BOTANICHESKII ZHURNAL, 2021, Vol. 106, N 7, pp. 627–657

ANGIOSPERM FEATURES IN PRE-CRETACEOUS POLLEN

N. E. Zavialova[a,#] and M. V. Tekleva[a,##]

[a] *A.A. Borissiak Paleontological Institute of the Russian Academy of Sciences*
Profsoyuznaya Str., 123, Moscow, 117647, Russia
[#]*e-mail: zavial@mail.ru*
[##]*e-mail: tekleva@mail.ru*

DOI: 10.31857/S0006813621070115

Dispersed pollen grains are the most likely source of information about a possible hidden period of angiosperm history, since they are numerous, diverse, and transported for long distances; in addition, a wealth of information has been accumulated on palynological assemblages. We reviewed angiosperm-like pollen reported from the deposits that lack angiosperm macroremains. The general morphology, sculpture, exine ultrastructure, as well as some available data on associations with macroremains allow us to interpret with sufficient confidence an overwhelming majority of such finds as gymnosperm pollen. They occur sporadically in the paleontological record without forming a chain that would have corresponded to any reconstructed evolutionary sequence; they rather represent detached and quite advanced links of this chain. On the other hand, the consecutive appearance of angiosperm pollen types in the Cretaceous nicely agrees with the molecular phylogeny reconstructed for the group. The finds of Pre-Cretaceous reticulate pollen seem the most controversial; however, those from the Permian are also known from conifer sporangia, and a gymnosperm variant of the endexine was revealed in one of Triassic reticulates.

Keywords: dispersed pollen grains, LM, SEM, TEM, fossils, angiosperms

ACKNOWLEDGMENTS

We are thankful for help with literature to Jean Dejax and Emmanuel Côtez (Muséum national d'Histoire naturelle, Paris, France), James Doyle (University of California, Davis, USA), and Evelyn Kustatscher (Museum of Nature South Tirol, Italy); for permission to reproduce illustrations to Silvia Ulrich (University Vienna) from Halbritter et al. (2018), Michael Zavada (University of Texas) from Taylor, Zavada (1986), Susanne Feist-Burkhardt (University of Geneva) from Hochuli, Feist-Burkhardt (2013), Tamara Surova from Chlonova, Surova (1988), Bruce Cornet from Cornet (1989), James Doyle from Doyle et al. (1975) and Doyle, Hutton (1991), Mario Coiro (Université de Fribourg) from Coiro et al. (2019), Palaeontological Association and Jo Hellawell from Hughes (1961); for a photo of *Oculipollis* to France Polette (Université de Rennes 1); for a photo once made by Peter Hochuli for Hochuli, Feist-Burkhardt (2013) and found in laboratory archive in publicable resolution to Elke Schneebeli-Hermann (University of Zurich); for photos of Circumpolles pollen (unpublished materials of collaborative study with Natalia Zavialova) to Guido Roghi (Padua University); for photos of *Eucommia* from Information system... (2021) and photographing *Welwitschia* pollen to Elena Severova (MSU); for photographing of a thick section of *Achillea* pollen to Svetlana Polevova (MSU); and for valuable comments on the manuscript to Dmitry Sokoloff (MSU). The study was supported by the Russian Foundation for Basic Research, project No. 19-04-00498.

REFERENCES

Afonin S.A., Rasnitsyn A.P., Krassilov V.A. 2007. Pollen eaters and pollen morphology: co-evolution through the Permian and Mesozoic. – African Invertebrates. 48 (1): 3–11.

Alvin K.L. 1982. Cheirolepidiaceae: biology, structure and paleoecology. – Rev. Palaeobot. Palynol. 37: 71–98. https://doi.org/10.1016/0034-6667(82)90038-0

Balme B.E. 1995. Fossil in situ spores and pollen grains: an annotated catalogue. – Rev. Palaeobot. Palynol. 87 (2–

4): 81–323.
https://doi.org/10.1016/0034-6667(95)93235-X

Barnard P.D. 1968. A new species of *Masculostrobus* Seward producing *Classopollis* pollen from the Jurassic of Iran. – Bot. J. Linn. Soc. 61 (384):167–176.
https://doi.org/10.1111/j.1095-8339.1968.tb00114.x

Batten D.J., Koppelhus E.B. 1996. Biostratigraphic significance of uppermost Triassic and Jurassic miospores in Northwest Europe. – In: Palynology: principles and applications. AASP. Vol. 2, Texas. P. 795–806.

