



Lagenella martini from the Triassic of Austria – Exine structure and relationships with other striate palynomorphs

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ARTICLE INFO

Article history:

Received 16 December 2017

Received in revised form 7 May 2018

Accepted 28 June 2018

Available online 30 June 2018

Keywords:

Upper Triassic

Lagenella martini

Striate pollen

Exine ultrastructure

Granular infratectum

ABSTRACT

Dispersed pollen grains of *Lagenella martini* from the Upper Triassic of Austria were studied by means of light, scanning and transmission electron microscopy. Pollen grains are medium-sized, monosulcate, finely striate with differently directed striations on distal and proximal surfaces. The aperture is usually broadly open with rounded ends. The ectexine is composed of a thick tectum, granular infratectum, and thin foot layer. The endexine shows fine lamellation in its outer part. Reported association of *Lagenella martini* with *Stachyotaxus* reproductive structures needs a more detailed investigation of the morphology and ultrastructure of the found pollen to make reliable conclusions. A comparison with known fossil and modern non-saccate striate pollen has shown that the studied pollen grains share a number of characters with some gymnosperms and angiosperms with most similarity to *Vittatina*-like pollen.

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1. Introduction

Striate non-saccate pollen grains represent one of the most interesting and enigmatic morphotypes among fossil microremains. Although this type of morphology is found in unrelated species of modern angiosperms and gymnosperms (e.g., Arales, Laurales, Zingiberales, Gnetales, Hesse et al., 2000) the affinities of most striate fossil pollen remained uncertain. Which plants produced such pollen grains, were they related or did this morphotype evolve repeatedly and independently in different phylogenetic lineages?

In such cases the most reliable information can be obtained by studying in situ material. However, there are few in situ findings of striate fossil pollen so far; most information rested on dispersed material (e.g., Stover, 1964; Osborn et al., 1993; Burger, 1994). While affinities of *Ephedripites*, *Ephedra*, *Welwitschia*-like pollen and some *Equisetosporites* were more or less safely recognized (with some recently re-interpreted, see Hesse and Zetter, 2007) among fossil striate palynomorphs, relationships of other morphotypes, e.g., *Vittatina*, *Weylandites*, *Lagenella*, and *Jugella*, remained completely unclear. A few findings of *Vittatina*-type or *Weylandites*-type pollen were reported in pollen chambers or inside sporangia but no conclusive data were obtained from such plant associations (e.g., Pant and Basu, 1977; Gomankov and Meyen, 1986; Zavada, 1984; Bhowmik and Parveen, 2012). Studies of fine structure of such pollen grains are definitely in demand to elucidate their botanical affinity and evolution of striate pollen in different plant lineages.

In this paper we studied the pollen morphology and ultrastructure of dispersed *Lagenella martini* from the Triassic of Austria. This is one of such non-saccate striate morphotypes which were mostly found dispersed. An association of *Decussatisporites martini* Leschik (later considered as *Lagenella martini* by Klaus (1960)) with macroremains of *Stachyotaxus lipoldi* (Stur) Kräusel had been documented (Klaus, 1966). No clear botanical affinity or studies on fine pollen morphology and sporoderm ultrastructure of these pollen grains by means of electron microscopy had been done so far. This study fills the gap and discusses possible relationships of *Lagenella* pollen with other striate palynomorphs.

2. Material and methods

Pollen grains of *Lagenella martini* Klaus and *Equisetosporites chinleanus* Daugherty come from the first basal shale of the Raibler Schichten outcropping in the Northern Calcareous Alps near the village of Rubland (Southern Austria, Fig. 1). The age is uppermost Julian (Upper Triassic; Roghi et al., 2010) (Fig. 2). The first shale of the Raibler Schichten showed a rich palynoflora with abundant monosaccate (*Patinasporites*, *Enzonasporites*, *Vallasporites*) and monosulcate (*Cycadopites*) pollen. The possibly bennettitalean pollen *Aulisporites astigosus* was also present and abundant only in the first shale together with striate *Lagenella martini* and *Equisetosporites chinleanus* (Jelen and Kusej, 1982; Roghi et al., 2010).

The sample was macerated and treated with HCl and HF. After washing and sieving (15 µm), the residue was stored in water. Pollen grains were picked up from the residue and subsequently studied with light

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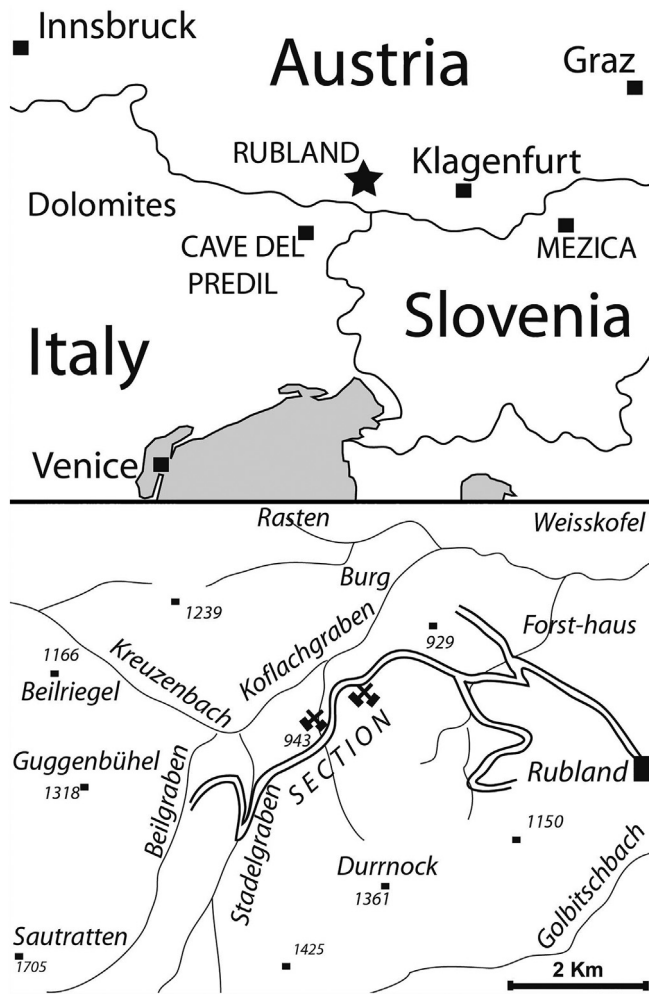


Fig. 1. Location map of Rubland area showing the position of the section (943 m s.l.) in the Koflachgraben.

