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Recognition of an extended record of euglenoid cysts: Implications for the end-Triassic mass extinction

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ABSTRACT

The enigmatic non-pollen palynomorph *Chomotriletes,* occurs consistently within sediments associated with the end-Triassic mass-extinction. Based on a detailed palynological survey and other published records from Europe, *Chomotriletes* is prevalent within the uppermost Rhaetian Contorta and Triletes Beds and its equivalents elsewhere. *Chomotriletes* is now a senior synonym for Permian *Circulisporites,* Meso- to Cenozoic *Pseudoschizaea*, and Quaternary to Recent *Concentricystes*. Its widespread occurrence has significance for our understanding of the end-Triassic mass-extinction, but its biological affinity and ecological preference have remained contentious for almost a century. We undertook a TEM examination of a Holocene and a Pliocene example of *Concentricystes* and found their structure to be a close match to the wall of Jurassic *Pseudoschizaea* from Italy that has been interpreted to belong to cysts of the Euglenophyceae. Together with a nascent understanding of a deep time record of the euglenoid, *Moyeria*, *Chomotriletes* helps document a terrestrial signature of the Euglenophyceae in the fossil record. An extensive literature survey indicates that *Chomotriletes* is associated with wetlands and riverine floodplain soils, and that it inhabited mainly temperate to tropical latitudes and continues to do so to the present day. Its presence in ancient marine sediments therefore indicates transport via weathering and erosion. The association with wetlands is in line with the ecological preferences of species of the Euglenophyceae. The presence of euglenoid cysts in association with the end-Triassic extinction fits a scenario in which enhanced rainfall followed by strong soil erosion resulted in the release and redeposition of *Chomotriletes* into shallow marine settings.

1. Introduction

The presence of the enigmatic palynomorph *Pseudoschizaea* in Triassic-Jurassic boundary beds in cored successions from Germany and France has prompted us to investigate these non-pollen palynomorphs (NPPs), exploring their potential as a proxy for environmental change during the end-Triassic mass-extinction event (ETME; 201.6 Ma). We attempt to disentangle confusion surrounding this long-ranging taxon and determine its systematic affinity as well as assessing its consistency as a paleo-environmental indicator. The introduction of the genus *Pseudoschizaea* by Thiergart and Frantz (1962) was not accompanied by the designation of a holotype. Thus began a history of confusion about the nomenclatural status of these circular, thick-walled and ribbed "spores" or "algal cysts", which has inhibited an exact understanding of their biology and systematic affinities (Christopher, 1976; Scott, 1992). Morphologically similar taxa to *Pseudoschizaea* are variously known as *Chomotriletes, Circulisporites, Concentricystes* and *Brodispora* (Scott, 1992). These designations follow a roughly stratigraphic scheme with *Chomotriletes* and *Circulisporites* as the Paleozoic endmembers, followed by the Mesozoic/Cenozoic *Pseudoschizaea* and Cenozoic-Recent *Concentricystes*. Collectively, these palynomorphs have left an extensive paper trail in the literature, and many individual authors have noted the

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similarities between sets of these genera (Scafati et al., 2009). Establishing synonymy between all these taxa would be significant, because these palynomorphs may range from the Cambrian to the recent, effectively making the organism that produced the spore or cyst, respectively, a *living fossil*.

The organisms producing the palynomorphs known as *Chomotriletes, Pseudoschizaea, Circulisporites*, and *Concentricystes* must be common constituents in the modern environment, given the widespread occurrence of the cysts in modern sediments. They can occur in great abundance in palynological preparations, such as for example in Upper Cretaceous caliche-bearing paleosols from the central foothills of Alberta, Canada (Jerzykiewicz and Sweet, 1988), where *Concentricystes* sp. constitutes up to 70% of the assemblage. *Concentricystes* is also widely observed in studies on subrecent palynological records from the Yangtze River in China, where it is connected to riverbank soils (Tang et al., 2013). *Concentricystes* has shown up in some unlikely places, including Maori coprolites studied for their palynological contents that provide insight on the diet and behavior of the original inhabitants of New Zealand (Horrocks et al., 2002). The Maori likely ingested these algal cysts while drinking water from ponds in the area. A link with wetlands and soils is mentioned in several papers (Chen et al., 2008; Norström et al., 2014), and it is notable that the earliest occurrence of the taxon *Sporites* described by Wolff (1934), and which gave rise to the genus *Circulisporites*, was sampled from a brown coal in Germany. And, of course, brown coal is a product of vegetation accumulation in a prior wetland environment.

In this paper, we first review the nomenclatural history of these striated, circular palynomorphs. It should be noted, however, that we are far from the first palynologists to recognize the overlapping morphology of these similar taxa. Both Jansonius and Hills (1976) and Fensome et al. (1990), have provided the nomenclatural basis for synonymy of these genera. We follow the recommendation by Fensome et al. (1990), who found *Chomotriletes* to be the senior synonym, which we designate as *Chomotriletes* s.l. throughout the remainder of the text, when referring to the collective taxon. Next, we focus on the various interpretations of the biological (and phylogenetic) origins of *Chomotriletes* s.l. Although the evidence from extant encystment studies in the Euglenophyceae is scant, in combination with an overwhelming preponderance of environmental data, we conclude that these forms are, indeed, the fossilized remains of freshwater euglenoids. Lastly, we present a compilation of literature that supports a restrictive environmental signal associated with the distribution of *Chomotriletes* s.l. as an indicator of stagnant freshwater and soil environments through geologic time.

2. Materials and methods

The material examined in this report comes from four different time slices – 1) drill cores spanning the Triassic-Jurassic boundary in Northern Europe, 2) Pliocene sediments from the Mozambique Channel, 3) Holocene samples from Lake Vouliagmeni, Greece, and, 4) living material from a pond in Mardi, NSW Australia (see Fig. 2).

Mesozoic samples were collected from the Schandelah-1 core (northern Germany), Mingolsheim core (southern Germany), Boust core (Paris Basin, France), and the Winterswijk WINT15-02 core (Netherlands). Core samples were treated to normal palynological preparations methods, that included acid digestion in HCl and HF, followed by sieving. The cores are all situated in the Central European Basin, in a broad area marked by Late Triassic shallow marine conditions (Fig. 1). All these cores span the uppermost Rhaetian to lowermost Jurassic and have a robust biostratigraphy based on palynological marker species, including pollen, spores, and dinoflagellates.

The sedimentary succession in all studied cores is generally similar and has been described in detail by van Eldijk et al. (2018), van de Schootbrugge et al. (2020), and Bos et al. (2023) for the Schandelah-1 core and by van de Schootbrugge et al. (2020) for the Boust core. The lithostratigraphy of the Mingolsheim core has been described in van de Schootbrugge et al. (2009, 2008). Samples from the Winterswijk WINT15-02 drilling that targeted the Lower Muschelkalk exploited at the nearby quarry, were derived from overlying Rhaetian sediments that are also exposed in the quarry. In addition, further occurrences were noted in the Boust core drilled in the Paris Basin in Northern France.

In the Schandelah-1 core *Chomotriletes* s.l. is common in the Upper Rhaetian at depths 338.00, 337.50, 337.20, and 336.80 mbs (Fig. 3). It also occurs in lower abundance in samples 336.00, 335.50, 329.50, 327.30 and 321.10 mbs in the Triletes Beds. *Chomotriletes* s.l. is prevalent in the Mingolsheim core at the following levels within the Triletes Beds: 203.00, 202.95, 202.00, 199.60 and 199.00 mbs. In the Boust core *Chomotriletes* s.l. occurs at depths 44.58, 43.26, and 42.40 mbs at the start and in the middle part of the Argiles de Levallois Member, where it is co-occurring with high abundances of *Polypodiisporites polymicroforatus* and *Concavisporites* spp. In addition, single occurrences are reported for samples from levels at 40.66, 40.47, 39.92 and 39.50 mbs where it is co-occurring with numerous reworked Carboniferous spores (van de Schootbrugge et al., 2020). In the WINT15–02 core from

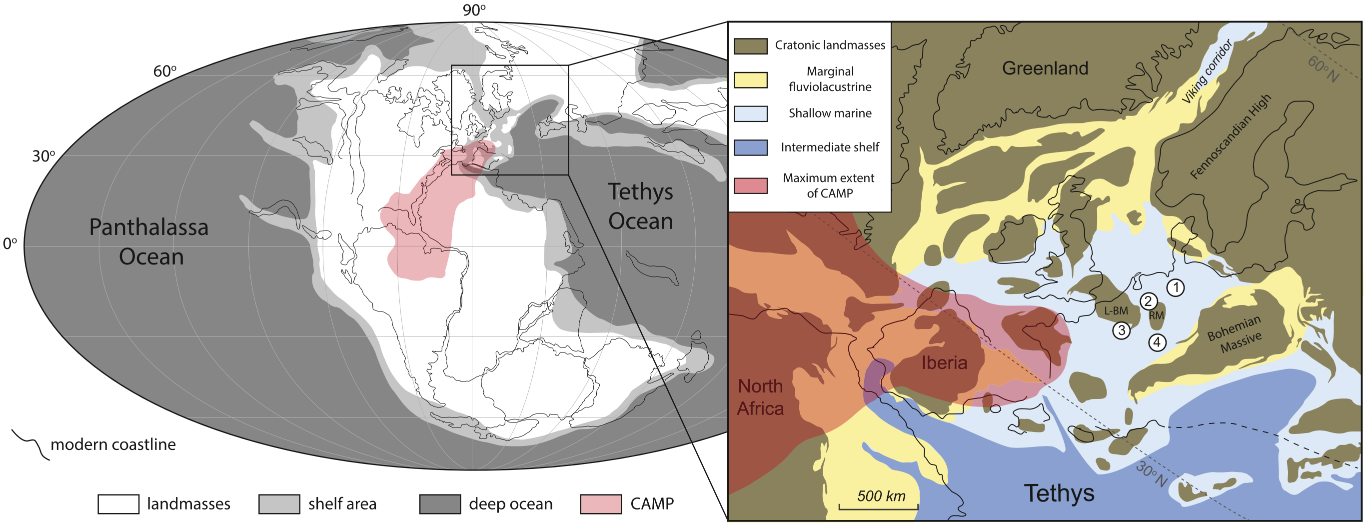

Fig. 1. Reconstructed palaeographic map of the Triassic-Jurassic boundary interval. The map insert shows the location of the four sampled cores in Europe: (1) Schandelah-1 core (Germany), (2) Winterswijk core (Netherlands), (3) Boust core, (France), (4) Mingolsheim core (Germany). Map is modified from van de Schootbrugge et al. (2020) and Bos et al. (2023).

Winterswijk *Chomotriletes* s.l. was observed in just one sample (15.5 mbs) in the equivalent of the German Triletes Beds (uppermost Rhaetian).

Pliocene material was derived from IODP Site U1478 in the Mozambique Channel (25°49.26′ S; 34°46.16′ E) from a water depth of 488 m below sea level. The record spans the past 4 Ma (Koutsodendris et al., 2021) and is characterized by high concentrations of terrestrial palynomorphs of excellent preservation originating from the Limpopo River catchment area in SE Africa (Taylor et al., 2021). Samples were processed at Palynological Laboratory Services Ltd. (Gwalchmai, UK) as described in Taylor et al., 2021.

More recent material was studied from sediment cores recovered from Lake Vouliagmeni (38°1′42"N, 22°52′58″E) in Greece spanning the Meghalayan Stage (latest Holocene). Lake Vouliagmeni is a deep coastal lake (c. 50 m) with permanent connection to the sea and year-round anoxic bottom waters (Koutsodendris et al., 2023). Samples from these sediment cores were processed in Heidelberg as described in Koutsodendris et al., 2023.

