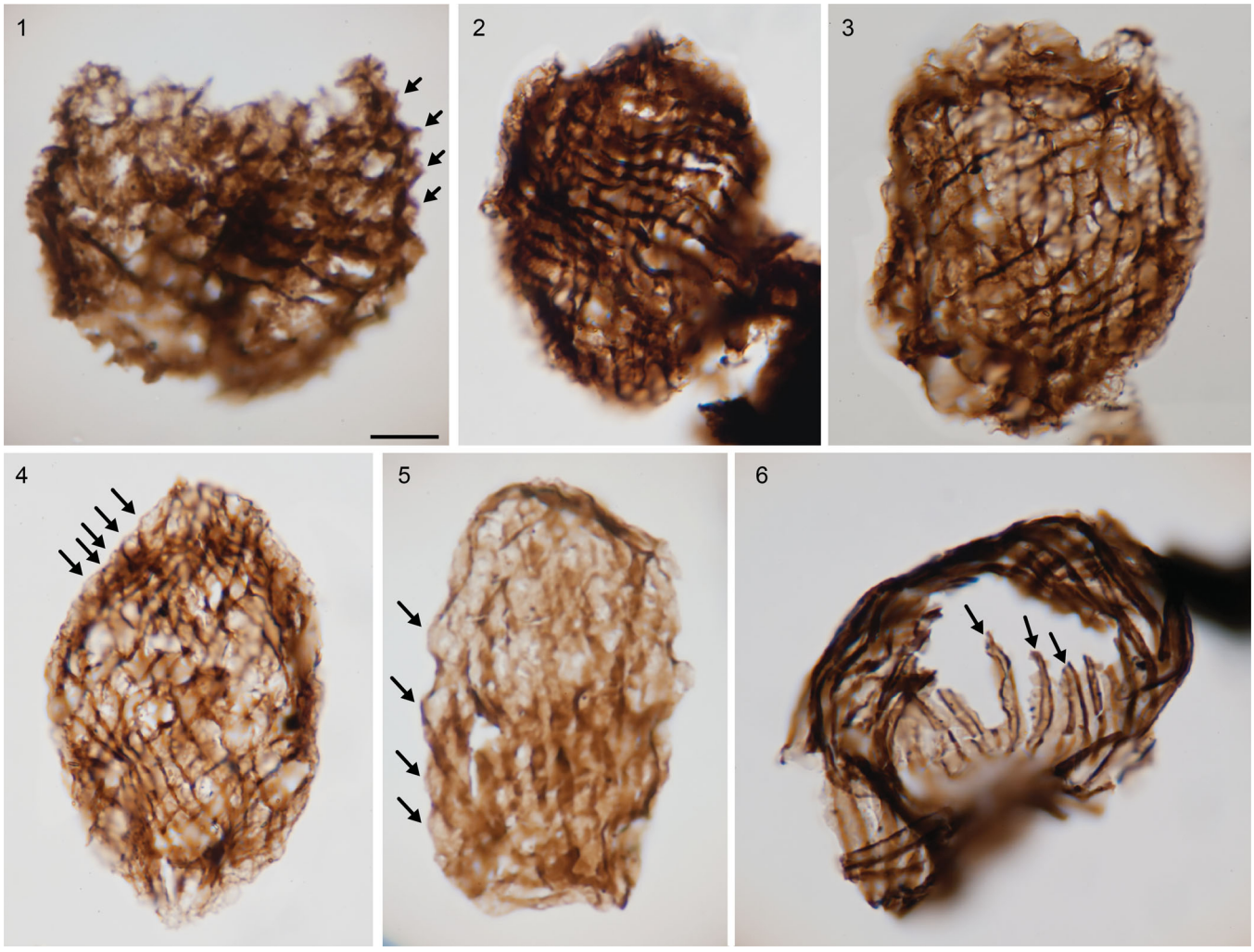

Plate 1. Transmitted white light micrographs of *Moyeria* sp. and *M. cabottii* from the Upper Silurian of the Hagshaw Hills inlier. All specimens are from sample CH1 collected from the Glenbuck Loch locality, sample 12CW156, slide BH4/1. Scale bar in 1 = 10 μm in all images. Slide loc. refers to England Finder coordinates. Figure 1. A nearly spherical specimen showing distinctly serrated/crenulate margin where strips wrap around the cell (arrows), loc. ca. H20. Figure 2. A typical prolate specimen, loc. L51. Figure 3. This squarish specimen clearly shows the cross-hatched nature of the compressed top and bottom walls, loc. L61. Figure 4. A subfusiform specimen with crenulated margin where pellicle strips wrap around the cell (arrows), loc. Q43. Figure 5. A subrectangular form with somewhat wider pellicle strips and distinctly crenulated margin (arrows), loc. D21. Figure 6. A damaged specimen with distinctive, wider pellicle strips. Individual strips are discernible in the centre of the specimen (arrows) where it is broken and only a single layer of the pellicle is present and unobscured by the opposing layer, loc. T59.

