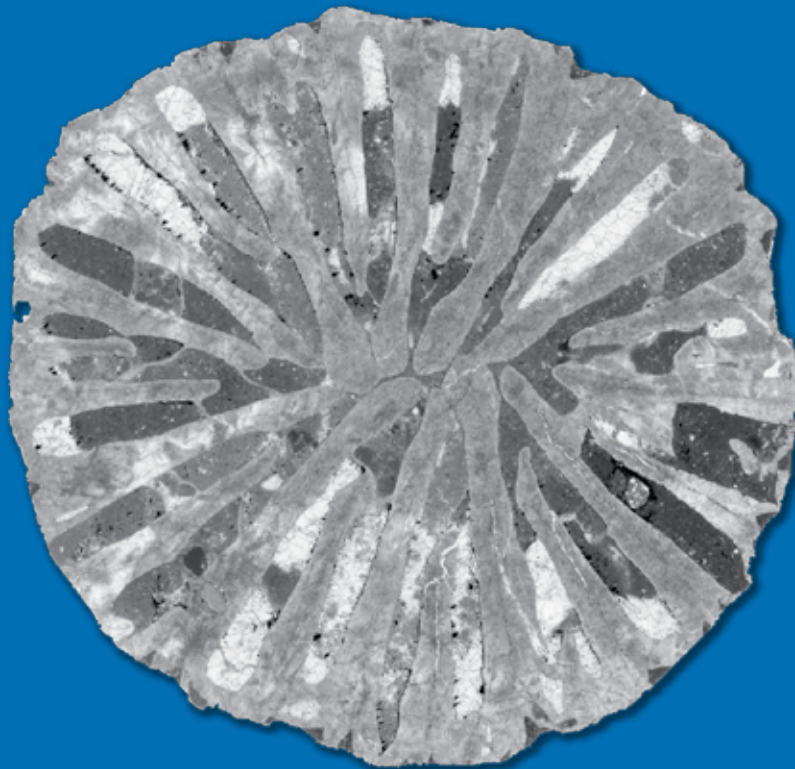


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***Frankbaronia velata* nov. sp., a putative peronosporomycete oogonium containing multiple oospores from the Lower Devonian Rhynie chert**

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Abstract

Spherical to pyriform microfossils containing multiple smooth-walled spherules from the Lower Devonian Rhynie chert are described as oogonia of a new fossil peronosporomycete based on congruencies in basic morphology to the polyoosporous oogonia of certain extant Saprolegniales. Because the new fossils also resemble *Frankbaronia polyspora*, a putative peronosporomycete described previously from the Rhynie chert, they are assigned to the fossil genus *Frankbaronia* and formally proposed as a new species, *F. velata*. Surrounding the oogonium is a conspicuous sheath of consolidated mucilage, produced and secreted by the oogonium during development. The discovery of *F. velata* adds to our understanding of the microbial diversity in early terrestrial ecosystems, and contributes to the documentation of the evolutionary history of the Peronosporomycetes.

Key words: mucilage sheath, Oomycota, polyoosporous oogonium, Saprolegniales

Zusammenfassung

Kugelige bis tropfenförmige, glattwandige kugelige Strukturen in großer Zahl enthaltende Mikrofossilien aus dem unterdevonischen Rhynie Chert werden als Oogonien eines neuen fossilen Peronosporomyceten beschrieben, da sie den polyoosporigen Oogonien einiger heutiger Saprolegniales morphologisch sehr ähnlich sind. Da die Fossilien auch mit *Frankbaronia polyspora*, einem bereits früher aus dem Rhynie Chert beschriebenen vermeintlichen Peronosporomyceten, gut vergleichbar sind, werden sie ebenfalls in die Gattung *Frankbaronia* gestellt und als neue Art, *F. velata*, eingeführt. Die Oogonien sind von einer auffälligen Hülle aus konsolidiertem Schleim umgeben, welcher vom sich entwickelnden Oogonium produziert und sekretiert wurde. *Frankbaronia velata* trägt zu einem besseren Verständnis der mikrobiellen Diversität in frühen terrestrischen Ökosystemen sowie zur Dokumentation der Evolutionsgeschichte der Peronosporomycetes bei.