Individual palynomorphs for TEM study were picked from both the Lake Vouliagmeni (core section LVL15–1, 60–61 cm) and IODP (Hole B Core 34F Section 2W, 137–139 cm) cores. Strew mounts were prepared on 1 × 3″ glass slides using melted agar as a mounting medium. We first photographed specimens of interest under light microscopy (LM), removed the coverslip from the agar slides, and then cut out a small chunk of agar which contained specimens of interest. The agar pieces were then embedded in epoxy (Spurr replacement formulation; Ellis, 2006) for TEM using standard procedures.

3. Results

3.1. Historical review of proposed euglenoid cyst taxa

In the following overview we provide a concise history of the taxonomy of each of the genera that have been intermittently used to describe what we now conclude to be cysts of Euglenophyceae. The text is not meant as a formal taxonomic revision as this has largely been addressed previously by Jansonius and Hills (1976) and Fensome et al. (1990). Takahashi (1979) also provides a concise narrative of the historical recognition of synonymy within the taxa presented here: *Chomotriletes*, *Pseudoschizaea*, *Concentricystes*, and *Circulisporites*. Here, we attempt to provide a justification for recognizing the biological provenance of these taxa specifically as encysted stages of members of the freshwater Euglenophyceae.

3.1.1. Genus Chomotriletes Naumova, 1939, ex Naumova, 1953

The genus *Chomotriletes*, first introduced by Naumova (1939), suffers from its initial designation as a trilete spore. The diagnosis of the type genus *Chomotriletes* reads as follows (from Jansonius and Hills, 1976), "azonotrilete spores, with concentric projections". Initially Naumova failed to provide a description of a type species, but this was later corrected by Naumova (1953) with the introduction of the type species, *Chomotriletes vedugensis*, from the Upper Devonian (Frasnian) of the Russian Platform. The diagnosis of the type species from Jansonius and Hills (1976) reads, "30–60 microns, yellow; spore circular, exine with thin fine costae, the ridges and grooves arranged as concentric circles; surface of ribs chagrinate; dehiscence mark indistinct." The remark on the dehiscence in the diagnosis has led to considerable confusion because the holotype depicted by Naumova (1953) is clearly alete, and there is no record elsewhere of any trilete *Chomotriletes.* In addition, Naumova (1953) used an image of a ribbed trilete spore, comparable to *Cicatricosiporites,* to underpin the description of the holotype, adding further to the confusion with respect to the trilete character of *Chomotriletes*.

The alete nature of *Chomotriletes* was firmly established by Stover (1962), who emended the genus to include only alete spores. This was done in the process of distinguishing a new, Lower Cretaceous ornamented subtriangular spore, *Taurocusporites*, from *Chomotriletes*. Stover (1962) also suggested that the Mesozoic species *Chomotriletes genuinus* was more similar to *Corrugatisporites*. This left *Chomotriletes* as a largely Paleozoic alete "spore" in terms of its stratigraphic position and botanical affinities.

Chomotriletes continued to persist as an alete form recovered in both Paleozoic and Mesozoic deposits. For example, isolated specimens assigned to *Chomotriletes minor* occur in the Lower to Middle Jurassic Baga Formation on Bornholm (Denmark) (Batten et al., 1994; Hoelstad, 1985). Its problematic systematic position was also commented on by Batten et al. (1994) who suggested that placing the genus in synonymy with *Concentricystes* and *Pseudoschizaea* as recommended by Fensome et al. (1990) is only valid if all of these taxa represent algal cysts, rather than plant spores. Specimens of *Chomotriletes minor* that were clearly alete are also depicted from Upper Jurassic to Lower Cretaceous sediments from northern Norway (Vigran and Thusu, 1975).

Paleozoic species of *Chomotriletes vedugensis* Naumova are occasionally found in the Silurian (e.g. Plate I, 1), but they become relatively abundant during the Devonian and most occurrences of this species are Devonian in age (Filipiak and Krawczyński, 2018). There are a few important occurrences in Ordovician and Cambrian sections too, indicating that we probably do not know the full extent of the taxon range. The oldest occurrence could be *Chomotriletes* cf. *C. vedugensis* which has been found in the Tempe Formation, Amadeus Basin, South Australia (Zang in Shergold et al., 1991). This assemblage, which is dominated by sphaeromorphs, is of middle Cambrian age. Another significant early occurrence is *Chomotriletes*? from the Ordovician Zanjón Fm of Argentina (Rubinstein et al., 2010), which, along with four additional presumed non-marine genera, is a component of the assemblage that is often cited as fossil evidence of the first land plants (e.g Morris et al., 2018). But, in general, *Chomotriletes* remains rare in rocks of Cambro-Ordovician age, possibly reflecting a global paucity of non-marine strata (Davies and Gibling, 2010).

3.1.2. Genus Pseudoschizaea Thiergart and Frantz 1962 ex. Potonié, 1966 emend. Christopher, 1976

The genus *Pseudoschizaea* was first introduced by Thiergart and Frantz (1962) based on the type species *Pseudoschizaea ozeanica* from a Pliocene brown coal from Kashmir (India). Curiously, the species name "*ozeanica*" was chosen even though the type species originated from a terrestrial sediment. Thiergart and Frantz (1962) provided neither a diagnosis of the genus nor of the type species, rendering them both *nomini nudii*. This situation was resolved by Potonié (1966), who effectively validated the taxon. The original diagnosis (combined description) given by Jansonius and Hills (1976) is, "Exospore ornamented with striates which run parallel to the wall of the spore. The spore looks like those of the Schizaeaceae, but it is neither monolete nor trilete. Perhaps this sporomorph belongs to the 'algae' ". The taxonomy of *Pseudoschizaea* was revised by Christopher (1976) who combined *Pseudoschizaea* with the original species description of *Sporites circulus* from Wolff (1934). *Sporites circulus* was first described as a circular spore with concentric ornamentations from a Tertiary brown coal from Germany. It is significant that both *P. ozeanica* and *P. circulus* were first described from brown coals, which suggests that the species are terrestrial rather than marine organisms.

Pseudoschizaea was regarded as a junior synonym of *Circulisporites circulus* by Krutzsch and Pacltová (1990), while Colbath and Grenfell (1995) considered *Pseudoschizaea* a junior synonym of *Concentricystes* and classified it with several other zygnematacean algal zygospores. However, they specifically did not group *Concentricystes* with *Chomotriletes* based on the observation that "specimens of *Chomotriletes* apparently do not exhibit a definite equatorial rupture" citing Playford and Dring (1981). The implication being that zygnematacean algal zygospores are characterized by equatorial splitting.

A number of examples of *Pseudoschizaea* from Triassic-Jurassic boundary sequences in Europe are shown here in Plate I, 2–7.

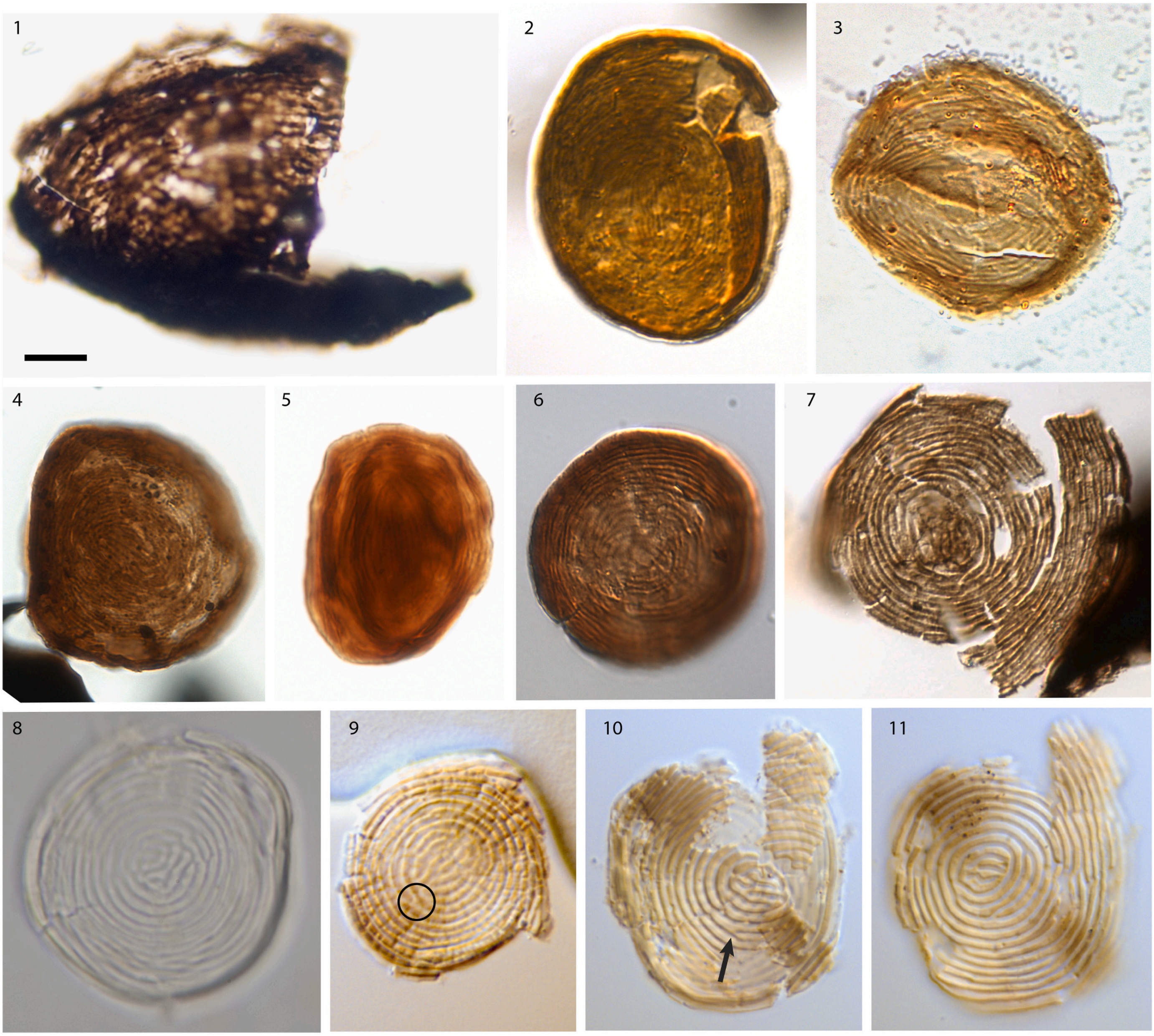

Plate I. 1–11. Stratigraphical examples of *Chomotriletes* s.l. 1. *Chomotriletes* sp. Illion Shale (Utica, New York, USA); sample S14–2, Silurian (Wenlock). 2. *Pseudoschizaea* sp., Winterswijk core (Netherlands) WINT15–02; sample 15.5 mbs, upper Rhaetian (Triassic) 3. *Pseudoschizaea* sp. Boust core (N France); sample BOUST_44_58 from the Argiles de Levallois, upper Rhaetian (Triassic). 4. *Pseudoschizaea* sp. Schandelah-1 core (N Germany); sample SCH_338_00 from the Contorta Schichten, middle Rhaetian (Triassic). 5 *Pseudoschizaea* sp. Schandelah-1 core (N Germany); sample SCH_338_00 from the Contorta Schichten, middle Rhaetian (Triassic). 6. *Pseudoschizaea* sp. Schandelah-1 core (N Germany); sample SCH_335_50 from the Contorta Schichten, middle Rhaetian (Triassic). 7. *Pseudoschizaea* sp. Mingolsheim core (S Germany); sample MING41A from the Triletes Beds, uppermost Rhaetian (Triassic). 8. *Concentricystes* sp. from Lake Vouliagmeni, Greece. (Holocene). 9. *Concentricystes* sp. IODP core U1478, Mozambique Channel (Pliocene), showing truncated costae (circle). 10. *Concentricystes* sp. IODP core U1478, Mozambique Channel (Pliocene), showing costae branching (arrow). 11. *Concentricystes* sp. IODP core U1478, Mozambique Channel (Pliocene).