(LM), scanning (SEM) and transmission (TEM) electron microscopy. Each studied pollen grain was photographed with a Carl Zeiss Axioplan-2 light microscope equipped with a 100 \times oil immersion objective and a Leica DFC-420 digital camera. Then the same pollen grain was transferred from the LM slide to a SEM stub, covered with gold and observed under a Tescan Vega-II XMU SEM (accelerating voltage 30 kV).

Some of the studied pollen grains were then removed from the stubs and prepared for TEM according to standard methods (Meyer-Melikian et al., 2004). Some of them were first stained with 1% OsO₄; others were directly embedded in epoxy resin unstained. Pollen grains were sectioned with a Leica UC6 ultramicrotome. Some of the ultrathin sections were stained with lead citrate and uranyl acetate (others were studied unstained), and examined under a Jeol 100 B and Jeol 1011 TEMs (Jeol, Japan) at accelerating voltage 80 kV and with a CCD GATAN ES500W under control Digital Micrograph GATAN at the Laboratory of Electron Microscopy, Biological Faculty, Lomonosov Moscow State University.

Terminology follows Osborn (2000) and Hesse et al. (2009).

3. Results

3.1. LM (Fig. 3)

Pollen grains are ellipsoidal, monosulcate, finely striate. The aperture is usually broadly open with rounded ends. The direction of the

striations is different on both surfaces, they are longitudinal (parallel to the sulcus and to the longest pollen axis) in the area around the aperture on the supposedly distal surface (where the aperture is situated) and transversal on the periphery of the distal and on the entire proximal surface. These perpendicularly directed striations roughly stem from the middle part of the longest pollen axis (corresponding to the sulcus length) and expand to the supposedly proximal surface. The longest pollen axis is 34.3 (25.4–43.2) μm , the shortest axis is 24.2 (20.0–29.4) μm .

3.2. SEM (Plate I)

The longest pollen axis is 36.4 (25.1–48.8) μm , the shortest axis is 28.9 (21.6–40.6) μm . The exine sculpture is finely striate, striations are immediately adjacent to each other and smooth, their width is 0.55 (0.2–1.0 [rarely]) μm (Plate I, 1, 2, 4–8). The aperture membrane is smooth or scabrate (Plate I, 3).

3.3. TEM (Plate II, 1–8)

In many pollen grains the ectexine looks homogeneous. The exine stratification can be distinguished in some pollen grains or at some parts of the pollen grains (Plate II, 1, 2). The ectexine is less electron dense than the endexine and is from 0.28 to 0.86 μm thick in the crest region. The ectexine consists mostly of the foot layer in the valley region (Plate II, 3, 4). In the non-aperture region the tectum is from 0.11 to 0.54, it mainly composes most part of the ectexine (Plate II, 5, 6). The infratectum is granular, with granules from 0.1 to 0.18 μm in diameter, they are probably (mainly) situated in one row (Plate II, 5–7). The foot layer is thin, from 0.02 to (rarely) 0.12 μm thick. The endexine is about 0.31–0.43 μm , it is equal in thickness throughout the pollen grain. The endexine structure is probably finely lamellate (Plate II, 7, 8), but in most parts it looks homogeneous. In aperture region the exine consists of a thin foot layer and endexine (Plate II, 3, 4).

4. Discussion

4.1. Understanding of the exine structure

The studied pollen grains show mostly homogeneous structure of the exine that reflects the preservational conditions of the material. We also studied *Equisetosporites* pollen from the same sample and its exine structure also looked homogeneous in most cases (Plate III, 1–11) though it was known from published data that such pollen is characterized by granular or columella-like infratectal elements (Zavada, 1984; Pocock and Vasanthy, 1988; Osborn et al., 1993). The same problem was reported for various Upper Triassic taxa with known exine ultrastructure (N. Zavialova, pers. comm.). So far, few such data are known and we do not know what could have caused such preservational transformations in the exine structure. In our case the study of numerous ultrathin sections of the same pollen and of stained and unstained sections of different pollen grains has shown that *Lagenella martini* is characterized by a relatively thick tectum, granular infratectum and thin foot layer (Plate III, 5–7). The infratectal granules are probably sometimes fused into the tectum (Plate III, 5, 8). The endexine shows fine lamellations in its outer part near the aperture region in some pollen (Plate III, 3, 4, 7). This might be an evidence of its true (finely lamellated) structure.

4.2. Association with macroremains

Lagenella martini was found in association with macroremains of *Stachyotaxus lipoldii* from the Triassic of Switzerland and Austria (Kräusel, 1949; Klaus, 1966). Pollen grains were described as “oval, simple, monosulcate, finely costate, 35–40 μm ” (cited from Balme, 1995). Klaus (1966) indicated the pollen size as 30 \times 40 μm . This is in good

