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The 'seed-fern' *Lepidopteris* mass-produced the abnormal pollen *Ricciisporites* during the end-Triassic biotic crisis

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ABSTRACT

The end-Triassic mass extinction (ETE; ~201.6 million years ago) led to dramatic changes in terrestrial ecosystems including the extinction of several seed-plant groups. Among the most intriguing features in the vegetation signal is the dominance of the peculiar pollen, *Ricciisporites tuberculatus* Lundblad, across large areas of the Northern Hemisphere immediately prior to and during the ETE. The parent plant of this pollen has remained unknown for 70 years. Here, we demonstrate that the 'seed-fern' *Lepidopteris ottonis* (Göppert) Schimper (Peltaspermales) produced *R. tuberculatus* in permanent tetrads. We show that *R. tuberculatus* is a large, abnormal form of the small smooth-walled monosulcate pollen traditionally associated with *L. ottonis*, which disappeared at the ETE, when volcanism induced cold-spells followed by global warming. We argue that the production of aberrant *R. tuberculatus* resulted from ecological pressure in stressed environments that favoured asexual reproduction in peltasperms. The expansion of dry environments led to the dominance of drought-tolerant plants in the Early Jurassic of northern middle latitudes.

1. Introduction

The end-Triassic mass extinction (ETE; 201.564 ± 0.015 Ma (Schoene et al., 2010; Blackburn et al., 2013), represents one of the five largest crises in the history of life on Earth (Sepkoski et al., 1981; Kustatscher et al., 2018; Mangerud et al., 2021). The extinction episode affected both marine and continental ecosystems and has been linked to extensive volcanism in the Central Atlantic Magmatic Province (CAMP) during the initial opening of the Atlantic Ocean (Fig. 1a). This led to emissions of vast volumes of ash and aerosols that caused short intervals of cooling and low light levels (Olsen et al., 2022), before a subsequent rise in global temperatures resulting from the emission of greenhouse gases (McElwain et al., 2009; Akikuni et al., 2010; Sha et al., 2015; Soh et al., 2017).

The Late Triassic forest ecosystems of palaeo-Scandinavia, Greenland, and other mid-palaeolatitude regions of Eurasia were dominated by ferns, conifers, and various broad-leaved deciduous seed plants collectively called 'seed-ferns'(McElwain et al., 2009; Harris, 1937a, 1937b; Kustatscher and Van Konijnenburg-van Cittert, 2013; McLoughlin, 2021; Vajda et al., 2021). The long-term vegetation record through the Triassic–Jurassic transition in this region has been assessed by combined studies of plant macrofossils and dispersed spores, pollen and mesofossils (Peng et al., 2021 and references therein). One of the most prominent features characterizing the end-Triassic pollen record across this region is the overwhelming dominance of the pollen taxon *Ricciisporites tuberculatus* Lundblad, 1954 (Lundblad, 1954, 1959a, 1959b; Pedersen and Lund, 1980; Bonis et al., 2009; Mander et al., 2012; Vajda et al., 2013, 2021; Kürschner et al., 2014; Peterffy et al., 2016). This pollen- type is a highly distinctive form represented by four unusually large monosulcate grains united in a tetrad (a so-called permanent or obligate tetrad) with pronounced 'knobbly' surface ornamentation (Fig. 1b). These 'knobs', known as 'orbicules' or 'Ubisch bodies' in modern pollen grains, develop synchronously with other layers of the pollen wall (Ubisch, 1927).

Ricciisporites tuberculatus pollen existed for approximately 10 million years following its first consistent appearance in the Norian (~210 million years ago) but it increased to exceptional prominence at many sites across the Northern Hemisphere immediately prior to and during the ETE. This species then became a casualty of the extinction event making it an important stratigraphic marker species for uppermost Rhaetian and 'Triassic-Jurassic transitional zone' strata across northern Eurasia and Greenland (Lundblad, 1959b. Pedersen and Lund, 1980;

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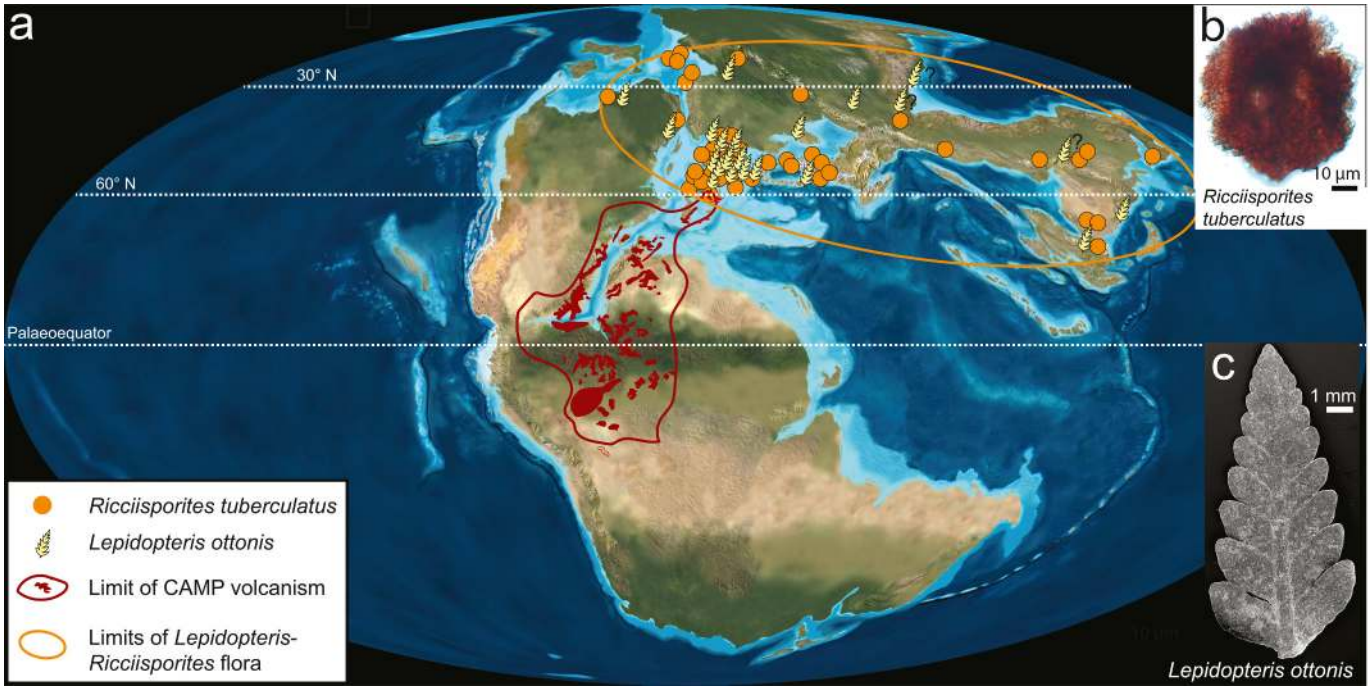


Fig. 1. Global palaeogeographic map. A. showing the distribution of B. *Ricciisporites tuberculatus* pollen and C. *Lepidopteris ottonis* foliage in relation to the Central Atlantic Magmatic Province (CAMP) volcanics in the Late Triassic (map modified from Blakey, 2005).

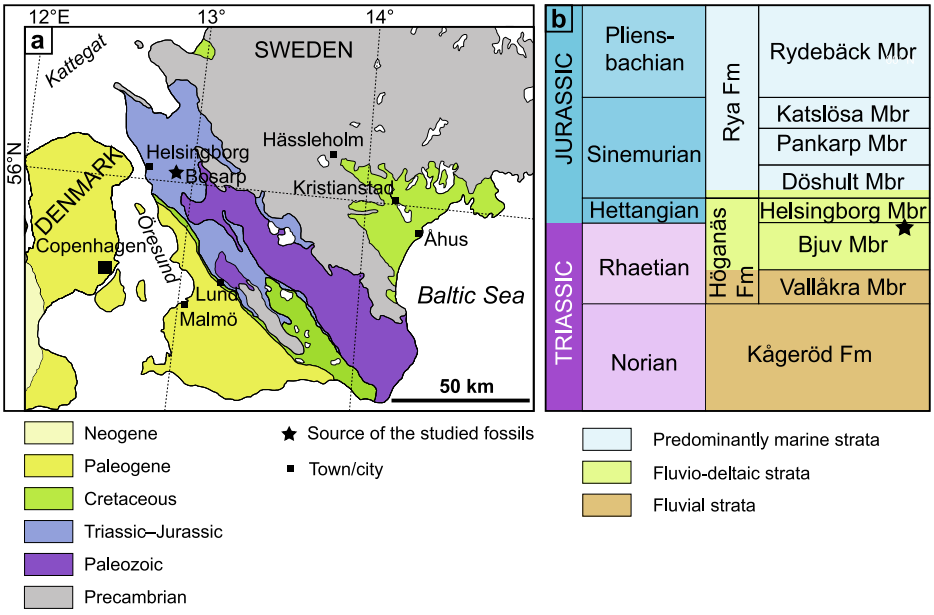


Fig. 2. Geological setting of the studied material.A. Simplified geological map of Skåne, southern Sweden showing the location of fossil leaves and pollen at Bosarp. B. Upper Triassic to Lower Jurassic stratigraphy of Skåne (Vajda and Wigforss-Lange, 2009), with star showing the level sampled for fossil leaves and pollen at Bosarp.

Bonis et al., 2009; Cirilli, 2010; Mander et al., 2012; Vajda et al., 2013, 2021; Kürschner et al., 2014). Although these pollen grains have been the focus of numerous investigations since their discovery 70 years ago, the parent plant has remained elusive, hampering interpretations of the terrestrial ecology for the most critical interval of the extinction event across a vast region.

Here we resolve the identity of the plant that produced *R. tuberculatus* pollen, clarify its distribution, and provide an ecological hypothesis for its abundance as a response to environmental changes during this mass extinction episode.