3.1.3. Genus Circulisporites de Jersey 1962 emend Norris, 1965

The genus *Circulisporites* has been mostly used to describe Permian–Triassic bi-hemispheric concentric palynomorphs with 5 to 6 circular ribs with a thickened disc at both poles and a rupture at the equator, causing the dorsal and ventral sides to split into two separate halves. In addition, *Circulisporites* has simple circular ribs which do not show the space-filling pattern seen in the central region of some specimens of *Chomotriletes*. Norris (1965) emended the genus as follows: “Test spheroidal, ornamented with a series of concentric ribs. Test separates into two hemispheres along an equatorial line. Shell of organic material in a single layer.” As is the case for all of these similar taxa, the term, “ornament,” really refers to ribs, muri or costae which are protrusions of integral wall structure rather than sculpture or ornament which is applied on top of a vesicle wall (see following discussion of wall ultrastructure).

Grenfell (1995) considered *Circulisporites parvus* de Jersey 1962 to be synonymous with *Chomotriletes* from the Permian of South Africa as described in Hart (1965), and he noted that some Devonian *Chomotriletes* species also tend to split into two halves along what should be an equatorial suture. This observation contrasts with Playford and Dring (1981) who specifically note that *Chomotriletes* does not possess an equatorial suture. That said, *Chomotriletes*, as illustrated by Playford and Dring (1981, pl. 2, fig. 10) does show a flattened vesicle with isomorphic proximal and distal halves. In our observations, the tendency for

Chomotriletes (*Circulisporites*) to split into two hemispheres may not necessarily indicate the presence of a pre-formed equatorial suture, but, rather, may be due to the somewhat brittle nature of the cyst wall in combination with its discoidal to extremely oblate shape. This feature can be seen in our examples of *Pesudoschizaea*, which show brittle fracture and tearing (Plate I, 2, 7).

3.1.4. Genus Concentricystes Rossignol, 1962

The genus *Concentricystes,* with the type species *C. rubinus,* was first described and illustrated by Rossignol (1962) from Pleistocene sediments from Israel. She noted that *C. rubinus* occurred in modern soils and considered it as fluvial in origin. However, as later pointed out by Christopher (1976), the introduction of *C. rubinus* constituted a *nomen nudum* as no diagnosis was provided, although the genus was subsequently validated by the designation of a lectotype (Jansonius and Hills, 1976). Rossignol appears to have been unaware of the introduction of the morphologically similar *Pseudoschizaea* (Thiergart and Frantz, 1962), and *Circulisporites* (de Jersey 1962), but she considered *Sporites circulus* Wolf 1934 and *Concentricystes rubinus* to be synonymous.

Examples of Holocene and Pliocene *Concentricystes* as seen in LM are illustrated in Plate I, 8–11.

3.1.5. Genus Brodispora Clarke, 1965

The genus *Brodispora* was first described from the British Upper Keuper (Late Triassic) Arden Sandstone and diagnosed as follows: “Oval striate body. Striations localized in a median zone; remainder of body laevigate” (Clarke, 1965). The diagnosis for the type species *Brodispora striata* reads, “Exine thin, outline oval, striae thin and polar areas unsculptured. Size 30–40 μm x 20–30 μm (mean of seventeen specimens, 35 x 28 μm)”. The co-occurrence of *Brodispora* with other Triassic pollen and spores led Clarke (1965) to suggest that the specimens do not represent acritarchs, but rather alete spores. Based on the morphological description it appears that *Brodispora* is unrelated to *Chomotriletes* and its junior synonyms. We therefore refrain from using it in this review.

3.1.6. Summary of the taxonomic history

The above review of the literature on the taxonomic confusion regarding *Chomotriletes*, *Concentricystes*, *Pseudoschizaea* and *Circulisporites* suggests that all four genera have at some point in time been classified as senior or junior synonyms of each other. We propose to use the taxon, *Chomotriletes* s.l. when referring to these genera collectively, given the priority of *Chomotriletes* as established by Fensome et al. (1990), to provide a simple label when referring to these genera collectively. The use of the name, *Chomotriletes* s.l. is not meant to introduce a new formal taxonomic name, but, rather, simply to facilitate a collective reference to all four genera. Although the genus *Sporites* Wolff, 1934 might seem to have priority based on date of publication, it was Christopher (1976) who transferred and emended *Sporites circulus* to *Pseudoschizaea* (as *P. circula*). He noted that the generic name, *Sporites*, having become elevated to a “suprageneric taxonomic ranking” by Potonié in 1952, was subsequently abandoned by palynologists for use as a genus name.

3.2. Studies of the wall of Chomotriletes s.l.

The fundamental nature of wall structure in palynology is a principal feature of morphology that is critical for distinguishing between spores and pollen grains of plants with cysts of protistan (algal) origin or spores of fungi. One particular distinction to spore and pollen morphology is the nature of sculpture patterning, which is due to sporopollenin deposition on the surface of the spore or pollen wall. Thus, sculpture, in the conventional sense as used in descriptive palynology, is an applied structure that rests on top of the wall itself. The morphological descriptions of *Chomotriletes* s.l. throughout the literature refer to concentrically arranged costae or striae as a fundamental taxonomic character. Therefore, it is important to make the distinction as to whether the concentric pattern refers to sculptural elements or to the fundamental structure of the wall itself. To that end, we undertook a Transmission Electron Microscopy (TEM) examination of two different specimens of *Chomotriletes* s.l. The first is a Holocene specimen from a core taken at Lake Vouliagmeni (Greece) that spans the Holocene. The second specimen derives from Pliocene cores of IODP Site U1478. Together with a comprehensive microscopic study of *Pseudoschizaea* from the Lower Jurassic of Italy (Tekleva et al., 2021), there are now three distinct examples of the wall ultrastructure of *Chomotriletes* s.l.

3.2.1. Holocene Chomotriletes s.l.

Specimens were collected from Lake Vouliagmeni, Greece (see Koutsodendris et al., 2023 for details of specimen collection and preparation). The specimen examined under TEM is similar to that seen in the light micrograph in Plate I, 8. Concentric costae are clearly delineated in the TEM cross section (Plate II, 1), showing that the principal morphological feature that defines *Chomotriletes* s.l., is, in fact, an integral part of the wall itself and not an applied sculptural element as would be expected in the case of a pollen grain or spore. In LM the surficial costae are quite distinct from each other in the center (=pole), becoming more crowded together at the equatorial margin. This can be seen clearly in the TEM cross section in Plate II, 1. Costae are spaced approximately 1 μm apart; slightly more at the pole, slightly less at the equator. When viewed at higher magnification under TEM, it is apparent that the wall is comprised of a series of fused units, but the external projecting tips (costae) represent the fused tips of adjacent underlying wall units (Plate II, 2–4). The modular wall units are demarcated internally by an electron dense layer, designated here as a projecting line (pl, in Plate II, 2–4). The projecting lines are usually more prominent (darker) on one side of each wall unit, but they always appear to run through the middle of the outwardly projecting costae. Thus, the external costal projections are essentially aligned with depressions in the interior part of the wall, i.e., the cyst lumen extends up into the peaks of the costae. The protruding costae appear to be laterally fused adjacent tips of the wall units. The contribution of the adjacent units that form a costa is not exactly equal; the projecting lines do not exactly bisect the costa. The wall units themselves are characterized by a diffuse, fibrillar, U-shaped, nested pattern with the base of the “U” pointing inward (toward the geometric center of the cyst) and the tips of the “U” fused to adjacent wall units. It is these fused tips that appear as the outwardly projecting ribs or costae as seen in the LM images.

3.2.2. Pliocene Chomotriletes s.l.

The sectioned specimen as viewed in the light microscope (Plate I, 10–11) is about 40 μm in diameter - the maximum diameter is 48 μm and the smaller diameter is 37 μm, but the specimen is fragmented (torn) so the perimeter is incomplete. Overall, costae appear more-or-less concentric, but individual costae may be quite clearly branched (Plate I, 10, arrow). Sometimes the costae simply appear as truncated tapered tips wedged in-between adjacent costae (Plate I, 8, circle). This effectively blurs the distinction between concentric and helical arrangement of the costae; it is not generally easy to trace an individual costa around an entire specimen. At the poles the costae are more-or-less space-filling and here, too, they may appear to branch as they form a “fingerprint-like” pattern.

In cross-section individual costae appear flat-topped and may possess slight lateral extensions forming a keel (labeled ‘k’ in Plate II, 4). In the sectioned specimen the costate projections are considerable, so much so, that the wall thickness in between the costae may be less than half of the total wall thickness. The inner surface of the wall undulates with the convex (outward) undulations aligning with the high points of the costate projections. Thus, maximum wall thickness at the flattened peaks of the costae ranges from 1.2–2.0 μm, whereas the wall thickness between the costae is slightly less than 1 μm.

The overall organization of this specimen is nearly identical to the Holocene specimen (Plate II, 5). Internally, the wall appears to be