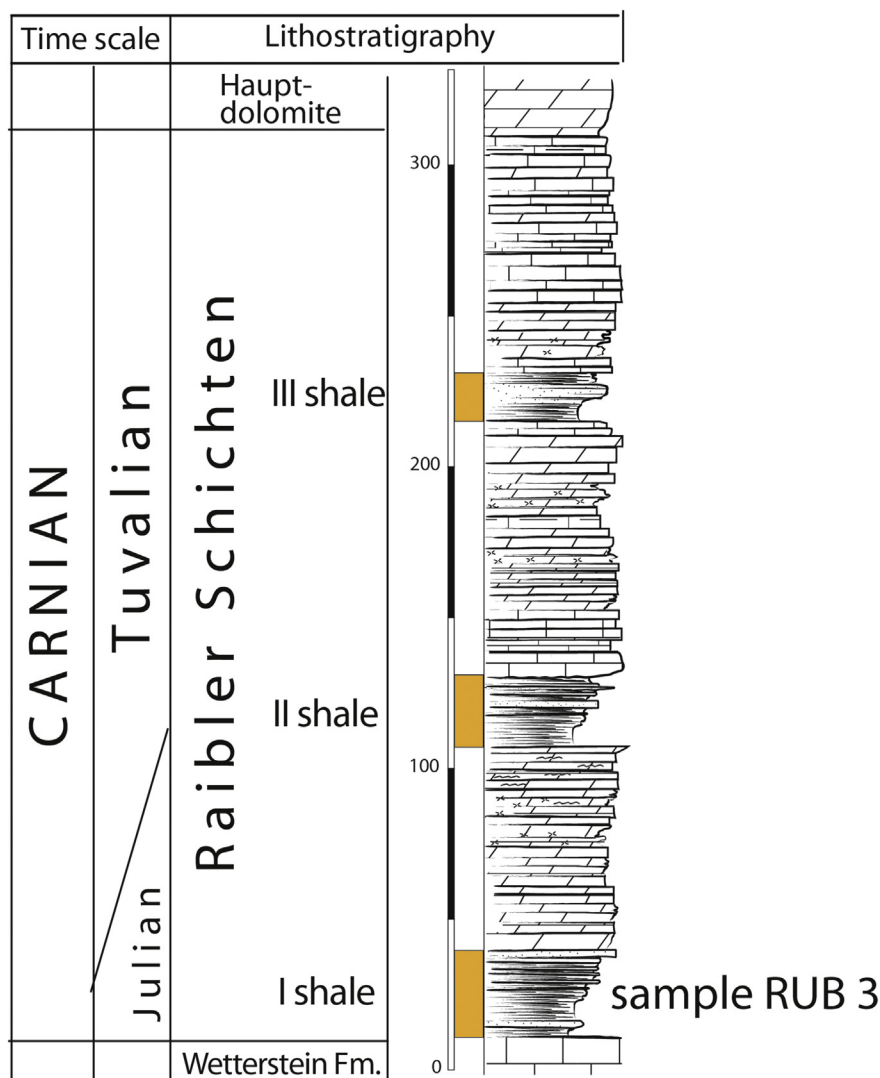


Fig. 2. Stratigraphic column of the Raibler Schichten with the position of the sample RUB 3 in the first shale.

accordance with our material. The occurrence of the associated pollen in cluster with some smaller grains (immature?) as well as their compression on the epidermal side of the macroremains made Klaus (1966) conclude that these pollen grains most probably came from *Stachyopitys lipoldii* ("from a nearby growing male reproductive organ"). Klaus (1966) in his description wrote that their exine structure was identical to that of *Lagenella martini* (Klaus, 1960) but did not bring any illustrations of the pollen grains and instead referred to the figures of pollen grains in Kräusel (1949). Striation was absent or indistinguishable in the pollen figured in Kräusel (1949) though it was clearly seen by Klaus and showed in his drawings of *Lagenella martini* in Klaus (1960).

Stachyotaxus lipoldii belongs to the family Palissayaceae, which was considered within Voltziales s.l. (Balme, 1995), Pinales (Meyen, 1984), but mainly within Coniferales (e.g. Taylor et al., 2009; see review in Wang, 2012). Relationships of the family members seem to be still controversial and need further research (see review in Wang, 2012; Pattemore et al., 2014). Harris (1926, cited from Balme, 1995) showed small monosulcate pollen from the micropyle of *Stachyotaxus elegans* Nathorst but it is unknown whether the pollen grain corresponds to that found in association with *S. lipoldii*. Harris (1935) wrote in his genus description of *Stachyotaxus* that pollen grains in the male cone are "round and wingless"; pollen grains found in micropyles of several specimens of *S. elegans* from the Triassic of Greenland were mostly the same as those from the male cone, although in one of the seeds three

types of pollen and fern spores were found. In situ pollen grains from another member of this member, *Palissya harrisii* Hill from the Jurassic of UK, were reported as "monosulcate with a rather broad sulcus" and to be of the same type as those described for *S. lipoldii* and *S. elegans* (Van Konijnenburg-van Cittert, 2008). However, according to Prof. Dr. J. van Konijnenburg-van Cittert's pers. comm. and LM photos kindly given by her no striation was observed. Also no striation was mentioned by Harris for his findings of pollen grains (Harris, 1926, 1935); although this could have been resulted from a poorer quality of the equipment at that time. *Decussatisporites delineatus* Leschik figured in Balme (1995, Plate X, fig. 2) showed definite striation similarly to our material although the pollen on the photo seemed to have two apertures or folds near the sulcus instead of one sulcus usually observed in this type of pollen. Prof. Dr. J. van Konijnenburg-van Cittert (pers. comm.) also mentioned that she sometimes observed folds near the sulcus in the pollen grains from *Palissya harrisii*. This discrepancy in "pollen data" and inconsistencies in the Palissayaceae phylogenetic position impede a reasonable attribution of dispersed *Lagenella* pollen to any plant group so far.

4.3. Comparison with similar gymnosperm morphotypes

4.3.1. Comparison with *Vittatina* and so called *Vittatina*-like pollen

A number of dispersed striate non-saccate pollen genera are known, some of them were also found in situ (e.g., Stover, 1964; Osborn et al.,

