



In search of the correspondence between in situ and dispersed pollen

Natalia Zavialova^{a,*}, Patrick Blumenkemper^b, Hans Kerp^b, Benjamin Bomfleur^b, Natalya Nosova^c

^a A.A. Borissiak Paleontological Institute, Russian Academy of Sciences, Profsojuznaya str., 123, Moscow 117647, Russia

^b Institut für Geologie und Paläontologie, Westfälische Wilhelms-Universität, Münster, Germany

^c Komarov Botanical Institute, Russian Academy of Sciences, ul. Professora Popova 2, 197376 St. Petersburg, Russia

ARTICLE INFO

Article history:

Received 31 December 2021

Received in revised form 25 April 2022

Accepted 2 May 2022

Available online 6 May 2022

Keywords:

In situ pollen

Dispersed pollen

Whole-plant reconstruction

Vegetation reconstruction

ABSTRACT

The amount of information about the diversity of dispersed pollen grains and spores exceeds that about their in situ counterparts by several orders of magnitude. Strangely, there are several finds of in situ pollen types that are thus far unknown from dispersed palynomorph assemblages. Here we provide a brief discussion of this peculiar phenomenon based mainly on two examples from our recent studies, including a late Permian lyginopterid seed fern from Jordan and a Middle Jurassic conifer from Siberia. Several reasons could account for such “in situ only” pollen types, including the scarcity of the parent plants, low pollen productivity, entomophily, or immaturity of in situ pollen, although the last variant seems overestimated. Such pollen grains, when found dispersed, might also be considered as untypical, featureless or inadequately preserved specimens and, as a consequence, be reported without illustrations as undetermined specimens or even ignored altogether; this way, they receive little attention from the authors, remain unregistered, and cannot be analyzed by subsequent researchers. We stress the importance of publication of as complete as possible information about all components of palynological assemblages, including their photos, even if they do not belong to stratigraphically important taxa. We do not attribute the disparity to taphonomic differences between megafossil and microfossil deposition, because the ‘in situ only’ pollen types are absent not only in the same beds where the pollen organs were found, but are unknown from any other deposits.

© 2022 Elsevier B.V. All rights reserved.

1. ‘Very small islands’ of in situ pollen and an ‘ocean’ of dispersed pollen

Fossil pollen grains can be preserved in more or less close association with other types of plant remains, for example, attached to the surface of leaves, seeds, or fruits, or occurring within anthers of flowers or within the micropyles or pollen chambers of seeds. Similarly, spores can be found in sporangia of spore-bearing plants. Such associations can be of particular importance for whole-plant reconstructions, contributing greatly to our understanding of extinct plants. Also, establishing correspondence between in situ pollen grains and spores and their counterparts preserved as dispersed pollen or spores is crucial for accurate reconstructions of vegetation based on dispersed palynological assemblages. Our knowledge on in situ pollen and spores, however, is very limited by comparison to that on dispersed palynomorphs. Norman F. Hughes argues that “in case of land plants of the Mesozoic era, the record consists primarily of an ‘ocean’ of dispersed palynomorphs that has so far been very lightly assessed or even sampled; this ocean is studded with a very few ‘small islands’ of megafossils...” (Hughes, 1994: p. 22). As again much fewer of those megafossils are associated

with pollen and spores, the ‘islands’ of in situ pollen and spores are much rarer still; the latest comprehensive catalog of in situ pollen and spores lists about 400 palynological taxa ever mentioned associated with plant macrofossils (Balme, 1995), whereas Palynodata—a standard database that contains references on the overwhelming majority of papers on paleopalynology published since 1974 until 2006—names over 122 thousands taxa of dispersed miospores (<http://paleobotany.ru/palynodata>).

It is understood that not all palynological taxa describe pollen or spores of land plants. Furthermore, all these taxa are artificial and several palynological species may derive from one biological species, if too much significance was given to the observed variability. In addition, this database also includes typographic and orthographic variants. On the other hand, pollen grains of the same morphological type are known to have been produced by several plant groups. In any case, this rough approximation (400:122,000) conveys the scale on how much is still unknown about in situ pollen and spores.

2. Pollen types known only in situ

In this context, the problem we have now repeatedly faced appears unexpected. We studied in situ pollen from reproductive organs of

* Corresponding author.

E-mail address: zavial@mail.ru (N. Zavialova).

two gymnosperms from the upper Permian deposits of Jordan and from the Middle Jurassic of Siberia (Zavalova et al., 2021; Zavalova and Nosova, 2021). Both pollen types are unusual yet sufficiently well-preserved to provide robust information on their morphology and ultrastructure. Surprisingly, these pollen types have never been found in dispersed palynomorph assemblages from either the macrofossil host strata or from other beds elsewhere. For the Jordan material, a subsequent attempt to obtain dispersed pollen grains from the matrix of the same hand specimen that also contains the reproductive organ remained unfruitful (Mike Stephenson, pers. comm. 2021). Still, multiple palynological samples from various stratigraphic levels and from different depositional settings within the Umm Irna Formation have yielded rich and diverse assemblages of dispersed miospore assemblages in the past (e.g., Abu Hamad, 2004; Stephenson and Powell, 2013, 2014), and none contained dispersed pollen grains similar to our in situ pollen type described below. The same is true for our second example from the Middle Jurassic of the Irkutsk region; pollen assemblages, including some from the same beds where the studied macroremains were found, may comprise somewhat similar monosaccate pollen (Kiritchkova et al., 2020), but those forms still differ clearly in several characters from the conifer pollen we studied from this area. In addition, we screened numerous papers reporting palynological assemblages from coeval deposits as well as from older and younger deposits, discussed slides and images of our pollen grains with palynologists who study dispersed miospores, but failed to find close analogues among taxa of dispersed pollen.

2.1. Lyginopterid pollen from the upper Permian of Jordan

The studied in situ pollen from the Lopingian Umm Irna Formation in the Dead Sea region of Jordan derives from an isolated seed-fern pollen organ composed of numerous densely positioned, radiating pollen sacs that together form a characteristic honeycomb-like surface pattern, much like *Dictyothalamus* Göppert and *Melissiotheca* Meyer-Berthaud. No taxonomic treatment was made because of the fragmentary nature of the single specimen, but its morphology, pollen ultrastructure, and co-occurring foliage support a lyginopterid affinity (Zavalova et al., 2021).

The in situ pollen grains are small ($19.8\ \mu\text{m} \times 24.0\ \mu\text{m}$), rounded to oval, flattened in various positions, non-saccate, and with verrucate sculpture and alveolate wall ultrastructure with alveoli arranged in several tiers (Plate I, 1–10). The pollen grains show no remnants of a proximal scar, but neither demonstrate a clearly delineated aperture. However, TEM analysis revealed a considerably extended thinned area, such that the pollen grains could be best described as cryptoaperturate (Zavalova et al., 2021).