2. Materials and methods

2.1. Materials

Pollen, pollen-bearing organs and leaf fossils of *Lepidopteris ottonis* (Göppert) Schimper, 1869 (Fig. 1c) studied here derive mainly from historical museum collections but to some extent also from samples collected recently by the authors. The material (both historical and recent) derive from the same coal-rich deposits of Skåne, southern Sweden (Fig. 2a), dated to the late Rhaetian (latest Triassic) on the basis

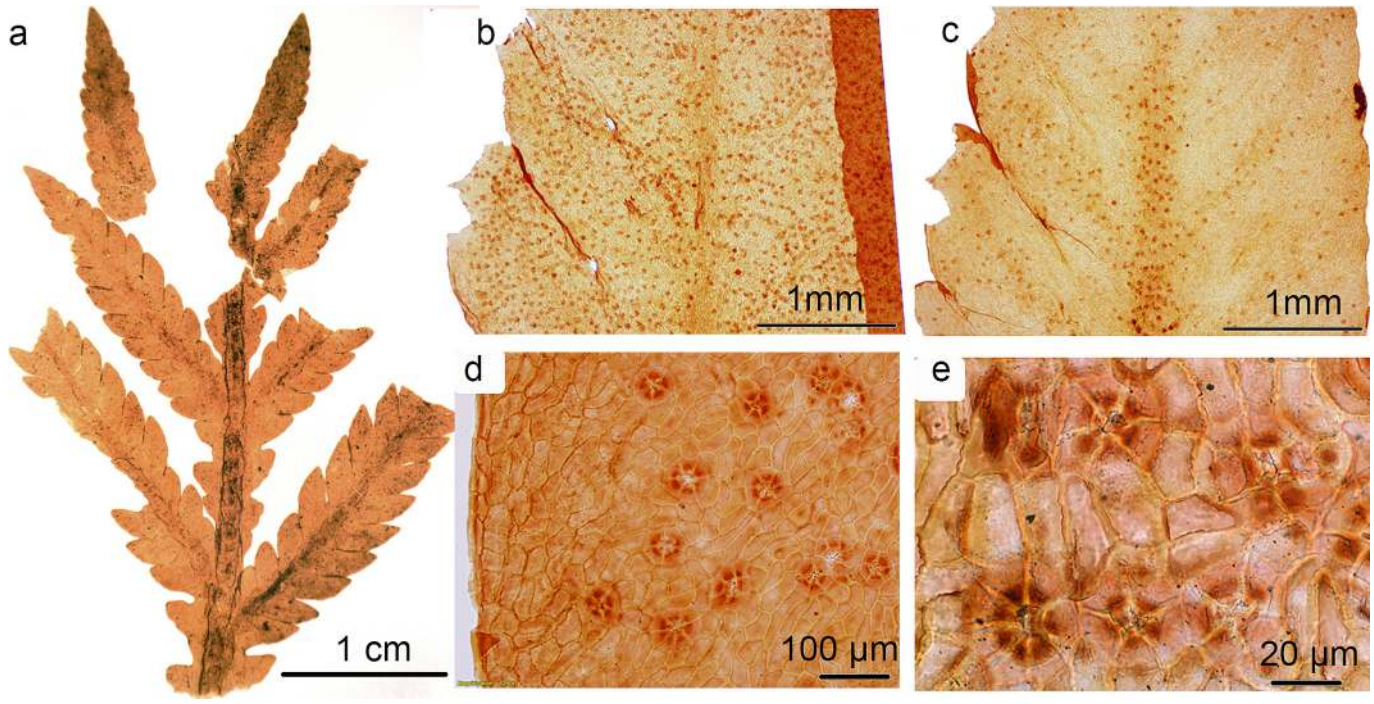


Fig. 3. Prepared cuticle of *Lepidopteris ottonis* from the uppermost Bjuv Member at Bosarp. A. Portion of frond; S079770. B. View of interior of abaxial (lower) cuticle showing rings of 5–7 papillate subsidiary cells around stomata; S057265–01.C. Pinnule adaxial (upper) cuticle showing stomata arranged over veins; S057265–01. D., E. Pinnule abaxial cuticle showing evenly distributed stomata; S057265–01.

of palynostratigraphy (Lindström and Erlström, 2006; Vajda et al., 2013).

The most productive samples for *L. ottonis* derive from paper shales in the uppermost portion of the Bjuv Member, Höganäs Formation, at Bosarp, near Billesholm, southern Sweden (Fig. 2b), especially represented by samples recovered in the 1950s from the now abandoned Bosarp coal mine. Fossils from this deposit include abundant mummified *L. ottonis* leaves, affiliated *Antevsia zeilleri* (Nathorst) Harris 1937 pollen organs (including the type specimen), and dispersed pollen prepared by Professor Britta Lundblad in 1954 (including the type specimen of *R. tuberculatus*). Several of the studied fossil pollen sacs in these collections are mounted in Canada balsam on glass slides. These historical samples were supplemented by new collections of *L. ottonis* from the Norra Albert Quarry. All studied fossil specimens are stored in the collections of the Department of Palaeobiology, Swedish Museum of Natural History, Stockholm.

In order to assess the palynological signal before and after the last occurrence of *L. ottonis*, two samples were analysed for their dispersed palynomorphs. One sample was collected from the thin bed hosting the uppermost leaf mats of *L. ottonis* (within the topmost *Lepidopteris ottonis* Assemblage Zone), and one from the mudstones 1.5 m above this bed (within the *Thaumatopteris schenkii* Assemblage Zone sensu Lundblad, 1959b).

2.2. Maceration of leaves and pollen sacs

Samples containing leaves were macerated in cold 38% HF for one week. The organic residues were then rinsed in distilled water and air-dried . Individual plant macro−/meso-fossils were then picked from the residue under stereo-dissecting microscope using a camel-hair brush.

2.3. Palynological processing and analysis

Five grams of sedimentary rock per sample were processed according to standard palynological procedures at Global Geolab Limited including treatment with hydrochloric acid (HCl) and hydrofluoric acid (HF). Organic residue (kerogen) was mounted in epoxy resin on two slides before light oxidation and sieving of the rest of the organic residues using a 5 µm mesh. The treated organic residues were mounted in epoxy resin on two microscope slides per sample. Two hundred palynomorphs (pollen, spores and algae) per sample were identified , and the percentage of each palynomorph taxon was calculated.

2.4. Transmitted light microscopy

Specimens that were mounted on glass slides and embedded in either epoxy resin (new specimens) or in Canada balsam (historical collections at the Swedish Museum of Natural History) were examined using an Olympus BX51 transmitted light microscope, and photographed with an Olympus DP71 camera.

2.5. Scanning electron microscopy (SEM)

Pollen sacs and pollen grains were examined using scanning electron microscopy . Specimens were mounted directly onto SEM stubs and gold coated for 50–120 s using an Agar high-resolution sputter coater. Specimens were studied using an ESEM FEI Quanta FEG 650 scanning electron microscope at the Swedish Museum of Natural History.

2.6. Transmission electron microscopy (TEM)

Fossil pollen and pollen sacs (*Antevsia zeilleri*) were immersed in epoxy resin (AGAR 100 Resin kit, R1031), which was left to polymerise at room temperature for 72 h, followed by 48 h at 60 °*C*. ultra-thin sections (60 nm) were cut using a Leica EM UC7 ultratome with a diamond knife. The sections were mounted on pioloform coated copper grids and stained with uranyl acetate (2%, 30 min) and lead citrate (4 min). The ultra-thin sections were examined in a JEOL JEM-1400 PLUS TEM at 100 kV. This was carried out at Lund University by O.G. Micrographs were recorded with a JEOL Matataki CMOS camera using TEM Centre for JEM1400 Plus software.

