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## Late Ordovician to early Silurian acritarchs from the Qusaiba-1 shallow core hole, central Saudi Arabia

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### Abstract

Well-preserved acritarchs are documented from Upper Ordovician and lower Silurian sections in the Qusaiba-1 shallow core hole of central Saudi Arabia. Sixty-nine genera comprising 68 named species and 62 forms under open nomenclature were recorded from forty core samples.

At the base of the Upper Ordovician and lower Silurian succession in Qusaiba-1 is the Quwarah Member of the Qasim Formation. This is overlain by glacio-marine deposits of the Sarah Formation, which are overlain in turn by the Qusaiba Member of the Qalibah Formation. Four distinct acritarch assemblages are informally numbered 1 to 4 from the base of the core upwards. Assemblage 1 is from the Quwarah Member, and is independently dated by Chitinozoa as being late Katian to early Hirnantian in age (Late Ordovician). The assemblage contains a number of new species, plus species reported from low-latitude Late

Ordovician Laurentia and Baltica as well as the Gondwanan margin. Assemblage 2 is from a glauconite at the base of the Sarah Formation and is early Hirnantian in age. Assemblage 3, from the Baq'a Shale Member of the Sarah Formation, is also Hirnantian in age and is characterized by a stratigraphically admixed Ordovician palynoflora. Assemblage 4 is restricted to three samples from the Qusaiba Member in the lowermost part of the Qalibah Formation and is dated as Rhuddanian (earliest Silurian). The highest of the three samples that comprise Assemblage 4 is from the same level as a gamma ray peak at 254.8 ft.

Reworking of Middle Ordovician forms is evident in Assemblage 3 and is attributed to processes of glacial erosion and re-sedimentation during glacial melting. Reworked specimens are probably from the Hanadir Member and possibly also the Kahfah Member of the Qasim Formation. The extent of later Ordovician reworking in Assemblage 3, for example reworking from the Quwarah Member, is unclear. However, given that glacial erosion extended to levels below the Quwarah Member, Late Ordovician palynomorphs present in Assemblage 3 might also be reworked. The extent of any reworking in assemblages 1 and 2 is uncertain. There is no evidence for reworking in Assemblage 4.

Two new acritarch genera, five new species and one new combination are proposed:

*Dorsennidium polorum* (Miller and Eames, 1982) comb. nov., *Falavia magniretifera* gen. et sp. nov., *Inflatarium trilobatum* gen. et sp. nov., *Nexosarium mansouri* sp. nov., *Orthosphaeridium orthogonium* sp. nov. and *Tunisphaeridium bicaudatum* sp. nov. Samples from the same set were used for chitinozoan, scolecodont and miospore studies (this volume). Eurypterid and graptolite remains are also present.

**Key words:**

## 1. Introduction

The acritarchs, as defined by Evitt (1963), are an artificial *incertae sedis* group of organic-walled microfossils with unknown biological affinities. Palaeozoic acritarchs have been recorded mainly from marine deposits, and they probably include microorganisms with different biological affinities, although many are thought to be the resting stages of marine phytoplankton (Tappan, 1980; Martin, 1993; Strother, 1996). The group possibly includes dinoflagellate cysts that lack diagnostic morphological features, but this hypothesis remains to be tested for the majority of genera (Sarjeant and Taylor, 1999). As the biological affinities of many forms included in the group remain unresolved, we continue to use the informal term acritarchs, rather than any of the alternatives terms that have been proposed such as organic-walled microphytoplankton.

Acritarchs were first reported from the Lower Palaeozoic succession in Saudi Arabia by Hemer (1968). Some of the forms illustrated by Hemer (1968) were attributed to named species such as *Baltisphaeridium* [now *Evittia* or *Diexallophasis*] *denticulatum*, *Leiofusa* [*Eupoikilofusa*] *striatifera*, *Veryhachium* [*Neoveryhachium*] *carminae* and *Peteinosphaeridium bergstroemii*. Other forms were unnamed at the time and were recorded under open nomenclature using terms such as ‘*Incertae sedis* Form B’ or ‘*Acritarch* sp. X’. From Hemer’s (1968) illustrations, these are now recognizable as actual or probable species of *Aremoricanium*, *Baltisphaeridium*, *Cymatiogalea* or *Stelliferidium*, *Dicrodiacrodium* and *Veryhachium*. Since then, Lower Palaeozoic acritarchs from Saudi Arabia have been studied

in more detail and with greater stratigraphic precision (McClure, 1988; Vaslet, 1989; Jachowicz, 1995; Le Hérissé et al., 1995; Al-Ruwaili, 2000; Le Hérissé, 2000; Molyneux and Al-Hajri, 2000; Miller and Melvin, 2005; Le Hérissé et al., 2007; Miller and Al-Ruwaili, 2007).

The present study investigates assemblages of Late Ordovician (Katian–Hirnantian) and early Silurian (Rhuddanian) acritarchs from the Qusaiba-1 shallow core section in the Qasim region of central Saudi Arabia (Fig. 1). They are very abundant, well preserved and form diverse assemblages throughout. The acritarchs of this interval are of interest for two reasons. First, Upper Ordovician–lower Silurian strata in North Africa and the Middle East are of economic importance. The Upper Ordovician glacial and related deposits constitute significant reservoirs (Le Héron et al., 2009) and the lower Silurian organic-rich ('hot') shales are the most important Palaeozoic petroleum source rocks in the region (Lüning et al., 2003). Second, acritarch records across the Ordovician–Silurian boundary document in part the probable phytoplankton response to climate-related environmental changes through a mass extinction event (Beuf et al., 1971; Deynoux et al., 1985; Vaslet, 1989; Ghienne et al., 2007; Le Heron and Craig, 2008). The clearest evidence for Late Ordovician glaciation and deglaciation (e.g. glacially related sediments, striated surfaces) comes from the Hirnantian, immediately before, during and immediately after the Late Ordovician ice maximum (Le Heron and Craig, 2008). Recent work, however, suggests that climate change in the Ordovician was gradual, with a cooling trend from the Early Ordovician onwards (Trotter et al., 2008; Vandenbroucke et al., 2010), and that ice-sheets could have formed as early as the early–middle Katian in Central and West Africa and eastern South America (Loi et al., 2010, fig. 14; Ghienne, 2011). Biostratigraphic and palaeoenvironmental studies are important for confirmation of this hypothesis. In addition, the Late Ordovician concluded with the oldest of the so-called 'Big

Five' extinction events, with extinction among marine families and genera at the end of the Ordovician being the second largest after the end-Permian extinction (Sepkoski, 1996; Sheehan, 2001). Two phases of faunal extinction and turnover have been recognized in the Hirnantian. The first is linked to the onset of the glaciation. The second is related to the melting of the Gondwanan ice sheet and the associated transgression that followed deglaciation (Delabroye and Vecoli, 2010). The mechanics of the end-Ordovician extinction and its relationship to the glaciation remain subjects of debate and research.

## 2. Stratigraphy

Qusaiba-1 was drilled to a total depth of 551.0 ft in the Qasim area, NNW of the abandoned Qusaiba village in central Saudi Arabia (Fig. 1). Graptolites collected from the core between 253.3 ft and 133.5 ft indicate a mid-Llandovery, Aeronian, *convolutus* Biozone age (Zalasiewicz et al., 2007), and hence the presence of MFS S10 of Sharland et al. (2001).

The detailed lithostratigraphy and depositional history of the Upper Ordovician and lowermost Silurian rocks in the core have been described by Melvin (this volume). At the base of the core is the Quwarah Member of the Qasim Formation. The base of the member was not reached in the borehole. The Quwarah Member comprises a lower interval, 74.2 ft thick, from 551.0 ft to 476.8 ft, and an upper interval of 15.5 ft from 476.8 ft to 461.3 ft. The contact between the lower and upper intervals is tentatively identified as a possible transgressive surface of erosion (Melvin, this volume). The lower interval consists of mudstone, sandstone and silty sandstone deposited in pro-delta, delta-front and non-deltaic, shallow marine, lower shoreface to offshore settings. The upper interval of the Quwarah

Member commences with a thin transgressive pebble-lag deposit overlain by sandstones with subordinate mudstones, and is interpreted as a prograding shoreface sequence.

Resting unconformably on the Quwarah Member, the Sarah Formation begins with a basal pebble conglomerate that is overlain by a grey-green sandy siltstone. These lithologies comprise a basal disrupted facies of the Sarah Formation between 461.3 ft and 436.0 ft (Fig. 2). The grey-green sandy siltstone is characterized by intense disruption, severe brecciation and rotation of bedding, and is interpreted as a glacitectorite that formed during the initial advance of the South Polar ice sheets in Arabia, at the onset of the Late Ordovician (Hirnantian) glaciation. The glaciogenic nature of the basal disrupted facies was noted by McClure (1978) and Young (1981).

Overlying the glacitectorite are thick sandstones of the Sarah Sandstone Member (436.0–351.4 ft), deposited subaqueously from glacial outwash during a phase (or phases) of glacial retreat. The Sarah Sandstone Member is succeeded by the Baq'a Shale Member (351.4–293.5 ft). The lower 2.4 ft of the Baq'a Shale Member comprises laminated sandy siltstone, interpreted as glaciogenic stratified diamictites deposited during initial terminal melting of the Hirnantian ice sheets. The succeeding 55.5 ft of the Baq'a Shale consists of silty mudstones with thin, fine-grained sandstones deposited from gravity flows from a prograding prodelta wedge.

Elsewhere in Saudi Arabia, the Hawban Member of the Sarah Formation, as restricted by Senalp et al. (2002), occupies a stratigraphical position above the Sarah Sandstone Member in some sections, but is interpreted as a glacial advance facies as opposed to the glacial retreat

facies of the Baq'a Shale Member (Melvin, this volume). The Hawban Member was not identified in the Qusaiba-1 core.

The Baq'a Sandstone Member (293.5–257.0 ft) is the stratigraphically highest unit of the Sarah Formation and consists of two distinct sandstone units. The lower unit was possibly deposited in a delta-front setting whereas the upper unit comprises fluvial deposits. The basal contact of the fluvial sandstones with the underlying delta-front deposits is tentatively identified as an isostatic rebound unconformity.

Overlying the Baq'a Sandstone Member, the lowermost deposits of the Silurian Qusaiba Member of the Qalibah Formation comprise mudstone of Rhuddanian age. The Rhuddanian mudstone occupies a 3.5 ft thick interval from 257.0 ft to 253.5 ft, beneath the graptolitic mudstones of Aeronian age referred to above (Zalasiewicz et al., 2007). The Rhuddanian section might be a condensed section, deposited during marine flooding that followed the retreat of the ice sheets in Saudi Arabia. The overlying Aeronian beds were deposited in a marine shelf setting.

### **3. Material and methods**

Samples from Qusaiba-1 were analysed to document and calibrate changes in the palynological record of acritarchs, chitinozoans, scolecodonts and miospores across the Ordovician–Silurian boundary. For the most part, the samples used to study each group were from the same depths. Forty core samples were collected below the Aeronian section in Qusaiba-1 for the study of acritarchs, and were prepared in the Palaeobiogeology,



Palaeobotany and Palaeopalynology (PPP) Research Unit, University of Liège, Belgium.

Twelve samples were collected and prepared from marine deposits of the Quwarah Member between 551.0 ft and 476.7 ft. Eleven samples are from the lower interval of the Quwarah Member in Qusaiba-1, and the remaining sample, from 476.7 ft, is just above the base of the upper interval. Four samples were collected and prepared from the basal disrupted facies of the Sarah Formation between 458.4 ft and 436.0 ft, and 21 samples from the Baq'a Shale Member between 350.6 ft and 292.3 ft. Three samples were collected and prepared from the Rhuddanian section of the Qusaiba Member, from 256.4 ft, 255.75 ft and 254.8 ft.

#### **4. Acritarch assemblages**

Microfloras comprising well-preserved acritarchs were recovered from all samples. The stratigraphic occurrence of genera and species in Qusaiba-1 is shown in Figure 2. The microfloras can be described in terms of four discrete assemblages, each of which corresponds to a sampled lithostratigraphic unit. Assemblage 1 comprises microfloras from the Quwarah Member of the Qasim Formation between 551.0 ft and 476.7 ft (cores 49 to 56). Assemblage 2 is from the basal glacitectorite deposits of the Sarah Formation between 458.4 ft and 436.0 ft (cores 45, 47). Assemblage 3 is from the Baq'a Shale Member of the Sarah Formation between 350.6 ft and 294.8 ft (cores 31 to 36). Assemblage 4 is from the Rhuddanian part of the Qusaiba Member of the Qalibah Formation and comprises acritarchs from the three samples between 256.4 ft and 254.8 ft (core 27).

Many Late Ordovician species recorded from the Quwarah Member and Sarah Formation have also been recorded from Late Ordovician assemblages of Laurentia (Loeblich and Tappan, 1978; Wright and Meyers, 1981; Jacobson and Achab, 1985; Wicander et al., 1999;

Playford and Wicander, 2006; Wicander and Playford, 2008). Their occurrence in Saudi Arabia supports suggestions (Vecoli and Le Hérisse, 2004) of cosmopolitanism among Late Ordovician acritarch assemblages.

#### 4.1. Assemblage 1 (Quwarah Member, 551.0–476.7 ft)

Assemblage 1 comprises microfloras of generally high diversity and abundance. In the eleven samples from the lower Quwarah interval recognized by Melvin (this volume), between 551.0 ft and 479.4 ft, diversity ranges from 23 to 46 species per sample, with a mean of 35. Above this interval, the microflora from a single sample from the upper Quwarah interval of Melvin (this volume), from 476.7 ft, comprises 14 taxa. The lower diversity in this sample possibly reflects the postulated change in the environment of deposition from a lower shoreface or offshore setting to a prograding shoreface environment.

Microfloras from the Quwarah Member are dominated by veryhachid acritarchs (species of *Neoveryhachium*, *Striatotheca*, *Veryhachium* and *Villosacapsula*) and leiospheres (*Leiosphaeridia* spp.). The veryhachids account for between 40% and 61% of counted specimens in some samples, with *Veryhachium* being the dominant genus. Leiospheres comprise between 26% and 43% in the same samples, but in all cases are less numerous than the veryhachids. *Leiofusa* is also relatively common, and particularly so in the lowest sample, from 551.0 ft, where the genus comprises 15% of counted specimens.

Stratigraphically important forms include *Actinotodissus longitaleosus*, *Actipilion druggii*, *Anomaloplaisium lumariacuspis*, *Cheleutochroa* spp., *Dactylofusa cucurbita*, *D. striatogranulata*, *Dorsennidium hamii*, *Fractoricoronula trirhetica*, *Leprotolypa evexa*,

*Multiplicisphaeridium bifurcatum*, *M. irregulare*, *Neoveryhachium carminae* s.l., *Ordovicidium elegantulum*, *Orthosphaeridium* spp., *Safirotheca safira*, *Sylvanidium?* *hawbanense*, *Veryhachium subglobosum*, *Villosacapsula irrorata* and *V. setosapellicula*. Of these, *Anomaloplaisium lumariacuspis*, *Dactylofusa cucurbita*, *D. striatogranulata* and *Safirotheca safira* are restricted to the Hirnantian Stage on the range charts published by Vecoli and Le Hérisse (2004), based on data from eastern Avalonia (England, Wales and north Germany) and the mid- to high-palaeolatitude Gondwanan margin (southern Europe, North Africa, Saudi Arabia, southeast Turkey). However, the range of *D. striatogranulata* extends in Algeria from the Upper Ordovician into the lower Silurian (zones F and G1 of Jardiné et al., 1974), and recent work on microfloras from Chad (Le Hérisse et al., 2013) has confirmed that *D. striatogranulata* ranges into the lower Silurian there as well. In addition, forms attributed to *D. striatogranulata* have been recorded from the Early Ordovician of northwest Argentina (Achab et al., 2006) and South China (*Azygograptus suecicus* Graptolite Biozone: Tongiorgi et al., 2003), and from the Middle Ordovician (Darriwilian) of the Canning Basin, Australia (Playford and Martin, 1984; Quintavalle and Playford, 2006a, b).

*Sylvanidium?* *hawbanense*, first recorded by Miller and Al-Ruwaili (2007) from the Hawban and Baq'a Shale members of the Sarah Formation, is well represented in the Quwarah Member in Qusaiba-1. It occurs in nine out of the 12 samples collected from that unit, and comprises more than 2% of counted specimens in samples from 528.3 ft and 488.3 ft, and more than 3% of counted specimens in the lowermost sample from 551.0 ft.

A number of species have their last appearance datums (LADs) in Assemblage 1 and therefore have the potential to distinguish Quwarah assemblages from those of overlying deposits. These include *Actinotodissus longitaleosus*, *Cheleutochroa clandestina?*,

*Fractoricoronula trirhetica*, *Petaloferidium* spp., *Striatotheca* aff. *monorugulata* and *Villosacapsula irrorata*. First and last appearance datums within the Quwarah Member might also be biostratigraphically significant. *Actinotodissus longitaleosus*, *Ampululla?* sp. and *Fractoricoronula trirhetica*, for example, do not occur above the lower part of the Quwarah Member in Qusaiba-1, whereas *Anomaloplaisium lumariacuspis*, *Caelatosphaera cerebella* and *Orthosphaeridium* cf. *chondrododora* have FADs higher in the member, at or above 488.3 ft. The FADs of a number of other species at 536.7 ft, 535.2 ft and 528.3 ft in the Quwarah Member (Fig. 2), notably those of *Inflatarium trilobatum* gen. et sp. nov., *Orthosphaeridium orthogonium* sp. nov. and *Safirotheca safira*, might serve to distinguish the upper part of the Quwarah Member from the lowermost sample at 551.0 ft. There are no FADs to distinguish the highest sample from the upper Quwarah interval in Qusaiba-1 from underlying samples, but only the reduction in diversity noted above.

**Age.** Assemblage 1 is typical of Late Ordovician acritarch assemblages from Gondwanan and Perigondwanan regions. The Quwarah assemblage is similar in some respects to the Hirnantian assemblage described from the Hawban Member of the Sarah Formation (Miller and Al-Ruwaili, 2007). That assemblage also has a high percentage of veryhachid acritarchs (about 50% of the assemblage) with leiospheres being the next most common forms. The occurrences of *Dactylofusa cucurbita*, *Safirotheca safira* and *Sylvanidium?* *hawbanense* in Assemblage 1 also suggest a Late Ordovician, possibly Hirnantian age. However, Miller and Al-Ruwaili (2007) have pointed out that acritarch ranges from the Ordovician of Arabia are too incompletely known to restrict species such as *Sylvanidium?* *hawbanense* to the Hirnantian.

In contrast, *Actinotodissus longitaleosus* and *Fractoricoronula trirhetica* are restricted largely to the Katian Stage in Vecoli and Le Hérissé's (2004) compilation of ranges, equivalent to the upper Caradoc Series and pre-Hirnantian Ashgill Series of the Anglo-Welsh succession, possibly just ranging into the base of the Hirnantian. *Dorsennidium hamii*, *Orthosphaeridium rectangulare* and *Veryhachium subglobosum* are also shown by those authors to have first appearance datums (FADs) in the upper Katian (= Ashgill) before ranging into the Hirnantian.

Chitinozoan assemblages from the Quwarah Member in Qusaiba-1 are attributed to the *Ancyrochitina merga* Biozone by Paris et al. (this volume), who also argue that much of the Quwarah Member in the borehole is late Katian–early Hirnantian in age, with a late Katian age suggested for the lowest sample (551.0 ft). Acritarch Assemblage 1 is accordingly considered to be of late Katian–early Hirnantian age.

Other species recorded from Assemblage 1 are potential stratigraphic markers for the upper Katian–lower Hirnantian in Saudi Arabia, but some are new and others have not yet been formally described. Consequently, their ranges are unknown. They include *Falavia magniretifera* gen. et sp. nov., *Striatotheca* aff. *monorugulata*, which resembles *S. monorugulata* recorded from the upper Floian to lower Darriwilian stages (i.e. the Anglo-Welsh Arenig Series) of South China and Pakistan (Yin et al., 1998; Quintavalle et al., 2000; Tongiorgi et al., 2003; Yan et al., 2011), and *Tunisphaeridium bicaudatum* sp. nov. These forms are described below in the discussion of Systematic Palaeontology.

#### 4.2. Assemblage 2 (*Sarah Formation, basal disrupted facies, 458.4–436.0 ft*)

Assemblage 2 occurs in the basal disrupted facies of the Sarah Formation and comprises 42 forms, 35 of which are also present in Assemblage 1 (Fig. 2). Diversity per sample tends to be slightly lower than that of Assemblage 1, with between 21 and 24 species per sample (mean 23), but the representation of certain groups such as the veryhachid or leiofusid acritarchs (principally species of *Eupoikilofusa*, *Leiofusa* and *Poikilofusa*) is comparable with that in the Quwarah Member.

Assemblage 2 is distinguished from Assemblage 1 by the first appearances in the Qusaiba-1 core of *Eupoikilofusa platynetrella*, *Moyeria cabottii*, *Oppilatala cf. frondis*, a large *Poikilofusa* sp. and *Veryhachium mareki*. Of these, *Eupoikilofusa platynetrella*, *Oppilatala cf. frondis* and *Veryhachium mareki* are present in at least two of the four samples. A number of other species have their last appearance datums in Assemblage 1, as noted above, and therefore have the potential to distinguish that assemblage from Assemblage 2.

Forms that were recorded from the Quwarah Member and are present in at least three samples from the basal Sarah Formation include *Actinotodissus crassus*, *Eupoikilofusa* spp. (including *Eupoikilofusa striatifera*), *Evittia denticulata denticulata*, *Ferromia pellita*, *Leprotolypa evexa*, *Lophosphaeridium* spp., *Neoveryhachium carminae constricta*, *Safirotheca safira*, *Veryhachium europaeum*, *Veryhachium lairdii*, *Veryhachium oklahomense*, *Veryhachium subglobosum*, *Veryhachium trispinosum* and *Villosacapsula setosapellicula*. Veryhachid acritarchs (species of *Neoveryhachium*, *Veryhachium* and *Villosacapsula*) are well represented.

A number of forms recorded from the basal Sarah Formation are present in the lower interval of the Quwarah Member, but not in the upper interval of that member from 476.8 ft to 461.3

ft (Fig. 2). These include *Actinotodissus crassus*, *Actipilion druggii*, *Baltisphaeridium perclarum*, *Caelatosphaera cerebella*, *Cheleutochroa gymnobrachiata*, *Eupoikilofusa* spp., *Evittia denticulata denticulata*, *Ferromia pellita*, *Leprotolypa evexa*, *Nexosarium parvum*, *Pirea* spp., *Safirotheca safira* and *Tunisphaeridium* spp. However, only one sample was included from the upper Quwarah interval (476.7 ft), and no samples were collected from the uppermost part of the member between 476.7 ft and 461.3 ft. In view of this, it is difficult to evaluate the significance, or otherwise, of the absence of these forms from the upper Quwarah Member and their reappearance in the basal Sarah Formation. The possibility that they might be reworked in the basal Sarah Formation is discussed below.

**Age and discussion.** Assemblage 2 has a number of taxa in common with Assemblage 1, indicating a Late Ordovician, late Katian–Hirnantian age. The large *Veryhachium mareki*, which appears for the first time in the succession, was previously described from the Prague Basin of Bohemia (Vavrdová, 1989), where it is present in pre-glacial (Kraluv Dvur Formation), glacial and post-glacial deposits (Kosov Formation), i.e. in the Asghill Series (late Katian to Hirnantian). The species has also been recorded in many Late Ordovician high palaeolatitude Gondwanan sections, but is only associated with the major Hirnantian glacial advance (Vecoli and Le Hérisse, 2004). The Chitinozoa from this interval (Paris et al., this volume) indicate an early Hirnantian age.

#### 4.3. Assemblage 3 (Baq'a Shale Member, 350.6–292.3 ft)

Assemblage 3 is from the Baq'a Shale Member of the Sarah Formation and is characterized by stratigraphic admixing of Middle and Late Ordovician taxa. The Baq'a Shale Member is

the most intensively sampled part of the core from Qusaiba-1. Twenty-one samples were collected between 350.6 ft and 292.3 ft.

Excluding recognizably reworked Middle Ordovician forms, the number of taxa recorded per sample ranges from nine to 25, with a mean of 18. Many range up from the Quwarah Member and/or the basal Sarah Formation (Fig. 2). Taxa that have FADs in the Baq'a Shale include *Cymbosphaeridium* spp., *Disparifusa* sp. A, *Dorsennidium* spp., *Evittia* sp. 1, *Leiofusa* sp. A, *Leiofusa* sp. B, *Multiplicisphaeridium paraguaferum*, *Multiplicisphaeridium ramusculosum* and *Sol* sp. 2, although the last might be another form that is reworked from the Middle Ordovician. Most of these are present in no more than three or four samples, although *Dorsennidium* spp. occur more frequently. *Cymbosphaeridium* spp., *Multiplicisphaeridium paraguaferum* and *Multiplicisphaeridium ramusculosum*, which are more characteristic of Silurian assemblages, have FADs in the upper half of the sampled section.

Of the other forms recorded, leiofusid (*Eupoikilofusa* spp., including *E. platynetrella*, *Leiofusa* spp.) and veryhachid acritarchs (*Neoveryhachium carminae* sl, *Veryhachium* spp., including *V. lairdii*, *V. subglobosum* and *V. trispinosum*) are present in most samples, together with leiospheres (*Leiosphaeridia* spp.). *Sylvanidium?* *hawbanense* is also present in most samples from the Baq'a Shale, despite being absent from Assemblage 2, and *Veryhachium oklahomense* and *Villosacapsula setosapellicula* occur in nearly 50% of samples.

A distinguishing feature of Assemblage 3 is the large number of reworked Middle Ordovician forms. Between 12% and 38% of species in each sample from the Baq'a Shale Member are considered to be reworked from the Middle Ordovician, and they outnumber Late Ordovician forms in terms of abundance. The occurrence of reworked Middle Ordovician taxa is



attributed to glacial erosion and re-deposition during final melting of the Hirnantian Gondwanan ice sheets. Reworked Chitinozoa, including Middle Ordovician species, are also present in the Baq'a Shale Member (Paris et al., this volume). Erosion of older Ordovician strata during the Hirnantian glaciation has been previously documented in Saudi Arabia (Miller and Al-Ruwaili, 2007; Melvin and Miller, 2009) and other high-palaeolatitude Gondwanan localities (Vecoli and Le Hérissé, 2004; Videt et al., 2010). The evidence for such erosion, probably the result of both deep glacial incisions and erosion by meltwater, includes admixed palynological assemblages.