With regard to the rounded outline and the surface patterning, these pollen grains are superficially similar to dispersed palynomorph taxa of the Circumpolles (Pocock et al., 1990) and Protomonosaccites (Scheuring, 1974) groups (Table 1). Nonetheless, Circumpolles members differ not only in the exine ultrastructure (Scheuring, 1978; Zavalova and Roghi, 2005; Zavalova et al., 2010; Zavalova, 2015), but also in features assessable via LM. In particular, they have an exine that is uneven in thickness laterally and over the poles, which usually determines the position in which pollen grains become flattened. This structurally controlled, preferred orientation distinguishes them from the randomly flattened pollen grains of the lyginopterid under discussion. Members of Protomonosaccites are, unlike the Jordan pollen, characterized by a developed saccus (Scheuring, 1974). Further unlike the Jordan pollen, genera of the Circumpolles (e.g., Zavalova et al., 2010) and Protomonosaccites (e.g., Zavalova et al., 2004; Zavalova and Stephenson, 2006) groups usually retain a small trilete scar and, in our opinion, appear to be more specialized. *Spheripollenites* Couper from the Jurassic and Cretaceous is similar in size and outline, but its exine does not show an alveolate pattern in transmitted light (Hoelstad, 1985) and rather resembles the columellate-like exine of *Classopollis*

Pflug in ultrathin sections (Kedves, 1990; Batten and Dutta, 1997). Some Jordan pollen grains are preserved in a boat-shaped position, appearing as if they bear a sulcus and, thus, being reminiscent of *Cycadopites* Wodehouse. However, observations on the entire pool of the pollen grains show that a clearly delineated aperture that can be interpreted as a sulcus is lacking, the thinning which presence was proved with TEM allowed us to describe the pollen as cryptoaperturate, and, thus, *Cycadopites* is an inappropriate genus for accommodation of such pollen grains. The Jordan pollen is strikingly similar to lyginopterid prepollen of *Telangioopsis* Eggert et Taylor in showing characteristic alveoli arranged in several tiers (Orlova et al., 2009), which was an argument for the lyginopterid affinity of the macrofossil, but *Telangioopsis* prepollen grains (ascribed to *Geminospora* Balme if found dispersed) are larger ($27.8 \times 32.0\ \mu\text{m}$) and possess a proximal trilete scar with unelevated but long arms reaching 3/4–4/5 of the radius.

2.2. Conifer pollen from the Middle Jurassic of Siberia

The genus *Schidolepium* Heer with one species, *Schidolepium gracile* Heer, was established for cones from the Ust'-Baley locality in the Irkutsk Coal Basin, the south-west of East Siberia, Russia (Heer, 1880). Since then, its nature as a pollen organ was revealed, and it has been registered in three more localities of the basin, dated to the Aalenian and Aalenian-Bajocian (Nosova et al., 2017). The cones are quite rare: eight samples from the Vladimirovka locality, seven from the Ust'-Baley locality, and solitary from the Idan and Topka localities. Vladimirovka is rich in plant remains, with prevailing foliage of *Phoenicopsis* Heer and *Czekanowskia* Heer, occasional fragments of *Pityophyllum* (Nathorst) Seward leaves and fern fronds, and several cones of *Ixostrobus* Raciborski and *Sorosaccus* Harris. Ovule-bearing structures of *Karkenia irkutensis* Nosova, numerous leaves of *Sphenobaiera* Florin, and rare capsules of *Leptostrobus* Heer were found in Idan (Kiritchkova et al., 2020; Nosova et al., 2021). Although only one cone of *Schidolepium* was found in the Topka locality, it is attached to a supposed *Elatocladus heerianus* Nosova et Kiritchkova shoot. Numerous leafy shoots of this species are present in the same beds of this locality as well as in the same formation in one more locality in the Irkutsk Basin (Nosova et al., 2017). We can conclude that the parent plant of *Schidolepium* was a rare, but not very rare plant, particularly if the presumable relation between *Schidolepium gracile* and *Elatocladus heerianus* is correct (and occurrences of the latter would testify to the presence of this parent plant).

Pollen grains from cones of *Schidolepium gracile* (Plate II, 1–12) from the Idan locality are $48.8\ \mu\text{m}$ in average, and those from the Vladimirovka locality are slightly larger, $58.7\ \mu\text{m}$ in average. The pollen grains demonstrate an unusual combination of morphological and ultrastructural traits (Zavalova and Nosova, 2021). The pollen grains appear quite different when observed in pollen masses and as detached monads. In clumps, they appear circular in outline, asaccate, and flattened in polar position (however, we should point out that pollen grains were lying on each other and their morphology was difficult to evaluate in transmitted light). Detached monads are rounded, oval, or irregular in outline, possess a narrow equatorial-distal saccus and are equally often preserved in polar and in equatorial position. The lateral position is unusual for monosaccate dispersed pollen types, which are usually flattened in polar position. This wide variability could readily be assessed from the in situ material, but such variably compressed forms would likely be attributed to several taxa if found in dispersed state (and the palynologist will not be able to evaluate the entire range of variability of such pollen grains). A small trilete scar is occasionally present in the otherwise non-aperturate pollen. The surface is fossulate, with finer proximal sculpturing. The ectexine is formed by elements that are fused to one another by their lateral surfaces; these solid elongated cylinders are arranged along their length, perpendicularly to the pollen surface. The endexine is more electron-dense than the ectexine, prominent, and appears homogeneous.

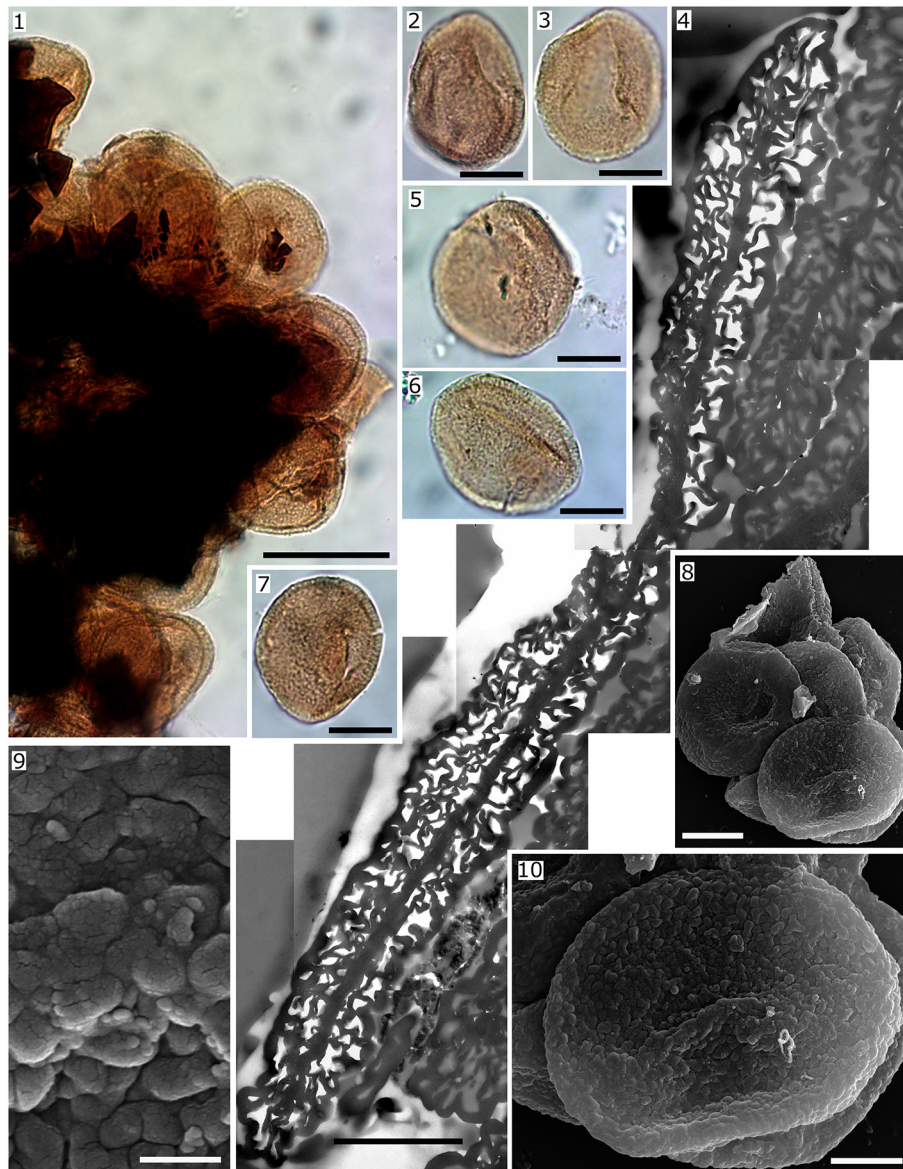


Plate I. In situ pollen grains from a lyginopterid pollen organ, Umm Irna Formation, upper Permian, Jordan. 1. Clump of pollen grains, LM. 2, 3, 5–7. Detached monads, LM. 4. Ultrathin section showing the characteristic ectexine with alveoli arranged in several tiers. 8. Several pollen grains, SEM. 9. Surface pattern, SEM. 10. Pollen grain, SEM. Scale bar: (1) 20 μm , (2, 3, 5–7, 8) 10 μm , (4) 2 μm , (9) 1 μm , (10) 5 μm .