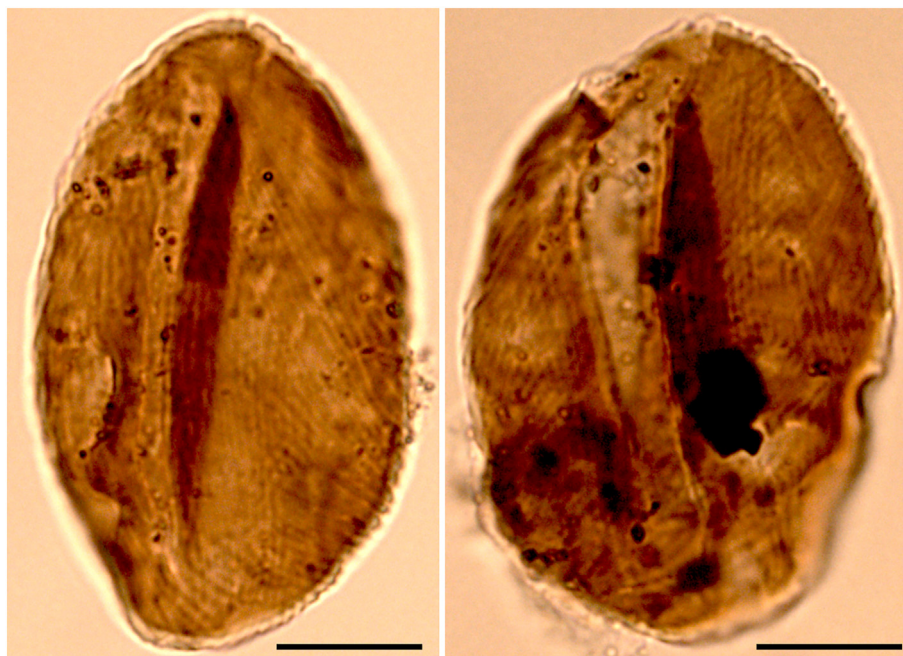


Fig. 3. *Lagenella martini*, light microscopy. Scale bar: 10 μ m.

1993; Burger, 1994). Similar pollen grains with differently directed striations/taeniae were found among ?*Rugapites*, *Vittatina*, *Weylandites* or so called *Vittatina*-like pollen (Koloda and Molin, 1986; Koloda, 1997; Afonin, 1999; Gomankov and Tarasevich, 2008, 2011, 2014; Bhowmik and Parveen, 2012).

Pollen grains of ?*Rugapites*, *Vittatina*, *Weylandites* or so-called *Vittatina*-like pollen were mostly larger than those of *Lagenella*. Morphologically all of them also differed from *Lagenella* in much thicker striations/taeniae. Besides, unlike *Lagenella*, striations on the proximal side were parallel to the longest axis of the pollen grain, while distal striations were perpendicular to the axis in these genera. Some of them additionally differed in the presence of small sacchi or remained “terminal ends”, a ?trilete or monolet scar, distal or transversal/equatorial “rim” (e.g., Gomankov and Meyen, 1986; Zavialova, 1998; Koloda, 1997; Lupia et al., 2015). Some *Vittatina* species additionally differed in verrucate sculpture (Koloda, 1997; Gomankov and Tarasevich, 2008, 2011).

All these genera were described on the basis of pollen grains and were mostly known as dispersed pollen, so their botanical affinity is unclear. Only *Rugapites* pollen grains, which Balme (1995) considered in fact as *Weylandites*, were found in *Rugospermum* seeds (Bhowmik and Parveen, 2012) and inside sporangia of *Rugatheca nidpurens* D.D. Pant et Basu (Pant and Basu, 1977). These remains, however, were mainly referred to as a “plant of gymnospermous affinity”. Bhowmik and Parveen (2012) put “Gnetales?” in the systematic heading describing *Rugospermum minuta* Bhowmik et Parveen, but did not discuss possible gnetalean affinities further. Later, Bhowmik et al. (2014, p. 379) described another *Rugospermum* species with *Rugapites* pollen inside pollen chambers and indicated that these pollen grains were “remotely comparable to the polyplicate pollen types of gnetophytes” and that “Rather presence of *Rugapites* grains of sporae dispersae within the pollen chamber of seeds indicate a gnetalean than a corystospermous affinity”.

Pollen grains of *Vittatina*-type were found in pollen chambers of seeds of possible peltasperm affinities (e.g., Gomankov and Meyen, 1986) but their reliable belonging to this plant species had never been proved as other pollen types were also found in the pollen chambers of the same species. Thus, no reliable evidence on possible botanical

affinities of such pollen grains (*Vittatina*, *Weylandites*, *Rugapites*, *Lagenella*) exists so far and the detailed study of their pollen morphology and ultrastructure is the only way to clarify the situation.

The exine ultrastructure was studied only for several species of *Vittatina* and *Weylandites* (Meyer, 1977; Koloda and Molin, 1986; Zavialova, 1998; Afonin, 1999; Gomankov and Tarasevich, 2008, 2011; Lupia et al., 2015). There were differences in the structure of exine layers in the studied *Vittatina* species. Meyer (1977) described the infratectum as alveolar and alveolar-granular for pollen grains of *Vittatina* sp. from the Permian of Russia with and without small sacchi; the tectum was relatively thin, the endexine was uniformly thick and lamellate. Koloda and Molin (1986) described a columellate infratectum, rather thin tectum and endexine for *Vittatina subsaccata* Sam. ex Wil. from the Permian of Russia. Afonin (1999) described a granular infratectum in the proximal region and alveolar infratectum in the distal region with a thick tectum, thin foot layer, and lamellate endexine which was preserved mainly in the aperture region for *Vittatina connectivalis* (Sauer) Warjuchina ex Utting from the Permian of Russia. Gomankov and Tarasevich (2008, 2011) described a rather thin tectum, granular-columellate infratectum and uniformly thick endexine for their *Vittatina costabilis* Wilson emend. Tschudy et Kosanke from the Permian of Russia. Lupia et al. (2015) figured the exine ultrastructure of *V. costabilis* from the Permian of the USA. They did not describe the infratectum but it appeared to consist of granules and columella-like elements in the proximal region and granular-alveolar in the lateral/equatorial region (“rim”). The tectum was relatively thin, the nexine (? = lamellate endexine) was thick and uniform throughout the pollen.