interpreted as accumulating in a freshwater lake. It is confidently dated as Early Wenlock (Late Silurian) based on invertebrate biotas in the marine deposits below and dispersed spore assemblages recovered from the actual Fish Bed Formation. The geology and palynology of the Fish Bed Formation are detailed in Wellman and Richardson (1993). Isolated specimens were analysed under LM (Plate 1, figures 1–6) and individual specimens picked, embedded, and sectioned for analysis of wall ultrastructure using TEM (Plate 2).

Examination using LM demonstrates that *Moyeria* consists of a flattened organic-walled vesicle, which varies in outline from circular (Plate 1, figure 1) to prolate (Plate 1, figures 2, 3) to somewhat fusiform but with rounded apices (Plate 1, figure 4); however, there is a considerable range of shapes between such ideal forms, including almost square (Plate 1, figures 5, 6). Palynologists originally interpreted the *Moyeria* vesicle to be ornamented with a series of parallel striae arranged helically, which take on a crosshatched appearance forming a diamond-shaped pattern when compressed (e.g. Thusu 1973). It is apparent, from the crenulated nature of the specimen margins (arrows in Plate 1, figures 1, 4, 5), that the 'striae' wrap around the vesicle and are integral to both the top and bottom walls of the compressed microfossil. Here, we interpret the 'striae' as the surface manifestation of a series of parallel strips (frames) that are fused together to form the vesicle wall. Each strip is delineated by a marginal bead, or darker strip edge, that is probably what has been interpreted in the past as 'striae'. However, some specimens possess strips that are pleated (Plate 1, figure 5) as paired sets of thickened 'striae'. This latter form is apparent in Plate 1, figure 6 (arrows) where the paired strips are broken away from the wall, leaving a ragged edge.

TEM imaging of a transverse section of the Hagshaw Hills specimen in Plate 2, figure 1 demonstrates a distinctive ultrastructure, which is depicted in its entirety in Plate 2, figure 2. Although there is distortion, likely induced during burial and compression, the morphology is similar enough to modern euglenid pellicles that the common terminology proposed