A number of taxa, including *Beromia clipeata* and *Saharidia munfarida*, which are important in high palaeolatitude Gondwanan assemblages associated with the second phase of Hirnantian glacial advance, and particularly with final melting, were not recorded in this study. Their absence might indicate palaeobiogeographical differences in composition between Saudi Arabian and other high palaeolatitude Gondwanan assemblages. Alternatively, their absence could reflect different palaeoenvironmental conditions, with perhaps a more brackish environment for the Baq'a Shale Member (Paris et al., this volume) in contrast to more marine conditions elsewhere, for example in the Late Hirnantian Hassi el Hadjar Formation in the Algerian Sahara (Paris et al., 2000; Vecoli and Le Hérissé, 2004).

#### 4.4. Assemblage 4 (*Qusaiba Member, 256.4–254.8 ft*)

The highest assemblage is based on the three samples collected from 256.4 ft, 255.75 ft and 254.8 ft. The succession consists of grey fissile mudstones deposited during the earliest stage of the Silurian marine transgression on the Late Ordovician Baq'a Sandstone Member (Melvin, this volume). The palynofacies are variable in the three samples, but the higher two

samples, and particularly the highest from 254.8 ft, contain abundant clumps of amorphous organic matter that dilute the acritarchs on the slides. This latter sample is from the same depth as a gamma ray peak in the borehole.

Abundance and diversity are both relatively low in Assemblage 4. In terms of diversity, there are between 7 and 13 species per sample (mean 10). The assemblage is also distinct from the underlying assemblages in its composition. It contains several *Multiplicisphaeridium* species, including *Multiplicisphaeridium irregulare* and *Multiplicisphaeridium raspum* (the latter included in *Multiplicisphaeridium* spp. in Fig. 2), *Evittia denticulata denticulata* morphotypes, simple *Micrhystridium* species, rare *Leprotolypa evexa* and *Salopidium* spp. The genus *Salopidium* has not been reported below the Silurian.

The presence in two samples of *Dorsennidium polorum* comb. nov. is of particular interest. This species, described as *Micrhystridium? polorum* by Miller and Eames, 1982, has a rectangular to quadrangular vesicle with more processes concentrated on one side of the vesicle than the other and a process-free area on the centre of the vesicle. The species was described from the early Silurian (Rhuddanian) Medina Group of the Niagara Gorge, New York, USA. Recently, it has also been described in a cored succession in northern Chad, in an interval referred to a post-*elongata*, pre-*fragilis* chitinozoan biozone of latest Hirnantian to earliest Rhuddanian age (Le Hérisse et al., 2013).

Other characteristic elements encountered in this interval are *Nexosarium mansouri* sp. nov. and a single specimen of *Hoegklintia* attributed to *Hoegklintia* aff. *digitata*. The assemblage also contains leiofusid acritarchs, *Leiosphaeridia* spp. and a few triapsidate and quadrangular veryhachid acritarchs. A few rounded forms are referred to *Veryhachium* aff. *subglobosum*

because of their strongly convex vesicle sides, but they have shorter processes than true *V. subglobosum*. *Nexosarium mansouri* sp. nov. resembles a species from the early Silurian *acuminatus* Graptolite Biozone in the Zelkovice Formation of Bohemia, described as *Oppilatala* cf. *frondis* (Dufka and Fatka, 1993), but the latter is too poorly preserved to be certain that they are the same species.

Among the leiofusid acritarchs, *Leiofusa* sp. B (Plate XIV, 10) is a large fusiform species with a slightly asymmetrical vesicle, a thin vesicle wall that is commonly folded, and short polar processes. The vesicle is 90  $\mu\text{m}$  long by 50  $\mu\text{m}$  wide, and the processes are 30  $\mu\text{m}$  long. A second form, *Leiofusa* sp. C (Plate XIV, 11), is a very thin-walled and folded leiofusid with a total length of 230–250  $\mu\text{m}$  and a width of 42–45  $\mu\text{m}$ .

**Age and significance.** The occurrence of *Dorsennidium polorum* and the absence of species with true Ordovician character constitute the best evidence to suggest a Rhuddanian age, and possibly earliest Rhuddanian, for Assemblage 4 in Qusaiba-1. This is consistent with the conclusion reached from the study of Chitinozoa (Paris et al., this volume). The lowest graptolites identified in the Qusaiba-1 core are assigned to the mid-Aeronian *convolutus* Biozone, at 253.3 ft, only 1.5 ft above the highest sample studied here (Zalasiewicz et al., 2007).

Publications that document the abundance and diversity of acritarchs at high palaeolatitudes in Rhuddanian sections with independent stratigraphic control (e.g. by graptolites of the *persculptus-ascensus-acuminatus* biozones or Chitinozoa) are rare. In Saudi Arabia, assemblages from 8171.0–9468.9 ft in well HWTH-1, for which an early Rhuddanian age was proposed by Le Hérissé et al. (1995), yielded only long ranging species of little stratigraphic

value. Subsequently, a tentative Ordovician age was suggested by Molyneux and Al-Hajri (2000) for a sample from 8549.0 ft. The other reference to earliest Rhuddanian acritarchs in Saudi Arabia (Le Hérissé, 2000), with independent age control provided by Chitinozoa, was concerned with an interval in the lower part of core 12 in well MKSR-1. This has since been re-interpreted as being late Hirnantian in age, following re-attribution of *Spinachitina fragilis* to *S. oulebsiri* (Paris et al., this volume). The assemblage of acritarchs described by Le Hérissé (2000), rich in sphaeromorph acritarchs (leiospheres), is different from the assemblage described in Qusaiba-1, which is richer in acanthomorphic acritarchs with taxa of better biostratigraphic value.

Other relevant data come from Libya, Tunisia and Bohemia. The assemblage from the L11 Local Biozone in northeast Libya and dated as Rhuddanian *s.l.* (Hill and Molyneux, 1988) does not enable precise correlation with Qusaiba-1. In Tunisia, acritarch-poor samples have been recorded from a Rhuddanian interval below and within a ‘hot-shale’ (Vecoli et al., 2009), but are attributed to the *vesiculosus* and younger graptolite biozones and are apparently younger than the interval studied here. Results of palynological studies across the Ordovician-Silurian boundary in Bohemia (the local boundary between the Kosov and Llandovery series) were published by Dufka and Fatka (1993). *Oppilatala cf. frondis*, from the *acuminatus* Graptolite Biozone in the Zelkovic Formation of Bohemia, is possibly comparable to *Nexosarium mansouri* sp. nov. recorded herein, but no acritarch species were described from the *ascensus* Graptolite Biozone of Bohemia.

Environmental conditions under which beds across the Ordovician–Silurian boundary were deposited varied along the Gondwanan margin, controlled, for example, by position in relation to the continental margin, position in each basin, and isostatic readjustments during

deglaciation. Variable environmental conditions explain variations in the composition of assemblages. The Qusaiba-1 assemblage most closely resembles an assemblage from the late Hirnantian to earliest Rhuddanian in northern Chad (Le Hérisse et al., 2013), which also contains *Dorsennidium polorum* comb. nov., even though the deposits in northern Chad are from a marginal-marine environment whereas those from Qusaiba-1 are from a more open marine setting.

Phytoplankton dynamics across the Ordovician–Silurian boundary and from the early Silurian at low palaeolatitudes, with reference to acritarch data, have also been discussed (Delabroye et al., 2011; Johnson, 1985; Hill and Dorning, 1984; Masiak et al., 2003; Martin, 1988; Miller and Eames, 1982). For the Rhuddanian, the closest similarity is with western New York State (Miller and Eames, 1982).

## 5. Reworking

Reworking of Middle Ordovician acritarchs is evident in the Baq'a Shale Member in the Qusaiba-1 core, and is attributed to processes of glacial erosion and resedimentation during glacial melting. The extent of reworking at other levels in the Qusaiba-1 core is uncertain. Three questions arise in connection with this. 1. Are Late Ordovician forms reworked in the Baq'a Shale Member as well as Middle Ordovician forms, or are the Late Ordovician forms in place? 2. Is there any evidence for reworking in the basal Sarah Formation? 3. Is there any evidence for reworking in the Quwarah Member?

### 5.1. Baq'a Shale Member

Species of *Acanthodiacrodium*, *Arkonina*, *Cymatiogalea*, *Dicrodiacrodium*, *Frankea*, *Peteinosphaeridium*, *Stelliferidium* and *Uncinisphaera*, together with *Aremoricanium rigaudae*, *Dasydorus cirritus*, *Stellechinatum celestum*, *Striatotheca quieta* and *S. rarirrugulata*, are all known from the Middle Ordovician (Darriwilian) Hanadir Member of the Qasim Formation (Le Hérissé et al., 2007). They are considered to be reworked in the Baq'a Shale Member (Fig. 2), probably from the Hanadir Member and possibly also from higher members of the Qasim Formation such as the Kahfah Member. They were most likely reworked during the second phase of Hirnantian glaciation and re-deposited in the Baq'a Shale Member during deglaciation (Melvin, this volume). The Middle Ordovician origin of these forms is consistent with the derivation of reworked chitinozoans in the same deposits (Paris et al., this volume).

Determining whether any of the Late Ordovician taxa recorded from the Baq'a Shale Member are reworked is more difficult, especially as there is no difference in preservation to distinguish possible reworked forms. Excluding those forms considered to be reworked from the Middle Ordovician, 64 acritarch taxa were recorded from the Baq'a Shale Member. The majority (33) were also recorded from the Quwarah Member and basal Sarah Formation. A further 15 taxa were recorded from the Baq'a Shale and the Quwarah members but not from the basal Sarah Formation. Six taxa were recorded from the Baq'a Shale Member and the basal Sarah Formation, but not from the Quwarah Member. The remaining 10 forms were not recorded below the Baq'a Shale.

Paris et al. (this volume) have postulated that the environment of deposition of the Baq'a Shale was unfavourable for the development of an indigenous chitinozoan fauna, and that it

was not an open marine environment, but was possibly brackish due to the influx of glacial meltwater. If so, the environment of deposition would have been quite different from that of the Quwarah Member, with the implication that many of the forms recorded from that member would be out of their optimum environment in the Baq'a Shale. In this context, it might be significant that Miller and Al-Ruwaili (2007) recorded leiosphere-dominated assemblages in shales of the Baq'a Member, and these would be more consistent with a brackish environment of deposition.

Furthermore, as there is reworking from the Hanadir Member into the Baq'a Shale Member, reworking might also be expected from higher members of the Qasim Formation as a result of glacial erosion and redeposition. Miller and Al-Ruwaili (2007) reported subordinate numbers of reworked Ordovician palynomorphs in the leiosphere-dominated Baq'a assemblages, and several distinct assemblages of reworked Ordovician acritarchs in the Hawban Member. The latter comprised genera and species from the Hanadir, Kahfah and Quwarah members of the Qasim Formation.

Interpretation of the environment of deposition as possibly brackish, coupled with the likelihood that glacial erosion down to Middle Ordovician levels would have also affected Upper Ordovician beds, supports the interpretation that many Late Ordovician genera and species recorded from the Baq'a Shale are reworked. Nevertheless, *Multiplicisphaeridium paraguaferum*, which has its first appearance in Qusaiba-1 in the Baq'a Shale but is more typical of Silurian assemblages, suggests that conditions were not entirely inimical to non-leiospherid acritarchs, and that some component of the non-leiosphere assemblage is in place. Hence, although it is quite likely that Late Ordovician taxa are reworked in the Baq'a Shale Member, the extent of any such reworking remains uncertain.

## 5.2. Basal Sarah Formation

A number of forms are present in the lower interval of the Quwarah Member and in the basal disrupted facies of the Sarah Formation, but are absent from the upper interval of the Quwarah Member between 476.8 ft and 461.3 ft (Fig. 2). Given that only one sample was examined from the upper Quwarah interval, the significance of their absence from the upper part of the member is unclear. However, the possibility that their reappearance in the basal Sarah Formation is due to reworking must be considered.

The basal disrupted facies of the Sarah Formation is interpreted as a glacitectorite (Melvin, this volume), a subglacially sheared deposit that retains some of the structure and characteristics of the parent material (Benn and Evans, 1998; Evans et al., 2006). In this case, the parent material of the facies between 461.1 ft and 436.0 ft comprises grey-green sandy siltstone. Where the original depositional fabric of the rock can be recognized, it is comparable with Facies 1 of the Quwarah Member (Melvin, this volume).

Interpretation of the basal disrupted facies as a glacitectorite raises the question of which pre-glacial sedimentary units might have been incorporated. Three possibilities are considered. The first is that shearing at the base of the ice sheet incorporated sediment from sub-Sarah Formation units such as the Quwarah Member. This could explain why many of the taxa found in Assemblage 1 are also recorded from Assemblage 2, why the chitinozoans from the basal disrupted facies are included in the same assemblage as those from the upper Quwarah Member, and why the sediments incorporated in the basal disrupted facies are comparable with facies recognized in the Quwarah Member. The implication is that many of the forms



found in Assemblage 2 are reworked from pre-Sarah Formation, pre-glacial deposits along with the sediment in which they are contained.

The second possibility is that the sediments incorporated into the basal disrupted facies of the Sarah Formation represent a post-Quwarah but pre-glacial depositional unit. In this scenario, deposition of the basal Sarah Formation followed post-Quwarah erosion, with the basal pebble conglomerate of the former overlying an eroded surface of the Quwarah Member (Melvin, this volume). The basal conglomerate is succeeded by siltstone that was subsequently sheared, brecciated and rotated as the ice sheet rode over it. The implication of this scenario is that Assemblage 2 could be an in place, post-Quwarah, pre-glacial assemblage contained within sediments that were subsequently deformed subglacially.

The third possibility is some combination of the previous two, in which a post-Quwarah component is admixed with older reworked elements. Discriminating between these three scenarios is beyond the scope of the present work and requires further investigation to understand the processes leading to the occurrence of Assemblage 2 in the basal Sarah Formation. Hence, there remains uncertainty over whether Assemblage 2 comprises taxa that are reworked, in place, or a combination of the two.

### 5.3. *Quwarah Member*

A very few forms recorded from the Quwarah Member, notably *Ferromia pellita*, *Impluviculus?* sp., *Pirea* spp. and *Baltisphaeridium ternatum*, might be reworked, but there is no obvious stratigraphic admixing at this level and the forms listed are all rare. The alternative hypothesis is that they are in place in the late Katian or early Hirnantian.

Paris et al. (2007) reported *Baltisphaeridium ternatum*, *Ferromia pellita* and *Pirea* spp. to be reworked in Late Ordovician deposits in Turkey, but in these instances there is more evidence for stratigraphic admixing. *Baltisphaeridium ternatum*, for example, was reported to be reworked in a late Sandbian–early Katian assemblage from the Sort Tepe Formation of the Taurus Range, and is accompanied there by species of *Acanthodiacrodium*, *Arkonina*, *Dicrodiacrodium*, *Stelliferidium* and *Striatotheca*. Similarly, *Ferromia pellita* and *Pirea* spp. were recorded by Paris et al. (2007) as reworked in Hirnantian glacio-marine sediments of the Border Folds in Turkey, along with *Cymatiogalea* spp., *Dasydorus cirritus*, *Frankea longiuscula*, the late Cambrian form *Lusatia dendroidea* (see Albani et al., 2007) and the late Cambrian–Early Ordovician genus *Vulcanisphaera*.

The extent of reworking in pre-glacial Ordovician sedimentary rocks elsewhere in Saudi Arabia is unclear. Jachowicz (1995) reported reworking in acritarch assemblages from central and northwestern Saudi Arabia, and at the time the assemblages were considered to be from rocks of early Caradoc (Sandbian) and early Ashgill (late Katian) age. In both cases, Tremadocian forms were reported to dominate or to be the most common elements in the reworked component of the assemblages. Miller and Al-Ruwaili (2007), however, have pointed out that Jachowicz's (1995) study did not benefit from parallel sedimentological work, which would have identified the sampled units as being glacial in origin.

#### 5.4. Discussion

There is no clear answer to any of the three questions posed at the beginning of this section. It is evident that Middle Ordovician forms are reworked into the Baq'a Shale Member, probably

from the Hanadir Member and perhaps also from the Kahfah Member of the Qasim Formation, and this fits the pattern of reworking seen regionally in Late Ordovician glaciogenic successions. It is also consistent with the reworking of chitinozoans in Qusaiba-1. Whether any of the Late Ordovician taxa recorded from the Baq'a Shale are reworked is less clear, although it seems likely. Interpretation of the environment of Baq'a Shale deposition as brackish suggests that many forms might be reworked as they would be out of their normal environmental range. Furthermore, reworking should be expected from higher members of the Qasim Formation, given that glacial erosion cut down through lower levels in the formation. Nevertheless, there remains some uncertainty over the extent of Late Ordovician reworking in the Baq'a Shale Member, especially as some non-leiosphere acritarchs such as *Multiplicisphaeridium paraguaferum* appear to be in place in the Baq'a Shale.

The extent of any reworking in assemblages from the basal Sarah Formation and the Quwarah Member is even less certain. The absence of genera and species from the upper part of the Quwarah Member and their reappearance in the basal Sarah Formation might indicate reworking in the latter. Alternatively, their absence from the upper Quwarah interval could indicate no more than normal fluctuations in taxon occurrences controlled by shifting palaeoenvironmental conditions, compounded by sampling bias.

The problem of determining whether occurrences in the basal Sarah Formation might be due to reworking is exemplified by *Aremoricanium squarrosom*. This species was not recorded from the Quwarah Member in Qusaiba-1, and its occurrences in Hirnantian deposits elsewhere (e.g. in Bohemia, as *Aremoricanium syringosagis*, by Vavrdová, 1982; see also Vecoli and Le Hérissé, 2004, fig. 6) have been attributed to reworking. Consequently, it might be regarded as reworked in the basal disrupted facies of the Sarah Formation. On the other

hand, *Aremoricanium squarrosus* has been recorded from the Quwarah Member in several wells by one of us (M.M.), which suggests that its absence from the Quwarah Member in Qusaiba-1 might be due to local environmental factors.

Reworking in the Quwarah Member is uncertain, especially as there is no conclusive evidence for stratigraphic admixing. Previous suggestions of reworking in pre-glacial, early Caradoc (Sandbian) and early Ashgill (late Katian) assemblages in Saudi Arabia have been discounted (Miller and Al-Ruwaili, 2007).

## 6. Systematic Palaeontology

Two new acritarch genera, five new species and one new combination are described and discussed below: *Dorsennidium polorum* (Miller and Eames, 1982) comb. nov., *Falavia magniretifera* gen. et sp. nov., *Inflatarium trilobatum* gen. et sp. nov., *Nexosarium mansouri* sp. nov., *Orthosphaeridium orthogonium* sp. nov. and *Tunisphaeridium bicaudatum* sp. nov.

The palynomorphs described herein are fossil-taxa under the terms of the International Code of Nomenclature for algae, fungi, and plants (formerly the International Code of Botanical Nomenclature [I.C.B.N.]; McNeill et al., 2012), and are arranged alphabetically by genera in the informal *incertae sedis* group Acritarcha. The material is housed in the palynological collections of the Department of Geology, “Laboratoire de Paléontologie de Brest” (LPB), University of Brest, France, with the prefix LPB, and repository numbers LPB 13200 to LPB 13231. England finder co-ordinates are provided for all illustrated specimens.

Group Acritarcha Evitt, 1963

Genus *Actipilion* Loeblich, 1970

*Type species: Actipilion druggii* Loeblich, 1970, by original designation.

*Actipilion druggii* Loeblich, 1970 (Plate IV, 8–9; Plate V, 1)

1970 *Actipilion druggii* Loeblich, p. 711, fig. 3A–E

*Description:* The vesicle is large, subcircular in outline, and has a relatively thick wall. It bears a variable number of cylindrical, fibrous, thin-walled, diaphanous processes. The processes are distributed at random and are clearly differentiated from the vesicle.

*Dimensions* (22 specimens):

Vesicle diameter: 36–70  $\mu\text{m}$  (mean 49.6  $\mu\text{m}$ , median 50  $\mu\text{m}$ ).

Process length: 15–40  $\mu\text{m}$  (mean 28.5  $\mu\text{m}$ , median 28  $\mu\text{m}$ ).

Process number: 7–21 (mean and median 14).

*Comparison:* The thin-walled, diaphanous, fibrous processes are a characteristic feature of *Actipilion druggii*. The holotype of *A. druggii* Loeblich, 1970, is larger than the Quwarah specimens and has longer processes (Fig. 3). The number of processes on the holotype, however, approximately 14, falls within the range recorded on specimens from the Quwarah Member. Two of the isotypes (Loeblich, 1970, isotype 1, isotype 2), the specimen recorded from northeast Libya by Molyneux (1988), and several of the specimens figured by Playford and Wicander (2006) all fall within or around the range of variation of the Quwarah specimens in terms of vesicle diameter, process length and process number (Fig. 3).

*Occurrence:* *Actipilion druggii* is present in the lower interval of the Quwarah Member, in the basal disrupted facies of the Sarah Formation, and in the Baq'a Shale Member.

Genus *Dorsennidium* Wicander, 1974 emend. Sarjeant and Stancliffe, 1994

*Type species:* *Dorsennidium patulum* Wicander, 1974, by original designation.

*Dorsennidium polorum* (Miller and Eames 1982) comb. nov. (Plate XIV, 1–2)

*Basionym:* *Micrhystridium? polorum* Miller and Eames, 1982, *Palynology*, v. 6, p. 239–240, pl. 2, figs. 10–12.

1982 *Micrhystridium? polorum* Miller and Eames, pp. 239–240, pl. 2, figs. 10–12.

2013 “*Dorsennidium polorum* Miller and Eames 1982 nov. comb.” in Le Hérisse et al., fig. 8I, J, M.

*Remarks:* Miller and Eames (1982) originally placed this species tentatively in the genus *Micrhystridium*. The original diagnosis refers to the vesicle as having a subrectangular to subquadrate outline, with acuminate homomorphic processes that are generally distributed around the vesicle margin. More processes may be concentrated on one side of the vesicle than on the other. The disposition of the processes recalls the supplementary processes drawn out from the vesicles faces of *Dorsennidium hamii* (Loeblich, 1970) Sarjeant and Stancliffe, 1994.

The recombined species name, *Dorsennidium polorum*, was used by Le Hérisse et al. (2013), who recorded the species in an assemblage of latest Ordovician–earliest Silurian age from

northern Chad. However, Le Hérisse et al. (2013) did not cite the basionym and did not provide a full and direct reference to the authors and place of valid publication, with page, plate reference and date. The new combination was therefore not validly published in Le Hérisse et al. (2013) under Article 41.5 of the International Code of Nomenclature for algae, fungi, and plants (McNeill et al., 2012), and so is validated here.

Genus *Falavia* gen. nov.

*Type species: Falavia magniretifera* sp. nov.

*Derivation of name:* Latin *fallus*, false, and *avis*, bird, referring to the superficial resemblance to a shuttlecock used in badminton.

*Diagnosis:* Vesicle spherical. The processes are restricted to one half of the vesicle and bear a network of anastomosing filaments that arise along their lengths and from their distal terminations, and which connect the processes.

*Comparison:* The distinguishing feature of *Falavia* gen. nov. is the restriction of its major ornament to one half of the vesicle. Other genera that also have processes or other major structures restricted to one half of the vesicle are *Chuttecloska* Loeblich and Wicander, 1976, *Hemibaltisphaeridium* Cramer, 1971, and *Ooidium* Timofeev, 1957. *Chuttecloska*, described from the Lower Devonian (Gedinnian) of Oklahoma (Loeblich and Wicander, 1976), has a vesicle that is pear-shaped, subovate, ovate or subcircular in outline, with one pole surrounded by a thin, flaring, skirt-like vellum or membrane that extends beyond the vesicle.

*Hemibaltisphaeridium*, described from the middle and upper Silurian of Spain (Cramer, 1971), has a subspherical to ellipsoidal vesicle, with one smooth pole and the other bearing a number of ramusculose processes (3–10 in the type and only species, *H. dedosmuertos* (Cramer) Cramer, 1971). *Ooidium*, originally described by Timofeev (1957) from the Lower

Ordovician of Baltic Russia, has subcircular, ovate or elongate vesicles, one pole of which is crowned with anastomosing trabeculae. Of the three genera, *Ooidium* is morphologically closest to *Falavia* gen. nov. because of its anastomosing ornament, but in *Ooidium* this is a comparatively low structure and is not supported by stout processes. Species of *Ooidium* also commonly have striate vesicles, with the striations extending between the poles.

***Falavia magniretifera*** gen et sp. nov. (Plate VI, 8–9)

*Derivation of name:* From Latin *magnus*, large, and *retiferum*, net-bearing, referring to the large net-like structure that the vesicle bears at one pole.

*Type locality:* Qusaiba-1 core hole, Qusaiba, central Saudi Arabia.

*Stratum typicum:* Quwarah Member of the Qasim Formation, cores 56 to 50, 551.0–488.3 ft, Late Ordovician, late Katian–early Hirnantian.

*Holotype:* Qusaiba-1, Quwarah Member, Qasim Formation, core 50, 488.3 ft, slide 64143, England Finder co-ordinate T42/1 (Plate VI, 8), LPB 13221. Late Katian–early Hirnantian.

*Paratype:* Qusaiba-1, Quwarah Member, Qasim Formation, core 52, 503.1 ft, slide 64089, England Finder co-ordinate U39/2-U40/1 (Plate VI, 9), LPB 13223. Late Katian–early Hirnantian.

*Diagnosis:* The vesicle is subcircular in outline and is inferred to have been originally spherical. It is thin-walled and bears an ornament of fine grana. Processes are restricted to one



half of the vesicle. About 25 stout, apparently solid, rod-like processes that taper distally are present. The processes bear a network of anastomosing filaments that arise along their lengths and from their distal terminations, and these connect the processes. The height of the filamentous net is approximately  $1.5 \times$  the maximum vesicle diameter.

*Dimensions* (6 specimens):

Vesicle diameter: 28–35  $\mu\text{m}$  (mean 31.7  $\mu\text{m}$ , median 32  $\mu\text{m}$ )  $\times$  18–33  $\mu\text{m}$  (mean 27.2  $\mu\text{m}$ , median 27.5  $\mu\text{m}$ ).

Net height: 40–53  $\mu\text{m}$  (mean 48  $\mu\text{m}$ , median 50  $\mu\text{m}$ ).