There are several dispersed morphotypes that resemble pollen of *Schidolepium*, or, at least, some specific compression variants of its pollen grains (Table 2). As such, *Perinopollenites* Couper, *Araucariacites* Cookson, *Callialasporites* Sukh Dev can be named. Pollen grains of *Schidolepium* have something in common with pollen grains ascribed to these dispersed genera, such as more or less rounded outlines in polar view and the saccate state that is often difficult to understand. However, keeping in mind their diagnoses, general appearance, as well as currently available information about their ultrastructure, we cannot associate pollen grains of *Schidolepium* with any of them.

Thus, specimens that are compressed in a more or less polar position and show a distinct gap between the outer and inner exine layers appear similar to pollen grains of *Perinopollenites*. However, the latter genus was described as comparable with in situ pollen of taxodiaceous *Elatides williamsonii* (Lindley et Hutton) Nathorst (Couper, 1958). A distal pore should be present, although in practice it is nearly never observed in dispersed pollen grains (e.g. Il'ina, 1985); our experience with taxodiaceous pollen also shows that their exine is so repeatedly folded that their very small aperture is difficult to detect even in a rich in situ material

(Sokolova et al., 2017). Taxodiaceous pollen grains often demonstrate a cleavage between the outer and inner exine layers, but, unlike our pollen, they are non-saccate. Laterally compressed pollen grains of *Schidolepium* do not resemble *Perinopollenites*. A trilete scar occurs rarely in *Schidolepium* pollen, but is absent in *Perinopollenites*.

The same is true for *Araucariacites*. *Schidolepium* pollen grains compressed in polar position are quite reminiscent of *Araucariacites*, but their equatorial-distal saccus and occasional proximal trilete scar differentiate them from this asaccate pollen type.

Monosaccate (and also trisaccate) pollen grains are ascribed to *Callialasporites* (Potonié, 1966). However, the saccus in monosaccate *Callialasporites* is equatorial, which results in the predominantly polar compression of *Callialasporites* pollen. It seems that it is not developed distally.

The most important dissimilarities concern the ectexine ultrastructure, which to the present knowledge was found to be granulate in all studied specimens of the three dispersed genera, with irregularly distributed granules of various size (e.g., Zavada, 1992; Archangelsky, 1994; Batten and Dutta, 1997).

Table 1

Comparison between Jordan pollen and several pollen types. Pollen grains are ranged as small (10–25 µm), medium (26–50 µm), or large (51–100 µm) after Halbritter et al. (2018). See the text for the references.

Character \ taxon	Jordan pollen	Circumpolles members	Protomonosacciti members	<i>Spheripollenites</i>	<i>Cycadopites</i>	<i>Telangiopsis</i> prepollen
Size	Small	Small to medium	Medium and, more often, large	Small	Small and medium	Medium
Outline	Rounded to oval	Rounded	Rounded	Rounded	Oval	Rounded -triangular
Variants of compression	Flattened in various positions	Predominantly polar	Predominantly polar	Predominantly polar	Polar (boat-shaped)	More often polar
Saccus	No saccus, but the exine is airy	Absent	One saccus	Absent	Absent	No saccus, but the exine is airy
Sculpturing	Verrucate	Several variants, including verrucate , usually distinct	Several variants, more often indistinct	Indistinct, smooth?	Typically indistinct, can be smooth	Verrucate , folded, echinate
Ectexine ultrastructure	Characteristic alveoli in several tiers	Several dissimilar variants (e.g., large granules or columella-like elements)	Several dissimilar variants	Dissimilar (columellate-like)	Several dissimilar variants (e.g., a row of elongated alveoli or of large granules)	Characteristic alveoli in several tiers
Proximal scar	Absent	Small trilete often present	Small trilete or monolete often present	Absent	Absent	Long trilete
Distal aperture	Thinning is detected by TEM only	Usually absent, in some pseudopore is present	Absent?	?	Sulcus	Thinning is detected by TEM only

Pollen assemblages from the studied area comprise members of *Araucariacites* and *Perinopollenites* (Kiritchkova et al., 2020), but illustrated specimens are compressed in irregular polar position. We suppose that if pollen grains are compressed in preferred orientation, their exine includes areas that are more and less resistant to compression. The exine is probably harder or thicker in more resistant regions and become compressed in weaker regions. If this is true, the preferred orientation is a function of the inner arrangement of the exine and can be used for the pollen characteristics. Kiritchkova et al. (2020) illustrated a pollen grain defined as *Quadraeculina anellaeformis* Malyavkina, not very typical of this taxon, but resembling some of the irregularly folded specimens of *Schidolepium* pollen. The only available TEM report on this pollen type revealed a very different ultrastructure with protosacci filled with thin undulated partitions and a thin endexine that appears fine-grained (Batten and Dutta, 1997).

Those pollen grains of *Schidolepium* that are compressed in polar position are similar to *Cerebropollenites* Nilsson in the rounded outline, medium (to large) size, and relatively prominent sculpturing. However, we have not seen any photo of *Cerebropollenites* pollen compressed in lateral position; the polar position totally prevails, which is certainly predetermined by the inner structure of the exine. The ectexine of *Cerebropollenites* is formed by irregularly shaped and tightly packed elements (Batten and Dutta, 1997), being quite similar to the ultrastructure of the pollen grains of *Schidolepium*. The most important difference is related to the orientation of pollen features: our pollen has a proximal scar, no distal aperture, and an equatorially-distal saccus, whereas *Cerebropollenites* does not possess a scar, bears a distal leptoma, which is easily detectable by a characteristic invagination, and many saccus-like extensions situated proximally and equatorially.

Similar to the pollen grains of *Schidolepium*, taxodiaceous pollen grains (in dispersed state attributable to *Sequoiapollenites* Thiergart, *Exesipollenites* Balme, or *Perinopollenites*; Balme, 1995) have rounded outlines; commonly they are folded, appear non-aperturate, and bear numerous orbicules (e.g., Sokolova et al., 2017). However, although it is often difficult to detect their aperture, they do have a distal leptoma and a small pore or papilla on the distal pole (Zavialova and Sokolova, 2017), unlike truly non-aperturate pollen grains of *Schidolepium*. Occasionally, taxodiaceous pollen grains can reach moderate size, but they are typically small, unlike the larger pollen grains of *Schidolepium*. Many pollen grains of *Schidolepium* appear asaccate, but the saccus is present as TEM shows, whereas taxodiaceous pollen grains do not possess a saccus. The ectexine of any taxodiaceous pollen is granulate, and

the endexine is distinctly multilamellate (e.g., Sokolova et al., 2017), whereas the ectexine of *Schidolepium* pollen lacks granules and the endexine appears homogeneous.