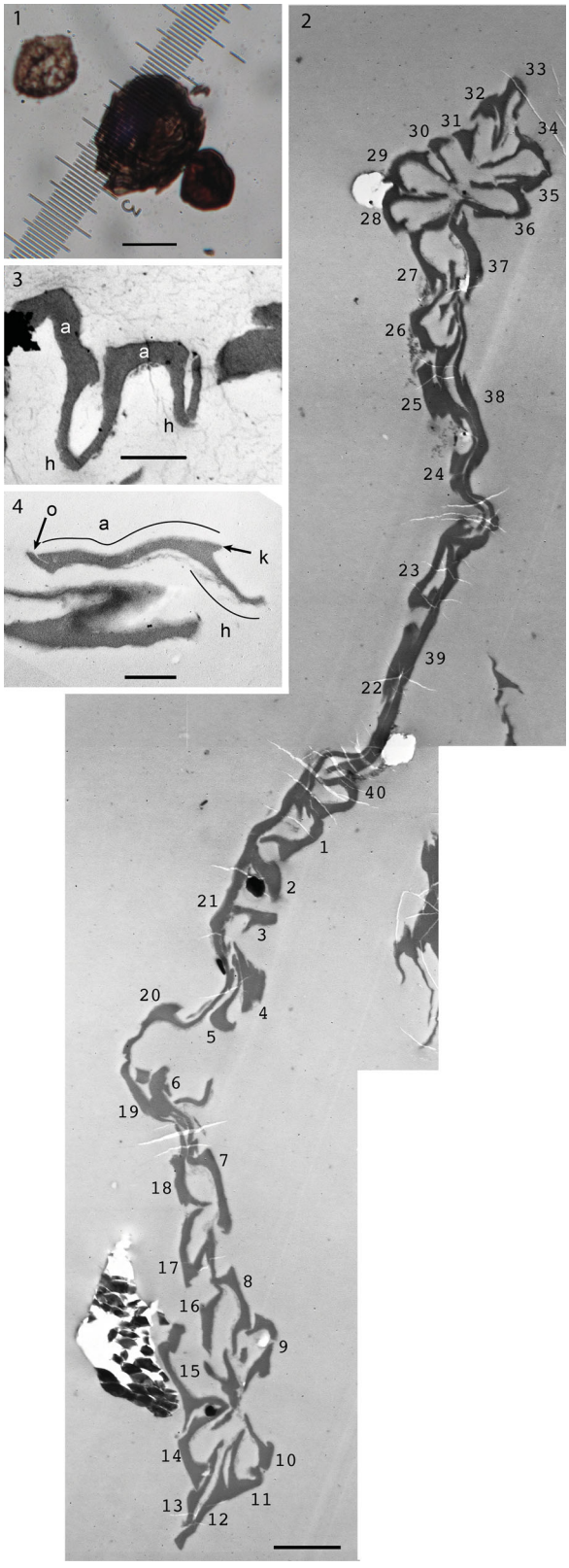

Plate 2. Wall ultrastructure of a specimen of *Moyeria* sp. from the Hagshaw Hills inlier. Figure 1. A low-resolution image of embedded specimen prior to sectioning; scale bar = 20 μm. Figure 2. A composite transmission electron microscopy image of entire specimen; scale bar = 2 μm. Figure 3. A close-up of a pair of pellicle frames; a = frame arch, h = frame heel; scale bar = 1 μm. Figure 4. Another close-up of an isolated pellicle frame; o = overhang, a = frame arch, h = frame heel, k = keel; scale bar = 1 μm. Terminology follows Leander and Farmer (2001).

by Leander and Farmer (2001) can be applied to the fossil. Many individual frames are detached from each other, so the exact number of frames in the specimen was difficult to determine with complete certainty. Nevertheless, we provisionally counted and labelled 40 frames, which are numbered in Plate 2, figure 2. The width of the frames varies considerably, of course, depending upon the angle of the a–a section. When cut transverse to the strip, it appears that the frames have a plateau-shaped arch (a) laterally fused to a somewhat thinner, shallow U-shaped heel (h). In the complete specimen this is most clearly seen in frames 1 and 7–9. These features can be seen in two different enlargements of the larger wall (Plate 2, figures 3, 4). In Plate 2, figure 3, two isolated frames from a different ultrathin section show the basic structure of plateau-shaped arches (a) connected by U-shaped heels (h). In Plate 2, figure 4, a different section (corresponding to frame 8 in Plate 2, figure 2) demonstrates a plateau-shaped arch (a) attached to a thinner heel (h), but in this case both a keel (k) and a notch corresponding to an overhang (o) are preserved. At the margins of the compressed vesicle, where the pellicle frames wrap around, the frames are deformed and often broken, forming inward projections (Plate 2, figure 2, frames 10–14 and 28–36).

3.2. The Ilion Shale specimen

The south branch of Moyer Creek (Figure 2) contains an 11-m section of the Lockport Formation that was described as the Ilion Member by Zengler (1965). Thusu (1973) reported the stratigraphical source of the original samples as deriving from the basal section of the Ilion Member, which consists largely of grey to dark grey mudstones along with some dolomitic shales and sandstones. The Ilion Member is an eastern extension of the Lockport Formation. It was considered by Thusu (1973) to be a littoral sequence with paper shales indicative of subtidal quiescent waters. However, as the Lockport Formation thins to the east, it is in effect reaching its proximal limit as it pinches out less than 20 km from the section at the south branch of Moyer Creek. Dark grey shales (Figure 3) were collected again during November 2014 and October 2017, resulting in a total of 10 samples. The samples closest to the overlying Vernon Shale, a red shale unit, contain a few trilete spores along with abundant phytodebris, especially tubular remains (nematoclasts, *sensu* Gensel et al. 1988), which although of unknown systematic affinity are universally agreed to be terrestrial in provenance. The samples from the lower part of the section, which contain *Moyeria*, are dominated by well-preserved acritarchs including *Domasia*, *Tylotopalla*, *Eupoikilofusa*, *Multiplicisphaeridium* and *Hoeglintia*, but some phytodebris attests to a continued terrestrial influx into this shallow marine setting.

LM of *Moyeria uticana* collected from the south branch of Moyer Creek shows a set of forms that are distinctly spherical to globular in shape (Plate 3, figures 1–3), closely matching the original specimen illustrated in Thusu (1973, plate 2, figures 18–21). Others are somewhat more ellipsoidal (Plate 3, figure 4) to squarish (Plate 3, figures 5, 6). One of the