Ratio of net height:maximum vesicle diameter: 1.38–1.79 (mean 1.52, median 1.49).

*Occurrence*: Quwarah Member, Qasim Formation. This form is very rare. Only six specimens were recorded, one each from 551.0 ft, 536.7 ft, 535.2 ft, 528.3 ft, 503.1 ft and 488.3 ft.

Genus *Ferromia* Vavrdová, 1979

*Type species*: *Ferromia pellita* (Martin) Martin, 1996, originally designated as *Ferromia filosa* Vavrdová, 1979, by Vavrdová (1979, p. 62).

*Ferromia pellita* (Martin) Martin, 1996 (Plate IV, 3–5)

1977 *Micrhystridium pellitum* Martin, pp. 7–8, pl. II, fig. 18, pl. IV, figs. 7, 16, figs. 5, 6 in the text.

1979 *Ferromia filosa* Vavrdová, p. 64, pl. 11, fig. 9, pl. 12, figs. 3–5, pl. 13, figs. 1–3.

1996 *Ferromia pellita* (Martin); Martin, pp. 27–30, pl. I, figs. 1-3, 5, 6, 9-12, 14-21, pl. II, figs. 1–12.

*Description:* The vesicle is subcircular to subpolygonal in outline, bearing between 9 and 23 processes. The processes are narrow, rigid and conical, taper to acuminate tips, and have angular proximal contacts. They are hollow and communicate with the vesicle cavity. In addition to the processes, the vesicle bears an ornament of short spines, about 1 µm long, that are stout and thorn-like with apparently simple distal terminations.

*Dimensions* (12 specimens):

Vesicle diameter: 14–21 µm (mean 17.2 µm, median 17 µm).

Process length: 10–15 µm (mean 13.3 µm, median 14.5 µm).

Process length/vesicle diameter: 0.59–0.94 (mean 0.78, median 0.76).

Process number: 9–23 (mean 15, median 14).

*Comparison:* The specimens from the Qusaiba-1 core differ in some respects from the specimens of *F. pellita* recorded by Martin (1996) and from the synonymous *F. filosa* of Vavrdová (1979). Vesicle dimensions of *F. pellita* in Martin (1996) and *F. filosa* in Vavrdová (1979) are slightly smaller than those of the Qusaiba-1 specimens, although with a degree of overlap. Martin (1996) gave a range of 8–18 µm for the vesicle diameter, with a mean of 13 µm, and Vavrdová (1979) recorded vesicle diameters of 8–16 µm. In contrast, the processes of *F. pellita* in Martin (1996) and *F. filosa* in Vavrdová (1979) are slightly longer in both absolute and relative terms than those of the specimens from Qusaiba-1, but again with some overlap. Martin (1996) indicated process lengths of 10–22 µm, and process length:vesicle diameter ratios of 0.75–1.20, and Vavrdová (1979) recorded process lengths of 10–20 µm for *F. filosa*. Also, the number of processes on some specimens from the Qusaiba-1 core exceeds the number of seven to about 15 specified in the emended diagnosis (Martin, 1996).

In the emended diagnosis, Martin (1996) described the secondary ornament of *F. pellita* as being a dense, hair-like ornamentation showing minute, possible anastomosed lateral ramifications, although under the heading of remarks and comparisons she also noted that the hair-like ornament might appear simple under the light microscope. Vavrdová (1979) described the secondary ornament as a thick cover of echinate to capitate hair-like outgrowths. In comparison, the ornament on the Qusaiba-1 specimens comprises relatively short, stout, conical, thorn-like elements with simple terminations. There is no indication under the light microscope, including under differential interference contrast, of branching or capitate tips.

*Remarks:* Martin (1996) commented that the last appearance datum of *F. pellita* as an autochthonous element of acritarch assemblages was probably pre-Caradoc (pre-Sandbian). If so, the range of the species would have to be extended upwards to accommodate the specimens from Qusaiba-1, or else they might be interpreted as reworked. Given the differences outlined above, however, it is also possible that the Qusaiba-1 specimens represent a distinct Late Ordovician morphotype, but one that is closely similar to *F. pellita*.

*Occurrence:* Specimens of *Ferromia pellita* were recorded from the Quwarah Member at 551.0 ft, 536.7 ft, 535.2 ft, 528.3 ft, 507.15 ft and 488.3 ft, from the basal disrupted facies of the Sarah Formation at 458.4 ft, 438.7 ft and 436.0 ft, and from the Baq'a Shale Member at 338.4 ft, 335.7 ft, 302.4 ft, 301.1 ft and 292.3 ft.

Genus *Glyptosphaera* Kiryanov, 1978

*Type species:* *Glyptosphaera speciosa* Kiryanov, 1978, by original designation.

*Glyptosphaera?* sp. (Plate VI, 5, 7)

*Description:* The vesicle is large, oval to subcircular in outline, and is inferred to have been originally spherical. The vesicle walls are thick and bear an ornament of low, angular ridges that form an irregular zigzag pattern on the surface, giving it the appearance of a maze. Segments of adjacent ridges can be parallel to each other, although the pattern is complex and adjacent ridges are generally not parallel for their entire lengths. Ridges might also bifurcate, with branches apparently terminating abruptly.

*Dimensions:* The vesicle dimensions of the two specimens recorded are 50×34 µm and 59×44 µm.

*Remarks:* The diagnosis of *Glyptosphaera* Kiryanov, 1978, stipulates that the surface of the vesicle be covered by low crests or ridges that form a characteristic pattern, reminiscent of subparallel meanders (Mullins, 2001). In the type species, *G. speciosa* Kiryanov, 1978, the vesicle surface is covered by low ridges that are arranged in a manner described as being reminiscent of the folds of a brain and as forming a characteristic labyrinth-like pattern (Mullins, 2001, p. 46). *Glyptosphaera helterskelter* Mullins, 2001, has membranes that appear crenulate along their length and swirl around the vesicle in a concentric pattern. The ornament on the Quwarah specimens is more irregular and maze-like than the ornament on either of these species.

*Occurrence:* Two specimens from the Quwarah Member at 535.2 ft.

**Genus *Impluviculus*** Loeblich and Tappan, 1969

*Type species: Impluviculus milonii* (Deunff) Loeblich and Tappan, 1969.

***Impluviculus?* sp.** (Plate V, 2–4)

*Description:* Small, hollow, thin-walled vesicle, bearing 7 or 8, long, slender, tapering, hollow, variably flexible and acuminate processes that communicate with the vesicle cavity. The vesicle is polygonal or rounded-polygonal in outline, and in the case of the three specimens recorded is perhaps best described as irregularly octagonal or heptagonal. Processes arise from the angles of the polygon and extend in the same plane as the vesicle. Processes tend to be clustered in pairs, with a short side between each process in a pair, and a longer side between adjacent pairs, i.e. the sides of each polygon alternate between short and long. The shorter vesicle sides tend to be straight to slightly concave. Longer sides are straight to slightly concave or slightly convex.

*Dimensions:*

Specimen 1 (Plate V, 2). Vesicle: octagonal, 10×9 µm; process length: 10 µm; process number: 8.

Specimen 2 (Plate V, 3). Vesicle: octagonal, 11×11 µm; process length: 11 µm; process number: 8.

Specimen 3 (Plate V, 4). Vesicle: heptagonal, 11×11 µm; process length: 9 µm; process number 7.

*Remarks:* The original diagnosis of *Impluviculus* Loeblich and Tappan, 1969, refers to a flattened subquadrate vesicle with a process extending from each corner, vesicle sides that are slightly concave between processes, and a quadrangular or rounded opening in the centre of the vesicle that resembles a skylight. The diagnosis was emended by Martin (1977) to refer to the number of processes (4–12) and to encompass the variability of the vesicle morphology (lenticular, polygonal or nearly circular, generally <20 µm). The overall morphology of the three specimens recorded from Qusaiba-1 is that of *Impluvuculus*; they have small, polygonal vesicles with simple processes arising from the angles of the polygon and extending in the

same plane as the vesicle. There is no clear evidence for an opening on any specimen. It might be represented by an indistinct structure on the upper surface of the vesicle of one specimen (Plate V, 2), and by indistinct folds on the surface of the vesicles of the other two specimens, but this is far from certain.

The occurrence of specimens assigned to *Impluviculus*, albeit questionably, is unusual for Late Ordovician assemblages. *Impluviculus* is more characteristic of late Cambrian and Early Ordovician assemblages (Loeblich and Tappan, 1969; Martin, 1977; Rasul, 1979; Pittau, 1985; Volkova, 1990; Vecoli and Playford, 1997; Parsons and Anderson, 2000). It is possible that these three specimens are reworked into the Quwarah Member. Alternatively, they might be a rare morphotype that is characteristic of the lower part of the Quwarah Member in Qusaiba-1 (see discussion of Reworking, above).

*Impluviculus lenticularis* Martin, 1977, from the Tremadocian of the Brabant Massif, Belgium, resembles the specimens recorded here in that it has a small polygonal vesicle (8–10 sides) with the processes arising from the angles of the polygon. However, it also has a distinctive operculum in the centre of the flattened vesicle surface, and has less regularly distributed and possibly also relatively shorter processes.

*Occurrence:* Three specimens from the lowermost cores in Qusaiba-1 (cores 56, 55), one each from 551.0 ft, 536.7 ft and 535.2 ft.

Genus *Inflatarium* gen. nov.

*Type species:* *Inflatarium trilobatum* sp. nov.

*Derivation of name:* Latin *inflatus*, swollen, distended, referring to the morphology of the vesicle.

*Diagnosis:* Vesicle lobate, formed by the coalescence of a number of lobes. The rounded terminations of the lobes bear one or several short spines. The surface of the vesicle is smooth.

*Comparison:* The genus *Inflatarium* differs from *Pulvinosphaeridium* Eisenack, 1954, in having a distinct ornament on the distal part of the lobes. *Rhiptosochema* Loeblich and Tappan, 1978, has a stellate outline with elongate processes, a clear differentiation of processes from vesicle, and no spinose ornamentation on the processes.

***Inflatarium trilobatum*** sp. nov. (Plate X, 3–7)

*Derivation of name:* From Latin *tres*, *tria*, *trium*, three and *lobatum*, lobed, referring to the predominantly three-lobed morphology of the species.

*Type locality:* Qusaiba-1 core hole, Qusaiba, central Saudi Arabia.

*Stratum typicum:* Quwarah Member of the Qasim Formation, cores 55 to 49, 536.7–476.7 ft, Late Ordovician, late Katian–early Hirnantian.

*Holotype:* Qusaiba-1, Quwarah Member, Qasim Formation, core 53, 518.5 ft, slide 64036, England Finder co-ordinates G50/3 (Plate X, 3). Late Katian–early Hirnantian.

*Paratype:* Qusaiba-1, Quwarah Member, Qasim Formation, core 52, 507.15 ft, slide 64193, England Finder co-ordinates C34/1 (Plate X, 4). Late Katian–early Hirnantian.

*Diagnosis:* The vesicle is hollow, inflated and formed from three bluntly rounded, lingulate lobes, all lying in the same plane. One of the lobes is usually longer and more pronounced than the other two, with the axes of the two shorter lobes extending more or less perpendicular to the axis of the longer lobe. The vesicle wall is thin and smooth. An ornament of short spines, variable in number, is developed mainly on the distal part of the two shorter lobes, but can be observed also on the longer one.

*Dimensions* (8 specimens):

Longer lobe length: 38–65  $\mu\text{m}$ .

Shorter lobe length: 18–22  $\mu\text{m}$ .

Lobe width: 22–28  $\mu\text{m}$ .

Spinose ornament length: 3–6  $\mu\text{m}$ .

*Occurrence*: Qasim Formation, Quwarah Member: 536.7 ft, 518.5 ft, 507.15 ft, 503.1 ft, 479.4 ft and 476.7 ft; Sarah Formation, Baq'a Shale Member: 341.0 ft, possibly reworked.

Genus *Leiofusa* Eisenack, 1938

*Type species*: *Leiofusa fusiformis* (Eisenack, 1934) Eisenack, 1938.

*Leiofusa litotes* Loeblich and Tappan, 1978 (Plate I, 6–7)

1978 *Leiofusa litotes* Loeblich and Tappan, p. 1271, pl. 12, figs. 1, 2.

aff. 1988 *Leiofusa* aff. *litotes* Loeblich and Tappan; Molyneux, p. 49, pl. 9, figs. 8, 9, pl. 10, fig. 1.

?1988 *Leiofusa* aff. *fusiformis* (Eisenack 1934) Eisenack 1938; Molyneux, p. 49, pl. 9, figs. 1, 6.

*Description*: Large, slender, elongate leiofusid acritarchs in which the processes are poorly differentiated from the vesicle. The vesicle extends into the processes through a zone of very gradual narrowing. The walls of the vesicle and processes are uniformly and moderately thick.

*Dimensions* (14 specimens):



Length: 180–400  $\mu\text{m}$  (mean 270  $\mu\text{m}$ , median 275  $\mu\text{m}$ ).

Width: 12–30  $\mu\text{m}$  (mean 19.6  $\mu\text{m}$ , median 20  $\mu\text{m}$ ).

Length/width: 9.60–22.22 (mean 14.3, median 15.0).

*Comparison:* The specimens from the Quwarah Member resemble *Leiofusa litotes* in that the vesicle extends gradually into the processes so that the boundary between them is difficult to determine. This is a diagnostic feature of the species. The original diagnosis and description of *L. litotes* by Loeblich and Tappan (1978) was based on only two specimens. A much greater range of variability was recorded among the Quwarah specimens in terms of overall length, maximum width and the ratio between them. Nevertheless, the holotype and the second of Loeblich and Tappan's (1978) specimens fall within the range of variation shown by the Quwarah specimens and plot close to Quwarah specimens on bivariate plots of overall length against maximum width (Fig. 4). Loeblich and Tappan's (1978) specimens of *L. litotes* have lengths of 208  $\mu\text{m}$  and 235  $\mu\text{m}$ , and widths of 18  $\mu\text{m}$  and 25  $\mu\text{m}$ .

Specimens of *L. aff. litotes* recorded by Molyneux (1988) from the Late Ordovician of northeast Libya are generally shorter than the Quwarah specimens (length 125–185  $\mu\text{m}$ , mean 160  $\mu\text{m}$ ; Fig. 4), but are comparable in width, although with a greater mean (15–30  $\mu\text{m}$ , mean 26  $\mu\text{m}$ ). *Leiofusa aff. fusiformis* in Molyneux (1988), from the Late Ordovician of Libya, is similar, but is generally larger (length: 250–470  $\mu\text{m}$ ; width: 20–35  $\mu\text{m}$ ) with a greater mean length and width (360  $\mu\text{m}$  and 30  $\mu\text{m}$ , respectively). Nevertheless, there is overlap in the dimensions of *Leiofusa aff. fusiformis* from Libya and *L. litotes* from Qusaiba-1, and the length/width ratio of the Libyan specimens is 12 and close to that of the specimens from the Quwarah Member (Fig. 4).

*Occurrence:* Large leiofusid acritarchs assigned to *Leiofusa litotes* are common in the Quwarah Member. They comprise 15% of counted specimens in the sample from 551.0 ft and between 3.3% and 8.4% of specimens in samples from 536.7 ft to 448.3 ft.

*Leiofusa* aff. *tumida* Downie, 1959 (Plate I, 2–3, 5)

aff. 1959      *Leiofusa tumida* Downie, p. 65, pl. 11, fig. 5.

?1988      *Leiofusa* aff. *tumida* Downie 1959; Molyneux, p. 49, pl. 9, fig. 5.

*Description:* Vesicles are small, oval in outline and have smooth, thin walls. Processes are differentiated from the vesicle but the contact is gradual. Processes are long, slender and flexible with acuminate distal terminations. They are hollow, at least proximally, and are in communication with the vesicle cavity.

*Dimensions* (19 specimens):

Vesicle length: 16–30  $\mu\text{m}$  (mean 20.3  $\mu\text{m}$ , median 20  $\mu\text{m}$ ).

Vesicle width: 8–13  $\mu\text{m}$  (mean 11.6  $\mu\text{m}$ , median 12  $\mu\text{m}$ ).

Process length: 20–50  $\mu\text{m}$  (mean 32  $\mu\text{m}$ , median 30  $\mu\text{m}$ ).

Process length/vesicle length: 1–2.35 (mean 1.59, median 1.67).

Overall length: 57–125  $\mu\text{m}$  (mean 80.2  $\mu\text{m}$ , median 78  $\mu\text{m}$ ).

*Remarks:* Specimens are variable in terms of the length of their processes relative to the length of the vesicle (Fig. 5), but are characterized by their small, oval vesicles and long, slender, flexible processes that are clearly differentiated from the vesicle.

*Comparison:* Specimens recorded by Molyneux (1988) as *Leiofusa* aff. *tumida* from the Late Ordovician of northeast Libya are similar in having an oval vesicle that is drawn out into two long, flexible processes. Among the Libyan specimens are some that are larger than those from the Quwarah Member, although the ranges overlap. Vesicle lengths of the Libyan specimens are 25–35  $\mu\text{m}$  (mean 29  $\mu\text{m}$ ), vesicle widths are 7–25  $\mu\text{m}$  (mean 15  $\mu\text{m}$ ), and process lengths are 25–45  $\mu\text{m}$  (mean 33  $\mu\text{m}$ ). The type material of *Leiofusa tumida* Downie,

1959, has an overall length of about 110  $\mu\text{m}$ , and each process was reported to be about one-third of the total length (i.e. process length is equal to vesicle length).

Similar morphospecies include *Leiofusa banderillae* Cramer, 1964a, and *L. berneseae* Cramer, 1964a. *Leiofusa banderillae* has an inflated vesicle, almost oval in outline, with a single, very long and thin process at each pole. Specimens figured by Cramer (1971, pl. IV, figs. 75, 81) are similar to those from the Quwarah Member considered here, although apparently larger given the reported dimensions. Cramer (1971) indicated vesicle lengths of 30–50  $\mu\text{m}$  for *L. banderillae*, with process lengths of up to 100  $\mu\text{m}$  and generally about twice the vesicle length. *Leiofusa berneseae* also has an inflated, almost oval vesicle, but has processes of variable length that are generally curved. Measurements of vesicle length provided by Cramer (1971) are 25–45  $\mu\text{m}$ , and process lengths were reported to be between 10% and 200% of vesicle length. Processes on specimens figured by Cramer (1971, pl. III, figs. 55–57, 63, pl. IV, figs. 76–80) are variable in length, although those on the specimen in pl. IV, fig. 80 are relatively long and flexible. Some of these specimens also show an equatorial split.

*Occurrence:* Small leiofusid acritarchs recorded here as *Leiofusa* aff. *tumida* occur in the Quwarah Member (Qasim Formation) in samples from 536.7 ft, 535.2 ft, 528.3 ft, 518.5 ft, 507.15 ft, 503.1 ft, 497.8 ft and 488.3 ft, but are uncommon ( $\leq 1.0\%$  of counted specimens).

Genus *Leprotolypa* Colbath, 1979

*Type species:* *Leprotolypa evexa* Colbath, 1979, by original designation.

*Leprotolypa evexa* Colbath, 1979 (Plate IV, 2)

1979 *Leptolypha evexa* Colbath, pp. 16–17, pl. 6, figs. 1–3, 5.

*Description:* The vesicle is subcircular in outline, and the vesicle wall is relatively thin but has a wrinkled appearance. The processes are stout, hollow, simple, and cylindrical to conical, with evexate distal terminations and angular contacts with the vesicle. They communicate freely with the vesicle cavity. The process walls are thin and usually bear faint striae parallel to the process length, especially on the proximal parts of the processes. In some cases, they might also appear faintly granulate.

*Dimensions* (10 specimens):

Vesicle diameter: 15–31  $\mu\text{m}$  (mean 22.6  $\mu\text{m}$ , median 22.5  $\mu\text{m}$ ).

Process length: 8–28  $\mu\text{m}$  (mean 17.9  $\mu\text{m}$ , median 18  $\mu\text{m}$ ).

Process width (base): 3–6  $\mu\text{m}$  (mean 4.3  $\mu\text{m}$ , median 4  $\mu\text{m}$ ).

Process length/vesicle diameter: 0.53–1.12 (mean 0.79, median 0.82).

Process number: 3–7 (mean and median 5).

*Comparison:* The original description of *Leptolypha evexa* was based on 11 specimens. The wrinkled appearance of the vesicle wall and the stout, broad-based, bluntly rounded processes are characteristic of the species. Some specimens from the Quwarah Member fall within the range of variation recorded by Colbath (1979) for the type material (vesicle diameter: 17–25  $\mu\text{m}$ , mean 21  $\mu\text{m}$ ; process length: 8–15  $\mu\text{m}$ ; process width (base): 2–4  $\mu\text{m}$ ; process length/vesicle diameter: approximately 0.5; process number: 5–11, mean 8). The Quwarah specimens have, on average, fewer processes than the type material, although with some overlap. Colbath (1979) reported process length of the type material to be roughly half of the vesicle diameter, whereas the processes on some Quwarah specimens are greater than the vesicle diameter. The basal widths of the processes on the type material, 2–4  $\mu\text{m}$ , also tend to be narrower than those of the Quwarah specimens, although they overlap. Finally, the process

walls of at least some of the Quwarah specimens appear to be faintly striate rather than granulate, although in some instances faint grana were also observed. Given that some Quwarah specimens fall within the range of variation reported for the type material, none of these differences is considered to be significant. They most probably reflect morphological variation within a single taxon.

*Occurrence:* *Leprotolypa evexa* was recorded from the lower interval of the Quwarah Member, the basal disrupted facies of the Sarah Formation, the Baq'a Shale Member, and the Qusaiba Member of the Qalibah Formation.

Genus *Lophosphaeridium* Timofeev, 1959 ex Downie, 1963 emend. Lister, 1970

*Lophosphaeridium?* sp. 1 (Plate VI, 2–4)

*Description:* The vesicle is generally oval, rarely subcircular in outline and is inferred to have been originally spherical. It has a relatively thick wall and bears an ornament of closely spaced, coarse grana. Many of the grana have a shallow pit or dimple on their top surface, giving them a crater-like appearance.

*Dimensions* (15 specimens):

Vesicle diameter (longer dimension): 34–58  $\mu\text{m}$  (mean 45.1  $\mu\text{m}$ , median 45  $\mu\text{m}$ ).

Vesicle diameter (shorter dimension): 27–55  $\mu\text{m}$  (mean 39.3  $\mu\text{m}$ , median 37  $\mu\text{m}$ ).

Ornament height: 0.5–1.5  $\mu\text{m}$  (mean 1.2  $\mu\text{m}$ , median 1.3  $\mu\text{m}$ ).

Ornament width: 1–2  $\mu\text{m}$  (mean 1.5  $\mu\text{m}$ , median 1.8  $\mu\text{m}$ ).

*Remarks:* The coarseness of the grana and the presence of pits on their summits are characteristic of these specimens.

*Occurrence:* Twenty specimens of this distinctive form were recorded from the Quwarah Member at 551.0 ft, 536.7 ft, 535.2 ft, 528.3 ft, 507.15 ft, 503.1 ft, 497.8 ft and 488.3 ft.

Genus *Nexosarium* Turner, 1984

*Type species:* *Nexosarium parvum* Turner, 1984.

*Nexosarium mansouri* sp. nov. (Plate XIV, 4–6)

*Derivation of name:* In honour of Mansour Al-Ruwaili, for his contributions to Saudi Arabian palynology.

*Type locality:* Qusaiba-1 core hole, Qusaiba, central Saudi Arabia.

*Stratum typicum:* Qusaiba Member of the Qalibah Formation, core 27, 256.4–255.75 ft, earliest Rhuddanian.

*Holotype:* Qusaiba-1, Qusaiba Member, Qalibah Formation, core 27, 256.4 ft, slide 64376, England Finder co-ordinates P45/1 (Plate XIV, 4), LPB 13202. Rhuddanian.

*Paratypes:* Qusaiba-1, Qusaiba Member, Qalibah Formation, core 27, 255.75 ft, slide 64379, England Finder co-ordinates O39, J56/1 (Plate XIV, 5–6), LPB 13201.

*Diagnosis:* Vesicle circular in outline, with 12–18 slender processes, simple or multifurcate, clearly differentiated from the vesicle. Processes are plugged for a short distance above the vesicle surface and so do not communicate with the vesicle interior. The distal surfaces of the plugs form concave depressions. Vesicle wall granulate to granulo-reticulate.

*Dimensions* (15 specimens):

Vesicle diameter: 19–24  $\mu\text{m}$ .

Process length: 8–12  $\mu\text{m}$ .

Process width: 1.5  $\mu\text{m}$ .

*Comparison:* This species has characteristics of the genus *Nexosarium*, which is, by definition, differentiated from the genus *Oppilatala* by the absence of a constriction at the base of the processes and the lack of a double-layered vesicle wall. The type species, *Nexosarium parvum*, has a similar vesicle ornament and heteromorphic processes, but *Nexosarium mansouri* has more numerous and shorter processes. Branches are only in the distal part of the processes. Some specimens illustrated as *Oppilatala cf. frondis* by Dufka and Fatka (1993), from the Rhuddanian of Bohemia, are similar to the material found here, but the poor preservation of the Bohemian specimens makes it difficult to determine whether they might be conspecific.

*Remarks:* The genus *Nexosarium* was described from the Caradoc Series (Sandbian to Katian stages) of Great Britain (Turner, 1984), but is also found in the Katian of the Baltic area (Le Hérissé, unpublished). We propose an extension of the range of the genus into the basal Silurian with the creation of this new species.

*Occurrence:* Qusaiba Member of the Qalibah Formation, core 27, 256.4–255.75 ft, earliest Rhuddanian.

Genus *Orthosphaeridium* Eisenack, 1968

*Type species:* *Orthosphaeridium rectangulare* (Eisenack, 1963) Eisenack, 1968, by original designation.

*Orthosphaeridium orthogonium* sp. nov. (Plate X, 1–2)

*Derivation of name:* Latin *orthogonium*, rectangle, referring to the elongate rectangular outline of the vesicle.

*Type locality:* Qusaiba-1 core hole, Qusaiba, central Saudi Arabia.

*Stratum typicum:* Quwarah Member of the Qasim Formation, cores 49 to 55, 536.7–476.7 ft, Late Ordovician, late Katian–early Hirnantian.

*Holotype:* Qusaiba-1, Quwarah Member, Qasim Formation, core 52, 503.1 ft, slide 64197, England Finder co-ordinate K34/2 (Plate X, 1), LPB 13222. Late Katian–early Hirnantian.