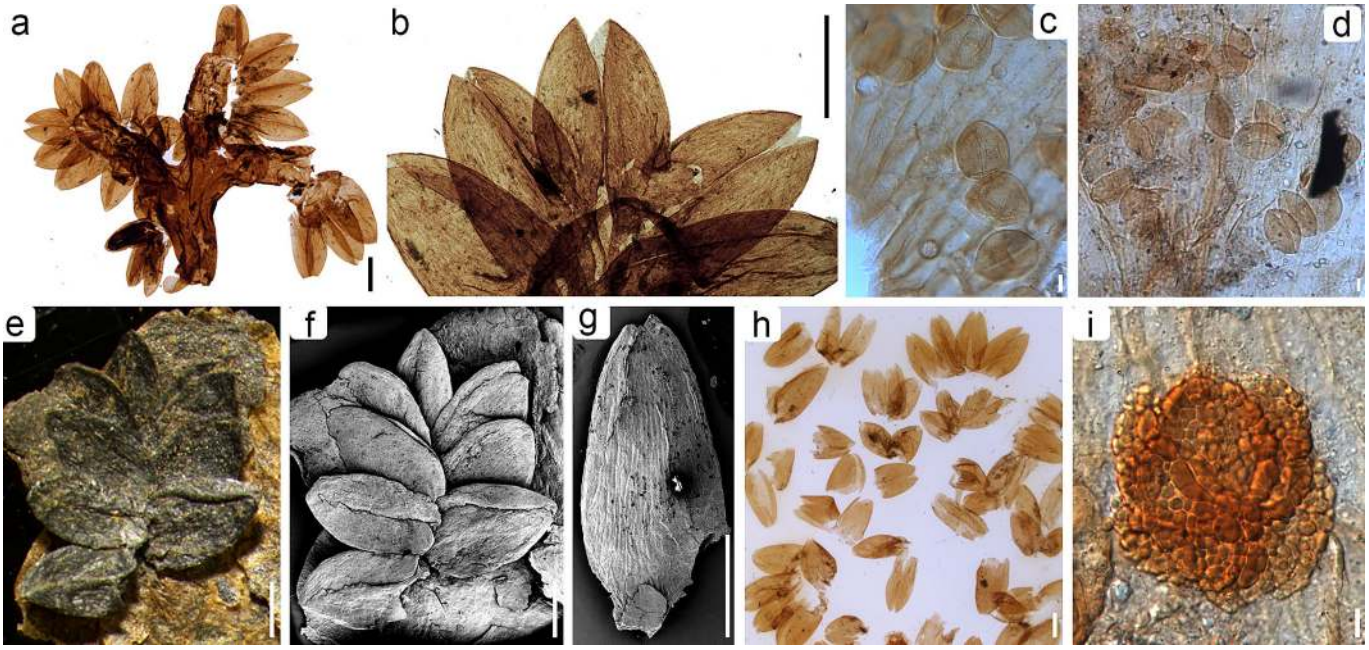


Fig. 4. Microsporophyll *Antevsia zeilleri* and microsporangia (pollen sacs) with contained pollen linked to the *Lepidopteris ottonis* plant. A. Branched microsporophyll bearing clusters of microsporangia (pollen sacs). B. Enlargement of microsporophyll with longitudinal line of dehiscence. C, D. 'Typical' smooth monosulcate pollen preserved within *A. zeilleri*. E, F. Cluster of pollen sacs imaged with e stereo microscope (incident light) and f scanning electron microscope (SEM). G. SEM of single detached ovoid pollen sac showing outer wall composed of longitudinally elongate cells. H. Large assemblage of acid-macerated pollen sacs. I. *Ricciisporites tuberculatus* pollen preserved within an *A. zeilleri* pollen sac. Scale bars = 1 mm for A, B, E–H, 10 μm for C, D, I. Specimen numbers: A, B.S062276; C. SO62285; D, E, F, G. S062265; H. S062267; I. S062271.

2.7. Confocal microscopy

Microscopy slides with pollen sacs and pollen grains mounted in Canada balsam were scanned with a confocal microscope (Leica TCS SP8 DLS), objective: HC PL APO 63×/1.4 OIL CS2) with Leica LAS-X software, at Lund University, Sweden. A 488 nm solid-state laser was used to excite auto-fluorescence from the samples.

3. Geological setting

The Upper Triassic to Lower Jurassic Höganäs Formation of the eastern Danish Basin (southern Sweden) accumulated in a coastal plain setting in middle northern palaeolatitudes. The formation incorporates the fluvio-paralic Vallåkra Member (lower Rhaetian), coal-rich, upper deltaic Bjuv Member (middle–upper Rhaetian) and coal-poor, lower deltaic Helsingborg Member (uppermost Rhaetian to Hettangian) in conformable succession (Fig. 2b). The Bjuv Member, hosting the fossils studied herein, comprises interbedded claystones, siltstones, thin sandstones and coals with local lenses and nodules of sideritic mudstone that attest to stagnant, waterlogged, reducing conditions during the early stages of diagenesis (Pieńkowski, 1991; Vajda and Wigforss-Lange, 2009; Petersen et al., 2013). Apart from a few sandy channel deposits with large trough cross-bed sets, the bulk of the Bjuv Member is characterized by diverse low-energy sedimentary structures including current and wave ripple cross-laminations, planar laminations, wavy interlaminations and flame structures reflecting mostly fluviodeltaic coastal floodplain deposition (Petersen et al., 2013). The unit hosts a rich fossil flora of leaves, stems and root traces, together with small vertical to horizontal invertebrate burrows typical of relatively low-energy, peat-forming wetland environments (Lundblad, 1950; Pieńkowski, 1991). The overlying Helsingborg Member, incorporating the informally defined 'Boserup beds' at the base, was deposited in a mix of coastal plain and lower deltaic environments with minor marine incursions (Ahlberg et al., 2003; Peterffy et al., 2016). This unit also hosts a relatively rich fossil flora (Nathorst, 1876). Thus, the Triassic–Jurassic transition in Skåne is represented primarily within coastal deposits that host a relatively rich and continuous succession of fossil floras.

4. Results and interpretation

Following a literature search for the stratigraphic and geographic distributions of *Ricciisporites tuberculatus* pollen and all gymnosperm leaf taxa available with equivalent distributions, we identified the seed fern (peltasperm) *Lepidopteris ottonis* (Fig. 3a–e), as the foliage most probably affiliated with this pollen. To test this hypothesized association, we used traditional palaeontological techniques, including transmitted light microscopy and scanning electron microscopy, together with a range of techniques typically used for studies of extant plants, e.g., fluorescence- and laser scanning confocal microscopy, and transmission electron microscopy to study pollen grains preserved in situ within pollen sacs linked to *L. ottonis*.

4.1. Antevsia

Pollen sacs affiliated with the seed fern *Lepidopteris ottonis* are borne on the microsporangiate organ *Antevsia zeilleri* (Nathorst) Harris 1937. This microsporophyll is the most abundant pollen-bearing organ in the Upper Triassic sediments of southern Sweden and its affiliation with L. *ottonis* is based on their co-occurrence and equivalent cuticular anatomy (Antevs, 1914; Harris, 1932; Lundblad, 1950; Anderson and Anderson, 2003). The rachis of the microsporophyll, bearing numerous pollen sacs can reach up to 90 mm long. It produces short (10–20 mm), widely angled, lateral branches (Fig. 4a) bearing ~1-mm-wide and 2-mm-long pollen sacs clustered in two-rows near the tips of these lateral branches (Fig. 4a). Each pollen sac has a wall consisting of a single layer of elongate cells that give the surface a longitudinally striate appearance. Empty pollen sacs have a single longitudinal line of dehiscence extending from base to apex (Fig. 4b, e–h). The pollen sacs bear no stomata.

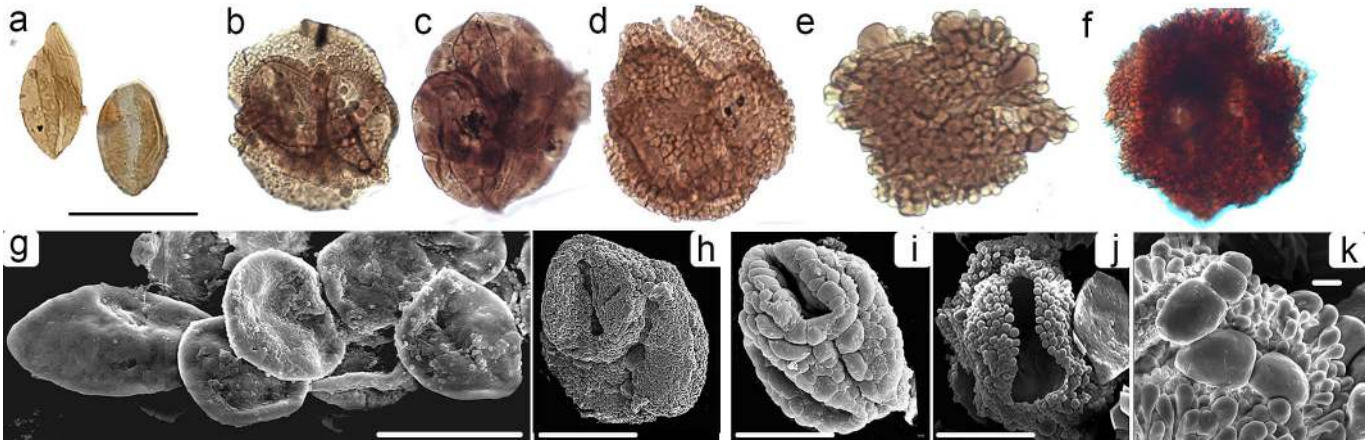


Fig. 5. Various pollen grains linked to *Antevsia zeilleri*. AF. Light micrographs. A. Dispersed, typical normal monosulcate pollen grains from the paper shale hosting abundant *Lepidopteris ottonis* leaves. B–F. Dispersed *Ricciisporites tuberculatus* pollen, note the intraspecific variation. B. Permanent tetrad with two smaller grains and two larger ones. C. Permanent tetrad with four pollen of roughly same size, note the exceptionally few and large orbicules. D. Specimen with many small orbicules E. Rare, atypical form of *R. tuberculatus*, completely covered with heterogenous orbicules. F. Holotype of *R. tuberculatus* with equal-sized grains bearing dense, small orbicules. g-k Scanning electron microscope photos. G. Morphological continuum of monosulcate pollen found in situ within *Antevsia zeilleri* pollen sacs. H–I. Dispersed specimens bearing two small and two large constituent monosulcate grains that comprise the *Ricciisporites tuberculatus* tetrad. J. Typical dispersed *Ricciisporites tuberculatus*-type grains in a permanent tetrad. K. Enlargement of gemmate ornament on a dispersed *Ricciisporites tuberculatus*-type pollen grain.

4.2. Monosulcites

The pollen sacs contain abundant smooth-walled monosulcate pollen that would typically be referred to *Cycadopites/Monosulcites* spp., but some also to *Chasmatosporites*, when found as dispersed grains (Fig. 5a; Fig. 6a-f). These monosulcate grains occur in clusters inside the pollen sac, but are consistently detached from sister grains when dispersed. *Monosulcites*-type grains found within *Antevsia zeilleri* pollen sacs are 28–45 μm long and 20–23 μm wide (Supplementary Table 1).

4.3. Ricciisporites tuberculatus

The pollen sacs also contain common examples of pollen aggregates consisting of four monosulcate grains that are distally fused into a permanent tetrad, collectively forming spheres with a diameter of 64–148 μm (average 100 μm, based on 80 specimens), i.e., considerably larger than the normal smooth monosulcate grains (Fig. 5a; Supplementary Table 1). The outer wall layer is elaborated into numerous solid 'blisters' called orbicules or Ubish bodies. In some specimens, however, the tetrad comprises two smaller grains, similar to the size of the normal monosulcate pollen grains, and two larger pollen grains (Figs. 5c, h, i).