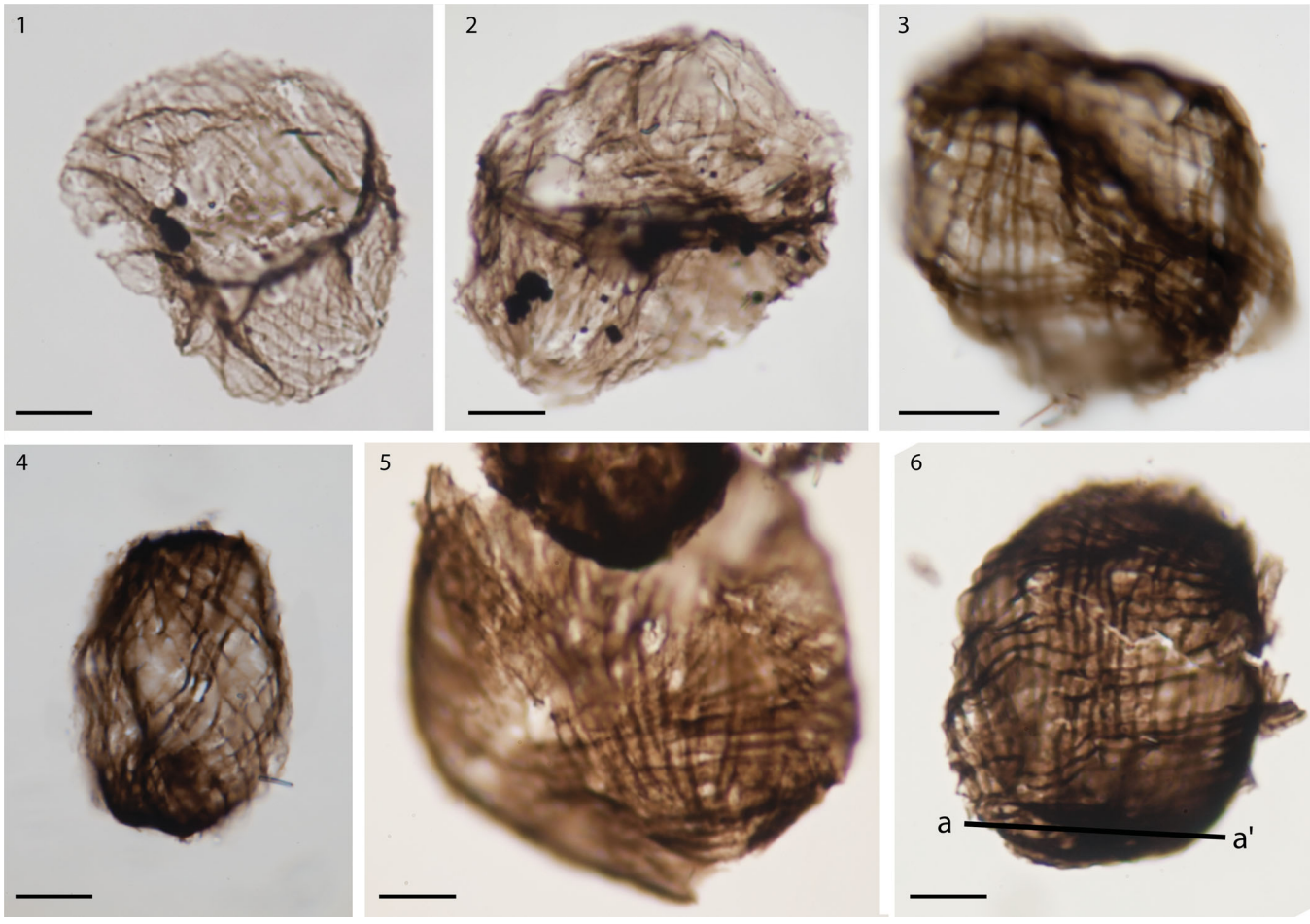

Plate 3. Transmitted white light micrographs of *Moyeria* from the type section along the south branch of Moyer Creek, New York State, USA. Scale bar = 10 μm in all images. Slide loc. refers to England Finder coordinates. Figure 1. A globular specimen of *Moyeria uticana* Thusu that clearly shows the diamond-shaped cross-hatching that characterises this taxon. It also shows the rucked-up, thickened bands that form during compression and traverse the entire specimen. This specimen is quite similar in all aspects to the holotype (Thusu 1973, plate 2, figure 19). Sample S14-2/10, loc. M33. Figure 2. This additional example of a globular *M. uticana* is similar in appearance to the holotype. This photograph is a montage of different focal planes. Sample S14-2/7, loc. D34. Figure 3. Another roughly spherical to globular specimen of *M. uticana*. Sample S14-2/11. Figure 4. A prolate form of *Moyeria* sp., which is smaller than the more globular forms that are closer in form to the holotype of *M. uticana*. This photograph is a montage of different focal planes. Sample S14-2A/2, loc. U29. Figure 5. This nearly spherical form, which is nearly 60 μm in diameter, is slightly larger than the typical *M. uticana* specimens illustrated in Thusu (1973). Sample S14-2/6, loc. E36. Figure 6. A somewhat ellipsoidal specimen of *Moyeria uticana* Line a–a′ shows the approximate line of section for the transmission electron microscopy image in Plate 4, figure 1. Sample S14-2/1, loc. P30.

distinctive features originally noted by Thusu (1973) is the tendency of the vesicle wall to form thickened bands of folded portions of the wall that cross the entire specimen. This rucked-up feature is most evident in Plate 3, figures 1–3. These seem to be taphonomic in nature because of flattening of the delicate pellicle during compression. Indeed, most specimens show some form of thinning (holes), tears, or other signs of physical damage. The specimen illustrated here in Plate 3, figure 1 is closest in appearance to the newly confirmed holotype in plate 2, figure 19 of Thusu (1973).