*Paratype:* Qusaiba-1, Quwarah Member, Qasim Formation, core 52, 503.1 ft, slide 64197 England Finder co-ordinate K55 (Plate X, 2), LPB 13222. Late Katian–early Hirnantian.

*Diagnosis:* Vesicle inflated, subrectangular in outline, with 10–12 processes, of which four primary processes lie in the plane of the central body and others, variable in length, arise from the faces. The processes are subcylindrical with acuminate tips. They do not communicate with the central body, but are closed by a solid plug that extends a short distance above the base. The vesicle wall is psilate, and the process walls are psilate or covered by small grana. Excystment is by median splitting of the vesicle into subequal hemicysts.

*Dimensions* (25 specimens):

Vesicle length: 67–75  $\mu\text{m}$  (mean 71  $\mu\text{m}$ ).

Vesicle width: 39–42  $\mu\text{m}$  (mean 40  $\mu\text{m}$ ).

Process length: 44–55  $\mu\text{m}$  (mean 49  $\mu\text{m}$ ).

*Remarks:* *Orthosphaeridium orthogonium* sp. nov. differs from *O. octospinosum* Eisenack, 1968, in having a central body of greater length and proportionally shorter processes. It differs also in having more secondary processes arising from the faces of the vesicle.

*Occurrence:* Qasim Formation, Quwarah Member: 536.7 ft, 528.3 ft, 518.5 ft, 503.1 ft, 497.8 ft, 484.7 ft and 476.7 ft. Sarah Formation, basal disrupted facies: 458.4 ft and 436.0 ft. Sarah Formation, Baq'a Shale Member: 310.2 ft, 307.7 ft and 305.0 ft. Occurrences in the Baq'a



Shale Member and basal disrupted facies of the Sarah Formation might be due to reworking, and especially so in the Baq'a Shale Member. See discussion of reworking above.

Genus *Pirea* Vavrdová, 1972

*Type species: Pirea dubia* Vavrdová, 1972, by original designation.

*Pirea?* sp. 1 (Plate IV, 7; Plate V, 7)

*Description:* Vesicle large, elongate, cylindrical, with convex rounded base and straight to slightly convex sides. The vesicle narrows towards the apex, extending through a short neck into an expanded distal termination. At its tip, the distal expansion appears either to be open (e.g. Plate IV, 7) or to have a much thinner wall. Otherwise, the wall of the vesicle, neck and lower part of the distal expansion is relatively thick and shagrinated.

*Dimensions* (7 specimens):

Overall length: 80–173  $\mu\text{m}$  (mean 112.6  $\mu\text{m}$ , median 114.5  $\mu\text{m}$ ).

Vesicle width: 29–45  $\mu\text{m}$  (mean 32.7  $\mu\text{m}$ , median 30.5  $\mu\text{m}$ ).

Neck width: 6–12  $\mu\text{m}$  (mean 8.9  $\mu\text{m}$ , median 9  $\mu\text{m}$ ).

Distal termination width: 7–15  $\mu\text{m}$  (mean 11.5  $\mu\text{m}$ , median 11.2  $\mu\text{m}$ ).

*Comparison:* The specimens resemble *Pirea* in general morphology, but are characterized and possibly distinguished from that genus by their large size and the thin-walled and possibly open distal termination.

*Occurrence:* Quwarah Member at 551.0 ft, 488.3 ft and 484.7 ft ; the basal disrupted facies of the Sarah Formation at 438.7 ft; and the Baq'a Shale Member at 335.7 ft and 333.4 ft.

Genus *Striatotheca* Burmann, 1970

*Type species: Striatotheca principalis* Burmann, 1970, by original designation.

*Striatotheca aff. monorugulata* Yin, Di Milia and Tongiorgi, 1998 (Plate II, 5, 8–9, 11–12)

aff. 1998 *Striatotheca monorugulata* Yin, Di Milia and Tongiorgi, pp. 241–242, pl. IV, figs. 7, 8, pl. V, fig. 5, pl. VI, figs. 2, 3.

aff. 2000 *Striatotheca monorugulata* Yin, Di Milia and Tongiorgi; Quintavalle, Tongiorgi and Gaetani, pl. 3, fig. 3.

aff. 2003 *Striatotheca monorugulata* Yin, Di Milia and Tongiorgi; Tongiorgi, Yin and Di Milia, p. 120, pl. 36, figs. 1, 4.

*Description:* The vesicle is quadrangular and usually elongate in outline, with a relatively thin wall. The shorter sides of the vesicle are more or less straight. The longer sides are generally concave, although this might be a function of preservation. The vesicle surface is ornamented by one or two closely spaced striae that are parallel to and close to the sides of the vesicle, forming a quadrangular pattern just inside the edge of the vesicle. The corners of the vesicle extend into low conical projections, generally with rounded distal terminations, and sometimes these extend into short hollow processes that have more acuminate distal terminations and communicate with the vesicle cavity.

*Dimensions* (8 specimens):

Vesicle length: 23–29  $\mu\text{m}$  (mean and median 26  $\mu\text{m}$ ).

Vesicle width: 12–26  $\mu\text{m}$  (mean 17.3  $\mu\text{m}$ ; median 16.5  $\mu\text{m}$ ).

Height of conical projections at vesicle corners: 1.5–2.5  $\mu\text{m}$  (mean and median 2  $\mu\text{m}$ ).

*Comparison:* The striations on the vesicle surface are very similar to those of *Striatotheca monorugulata* Yin et al., 1998, in terms of their number and distribution. Unlike the Quwarah specimens, however, *S. monorugulata* has distinct processes, one at each corner, reported by Yin et al. (1998) to range from about a third up to almost equal to the length of the longer vesicle dimension (Fig. 6). Processes on the holotype of *S. monorugulata* are 9.9–10.4  $\mu\text{m}$  long, and those of the paratypes are 14.5–16.2  $\mu\text{m}$  and 9.8–11.6  $\mu\text{m}$ . Process lengths among the population containing the type specimens range from 5.6  $\mu\text{m}$  to 17.3  $\mu\text{m}$ , with a mean of 10.5  $\mu\text{m}$ . Tongiorgi et al. (2003) recorded process lengths of *S. monorugulata* ranging from 3.5  $\mu\text{m}$  to 17.5  $\mu\text{m}$ . The lack of such processes distinguishes the Quwarah specimens from *Striatotheca monorugulata* s. s., and the distinction makes it very unlikely that the Quwarah specimens are conspecific with *S. monorugulata*.

*Occurrence:* This morphospecies is rare in the Quwarah Member. Only eight specimens were recorded, from 551.0 ft, 536.7 ft, 535.2 ft, 528.3 ft and 488.3 ft.

*Striatotheca monorugulata* has been recorded from the Lower–Middle Ordovician of South China and Pakistan. It ranges from the *Didymograptus deflexus* Graptolite Biozone (late Floian, early mid-Arenig) to the *Undulograptus austrodentatus* Graptolite Biozone (early Darriwilian, late Arenig) in South China (Yin et al., 1998; Tongiorgi et al., 2003; Yan et al., 2011) and from the *Azygograptus suecicus* Graptolite Biozone (late Floian, late mid-Arenig) to the *austrodentatus* Biozone in Pakistan (Quintavalle et al., 2000).

Genus *Tunisphaeridium* Deunff and Evitt, 1968

*Type species: Tunisphaeridium tentaculaferum* (Martin, 1967) Cramer, 1971, originally designated as *Tunisphaeridium concentricum* Deunff and Evitt, 1968 (junior synonym of *T. tentaculaferum* according to Eisenack et al., 1973, p. 1057–1059).

***Tunisphaeridium bicaudatum*** sp. nov. (Plate VII, 1–2, 4)

*Derivation of name:* Latin *bi-*, two, and *caudatum*, tail, referring to the twin ‘tails’ of elongate processes that arise from opposite poles of the vesicle.

*Type locality:* Qusaiba-1 core hole, Qusaiba, central Saudi Arabia.

*Stratum typicum:* Quwarah Member of the Qasim Formation, cores 55 to 50, 536.7–488.3 ft, Late Ordovician, late Katian–early Hirnantian.

*Holotype:* Qusaiba-1, Quwarah Member, Qasim Formation, core 50, 488.3 ft, slide 64143, England Finder co-ordinate W51/3 (Plate VII, 2), LPB 13221. Late Katian–early Hirnantian.

*Paratypes:* Qusaiba-1, Quwarah Member, Qasim Formation, core 50, 488.3 ft, slide 64143, England Finder co-ordinate T43/1 (Plate VII, 1), LPB 13221; core 55, 535.2 ft, slide 64076, England Finder co-ordinate L22/4 (Plate VII, 4), LPB 13229. Late Katian–early Hirnantian.

*Diagnosis:* The vesicle is subcircular in outline and inferred to have been originally spherical, with a thin, smooth wall. The vesicle bears numerous, rod-like, solid processes that are expanded or capitate at their distal tips and are joined distally by thin filaments or a thin diaphanous membrane. Much longer processes are present at opposite poles of the vesicle, and in some instances, these appear to be enclosed within a thin diaphanous membrane. The presence of groups of longer processes at opposite poles of the vesicle is diagnostic of the species.

*Dimensions* (based on 6 specimens):

Vesicle diameter: 18–32  $\mu\text{m}$  (mean 23  $\mu\text{m}$ , median 22.5  $\mu\text{m}$ ).

Process length: 4.5–11.5  $\mu\text{m}$  (mean 6.9  $\mu\text{m}$ , median 6.3  $\mu\text{m}$ ).

Polar process length: 18–54  $\mu\text{m}$  (mean 29.7  $\mu\text{m}$ , median 20.5  $\mu\text{m}$ ).

*Comparison:* This form is comparable to *Tunisphaeridium caudatum* Deunff and Evitt, 1968, in terms of vesicle size and in having numerous slender, wiry, rod-like, apparently solid processes, the distal terminations of which are evidently connected by a diaphanous membrane and/or filaments. *Tunisphaeridium caudatum* is distinguished by a single process or a small group of neighbouring processes that are conspicuously longer than the rest, but the specimens from the Quwarah Member have two such groups of longer processes arising from opposite poles of the vesicle.

*Tunisphaeridium bicaudatum* sp. nov. also resembles the genus *Carminella* Cramer, 1968, particularly the type species, *C. maplewoodensis* Cramer, 1968. Points of similarity include the slender, wiry processes that increase in length at opposite poles and their possible enclosure within a membrane. The longer processes at each pole, in particular, seem to support a membrane that is stretched between them. The enveloping membrane is much better developed in *Carminella*, however, and the shorter processes on the figured specimens (Plate VII, 1–2, 4) all appear to be connected distally by filaments, which is a characteristic of *Tunisphaeridium* rather than *Carminella*.

*Occurrence:* This form is rare in the Quwarah Member. Seven specimens were recorded from 536.7 ft, 535.2 ft and 488.3 ft. They are most numerous in the highest sample.

Genus *Veryhachium* Deunff, 1954

*Type species:* *Veryhachium trisulcum* (Deunff, 1951) ex Deunff, 1959. Subsequent designation by Downie (1959).

*Veryhachium cf. elongatum* Downie, 1963 (Plate III, 1–2, 4)

cf. 1963 *Veryhachium elongatum* Downie, p. 637, pl. 92, fig. 10.

*Description:* The vesicle is small and triangular, but distinctly elongate. The longer vesicle sides tend to be convex, and the shorter side straight to concave. A single long, narrow, flexible process arises gradually from each corner, and tapers to a simple acuminate tip. The processes are hollow and in communication with the vesicle cavity. The vesicle and processes are unornamented.

*Dimensions* (22 specimens):

Vesicle length: 15–20  $\mu\text{m}$  (mean 17.4  $\mu\text{m}$ , median 17.5  $\mu\text{m}$ ).

Vesicle width: 10–15  $\mu\text{m}$  (mean 11.9  $\mu\text{m}$ , median 11.5  $\mu\text{m}$ ).

Vesicle length:vesicle width: 1.15–1.82 (mean 1.48, median 1.46).

Process length: 16–45  $\mu\text{m}$  (mean 29.2  $\mu\text{m}$ , median 26.5  $\mu\text{m}$ ).

Process length/vesicle length: 1.00–2.65 (mean 1.68, median 1.52).

*Remarks:* This form is characterized by its small, triangular but elongate vesicle and its long processes. A histogram of process length/vesicle diameter ratios, however, reveals a possible further differentiation into forms with ratios of between 1 and 2, and those with ratios  $>2$  (Fig. 7). Bivariate plots of process length against vesicle length also show two distinct categories (Fig. 8). Given that only 22 specimens were measured, this could be an artefact of the data. Nevertheless, within this limited data set, individual samples are characterized by forms with process length/vesicle diameter ratios of  $<2$  or  $>2$ . For example, all the specimens measured from 536.7 ft, 528.3 ft and 488.3 ft, and three of the four specimens measured from 507.15 ft, have process length/vesicle diameter ratios of  $<1.66$ . Conversely, all the specimens measured from 503.1 ft and four of the five specimens measured from 535.2 ft have ratios  $>2$ , and the

fifth specimen from 535.2 ft has a ratio of 1.73. While we cannot draw any conclusions from this, it is nevertheless an observation worth recording as it might signal systematic variation in process length/vesicle diameter ratios through the member, perhaps in response to fluctuating palaeoenvironmental conditions.

*Comparison:* The forms recorded from the Quwarah Member are larger than the specimens of *Veryhachium elongatum* recorded by Downie (1963) from the lower Wenlock Series (Silurian) of the Welsh Borderland in the U.K. Downie (1963) recorded vesicle lengths of 10–16  $\mu\text{m}$ , with a mean of 10  $\mu\text{m}$ , and vesicle widths of 4–7  $\mu\text{m}$ . He also reported the vesicle length to be about three times the width, which is greater than the ratio for specimens from the Quwarah Member. The small size and elongate triangular vesicle of the specimens from the Quwarah Member are comparable with *V. elongatum*, as is the process length/vesicle length ratio, which Downie (1963) reported to be between 1.0 and 2.5 for his specimens.

*Occurrence:* Quwarah Member, Qasim Formation. *Veryhachium cf. elongatum* forms between 0.7% and 3.6% of counted specimens in samples from 536.7 ft, 535.2 ft, 528.3 ft, 518.5 ft, 507.15 ft, 503.1 ft, 497.8 ft and 488.3 ft. The highest percentages, respectively 3.0% and 3.6% are from the lowest two samples in this range at 536.7 ft and 535.2 ft. No specimens were recorded from the lowermost sample in Qusaiba-1, from 551.0 ft.

*Veryhachium oklahomense* Loeblich, 1970 (Plate II, 1–3)

1970 *Veryhachium oklahomense* Loeblich, pp. 742–743, fig. 36F, G.

*Description:* Veryhachid acritarchs with small (usually  $<20 \mu\text{m}$ ), quadrangular, generally rectangular, thin-walled and smooth vesicles, and four long, thin, flexible, simple and unornamented processes, one arising from each corner of the vesicle. The processes have

acuminate or evexate distal tips. They are hollow, at least proximally, and communicate with the vesicle cavity.

*Dimensions* (28 specimens):

Vesicle length: 12–18  $\mu\text{m}$  (mean 15.6  $\mu\text{m}$ , median 16  $\mu\text{m}$ ).

Vesicle width: 9–15  $\mu\text{m}$  (mean and median 12.5  $\mu\text{m}$ ).

Vesicle length/width: 1–1.6 (mean and median 1.26).

Process length: 10–45  $\mu\text{m}$  (mean 26.6  $\mu\text{m}$ , median 27  $\mu\text{m}$ ).

Process length/vesicle length: 0.71–2.92 (mean 1.71, median 1.66).

*Remarks:* The combination of small vesicle size and long flexible processes is characteristic of this veryhachid morphospecies.

*Comparison:* Similar forms have been referred in the literature to *Veryhachium oklahomense* Loeblich, 1970. Turner (1984), for example, recorded specimens with vesicle dimensions of 9–20  $\times$  9–16  $\mu\text{m}$  (mean 14  $\times$  12  $\mu\text{m}$ ) and process lengths of 18–33  $\mu\text{m}$  (mean 26  $\mu\text{m}$ ) from the type Caradoc Series in Shropshire, England, as *V. oklahomense*. Molyneux (1988) assigned similarly small, rectangular forms with long flexible processes from the Upper Ordovician of northeast Libya, with vesicle dimensions of 12–24  $\times$  12–20  $\mu\text{m}$  (mean 18  $\times$  15  $\mu\text{m}$ ) and process lengths of 20–48  $\mu\text{m}$  (mean 35  $\mu\text{m}$ ), to the same species. These specimens fall within the range of variation seen in the Quwarah Member (Fig. 9). Playford and Wicander (2006), however, considered the records of *V. oklahomense* by Turner (1984) and Molyneux (1988) to be “...almost certainly misidentifications, mainly due to their appreciably greater process length/vesicle diameter ratio”.

The original description of *Veryhachium oklahomense* Loeblich, 1970, records it as having relatively long, thin, flexible processes, a vesicle diameter of 16–22  $\mu\text{m}$ , and an overall diameter of 61–84  $\mu\text{m}$ . The holotype and paratype of *Veryhachium oklahomense* Loeblich, 1970, both have larger vesicles than the specimens recorded from the Quwarah Member,



measured from the illustrations in Loeblich (1970) as  $25 \times 19 \mu\text{m}$  and  $29 \times 29 \mu\text{m}$  respectively (longer dimensions plotted in Fig. 9). The process lengths, however, fall within the range of variation recorded for the Quwarah specimens,  $28 \mu\text{m}$  for the holotype and  $33 \mu\text{m}$  for the paratype (Fig. 9), but the vesicle dimensions of the type material means that their processes are relatively short compared with the Quwarah specimens.

Playford and Wicander (2006) recorded vesicle lengths of  $17\text{--}28 \mu\text{m}$  (mean  $22 \mu\text{m}$ ), process lengths of  $15\text{--}31 \mu\text{m}$  (mean  $22 \mu\text{m}$ ) (Fig. 9), and process length/vesicle diameter ratios of  $0.7\text{--}1.1$ . They also described the processes as being spine-like and straight or curved, although their illustrations show them as being perhaps more flexible. Although some of the specimens recorded from the Quwarah Member have greater process length/vesicle diameter ratios than the ratios of  $0.7\text{--}1.1$  reported by Playford and Wicander (2006), and the Quwarah mean and median ratios are both outside the range reported by those authors, there is nevertheless some overlap between the Quwarah population and Playford and Wicander's (2006) specimens.

*Veryhachium longispinosum* Jardiné et al. (1974) is also comparable with the Quwarah specimens in the sense that it has a quadrangular vesicle with relatively long processes, but is larger. The type material of *V. longispinosum* Jardiné et al. (1974) has vesicle dimensions of  $25\text{--}40 \mu\text{m}$  and process lengths of  $50\text{--}65 \mu\text{m}$ . Turner (1984) recorded specimens of *V. longispinosum* with vesicle dimensions of  $32 \times 26 \mu\text{m}$  and process lengths of  $50 \mu\text{m}$ , and  $22 \times 20 \mu\text{m}$  with process lengths of  $80 \mu\text{m}$  (Fig. 9).

*Occurrence:* Small quadrangular veryhachid acritarchs with long flexible processes, assigned here to *Veryhachium oklahomense*, are common in the Quwarah Member. They range from 5.9% to 11.5% of counted specimens in samples from 551.0 ft, 536.7 ft, 535.2 ft, 528.3 ft, 507.15 ft, 503.1 ft and 488.3 ft. *Veryhachium oklahomense* is present throughout the Quwarah

Member, and is also found in the basal disrupted facies and the Baq'a Shale Member of the Sarah Formation.

### Notes on other figured specimens

#### *Actinotodissus* spp. (Plate I, 1, 4)

Two specimens assigned to *Actinotodissus* are figured. One specimen (Plate I, 1) has a thin-walled vesicle with straight to slightly convex sides along its length, and more or less straight vesicle sides between the process bases, giving it an elongate, subpolygonal outline. The processes are long, slender, tapering and flexible, with narrow bases, angular contacts with the vesicle, and evexate distal terminations. They are hollow and in communication with the vesicle cavity. Nine processes are present at one pole, and fifteen at the other. The vesicle and process walls are smooth, apart from six faint, widely spaced striae that are subparallel to the long axis of the vesicle. The vesicle is 35  $\mu\text{m}$  long  $\times$  25  $\mu\text{m}$  wide; processes are 21–24  $\mu\text{m}$  long. The specimen is slightly larger and more elongate than the type material of *Actinotodissus crassus* Loeblich and Tappan, 1978, but is otherwise comparable.

The second specimen (Plate I, 4) has a large, quadrate vesicle with straight to slightly convex sides, including the lengths between the process bases at the poles. The processes taper from wide bases to acuminate or evexate tips, and are slightly flexible, with angular to curved contacts with vesicle. They are hollow and in communication with the vesicle cavity. There are nine processes at one pole, and ten at the other. Faint spaced striae are present on the surface of the vesicle, subparallel to the long axis. Vesicle and processes bear an ornament of fine grana. The vesicle is 41  $\mu\text{m}$  long  $\times$  35  $\mu\text{m}$  wide; processes are 28–34  $\mu\text{m}$  long. This specimen is much larger than described species of *Actinotodissus*, particularly *A.*

*longitaleosus* Loeblich and Tappan, 1978, which was distinguished from *A. crassus* on the basis of its granulate ornament.

***Comasphaeridium* spp.** (Plate IV, 1, 6)

Two specimens are figured. One (Plate IV, 1) has a vesicle that is ovate to elliptical in outline. The vesicle is hollow, with a relatively thin, folded wall, and bears an ornament of short, very densely and uniformly distributed hairs that are possibly capitate, possibly solid, and are flexible and parallel-sided. The vesicle diameter is  $53 \times 41 \mu\text{m}$  and the ornament height  $<2 \mu\text{m}$ . The second specimen (Plate IV, 6) is similar, but is smaller and has a correspondingly finer ornament. Its vesicle diameter is  $38 \times 29 \mu\text{m}$ , and its ornament height is c.  $1 \mu\text{m}$ .

***Dactylofusa cucurbita*** Jardiné et al., 1974 (Plate VIII, 1–2)

*Dactylofusa cucurbita* is characterized by its large, aligned, irregularly spaced tubercles, which are evident on this specimen.

***Dactylofusa striatogranulata*** Jardiné et al., 1974 (Plate VIII, 5–7)

Jardiné et al. (1974) described *Dactylofusa striatogranulata* as having a fusiform vesicle with pointed ends and an ornament of longitudinal striae formed by the alignment of closely spaced grana. Specimens recorded have rounded rather than pointed ends. *Eupoikilofusa rochesterensis* Cramer, 1971, is similar in that the central part of its elongately fusiform vesicle is covered by stout, digitate sculptural elements, aligned roughly parallel to the long axis of the vesicle, but the wall becomes smooth towards the poles through a transition zone.

***Dictyotidium* sp.** (Plate VI, 1)

The vesicle is interpreted as being originally spherical, and is now subcircular in outline and hollow, with a relatively thick wall that is covered by a network comprising small polygonal fields. The polygonal fields are generally pentagonal or hexagonal, and are 2–4  $\mu\text{m}$  in diameter. The vesicle diameter is  $42 \times 34 \mu\text{m}$ . The specimen differs from *D. faviforme* Schultz, 1967, in having larger fields, and from *D. stenodictyum* Eisenack, 1965, in lacking larger solid projections at the corners of (some) fields (see Mullins, 2001).

***Helosphaeridium* sp.** (Plate VI, 6)

The vesicle of this specimen is interpreted as being originally spherical, and is subcircular in outline, hollow, and relatively thin-walled. It bears a uniformly and densely distributed ornament of short, stout elements that are nail or stud-like in cross-section with cylindrical stems and a flat distal termination. The vesicle diameter is  $57 \times 47 \mu\text{m}$ , and the ornament is c.  $0.6 \mu\text{m}$  high and  $0.6 \mu\text{m}$  wide. The specimen is similar to *Helosphaeridium citrinipeltatum* Lister, 1970, but is larger and has a relatively smaller ornament. For comparison, *H. citrinipeltatum* has a spherical, hollow, thin-walled vesicle, with a diameter of 30–50  $\mu\text{m}$ , and an ornament of dense, peltate, uniformly distributed, apparently solid elements, up to 2  $\mu\text{m}$  high and equally wide at the base and top.

***Neoveryhachium carminae constricta*** Le Hérissé et al., 1995 (Plate II, 6, 10)

Some specimens of *Neoveryhachium* recorded from the Quwarah Member have the constricted vesicles typical of *N. carminae constricta*. Some of these specimens also appear to be enclosed within a thin membrane.

***Oppilatata* sp.** (Plate VII, 5–6)

A single specimen was recorded. The vesicle is circular in outline, and was probably originally spherical. It has a thick wall with a granulate ornament over most of the surface, but has striae at the base of the processes that radiate away from the process bases. The processes have thinner walls and are hollow, but are plugged at the base or arise from an outer vesicle layer. The process stems are cylindrical and parallel-sided, and have widely diverging branches in their distal third. Branching is irregular to the second order. The final branching is often a bifurcation. Branches taper to acuminate or narrowly rounded tips. The vesicle diameter is c. 28  $\mu\text{m}$ , and processes are c. 22  $\mu\text{m}$  from their contact with the vesicle to the first branches. Branches are c. 12  $\mu\text{m}$  long. There are seven processes.

***Pirea* spp.** (Plate III, 5–6)

In addition to *Pirea?* sp. 1, more typical specimens of *Pirea* were recorded from the Quwarah Member, from the basal disrupted faciés of the Sarah Formation, and from the Baq'a Shale Member. The two specimens figured are both from the Quwarah Member at 488.3 ft. One specimen (Plate III, 5) has a thin-walled, ovoid vesicle with a fine granulate ornament that is distributed uniformly and randomly on the vesicle. The grana diminish towards the process, where longitudinal striations extend from the upper part of the vesicle towards the neck. The process is smooth. There is a slight constriction at the neck, where the vesicle joins the process. The process termination is rounded and capitate. The overall length of this specimen is 47  $\mu\text{m}$ , of which the vesicle length is 40  $\mu\text{m}$  and the process length is 7  $\mu\text{m}$ . The vesicle width is 24  $\mu\text{m}$ , the neck width is 4  $\mu\text{m}$ , and the width of the process tip is 5  $\mu\text{m}$ . The specimen resembles *Pirea ornatissima* Cramer and Díez, 1977, in having an ornament of dense, solid, coarse grana or spines on the 2/3rds of vesicle furthest from process, but reduced or not present adjacent to the process or on the process, and in having a few widely spaced

striations that extend from the process onto the vesicle. Cramer and Díez (1977), however, recorded much greater dimensions for *P. ornatissima* (length: 110–130  $\mu\text{m}$ ).