Schlüsselwörter: Schleimhülle, Oomycota, polyoosporiges Oogonium, Saprolegniales

1. Introduction

Peronosporomycetes (Oomycota) are fungus-like microorganisms that are ubiquitous in aquatic and terrestrial environments where they are important saprotrophs and disease causative agents in plants and animals (Margulis & Schwartz 1998; Dick 2001). Within the group are economically important phytopathogens such as the root-rotting fungi and downy mildews (Kamoun 2003). As a result of the ecological significance of Peronosporomycetes today, a thorough documentation of the fossil record of these organisms, including the roles they played in biological and ecological processes in the past, is important in accurately assessing the complexity of ancient ecosystems.

The fossil record of the Peronosporomycetes has been slow to accumulate. Virtually all fossils historically assigned to this group have later been dismissed or remain inconclusive (reviewed in Krings et al. 2011a). In recent years, several persuasive fossil representatives of the Peronosporomycetes have been described based on permineralized remains in Devonian, Carboniferous, and Triassic cherts and coal balls that have been interpreted as oogonia, some with antheridia still attached (Taylor et al., 2006; Dotzler et al. 2008; Schwendemann et al. 2009; Krings et al. 2010, 2012; Strullu-Derrien et al. 2011).

Among these fossils is *Frankbaronia polyspora* M Krings et al. from the Lower Devonian Rhynie chert (Krings et al. 2012). The Rhynie chert Lagerstätte in

Aberdeenshire, Scotland, has preserved a remarkable diversity of fungi in exquisite condition, but has also yielded the oldest fossil evidence to date of definitive Peronosporomycetes (Taylor et al. 2004, 2006). *Frankbaronia polyspora*, which occurs singly or arranged in short chains in plant litter and as a component of microbial mats, is a spherical to elongate-cylindrical microfossil, usually approximately 50 µm wide or in diameter that may possess one to several conical or column-like surface projections. Each specimen in turn contains between 3 and >80 smooth-walled spherules, each of which includes a (sub)centric opaque inclusion. The fossils have been interpreted as polyoosporous oogonia, with the most compelling modern analogues occurring within the Saprolegniales.

In this paper, we describe *Frankbaronia velata* nov. sp., a second putative peronosporomycete oogonium containing multiple oospores. *Frankbaronia velata* resembles *F. polyspora* in general appearance, but differs in several morphological features, including a prominent sheath enveloping the oogonium and the lack of surface projections. This discovery adds to our understanding of the diversity of microorganisms in early terrestrial ecosystems, and contributes to a more accurate documentation of the evolutionary history of the Peronosporomycetes.

2. Material and methods

The Rhynie chert is located in the northern part of the Rhynie Outlier of Lower Old Red Sandstone in Aberdeenshire, Scotland, within a sequence of sedimentary and volcanic rocks. The cherts occur in the upper part of the Dryden Flags Formation, in the so-called Rhynie Block, located northwest of the village of Rhynie. The Lagerstätte consists of several fossiliferous beds containing lacustrine shales and cherts that have been interpreted as a series of ephemeral freshwater pools within a hot spring environment (Rice et al. 2002; Rice & Ashcroft 2004). Preserved in the cherts are both aquatic (freshwater) facies from the pools and subaerial soil/litter horizons with in situ plants that occupied the edges of the pools; it is hypothesized that the latter became preserved as a result of temporary flooding of silica-rich water, or by silica-rich groundwater that percolated to the surface. The cherts have been dated as Pragian-?earliest Emsian based on dispersed spore assemblages (Wellman 2006; Wellman et al. 2006). A high-precision U-Pb age constraint on the Rhynie Lagerstätte indicates an absolute age of 411.5 ± 1.3 Ma (Parry et al. 2011). Another age constraint using $^{40}\text{Ar}/^{39}\text{Ar}$ yields a mean age (U-Pb comparable) of the fossilized biota of 407.1 ± 2.2 Ma (Mark et al. 2011). Details about the geological setting, sedimentology, and development of the Rhynie chert Lagerstätte can be found in Rice et al. (2002), Rice and Ashcroft (2004), and Trewin and Rice (2004).

The fossils described here were identified in a thin section prepared from a chert block by cementing a thin wafer of the chert to a glass slide and then grinding the rock slice with silicon carbide powder until sufficiently thin to transmit light. The slide is deposited at the Bayerische Staatssammlung für Paläontologie und Geologie (BSPG) at Munich, Germany, under accession number BSPG 2013 V 12.