4.4. Proportions of pollen types

Of the 277 *Antevsia zeilleri* pollen sacs examined, 49 contained some pollen grains. Twenty-nine sacs contained numerous, small, smooth, monosulcate pollen grains (Figs. 4c, d; Fig. 6 a–f and Supplementary Table 2). These grains are morphologically consistent with specimens found in the dispersed pollen record assigned to *Monosulcites* spp. or referred to the '*Cycadopites-Monosulcites* complex'. Such grains have been considered by previous authors to be the only pollen produced in *Antevisa* pollen sacs (Antevs, 1914; Harris, 1932; Anderson and Anderson, 2003). However, 15 pollen sacs in our study contained exclusively *Ricciisporites tuberculatus* pollen grains (Figs. 4i; Fig. 6g–o; Supplementary Table 2), and five sacs contained pollen of both morphotypes (Fig. 7a–c; Supplementary Video 1). *Ricciisporites tuberculatus*-type grains are retained in meiotic tetrads indicating an atypical pollen developmental pathway in which the pollen grains failed to separate. In addition to the occurrence of morphologically distinct, end-member pollen types preserved within the same pollen sacs (Fig. 5g), SEM analysis revealed examples of grains in some sacs that bridge the full spectrum of morphologies from 'normal', smooth-walled, monosulcate forms to 'aberrant' large grains covered by minute to greatly enlarged orbicules (Figs. 5g). Most of the intermediate pollen are similar in size to 'normal' grains and are generally smooth-walled but bear sparse and irregularly distributed surficial orbicules (Fig. 5g). In atypical cases, where *Ricciisporites*-type tetrads consist of two larger, and two smaller, grains (Fig. 5b, c, h, i), the smaller grains match the size of normal monosulcate grains if disregarding the orbiculate ornamentation (Fig. 5a, b).

4.5. Ultrastructure of pollen walls

Although a destructive technique, transmission electron microscopy enables the investigation of the ultrastructure of the pollen walls. Numerous terminological schemes have been used for subdividing pollen wall structure, but for consistency, we follow Mander et al. (2012), i.e., (inner layer = nexine; middle layer = sexine 1; outer layer = sexine 2). The inner layer (nexine) of *R. tuberculatus*-type grains constitutes a thin, electron-dense wall (Fig. 8h, j, k). The middle layer (sexine 1) comprises a spongy, thick layer incorporating micro-alveoli. The outer layer (sexine 2), forms a less electron dense but solid layer that, generally, is greatly enlarged, forming spherical to club-shaped sculptural elements ('orbicules': Fig. 8h, i, k). The individual pollen grains remain connected, as expressed by continuity of the spongy layer (Fig. 8j), forming permanent tetrads (Fig. 8i; Supplementary Videos 2 and 3).

A comparison between the ultrastructures of *R. tuberculatus* and the monosulcate-type pollen reveals that, although both forms have a similar dark electron dense inner layer, the middle layer in *R. tuberculatus* is micro-alveolate (spongy), whereas this layer is dense in the monosculate pollen. At the boundary between the middle and the outer layers (sexine 1 and sexine 2) prominent alveoli occur only in *Monosulcites* grains. This is consistent with previous ultrastructural studies of *Monosulcites* (Zavialova and van Konijnenburg-van Cittert, 2011). In *R. tuberculatus*, the outermost layer is expanded into orbicules or gemmae as noted by (Mander et al., 2012). Thus, our TEM results show that the walls of both pollen types, found in situ in *Antevsia zeilleri* pollen sacs have an equivalent three-layered architecture but differ significantly in the thickness of the wall layers and the development of intervening alveoli and external orbicules.

Confocal microscopy enabled a detailed, non-destructive analysis of the in situ constituents of the pollen sacs, owing to the strong degree of

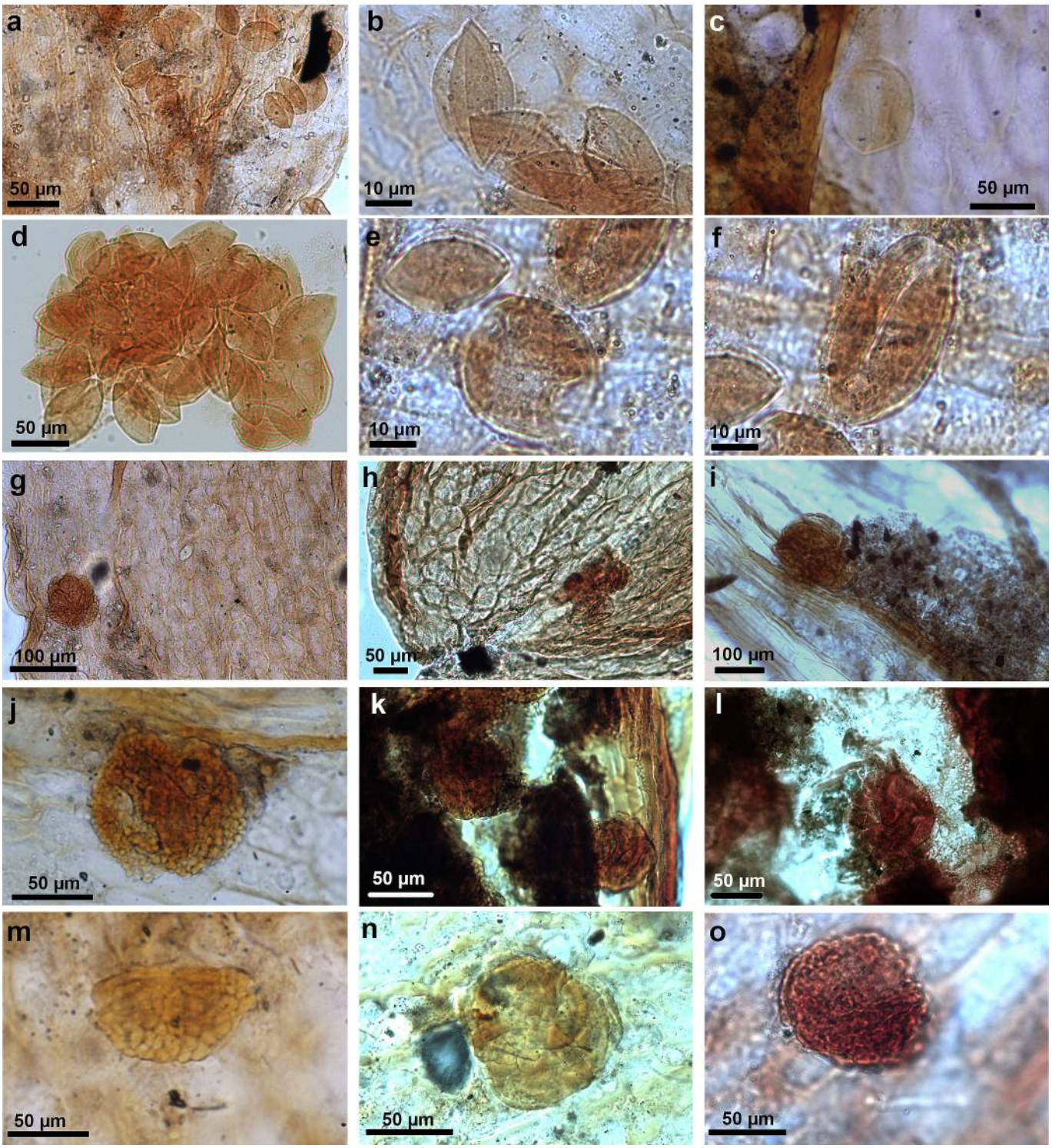


Fig. 6. Light micrographs of microsporangia with pollen grains. (Description, slide number, England finder reference) A. Mature disaggregated monosulcate pollen grains within pollen sac prior to dispersal, S062265, Q48. B. Enlargement of aggregated monosulcate pollen grains inside the sac, S062265, Q48. C. Monosulcate pollen of *Chasmatosporites* type inside pollen sac, S062278, V32. D. Cluster of nearly mature monosulcate pollen grains in the same slide as several pollen sacs, dispersed during preparation, S062265, J30. E. Enlargement of monosulcate pollen inside pollen sac, note the varied morphologies representing both *Monosulcites*-type and *Chasmatosporites*-type grains, S062267, J42. F. Aberrant monosulcate pollen grain, with enlarged dimensions and thickened wall, S062267, V22. G. *Ricciisporites tuberculatus* pollen grain in pollen sac (in situ position verified by analysis at different focal plains), S062271, K43. H. Cluster of *R. tuberculatus* tetrads inside sac, in process of being dispersed, S062268, N38. I. *Ricciisporites tuberculatus* within pollen sac, adjacent to pollen wall, note the tapetal cells partly embracing the pollen. S062285, V27, J. *Ricciisporites tuberculatus* tetrad with prominent orbicules inside the sac, S062282, V22. K. Several *R. tuberculatus* tetrads inside pollen sac, adjacent to pollen wall and some still embedded in tapetum, S062275–1, U40. L. *Ricciisporites tuberculatus* tetrad with very coarse orbicules inside the pollen sac S062275, N39. M. Enlargement of *R. tuberculatus* within pollen sac, S062278, V44. N. Enlargement of *R. tuberculatus* tetrad in pollen sac, note the very large orbicules in this specimen, S057164, G38. O. Enlargement of *R. tuberculatus* tetrad in pollen sac, note the small orbicules in this specimen,S062285, Q41.