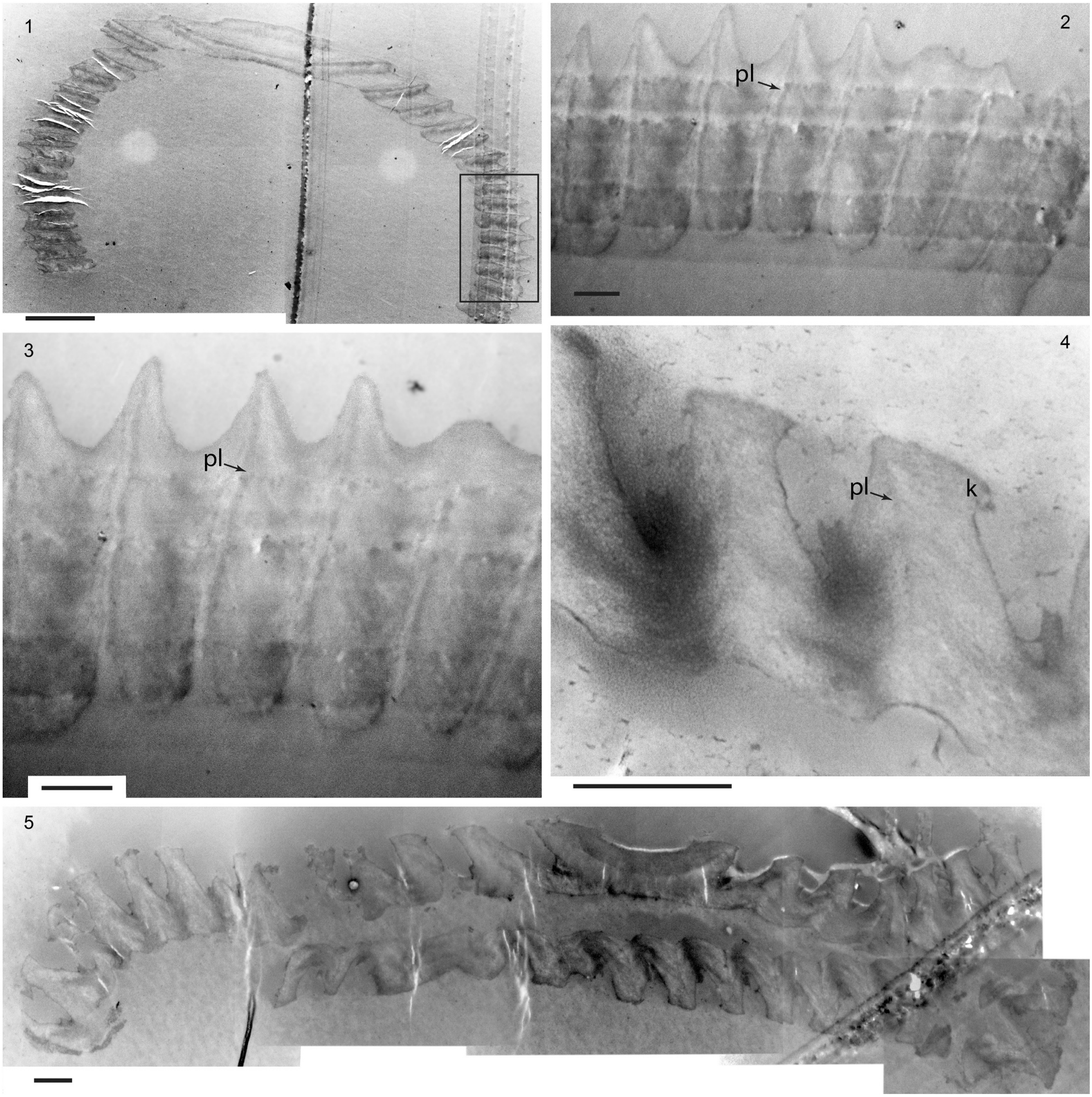

Plate II. TEM sections, showing wall ultrastructure of *Chomotriletes* s.l. Key to abbreviations: pl = projecting line; k = keel.

1–3. Holocene *Chomotriletes* s.l. from Lake Vouliagmeni like that shown in Plate I, 8.

1. TEM cross-section of cyst wall. The pole of the cyst is oriented at an angle of approx. 10° clockwise from vertical in the image; the equator is oriented at 90° to the pole. The costae seen in LM project from the outer surface of the cyst. They directly overlie outward projections of undulations on the inside of the cyst wall. Costae are relatively more widely spaced toward the pole than at the equator. The inset at right is seen at higher magnification in fig. 2 (rotated anticlockwise 90° degrees), and again in fig. 3. The dark line running down the center of the image, as well as the wider, lighter line just off the right edge are artifacts of preparation (knife marks). The very white arcs that appear on the specimen proper (most clearly seen at middle left) are tears in the epoxy section. Scale bar = 2 μm. 2. High outward-projecting costae (top) and undulations on the inner surface of the cyst wall (bottom) can be seen. A differentially processed version of this area appears in fig. 3. Scale bar = 500 nm. 3. Additional detail from cyst wall cross section near cyst equator (a smaller area of the inset in fig. 1) showing projecting line and hints of fibrillar substructure. This image is differentially processed to minimize the horizontally oriented knife marks. Scale bar = 500 nm. 4–5 Pliocene *Chomotriletes* s.l. from IODP core U1478, Mozambique Channel. 4. Detail of cyst wall from fig. 5 showing fainter projecting line than in the Holocene specimen, but similar alignment of the costal peaks with inner surface undulations. In this specimen, the costal peaks may show a slight asymmetric keel (k). The fibrillar substructure is evident. Scale bar = 1 μm. 5. TEM cross-section of flattened cyst wall. The pole of the cyst is just slightly clockwise from vertical in the image; the equator is nearly horizontal. Scale bar = 1 μm.

fibrillar, although the "fibrils" themselves are not particularly distinct. This can be seen in higher magnification TEM images (Plate II, 4). The fibrils form a stacked chevron pattern which appears to be centered around the projecting lines, which cross the wall from the apex of the inner wall undulations to the margin of the flattened costate projections (labeled 'pl' in Plate II, 4). This conveys a sense of asymmetry to the costae, in that the projecting lamina is not centered within the projection itself. There are hints of "U-shaped" structure in the fibrils that connect between the costate projections, but the sense of distinct wall units as seen in the Holocene specimen (Plate II, 1–3) is not evident here. Instead, the structural units seem to be centered around the pl and their external manifestation as projecting costae.

3.2.3. Jurassic Pseudoschizaea

Jurassic specimens of *Pseudoschizaea* were examined with TEM by Tekleva et al. (2021). They refer to the ribbed nature as being composed of "denticles", which is confusing from our perspective as the surface pattern is more striate, not "tooth-like" as would be implied by the term, denticle. Tekleva et al. (2021) also noted the electron dense lines (our pl) that traverse the wall radially, which they describe as, "… a striation through the wall thickness…" (Tekleva et al., 2021, p. 225). They discuss the importance of this structural feature which they noted is fundamentally in contrast to the concentric lamination seen in cross sections of the walls of land plant spores and pollen grains. Aside from the exact shape of the costate projections in cross-section, the Jurassic specimens appear structurally similar to those we have described above.

3.2.4. The wall ultrastructure of Chomotriletes s.l.

All three samples examined to date possess a set of common characteristics. The costate projections all appear to lie on top of positive (outwardly projecting) undulations of an inner wall surface. The internal, fibrillar nature of the wall material seems to align with an electron dense zone (the pl) that traverses the wall, again, projecting outwardly from positive undulations of the inner wall surface. The wall itself is constructed of modular units that correspond to the projecting costae. These units are generally arranged concentrically, corresponding to the ribbed appearance of *Chomotriletes* s.l. in LM, but they are rarely perfectly so, and all specimens show some form of costal branching or intercostal originations. This space-filling pattern could be explained by a very low helical organization of the costae. The wall-ultrastructural organization of *Chomotriletes* s.l. is, as far as we are aware, unlike any other protist group examined to date. And, as noted by Tekleva et al. (2021), it is clearly distinct from any known embryophyte spore or pollen grain.

4. Discussion

4.1. On the systematic affinity of Chomotriletes s.l.

The unique wall structure established above leads to a more general question as to the systematic affinity of this fossil. The new TEM data presented here affirms what was discovered by Tekleva et al. (2021), who made a comparison of their results with a range of NPPs of known provenance. They first eliminated embryophytic spores and pollen grains as a possible source, due primarily to the incompatibility of basic wall structure. This is consistent with the findings of prior palynological studies of fossil *Pseudoschizaea* that found no good evidence of a trilete or monolete laesura (e.g. Potonié, 1966), hence eliminating an embryophyte origin to *Pseudoschizaea*. Next, they made comparisons with algae, fungi and invertebrate eggs, but found no convincing homologs outside of the algae. Within the algae, prior studies based on LM have resulted in weakly supported proposals of zygnematalean affinities for members of the *Chomotriletes* s.l. group (Colbath and Grenfell, 1995), but there is no convincing evidence that wall ultrastructure is at all similar to zygospores of the Zygnemataceae. In fact, ultrastructural studies of multiple species of zygnematacean zygospores by Permann et al. (2022, 2021a, 2021b) show a three parted wall that is quite distinct from that seen in *Chomotriletes* s.l. as documented here. Mays et al. (2021) present the latest summary of the prior evidence that supports a zygnematacean affinity for *Chomotriletes* s.l., but they provide no additional new evidence in support of this interpretation. In addition, surface sculpture patterning in zygnematacean zygospores, such as *Debarya*, which is characterized by fine, radially-aligned partial striae, are not at all like those of *Chomotriletes* s.l. with their robust to fine concentric costae. In the end, Tekleva et al. (2021), concluded that the closest match to *Pseudoschizaea* was within the euglenoids.

It is curious that there are no ultrastructural studies on the walls of extant euglenoid cysts, perhaps reflecting the rarity of cyst formation in living members of the Euglenophyceae. Cyst formation is mentioned to occur in Euglena (Gojdics, 1953; Graham and Wilcox, 2000; Leander et al., 2017; Smith, 1933) – where they are sometimes associated with palmelloid stages in the life cycle. Bower (1919, fig. 266 D) illustrated a drawing of a circular cyst that shows an interior ball of refractile granules and a thick, clear outer wall, but, as an illustration in cross section, it did not show distinct concentric surface patterning. Bower's figure is reproduced here as Fig. 2A.

In Fig. 2B we illustrate an example of two extant euglenoid cysts that were found in a pond in New South Wales, Australia. The encystment process was filmed in a microscope strew slide and is available as Supplementary Video 1in the On-line Supplementary Information. Here, individuals from a population of *Euglena* sp. are seen to first ball up, and then transform into a spherical cyst with a thick, articulated wall (*w*) and a densely packed central zone of highly refractile bodies. The remnant of the red eyespot (*r*) can also be seen within the spherical mass. In optical section the wall is comprised of a radially oriented series of homogeneous material which is topologically comparable to the wall ultrastructures presented in Plate II, although the number of articulations is fewer in the living species. In Fig. 2C, the striated pellicle (*p*) is still visible on the cyst surface.

Hindák et al. (2000), directly observed cyst formation in two species of *Euglena*. Their illustrations show discoidal, circular cysts with concentric costae and with the polar "fingerprint-like" patterning that is characteristic of some *Chromotriletes* s.l. Although they did not provide LM illustrations, the SEM illustrations show an unambiguous similarity to *Chomotriletes* s.l. Comparison of the SEM illustrations of Hindák et al. (2000), with the Jurassic specimens of *Pseudoschizaea*, also helped lead Tekleva et al. (2021) to conclude that *Pseudoschizaea*, was a euglenoid, rather than a zygnematacean cyst.

Recent work on the fossil record of the Euglenophyceae has shown that *Moyeria* Thusu, formerly considered as an acritarch (Gray and Boucot, 1989), belongs to the Euglenida (Strother et al., 2020). Thus, the stratigraphic distribution of *Moyeria* provides a proxy record of the euglenoids through geologic time. Intriguingly, based on ultrastructure of the pellicle wall (Strother et al., 2020), *Moyeria*, was probably the vegetative form of a euglenoid – not a cyst. And *Moyeria*, which was originally described from the middle Silurian of New York state (Thusu, 1973), clearly overlaps in geologic time with *Chomotriletes* s.l. There are reports citing *Moyeria*, or OWMs similar to *Moyeria*, extending as far back as the Cambrian-Precambrian boundary (Yin, 1987) and possibly to the 1.1 Ga Nonesuch Formation (Slotznick et al., 2023; Strother and Wellman, 2020).