TEM cross sections of the paratype *Moyeria uticana* from New York were not as well preserved as the Hagshaw Hills specimen; however, Plate 4, figure 1 shows a cross section of a portion of one specimen showing seven successive frames, numbered 1–7 (each frame is numbered at its thickest region in Plate 4, figure 1). The frames are variously distorted by compression and some fragmentation. The exact structural correspondence between the dark lines (striae) on the LM images and the thickened areas seen in TEM cross sections is not always clear. But, apparently, very subtle differences in pellicle thickness (as seen in TEM) result in a noticeable effect in transmitted light. A single frame can be seen in Plate 4, figure 2. This frame has a thickened arch (a) that is approximately 1.5 μm wide and 400–800 nm thick. The arch thins somewhat abruptly to a thinner portion (heel – h in Plate 4, figure 2; approx. 200 nm thick). A second frame of slightly different morphology (Plate 4, figure 3) illustrates some of the variation seen.

4. Systematic palaeontology

Moyeria has always been treated as an acritarch in the literature. Acritarchs are defined as vesicular OWMs of unknown phylogenetic affinity (Evitt 1963). They are widely considered among palynologists to be the resting cysts of marine phytoplankton (Downie et al. 1963; Martin 1993; Colbath and Grenfell 1995; Strother 1996; Talyzina et al. 2000; Servais et al. 2016). The intention of Evitt (1963), who created the informal taxon Acritarcha, was that individual acritarch taxa (genera and species) would eventually be transferred