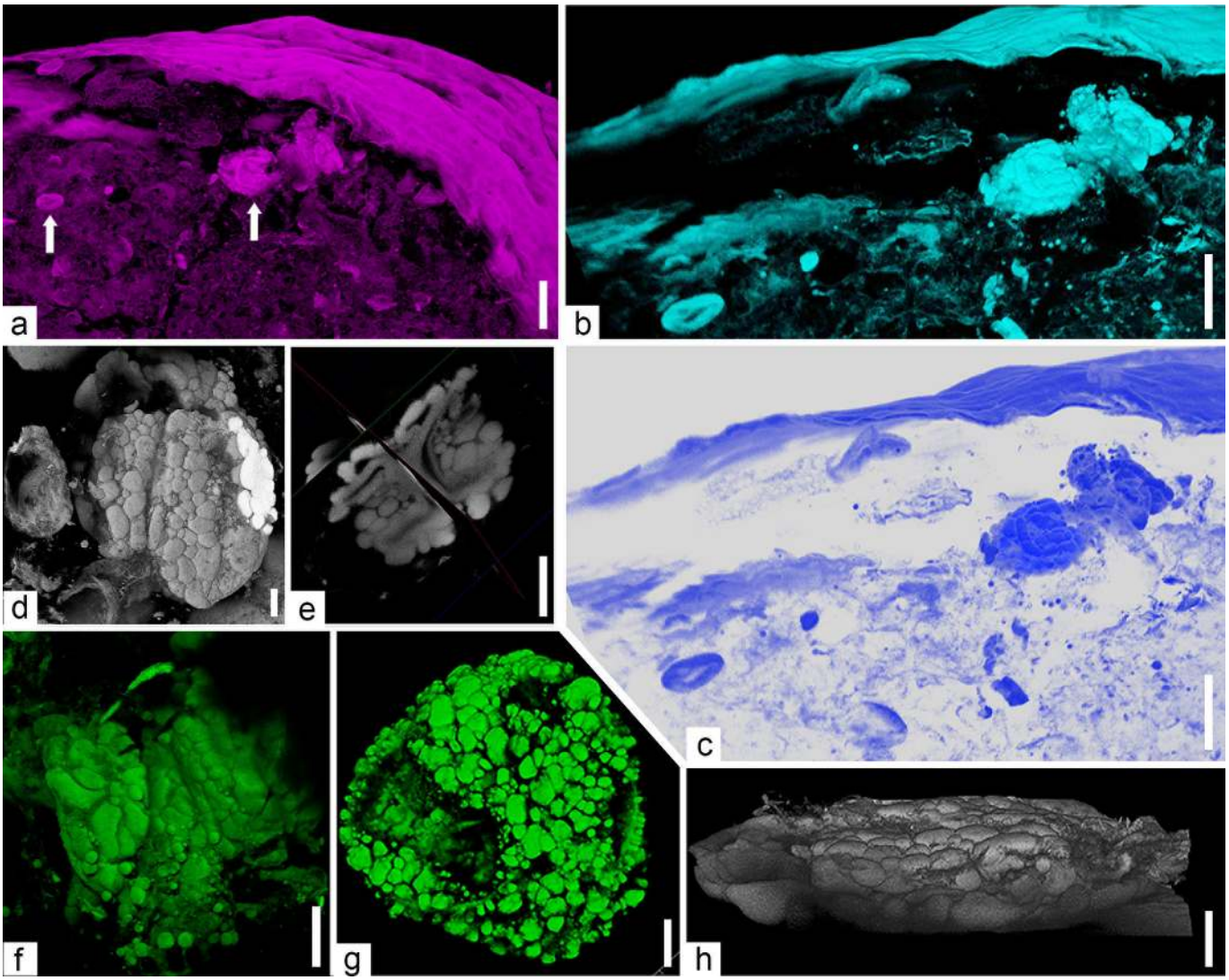


Fig. 7. Confocal micrographs of pollen grains located inside an *Antevsia zeilleri* pollen sac. Note the strong autofluorescence. A. Section through an *Antevsia zeilleri* pollen sac showing isolated monosulcate pollen grain (left arrow) and tetrad of *Ricciisporites tuberculatus*-type pollen (right arrow) within the same sac. B. enlargement of in situ monosulcate pollen grain (lower left) and tetrad of *Ricciisporites tuberculatus*-type pollen (centre right). C. Inverted colour image of B. highlighting the in situ pollen and pollen sac wall. D. *Ricciisporites tuberculatus* tetrad showing variation in grain size. E. Section through *Ricciisporites tuberculatus* tetrad showing amalgamation of grain walls. F. *Ricciisporites tuberculatus* tetrad showing varied sizes of orbicules. G. *Ricciisporites tuberculatus* tetrad showing reduced ornament in sulci. H, *Ricciisporites tuberculatus* tetrad showing flattened to gently rounded crests of orbicules. Scale bars = 100 μm for A, 10 μm for B, C.

autofluorescence of the pollen sac wall and the pollen. Strong fluorescence is likely due to the incorporation of a high proportion of cutin and/or flavonoids in the exine (Donaldson, 2020). Notably, the tapetum cells inside the pollen sac do not fluoresce (Fig. 7a, b). Confocal microscopy confirms that *Ricciisporites* and monosulcate grains occur together in the same sac, a trait that was identified in multiple sacs (Fig. 7a–c; Supplementary Table 2, Supplementary Video 1).

4.6. Spore-pollen analysis of beds spanning the last appearance of *L. ottonis*

One sample each from beds above and below the last occurrence of *L. ottonis* at Norra Albert Quarry (Fig. 9) yielded well-preserved assemblages of pollen and spores of moderate diversity (Table 1). The sample from the bed within the *Lepidopteris ottonis* Zone containing *Antevsia zeilleri* (NRM—S054366) is dominated by gymnosperm pollen (61%), of which *Ricciisporites tuberculatus* represents 31% of the total count. Spores reach 39% and are dominated by *Deltoidospora toralis* Lund 1977 and *Cyathidites australis* Couper, 1953, produced by ferns, such as *Dictyophyllum* spp. Monosulcate pollen grains that can be linked to the *Antevsia* pollen sacs include representatives of the genera *Chasmatosporites*, *Cycadopites* and *Monosulcites*. These collectively reach a relative abundance of 15%.

The second sample (NRM—S064694), collected 1.5 m above the previous, derives from the *Thaumatopteris schenkii* Assemblage Zone, which lacks *Lepidopteris ottonis* leaves. Fern spores dominate (65%) the palynoflora of this bed—a feature typical of the 'Transitional spore-spike interval' sensu Larsson (2009). The spore *Deltoidospora toralis* overwhelmingly dominates the assemblage. Gymnosperm pollen constitutes 33% of the total assemblage and is dominated by *Pinuspollenites minimus* Kemp, 1970. Importantly, *R. tuberculatus* makes up only 2% of the assemblage and the small smooth monosulcate pollen grains comprise 3% (Table 1).

4.7. Lepidopteris ottonis

Lepidopteris belongs to Peltaspermales, an extinct group variably resolved as a relatively basal or derived clade of seed plants depending