3. Systematic paleomycology

Kingdom Straminipila MW Dick, 2001
Phylum Heterokonta Cavalier-Smith, 1986
Subphylum Peronosporomycotina MW Dick, 2001
Class Peronosporomycetes MW Dick, 2001
Order and family uncertain

Genus *Frankbaronia* M Krings, TN Taylor, EL Taylor, Kerp, Hass, Dotzler et CJ Harper, 2012

Type species: *Frankbaronia polyspora* M Krings, TN Taylor, EL Taylor, Kerp, Hass, Dotzler et CJ Harper, 2012

Frankbaronia velata nov. sp.
Figs 1–3

Mycobank: MB 804696.

Diagnosis: Oogonium spherical, ovoid, or pyriform, up to 110 µm wide or in diameter; attachment to parental hypha or stalk via truncated extension; oogonium enveloped in prominent sheath; sheath translucent, uniform or indistinctly layered to discontinuously stratified; periphery of sheath smooth to irregularly wrinkled, bounded on outside by delicate but distinctly more opaque boundary layer; oogonium wall thin, layered, smooth; oogonium with 6 to >150 smooth-walled oospores >10 µm in diameter.

Holotype: Specimen illustrated in Fig. 2d; slide BSPG 2013 V 12, deposited in the Bayerische Staatssammlung für Paläontologie und Geologie at Munich, Germany.

Paratypes: Specimens illustrated in Figs 1b and 2a; slide BSPG 2013 V 12, deposited in the Bayerische Staatssammlung für Paläontologie und Geologie at Munich, Germany.

Etymology: The epithet *velata* (Lat.: *velatus*, -a, -um = covered, wrapped, veiled, or consealed) refers to the prominent sheath surrounding the oogonium.

Occurrence: Rhynie, Aberdeenshire, Scotland; National Grid Reference NJ 494276.

Age: Early Devonian (Pragian-?earliest Emsian).