Pollen grains of Permian *Cladaitina* Maheshwari et Meyen demonstrate a variable general morphology from monosaccate to more or less clearly asaccate forms and potential to compress in various positions, including even boat-shaped variants (Maheshwari and Meyen, 1975), resembling the *Schidolepium* material. A small proximal scar was detected in some specimens. However, ultrastructural data revealed a solid continuous tectum, an infratectum of large and not numerous granules, a thinning that might have corresponded to a distal germination area, and an endexine with evident layering (Afonin, 2000; Zavialova and Gomankov, 2002). The surface of *Cladaitina* pollen differs from the characteristic fossulate surface of *Schidolepium* pollen; it is obvious with SEM, but also accessible to a certain extent in transmitted light, under greater magnification of the microscope. Permian *Marsupipollenites* Balme is rounded, bears a rudimentary trilete scar, and folds in various positions including a boat-shaped variant, but it is asaccate and has a distal sulcus (Foster and Price, 1981). Pollen grains of *Schidolepium* are similar to Circumpolles in their more or less rounded outlines, a small rudimentary proximal scar, and in a fine but distinct sculpturing, but differ in the presence of a saccus and compression in various positions; the exine ultrastructure is also dissimilar (Scheuring, 1978; Zavialova and Roghi, 2005; Zavialova et al., 2010; Zavialova, 2015).

2.3. Voltzialean pollen from the Upper Triassic of Poland

Patokaea Pacyna, Barbacka et Zdebska, a representative of a new voltzialean family, was described from the Norian of Silesia (Pacyna et al., 2017). The in situ pollen grains are medium in size (average size is 32–35 µm), circular in polar view to oval in equatorial or oblique view, with a rugulate surface and without sacchi; neither proximal scar nor distal aperture was detected. Ultrastructural observations revealed a convoluted ectexine with some similarities to pollen grains of modern *Tsuga* (Endl.) Carrière and to *Cerebropollenites*; the endexine is very thin, fine-grained, more electron-dense than the ectexine. Similar to us, Pacyna et al. (2017) also faced difficulties in finding a corresponding dispersed taxon. Most closely comparable appeared *Enzonalasporites* Leschik emend. Scheuring, *Vallasporites* Leschik emend. Scheuring, *Pseudoenzonasporites* Scheuring, and *Patinasporites* Leschik emend. Scheuring; the authors decided in favor of the first one not because it

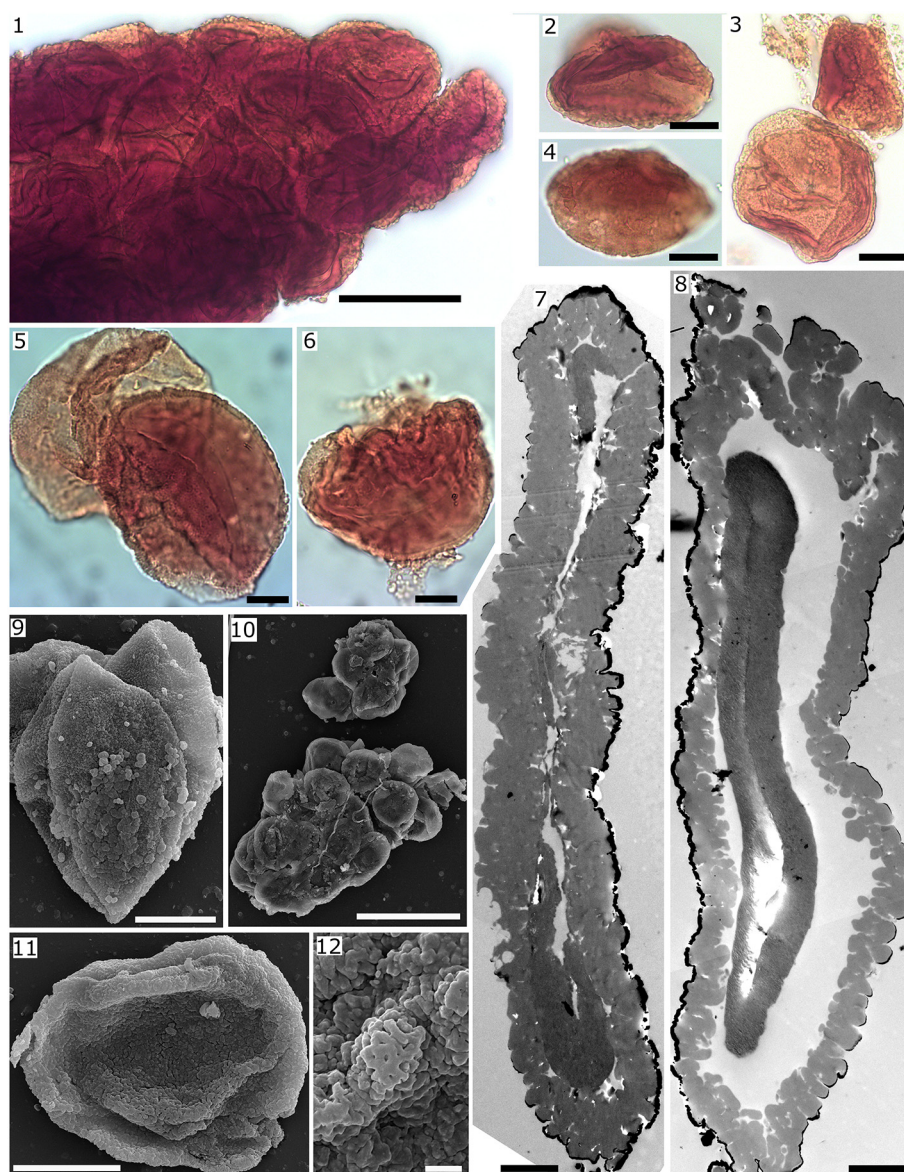


Plate II. In situ pollen grains of *Schidolepium gracile* Heer, Prisayan Formation, Aalenian-Bajocian, Irkutsk Coal Basin, Siberia. 1. Pollen grains in a clump that reproduces the outlines of the sporangium, LM. 2. Detached monad, note a small trilete scar, LM. 3. Detached pollen grains, a saccus cavity is evident, LM. 4. Pollen grain in boat-shaped preservation, a small trilete scar is visible, LM. 5. Two pollen grains, equatorially-distal position of the saccus is evident, LM. 6. Detached pollen, note the saccus and orbicules, LM. 7. Composite image of a section made in non-saccate region, TEM. 8. Composite image of a section, a saccus cavity is present between the ectexine and prominent, more electron-dense endexine, TEM. 9. Pollen grains in boat-shaped preservations, SEM. 10. Two groups of pollen grains, most of them are rounded in outlines, SEM. 11. Monad in polar position, SEM. 12. Pollen surface pattern, SEM. Scale bar: (1) 50 μm , (2–4, 9, 11) 20 μm , (5, 6) 10 μm , (7, 8, 12) 2 μm , (10) 100 μm .

fully corresponds to the *Patokaea* pollen, but because others correspond to a lesser degree.

Pollen grains that are conventionally incorporated in these taxa are more or less rounded and medium in size; there is no general agreement in the interpretation of their exine architecture: monosaccate, monosaccoid, velate and asaccate states were named (see Pacyna et al., 2017 for references). *Vallasporites* differs by a bulging proximal trilete scar that reaches the equator; *Pseudoenzonalasporites*, by a different exine pattern and distinctly dark inner body; and *Patinasporites*, by a wide ectexine that can be described as an equatorial zone or saccus (Pacyna et al., 2017).