The second figured specimen (Plate III, 6) has a thin-walled, ovoid vesicle. A fine granulate ornament is distributed uniformly and randomly on the vesicle and extends onto the process, but there are no longitudinal striations and no constriction at the base of the process. The vesicle passes into the process at a slight flexure. The process is rounded distally, but is not capitate. The overall length of the specimen is 52  $\mu\text{m}$ , with a vesicle length of 45  $\mu\text{m}$  and a process length of 7  $\mu\text{m}$ . The vesicle width is 24  $\mu\text{m}$ , the width of the neck, measured at the base of the process is 6  $\mu\text{m}$ , and the process is 4  $\mu\text{m}$  wide at its distal termination.

***Striatotheca* cf. *S. sp. B*** of Molyneux, 1988 (Plate II, 7)

A specimen of *Striatotheca* recorded from 507.15 ft has very fine striations and long flexible processes. The vesicle measures  $22 \times 18 \mu\text{m}$  and the processes are about 23  $\mu\text{m}$  long (i.e. about the same as the maximum vesicle dimension). The specimen resembles *Striatotheca* sp. B of Molyneux (1988), from the Late Ordovician of northeast Libya, which also has fine striations and flexible processes that are approximately equal in length to the vesicle dimensions (*Striatotheca* sp. B, vesicle dimensions:  $18\text{--}20 \times 14\text{--}16 \mu\text{m}$ ; process length 16–20  $\mu\text{m}$ ).

***Veryhachium fakirum?*** Martin, 1969 (Plate V, 5–6; Plate XIII, 2)

Rare specimens resembling *Veryhachium fakirum* Martin, 1969, were recorded from the Quwarah Member at 551.0 ft and 448.3 ft, and are also present in the Baq'a Shale Member (Plate XIII, 2), where they might be reworked. A specimen illustrated from 551.0 ft (Plate V, 5) bears an ornament of short hairs on the vesicle and processes that are apparently distributed

at random, but are actually aligned in indistinct rows subparallel to the sides of the vesicle.

Vesicle dimensions are  $23 \times 19 \mu\text{m}$ , process length is  $10 \mu\text{m}$  and the processes are about  $5 \mu\text{m}$  wide at the base. A second illustrated specimen, from 488.3 ft (Plate V, 6), has relatively long, broad-based, narrowly conical processes, and grana rather than hairs. The specimens resemble *V. fakirum* (vesicle dimensions  $20\text{--}50 \mu\text{m}$ , process length  $13\text{--}22 \mu\text{m}$ , often about  $0.5 \times$  vesicle sides), which also has a vesicle surface and processes covered by hairs (with robust bases and up to  $4 \mu\text{m}$  long). However, the processes of *V. fakirum* are described as having narrow bases and as tapering very gradually to a simple termination, unlike the wider-based processes of these specimens.

#### ***Veryhachium* sp. A** (Plate V, 8)

Large quadrate veryhachids with smooth walls, slightly concave sides and long processes with wide bases that arise gradually from the corners of the vesicle and taper to acuminate or bluntly rounded tips, are present in small numbers in the Quwarah Member at 528.3 ft, 507.15 ft, 503.1 ft and 488.3 ft. The vesicle dimensions of the figured specimen are  $27 \times 24 \mu\text{m}$ , the process length is  $25 \mu\text{m}$  and the process width at the base is  $10 \mu\text{m}$ . For specimens of this type as a whole, the vesicle dimensions are  $19\text{--}27 \times 15\text{--}24 \mu\text{m}$  (mean  $23 \times 19.4 \mu\text{m}$ , median  $23 \times 20 \mu\text{m}$ ), the process length is  $16\text{--}25 \mu\text{m}$  (mean 19, median 18), and the process width (base) is  $4\text{--}10 \mu\text{m}$  (mean  $7 \mu\text{m}$ , median  $6 \mu\text{m}$ ).

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## Figure captions

Fig. 1. Location maps for the Qusaiba-1 core hole. (a) Map of the Arabian Peninsula showing the location of the north-western part of the Buraydah quadrangle in Qasim region, central Saudi Arabia (red box). (b) Geological sketch map of the north-western part of the Buraydah quadrangle, showing location of the Qusaiba-1 core hole. Modified after Zalasiewicz et al. (2007).

Fig. 2. Ranges of acritarchs in the Late Ordovician (Upper Qasim and Sarah formations) and early Silurian, early Rhuddanian (basal Qalibah Formation) succession in the Qusaiba-1 shallow borehole (parts 1 and 2). Reworked Middle Ordovician forms are plotted separately in part 2. It is likely that a number of Late Ordovician taxa are also reworked in the Baq'a Shale Member, but reworking of Late Ordovician forms at this level is not so easy to identify.

Fig. 3. Bivariate plot of vesicle diameter against process length for specimens of *Actipilion druggii* Loeblich, 1970, from the Quwarah Member, Qusaiba-1 (black dots). Also plotted for comparison are dimensions of the holotype and isotypes of *A. druggii*, dimensions of specimens figured by Playford and Wicander (2006), and the dimensions of *Actipilion* cf. *druggii* in Molyneux (1988) from the Late Ordovician of Libya.

Fig. 4. Bivariate plot of overall length against maximum width for specimens identified as *Leiofusa litotes* Loeblich and Tappan, 1978, from the Quwarah Member, Qusaiba-1 (black dots). Also plotted for comparison are the dimensions of two specimens recorded by Loeblich and Tappan (1978), including the holotype, and the mean dimensions of specimens from the Late Ordovician of Libya identified by Molyneux (1988) as *Leiofusa* aff. *litotes* and *Leiofusa* aff. *fusiformis* (Eisenack) Eisenack, 1938.

Fig. 5. Bivariate plot of vesicle length against overall length for specimens identified as *Leiofusa* aff. *tumida* Downie, 1959, from the Quwarah Member, Qusaiba-1 (black dots). Also plotted are the mean dimensions of specimens recorded by Molyneux (1988) from Libya as *Leiofusa* aff. *tumida* Downie 1959.

Fig. 6. Bivariate plots of vesicle length against process length for *Striatotheca monorugulata* Yin et al., 1998, (red dots) and *Striatotheca* aff. *monorugulata* (black dots) from the Quwarah Member in Qusaiba-1. Dimensions of *Striatotheca monorugulata* are from (1) the holotype, (2) the paratypes, (3) the population mean and (4) other figured specimens in Yin et al. (1998), and specimens figured by (5) Quintavalle et al. (2000) and (6) Tongiorgi et al. (2003).

Fig. 7. Histogram and kernel density of process length/vesicle length ratios for *Veryhachium* cf. *elongatum* Downie, 1963, from the Quwarah Member in Qusaiba-1.

Fig. 8. Bivariate plot of vesicle length against process length for *Veryhachium* cf. *elongatum* Downie, 1963, from the Quwarah Member in Qusaiba-1. Specimens with process length/vesicle length ratios of  $>2$  (red dots) are differentiated from those with ratios  $<2$  (black dots).

Fig. 9. Bivariate plot of vesicle length against process length for specimens of *Veryhachium oklahomense* Loeblich, 1970, from the Quwarah Member of Qusaiba-1 (black dots). Also plotted for comparison are the values of vesicle length against process length for the holotype and paratype of *Veryhachium oklahomense* Loeblich, 1970, the mean values of vesicle length against process length for populations of specimens assigned to *V. oklahomense* by Turner



(1984), Molyneux (1988) and Playford and Wicander (2006), and vesicle length against process length for specimens of *Veryhachium longispinosum* Jardiné et al. (1974) recorded by Turner (1984).

### Plate captions

Plate I. Scale bar = 10  $\mu\text{m}$  for Figs. 1–5; 20  $\mu\text{m}$  for Figs. 6–7.

1. *Actinotodissus* cf. *crassus* Loeblich & Tappan, 1978, 536.7 ft, slide 64183, LPB 13230, C19/1.
2. *Leiofusa* aff. *tumida* Downie, 1959, 528.3 ft, slide 64191, LPB 13227, T28/0.
3. *Leiofusa* aff. *tumida* Downie, 1959, 528.3 ft, slide 64191, LPB 13227, O20/2.
4. *Actinotodissus* sp., 503.1 ft, slide 64089, LPB 13223, U40/2.
5. *Leiofusa* aff. *tumida* Downie, 1959, 488.3 ft, slide 64143, LPB 13221, W29/0.
6. *Leiofusa litotes* Loeblich and Tappan, 1978, 528.3 ft, slide 64191, LPB 13227, X36/1.
7. *Leiofusa litotes* Loeblich and Tappan, 1978, 528.3 ft, slide 64191, LPB 13227, N23/0.

Plate II. Scale bar = 10  $\mu\text{m}$ .

1. *Veryhachium oklahomense* Loeblich, 1970, 488.3 ft, slide 64143, LPB 13221, T47/0.
2. *Veryhachium oklahomense* Loeblich, 1970, 528.3 ft, slide 64191, LPB 13227, M39/0-3.
3. *Veryhachium oklahomense* Loeblich, 1970, 528.3 ft, slide 64191, LPB 13227, X35/2.

4. *Veryhachium lairdii* Deflandre ex Loeblich, 1970, 488.3 ft, slide 64143, LPB 13221, S24/3-4.
5. *Striatotheca* aff. *monorugulata* Yin Leiming et al., 1998, 551.0 ft, slide 64068, LPB 13231, N24/1.
6. *Neoveryhachium carminae constricta* Le Hérissé et al., 1995, 488.3 ft, slide 64143, LPB 13221, V38/0.
7. *Striatotheca* aff. *S.* sp. B of Molyneux, 1988, 507.15 ft, slide 64085, LPB 13224, J40/0.
8. *Striatotheca* aff. *monorugulata* Yin Leiming et al., 1998, 488.3 ft, slide 64143, LPB 13221, S25/0-4.
9. *Striatotheca* aff. *monorugulata* Yin Leiming et al., 1998, 528.3 ft, slide 64191, LPB 13227, G45/2-4.
10. *Neoveryhachium carminae constricta* Le Hérissé et al., 1995, 536.7 ft, slide 64183, LPB 13230, T34/0.
11. *Striatotheca* aff. *monorugulata* Yin Leiming et al., 1998, 535.2 ft, slide 64076, LPB 13229, B49/4.
12. *Striatotheca* aff. *monorugulata* Yin Leiming et al., 1998, 536.7 ft, slide 64183, LPB 13230, K19/2.

Plate III. Scale bar = 10  $\mu$ m for Figs. 1–8; 20  $\mu$ m for Figs. 9–11.

1. *Veryhachium* cf. *elongatum* Downie, 1963, 528.3 ft, slide 64191, LPB 13227, O24/0.
2. *Veryhachium* cf. *elongatum* Downie, 1963, 528.3 ft, slide 64191, LPB 13227, O33/3.
3. *Sol?* sp., 488.3 ft, slide 64143, LPB 13221, X22/0-1-3.
4. *Veryhachium* cf. *elongatum* Downie, 1963, 488.3 ft, slide 64143, LPB 13221, R46/4.
5. *Pirea* sp., 488.3 ft, slide 64143, LPB 13221, U46/2.

6. *Pirea* sp., 488.3 ft, slide 64143, LPB 13221, S38/3.
7. *Villosacapsula setosapellicula* (Loeblich) Loeblich and Tappan, 1976, 488.3 ft, slide 64143, LPB 13221, Y42/0.
8. *Villosacapsula setosapellicula* (Loeblich) Loeblich and Tappan, 1976, 507.15 ft, slide 64085, LPB 13224, U38/3.
9. *Fractoricoronula* cf. *trirhetica*? Turner, 1984, 528.3 ft, slide 64191, LPB 13227, R19/1.
10. *Veryhachium subglobosum* Jardiné et al., 1974, 507.15 ft, slide 64085, LPB 13224, P48/1-P47/2.
11. *Dorsennidium hamii* (Loeblich) Sarjeant and Stancliffe, 1994, 536.7 ft, slide 64183, LPB 13230, G45/0.

Plate IV. Scale bar = 10  $\mu$ m for Figs. 1-6, 8-9; 12  $\mu$ m for Fig. 7.

1. *Comasphaeridium* sp., 488.3 ft, slide 64143, LPB 13221, S36/4.
2. *Leptolypha evexa* Colbath, 1979, 535.2 ft, slide 64076, LPB 13229, K20/0.
3. *Ferromia pellita* (Martin) Martin, 1996, 536.7 ft, slide 64183, LPB 13230, M21/4.
4. *Ferromia pellita* (Martin) Martin, 1996, 536.7 ft, slide 64183, LPB 13230, M28/0.
5. *Ferromia pellita* (Martin) Martin, 1996, 528.3 ft, slide 64191, LPB, 13227, K25/2.
6. *Comasphaeridium* sp., 528.3 ft, slide 64191, LPB 13227, E48/4-F48/2.
7. *Pirea*? sp. 1, 488.3 ft, slide 64143, LPB 13221, K42/0.
8. *Actipilion druggii* Loeblich, 1970, 488.3 ft, slide 64143, LPB 13221, X24/0.
9. *Actipilion druggii* Loeblich, 1970, 507.15 ft, slide 64085, LPB 13224, W22/0.

Plate V. Scale bar = 10  $\mu$ m.

1. *Actipilion druggii* Loeblich, 1970, 488.3 ft, slide 64143, LPB 13221, W25/0-4.
2. *Impluviculus?* sp., 535.2 ft, slide 64076, LPB 13229, Y31/4.
3. *Impluviculus?* sp., 536.7 ft, slide 64183, LPB 13230, V19/1.
4. *Impluviculus?* sp., 551.0 ft, slide 64068, LPB 13231, L38/3.
5. *Veryhachium fakirum?* Martin, 1969, 551.0 ft, slide 64068, LPB 13231, J47/2.
6. *Veryhachium fakirum?* Martin, 1969, 488.3 ft, slide 64143, LPB 13221, S18/0-4.
7. *Pirea?* sp. 1, 488.3 ft, slide 64143, LPB 13221, T41/1.
8. *Veryhachium* sp., 488.3 ft, slide 64143, LPB 13221, T48/0.

Plate VI. Scale bar = 10  $\mu$ m.

1. *Dictyotidium* sp., 503.1 ft, slide 64089, LPB 13223, W17/0.
2. *Lophosphaeridium?* sp. 1, 503.1 ft, slide 64089, LPB 13223, E40/0.
3. *Lophosphaeridium?* sp. 1, 536.7 ft, slide 64183, LPB 13220, J45/1.
4. *Lophosphaeridium?* sp. 1, 488.3 ft, slide 64143, LPB 13221, R32/3.
5. *Glyptosphaera?* sp., 535.2 ft, slide 64076, LPB 13229, X33/4.
6. *Helosphaeridium* sp., 528.3 ft, slide 64191, LPB 13228 O21/2.
7. *Glyptosphaera?* sp., 535.2 ft, slide 64076, LPB 13229, J47/0.
8. *Falavia magniretifera* gen. et sp. nov., Holotype, 488.3 ft, slide 64143, LPB 13221, T42/1.
9. *Falavia magniretifera* gen. et sp. nov., Paratype, 503.1 ft, slide 64089, LPB 13223, U39/2-U40/1.

Plate VII. Scale bar = 10  $\mu$ m for Figs. 1–6; approximately 5.6  $\mu$ m for Fig. 6 inset.

1. *Tunisphaeridium bicaudatum* sp. nov., Paratype, 488.3 ft, slide 64143, LPB 13221, T43/1.
2. *Tunisphaeridium bicaudatum* sp. nov., Holotype, 488.3 ft, slide 64143, LPB 13221, W51/3.
3. *Stellechinatum helosum* Turner, 1984, 488.3 ft, slide 64143, LPB 13221, E21/4.
4. *Tunisphaeridium bicaudatum* sp. nov., Paratype, 535.2 ft, slide 64076, LPB 13229, L22/4.
5. *Oppilatala* sp., 503.1 ft, slide 64089, LPB 13223, Q50/0-3.
6. *Oppilatala* sp., 503.1 ft, slide 64089, LPB 13223, Q50/0-3; inset showing details of ornament and striations at base of process.

Plate VIII. Scale bar = 10  $\mu\text{m}$  for Figs. 3–4, 7–8; 20  $\mu\text{m}$  for Fig. 1; approximately 5.6  $\mu\text{m}$  for Figs. 2, 5–6.

1. *Dactylofusa cucurbita* Jardiné et al., 1974, 528.3 ft, slide 64191, LPB 13227, W49/0; box indicates area of Fig. 2.
2. *Dactylofusa cucurbita* Jardiné et al., 1974, 528.3 ft, slide 64191, LPB 13227, W49/0; detail of Fig. 1.
3. *Eupoikilofusa striatifera* (Cramer) Cramer, 1971, 528.3 ft, slide 64191, LPB 13228, X45/0.
4. *Navifusa similis?* (Eisenack) Turner, 1984, 528.3 ft, slide 64191, LPB 13228, F38/4.
5. *Dactylofusa striatogranulata* Jardiné et al., 1974, 488.3 ft, slide 64143, LPB 13221, S43/3-T43/1; detail of Fig. 7.
6. *Dactylofusa striatogranulata* Jardiné et al., 1974, 488.3 ft, slide 64143, LPB 13221, S43/3-T43/1; detail of Fig. 7.

7. *Dactylofusa striatogranulata* Jardiné et al., 1974, 488.3 ft, slide 64143, LPB 13221, S43/3-T43/1; boxes indicate areas of Figs. 5, 6.
8. *Safirotheca safira* Vavrdová, 1989, 535.2 ft, slide 64076, LPB 13229, Z41/0-1.

Plate IX. Scale bar = 10  $\mu\text{m}$  for Figs. 1–4, 6; 15  $\mu\text{m}$  for Fig. 5; 20  $\mu\text{m}$  for Fig. 7.

1. *Petaloferidium* sp. 1, 551.0 ft, slide 64068, LPB 13231, W52/4.
2. *Petaloferidium* sp. 2, 551.0 ft, slide 64068, LPB 13231, C28/2.
3. *Nexosarium parvum* Turner, 1984, 528.3 ft, slide 64081, LPB 13228, M47.
4. *Sylvanidium?* *hawbanense* Miller and Al-Ruwaili, 2007, 551.0 ft slide 64068, LPB 13231, C27.
5. *Ordovicidium* sp., 535.2 ft, slide 64186, LPB 13229, G35/4.
6. *Coenobium* sp. A, 551.0 ft, slide 64068, LPB 13231, J46/1.
7. *Baltisphaeridium ternatum* (Burmam) emend. Rauscher, 1973, 507.15 ft, slide 64193, LPB 13225, P29.

Plate X. Scale bar = 10  $\mu\text{m}$ .

1. *Orthosphaeridium orthogonium* sp. nov., Holotype, 503.1 ft, slide 64197, LPB 13222, K34/2.
2. *Orthosphaeridium orthogonium* sp. nov., Paratype, 503.1 ft, slide 64197, LPB 13222, K55.
3. *Inflatarium trilobatum* gen. et sp. nov., Holotype, 518.5 ft, slide 64036, LPB 13226, G50/3.
4. *Inflatarium trilobatum* gen. et sp. nov., Paratype, 507.15 ft, 64193, LPB 13225, C34/1.

5. *Inflatarium trilobatum* gen. et sp. nov., 518.5 ft, slide 64036, LPB 13226, T57/1.
6. *Inflatarium trilobatum* gen. et sp. nov., 518.5 ft, slide 64036, LPB 13226, H50.
7. *Inflatarium trilobatum* gen. et sp. nov., 503.1 ft, slide 64197, LPB 13222, D40/2.

Plate XI. Scale bar = 10  $\mu\text{m}$  for Figs. 3, 5–7; 15  $\mu\text{m}$  for Fig. 2; 20  $\mu\text{m}$  for Figs. 1, 4.

1. *Eupoikilofusa platynetrella* Loeblich and Tappan, 1978, 436.0 ft, slide 64234, LPB 13217, H47.
2. *Veryhachium mareki* Vavrdová, 1989, 452.75 ft, slide 64228, LPB 13219, F54.
3. *Oppilatala* sp. 1, 438.7 ft, slide 64231, LPB 13218, M26/3.
4. *Aremoricanium squarrosus* Loeblich and MacAdam, 1971, 438.7 ft, slide 64231, LPB 13218, M45/4.
5. *Actinotodissus longitaleosus* Loeblich and Tappan, 1978, 528.3 ft, slide 64081, LPB 13228, U31.
6. *Anomaloplaisium lumariacuspis* Tappan and Loeblich, 1971, 476.7 ft, slide 64034, LPB 13220, N39.
7. *Anomaloplaisium lumariacuspis* Tappan and Loeblich, 1971, 488.3 ft, slide 64143, LPB 13221, R26/1.

Plate XII. Scale bar = 10  $\mu\text{m}$  for Figs. 1–7, 9, 10; 15  $\mu\text{m}$  for Fig. 8.

1. *Virgatasporites rudii* Combaz, 1967, 342.3 ft, slide 64243, LPB 13214, O48.
2. *Stelliferidium* sp., 318.2 ft, slide 64278, LPB 13207, L47/3.
3. *Cheleutochroa gymnobrachiata* Loeblich and Tappan, 1978, 341.0 ft, slide 64246, LPB 13213, N47/2.

4. *Aremoricanium rigaudae* Deunff, 1955, 323.1 ft, slide 64272, LPB 13209, E51.
5. *Peteinosphaeridium* cf. *velatum* Kjellström, 1971 emend. Playford et al., 1995, 345.85 ft, slide 64031, LPB 13215, K26/1.
6. Sphaeromorph with concentric striations in Le Hérisse et al., 2007, 327.9 ft, slide 64028, LPB 13211, G42/4.
7. ?*Clypeolus* sp. A in Le Hérisse et al., 2007, 323.1 ft, slide 64272, LPB 13209, C27/4.
8. *Baltisphaeridium perclarum* Loeblich and Tappan, 1978, 348.8 ft, slide 64240, LPB 13216, B52/4.
9. *Dicrodiacrodium ancoriforme* Burmann, 1968, emend. Servais et al., 1996, 348.8 ft, LPB 13216, slide 64240, N46/1.
10. *Sol* sp. 2. 348.8 ft, slide 64240, LPB 13216, W58/4.

Plate XIII. Scale bar = 10  $\mu$ m.

1. *Arkonina virgata* Burmann, 1970, 335.7 ft, slide 64260, LPB 13212, S28/1.
2. *Veryhachium fakirum*? Martin, 1969, 305.0 ft, slide 64025, LPB 13205, U40/1.
3. *Comasphaeridium* cf. *denseprocessum* Cramer and Diez, 1977, 319.1 ft, slide 64275, LPB 13208, R55/4.
4. *Cymbosphaeridium* sp., 301.1 ft, slide 64367, LPB 13204, F52.
5. *Oppilatala* sp. 2., 294.8 ft, slide 64370, LPB 13203, R40/1.
6. *Leiofusa* sp. A, 307.7 ft, slide 64330, LPB 13206, H42/2.
7. *Frankea longiuscula* Burmann, 1970, 305.0 ft, slide 64025, LPB 13205, V43/1.
8. Abnormal form (teratological case) of a *Veryhachium* sp., 325.4 ft, slide 64269, LPB 13210, Q41/2.



9. *Dorsennidium* sp. 1, 341.0 ft, slide 64246, LPB 13213, H50/4.
10. *Dorsennidium* sp. 1, 341.0 ft, slide 64246, LPB 13213 P46.
11. *Striatotheca quieta* (Martin) Rauscher, 1973, 348.8 ft, slide 64240, LPB 13216, D43/2.

Plate XIV. Scale bar = 10  $\mu$ m for Figs 1–6, 8; 15  $\mu$ m for Figs 7, 9–11.

1. *Dorsennidium polorum* Miller and Eames, 1982, comb. nov., 256.4 ft, slide 64376, LPB 13202, M27/3.
2. *Dorsennidium polorum* Miller and Eames, 1982, comb., nov., 254.8 ft, slide 64022, LPB 13200, K31/4.
3. *Multiplicisphaeridium raspum* (Cramer, 1964b) Eisenack et al., 1973, 256.4 ft, slide 64376, LPB 13202, F30/4.
4. *Nexosarium mansouri* sp. nov., Holotype, 256.4 ft, slide 64376, LPB 13202, P45/1.
5. *Nexosarium mansouri* sp. nov., Paratype, 255.75 ft, slide 64379, LPB 13201, O39.
6. *Nexosarium mansouri* sp. nov., Paratype, 255.75 ft, slide 64379, LPB 13201, J56/1.
7. *Leiosphaeridia* cf. *acerscrabella* Johnson, 1985, 256.4 ft, slide 64376, LPB 13202, J46/2.
8. *Salopidium* sp., 256.4 ft, slide 64376, LPB 13202, D40/3.
9. *Hoegklintia* aff. *H. digitata* (Eisenack, 1938) Dorning, 1981, 256.4 ft, slide 64376, LPB 13202, F50.
10. *Leiofusa* sp. B, 256.4 ft, slide 64376, LPB 13202, L38/3.
11. *Leiofusa* sp. C, 256.4 ft, slide 64376, LPB 13202, P29.