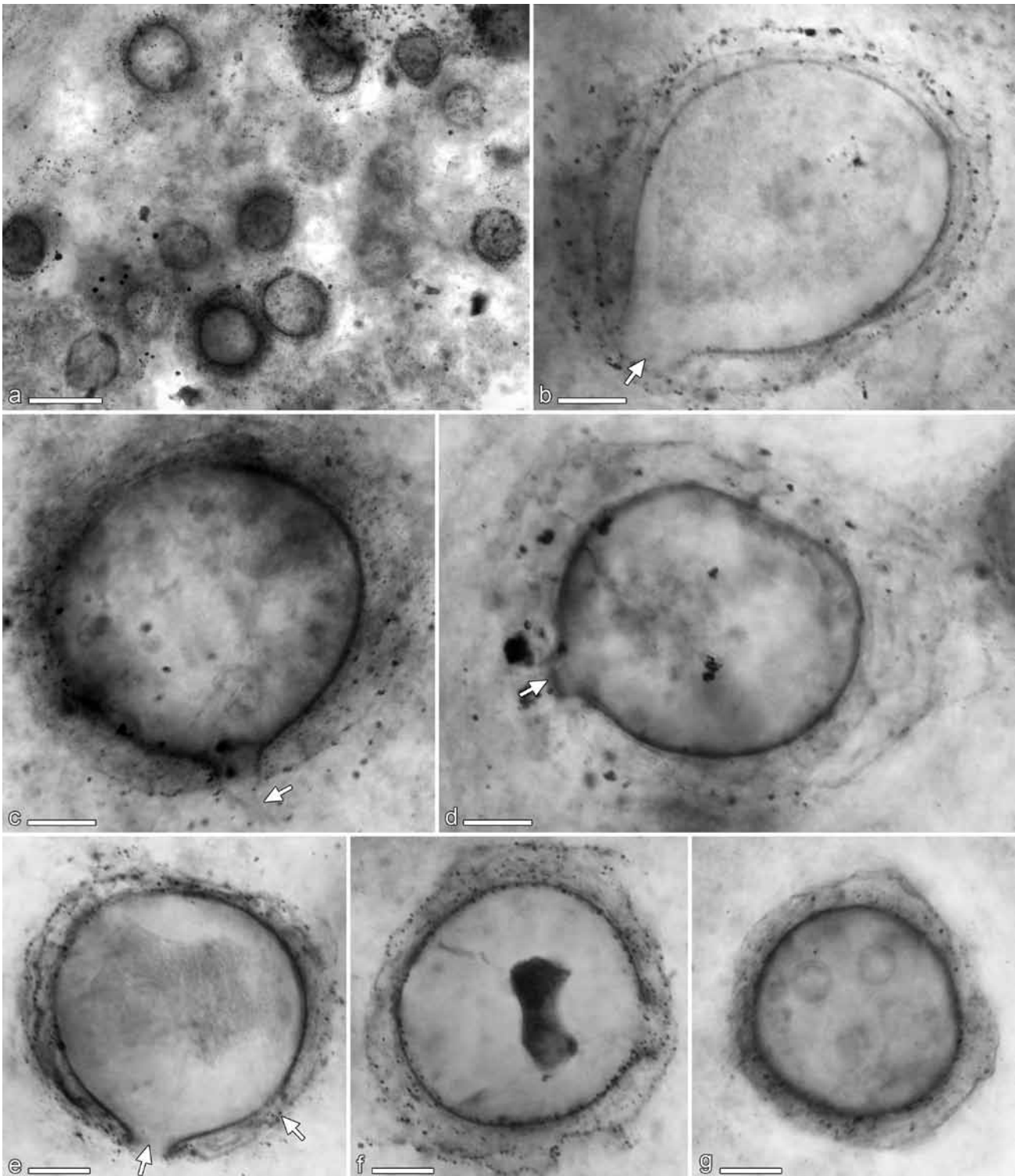


Figure 1: *Frankbaronia velata* nov. sp. from the Lower Devonian Rhyne chert; **(a)** Cluster of several specimens within microbial mat; scale bar = 100 µm; **(b–d)** Specimens showing prominent sheath enveloping the oogonium and truncated extension (arrows); note stratification of sheath in (b) and (d), as well as part of subtending hypha or oogonial stalk in (c) (arrow); b: paratype; scale bars = 20 µm; **(e–g)** Specimens showing the prominent sheath enveloping the oogonium; note two openings (arrows) in specimen illustrated in (e) and empty oospores in (g); scale bars = 20 µm

Description: *Frankbaronia velata* is represented by a single assemblage (Fig. 1a) of approximately 250 specimens that occur within a microbial mat dominated by filamentous bacteria or cyanobacteria similar to *Croftalania venusta* Krings et al. (2007). Speci-

mens occur solitarily; they are ovoid, up to 90–100 µm long and 60–80 µm wide (Figs 1b, 2c), or, more often, spherical to drop-shaped, (50–)60–90–110 µm in diameter (Figs 1c–g, 2a, b, e–g). The outer wall is thin and smooth (e.g., Fig. 1b–g); in some speci-

mens the wall appears to be composed of at least two separate components or layers (arrows in Figs 2c, 3b). Projections of the wall or other patterns of surface ornament are absent. Approximately 75% of the specimens display a single truncated extension up to 21 μm wide and 12 μm long (arrows in Figs 1b, d, 2d, e, g), which most likely represents the attachment point of a stalk or parental hypha. However, we have found only one specimen in which a short segment of the parental structure is physically connected to the truncated extension (arrow in Fig. 1c). In the specimens that appear to lack an extension we suggest that this simply reflects the plane of the section through the specimen. In a few specimens, two truncated extensions may be present (arrows in Fig. 1e). Each specimen is enveloped by a prominent, translucent sheath, in some areas up to 35 μm thick (Figs 1b–g, 3b–f). The sheath may be uniform in texture (Fig. 3b, e), indistinctly differentiated into a more opaque inner and less opaque outer portion (Fig. 3c, d), or discontinuously stratified (Figs 1b, d, e, 3f) with distinct demarcations between the individual layers (arrows in Fig. 3f). Numerous small opaque particles or tiny granules are irregularly distributed within the sheath (e.g., Figs 1b–f, 3b–d). The periphery of the sheath may be relatively smooth (Fig. 3b, c) or irregularly wrinkled (Fig. 3d, e), and bounded on the outside by a delicate but distinctly more opaque boundary layer (e.g., arrows in Fig. 3e). Specimens of *F. velata* may be devoid of structured contents (Fig. 1b, d, e) or, more often, contain between 6 and >150 small spherules (Figs 1g, 2a–g, 3a) that are smooth and bounded by a distinctive wall. The wall is typically more opaque than the central portion of the spherule (e.g., Fig. 3a), but sometimes may be translucent (e.g., arrows in Fig. 2a). The interior spherules vary from 11 to 18 μm in diameter, and each in turn contains a subcentric opaque inclusion that appears to be separate from the wall of the spherule (Figs 2a–g, 3a). There are only a few specimens in which the interior spherules lack this inclusion (e.g., Fig. 1g). Many specimens are closely associated with large numbers of smaller spheroidal structures (<10–20 μm in diameter) that may occur singly, or are arranged in short chains or clusters (Fig. 2b); some possess what appears to be a double wall up to 3 μm thick (Fig. 3g).