Indeed, *Enzonalasporites* appears more suitable to *Patokaea* pollen than the other genera. However, dispersed pollen grains of this genus often show a distinct inner body, that means that the inner portion of exine is considerably robust. We did not remark this in LM illustrations of *Patokaea* pollen, and its TEM sections show why: the endexine is very thin. In addition, the rugulate surface pattern of *Patokaea* pollen is very

peculiar, although it is better seen under SEM, but also easy to recognize in transmitted light. We examined about 50 images of *Enzonalasporites* from different literature sources that are present in Sporopollen database compiled by Jianguang Zhang, and none shows the same pattern (<http://www.sporopollen.com/>). Pacyna et al. (2017) also failed to find a suitable species among members of *Enzonalasporites*, which is remarkable keeping in mind that the genus is a long-known, common and very characteristic member of Triassic palynological assemblages.

3. Why we do not find such pollen grains in dispersed state

3.1. Scarcity or entomophily of the parent plants

The absence of the above-described pollen types from dispersed palynological assemblages can be due to the scarcity of their parent plants. This is more plausible for the Jordan lyginopterid, with a unique

Table 2
Comparison between *Schidolepium* pollen and several pollen types. Pollen grains are ranged as small (10–25 µm), medium (26–50 µm), or large (51–100 µm) after Halbritter et al. (2018). See the text for the references.

Character taxon	<i>Schidolepium</i> pollen	<i>Perinipollenites</i>	<i>Araucariacites</i>	<i>Callidaspores</i>	<i>Quadraculina</i>	<i>Cerebropollenites</i>	Taxodiaceous in situ pollen	<i>Cladaitina</i>	<i>Marsupipollenites</i>	Circumpollens members
Size	Medium to large	Medium	Large	Large	Large	Medium to large	Small to medium	Medium	Medium to large	Small to medium
Outline	Rounded, oval, irregular	More or less rounded	More or less rounded	More or less rounded	Irregular	Rounded	Rounded	Rounded, oval, irregular	Rounded	Rounded
Variants of compression	Equally occurring polar and equatorial positions	Irregularly polar?	Irregular, repeatedly folded	Predominantly polar	Predominantly polar	Only polar	Variable, numerous folds are present	Equally occurring polar and equatorial positions	Folded in various (including boat-shaped) positions	Predominantly polar
Saccus	One saccus is present, though it is not always detectable	Gap between outer and inner layers, but no saccus	No saccus	One trilobate saccus or three sacs	Two protosacci are saccate-like convolutions	No saccus, but there are saccate-like convolutions	No saccus, although some gaps between exine layers can be present	Cavities between the ect- and endexine	No saccus	No saccus
Saccus attachment	Equatorial-distal	n/a	n/a	Equatorial	Distal	Saccus-like convolutions occur equatorially and proximally	n/a	Cavities supposedly occur in proximal and equatorial regions	n/a	n/a
Sculpturing	Fossulate, proximal sculpturing is finer than distal	Granular?	Granular, microechinate	Smooth? Granular?	Fine wrinkles and folds	Gemmate, proximal sculpturing is coarser than distal	Granular	Microverrucate, quite variable	Granular	Several variants (including fossulate), usually distinct
Exetexine ultrastructure	Laterally fused cylinders arranged perpendicular to the pollen surface	Numerous small granules	Numerous irregularly arranged granules	Numerous irregularly arranged granules	Undulated partitions	Tightly packed elements	Numerous small granules	One row of large granules under a solid tectum	Fused small granules	Several dissimilar variants
Proximal scar	Small trilete, occasionally present	Absent	Absent	Absent	Two thinned areas	Absent	Absent	Trilete or monolete, occasionally present	Trilete, present	Small trilete, often present
Distal aperture	Absent	Pore should be present, though nearly never seen	Absent	Absent?	Sulcus?	Leptoma	Leptoma + pore	Thinned area revealed by TEM only, leptoma?	Sulcus	Usually absent, in some pseudopore is present

specimen so far known; as to *Schidolepium*, its parent plant was probably not too uncommon.

A further explanation for the absence of pollen grains of the Jordan lyginopterid (Zavalova et al., 2021) in the palynological assemblage could be entomophily of the plant; pollen grains would then probably have been produced in small amount, would not be conducive to extensive abiotic transport and would thus not be favorable to fossilize as dispersed pollen. Regardless of the actual pollination syndrome, if pollen grains were produced in small amounts or/and the parent plant was rare, such pollen grains would be unlikely to reach detectable amounts in palynological assemblages.

Friis et al. (1999) explored the diversity of pollen associated with angiosperm mesofossils from five localities dated to the Barremian or supposed Aptian of Portugal and compared it with dispersed pollen floras from the same deposits as well as with pollen grains of modern angiosperm families. The mesofloras comprised about 100 different kinds of flowers, fruits, seeds and stamens in three richer localities; and the diversity is poorer, but still significant in two others. Between 7 and 27 types of various angiosperm pollen associated with the mesofossils at each of the five localities; monocolpates (including trichomonocolpates), dicolpates, periporates and tricolpates were recognized, the first type being dominant. This diversity contrasts strongly with the paucity of angiosperm pollen in dispersed palynofloras, where only rare monocolpates were registered. Friis et al. (1999) related this discrepancy to insect pollination or herbaceous habit of the early angiosperms. One more observation was that the in situ pollen were very small, most were in the range of 12–16 µm. SEM was used as the principal instrument of their study, but dispersed assemblages are conventionally observed with LM, and characters of such minute pollen grains can be poorly distinguishable or undistinguishable at the light-microscopical level.

The pollen types under our discussion are not that small as the early angiosperm pollen and their morphology is assessable even in transmitted light; and, presumably, the producers of both pollen types were not herbs. Entomophily might serve as an explanation in case of the *Schidolepium* pollen (Zavalova and Nosova, 2021). However, these pollen grains possess a saccus and there are plenty of them in the pollen cones—features typically indicative of anemophily rather than entomophily. On the other hand, entomophilic plants do not necessarily produce small amounts of pollen; finds of saccate pollen in guts of fossil insects imply that entomophilic plants might have produced saccate pollen (Krassilov et al., 2007). Interestingly, we found a small group of *Cycadopites* pollen in the organic residue obtained from maceration of a *Schidolepium* pollen sac that otherwise contained masses of monosaccate pollen, which were preserved in clumps reproducing outlines of the sporangia. This small group of *Cycadopites* pollen could have been brought to the *Schidolepium* plant by a non-specialized pollinator.

Similarly to us, Friis et al. (1999) often did not find counterparts among dispersed pollen types for the in situ pollen. However, the task to find dispersed analogues for peculiar in situ types seems less important for the Cretaceous and younger materials than for pre-Cretaceous ones. Fossil angiosperm pollen grains can be compared with those of modern angiosperms, and this is more valuable for further reconstructions.