4.2. Paleo-environmental preferences

Several possible affinities have been suggested for concentrically sculptured hyaline non-pollen palynomorphs that belong to *Chomotriletes* s.l. The exhaustive catalog of plankton from European lakes produced by Huber-Pestalozzi (1955), contains line drawings of cysts that bear a superficial resemblance to *Chomotriletes* s.l. Attribution of these cysts to the Zygnemataceae by Huber-Pestalozzi has been followed by numerous later authors, including Scafati et al. (2009) and Grenfell (1995). The combination of a freshwater environment and closely

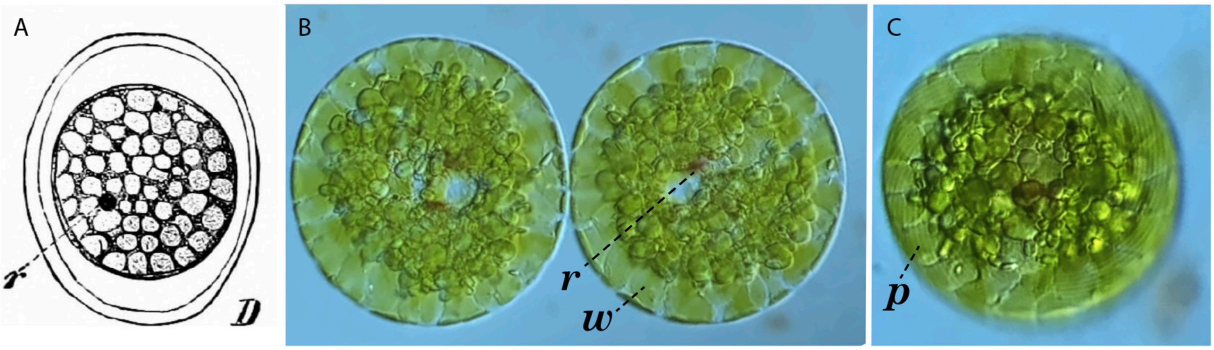

Fig. 2. Extant euglenoid cysts. A. Drawing of a Euglenid cyst illustrated as fig. 266 D in Bower (1919). B, C. *Euglena* sp. cysts from a small pond in Mardi NSW 2259 (33°16′33.2″S 151°23′56.5″E), Australia. B. Still image from Supplementary Video showing completed *Euglena* sp. cyst in medial section. C. Completed *Euglena* sp. cyst in surface section, *r* points to degraded eyespot, *w* points to an articulated wall segment, and p points to surficial pellicle strips.

spaced striae has led others to suggest a source with the euglenoids. Da et al. (2014) include a line drawing of a microscopic body (cyst?) that they attribute to *Trachelomonas anulifera* from Ivory Coast, which bears similar concentric patterning. The case for a euglenoid source was bolstered by Hindák et al. (2000) who studied surface blooms on fresh water in Slovakia that included cysts of *Euglena anabaena* and *E. agilis*. These authors figured a cyst of *Euglena anabaena* under SEM with a concentric appearance that closely resembles *Chomotriletes* s.l. (Hindák et al., 2000, fig. 37). This particular cyst appears to be substantially smaller than most other examples of *Chomotriletes* s.l. as discussed in this report, although we suspect this may be due to an inadvertent scale bar in the original figure.

We compiled literature data on occurrences of *Chomotriletes, Circulisporites, Pseudoschizaea* and *Concentricystes* to better understand the ecology of *Chomotriletes* s.l. and tabulated taxonomic, stratigraphic, biological, geographic, and ecological data in Table S1 (Online Supplementary Information). Table S1 contains nearly 500 citations to all literature reports that mention *Pseudoschizaea, Concentricystes*, *Chomotriletes* and *Circulisporites*. While we do not claim this literature survey to be exhaustive, clear patterns emerge, particularly on the (paleo)ecology of the organism producing the *Chomotriletes* s.l. cysts. The consistent occurrence of *Chomotriletes* s.l. in rivers and wetlands in Holocene samples indicates a freshwater or terrestrial environment for the organisms that produce these cysts. Fewer than 20% of the records are from marine settings, and, in most cases, these come from coastal settings, not open marine environments. The vast majority of records stem from riverine settings, wetlands, and soils. While many marine occurrences do not preclude a terrestrial origin, the predominant occurrence in many terrestrial settings does preclude a marine affinity.

The relationship with terrestrial environments is also shown by the disparity in the stratigraphic distribution of *Chomotriletes* s.l. The majority of reports stem from the Pleistocene and Holocene to Recent ($n = 324$), which is clearly an artifact of both preservation and the generally large community of Quaternary palynologists. But for older time intervals, the number of records of *Chomotriletes* s.l. per stage tracks the abundance of preserved terrestrial sediments through time. For example, there are astoundingly few records from the Jurassic ($n = 9$; Table S1), a time interval characterized by high spreading rates, high sea levels and predominantly marine sedimentation. On the other hand, periods which are characterized by abundantly preserved terrestrial sediments, such as the Permian to Triassic ($n = 50$), are overrepresented. Also, the (Lower) Cretaceous, a time interval of generally warm and humid climate conditions and widespread terrestrial deposition (e.g. the Wealden), is well represented ($n = 49$). While nearly all records from the Silurian, Ordovician and Devonian are from marine deposits, it is surprising that the Carboniferous with its extensive coal swamps shows very few records. This likely indicates that the organisms producing *Chomotriletes* s.l. did not thrive in the coal swamps that existed during that time.

Regardless of stratigraphic age, a vast majority of authors in our compilation suggest that the organism producing *Chomotriletes* s.l. is linked to freshwater environments. This is based either on the facies the microfossils occur in, which range from swamps to rivers and soils associated with riverine settings, or the fact that *Chomotriletes* s.l. occurs frequently in association with other freshwater indicators, such as zygospores from Zygnematacean algae or *Botryococcus* (e.g. Brenner and Foster, 1994; Hunt and Premathilake, 2012; Zippi, 1998). Based on our literature survey it is clear that most Holocene occurrences are linked with lacustrine and fluvial environments. This compares well with many deep time records, where some of the first descriptions of *Chomotriletes* s. l. were derived from brown coal deposits. The original *Sporites circulus* Wolf, described in 1934, stems from a Pliocene brown coal (Wolff, 1934), and the revision of the genus was based on material from a Pliocene brown coal in India (Thiergart and Frantz, 1962).

Numerous authors see the presence of *Chomotriletes* s.l. in marine sediments as the result of reworking from a terrestrial environment, for example during soil erosion and transport via rivers (Baroni et al., 2008; Kholeif, 2010; Munoz-Sobrino et al., 2012). Some authors have commented on the link between *Chomotriletes s.l.* and soil erosion events following strong run-off (Mercuri et al., 2010). The co-occurrence of *Concentricystes* and reworked Eocene lithoclasts in a paleolake in Northern Spain was linked to strong run-off and ensuing collapse of the lake margin (Lovlie and Leroy, 1995). But a link to reworking and run-off has also been suggested for Holocene occurrences in marine sediments in estuaries, such as for the Black Sea (Mudie et al., 2011) and the Mediterranean (Palanques et al., 1998). Some authors witness increases in *Chomotriletes s.l.* during the Holocene in response to early agricultural activities and increased erosion (López-Merino et al., 2010). Recent mass-occurrences in estuaries in southern France have been linked to soil erosion as a result of environmental management (Debenay et al., 2003). Reworking and run-off appear to be a fitting explanation for the occasional occurrences of *Chomotriletes* s.l. in marine offshore deposits, as pointed out by Takahashi (1979).

Reworking of cysts would likely be promoted if the cysts formed during drying of swampy or riverine settings, whereby the cysts would perennate in soils and would excyst during the rainy season. Such an explanation was initially proposed by Scott (1992) and later adopted by Puech et al. (2017) and Tripathi et al. (2018). Carrión et al. (2003) saw a clear link between desiccation of basins in southern Spain and occurrences of *Pseudoschizaea* in connection to the spread of steppic pollen types.

4.3. (Paleo)biogeographic considerations

Based on a selection of Plio-Pleistocene and Holocene occurrences, a paleobiogeographic map was constructed (Fig. 4) showing the very wide distribution of *Chomotriletes* s.l. A remarkably consistent distribution can be recognized for both the southern and northern hemispheres, whereby *Chomotriletes* s.l. occurs between approximately 45° North and 40° South. It thus has a temperate to tropical distribution, but is absent from colder higher latitudes. It is very common in studies dealing with organic rich sediments from coastal lagoons along Brazil's coastline (e.g. da Costa Spalding and Lorscheitter, 2009; Gonçalves de Freitas et al., 2015), while in China it occurs especially abundantly along the Yangtze River. There are also numerous records from around the Mediterranean in Italy, Spain, Greece, Israel and Egypt. Records from Spain and Italy are often linked to archeological investigations, such as at the famous dolines at Atapuerca (northern Spain), where *Chomotriletes* s.l. is often found in deposits containing hominid remains (Expósito et al., 2017).

Chomotriletes s.l. is clearly less abundant in the United States, New Zealand, and Africa. A certain degree of caution is needed because of possible sampling artifacts. There are very few records from equatorial Africa, while Spain and Italy are overrepresented, also compared to other circum-mediterranean countries. This is likely due to sizable communities of Quaternary palynologists spread unequally between these regions. Despite such biases, the distribution of *Chomotriletes* s.l. does point at a dominant temperature and humidity control. For example, a near absence from Australia (except for a site in northern Australia; Field et al., 2018) could be the result of generally very dry conditions governing large portions of that continent. A connection to wetlands and floodplain settings is evident from the biogeography of Holocene *Chomotriletes* s.l. in China, while in India occurrences are linked to coastal wetlands and mangroves (Sen and Banerjee, 1990). But also, occurrences further removed from the coastline, such as in the Himalaya, appear to be connected to tropical vegetation zones (Ghosh et al., 2017).

Some interesting outliers confirming the warm and humid constraints, include well preserved specimens of *Chomotriletes* s.l. from an atoll in the Easter Caroline Islands, in the middle of the Pacific (Ward, 1988), where it is linked to freshwater swamps on the atoll. The striking absence of *Chomotriletes* s.l. from high northern latitudes, regions that today and during the Quaternary are characterized by widespread peat bog accumulations, suggests that either lower temperatures or ecosystems like peat bogs were not and are not conducive to the presence of *Chomotriletes*. Although unlikely as an explanation, peat bogs may be too acidic to allow fossilization.

4.4. Implications for mass-extinction scenarios

The consistent presence of *Chomotriletes* s.l. in sediments in proximity to the end-Triassic mass-extinction in a number of sites across the Central European Basin has a bearing on discussions regarding the causes of the extinction. The Triassic-Jurassic transition was marred by large-scale flood basalt volcanism in the Central Atlantic Magmatic Province that led to widespread deforestation and a proliferation of ferns and fern allies across NW Europe (Lindström, 2021; van de Schootbrugge et al., 2009). A combination of extreme climate variability, tectonic instability, and collapse of vegetation together led to strongly increased weathering, erosion, and run-off (van de Schootbrugge et al., 2020). The onset of this period of major upheaval coincides with the appearance of *Chomotriletes* s.l. in coeval latest Triassic shallow marine deposits across NW Europe, such as in the basal Triletes Beds at Bonenburg (Germany; Gravendyck et al., 2020), the top of the Klettgau Formation (Switzerland; Schneebeli-Hermann et al., 2018), and in the Bjuv Member in the Lunnom Quarry (Sweden; Lindström and Erlström, 2006). Together with the records from Schandelah, Mingolsheim, Boust and Winterswijk presented here, it becomes clear that *Chomotriletes* s.l. is a widespread taxon in sediments straddling the end-Triassic mass-extinction (Fig. 3).