4. Discussion

The Early Devonian Rhynie chert has yielded the oldest fossil evidence to date of Peronosporomycetes, including *Hassliella monospora* TN Taylor et al., an ornamented oogonium to which are attached amphigynous antheridia borne on a coenocytic hyphal system (Taylor et al. 2006), and *Frankbaronia polyspora*, a microfossil strikingly similar morphologically to the polyoosporous oogonia produced by certain extant Saprolegniales (Krings et al. 2012).

The fossils described in this paper are interpreted as oogonia containing multiple oospores of a third representative of the Peronosporomycetes from the Rhynie chert that are similar to polyoosporous oogonia seen in certain extant peronosporomycetes, especially within the order Saprolegniales. The Saprolegniales is comprised of mostly saprotrophic organisms that thrive in both freshwater aquatic and soil habitats (Johnson et al. 2002). During sexual reproduction, they produce terminal or intercalary oogonia that can be variable in size and shape and contain one to several (up to 100 in some species; see Paul & Steciow 2004) oospores (e.g., Seymore 1970; Prabhujii 2010). Moreover, the overall appearance of the fossils described in this paper is closely reminiscent of the spheroidal and drop-shaped specimens of *Frankbaronia polyspora* (e.g., Krings et al. 2012: fig. 1.6, 1.7, 1.11). Especially interesting is the presence of a subcentric opaque inclusion in the interior spherules (oospores) of both forms that Krings et al. (2012) have interpreted as representing the ooplast. As a result of this morphological similarity, we have assigned the new form to the fossil genus *Frankbaronia* as defined by Krings et al. (2012), and proposed the name *F. velata* nov. sp. for the species.

Although *Frankbaronia velata* and *F. polyspora* are structurally similar, they differ from each other in several key features: *Frankbaronia velata* is typically larger than *F. polyspora*, contains a larger number of oospores, and appears to be morphologically more uniform in oogonium shape. Elongate specimens, as well as specimens arranged in interconnected pairs or short chains, which are common in *F. polyspora*, are not present in the new species. Moreover, individuals of *F. velata* usually display a prominent truncated extension (e.g., arrows in Fig. 2c–e, g), which most likely represents the point of attachment to a parental hypha or stalk. In extant peronosporomycetes, the point of attachment of the oogonium often consists of a collar-like extension that is identical in wall thickness and coloration to the oogonium wall (e.g., Krings et al. 2012: fig. 4). This peronosporomycete feature has not been documented in *F. polyspora*. In addition, most specimens of *F. polyspora* (except small ones) possess one to several hollow projections of the oogonial wall, whereas the oogonia of *F. velata* consistently lack projections or other patterns of surface ornamentation. The most interesting difference between *F. velata* and *F. polyspora*, however, concerns the prominent sheath that envelops the oogonia of the former, but has not been observed in *F. polyspora*.

Sheaths enveloping oogonia are not known in any other fossil peronosporomycete. However, it has been suggested that part of the oogonium ornament of the Carboniferous peronosporomycete *Combresomyces cornifer* Dotzler et al. was not formed by the oogonial wall proper, but rather that the distal, antler-like portions result from condensation of a mucilaginous extra-oogonial wall exudate at some