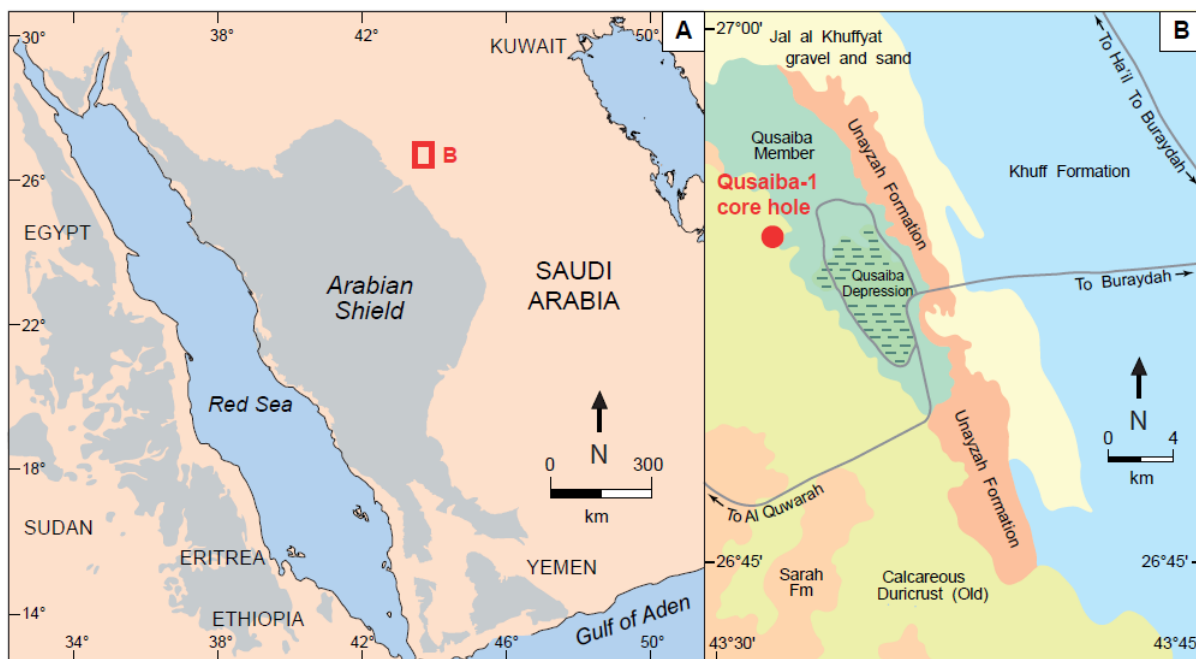


Figure 1

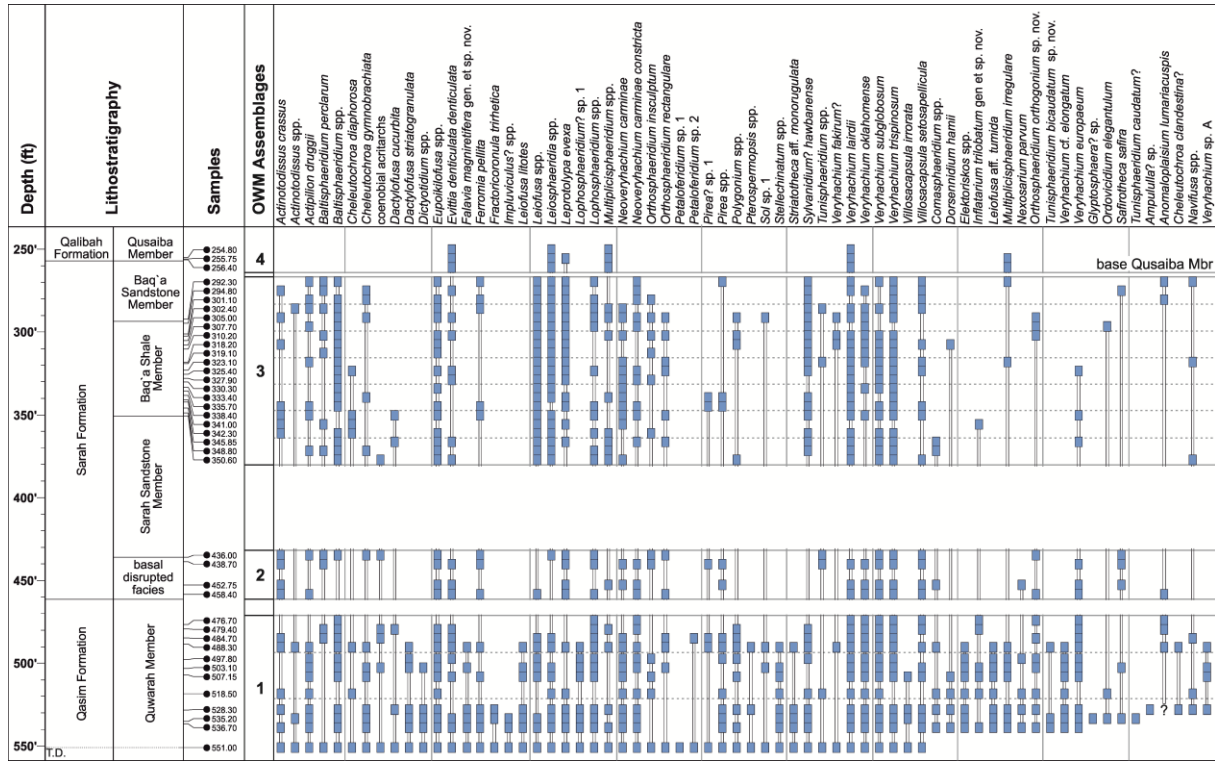


Figure 2i

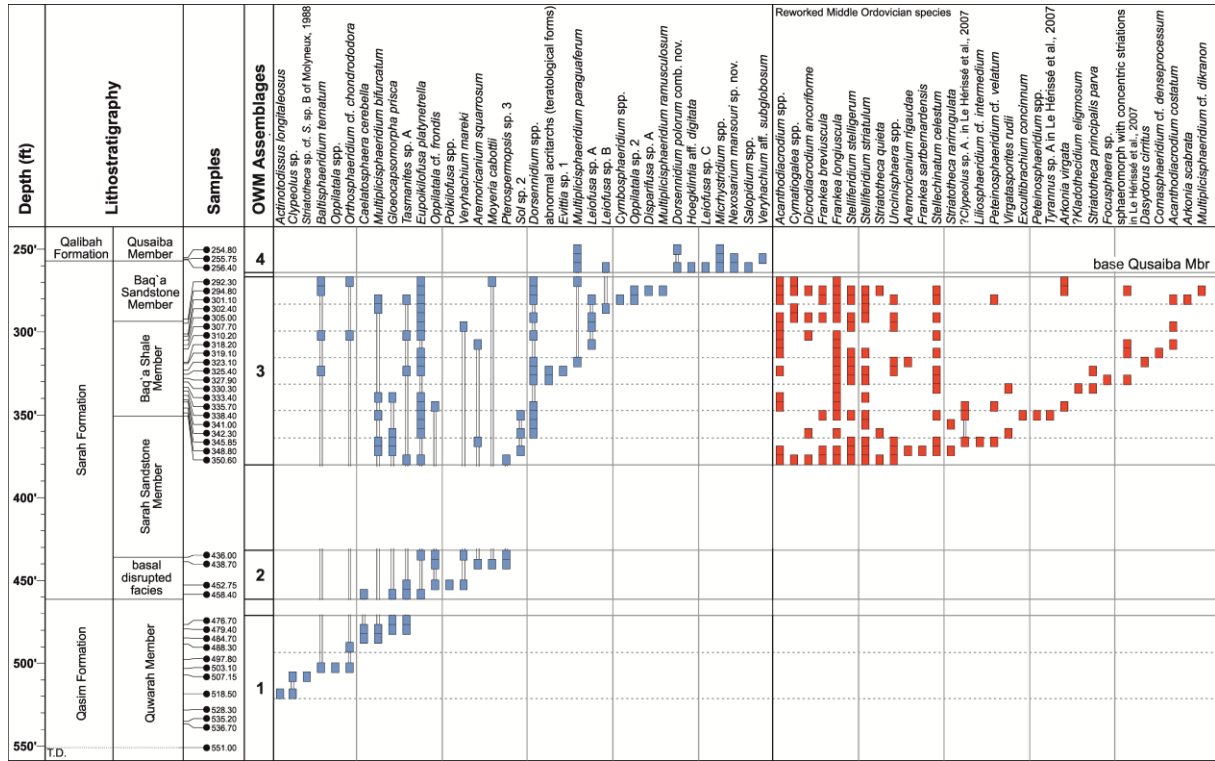


Figure 2ii

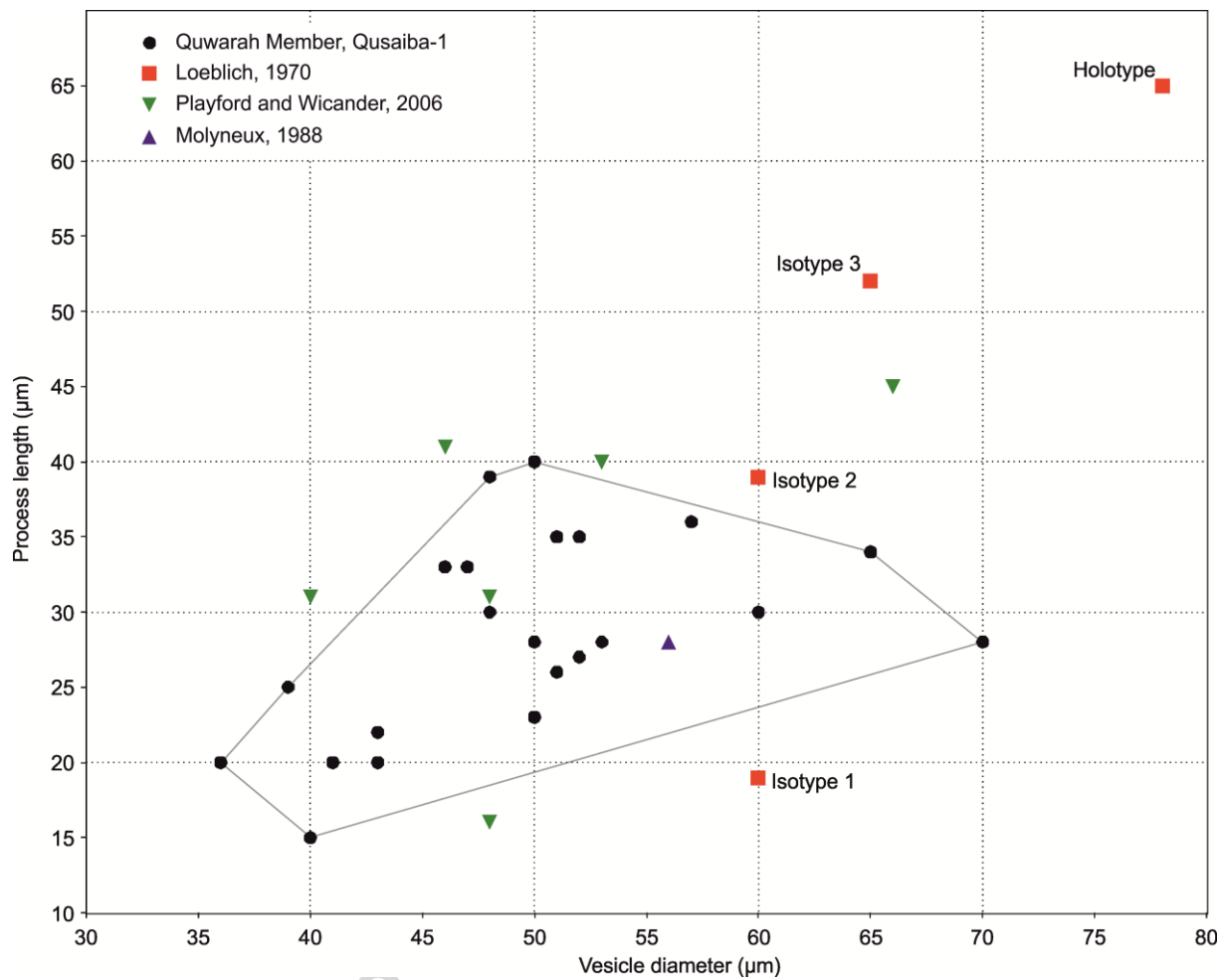


Figure 3

ACCEPTED

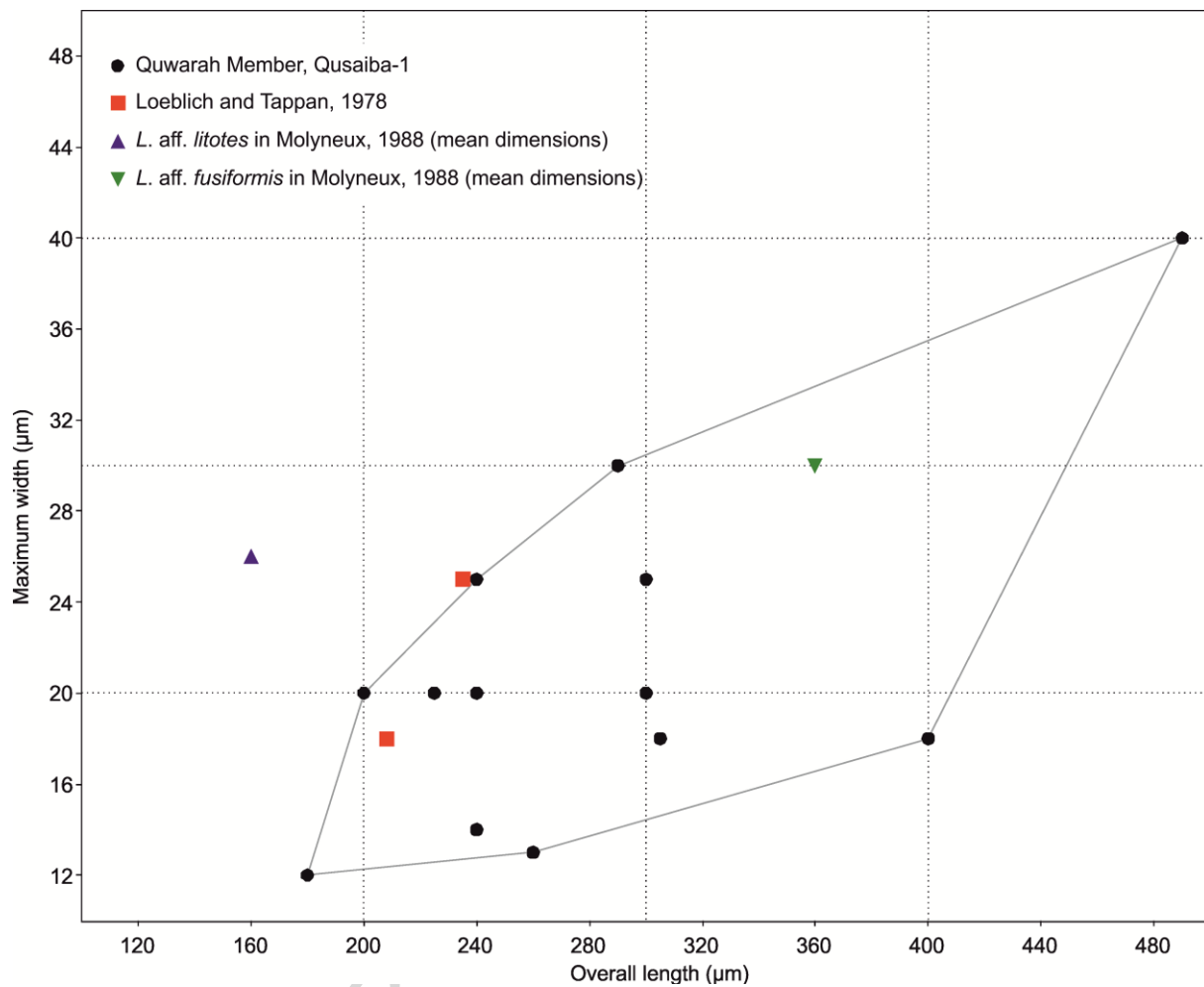


Figure 4

ACCEPTED

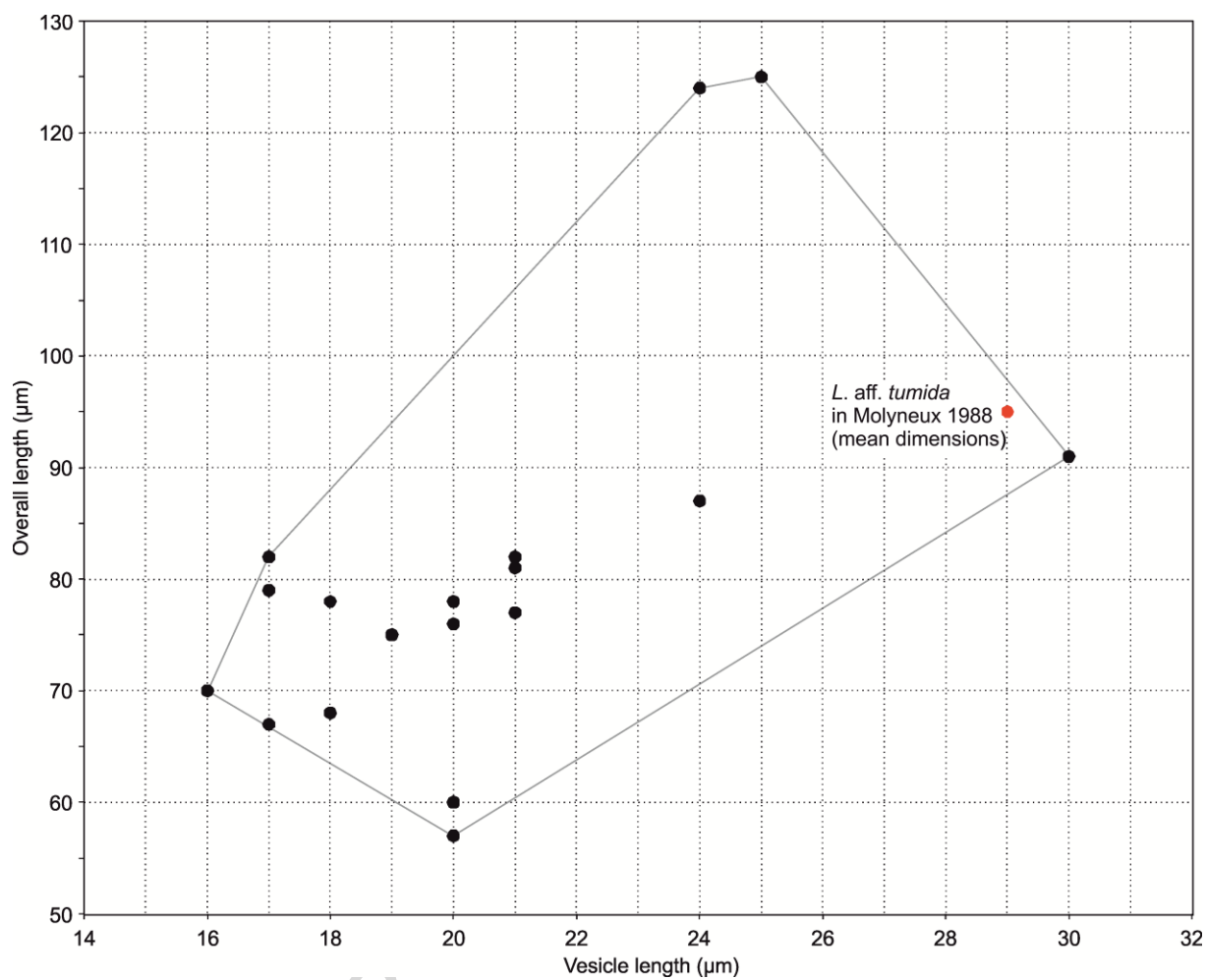


Figure 5

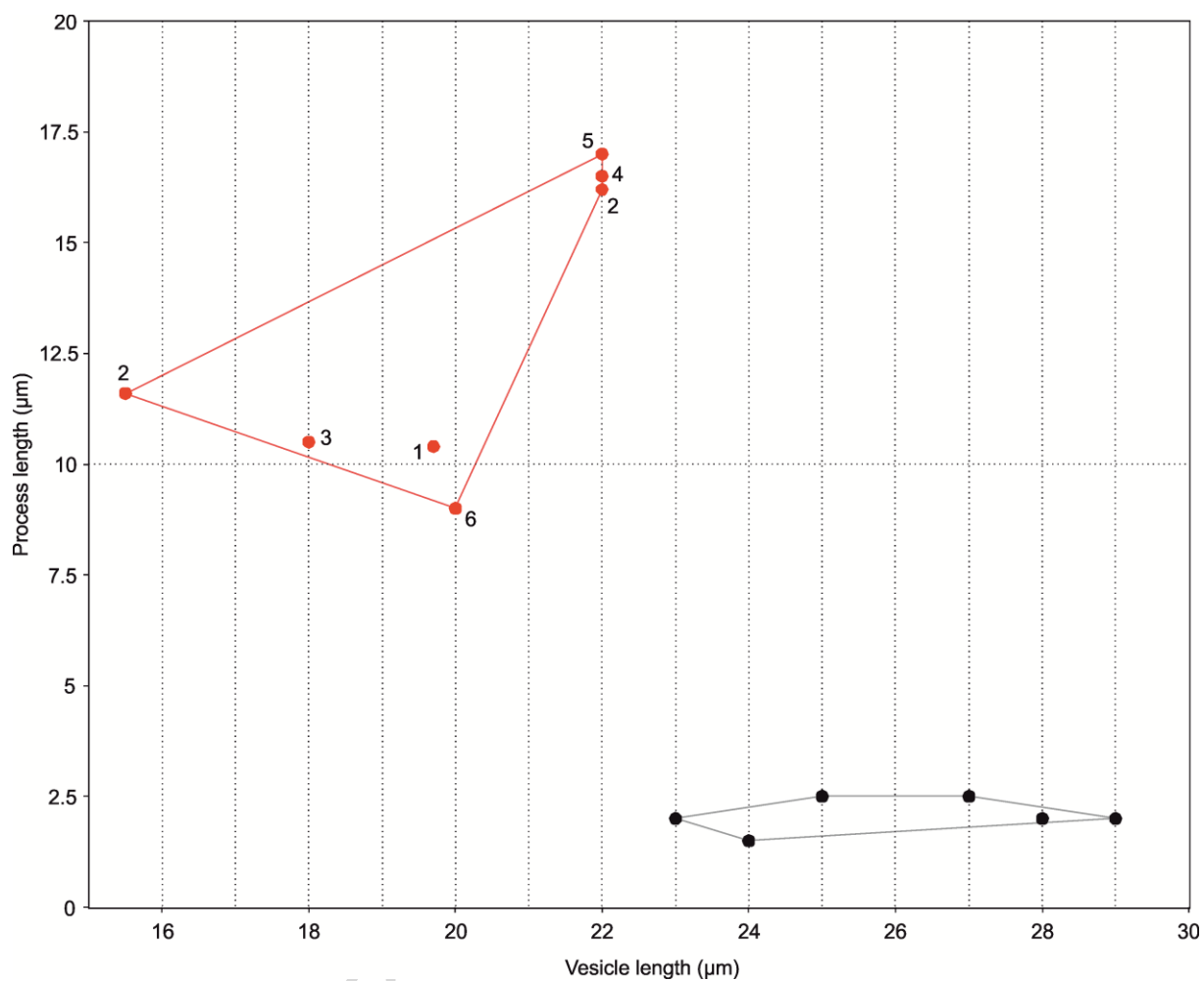


Figure 6



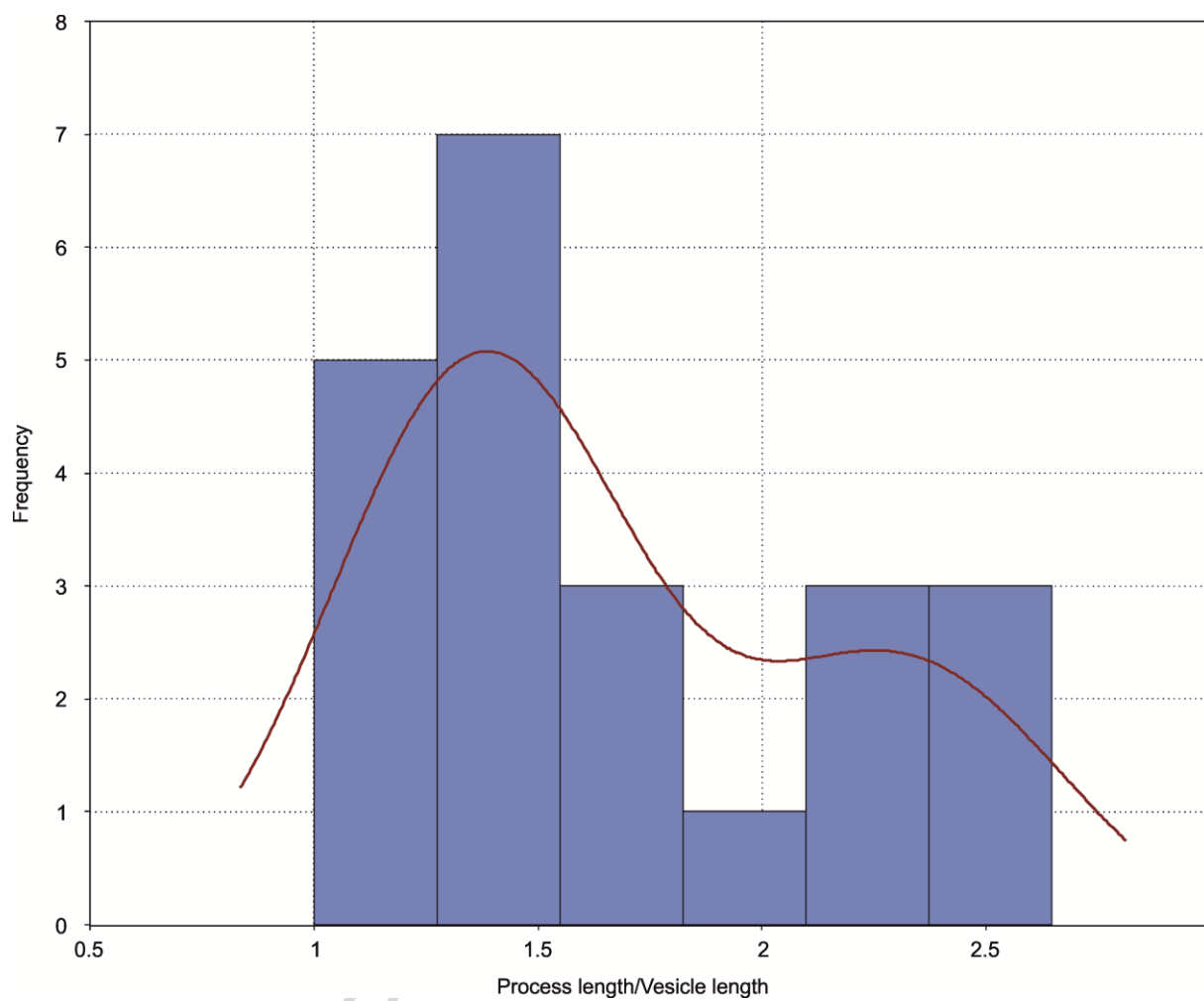