Zavialova (1998) studied Upper Permian pollen grains of *Weylandites* sp. from Russia and detected an exine consisting of a thick tectum and infratectum of large granules. Afonin (1999) reported on the exine ultrastructure of *Weylandites tataricus* Gomankov from the Permian of Russia with a relatively thin tectum consisting of fused granules and infratectum of mainly large granules; the lamellate endexine was preserved in the distal region only. Gomankov and Tarasevich (2008) described pollen grains of *Weylandites* sp. from the Permian of Russia as having a very similar ultrastructure to their *Vittatina costabilis*: with a tectum, granular-columellate infratectum, and thick uniform

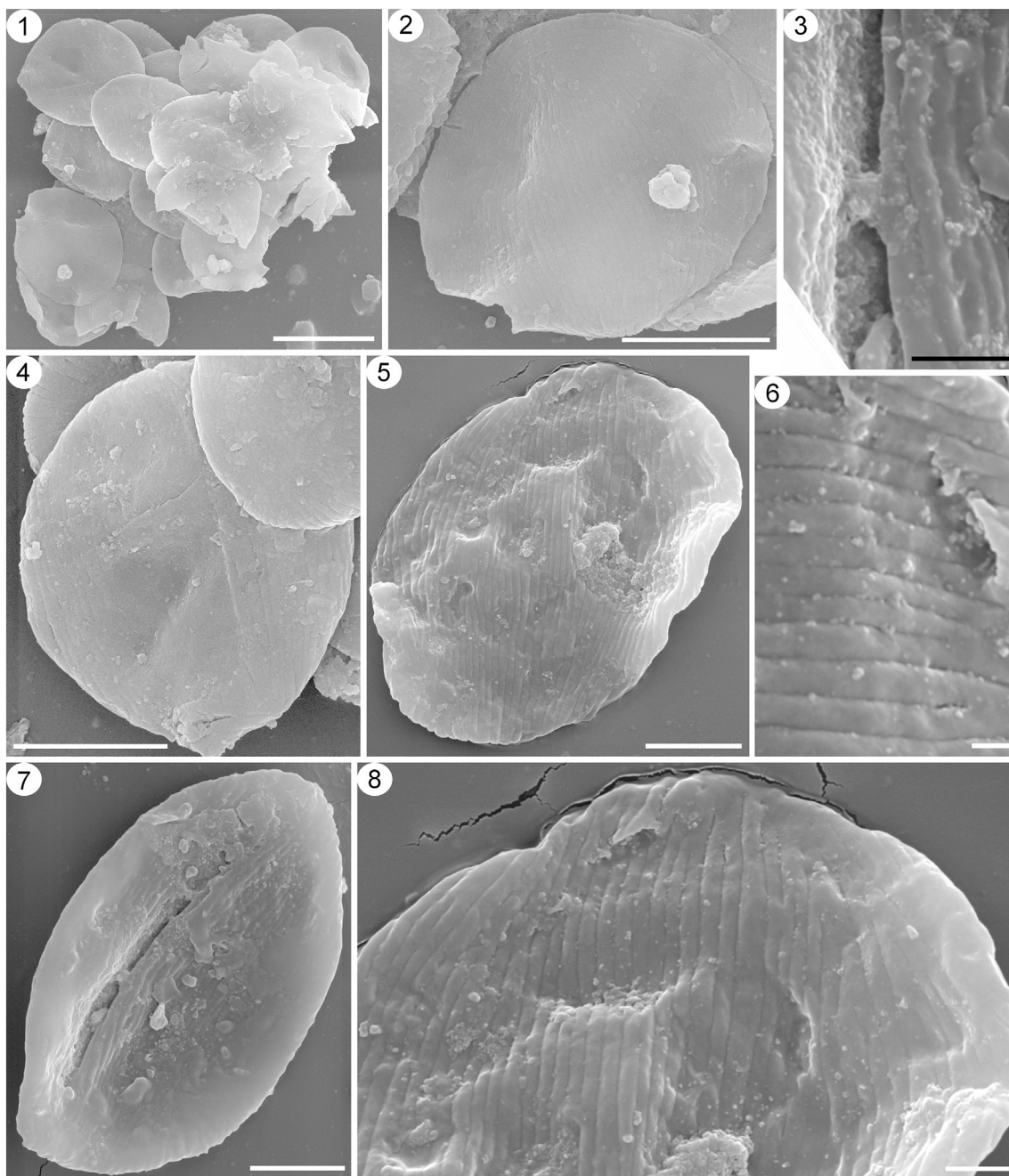


Plate I. *Lagenella martini*, scanning electron microscopy. 1. Group of pollen grains. 2, 5. Pollen grain, proximal view. 3. Aperture membrane. 4, 7. Pollen grain, distal view. 6, 8. Close-up of striation. Scale bar: (1) 20 μm ; (2, 4, 5, 7) 10 μm ; (3, 8) 3 μm ; (6) 1 μm .

inner layer (=endexine, in our opinion). Judging from the photos, the infratectal granules of *Weylandites* sp. were larger than those of *Vittatina costabilis*.

The exine ultrastructure in the aperture region and in the depressions between taeniae was similar in all studied specimens of *Vittatina* and *Weylandites*: it consisted of a lamellate endexine and thin foot layer (if present).

In our opinion, the infratectum of all studied so far pollen of *Weylandites* and *Vittatina* consisted of granular elements. So-called columellate state was rather composed of granules arranged in columella-like elements. The alveolate state in the distal region of *Vittatina connectivalis* and for *Vittatina* sp. reported by Afonin (1999) and Meyer (1977) was not clearly seen on the presented illustrations. The only clear alveolate structure of the infratectum was evident from

illustrations of the lateral/equatorial regions of *Vittatina costabilis* studied by Lupia et al. (2015).

Foster and Gomankov (1994) noted that detached cappa of *Protohaploxylinus* pollen grains resembled superficially members of other genera (including *Vittatina* and *Weylandites*) and could be confused with them or identified as such. *Vittatina*-like pollen grains can be imagined as a possible transitional state from bisaccate pollen grains like taeniate *Protohaploxylinus* to non-saccate pollen appearing like *Vittatina*-like pollen and the latter representing an oblate sort of *Lagenella* pollen. Indeed, some studied *Protohaploxylinus* pollen grains had rather small sacchi (Zavialova, 1998) and it was easy to imagine their change to *Vittatina* pollen with an equatorial rim instead of sacchi or to *Vittatina* pollen with small residual sacchi. The ultrastructure of the taeniate body of *Protohaploxylinus* often looked granular (Zavialova et al., 2001;