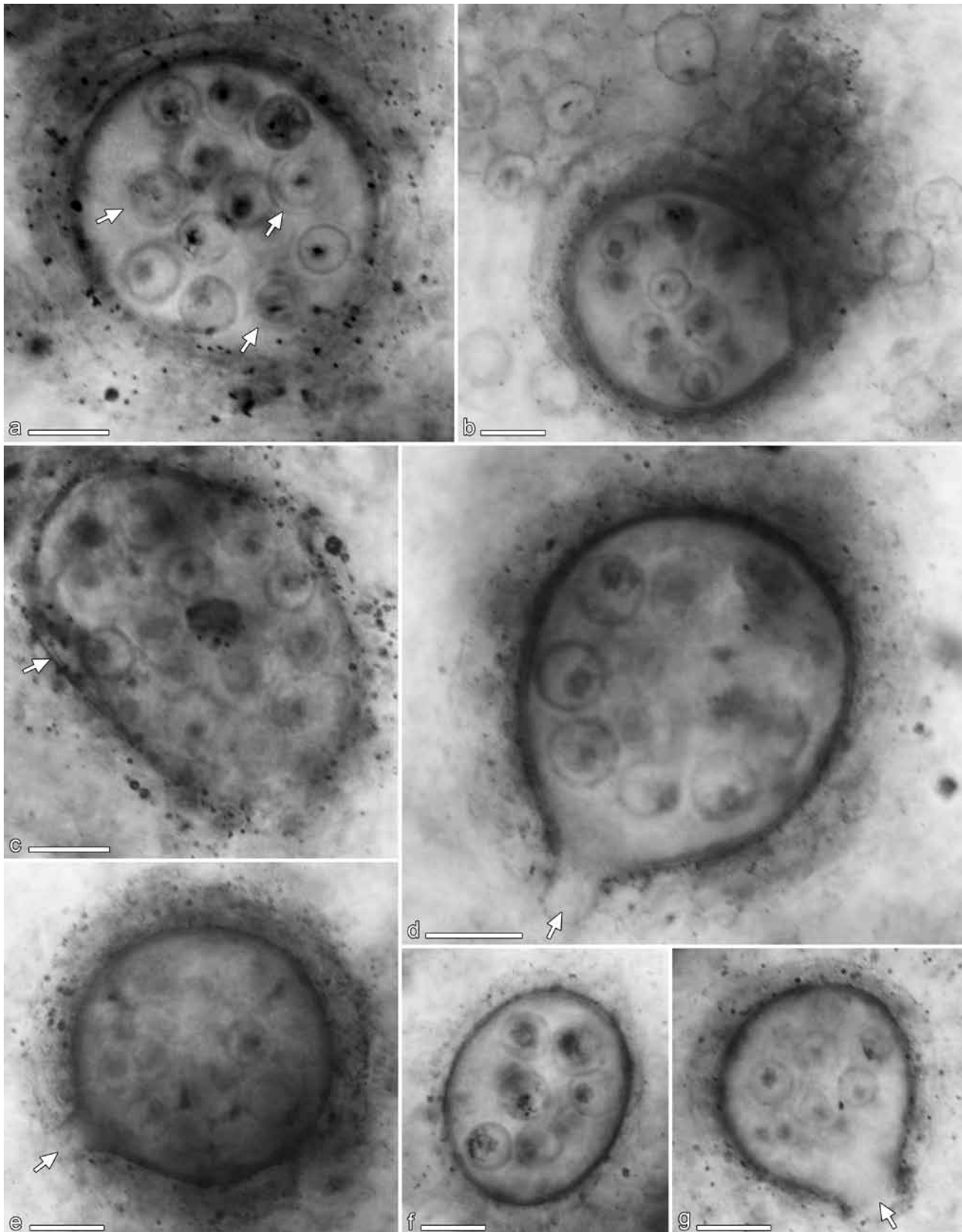


Figure 2: *Frankbaronia velata* nov. sp. from the Lower Devonian Rhynie chert; **(a–g)** Specimens containing multiple oospores; note oospores with translucent wall in (a) (arrows), layered oogonium wall in (c) (arrows), truncated extension in (e) and (g) (large arrow), and numerous spherules associated with specimen in (b); a: paratype, d: holotype; scale bars = 20 μ m.

stage during development (Dotzler et al. 2008). In several extant peronosporomycetes (e.g., *Aplanopsis terrestris* Höhnk, *Newbya pascuicola* MC Vick et MW Dick, and *Pythiopsis cymosa* de Bary), development of the oogonial initial is accompanied by a secretion of mucilage, which initially forms a spherical envelope with a sharply defined outer surface around the developing oogonium (e.g., Dick 2001: fig. 22). As development of the oogonium continues, the envelope subsequently becomes irregular, and finally collapses entirely or in part on the oogonium wall proper (Dick 1969; Johnson et al. 2002; Spencer et al. 2002). The mucilage may have an ecological function, i.e. cementing the oogonium to organic detritus (Dick 2001). We speculate that the developing oogonium of *Frankbaronia velata* may have exuded a mucilaginous secretion through the oogonial wall that gradually accumulated on the outer surface of the oogonium, eventually consolidating (to some degree) but not collapsing, and thus forming a continuous sheath. Moreover, small (?organic) particles present in the surrounding water may have become entangled in the mucilage and subsequently integrated into the sheath. An alternative hypothesis is that the sheaths were deposited onto the outer surface of the oogonium by some exterior source. Perhaps this external source included various microorganisms that colonized the oogonium surface, or the filamentous organisms that comprise the microbial mats in which *F. velata* occurred were in some way responsible for producing the sheath. Arguing against this hypothesis, however, is the consistent presence of a sheath in all specimens. For the same reason it is also unlikely that the sheaths represent preservational artifacts. Moreover, the sheaths are relatively uniform in thickness in all specimens, which seems unlikely if the sheaths were produced by some other organism and deposited onto the oogonium surface. In addition, there is no evidence of similar deposits on spores and other propagules of organisms that co-occur with *F. velata* in the microbial mats, including the small spheroidal structures closely associated with many of the *F. velata* specimens (Figs 2b, 3g). As to whether these structures and *F. velata* were produced by the same organism cannot be determined. The thickness and texture of the 'double wall' seen in some of the spheroidal structures clearly differs from that of the sheaths. Our lack of understanding of the processes leading to the formation of the sheaths make it currently impossible to explain the nature of the differences in texture and discontinuous stratification visible in some of the sheaths.