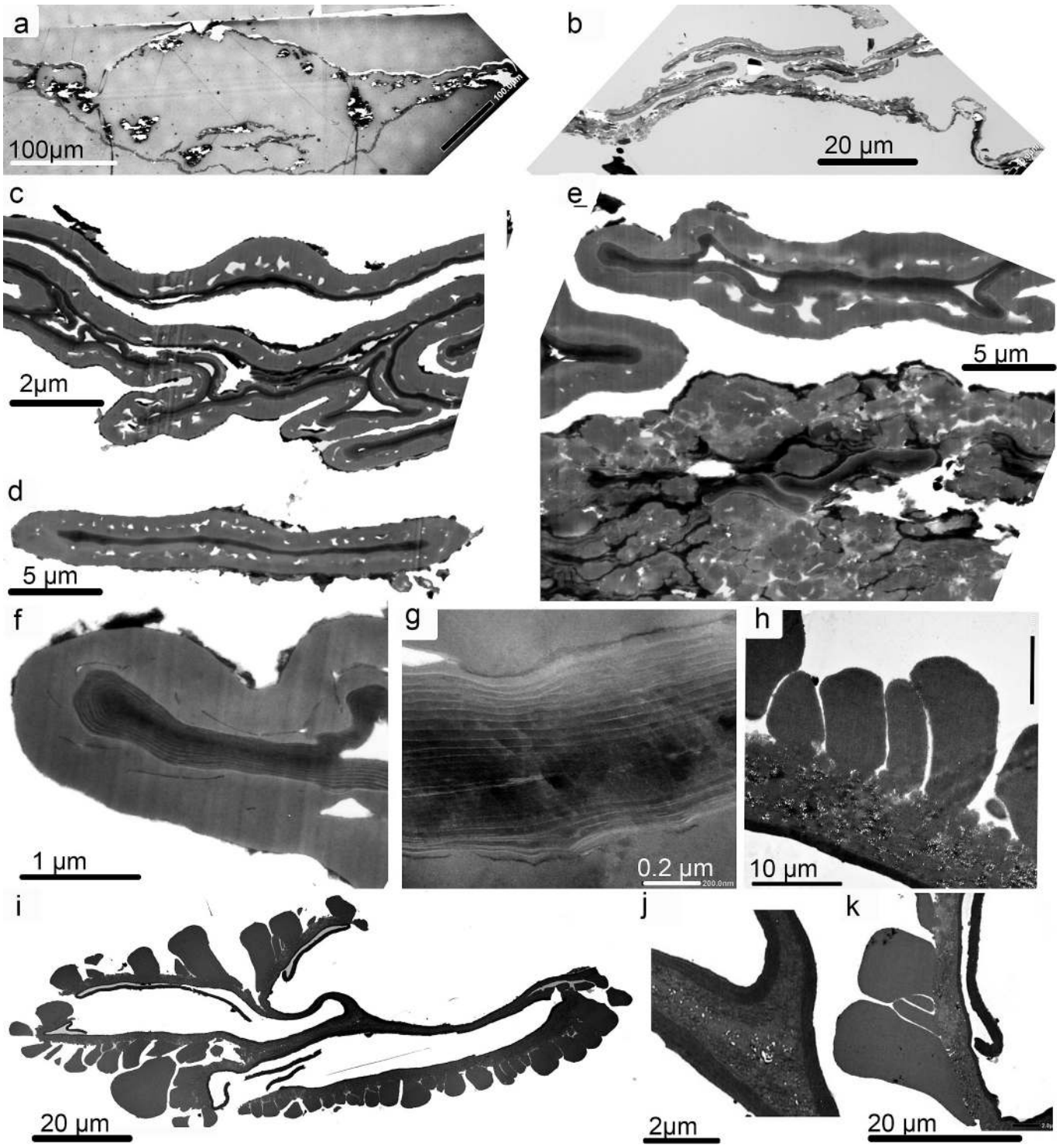


Fig. 8. Transmission electron microscopy photos of *Antevsia zellerii* pollen sac. A. Section of entire pollen sac with in situ smooth monosulcate pollen grains. B–G. successive enlargements of sections through 'normal' monosulcate pollen grains within pollen sac. C, D, E. Prominent alveoli developed between the middle layer (sexine 1) and the outer layer (sexine 2). F–G. Enlargement of monosulcate grain showing the electron dense, dark inner layer (foot layer = nexine) with numerous lamellae, succeeded by a lighter middle layer (sexine 1) and a less electron dense but solid outer Layer (Sexine 2) with prominent alveoli at the boundary between the middle and outer layers. H. Enlargement of section through the wall of an aberrant (*Ricciisporites tuberculatus*-type) pollen showing electron-dense inner layer (bottom), spongy sexine (centre) and homogenous orbicular outer layer (top). I. Section through a *R. tuberculatus* tetrad showing development of a continuous sporopollenin layer between individual grains. J. Enlargement of the centre of the tetrad showing continuity of spongy layer at the junction of three pollen grains. K. Section through the pollen wall showing development of orbicules from the outermost layer of the pollen wall. Specimen number: S066636.

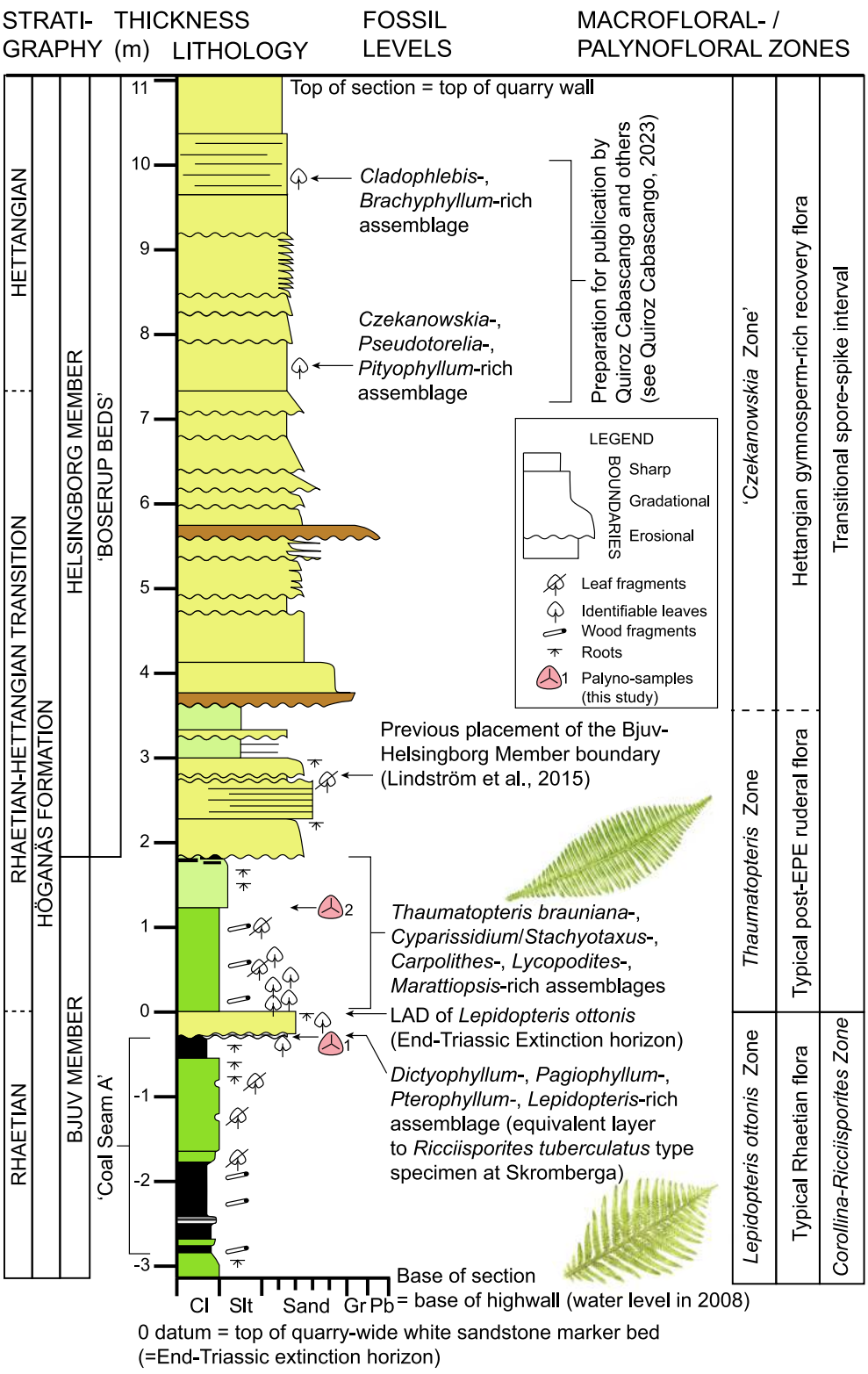


Fig. 9. Measured section through the Triassic–Jurassic transition in the Norra Albert Quarry, southern Sweden, showing the last appearance datum of *Lepidopteris ottonis*, key macroforal assemblages, palynozones, beds sampled for palynology, and stratigraphic subdivisions. Pollen and macrofossil data after Larsson (2009) and Quiroz Cabascango (2023) respectively, and from this study.

on how its features are coded in character matrices (Doyle, 2006; Hilton and Bateman' 2006). The origin of Peltaspermales dates to at least the Asselian (Wang et al., 2013). The group was confined mainly to the Northern Hemisphere in the Permian (Naugolnykh and Kerp, 1996; DiMichele et al., 2005) but penetrated Gondwana at the close of that period (Retallack, 2002; McLoughlin et al., 2021) to become a key element of global floras through the Triassic (Townrow, 19601956; Anderson and Anderson, 2003). Peltasperms were among the major plant casualties of the ETE (Anderson and Anderson, 2003; McElwain and Punyasena, 2007; Kustatscher and Van Konijnenburg-van Cittert,

Table 1
Palynological results, see Fig. 9 for stratigraphic position.

Age / zone	Rhaetian, *Lepidopteris* Zone (S054366)	Transitional interval, *Thaumatopteris* Zone (S064694)
Locality	Billesholm, Norra Albert (Bjuv Mbr)	Billesholm, Norra Albert (Helsingborg Mbr)
Spores	%	%
Camarozonosporites rudis	2	
Cibotiumspora juriensis		3
Cyathidites australis	16	9
Deltoidospora toralis	10	51
Marattisporites scabratus	1	
Punctatisporis globosus	8	
Trachysporites asper	1	
Trachysporites fuscus		2
Uvaesporites sp.	1	
Total spores %	**39**	**65**
Pollen except *Rturberculatus*	%	%
Alisporites radialis		2
Alisporites robustus	1	
Ovalipollis ovalis	1	1
Pinuspollenites minimus	2	18
Quadraeculina anaellaformis		1
Vitreisporites pallidus	1	
Classopollis classoides	1	2
Perinopollenites elatoides	9	6
Chasmatosporites sp.		1
Chasmatosporites elegans	4	
Cycadopites follicularis	4	1
Cycadopites granulatus	2	
Cycadopites major	1	
Monosulcites minimus	4	1
	30	**33**
Ricciisporites tuberculatus	31	2
Total pollen%	**61**	**35**
Total all %	**100.0**	**100.0**

2013; Kustatscher et al. 2018), *Lepidopteris ottonis* representing the last abundant representative of the order. The clade persisted into the Jurassic in the form of only two known relict populations in Argentina and Australia (Rozefelds, 1988; McLoughlin et al., 2015; Elgorriaga et al., 2016; Bomfleur et al., 2018). *Lepidopteris ottonis* is a widely used biostratigraphic index taxon for Rhaetian strata across northern Europe and Greenland (Harris, 1937a, 1937b; Lundblad, 1959b; Pacyna, 2014). A few studies have suggested precocious occurrences of this species in Norian strata (Vavrek et al., 2008; Świło et al., 2013; Barth et al., 2014; Li and Wang, 2015) but, in these cases, precise age controls on the sedimentary beds are lacking or identification of the leaf/cuticle fragments are equivocal. One difficulty in determining the earliest occurrence of *L. ottonis* is its strong morphological resemblance to its sister taxon *Lepidopteris stuttgardiensis* (Jaeger) Schimper, 1869. Some authors have postulated that the Middle Triassic to Carnian *L. stuttgardiensis*, which lacks obvious pustular ornament on its rachis, and *L. ottonis*, which is strongly pustulose, are synonymous (Kelber and van Konijnenburg-van Cittert, 1997; Kirichkova, 2006, 2008) but this has not been confirmed, since the cuticular micromorphology of the former species remains unknown. Although Peltaspermaceae survived the ETE at two locations in high southern latitudes (Bomfleur et al., 2018; Elgorriaga et al., 2019), there are no convincing records of *L. ottonis* from the Hettangian and this species was a key casualty of the ETE in mid-northern palaeolatitudes.