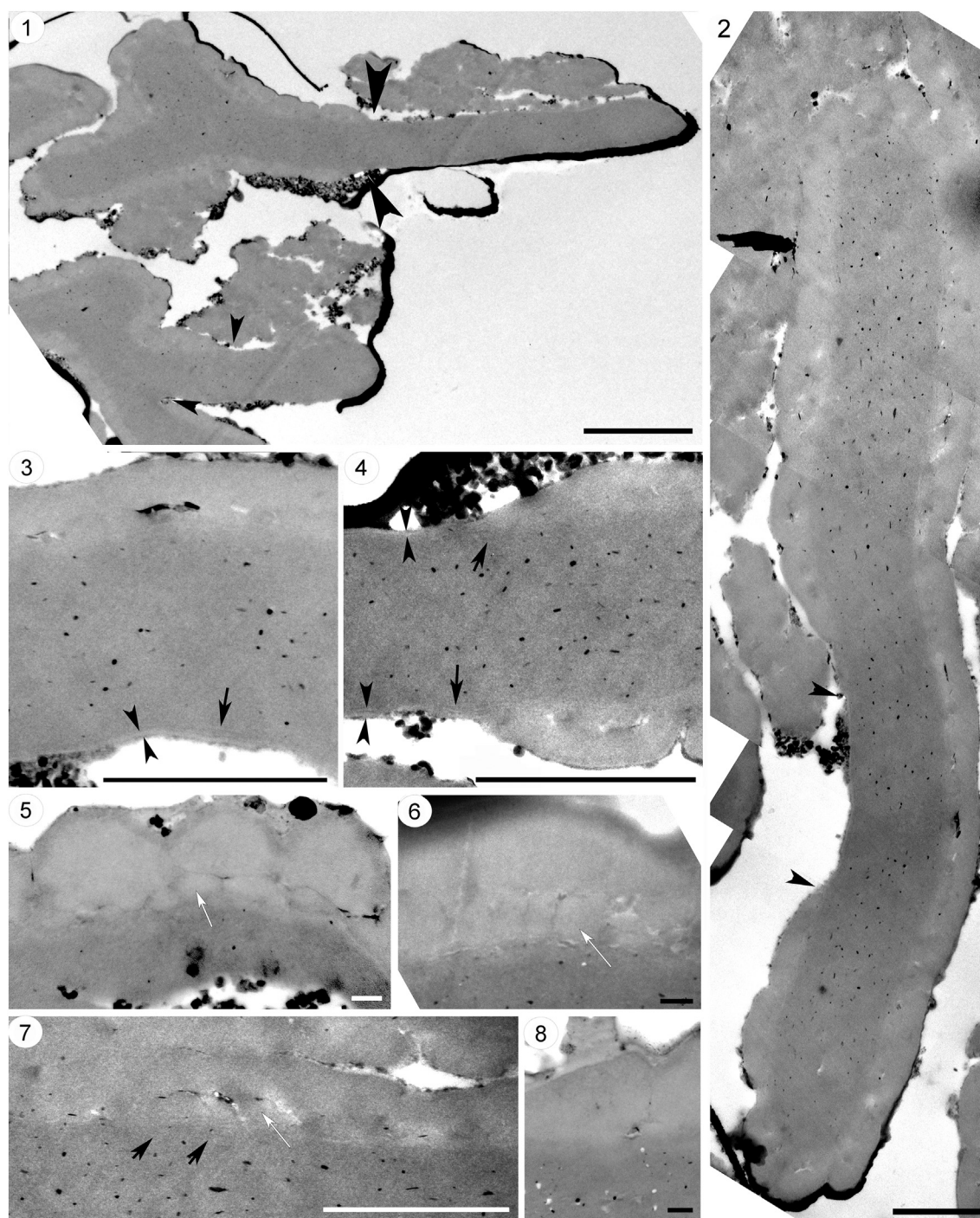


Plate II. *Lagenella martini*, transmission electron microscopy. 1. Section through the group of pollen grains, arrowheads indicate aperture regions. 2. Section through a whole pollen grain, arrowheads indicate aperture regions. 3, 4. Part of aperture and non-aperture sporoderm, arrowheads border thin foot layer in the aperture region; at places lamellations are seen in the outer part of the endexine at the transition from non-aperture to aperture sporoderm (arrows in 3, 4). 5–8. Non-aperture region, white arrows point to infratectal granules, black arrows point to the weakly seen lamellations in the outer part of the endexine, gaps in the endexine are often seen (7, 8). Scale bar: (1, 2) 2 μm ; (3, 4, 7) 1 μm ; (5, 6, 8) 0.2 μm .

Zavialova and Karasev, 2015) similarly to granular infratectum of *Vittatina*. The tectum was somewhat thicker at rib regions in comparison to other sporoderm regions and this, together with the one row of alveolae or granules, appeared to look similarly to the ultrastructure of *Lagenella* sporoderm. The endexine in studied *Protohaploxypinus* pollen grains was often represented by (or preserved as) a thin or discontinuous layer (Zavialova et al., 2001; Zavialova and Karasev, 2015), mostly different from what we observed in *Lagenella* pollen.

Leschik (1956) proposed for *Entylissa/Decussatisporites* pollen grains (later considered by Klaus (1960) under the generic name *Lagenella*)

affinities with cycadalean and bennettitalean plants. However, both pollen morphology (striate in *Lagenella* versus non-striate in cycadalean and bennettitalean pollen) and exine ultrastructure (medium-sized granules disposed in one row in *Lagenella* versus alveolate in cycadalean pollen and finely granular, often with numerous granules in bennettitalean pollen) contradict this idea.

4.3.2. Comparison with gnetophyte (ephedroid) pollen

Striate pollen of *Lagenella* as well as ?*Rugapites*, *Vittatina*, *Weylandites* evoked their comparison with gnetophyte (ephedroid)