3.2. Immature state of in situ pollen

Another possible explanation is that dispersed pollen usually becomes fossilized in fully developed state, whereas in situ pollen may be preserved in immature sporangia. If so, immature in situ pollen and mature dispersed pollen of the same plant may differ considerably in their morphology, and this is why we do not recognize in palynological assemblages the pollen types found in situ. However, we do not think that this is applicable to the materials under discussion, as well as to most other similar cases. Ontogenetic studies show that apertures always initiate at a very early stage of development, when pollen grains

are still in tetrads (e.g., Kurmann, 1990b; Plate III, 1–4). The same is true for air sacs (e.g., Kurmann, 1989; Plate III, 4), and also for proximal scars of spores (Tryon and Lugardon, 1991). If we deal with in situ pollen grains in monads, and do not find an aperture or air sacs, there is no reason to believe that they would have been developed at some later stage and to interpret such pollen as immature because of the absence of such features. If in situ pollen grains are found in clumps (Balme, 1995), they are commonly interpreted as immature. We insist that this conclusion is substantiated only if they are in tetrads. If during mechanical or ultrasound disintegration pollen clumps yield monads, the occurrence of clumps relates to preservation state of the material rather than to its immaturity.

TEM examination may add more information on the degree of pollen maturation. As a rule, the endexine is more electron dense than the ectexine in mature pollen grains. A reversed electron density was observed in slightly underdeveloped conifer pollen grains: more electron dense ectexine and less electron dense endexine (Kurmann, 1990a). A normal difference in electron density between the ectexine and endexine testifies to the mature state of the pollen. This is the case for our Jordan and Siberian pollen. The endexine of the Polish pollen is very thin, but also more electron-dense than the ectexine.

3.3. Is taphonomy an explanation?

It often happens that different types of plant remains occur with different frequency in beds. For example, beds that contain abundant shoots of *Elatocladus heerianus* rarely contain cones. Although we found quite many *Schidolepium* cones, only a single cone specimen was attached to a leafy shoot (Nosova et al., 2017). The explanation is related this way or another to the taphonomy. Cones and shoots might demand different conditions for successful fossilization. There is a possibility that they were detached from parent plants and started their 'post-mortem existence' in different seasons. Something like that might have happened to the pollen as well and explains why we do not find dispersed pollen of the types under present consideration in the same beds where we found them in situ in the macroremains. However, they are not reported in any literature sources as well, whatever were conditions for fossilization for described palynological assemblages.

3.4. Unusual (inconspicuous) pollen grains are not registered

In our opinion, however, the most probable explanation is that researchers who deal with palynological assemblages do not mention such rare palynomorphs of a quite untypical morphology that do not have any acknowledged stratigraphic (or palaeoecological) significance. Such pollen grains may end up hidden in those few percent of undetermined and undocumented specimens. One further option is that they are erroneously ascribed to other taxa based on superficial similarity only. Typical specimens of such taxa are photographed, whereas forms that are more unusual remain unshown. For example, attribution of boat-shaped specimens of the Jordan pollen grains to *Cycadopites* would affect the accuracy of paleoecological reconstructions based on palynological data, since *Cycadopites* will never be interpreted as a lyginopterid pollen. Likewise, their accommodation within Circumpolles would imply conifers such as cheirolepidiaceae or voltzialean plants in reconstructions, whereas comparison with *Cordaitina* would mean cordaites. If we find pollen grains of *Schidolepium* in the dispersed state and ascribe them to more or less similar *Araucariacites*, *Callialasporites*, or *Perinopollenites*, this would erroneously imply the presence of araucariaceous or taxodiaceous plants, but *Schidolepium* certainly did not belong to these groups. We do not only need to name the pollen type somehow, but to give it a meaningful name, which would lead to the correct parent group during vegetation reconstruction.

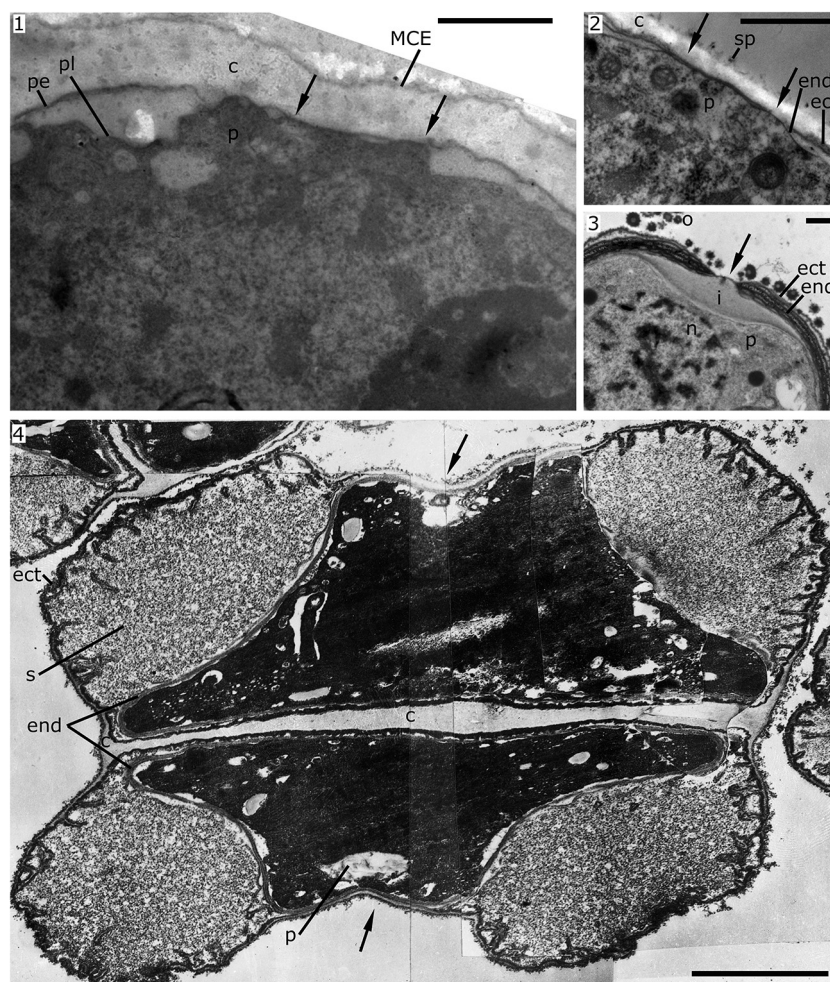


Plate III. Developing pollen grains of modern *Juniperus communis* L. and *Podocarpus hallii* Kirk. 1–3. Developing asaccate pollen grains of *J. communis*. The illustrations are kindly provided by Svetlana Polevova and derive from unpublished materials by Gabarayeva et al. (2014). 1. Early tetrad stage. Arrows indicate the position of the future aperture. Callose is prominent. Outermost layer of primexine is already visible. The plasmalemma invaginates into the protoplast of the microspore outside the aperture region. 2. Late tetrad stage. Callose is still prominent. The position of the aperture (arrows) is evident by much lesser developed exine. Outside the aperture a developing ectexine and a couple of endexine lamellae are already visible. 3. Distal pole of a pollen grain at free-spore stage. Callose is absent. Note starting from the outside: orbicules, thin ectexine, several loosely arranged lamellae of a more electron-dense endexine (end) with granules between them, a much less electron-dense intine, and protoplast (p). Arrow points to the pore, where the ectexine is lacking, endexine is reduced to one lamella, and the intine is strongly thickened. 4. Developing bisaccate pollen grains of *P. hallii*. Ultrathin section of a developing tetrad, two pollen grains with living protoplast are visible. Note a distal thinning in the aperture area (arrow), already developed prominent air sacci, and callose wall that is still present. The ectexine and endexine are already present. Reproduced from Meyer (1977, pl. 74). Abbreviations: (c) callose, (o) orbicules, (ect) ectexine, (end) endexine, (i) intine, (n) nucleus, (p) protoplast, (pe) outermost layer of primexine; (pl) plasmalemma; primary mother cell envelope (MCE); (s) air saccus, (sp) sporopollenin transporting through the callose wall to deposit and form the exine. Scale bars: (1–3) 1 μ m, (4) 5 μ m.