Lepidopteris ottonis has highly dissected leaves with small pinnules, very thick cuticle, tubercles over the major veins of the leaves but also on the rachis (Figs. 3a,b, 10). Stomata occur mainly on the abaxial (lower) side of the leaf protected by strong overarching beak-like papillae (Fig. 3c, e). Stomata are less abundant on the adaxial (upper) side of the leaf where they are concentrated over the veins (Fig. 3d).

The reproductive and foliar organs of Peltaspermales were not attached but borne separately on the parent plant and shed independently, such that it is unlikely that they will be found in physical connection. Nevertheless, the biological affiliation of *Lepidopteris ottonis* (leaf) and *Antevsia zeilleri* (pollen organ), has been confidently established by their shared cuticular features and co-preservation in various deposits in Greenland and northern Europe (Harris, 1937a, 1937b; Lundblad, 1959a, 1959b; Barbacka, 1991). Indeed, this linkage was so well resolved that these organ-based taxa were synonymized under the concept of a 'natural species' as *Peltaspermum ottonis* by Poort and Kerp (1990).

5. Discussion

5.1. Paleoecological implications

Our discovery that the 'seed-fern'*Lepidopteris ottonis* produced *Ricciisporites tuberculatus* pollen helps resolve the palaeobiology of this key early Mesozoic plant, and contributes to an understanding of the forces driving the end-Triassic mass extinction. The intense and geographically widespread volcanism associated with the initial opening of the central Atlantic led to pulses of cooling (Olsen et al., 2022) followed by global warming and depleted ozone shielding, collectively through increased



Fig. 10. Photographs and reconstruction of *Lepidopteris ottonis* plant from uppermost Rhaetian strata (Bjuv Member) of Sweden. A. *Lepidopteris ottonis* foliage, preserved on shale bedding plane from Gunnarstorp, Skåne. B. Macerated pinnae of *L. ottonis* showing thick cuticle from Bosarp, Skåne. C. Reconstruction of branch of male plant with short shoots bearing *Lepidopteris ottonis* foliage and *Antevsia zeilleri* microsporophylls. Scale bars = 10 mm. Specimen numbers: A, S064108; B, S079771.

atmospheric particulate matter, CO_2, thermogenic methane and SO_2. Particulate matter injected into the atmosphere by volcanism may also have contributed to elevated levels of metal toxins and other pollutants, such as HF, HCl, halocarbons and polycyclic aromatic hydrocarbons (van de Schootbrugge and Wignall, 2015).

The Early Jurassic was characterized by a hot climate with an atmospheric carbon dioxide concentration (pCO_2) around 900–1000 ppm (Beerling and Royer, 2002; Bonis et al., 2009; Steinthorsdottir et al., 2011; Steinthorsdottir and Vajda, 2015; Sha et al., 2015). Based on paleobotanical and palynological data, the End-Triassic environmental perturbations were expressed more strongly in the Northern Hemisphere (Kustatscher et al. 2018; Li et al., 2018, 2020) than in the Southern Hemisphere (Akikuni et al., 2010).

Complete fossilized plants of *Lepidopteris ottonis* have not been found but, based on the preservation of the leaves with slender axes in carbonaceous siltstones intercalated with coal seams in the upper Rhaetian strata of Sweden and Greenland, we interpret the plant to have been a woody shrub or small tree (Fig. 10c) that occupied relatively open mire and moist floodplain environments. The morphological characters, together with its abundance in peat deposits, suggests that *L. ottonis* was a plant adapted to high insolation, but also wetlands with consistently high groundwater moisture that could be regulated in the plant via transpiration through the vein-centred stomata.

We infer that the small, smooth, monosulcate pollen forms represent the 'normal' pollen of the *Lepidopteris ottonis/Antevsia zeilleri* parent plant, i.e., those having undergone regular meiosis, grain development, and separation. We interpret the highly ornamented, *Ricciisporites tuberculatus*-type grains to represent aberrant pollen produced by the same plant. *Ricciisporites* grains occur consistently united (shed as permanent tetrads) and are too large to represent immature forms. Several other distinctive morphological features of *R. tuberculatus*, including atypical surface structures (exaggerated ornamentation), skewed germinal apertures, and a thicker pollen wall, are considered characteristic of aberrant pollen grains of other plant groups (Kürschner et al., 2013; van de Schootbrugge and Wignall, 2015).

These atypical features of *R. tuberculatus* indicate significant disruption to the reproductive pathway of the parent plant. Various other pollen and spores across the Rhaetian–Hettangian transition potentially also represent aberrant forms of more common palynomorph taxa. Among these, *Rhaetipollis germanicus* Schulz, 1967 has prominent exinal thickenings and might represent a teratological variant of some other pollen type. *Classopollis* pollen is locally represented by elevated levels of aberrant permanent triads and tetrads of diverse sizes around the ETE (Kürschner et al., 2013; Li et al., 2018, 2020). The regular occurrence of aberrant pollen derived from diverse plant groups suggests a common environmental factor promoting mutagenic processes at that time.

5.2. Implications for Lepidopteris reproduction

We interpret *Ricciisporites tuberculatus* pollen to represent abnormal pollen produced by asexual *Lepidopteris* plants growing in stressed environments. The production of aberrant pollen is a well-documented phenomenon in both modern and ancient plants (Lindström et al., 1997; Benca et al., 2018;Vasilevskaya and Domakhina, 2018; Galasso et al., 2022), and such grains are commonly interpreted as mutant or immature forms that are infertile and produced by plants during periods of severe environmental stress (Smith and Zhao, 2016; Visscher et al., 2004; Zavattieri and Gutiérrez, 2023). The factors contributing to the high proportion of aberrant pollen produced by the *Lepidopteris ottonis* plant at the end of the Triassic are intriguing, since several other plants also produced elevated proportions of malformed spores and pollen at this time (Kürschner et al., 2013; Galasso et al., 2022). Moreover, similarly high levels of atypical grains have been reported around the end-Permian mass extinction event (van de Schootbrugge and Wignall, 2015; Foster and Afonin, 2005; Benca et al., 2018), and during the hyperthermal intervals of the Early Triassic (Galasso et al., 2022). Several causal factors have been postulated for the increased production of aberrant pollen during mass extinctions and hyperthermal events, including elevated levels of atmospheric pollutants, such as Hg (Lindström et al., 2019), high UV-B radiation linked to ozone depletion (Galasso et al., 2022; Smith and Zhao, 2016; Visscher et al., 2004; Benca et al., 2018), volcanism (Zavattieri and Gutiérrez, 2023), and heat, cold and drought stress (Smith and Zhao, 2016).

It is possible that any one, or a combination, of the environmental factors outlined above contributed to physiological stress in the *Lepidopteris ottonis* plant and induced the aberrancies recorded in its pollen, resulting in sterility and asexuality. The possession or adoption of an asexual reproductive strategy may have facilitated the survival of *Lepidopteris* under strengthening volcanic episodes leading up to the ETE and might have even provided this wetland-adapted lineage with short-term competitive advantages enabling proliferation over a broad swathe of the northern palaeotemperate belt. However, with a later shift to more stable drier conditions at the beginning of the Jurassic, sexually reproducing plant groups may have had advantages in adapting to the new environments over asexual plants with low genetic variation. Asexuality may also have led to an accumulation of deleterious mutations (Muller, 1964; Gabriel et al., 1993; Bengtsson, 2009), further decreasing the long-term fitness of *Lepidopteris*.

In some extant taxa, such as *Acacia*, rather than being detrimental to reproductive success, permanent tetrads or polyads can be beneficial to the plant by forming larger pollen packages that are more readily transported by insect vectors, and by increasing the number of viable pollen delivered to the stigma to fertilize multiple ovules in a carpel (Kenrick and Knox, 1982). Despite *Peltaspermum-Lepidopteris* being associated with relatively well preserved and well-studied ovules, there is no evidence for polyembryony in this group (Barbacka, 1991; Townrow, 1960).

The wall of the pollen sac and exine of the pollen are important protective barriers against various stresses but are also informative for pollen development and fertilization strategies (Chen et al., 2017). The innermost layer of the pollen sac wall, the tapetum, is where nutrients and enzymes are synthesized and transported to form the pollen (Wang et al., 2003; Ariizumi and Toriyama, 2011). Immediately after meiosis, as the tapetal cells degrade, segregation of individual grains takes place and original patterns leading to surficial orbicules or other ornamental features of the exine are laid down (Kurmann, 1990). A lack of separation of microspores after the tetrad stage will lead to aggregated pollen. Fertile aggregates have been observed in extant angiosperms and pteridophytes, but to the best of our knowledge, not in extant gymnosperms (Pacini et al., 1985; Fernando et al., 2010) emphasizing the aberrant nature of the tetrads observed here. Further, although there are differences between gymnosperms and angiosperms regarding how pollen surface coat material is deposited (Kurmann, 1990), knowledge of molecular mechanisms defining how the microspores separate at the end of the tetrad stage exists only for angiosperms. This separation demands an active process where the pollen mother cell is degraded (in the angiosperm *Arabidopsis* regulated by QUARTET genes) depending on cell-wall-loosening enzymatic activities, such as pectin methylesterase (QUARTET1) and polygalacturonidase (QUARTET3). As an example, the *quartet* mutants of *Arabidopsis thaliana* generate pollen complexes, each consisting of four microspores under a common exine layer (Francis et al., 2006; Shi et al., 2021). Further, a wide range of factors are known to induce tapetal cells of modern plants to secrete excessive sporopollenin, resulting in orbicule formation and, in some cases, fusion of pollen into permanent tetrads (Gómez et al., 2015). These unusual levels of sporopollenin secretion may result from abnormal hormonal instructions to the tapetum, and such signals can be induced by environmental stresses, such as elevated levels of metabolically harmful chemicals, dust, UV light, or excessively high or low temperatures (Benca et al., 2022).