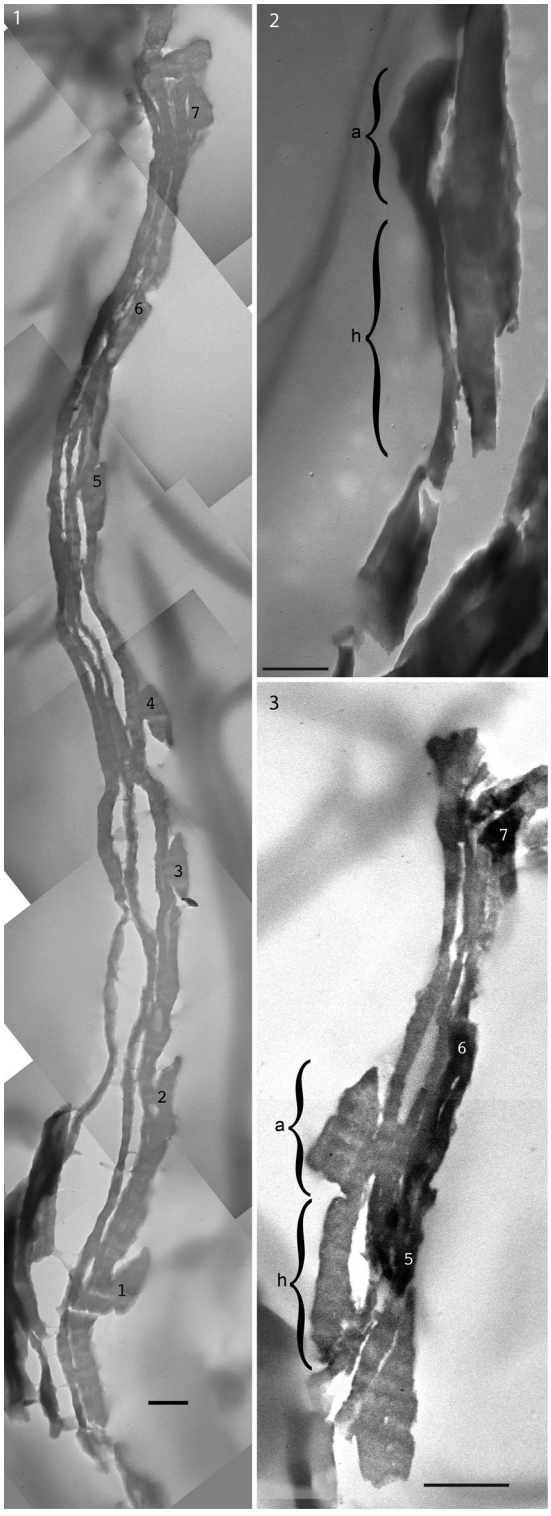

Plate 4. Wall ultrastructure of a specimen of *Moyeria* from the type locality. Figure 1. A composite transmission electron microscopy (TEM) image of a portion of the specimen illustrated in Plate 3, figure 6, showing seven successive frames. The wall largely appears to be fused, although some degree of articulation can be discerned in the thickened portions of the frames that are labeled 1 through 7; scale bar = 1 μm. Figure 2. A TEM image of a cross section of a single frame of the specimen illustrated in Plate 3, figure 6. This frame consists of a thickened portion (a) corresponding to an arch that abruptly thins to a thinner portion (h) corresponding to a heel; scale bar = 1 μm. Figure 3. A frame cross section with slightly different profile, but still showing thick (a) and thin (h) portions; scale bar = 1 μm.

into biologically meaningful taxa as evidence of their phylogenetic affinities became apparent with further study (Servais 1996).

Because of its distinctive morphology, especially with respect to wall ultrastructure, we can now assign *Moyeria* to the Euglenida. Additionally, we propose to re-establish *M. uticana* as the type species for the genus, based on the confirmation of the figured holotype as Plate 2, figure 19 in Thusu (1973). Although *Moyeria* is most commonly associated with *M. cabottii*, following the proposal of Miller and Eames (1982), it is apparent that the variation in basic morphology seen here in Plates 1 and 3 probably encompasses more than one species. Extant euglenid species vary in the number of pellicle strips they possess, for example, and even though the fossils present some difficulty in determining an exact number, it is clear that the specimens in Plate 1, figures 1 and 4 and Plate 3, figure 4 possess only about half the number of strips found in the 40 or so documented in Plate 2, figure 2. In any case, it is not our purpose here to document an expansion of the number of species in the genus, only to validate the genus and confirm its systematic placement within the Euglenida. To that extent we propose an abbreviated systematic note, following the taxonomic schema of Adl et al. (2012).

Domain EUKARYA Woese et al. 1990
Supergroup EXCAVATA Cavalier-Smith 2002, emend. Simpson 2003
Unranked group DISCOBA Simpson in Hampl et al. 2009
Unranked group DISCRISTATA Cavalier-Smith 1998
Unranked group EUGLENOZOA Cavalier-Smith 1981, emend. Simpson 1997
Unranked group EUGLENIDA Büschli 1884, emend. Simpson 1997

Discussion. The Euglenida all possess a pellicle comprised of proteinaceous strips. Because we can infer that the vesicle 'wall' of *Moyeria* was originally a proteinaceous pellicle, the Euglenida is the lowest ranked taxon in which we can confidently place *Moyeria*.

Genus *Moyeria* Thusu 1973

Original diagnosis (Thusu 1973, p. 142). 'Vésicle subsphérique à allongée, arrondie ovoïde, brun clair, paroi modérément épaisse, ornamentation comportant des stries spiralées et forment une reticulation apparente au moyen de deux ranges des crêtes se croissant l'une l'autre et figurant ansi des surfaces losangiques, carrées or rectangulaires dans les specimens comprimés'.

Emended diagnosis (Miller and Eames 1982, p. 242). 'Vesicle hollow, ovoidal to ellipsoidal in shape. Polar processes absent. Ornamented with helicoid folds which converge at the poles. Wall unilayered'.

Type. *Moyeria uticana* Thusu 1973

Discussion. Thusu (1973) originally referred to the species epithet as *uticaensis*, for which we propose an orthographic correction to *uticana*. It is now apparent that the helical 'striae' or 'folds' of the fossil are not really ornament in the

typical sense employed in the morphological terminology used to describe acritarchs. Ornament usually refers to wall materials that lie on top of a vesicle wall, whereas here the strips are an integral component of the wall (pellicle) itself. To that extent the above generic diagnoses represent an incorrect description of the morphology. Miller and Eames (1982) recognised that the outline shape of *Moyeria*, although variable, was distinctly different from that of *Eupoikilofusa*, which, as its name implies, tapers to a point at each end of its axis. As demonstrated here in Plates 1 and 3, the outline of *Moyeria* can be quite variable, a trait that is consistent with many living species of euglenids which possess the ability to dramatically change shape. Since our concern here is only with the type species, we provide a synonymy for the type species only.

Moyeria uticana Thusu 1973
Plate 3, figures 1–3

1973 *Moyeria uticaensis* Thusu: p. 142, pl. 2, figs 18–22.
1978 *Moyeria* cf. *M. uticaensis* Emo & Smith: pl. 1, figs 16–18.

Holotype. Thusu (1973, pl. 2, fig. 19), designated herein.