Better-preserved specimens of stratigraphically significant and typical taxa are always chosen for illustrations in palynological papers that aimed on stratigraphy and dating of host deposits. Unusual morphological types are reported only if they are very dissimilar from other members of the assemblage. Otherwise, they can easily be disregarded. In the past, monographic papers were more common, and undetermined, rare, and strange specimens were registered (e.g. Hacquebard, 1957; Higgs, 1975).

4. Conclusions

The situation described above seems to be one particular symptom of a greater problem. Nowadays, we are in such haste because of the publish-or-perish race that we include in papers only the information that is of immediate relevance to the claimed aims, to the effect that additional unexpected data of as-yet uncertain significance are too often omitted for the sake of a brief, concise story. We write this way and we review similarly. Potentially important information remains unknown for subsequent scientists. Other scientists who find something similar or face a similar problem erroneously think that their finding/

problem is unique, because it is not mentioned in the published literature.

Often, we look in articles for the information that is not considered among the most important achievements by their authors. For example, although one of us (NZ) constantly screens papers on palynostratigraphy, she is not interested in stratigraphical conclusions, but in as complete as possible information about the composition of palynological assemblages. Vice versa, a whole half of citations of her papers is not related to the sporoderm ultrastructure, although all her publications are about this topic. This is normal, or, at least, it happens commonly.

We believe that publication of the complete information obtained during studies is very important, including data that are at the time difficult to interpret or appear too remotely related to the main goals of the study. It is worth to illustrate all members of the assemblages, rather than merely the typical, common, and stratigraphically significant ones. It is needed to illustrate the observed variability of the taxa, rather than to show only specimens that fit the best the diagnoses and/or the conclusions of the authors. Nowadays, we mostly read electronic versions of publications; it is time to stop worrying about the shortage of

journal paper. It would be much more expensive to re-conduct study of a material that was published and illustrated too laconically. In addition, a restudy turns to be often impossible to accomplish by various reasons. Heroic efforts are often needed to find and reach the original material. This is even more pitiful if the original authors knew the answer on the question but considered it unimportant and did not mention it in the publication.

The last but not least remark: To the best of our knowledge, the in situ pollen types discussed above are unknown from palynological assemblages; however, we will be happy to be wrong about their uniqueness.

Declaration of Competing Interest

No potential conflict of interest was reported by the authors.

Acknowledgements

We acknowledge reproduction of an ultramicrograph of a developing *Podocarpus hallii* tetrad from the professor thesis by the late Nonna Meyer-Melikian (Meyer, 1977). We are thankful to Svetlana Polevova (Lomonosov Moscow State University) for allowing to reproduce unpublished ultramicrographs of pollen grains of *Juniperus communis* from her collaborative study (Gabarayeva et al., 2014), Elena Kostina (Geological Institute of the Russian Academy of Sciences, Moscow, Russia) for letting us to evaluate several original photos to Kiritchkova et al. (2020), and Janguang Zhang (Technische Universität Darmstadt, Darmstadt, Germany) for allowing to use his database *Sporopollen.com*. We are thankful to Sofia Kuhn (Farroupilha Federal Institute of Education, Science and Technology, Brazil), Guido Roghi (Istituto di Geoscienze e Georisorse IGG-CNR, Padua, Italy), Mike Stephenson (British Geological Survey, Keyworth, UK), Evelyn Kustatscher (Naturmuseum Südtirol, Bolzano, Italy), Elke Schneebeil-Hermann (Universität Zürich, Zürich, Switzerland), Dmitry Mamontov, Svetlana Polevova and Elena Severova (Lomonosov Moscow State University), and Janguang Zhang for valuable discussion. We are grateful to the anonymous reviewers and the editor for their helpful comments. The studies were supported by the Russian Foundation for Basic Research, projects 19-04-00498 and 20-04-00355. Further financial support was provided by the German Science Foundation (DFG Emmy Noether grant BO3131/1-1 “Latitudinal Patterns in Plant Evolution” to BB; DFG grants KE584/11-1 + 2 and KE584/20-1 to HK).