The presence of cysts of *Chomotriletes* s.l. in the extinction interval likely signals a general increase in freshwater influx into the Central European Basin. This influx of freshwater could have been a direct result of extreme climate swings as a result of a fourfold increase in pCO_2 reconstructed from leaf stomata (Steinthorsdottir et al., 2011). Run-off may have been exacerbated by the changes in the vegetation away from a stable forest biome toward a pioneering vegetation composed

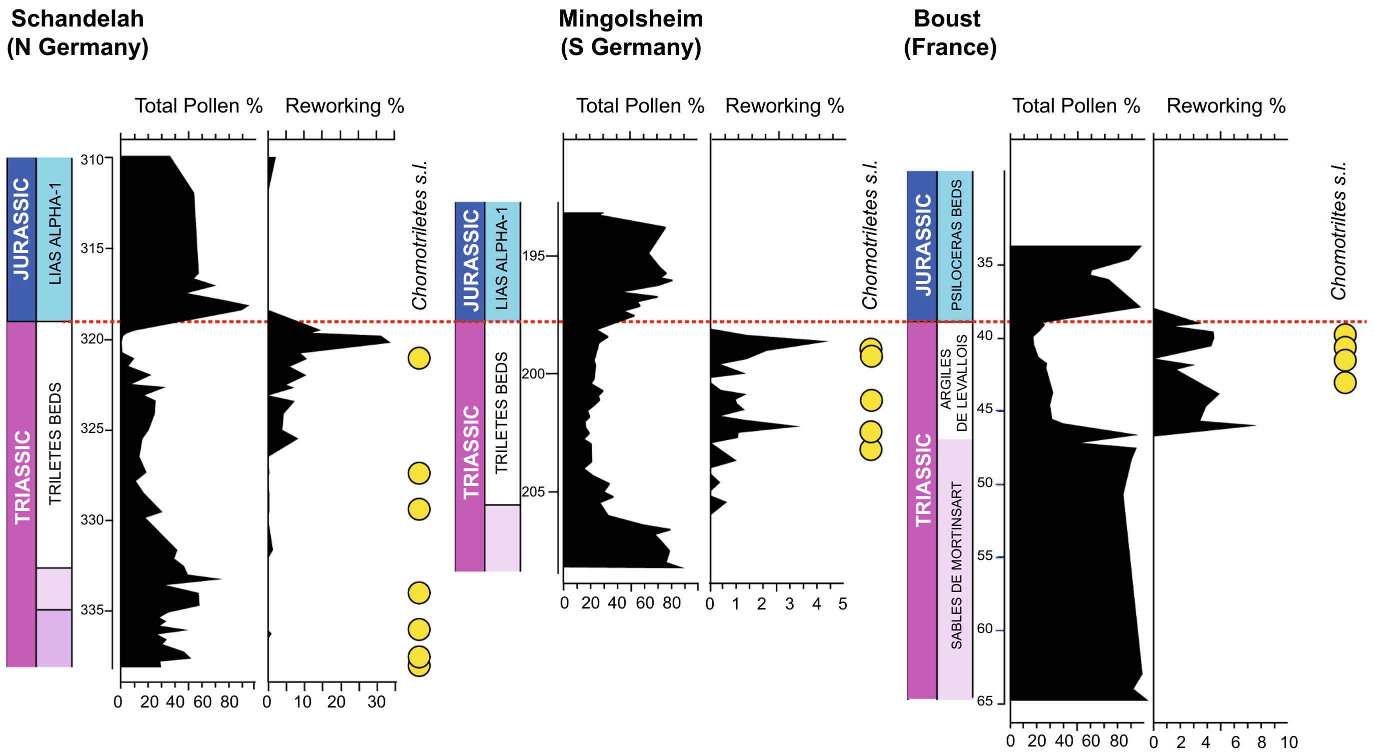

Fig. 3. Stratigraphic distribution of *Chomotriletes* s.l. in the Schandelah-1, Mingolsheim, and Boust cores. Yellow circles indicate samples where *Chomotriletes* s.l. was recovered. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

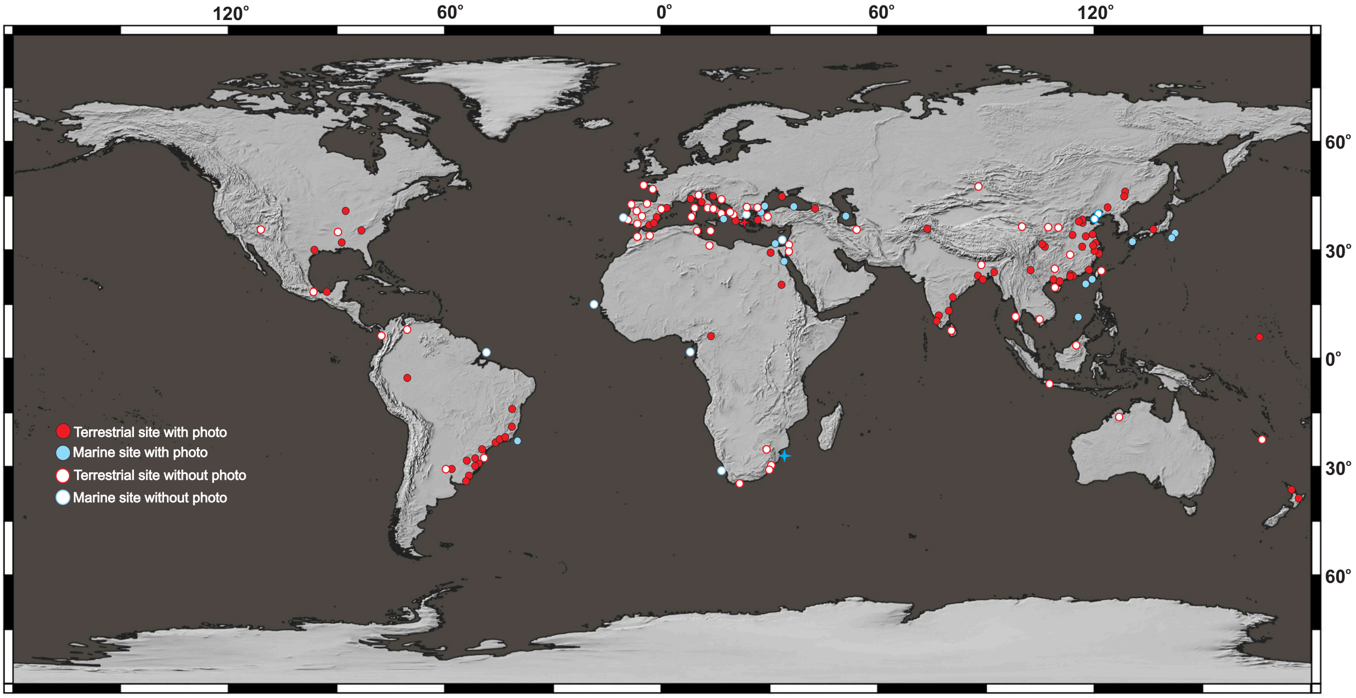

Fig. 4. Biogeography of *Chomotriletes* s.l. in Plio-Pleistocene and Holocene records. The distribution is based on a selection of the more than 300 compiled occurrences in order to show a maximum distribution. The data underlying the map are presented in Supplementary Table S2.

largely of ferns. Furthermore, periods of extreme drought interrupted by large storms are thought to have led to increased forest fire activity (Baker et al., 2020). Micro-charcoal (Williford et al., 2014) and PAHs (Marynowski and Simoneit, 2009) indicate biomass burning increased during the latest Triassic triggering the destruction of coastal wetlands (Petersen and Lindström, 2012).

"Ponding" due to strongly increased rainfall has recently been proposed as an additional stress factor during the end-Permian extinction (Mays et al., 2021). Deforestation resulting from environmental devastation at the Permian–Triassic boundary in Southern Australia led to strongly increased weathering, erosion, and run-off, causing eutrophication of freshwater lakes and rivers. These events are reflected in high recorded abundances of *Circulisporites*, a.k.a. *Chomotriletes* s.l. This scenario is thus similar to what we observe for the end-Triassic extinction, although we refrain from linking it to toxic microbial blooms since euglenoids are not known to produce such toxins. The euglenoids today are predominantly freshwater in distribution, where they are typically associated with ponds and freshwater settings that are rich in organic matter (Gojdics, 1953; Hindák et al., 2000; Leander et al., 2017). This distribution today is consistent with the paleoenvironmental distribution of *Chomotriletes* s.l., adding to the likelihood that this taxon is a preserved form of some species of the Euglenophyceae.

5. Conclusion

We conclude that *Chomotriletes* is the valid senior synonym of a variety of taxa, including *Circulisporites*, *Pseudoschizaea*, and *Concentricystes*. This observation effectively extends the fossil record of *Chomotriletes* s.l. from at least the Ordovician until today. The cysts are concentric and show a variable number of thicker or finer ribs or costae. Some species show a thickened disc at both poles, or a characteristic fingerprint-like pattern consisting of muri. *Chomotriletes* s.l. is considered to be a cyst of a freshwater organism that was, and is, prevalent in floodplain soils and ephemeral freshwater lakes. Marine occurrences are all indicative of transport from land, and high abundances in marine sediments may point to depositional conditions of intense erosion and run-off. TEM analyses show that the structure of the wall is unlike anything seen in any freshwater algal (protist) group. Therefore, an affinity with zygnematacean green algae appears unlikely, even though *Chomotriletes* s.l. often occurs together with zygospores of Zygnemataceae. These factors, including morphology, biogeographic distribution, and restricted depositional distribution, lead us to infer that *Chomotriletes* s.l. is most likely the encysted form of species belonging to the Euglenophyceae.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2023.105043.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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References

Baker, S., Dewhirst, R., McElwain, J., Haworth, M., Belcher, C., 2020. CO_2 driven changes in leaf biochemistry may have influenced fire behavior at the Triassic-Jurassic boundary. In: EGU General Assembly 2020, Online, 4–8 May 2020, EGU2020-8146. https://doi.org/10.5194/egusphere-egu2020-8146.

Baroni, C., Fasano, F., Giorgetti, G., Salvatore, M.C., Ribecai, C., 2008. The Ricker Hills Tillite provides evidence of Oligocene warm-based glaciation in Victoria Land, Antarctica. Global Planet. Change 60, 457–470. https://doi.org/10.1016/j.gloplacha.2007.05.004.

Batten, D.J., Koppelhus, E.B., Nielsen, L.H., 1994. Uppermost Triassic to Middle Jurassic palynofacies and palynomiscellanea in the Danish Basin and Fennoscandian border zone. Cah. Micropaleontol. 9, 21–45.

Bos, R., Lindström, S., van Konijnenburg-van Cittert, H., Hilgen, F., Hollaar, T.P., Aalpoel, H., van der Weijst, C., Sanei, H., Rudra, A., Sluijs, A., van de Schootbrugge, B., 2023. Triassic-Jurassic vegetation response to carbon cycle perturbations and climate change. Global Planet. Change 228, 104211. https://doi.org/10.1016/j.gloplacha.2023.104211.

Bower, F.O., 1919. Botany of the Living Plant. MacMillan Co., Ltd, London.

Brenner, W., Foster, C.B., 1994. Chlorophycean algae from the Triassic of Australia. Rev. Palaebot. Palynol. 80, 209–234.

Carrión, J.S., Sánchez-Gómez, P., Mota, J.F., Yll, R., Chaín, C., 2003. Holocene vegetation dynamics, fire and grazing in the Sierra de Gádor, southern Spain. Holocene 13, 839–849. https://doi.org/10.1191/0959683603hl662rp.

Chen, W., Wang, W.-M., Dai, X.-R., 2008. Holocene vegetation history with implications of human impact in the Lake Chaohu area, Anhui Province, East China. Veg. Hist. Archaeobotany 18, 137–146. https://doi.org/10.1007/s00334-008-0173-7.

Christopher, R.A., 1976. Morphology and Taxonomic Status of *Pseudoschizaea* Thiergart and Frantz ex R. Potonié Emend. Micropaleontology 22, 143–150.

Clarke, R.F.A., 1965. Keuper miospores from Worcestershire, England. Palaeontology 8, 16–28.