Discussion. *Moyeria uticana* as characterised by Thusu (1973) has a vesicle length of 35 to 45 μm. This is consistent with the specimens newly collected from Thusu's original locality that are illustrated here in Plate 3, figures 1–3. Although he did not specify the number of strips (striae), it is apparent, based on a count estimate from three of his four figured specimens, that this species possesses numerous strips, approximately 40 per cell. The shape of this species in outline is highly variable, being more or less globular and, most typically, without an apparent smooth or rigid outline. One might view this irregularity as a taphonomic artefact, but it may reflect the lack of a rigid wall in the source specimens themselves. None of the specimens originally illustrated in Thusu (1973) demonstrate clear axial polarity, and this is true as well for the additional specimens illustrated in Plate 3, figures 1–3. Likewise, both the original and the newly collected specimens possess walls which have rucked up into linear, somewhat sinuous folds and clumps.

Emo and Smith (1978) illustrated three examples of very dark and broken specimens of *Moyeria* cf. *M. uticaensis* from the Killanene Formation in Ireland. Their specimens range from 21 to 36 μm in size, but they are apparently globular in shape, and thus in essence appear more like *M. uticana* than *M. cabottii*. In fact, they considered their forms distinct from *Eupoikilofusa cabottii* Cramer 1971, because of the perceived size difference.

Eupoikilofusa cabottii Cramer 1971, now *Moyeria cabottii* (Cramer) Miller & Eames 1982, was originally described by Cramer (1971) as 100 to 200 μm in length and with about 20 strips per cell. If this size assessment is correct, this would render *M. cabottii* much larger and clearly different from *M. uticana* on the basis of size alone. Eisenack et al. (1976) reproduced the original drawing of *Eupoikilofusa cabottii* from Cramer (1971) with a scale bar that indicates the specimen is 96 μm in length. As illustrated by Miller and Eames (1982, plate 3, figure 3), *M. cabottii* is 60 μm × 33 μm, which falls well short of 100–200 μm as stated in Cramer (1971). So in our view, there is uncertainty in the size of *E. cabottii* as originally described by Cramer. In addition the original figured specimens in Cramer (1971), with 20 strips per cell, possess exactly half the number characterising *M. uticana*. The same is true for the specimen illustrated by Miller and Eames (1982, plate 3, figure 3). In addition, these specimens are not globular in outline, but are sub-elliptical, bordering on rounded rectangular in form. Finally, the specimens illustrated by Cramer (1971) and by Miller and Eames (1982) possess distinctly wide strips, which differ from those in *M. uticana* which are characterised by a single, darker bead, or leading edge to the strip itself.

After examining both the original slides used by Thusu (1973), new material collected from the same stratigraphical section, and additional examples of *Moyeria* from other Silurian rocks, we now consider the original proposal of synonymy by Eisenack et al. (1976) to be incorrect. The taxon *Eupoikilofusa cabottii* Cramer 1971 possesses about 20 helical striae, which is quite distinct from *Moyeria uticana* Thusu 1973 with approximately 40 striae. This character, when considered as a euglenid feature, has been used to differentiate species in living genera (Leander and Farmer 2001), so it is significant enough to reject the previously proposed synonymy.

Wicander and Loeblich (1977) described a murate acritarch, *Spurimoyeria falcilaculata*, from the Devonian of Indiana, which they contrasted with both *Moyeria* and *Eupoikilofusa*. However, *S. falcilaculata* is clearly spherical in overall shape and possesses laevigate muri which cross at a greater angle, close to 90°. This results in (compression to) a rectangular patterned surface instead of a diamond-shaped (losangiques) pattern as is more typical for *Moyeria uticana*. More importantly, as pointed out by Wicander and Loeblich (1977), the muri in *S. falcilaculata* do not extend around the circumference of the vesicle body as they do in *Moyeria*. So the resemblance in this case, regarding the fenestrate pattern, is not related structurally to any fundamental, helical pattern of strips or striae that make up the wall itself.

In any case, given the morphological variability seen here in Plates 1 and 3, it is likely that future taxonomic consideration of *Moyeria* will result in the recognition of additional fossil morphospecies based on shape, size, and strip number, especially since these are characters that can be used to diagnose extant euglenid taxa (Leander et al. 2001, 2007).