When vegetation comes under stress, perturbation of the genetic or

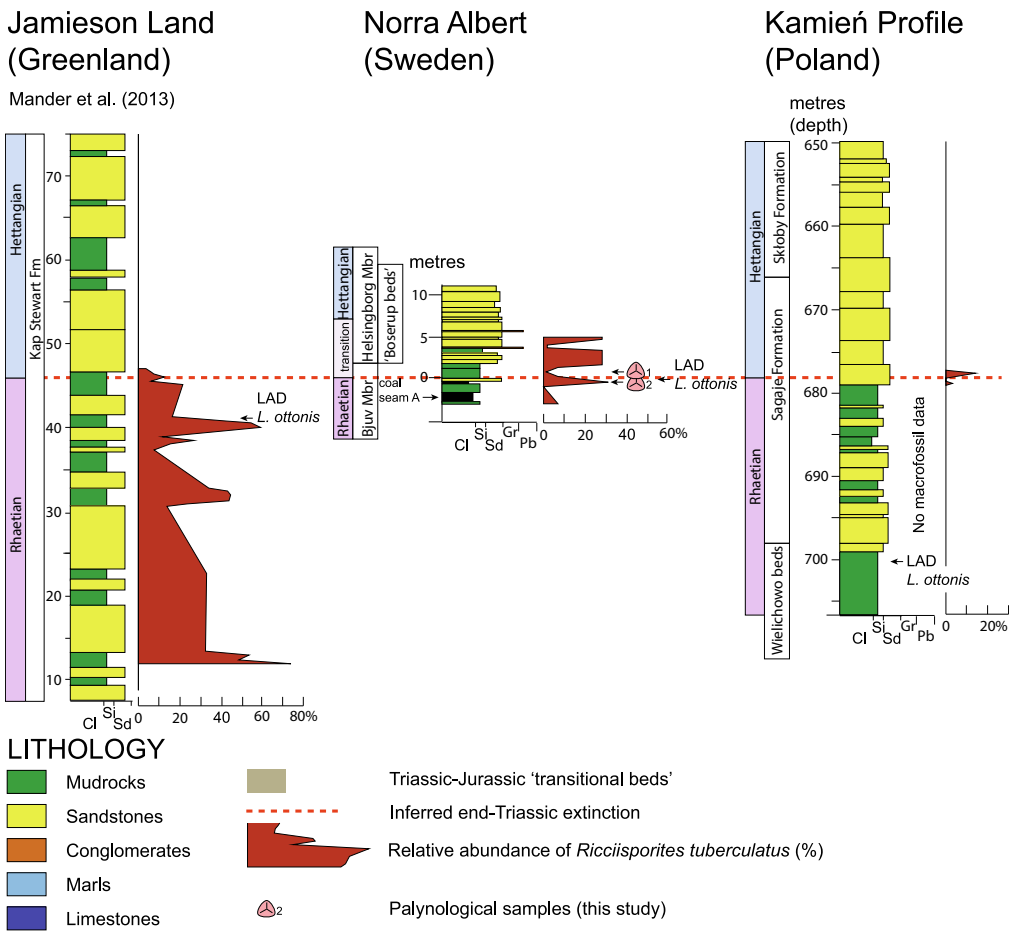


Fig. 11. Range and relative abundance of dispersed *Ricciisporites tuberculatus* grains in Greenland, southern Sweden and Poland in sections that contain the last appearance datum of *Lepidopteris ottonis*. Data after Mander et al. (2013), McElwain et al. (2007), Lindström and Erlström (2006), Pieńkowski et al. (2012), Barbacka et al. (2014), this study.

metabolic systems may cause infertility due to pollen aberrations, and an existing or induced asexual reproductive strategy becomes essential for short-term survival of the species (Visscher et al., 2004). Polyploidy, which gives advantages under environmentally stressful conditions (Van de Peer et al., 2017, 2021; Cheng et al., 2018; Stull et al., 2021), is commonly expressed by atypically large pollen (Kürschner et al., 2013) and can hinder fertilization by generating a collapse of genetic self-incompatibility systems (Amigo and Barker, 2012). With a rise in polyploid pollen production, asexual reproduction may have commenced vegetatively via layering, suckering or epicormic budding, all of which occur in extant angiosperms and conifers, or via pollen-independent apomixis. Self-fertilization and apomixis are the two major pathways of reproduction in angiosperms besides the normal sexual outcrossing system (Hojsgaard and Hörandl, 2015). Apomixis also occurs in gymnosperms, at least in the form of paternal apomixes (Pichot et al., 2001). Since Peltaspermales are resolved in relatively basal positions in most phylogenies of seed plants (Doyle, 2006; Hilton and Bateman, 2006; Nixon et al., 1994) and have no close extant relatives, their potential to perform maternal or paternal apomixes remains unclear. Apomictic plants may produce sexual or asexual offspring within the same generation, which means that asexuality is facultative (Hojsgaard and Hörandl, 2015). This may also have been the case for peltaspermalean 'seed ferns'.

Polyploidy can also induce the production of aberrant grains and the formation of obligate pollen tetrads or polyads (Baranyi et al., 2018). Polyploidy has long been considered important in driving long-term evolutionary trajectories in land plants (Stebbins, 1950; Levin, 1983; Soltis and Soltis, 2009). However, speciation via polyploidy has traditionally been considered rare among extant gymnosperms (Li et al., 2015). Nevertheless, recent studies have indicated that the natural history of most major extant gymnosperm lineages included whole-genome duplications and genome-size shifts and that these duplications, or their preferential selection, were concentrated during the Permian–Triassic interval and in the aftermath of the end-Cretaceous extinction event (Stull et al., 2021; Levin, 1983; Van de Peer et al., 2017, 2021).

Importantly, a transition to polyploidy and asexual reproduction via apomixis can promote rapid diversification and wide geographic distribution since polyploid organisms or populations are commonly more resilient to extreme conditions owing to increased genetic variation and rapid regeneration, thus allowing reproductively isolated genotypes to develop quickly (geographical parthenogenesis), providing reproductive success in the absence of, e.g., primary pollinators (Stull et al., 2021; Koutroumpa et al., 2021). The advantage of apomixis over other forms of vegetative reproduction is that it can enable a single plant to establish a viable new population and rapidly extend its range—an important trait in a stressed and changing environment. However, since asexual plant lineages are generally short-lived compared to sexual lineages (Koutroumpa et al., 2021), the pollen aberrations contributing to asexuality, may ultimately have led to the extinction of this briefly abundant species (*L. ottonis*) by the close of the Triassic.

5.3. Implications for pollen taphonomy

Where plant macrofossils and palynomorphs occur in the same section, the collapse of *R. tuberculatus* abundance coincides with the last appearance of *Lepidopteris ottonis* (Fig. 9). In some parts of Europe,

sparse occurrences of *R. tuberculatus* persist into inferred lowermost Hettangian) strata (van de Schootbrugge et al., 2020; Gravendyck et al., 2020) and even into much younger Pliensbachian (late Early Jurassic) beds (Polteau, 2020). However, palynomorphs are prone to sedimentary reworking, especially in fluvial depositional systems (Traverse, 2007). Consequently, last appearance datums of pollen can be unreliable and are rarely used to define palynostratigraphic zones (Vajda and Bercovici, 2014). The most parsimonious explanation for the sparse representation of *R. tuberculatus* grains in post-Triassic strata (Fig. 11), in the absence of *L. ottonis*, is that their occurrence has resulted from sedimentary reworking of uppermost Triassic strata rich in this microfossil taxon.

The relatively low abundance of *Monosulcites* pollen in northern temperate palaeolatitudes prior to the ETE is intriguing, since it dominates over *R. tuberculatus* in the studied *Antevsia zeilleri* pollen sacs. Even in the absence of peltasperms, smooth boat-shaped pollen of this type produced by Bennettitales, Cycadales, Leptostrobales, Pentoxylales and Ginkgoales ought to be very common in uppermost Triassic and lowermost Jurassic strata based on the macrofossil record of these groups, yet it is consistently sparse. There are several possible explanations for this including: (1) loss of the generally small and slender (~20 μm maximum diameter) boat-shaped grains during the sieving process of standard Mesozoic palynological sample processing; (2) preferential oxidation of these thin-walled pollen types during some sample maceration procedures; or (3) deficiency of sporopollenin in the pollen walls resulting in a negative preservational bias for such grains in the dispersed state, as is the case for Lauraceae pollen in Cenozoic strata (Traverse, 2007).

We used 5 μm mesh in this study in order to retain small grains and we prepared kerogen slides from unoxidized residues. This may explain why we obtained relatively high percentages of monosulcate pollen grains (15% of the pre-extinction assemblage) in contrast to some previous studies (Lindström and Erlström, 2006). The *Ricciisporites* pollen grains are large and robust, which favours their preservation and may explain their over-representation in palyno-assemblages. Their resistance to mechanical and chemical abrasion may also explain their persistence into post-ETE sandstones.

6. Conclusions

Our results solve a 70-year-old puzzle by recognizing a 'seed-fern' (Peltaspermales) affinity for the bizarre stratigraphic index pollen *Ricciisporites tuberculatus*. We conclude that this taxon represents aberrant pollen of probable (in part) asexually reproducing *Lepidopteris ottonis* plants. The marked peak in several aberrant gymnosperm pollen groups before and during the end-Triassic extinction probably reflects the competitive success of asexual plants under stressed environmental conditions, such as intervals of reduced insolation and short-term cooling due to massive volcanic emissions. The loss of *Lepidopteris* from the Northern Hemisphere during the end-Triassic mass extinction was probably the result of an inability to adapt by sexual recombination to the drier and more stable Jurassic environmental conditions, wherein competition increased from more genetically diverse, sexually reproducing plant groups.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2023.111723.

Declaration of Competing Interest

The authors declare no competing interests.

Data availability

No data was used for the research described in the article.

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