Colbath, C.K., Grenfell, H.R., 1995. Review of biological affinities of Paleozoic acid-resistant, organic-walled eukaryotic algal microfossils (including “acritarchs”). Rev. Palaebot. Palynol. 86, 287–314.

Da, K., Bambara, S., N’guessan, K., 2014. Étude de quelques *Trachelomonas* Ehr. (Euglenophyta) nouveaux ou peu connus pour la Côte d’Ivoire. Int. J. Biol. Chem. Sci. 8, 1730–1741. https://doi.org/10.4314/ijbcs.v8i4.32.

da Costa Spalding, B.B., Lorscheitter, M.L., 2009. Palinologia de sedimentos da turfeira do Banhado Amarelo, São Francisco de Paula, Rio Grande do Sul, Brasil. Fungos e criptógamas. Hoehnea 36, 219–232.

Davies, N.S., Gibling, M.R., 2010. Cambrian to Devonian evolution of alluvial systems: the sedimentological impact of the earliest land plants. Earth Sci. Rev. 98, 171–200.

Debenay, J.P., Carbonel, P., Morzadec-Kerfourn, M.T., Cazaubon, A., Denèfle, M., Lézine, A.M., 2003. Multi-bioindicator study of a small estuary in Vendée (France). Estuar. Coast. Shelf Sci. 58, 843–860. https://doi.org/10.1016/s0272-7714(03)00189-6.

Ellis, E., 2006. Corrected formulation for Spurr low viscosity embedding medium using the replacement epoxide ERL 4221. Microsc. Microanal. 12, 288–289. https://doi.org/10.1017/s1431927606062660.

Expósito, I., Burjachs, F., Allué, E., 2017. Filling in the gaps: the contribution of non-pollen palynomorphs to knowledge about the local environment of the Sierra de Atapuerca caves during the Pleistocene. Quat. Int. 433, 224–242.

Fensome, R.A., Williams, G.L., Barss, M.S., Freeman, J.M., Hill, J.M., 1990. Acritarchs and fossil prasinophytes: an index to genera, species and infraspecific taxa. A.A.S.P. Contrib. Ser. 25, 1–771.

Field, E., Tyler, J., Gadd, P.S., Moss, P., McGowan, H., Marx, S., 2018. Coherent patterns of environmental change at multiple organic spring sites in northwest Australia: evidence of Indonesian-Australian summer monsoon variability over the last 14,500 years. Quat. Sci. Rev. 196, 193–216.

Filipiak, P., Krawczyński, W., 2018. Palynological and microfacies analysis of the Famennian part of the Russkiy Brod Quarry section, Central Devonian Field, Russia. Rev. Palaebot. Palynol. 249, 50–60. https://doi.org/10.1016/j.revpalbo.2017.11.004.

Ghosh, R., Paruya, D.K., Acharya, K., Ghorai, N., Bera, S., 2017. How reliable are non-pollen palynomorphs in tracing vegetation changes and grazing activities? Study from the Darjeeling Himalaya, India. Palaeogeogr. Palaeoclimatol. Palaeoecol. 475, 23–40.

Gojdics, M., 1953. The genus *Euglena*. The University of Wisconsin Press, Madison WI.

Gonçalves de Freitas, A., de Araujo Carvalho, M., Bevilacqua de Toledo, M., Ferreira Mendonça, C.B., Gonçalves-Esteves, V., 2015. Bryophyte and pteridophyte spores and other palynomorphs in quaternary marine sediments from Campos Basin, southeastern Brazil: Core BU-91-GL-05. Acta Bot. Brasil. 29, 161–174. https://doi.org/10.1590/0102-33062014abb3734.

Graham, L.E., Wilcox, L.W., 2000. Algae. Prentice-Hall, Inc., Upper Saddle River, NJ.

Gravendyck, J., Schobben, M., Bachelier, J.B., Kürschner, W.M., 2020. Macroecological patterns of the terrestrial vegetation history during the end-Triassic biotic crisis in the central European Basin: a palynological study of the Bonenburg section (NW-Germany) and its supra-regional implications. Global Planet. Change 194, 103286. https://doi.org/10.1016/j.gloplacha.2020.103286.

Gray, J., Boucot, A.J., 1989. Is *Moyeria* a euglenoid? Lethaia 22, 447–456. https://doi.org/10.1111/j.1502-3931.1989.tb01449.x.

Grenfell, H.R., 1995. Probable fossil zygnematacean algal spore genera. Rev. Palaebot. Palynol. 84, 201–220. https://doi.org/10.1016/0034-6667(94)00134-6.

Hart, G.F., 1965. *Chomotriletes* from the lower Permian of South Africa. Ann. Geol. Surv. South Africa 3, 149–157.

Hindák, F., Wolowski, K., Hindáková, A., 2000. Cysts and their formation in some neustonic *Euglena* species. Ann. Limnol. Int. J. Limnol. 36, 83–93. https://doi.org/10.1051/limn/2000010.

Hoelstad, T., 1985. Palynology of the uppermost Lower to Middle Jurassic strata on Bornholm, Denmark. Bull. Geol. Soc. Den. 34, 111–132.

Horrocks, M., Jones, M.D., Beever, R.E., Sutton, D.G., 2002. Analysis of plant microfossils in prehistoric coprolites from Harataonga Bay, Great Barrier Island, New Zealand. J. R. Soc. New Zeal. 32, 617–628. https://doi.org/10.1080/03014223.2002.9517712.

Huber-Pestalozzi, G., 1955. Das Phytoplankton des Süßwassers 4: Euglenophyceen. Die Binnengewasser 16 (4) (Schweizerbart).

Hunt, C.O., Premathilake, R., 2012. Early Holocene vegetation, human activity and climate from Sarawak, Malaysian Borneo. Quat. Int. 249, 105–119. https://doi.org/10.1016/j.quaint.2011.04.027.

Jansonius, J., Hills, L.V., 1976. Genera File of Fossil Spores, Special Publication (with Supplements). Department of Geology and Geophysics, University of Calgary, Alberta.

Jerzykiewicz, T., Sweet, A.R., 1988. Sedimentological and palynological evidence of regional climatic changes in the Campanian to Paleocene sediments of the Rocky Mountain Foothills, Canada. Sediment. Geol. 59, 29–76.

Kholeif, S.E.A., 2010. Holocene paleoenvironmental change in inner continental shelf sediments, Southeastern Mediterranean, Egypt. J. Afric. Earth Sci. 57, 143–153. https://doi.org/10.1016/j.jafrearsci.2009.08.001.

Koutsodendris, A., Nakajima, K., Kaboth-Bahr, S., Berke, M.A., Franzese, A.M., Hall, I.R., Hemming, S.R., Just, J., LeVay, L.J., Pross, J., Robinson, R., 2021. A Plio-Pleistocene (c. 0–4 Ma) cyclostratigraphy for IODP Site U1478 (Mozambique Channel, SW Indian Ocean): exploring an offshore record of paleoclimate and ecosystem variability in SE Africa. Newsl. Stratigr. 54, 159–181. https://doi.org/10.1127/nos/2020/0608.

Koutsodendris, A., Brauer, A., Friedrich, O., Tjallingii, R., Putyrskaya, V., Hennrich, B., Kühn, B., Klemt, E., Pross, J., 2023. Natural and human-induced ecosystem change in SE Europe since 1700 AD derived from a partially varved sediment record from Lake Vouliagmeni (Greece). The Holocene 33, 1207–1220. https://doi.org/10.1177/095968362311830.

Krutzsch, W., Pacltová, P., 1990. Die Phytoplankton-Mikroflora aus den pliozänen Süsswasserablagerungen des Cheb-Beckens (Westböhmen, CSFR). Acta Univ. Carolinae – Geol. 34, 345–420.

Leander, B.S., Lax, G., Karnkowska, A., Simpson, A., G., B, 2017. Euglenida. In: Archibald, J.M., Simpson, A., G., B, Slamovits, C. (Eds.), Handbook of the Protists (2nd edition of the Handbook of Protoctista by Margulis et al.). Springer International Publishing, Dordrecht, The Netherlands, pp. 1–41.

Lindström, S., 2021. Two-phased mass rarity and extinction in land plants during the End-Triassic climate crisis. Front. Earth Sci. 9, 780343 https://doi.org/10.3389/feart.2021.780343.

Lindström, S., Erlström, M., 2006. The late Rhaetian transgression in southern Sweden: regional (and global) recognition and relation to the Triassic–Jurassic boundary. Palaeogeogr. Palaeoclimatol. Palaeoecol. 241, 339–372. https://doi.org/10.1016/j.palaeo.2006.04.006.

López-Merino, L., Cortizas, A.M., López-Sáez, J.A., 2010. Early agriculture and palaeoenvironmental history in the North of the Iberian Peninsula: a multi-proxy analysis of the Monte Areo mire (Asturias, Spain). J. Archaeol. Sci. 37, 1978–1988. https://doi.org/10.1016/j.jas.2010.03.003.

Lovlie, R., Leroy, S., 1995. Magnetostratigraphy of Lower Pleistocene Banyole paleolake carbonate sediments from Catalonia, NE Spain: evidence for relocation of the Cobb Mountain sub-chiron. Quat. Sci. Rev. 14, 473–485.

Marynowski, L., Simoneit, B.R.T., 2009. Widespread upper Triassic to lower Jurassic wildfire records from Poland: evidence from charcoal and pyrolytic polycyclic aromatic hydrocarbons. Palaios 24, 785–798. https://doi.org/10.2110/palo.2009.p09-044r.

Mays, C., McLoughlin, S., Frank, T.D., Fielding, C.R., Slater, S.M., Vajda, V., 2021. Lethal microbial blooms delayed freshwater ecosystem recovery following the end-Permian extinction. Nat. Commun. 12, 5511. https://doi.org/10.1038/s41467-021-25711-3.

Mercuri, A.M., Florenzano, A., N’siala, I.M., Olmi, L., Roubis, D., Sogliani, F., 2010. Pollen from archaeological layers and cultural landscape reconstruction: case studies from the Bradano valley (Basilicata, southern Italy). Plant Biosyst. Int. J. Dealing Aspects of Plant Biol. 144, 888–901. https://doi.org/10.1080/11263504.2010.491979.

Morris, J.L., Puttick, M.N., Clark, J.W., Edwards, D., Kenrick, P., Pressel, S., Wellman, C. H., Yang, Z., Schneider, H., Donoghue, P.C.J., 2018. The timescale of early land plant evolution. PNAS 115, E2274–E2283. https://doi.org/10.1073/pnas.1719588115.

Mudie, P.J., Leroy, S.A.G., Marret, F., Gerasimenko, N., Kholeif, S.E.A., Sapelko, T., Filipova-Marinova, M., 2011. Nonpollen palynomorphs: indicators of salinity and environmental change in the Caspian–Black Sea–Mediterranean corridor. In: Buynevich, I., Yanko-Hombach, V., Gilbert, A.S., Martin, R.E. (Eds.), Geology and Geoarchaeology of the Black Sea Region: Beyond the Flood Hypothesis, Geological Society of America Special Paper 473. https://doi.org/10.1130/2011.2473(07.

Munoz-Sobrino, C.M., García-Gil, S., Iglesias, J., Carreño, N.M., Costa, J.F.D., Varela, R. A.D., Judd, A., 2012. Environmental change in the Ría de Vigo, NW Iberia, since the mid-Holocene: new palaeoecological and seismic evidence. Boreas 41, 578–601. https://doi.org/10.1111/j.1502-3885.2012.00255.x.

Naumova, S.N., 1939. Spores and pollen of the coals of the USSR. XVIII International Geological Congress 1, 353–364.