The consistent absence of antheridia attached to the structures interpreted as oogonia challenges the assignment of *Frankbaronia velata* to the Peronosporomycetes because oogonium-antheridium complexes are regarded as the only morphological feature that can be used to safely identify Peronosporomycetes as fossils (Krings et al. 2011a). This challenge is further aggravated by the fact that an-

theridia have not been documented in *F. polyspora* to date (Krings et al. 2012). Krings et al. (2012) have suggested that perhaps oospores developed parthenogenetically in *F. polyspora*, or that the antheridia in *F. polyspora* were ephemeral and readily disintegrated. However, the absence of antheridia in both *F. polyspora* and *F. velata* renders the former hypothesis rather unlikely. On the other hand, the absence of reproductive characters is not uncommon in extant members of the Peronosporomycetes because the oogonium-antheridium complex may readily disintegrate post-fertilization in some species (Dick 1969, 1995). It is interesting to note in this context that the vast majority of specimens of *F. polyspora* and *F. velata* appear to have been more or less mature at the time of fossilization based on the presence of walled oospores. Moreover, both fossils do not only lack antheridia, but also evidence of a hyphal system on which the putative oogonia were produced. This suggests that all delicate parts of the organisms (hyphae, antheridia) disintegrated readily, perhaps before the fossilization process even started, and only the thicker-walled and more resistant mature oogonia persisted as fossils. Adding some support to this hypothesis is a report on fungi colonizing the leaves of cordaites preserved in a Pennsylvanian chert from France (Krings et al. 2011b). In one of these fungi, the hyphal system was at an advanced state of disintegration at the time of preservation, while the numerous terminal and intercalary propagules show little to no evidence of decay. There is no doubt that, if the fossilization process had started just slightly later, only the propagules were present as fossils.

5. Conclusions

As is true in many areas of paleontology, the systematic affinities of the organism, ecological niche occupied, and life history often take an extended period of time to fully document because fossil organisms are rarely preserved either in sufficient numbers, or in a way that provides insight into all phases of growth and reproduction. As a result, it is necessary to continue to catalogue organisms in time and space, especially in ecosystems like the Rhynie chert that afford extraordinary preservation. *Frankbaronia velata* is an excellent example of this dilemma since preservation is excellent and there are multiple specimens available to study. Still, the complete organism and precise affinities remain elusive. All specimens appear at approximately the same stage of development and there are no examples as yet recognized that might represent other stages in the life history. Moreover, *F. velata* occurs as an inhabitant of microbial mats dominated by filamentous microorganisms, but as to whether it also interacted with the mat builders or some other organism inhabiting the mat cannot be determined because the fossil evidence to date only includes isolated oogonia. Even in the