Figure 7

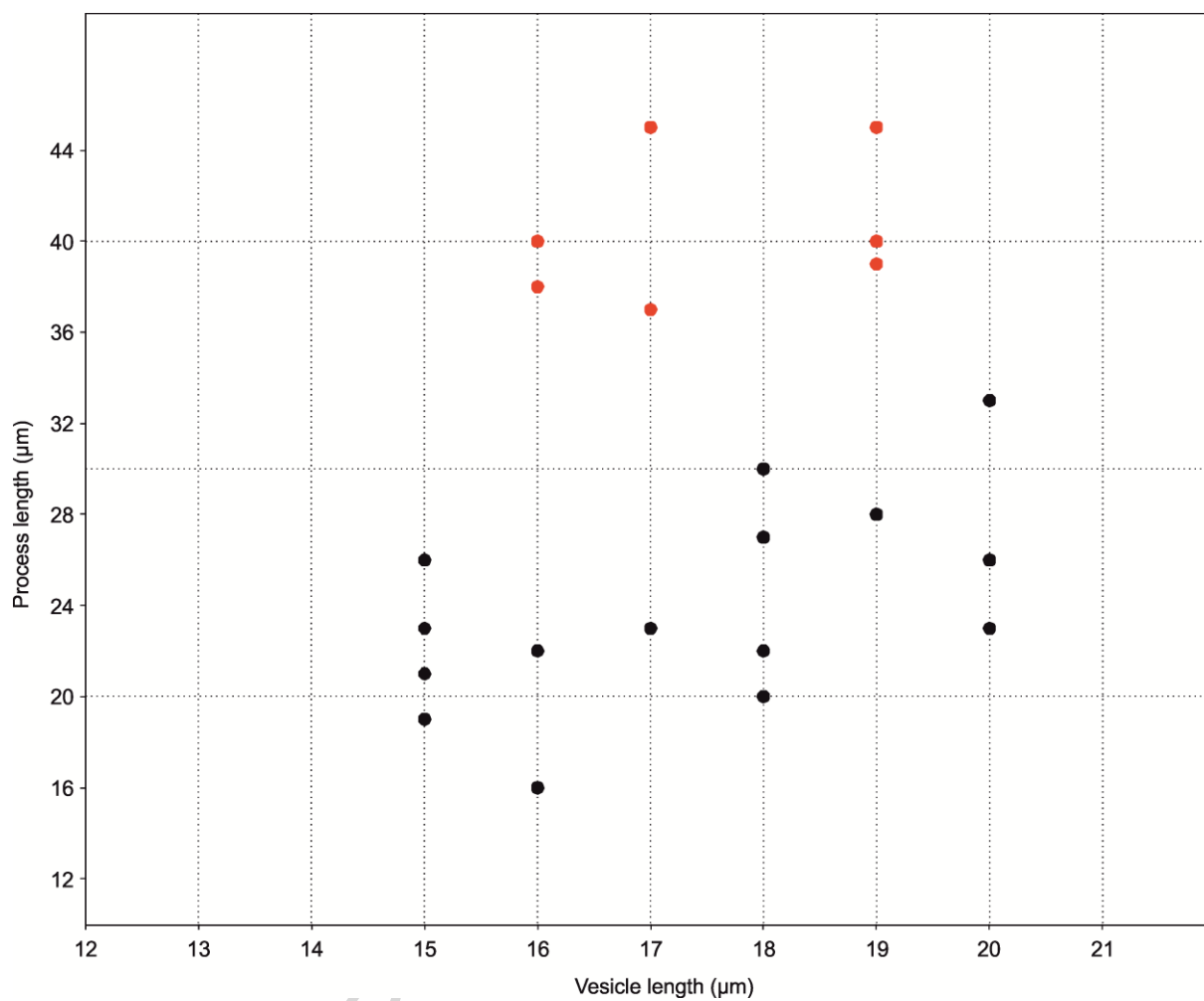


Figure 8

ACCEPTED

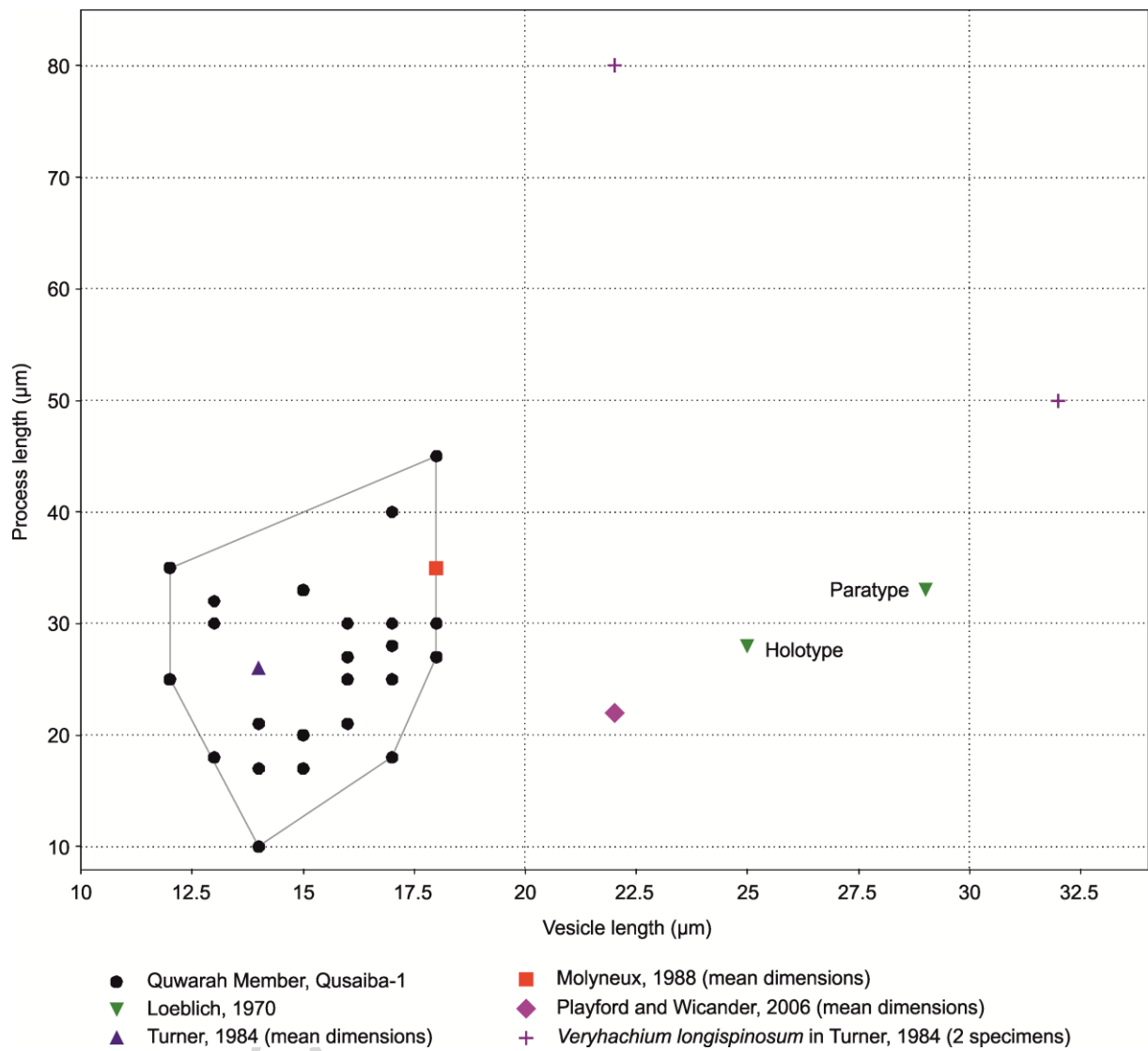


Figure 9

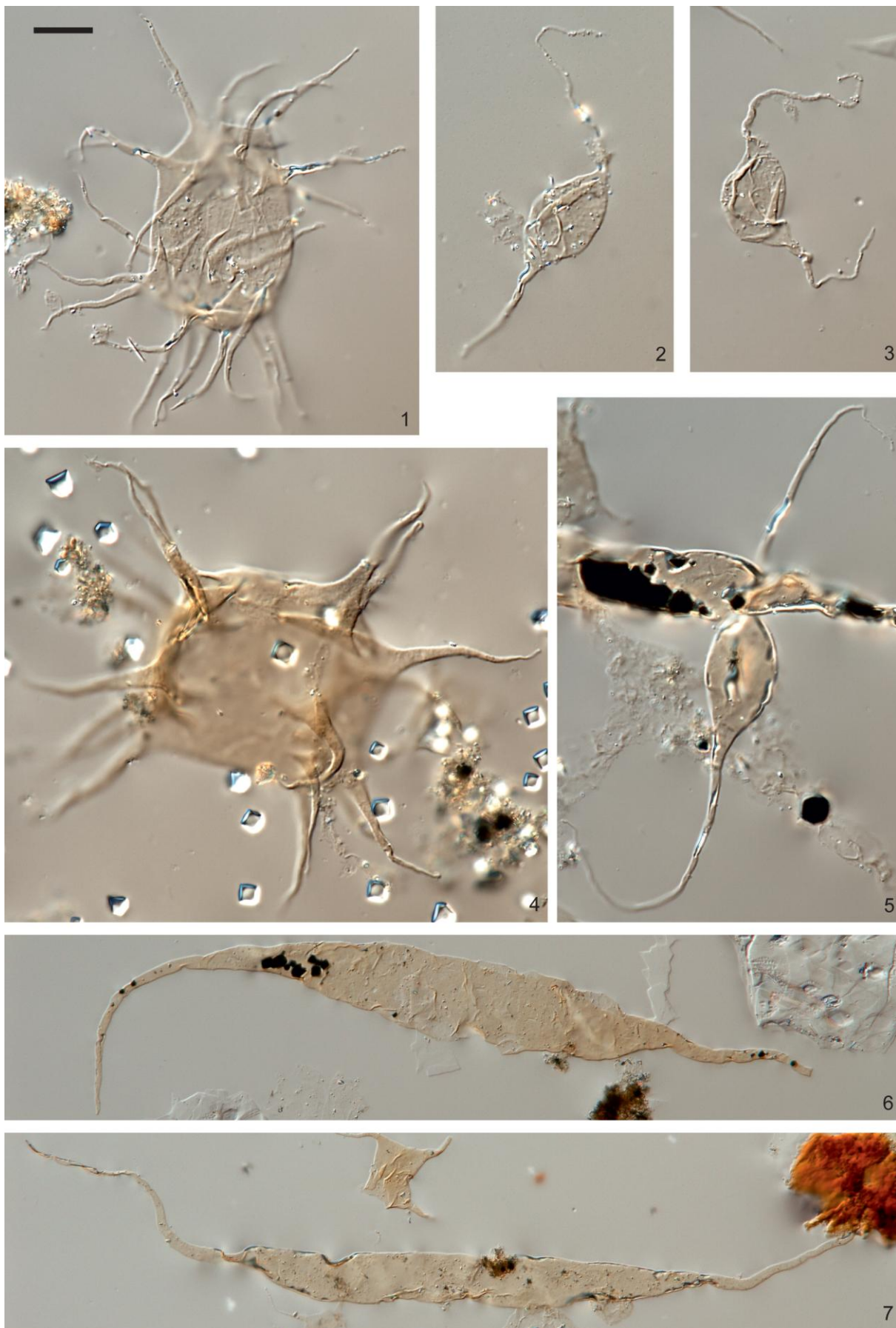


Plate I

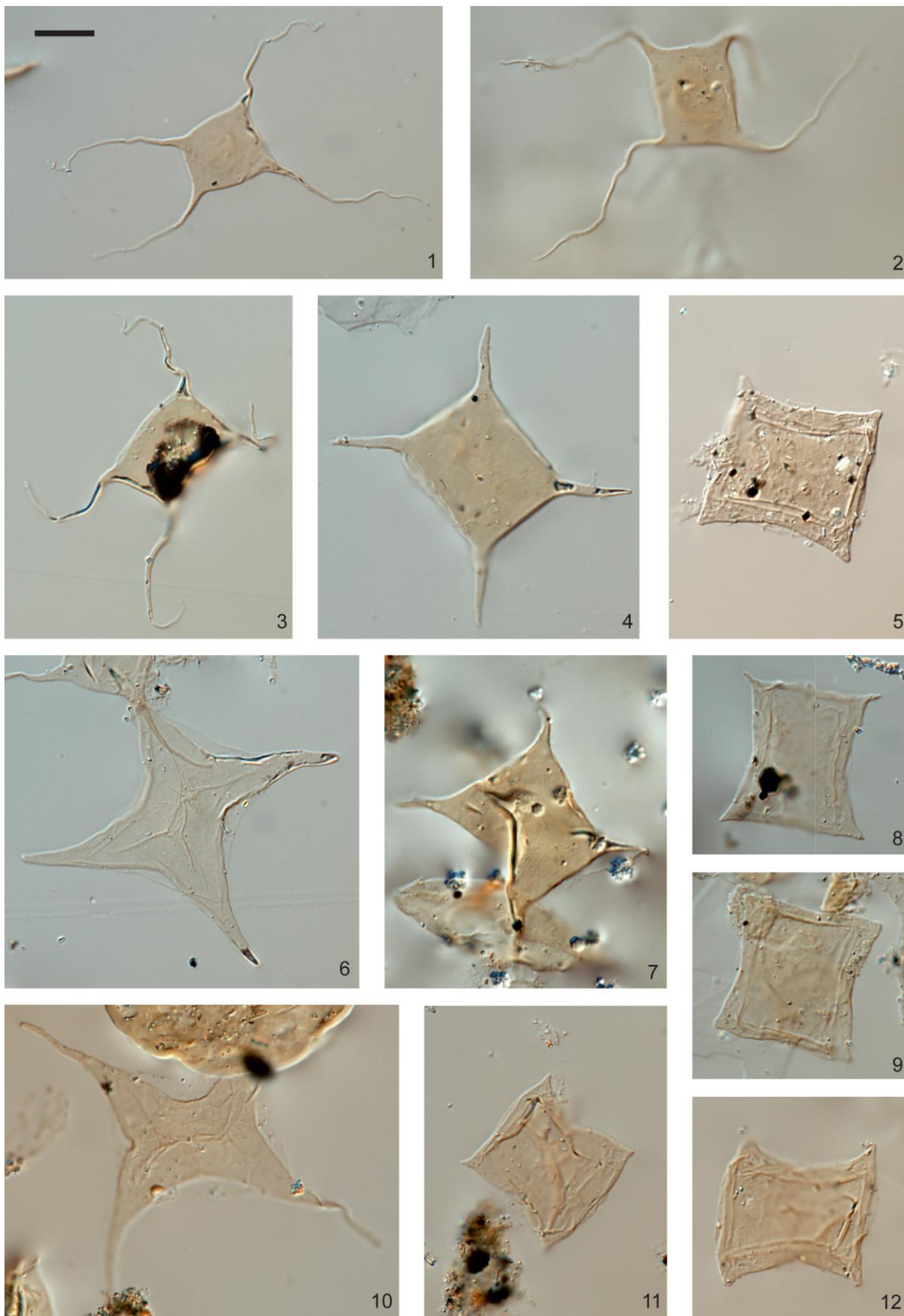


Plate II



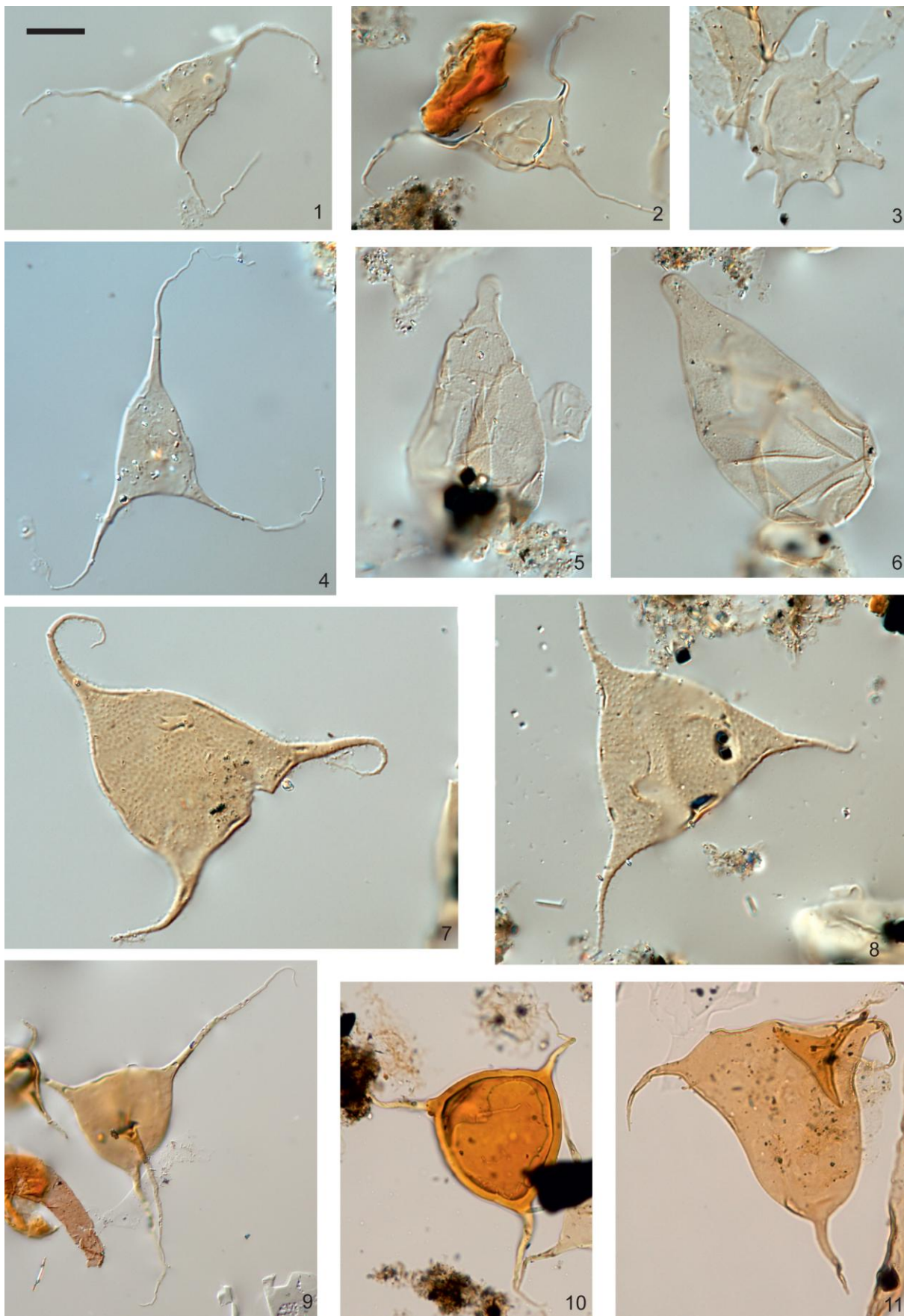


Plate III



Plate IV



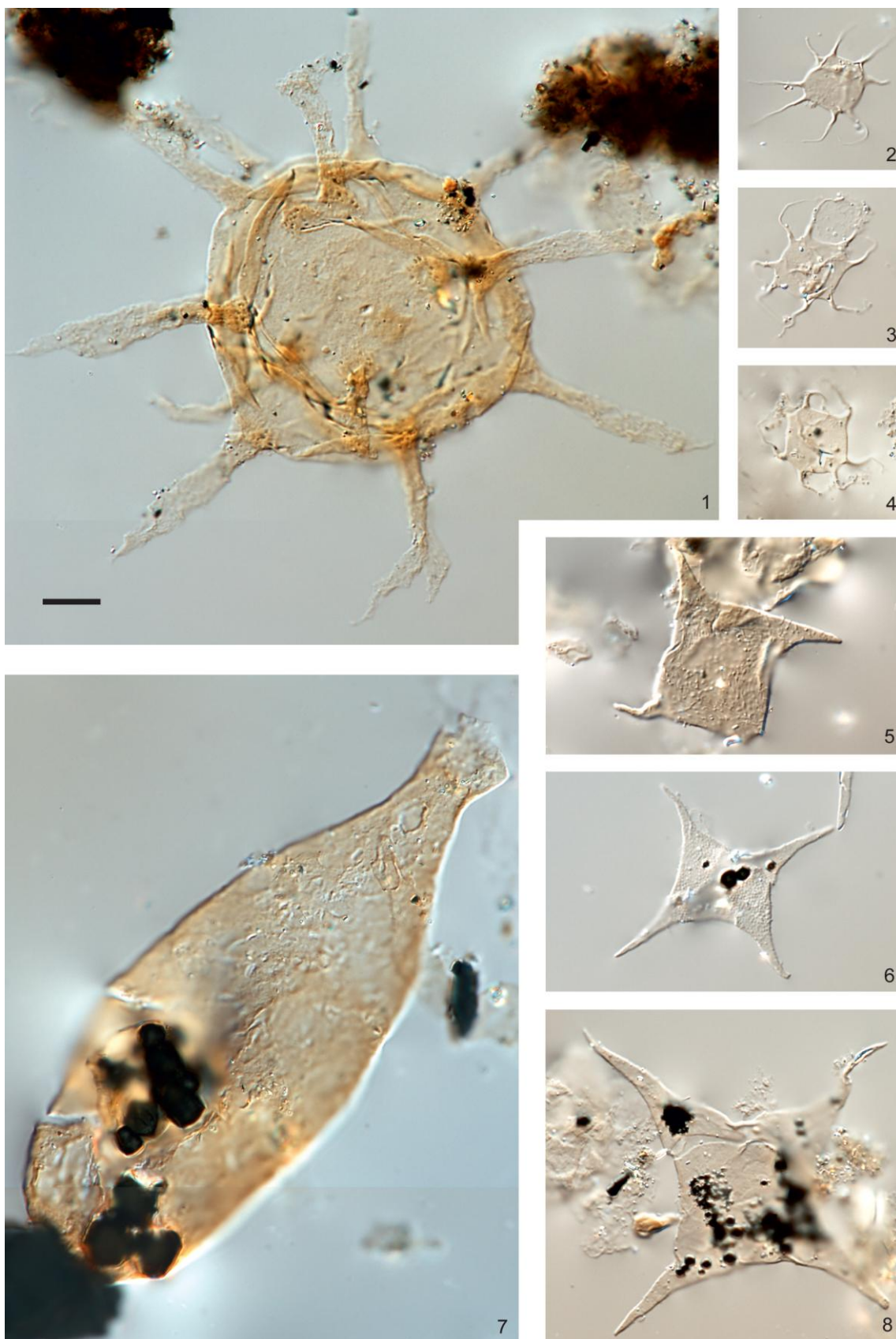


Plate V



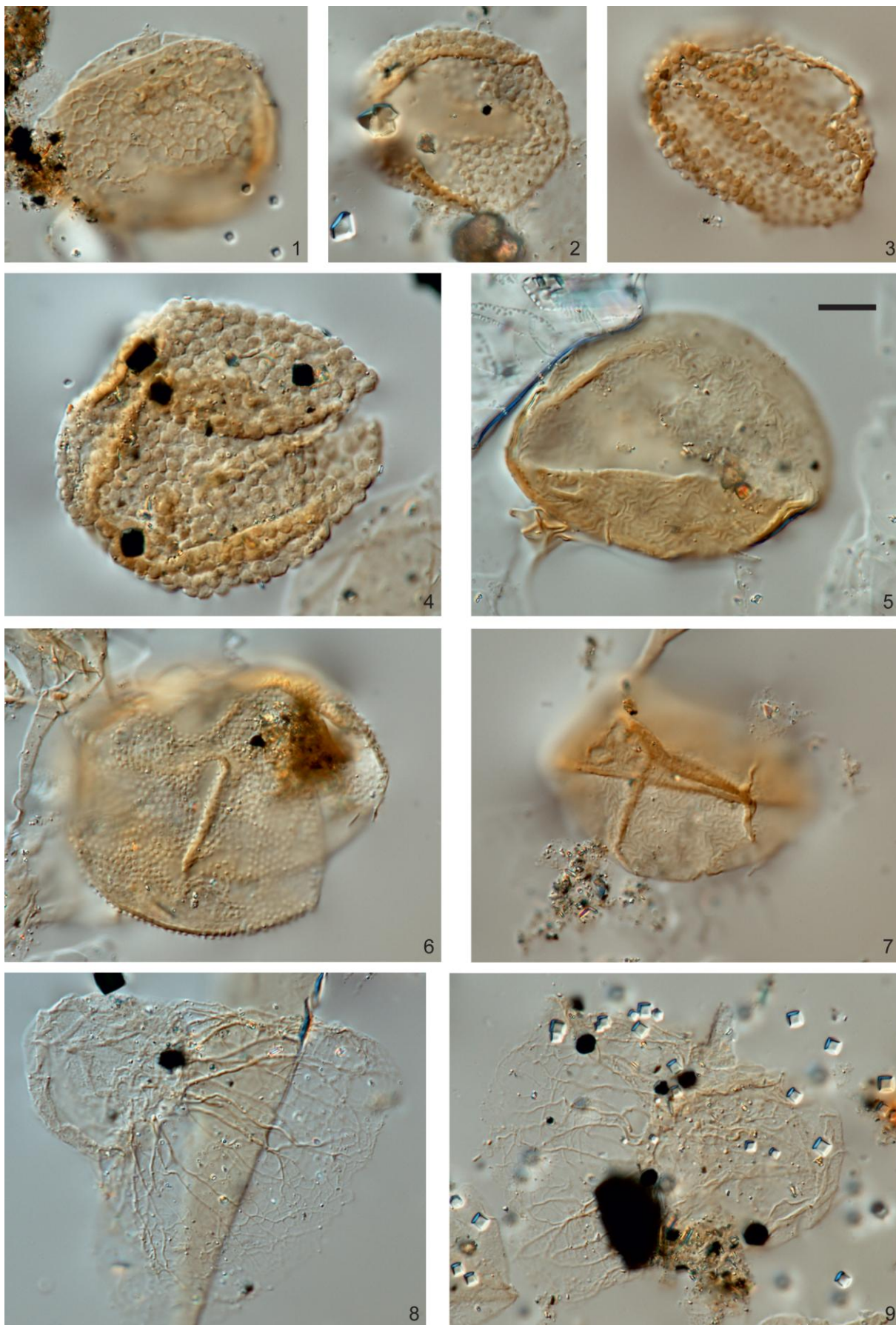


Plate VI