References

- Abu Hamad, A.M.B., 2004. Palaeobotany and Palynostratigraphy of the Permo-Triassic in Jordan. Unpublished PhD Thesis University of Hamburg, Hamburg, Germany.
- Afonin, S.A., 2000. Pollen grains of the genus *Cladaitina* extracted from the gut of the Early Permian insect *Tillyardembia* (Grylloblattida). *Paleontol. J.* 34 (5), 575–579.
- Archangel'sky, S., 1994. Comparative ultrastructure of three Early Cretaceous gymnosperm pollen grains: *Araucariacites*, *Balmeopsis* and *Callialasporites*. *Rev. Palaeobot. Palynol.* 83, 185–198.
- Balme, B.E., 1995. Fossil in situ spores and pollen grains: an annotated catalogue. *Rev. Palaeobot. Palynol.* 87 (2–4), 81–323.
- Batten, D.J., Dutta, R.J., 1997. Ultrastructure of exine of gymnospermous pollen grains from Jurassic and basal Cretaceous deposits in northwest Europe and implications for botanical relationships. *Rev. Palaeobot. Palynol.* 99, 25–54.
- Couper, R.A., 1958. British Mesozoic microspores and pollen grains, a systematic and stratigraphic study. *Palaeontogr. Abt. B* 103, 75–179.
- Foster, C.B., Price, P.L., 1981. Exine intrastructure of *Praecolpatites sinuosus* (Balme & Hennelly) Bharadwaj & Srivastava, 1969, and *Marsupipollenites triradiatus* Balme & Hennelly, 1956. *The Palaeobotanist* 28–29, 177–187.
- Friis, E.M., Pedersen, K.R., Crane, P.R., 1999. Early angiosperm diversification: the diversity of pollen associated with angiosperm reproductive structures in Early Cretaceous floras from Portugal. *Ann. Mo. Bot. Gard.* 86, 259–296.
- Gabarayeva, N., Grigorjeva, V., Polevova, S., 2014. Sporoderm and tapetum ontogeny in *Juniperus communis* (Cupressaceae). *Connective structures between tapetum and microspores*. *Rev. Palaeobot. Palynol.* 206, 23–44.
- Hacquet, P.A., 1957. Plant spores in coal from the Horton Group (Mississippian) of Nova Scotia. *Micropaleontology* 3, 301–324.
- Halbritter, H., Ulrich, S., Grímsson, F., Weber, M., Zetter, R., Hesse, M., Buchner, R., Svojtka, M., Frosch-Radivo, A., 2018. *Illustrated Pollen Terminology*. Springer, Cham.
- Heer, O., 1880. *Nachträge zur Jura-Flora Sibiriens*. *Mémoires de l'Académie Impériale des Sciences de St.-Petersbourg*. 27, pp. 1–34.
- Higgs, K., 1975. Upper Devonian and Lower Carboniferous miospore assemblages from Hook Head, County Wexford, Ireland. *Micropaleontology* 21, 393–419.
- Hoelstad, T., 1985. Palynology of the uppermost Lower to Middle Jurassic strata on Bornholm, Denmark. *Bull. Geol. Soc. Den.* 34, 111–132.
- Hughes, N.F., 1994. *The Enigma of Angiosperm Origins*. Cambridge University Press.
- Il'ina, V.I., 1985. *Palinologiya yury Sibiri* [Palynology of the Jurassic of Siberia]. Nauka, Moskva (in Russian).
- Kedves, M., 1990. Palynological studies on manganese ore layers in Úrkút (Transdanubia), Hungary. *Ore Geol. Rev.* 5, 491–507.
- Kiritchkova, A.I., Nosova, N.V., Kostina, E.I., Yaroshenko, O.P., 2020. *Kontinental'naya yura Irkutskogo uglenosnogo basseina* [Jurassic Continental Deposits of the Irkutsk Coal Basin]. VNIGRI, St. Petersburg (in Russian).
- Krassilov, V.A., Rasnitsyn, A.P., Afonin, S.A., 2007. Pollen eaters and pollen morphology: co-evolution through the Permian and Mesozoic. *Afr. Invertebr.* 48 (1), 3–11.
- Kurmann, M.H., 1989. Pollen wall formation in *Abies concolor* and a discussion on wall layer homologies. *Can. J. Bot.* 67, 2489–2504.
- Kurmann, M.H., 1990a. Exine formation in *Cunninghamia lanceolata* (Taxodiaceae). *Rev. Palaeobot. Palynol.* 64, 175–179.
- Kurmann, M.H., 1990b. Exine ontogeny in conifers. In: Blackmore, S., Knox, R.B. (Eds.), *Microspores Evolution and Ontogeny: Evolution and Ontogeny*. Academic Press, London, pp. 157–172.
- Maheshwari, H.K., Meyen, S.V., 1975. *Cladostrobus* and the systematics of cordaitalean leaves. *Lethaia* 8 (2), 103–123.
- Meyer, N.R., 1977. Professor thesis Comparative Morphological Studies of the Development and Ultrastructure in the Sporoderm of Gymnosperms and Primitive Angiosperms. Komarov Botanical Garden, Academy of Sciences of USSR, Leningrad (In Russian). 179 plates.
- Nosova, N.V., Kiritchkova, A.I., Kostina, E.I., 2017. Leafy shoots and pollen cones of conifers from the Middle Jurassic deposits of the Irkutsk Coal Basin. *Palaeobotany* 8, 5–27.
- Nosova, N., Crane, P.R., Shi, G., 2021. Ovule-bearing structures of *Karkenia* Archangelsky, associated dispersed seeds and *Sphenobaiera* leaves from the Middle Jurassic of East Siberia, Russia. *Rev. Palaeobot. Palynol.* 295.
- Orlova, O.A., Meyer-Melikian, N.R., Zavialova, N.E., 2009. A new microsporangiate organ from the Lower Carboniferous of the Novgorod region, Russia. *Palaeontol. J.* 43, 1316–1329 [English edition].
- Pacyna, G., Barbacka, M., Zdebska, D., Ziaja, J., Fijałkowska-Mader, A., Bóka, K., Sulej, T., 2017. A new conifer from the Upper Triassic of southern Poland linking the advanced voltzialean type of ovuliferous scale with *Brachyphyllum*-*Pagiophyllum*-like leaves. *Rev. Palaeobot. Palynol.* 245, 28–54.
- Pocock, S.A.J., Vasanthi, G., Venkatachala, B.S., 1990. Pollen of circumpoles—an enigma or morphotrends showing evolutionary adaptation. *Rev. Palaeobot. Palynol.* 65 (1–4), 179–193.
- Potonié, R., 1966. Synopsis der Gattungen der Sporae dispersae. Teil IV. Nachträge zu allen Gruppen (Turmae). *Beihefte zum Geologischen Jahrbuch* 72, 1–244.
- Scheuring, B.W., 1974. “Protosaccate” Strukturen, ein weitverbreitetes Pollenmerkmal zur frühen und mittleren Gymnospermenzeit. *Geologische und paläontologische Mitteilungen Innsbruck* 4 (2), 1–30.
- Scheuring, B.W., 1978. Mikrofloren aus den Meridekalken des Mte. San Giorgio (Kanton Tessin). *Schweizerische Paläontologische Abhandlungen* 100, 1–119.
- Sokolova, A., Gordenko, N., Zavialova, N., 2017. The most ancient member of the Sequoioideae: the new genus *Krassilovidendron* Sokolova, Gordenko et Zavialova (Cupressaceae sl) from the Albian-Cenomanian of western Siberia (Russia). *Cretac. Res.* 77, 1–27.
- Stephenson, M.H., Powell, J.H., 2013. Palynology and alluvial architecture in the Permian Umm Irna Formation, Dead Sea, Jordan. *GeoArabia* 18, 17–160.
- Stephenson, M.H., Powell, J.H., 2014. Selected spores and pollen from the Permian Umm Irna Formation, Jordan, and their stratigraphic utility in the Middle East and North Africa. *Riv. Ital. Paleontol. Stratigr.* 120, 145–167.
- Tryon, A.F., Lugardon, B., 1991. Spores of the Pteridophyta: surface, wall structure and diversity based on electron microscope studies. Springer Science & Business Media.
- Zavada, M.S., 1992. The wall ultrastructure of fossil discoid pollen. *Bull. Torrey Bot. Club* 119, 44–49.
- Zavialova, N.E., 2015. Evolutionary transformations of sporoderm ultrastructure in certain monophyletic lineages of higher plants. *Bot. Pacif. J. Plant Sci. Conserv.* 4 (2), 49–57.
- Zavialova, N.E., Gomankov, A.V., 2002. Dispersed pollen grains of the genus *Cladaitina* from the Permian of Russia. Abstracts of Papers on the Palaeozoic Palynology in the Third Millennium. New Directions in Acritarch, Chitinozoan, and Miospore Research. International Meeting and Workshops of the Commission Internationale de Microflore de Paléozoïque, Lille, 5–7 September, 2002, p. 74.
- Zavialova, N., Nosova, N., 2021. Pollen grains found in pollen cones of *Schidolepium* Heer (Pinopsida) from the Middle Jurassic of East Siberia, Russia. *Int. J. Plant Sci.* 182 (6), 468–489.
- Zavialova, N.E., Roghi, G., 2005. Exine morphology and ultrastructure of *Duplicisporites* from the Triassic of Italy. *Grana* 44 (4), 337–342.
- Zavialova, N.E., Sokolova, A.B., 2017. *Primeneniye priznakov morfologii i ultrastruktury pyll'tsevykh zeren v sistematike semeistva Cupressaceae* [Use of characters of morphology and ultrastructure of pollen grains in taxonomy of the family Cupressaceae]. In: Sokoloff, D. (Ed.), *Taxonomy and Evolutionary Morphology of Plants: Materials of the Conference Dedicated to 85th Anniversary of VN Tikhomirov* (January 31–February 3, 2017, Moscow). MAKSS Press, Moscow, pp. 168–171 (In Russian).

- Zavalova, N.E., Stephenson, M.H., 2006. The exine ultrastructure of *Plicatipollenites* Lele 1964. *Rev. Palaeobot. Palynol.* 139 (1–4), 241–252.
- Zavalova, N.E., Gomankov, A.V., Yaroshenko, O.P., Rovnina, L.V., 2004. Morphology and ultrastructure of monosaccate pollen grains from the genus *Cordaitina* Samoilovich 1953 from the Permian of Russia. *Acta Palaeobot. Polon.* 44 (1), 3–35.
- Zavalova, N., Buratti, N., Roghi, G., 2010. The ultrastructure of some Rhaetian Circumpolles from southern England. *Grana* 49 (4), 281–299.
- Zavalova, N., Blomenkemper, P., Kerp, H., Abu Hamad, A., Bomfleur, B., 2021. A lyginopterid pollen organ from the upper Permian of the Dead Sea region. *Grana* 60 (2), 81–96.