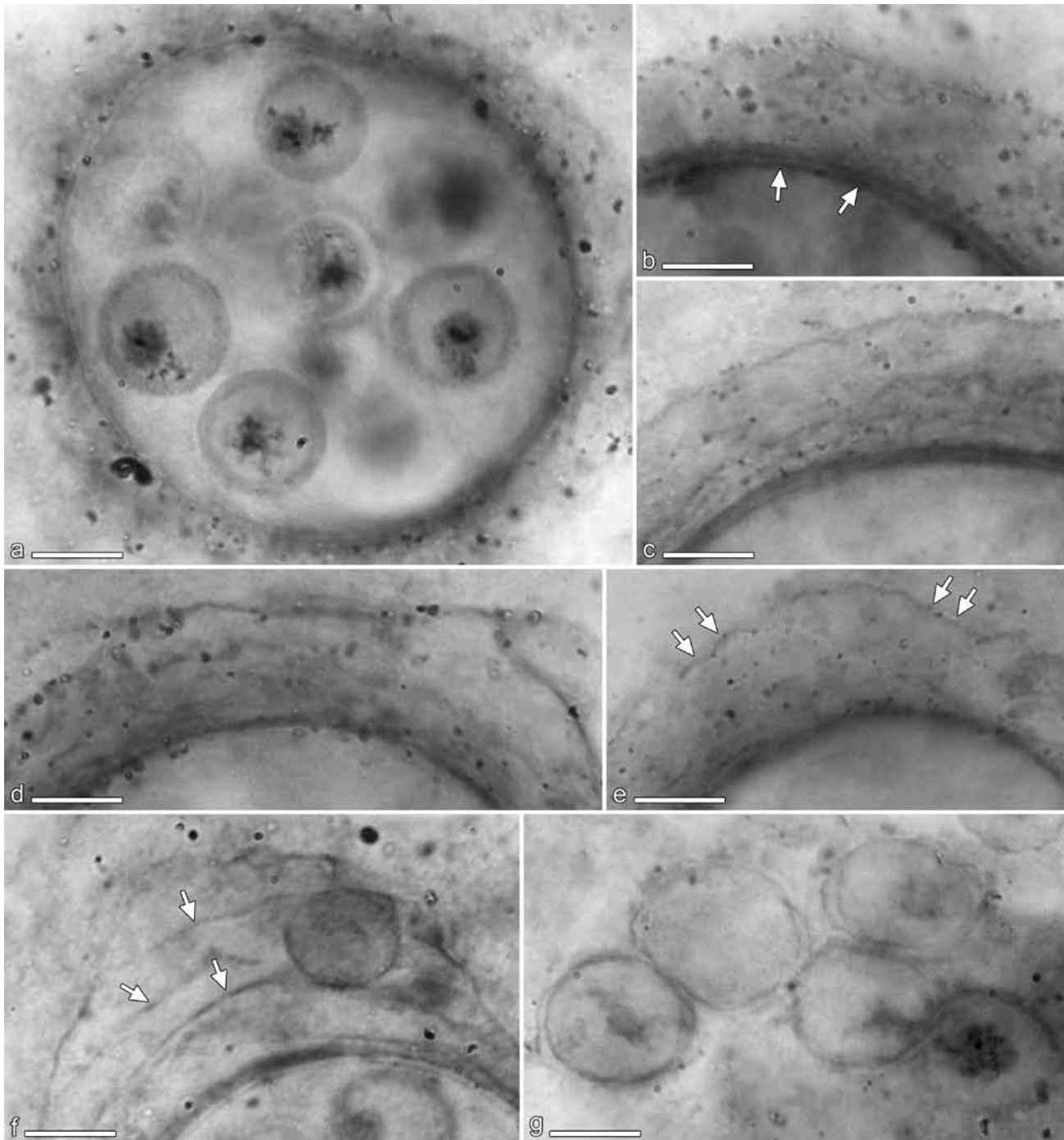


Figure 3: *Frankbaronia velata* nov. sp. from the Lower Devonian Rhyne chert; **(a)** Detail of Fig. 2a, different focal plane, showing oospores, each with a subcentric opaque inclusion; scale bar = 10 µm; **(b–e)** Oogonium wall and enveloping sheath; note layered wall in (b), irregularly wrinkled outer surface of sheath in (e); arrows in (e) indicate delicate boundary layer; scale bars = 10 µm; **(f)** Stratified sheath (arrows indicate demarcations between strata) with spherical inclusion; scale bar = 10 µm; **(g)** Associated spherules (see Fig. 2b); scale bar = 10 µm.

case of living microorganisms, some stages in the life history and/or interactions with other organisms remain incompletely known. In spite of these difficulties, the discovery of structures like those of *F. velata* indicate that during the Early Devonian there was an organism similar to an extant peronosporomycete, perhaps in the Saprolegniales, that was a significant component in this freshwater ecosystem. We belie-

ve that renewed efforts in documenting the microbial diversity preserved in the Rhyne chert will eventually provide the missing parts of this organism, and that this will lead to an increasing appreciation of not only the geologic history of the group, but also the ecological role of *F. velata* within the Rhyne ecosystem.

Acknowledgments

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