5. Discussion

The recovery of OWMs in ancient sediments is dependent upon the recalcitrant nature of the biopolymers that constitute vesicle walls. Classically, sporopollenin, which is found in the walls of land plant spores and pollen grains, is considered to be responsible for the retention of morphological detail. But sporopollenin is not the only resistant biopolymer found to preserve cell walls in the fossil record. Dinosporin, the resistant polymer associated with dinoflagellate cysts, has similar properties to sporopollenin, but functions in fundamentally aquatic organisms. Algaenans are another class

of resistant biomacromolecules that are found in various chlorophyte algae and in some dinoflagellate cysts (see de Leeuw et al. 2006 for an excellent review of this topic). Chitinous walls associated with higher fungi, both in spores and in hyphae, are responsible for the preservation of the fungi in the sedimentary record (Jarzen and Elsik 1986). Chitin also allows for the preservation of insect scales in palynological preparations (van Eldijk et al. 2018). Other biopolymers, associated with cyanobacterial sheaths for example, are well known to survive palynological preparation and extraction from siliciclastic rocks (Knoll 1996).

There are hints of the capability of modern euglenids to survive fossilisation in a study that indicated the lorica of *Trachelomonas* is resistant to acetolysis (Lindgren 1981), but a thorough investigation of the general fossilisation potential of extant euglenids has yet to be undertaken. Nevertheless, the retention of microscopic wall structure in *Moyeria*, as demonstrated here, now indicates that the proteinaceous pellicle of the euglenids is also capable of fossilisation.

Moyeria has a documented stratigraphical range of Katian to Ludlow age (Fensome et al. 1990), and thus appears to be restricted to this interval. However, other striate palynomorphs of younger and older ages have sometimes been compared to *Moyeria*, so one could reasonably speculate that euglenids might have a more extensive record than that recorded by *Moyeria* alone. For example, Martin (1974) noted in an addendum that her *Schizaeoisporites* sp. I was now *Eupoikilofusa cabottii* Cramer (1971). She also compared these forms to *Chomotriletes* Naumova, but rejected this assignment at the time. In any case, we consider it possible that a closer examination of alete, helically striate taxa from other parts of the column may establish a wider stratigraphical range for what we now consider to be fossil euglenids.

Moyeria has rarely been reported as a dominant member of any acritarch assemblage, which may be a reflection of its non-marine provenance in assemblages that are recovered from proximal marine settings. There is one exception, however, found in a study of upper Llandovery to Wenlock palynology of the Pentland Hills Inliers, Midland Valley, Scotland (Molyneux et al. 2008). Here, in the upper part of the Reservoir Formation, *Moyeria cabottii* and *Tylotopalla* spp. form a distinctive assemblage in which they constitute 26 to 74% of the total acritarchs. Molyneux et al. (2008) noted that *Moyeria* was possibly of continental origin, based on its occurrence in terrestrial sequences elsewhere in the Silurian of the Midland Valley (Wellman and Richardson 1993), and that its presence might be indicative of changing environmental conditions within their section, but they stopped short of considering *Moyeria* to be a definitive indicator of freshwater provenance. Gray and Boucot (1989) argued for a terrestrial (freshwater) origin to *Moyeria*, noting that it is most common in nearshore and non-marine settings. As part of an ongoing study, we have noted that *Moyeria* co-occurs with *Tapetisphaerites* Miller & Wood, a freshwater hydrodictyeacean colonial alga, in the Tuscarora Formation in central Pennsylvania, USA. The palynological assemblage recovered from this deposit is entirely non-marine in character (Strother and Traverse 1979; Johnson 1985). As a euglenid, it is likely that *Moyeria* is of freshwater origin, given the overwhelmingly freshwater distribution of extant species (Gojdics 1953). Thus, the determination of *Moyeria* as a euglenid should result in a potentially useful marker for non-marine provenance. In addition, *Moyeria*-like forms in younger assemblages may eventually be recognised as a minor component of the non-pollen palynomorph (NPP) fraction in terrestrial assemblages.

6. Conclusions

With the rise of molecular phylogenetics and its use in the construction of evolutionary (time-calibrated) trees, the role of fossils with well-known phylogeny has been crucial in the calibration of molecular clocks. And, while numerous nodes of plant and animal evolutionary trees have been calibrated, very few fossil protists have found their way into calibrated trees in an unquestioned manner (Berney and Pawlowski 2006). In that regard, *Moyeria* now takes on an enhanced level of importance as the sole representative of the eukaryotic supergroup Excavata. This is through its inclusion in both molecular phylogenetic reconstructions (Parfrey et al. 2011) and ancestral character state reconstructions with respect to chloroplast origins (Jackson et al. 2018).

The characteristic pellicle of the euglenids, which is clearly capable of fossilisation, provides a very distinctive morphology that is eminently recognisable in palynological assemblages. The character of an articulated wall, composed of elongate strips, or frames, is distinct from other forms of wall sculpture, and this feature will be helpful in the interpretation of other striate acritarchs. Even though *Moyeria*, as it is presently circumscribed, is known only from the lower mid-Palaeozoic, it is expected that distinctly euglenid forms will be recovered from both younger and older sediments in the future.

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No potential conflict of interest was reported by the authors.

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