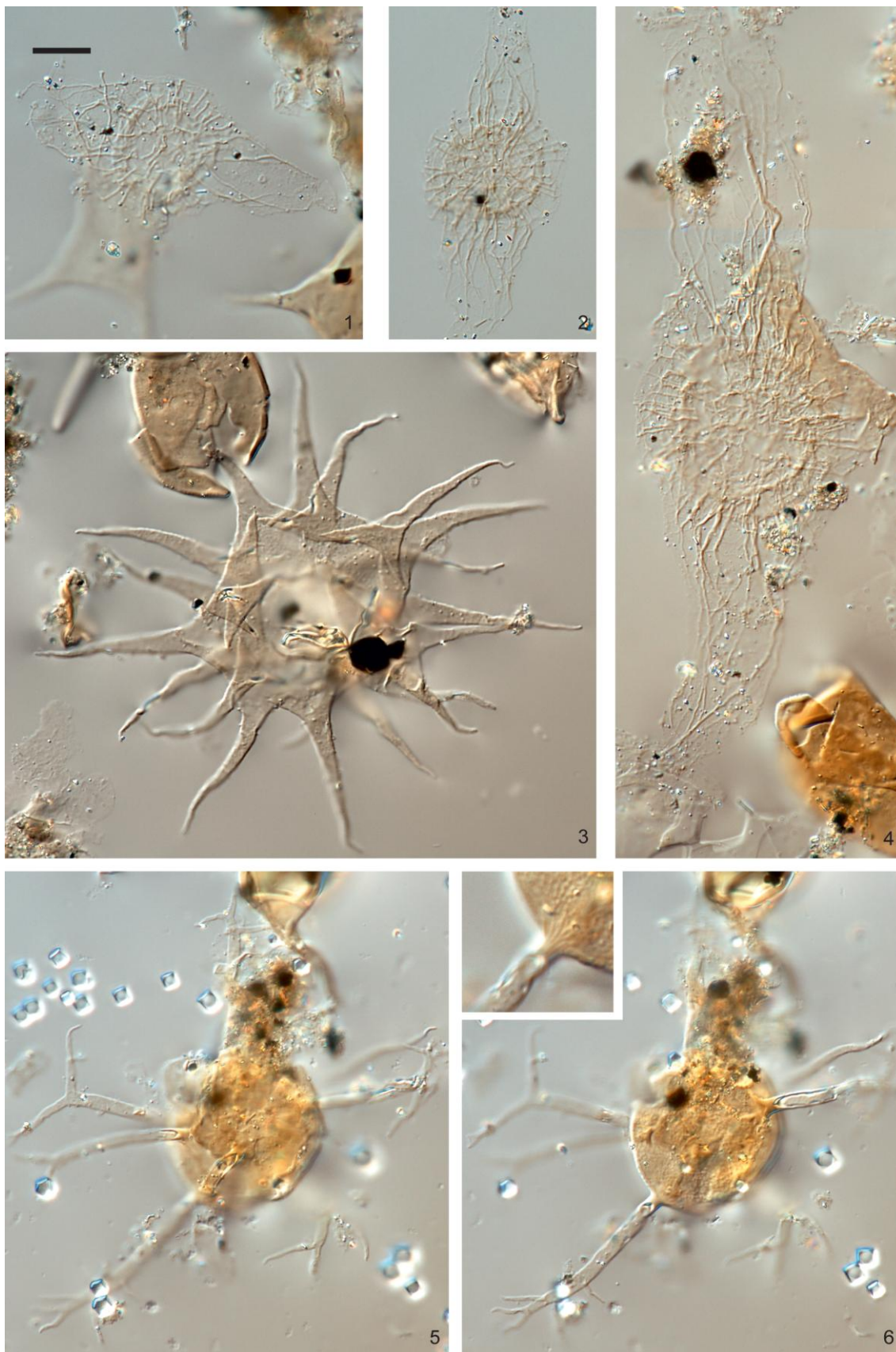


Plate VII





Plate VIII

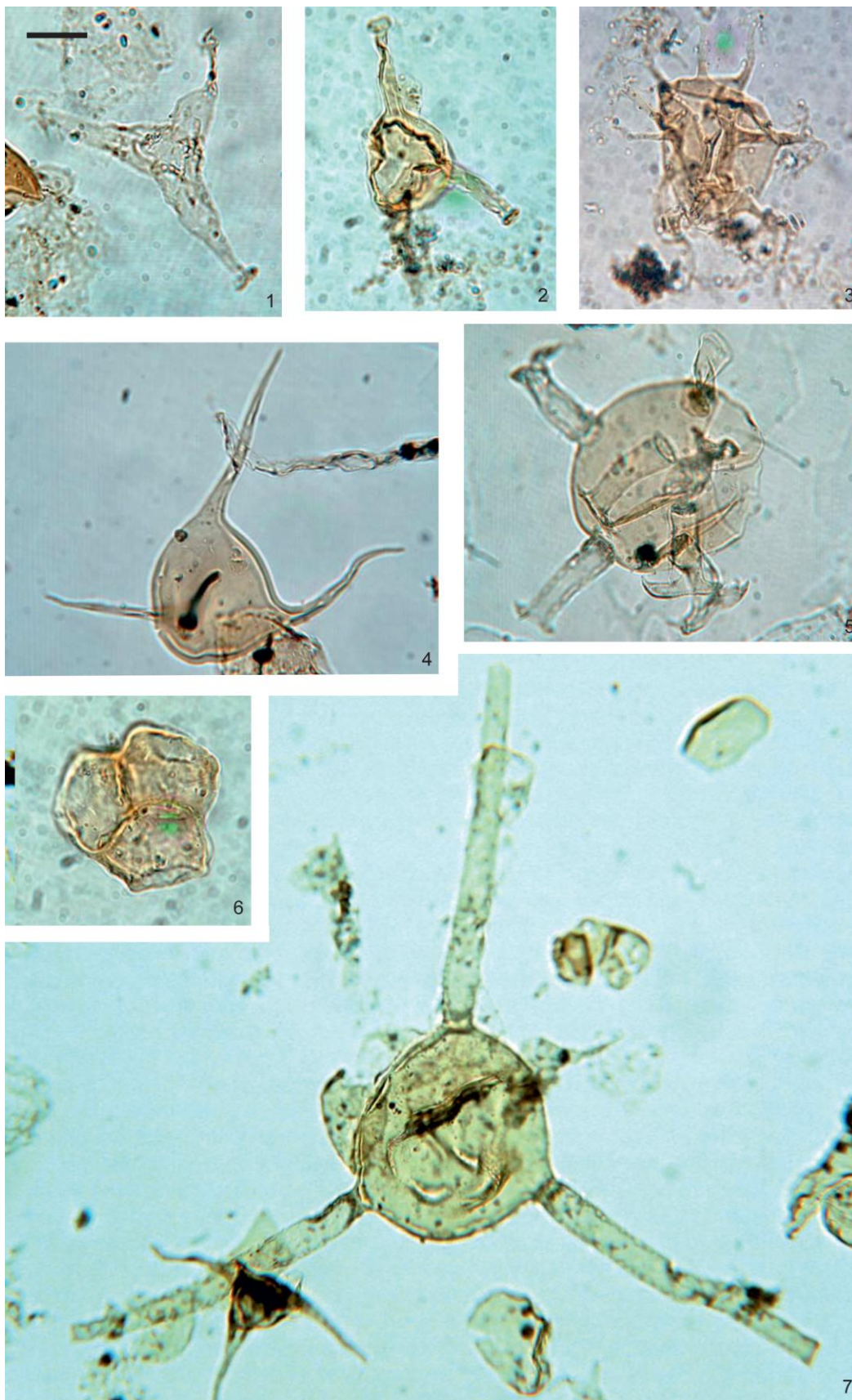


Plate IX



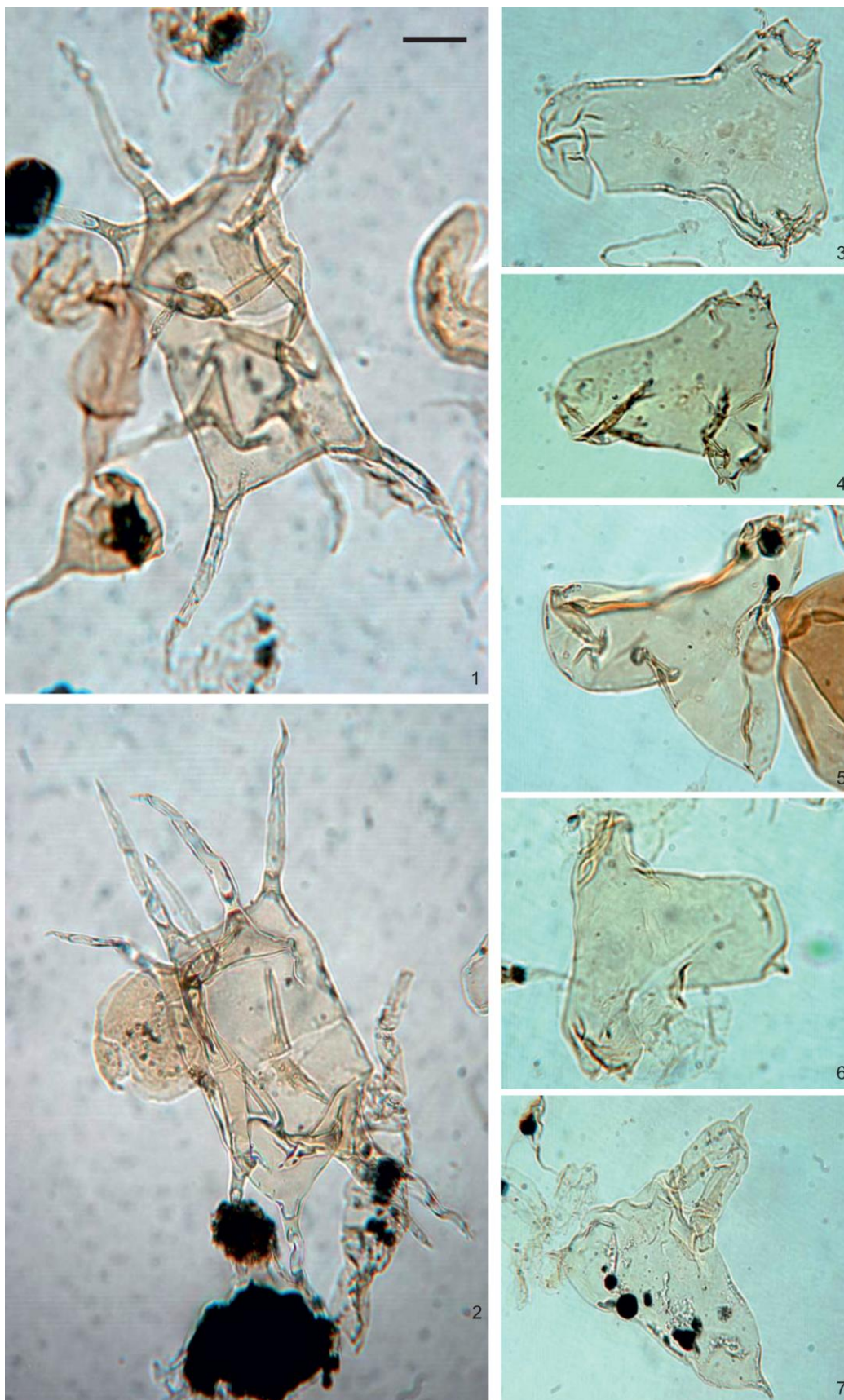


Plate X



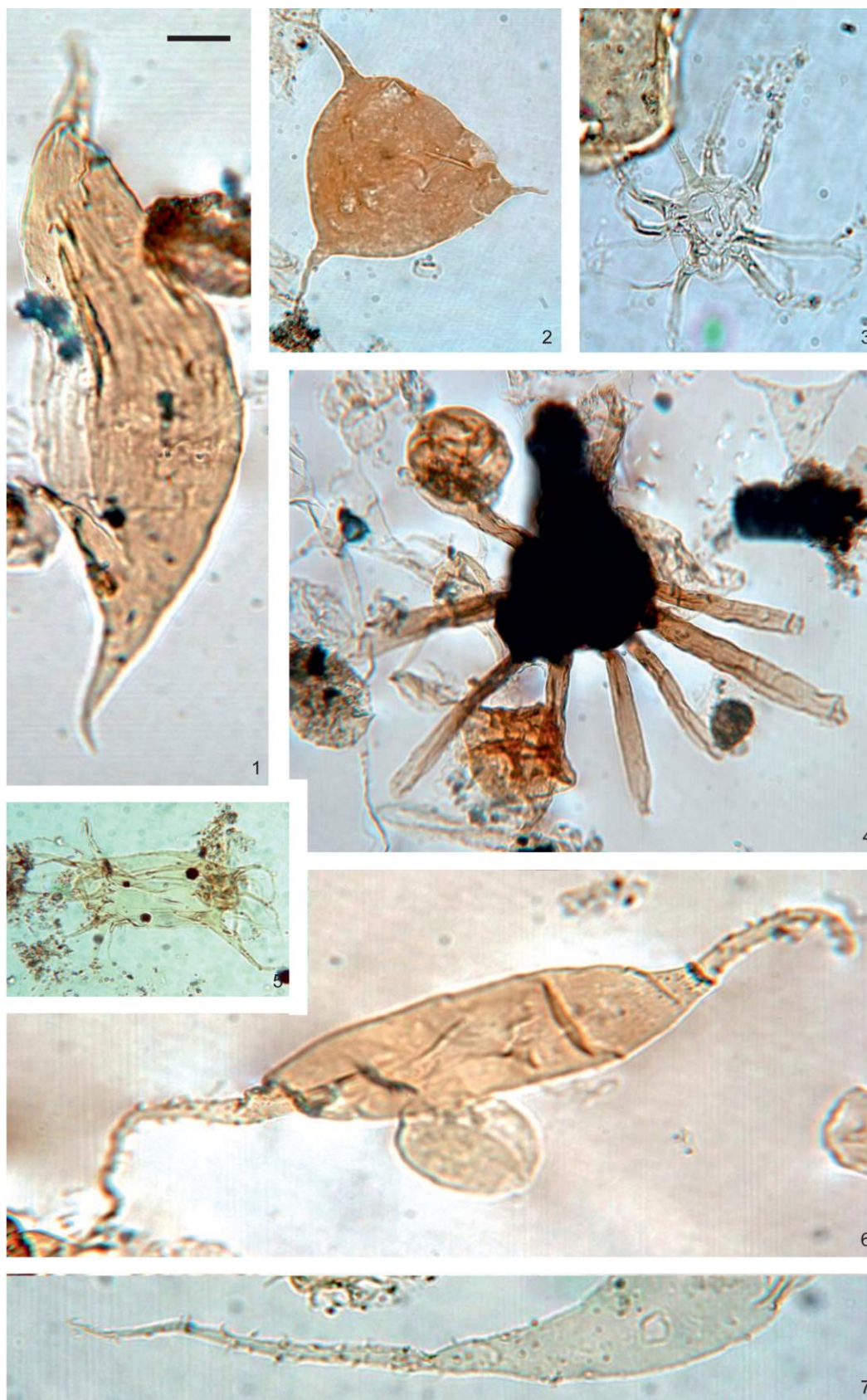


Plate XI



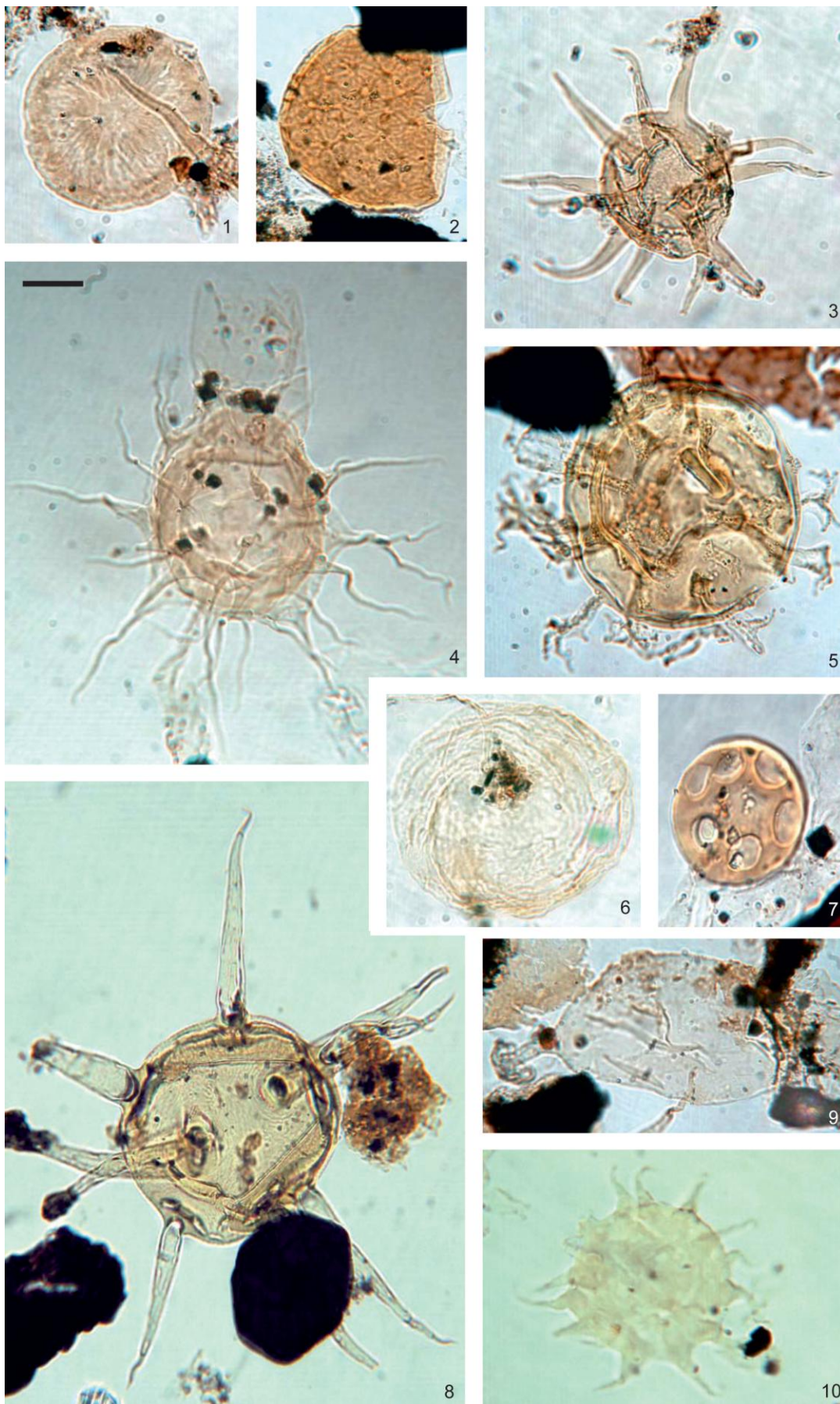


Plate XII



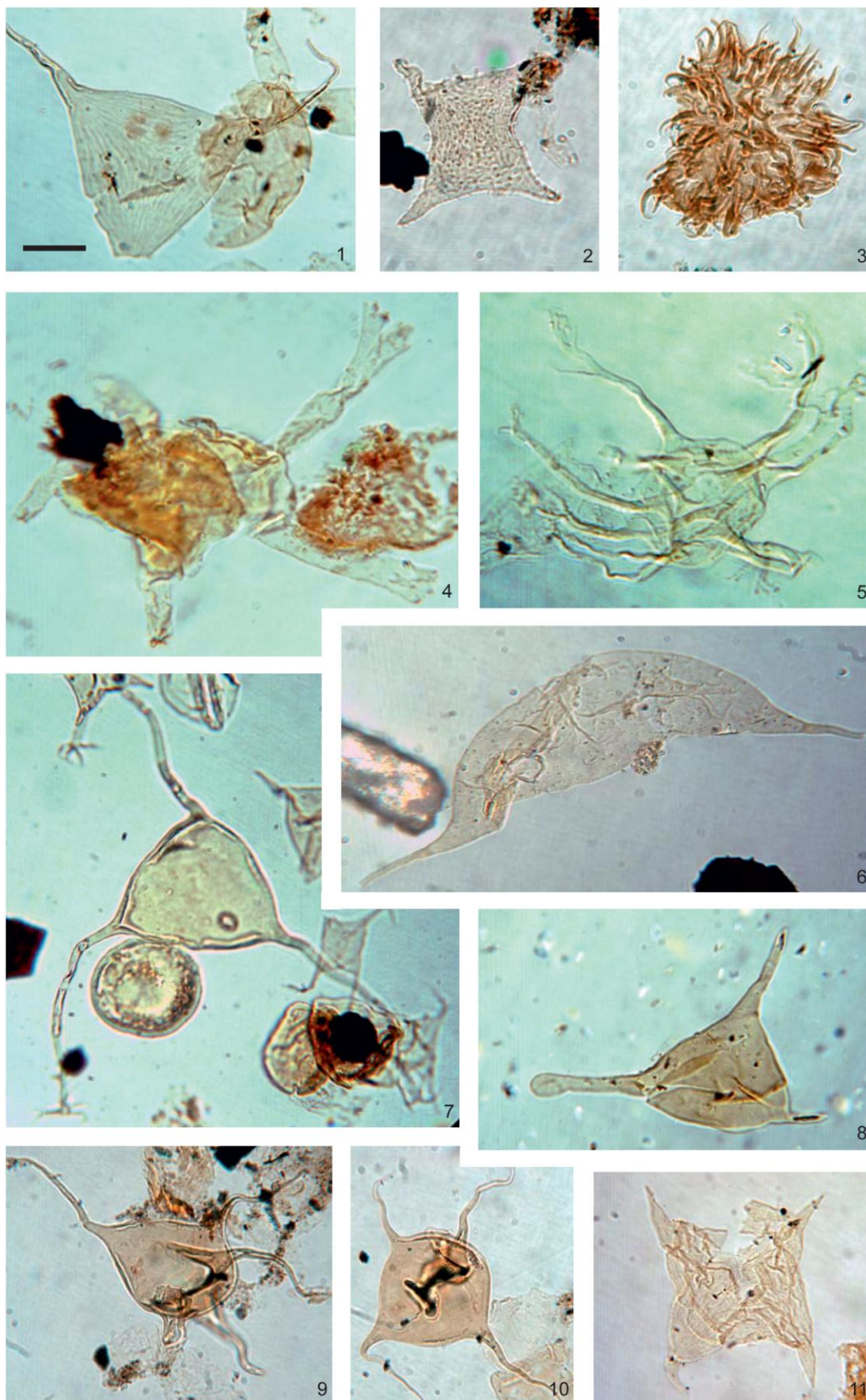


Plate XIII



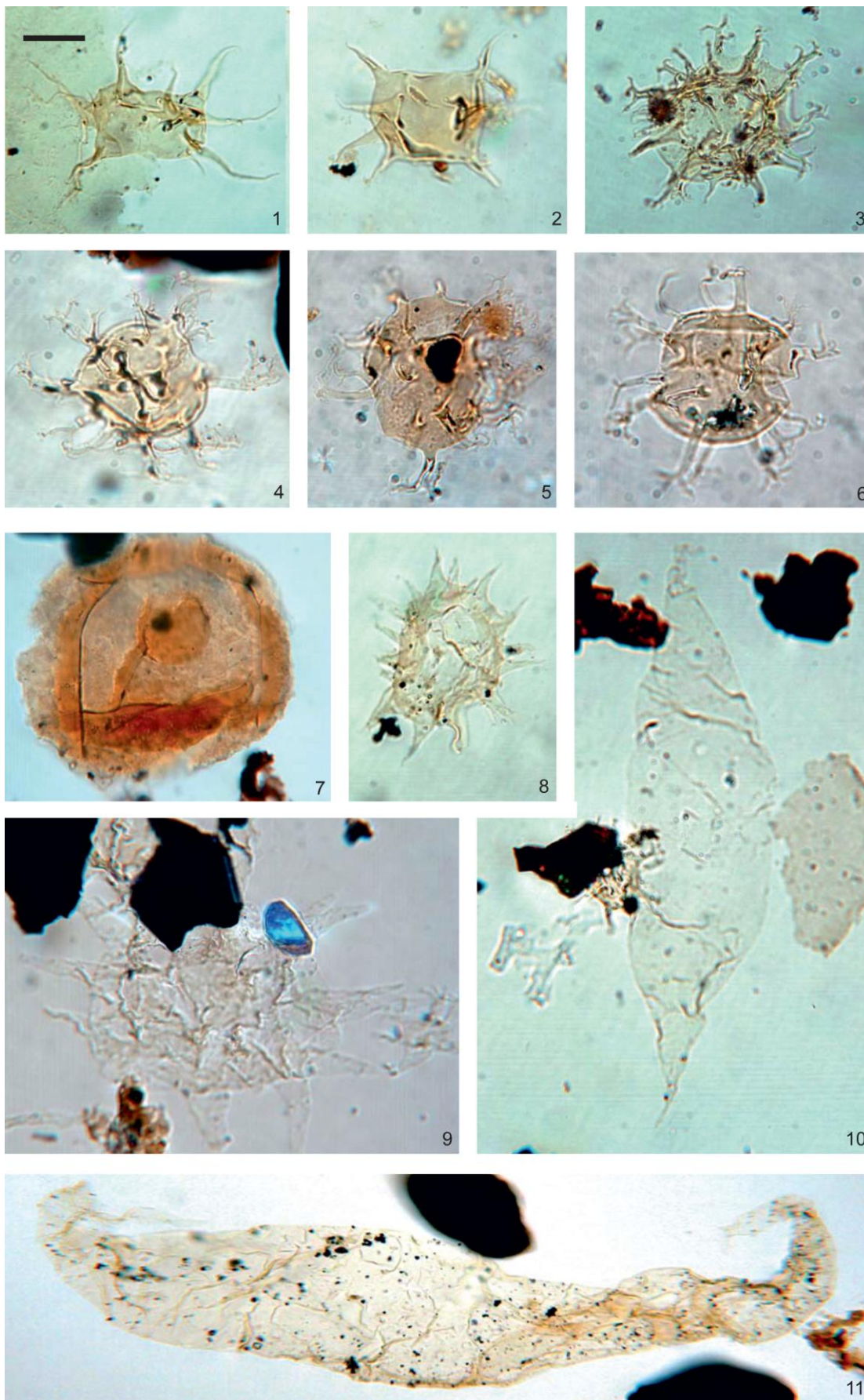


Plate XIV

ACCEPTED MANUSCRIPT