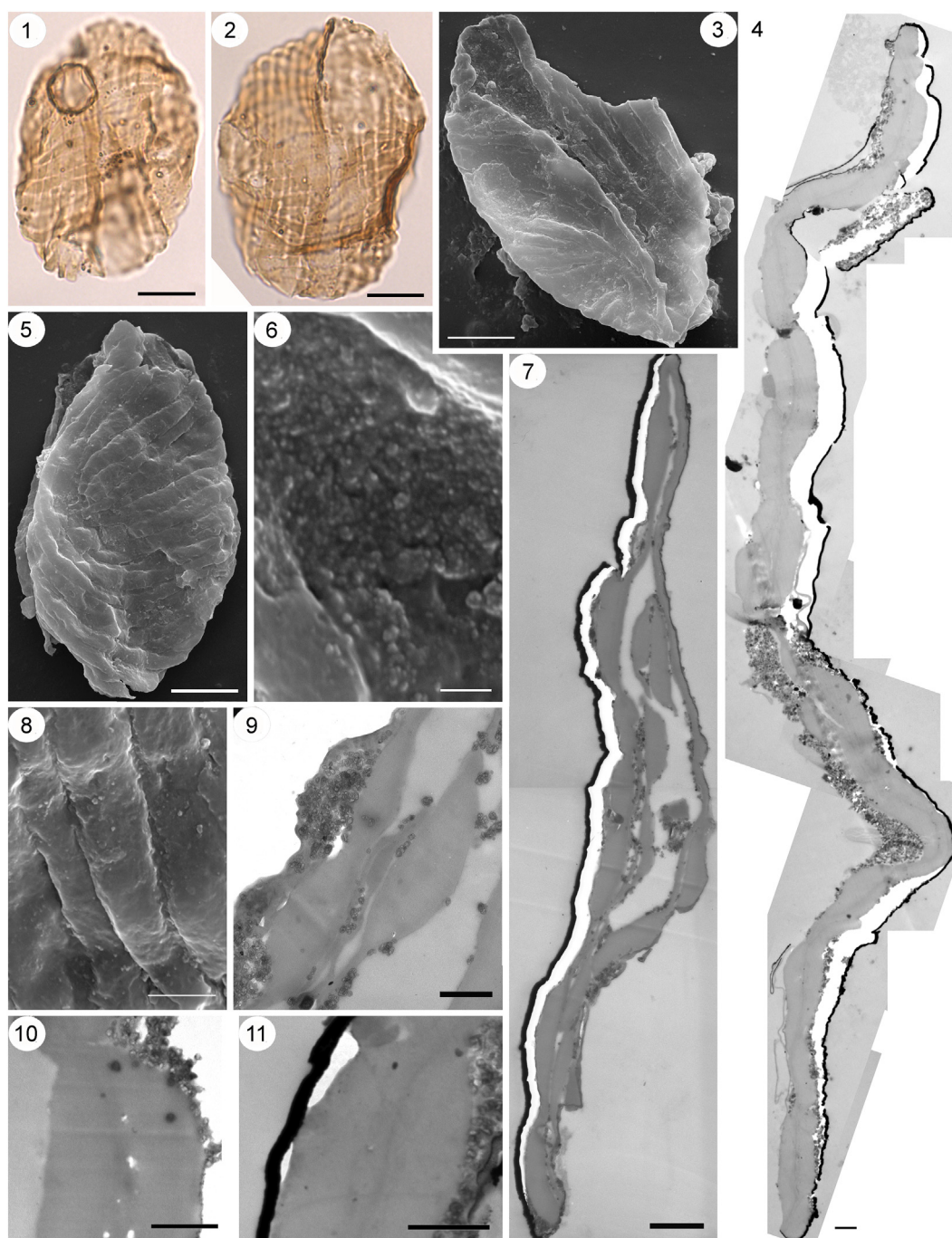


Plate III. *Equisetosporites chinleanus*. 1, 2. Light microscopy. 3. Scanning electron microscopy, distal view. 4, 7. Transmission electron microscopy, section through the whole pollen grain. 5. Scanning electron microscopy, lateral view. 6. Scanning electron microscopy, aperture membrane. 8. Scanning electron microscopy, close-up of exine sculpturing. 9–11. Exine structure in the plica region. Scale bar: (1–3, 5) 10 μm ; (4, 10, 11) 0.5 μm ; (6, 7) 1 μm ; (8) 3 μm ; (9) 0.4 μm .

pollen. Some authors considered them within gnetophytes with different degree of probability (e.g., Lindström et al., 2016). Fossil and modern striate pollen of gnetophytes were studied in a number of works, and there were several reviews on this topic (e.g., Osborn, 2000; Tekleva and Krassilov, 2009; Tekleva, 2016). Striate pollen grains of gnetophytes include *Welwitschia*, *Ephedra*, *Ephedripites*, *Equisetosporites*, and ?*Jugella*. The latter was of unclear botanical affinity but was believed to be related to gnetophytes (to *Welwitschia*, see Friis et al., 2004; Schrank, 2010). The striations were wider in striate gnetophyte pollen than those in *Lagenella*. Unlike *Lagenella*, ephedroid pollen grains *Ephedra*, *Ephedrites*, and *Equisetosporites* lacked a sulcus. Only one example of monosulcate *Ephedripites* was described by

Trevisan (1980) from the Early Cretaceous of Italy. Striations of *Welwitschia*, *Ephedra*, *Ephedripites* differed from those of *Lagenella* all being parallel to the longest pollen axis.

The exine ultrastructure in gnetophyte striate pollen was also characterized by a granular infratectum like in *Lagenella*, however, granules were usually much smaller and numerous in comparison to *Lagenella*. The tectum was thinnest at the crest within the plica in *Ephedra* species and more or less uniform in thickness within the plica in *Welwitschia*, *Ephedripites* and *Lagenella*. The tectum reduced in thickness toward furrow regions in all species. The endexine structure and exine ultrastructure of the aperture region (when present) were quite similar in gnetophyte striate pollen and *Lagenella*.

The furrow region was represented by a thin tectum, thin granular layer, foot layer and endexine in *Welwitschia*, thin ectexine layer (?foot layer) and endexine in *Ephedra* species, *Ephedripites*, and *Equisetosporites* described in Osborn et al. (1993) from Early Cretaceous of Brazil (see review in Osborn, 2000; Tekleva, 2016), and by an endexine alone in *Equisetosporites* from the Triassic of USA (Zavada, 1984; Pocock and Vasanthi, 1988).