Naumova, S.N., 1953. Spore-pollen complexes of the Upper Devonian of the Russian Platform and their stratigraphic value (in Russian). Akademii Nauk. SSSR, Trudy, seriya geologicheskaya 60, 1–154.

Norris, G., 1965. Triassic and Jurassic miospores and acritarchs from the Beacon and Ferrar groups, Victoria land, Antarctica. N. Z. J. Geol. Geophys. 8, 236–277. https://doi.org/10.1080/00288306.1965.10428110.

Norström, E., Neumann, F.H., Scott, L., Smittenberg, R.H., Holmstrand, H., Lundqvist, S., Snowball, I., Sundqvist, H.S., Risberg, J., Bamford, M., 2014. Late Quaternary vegetation dynamics and hydro-climate in the Drakensberg, South Africa. Quat. Sci. Rev. 105, 48–65. https://doi.org/10.1016/j.quascirev.2014.09.016.

Palanques, A., Sanchez-Cabeza, J.A., Masqué, P., Léon, L., 1998. Historical record of heavy metals in a highly contaminated Mediterranean deposit: the Besòs prodelta. Mar. Chem. 61, 209–217.

Permann, C., Herburger, K., Felhofer, M., Gierlinger, N., Lewis, L.A., Holzinger, A., 2021a. Induction of conjugation and zygospore cell wall characteristics in the alpine *Spirogyra mirabilis* (Zygnematophyceae, Charophyta): advantage under climate change scenarios? Plants 10, 1740. https://doi.org/10.3390/plants10081740.

Permann, C., Herburger, K., Niedermeier, M., Felhofer, M., Gierlinger, N., Holzinger, A., 2021b. Cell wall characteristics during sexual reproduction of Mougeotia sp. (Zygnematophyceae) revealed by electron microscopy, glycan microarrays and RAMAN spectroscopy. Protoplasma 258, 1261–1275. https://doi.org/10.1007/s00709-021-01659-5.

Permann, C., Gierlinger, N., Holzinger, A., 2022. Zygospores of the green alga Spirogyra: new insights from structural and chemical imaging. Front. Plant Sci. 13, 1080111. https://doi.org/10.3389/fpls.2022.1080111.

Petersen, H.I., Lindström, S., 2012. Synchronous wildfire activity rise and mire deforestation at the Triassic–Jurassic boundary. PloS One 7, e47236. https://doi.org/10.1371/journal.pone.0047236.

Playford, G., Dring, R.S., 1981. Late Devonian acritarchs from the Carnarvon Basin, Western Australia. Spec. Pap. Palaeontol. 27, 1–78 pl. 1–19.

Potonié, R., 1966. Synopsis der Gattungen der Sporae dispersae IV. Teil: Nachträge zu allen Gruppen (Turmae). Geol. Jahrb. Beih. 72, 1–255 pls. 1–15.

Puech, E., Urrego, D.H., Goñi, M.F.S., Backwell, L., d'Erricoc, F., 2017. Vegetation and environmental changes at the Middle Stone Age site of Wonderkrater, Limpopo, South Africa. Quat. Res. 88, 313–326. https://doi.org/10.1017/qua.2017.42.

Rossignol, M., 1962. Analyse pollinique de sediments Quaternaires en Israël. I : Sediments Pleistocenes. Pollen Spores 4, 121–148.

Rubinstein, C.V., Gerrienne, P., Puente, G.S. de la, Astini, R.A., Steemans, P., 2010. Early Middle Ordovician evidence for land plants in Argentina (eastern Gondwana). New Phytol. 188, 365–369. https://doi.org/10.1111/j.1469-8137.2010.03433.x.

Scafati, L., Melendi, D.L., Volkheimer, W., 2009. A Danian subtropical lacustrine palynobiota from South America (Bororó Formation, San Jorge Basin, Patagonia - Argentina). Geol. Acta 7, 35–61. https://doi.org/10.1344/105.000000270.

Schneebeli-Hermann, E., Looser, N., Hochuli, P.A., Furrer, H., Reisdorf, A.G., Wetzel, A., Bernasconi, S.M., 2018. Palynology of Triassic–Jurassic boundary sections in northern Switzerland. Swiss J. Geosci. 111, 99–115. https://doi.org/10.1007/s00015-017-0286-z.

Scott, L., 1992. Environmental implications and origin of microscopic *Pseudoschizaea* Thiergart and Frantz Ex R. Potonie emend. in sediments. J. Biogeogr. 19, 349–354.

Sen, P.K., Banerjee, M., 1990. Palyno-plankton stratigraphy and environmental changes during the Holocene in the Bengal Basin, India. Rev. Palaeobot. Palynol. 65, 25–35.

Shergold, J.H., Elphinstone, R., Laurie, J.R., Nicoll, R.S., Walter, M.R., Young, G.C., Zang, W., 1991. Late Proterozoic and Early Palaeozoic palaeontology and biostratigraphy of the Amadeus Basin. In: Kennard, J., Korsch, R.J. (Eds.), Bureau of Mineral Resources, Australia. Bulletin, pp. 97–111.

Slotznick, S.P., Swanson-Hysell, N.L., Zhang, Y., Clayton, K.E., Wellman, C.H., Tosca, N. J., Strother, P.K., 2023. Reconstructing the paleoenvironment of an oxygenated Mesoproterozoic shoreline and its record of life. Geol. Soc. Am. Bull. https://doi.org/10.1130/b36634.1.

Smith, G.M., 1933. The Freshwater Algae of the United States. McGraw-Hill Book Company, Inc.

Steinthorsdottir, M., Jeram, A.J., McElwain, J.C., 2011. Extremely elevated CO2 concentrations at the Triassic/Jurassic boundary. Palaeogeogr. Palaeoclimatol. Palaeoecol. 308, 418–432. https://doi.org/10.1016/j.palaeo.2011.05.050.

Stover, L., 1962. *Taurocusporites*, a new trilete spore genus from the Lower Cretaceous of Maryland. Micropaleontology 8, 55–59.

Strother, P.K., Wellman, C.H., 2020. The Nonesuch Formation Lagerstätte: a rare window into freshwater life one billion years ago. J. Geol. Soc. Lond. https://doi.org/10.1144/jgs2020-133 jgs2020-133.

Strother, P.K., Taylor, W.A., van de Schootbrugge, B., Leander, B.S., Wellman, C.H., 2020. Pellicle ultrastructure demonstrates that *Moyeria* is a fossil euglenid. Palynology 44, 461–471. https://doi.org/10.1080/01916122.2019.1625457.

Takahashi, K., 1979. *Pseudoschizaea* from the Pleistocene sediments in the Ariake Sea area, West Kyushu. Bull. Facult. Liberal Arts Nagasaki Univ. Nat. Sci. 19, 39–46.

Tang, L., Mao, L., Lü, X., Ma, Q., Zhou, Z., Yang, C., Kong, Z., Batten, D.J., 2013. Palaeoecological and palaeoenvironmental significance of some important spores and micro-algae in Quaternary deposits. Chin. Sci. Bull. 58, 3125–3139. https://doi.org/10.1007/s11434-013-5747-9.

Taylor, A.K., Berke, M.A., Castañeda, I.S., Koutsodendris, A., Campos, H., Hall, I.R., Hemming, S.R., LeVay, L.J., Sierra, A.C., O'Connor, K., Expedition 361 Scientists, E, 2021. Plio-Pleistocene continental hydroclimate and Indian Ocean sea surface temperatures at the southeast African margin. Paleoceanogr. Paleoclimatol. 36 https://doi.org/10.1029/2020pa004186 e2020PA004186.

Tekleva, M.V., Polevova, S.V., Gavrilova, O.A., Roghi, G., Neri, M., 2021. *Pseudoschizaea* sp. from the Early Jurassic of Italy: fine structure and comparison. Paleontol. J. 55, 224–234. https://doi.org/10.1134/s0031030121020155.

Thiergart, F., Frantz, U., 1962. Some spores and pollen grains from a Tertiary brown coal deposit in Kashmir. Palaeobotanist 10, 84–86.

Thusu, B., 1973. Acritarches provenant de l'Ilion Shale (Wenlockien), Utica, New York. Rev. Micropaleontol. 16, 137–146.

Tripathi, S., Singh, Y.R., Nautiyal, C.M., Thakur, B., 2018. Vegetation history, monsoonal fluctuations and anthropogenic impact during the last 2330 years from Loktak Lake (Ramsar Site), Manipur, North-East India: a pollen based study. Palynology 42, 406–419. https://doi.org/10.1080/01916122.2017.1375441.

van de Schootbrugge, B., Payne, J.L., Tomasovych, A., Pross, J., Fiebig, J., Benbrahim, M., Föllmi, K.B., Quan, T.M., 2008. Carbon cycle perturbation and stabilization in the wake of the Triassic-Jurassic boundary mass-extinction event. Geochem. Geophys. Geosyst. 9 https://doi.org/10.1029/2007gc001914.

van de Schootbrugge, B., Quan, T.M., Lindström, S., Püttmann, W., Heunisch, C., Pross, J., Fiebig, J., Petschick, R., Röhling, H.-G., Richoz, S., Rosenthal, Y., Falkowski, P.G., 2009. Floral changes across the Triassic/Jurassic boundary linked to flood basalt volcanism. Nat. Geosci. 2, 589–594. https://doi.org/10.1038/ngeo577.

van de Schootbrugge, B., van der Weijst, C.M.H., Hollaar, T.P., Vecoli, M., Strother, P.K., Kuhlmann, N., Thein, J., Visscher, H., Cittert, H. van K., Schobben, M.A.N., Sluijs, A., Lindström, S., 2020. Catastrophic soil loss associated with end-Triassic deforestation. Earth Sci. Rev. 103332 https://doi.org/10.1016/j.earscirev.2020.103332.

van Eldijk, T.J.B., Wappler, T., Strother, P.K., van der Weijst, C.M.H., Rajaei, H., Visscher, H., van de Schootbrugge, B., 2018. A Triassic-Jurassic window into the evolution of Lepidoptera. Sci. Adv. 4, e1701568 https://doi.org/10.1126/sciadv.1701568.

Vigran, J.O., Thusu, B., 1975. Illustrations of Norwegian microfossils: illustrations and distribution of the Jurassic palynomorphs of Norway. Royal Norwegian Council for Scientific and Industrial Research 65, 1–55.

Ward, J.V., 1988. Palynology of Kosrae, eastern Caroline Islands: recoveries from pollen rain and Holocene deposits. Rev. Palaeobot. Palynol. 55, 247–271.

Williford, K.H., Grice, K., Holman, A., McElwain, J.C., 2014. An organic record of terrestrial ecosystem collapse and recovery at the Triassic–Jurassic boundary in East Greenland. Geochim. Cosmochim. Acta 127, 251–263. https://doi.org/10.1016/j.gca.2013.11.033.

Wolff, L.V., 1934. Mikrofossilien des pliocänen Humodils der Grube Freigericht bei Dettingen a. M. und Vergleicht mit älteren Schichten der Tertiärs sowie posttertiären Ablangerungen. Inst. Paläobot. Petrogr. Brennsteine, Arbeit. 5, 55–101.

Yin, L., 1987. Microbiotas of latest Proterozoic in China. In: Stratigraphy and Palaeontology of Systemic Boundaries in China. Precambrian–Cambrian Boundary. Nanjing University Publishing House, Nanjing, pp. 415–522.

Zippi, P., 1998. Freshwater algae from the Mattagami Formation (Albian), Ontario: paleoecology, botanical affinities and systematic taxonomy. Micropaleontology 44, 1–78.