The infratectum of *Equisetosporites chinleanus* from the Triassic (Chinle Formation) was reported to be columellate unlike the infratectum of other gnetophyte striate pollen (Zavada, 1984; Pocock and Vasanthi, 1988; Vasanthi et al., 2004). The columellae were short and stout and often looked like large granules somewhat similar to those found in studied *Lagenella*. *Cornetipollis reticulata* Pocock et Vasanthi from the Triassic of USA, separated from *Equisetosporites chinleanus*, had quite a different morphology of striae and infratectum and was quite distinct from *Lagenella*. Pollen grains of *Equisetosporites* often fell into different bands (=rigged ectexine, e.g., Scott, 1960) most probably because there was no ectexine in the furrow region, thing that never happened to *Ephedripites*, *Ephedra* or *Lagenella* pollen. The infratectum of *Equisetosporites chinleanus* from the Lower Cretaceous, Brazil studied by Osborn et al. (1993) was finely granular and similar to that of *Ephedripites*. *Equisetosporites chinleanus* studied here shows homogenized ectexine and unfortunately does not add much information.

4.4. Comparison with similar angiosperm morphotypes

There was a detailed discussion of fossilization potential of Araceae pollen grains and their possible confusion with fossil ephedroid and similar pollen in Hesse et al. (1999), Hesse et al. (2000) and Hesse and Zetter (2007). Such similar pollen types also include *Lagenella*, as we can see. These authors concluded that among Araceae two genera possessed striate pollen with sporopolleninous ectexine which could be recognized in fossil record – *Spathiphyllum* and *Holochlamys*, and Hesse and Zetter (2007) gave a table with diagnostic criteria for extant *Spathiphyllum*, *Ephedra* sp., *Jugella* pollen, and fossil ephedroid pollen, among which they re-interpreted *Ephedripites vanegensis* Hammen and *Ephedripites elsikii* Hengreen as *Spathiphyllum* species.

Hofmann and Zetter (2010) indicated a similar morphology of *Lagenella* pollen and pollen of *Mayoa portugallica* Friis, Pedersen et Crane described from the Early Cretaceous of Portugal by Friis et al. (2004). This Cretaceous plant was assigned to the tribe Spathiphyllaeae (subfamily Monsteroideae), Araceae on the basis of pollen characters (Friis et al., 2004). The pollen grains were small, inaperturate, striate with differently oriented striations like those found in modern *Holochlamys* pollen from Araceae (Grayum, 1992; Hesse et al., 2000). *Lagenella* differed in the presence of a sulcus and more ellipsoidal shape and probably in the exine ultrastructure. The rib width was somewhat similar in *Lagenella*, *Mayoa*, and *Holochlamys*, though in *Holochlamys* the rib width was about 1 µm or slightly more, in *Mayoa* – from 0.5 to 1 µm, and in *Lagenella* – from 0.3 to 0.8 µm (rare up to 1 µm). The exine ultrastructure of *Holochlamys* was studied by Tarasevich (2008) but no photos or descriptions were brought, and she united *Holochlamys* and *Spathiphyllum* as having the same columellate exine ultrastructure. Hesse et al. (2000) also described the infratectum of *Holochlamys* and *Spathiphyllum* as columellate though on the given TEM micrograph of *Holochlamys* the infratectal elements looked like granules (Hesse et al., 2000, fig. 5). The ectexine thickness was similar in *Lagenella*, *Mayoa*, and *Holochlamys*, the infratectum was granular with granules from 0.1 to 0.2 µm in *Lagenella*, granular-rarely weakly columellate with elements of about 0.05–0.08 µm high in *Mayoa* (Friis et al., 2004; measured from fig. 11), and with infratectal elements of about 0.11 µm high in *Holochlamys beccarii* (Engl.) Engl. (figured in Hesse et al., 2000, not described in the article but measured from their fig. 5). The tectum was thick and similar in thickness in *Mayoa* and *Holochlamys*, and somewhat thinner (in relation to other ectexine

layers) in *Lagenella*. The foot layer was not mentioned but seems to be present and be thin (at least at rib regions) in *Mayoa* (about 0.03 µm as measured from Friis et al., 2004, fig. 11) and *Holochlamys* (about 0.05 µm as measured from Hesse et al., 2000, fig. 5), and 0.02 up to 0.12 µm in *Lagenella*. The endexine was thin and granular in *Mayoa*, thin and spongy in *Holochlamys*, and thick and probably lamellate in *Lagenella*.

The furrow region is represented by a thin foot layer and endexine in *Lagenella*, *Mayoa*, and probably in *Holochlamys* (or by an endexine alone).

5. Conclusions

The exine ultrastructure of *Lagenella martini* is characterized by a granular infratectum and lamellate endexine. The pollen grains mainly show homogenized exine structure. This reflects a preservational peculiarity rather than a real structure of the sporoderm; such a phenomenon had already been reported for a number of different taxa with non-homogeneous exine. Repeated sectioning and different staining reveal the true sporoderm structure of *Lagenella martini*.

Reported association of *Lagenella martini* with *Stachytaxus* reproductive structures needs a more detailed investigation of the morphology and ultrastructure of the found pollen to make reliable conclusions. So far, the data are scarce and incomplete.

A comparison with known fossil and modern non-saccate striate pollen has shown that the studied pollen grains share a number of characters with some gymnosperms and angiosperms with most similarity to *Vittatina*-like pollen. On the other hand, keeping in mind existing of such morphotypes as *Spathiphyllum* and *Holochlamys* as closely related taxa, gnetophytalean affinity of *Lagenella* cannot be fully discarded though the sporoderm ultrastructure does not support this idea.

Unfortunately, all ultrastructurally studied pollen grains of *Protohaploxylinus*, *Vittatina*, and *Weylandites* were described from the Permian deposits only, so far no Triassic material of such palynomorphs was studied with TEM. This impedes a direct corresponding of our studied species and published data. Gnetophyte pollen grains studied by means of TEM mostly come from the Cretaceous, with the only Triassic representatives such as *Equisetosporites chinleanus* and ?*Cornetipollis reticulata*, which differ noticeably from the studied species both in the morphology and ultrastructure.

Acknowledgements

We thank Prof. Dr. J.H.A. van Konijnenburg-van Cittert for sharing her unpublished results on in situ pollen from *Palissyia* male cone. We are grateful to Dr. Evelyn Kustatscher for her help. Valuable comment of an anonymous reviewer helped to improve our paper. The work was supported by the Russian Foundation for Basic Research, project # 17-04-01094.

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