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 (1): 25–54.
https://doi.org/10.1016/S0034-6667(97)00036-5

Bolinder B., Norbäck Ivarsson L., Humphreys A.M., Ickert-Bond S.M., Fang H., Hoorn C., Rydin C. 2016. Pollen morphology of *Ephedra* (Gnetales) and its evolutionary implications. – Grana. 55 (1): 24–51.
https://doi.org/10.1080/00173134.2015.1066424

Brenner G.J. 1963. The spores and pollen of the Potomac Group of Maryland. – Maryl. Dep. Geol. Mines and Water Res. Bull. 27: 1–215.
https://doi.org/10.1016/0034-6667(67)90215-1

Brenner G.J. 1967. The gymnospermous affinity of *Eucommiidites* Erdtman, 1948. – Rev. Palaeobot. Palynol. 5: 123–127.

Brenner, G.J. 1996. Evidence for the earliest stage of angiosperm pollen evolution: a paleoequatorial section from Israel. – In: Flowering plant origin, evolution and phylogeny Boston, MA. P. 91–115.

Budd G.E., Mann R.P., Doyle J.A., Coiro M.P., Hilton J. 2021. Fossil data do not support a long Pre-Cretaceous history of flowering plants. bioRxiv.
https://doi.org/10.1101/2021.02.16.431478

Chlonova A.F., Surova T.D. 1988. Pollen wall ultrastructure of *Clavatipollenites incisus* Chlonova and two modern species of *Ascarina* (Chloranthaceae). – Pollen et Spores. 30 (1): 29–44.

Coiro M., Doyle J.A., Hilton J. 2019. How deep is the conflict between molecular and fossil evidence on the age of angiosperms? – New Phytol. 223 (1): 83–99.
https://doi.org/10.1111/nph.15708

Cornet B. 1989. Late Triassic angiosperm-like pollen from the Richmond rift basin of Virginia, USA. – Palaeontographica. Abt. 213 (1–3): 37–87.

Cornet B., Habib D. 1992. Angiosperm-like pollen from the ammonite-dated Oxfordian (Upper Jurassic) of France. – Rev Palaeobot. Palynol. 71 (1–4): 269–294.
https://doi.org/10.1016/0034-6667(92)90167-F

Cornet B., Traverse A. 1975. Palynological contributions to the chronology and stratigraphy of the Hartford Basin in Connecticut and Massachusetts. – Geoscience and man. 11 (1): 1–33.
https://doi.org/10.1080/00721395.1975.9989753

Couper R.A. 1956. Evidence of a possible gymnospermous affinity for *Tricolpites troedssonii* Erdtman – New Phytol. 55: 280–285.
https://doi.org/10.1111/j.1469-8137.1956.tb05286.x

Doyle J.A. 2009. Evolutionary significance of granular exine structure in the light of phylogenetic analyses. – Rev. Palaeobot. Palynol. 156 (1–2): 198–210.
https://doi.org/10.1016/j.revpalbo.2008.08.001

Doyle J.A. 2012. Molecular and fossil evidence on the origin of angiosperms. – Annual review of earth and planetary sciences. 40: 301–326.
https://doi.org/10.1146/annurev-earth-042711-1053A13

Doyle J.A., Hotton C.L. 1991. Diversification of early angiosperm pollen in a cladistic context. – In: Pollen and spores: patterns of diversification. Systematics Association Special Volume, 44. Clarendon. P. 169–195.

Doyle J.A., Van Campo M., Lugardon B. 1975. Observations on exine structure of *Eucommiidites* and Lower Cretaceous angiosperm pollen. – Pollen et spores. XVII (3): 429–485.

Efremova G.D. 1967. Sporovo-pyl'tsevoi kompleks kungurskikh otlozhenii Zapadnogo Primugodzharya. [A spore and pollen assemblage from the Kungurian of the Western Cis-Mugojars]. – Trudy VNIGNI. LII: 63–72.

Erdtman G. 1948. Did dicotyledonous plants exist in Early Jurassic times? – Geologiska Föreningen i Stockholm Förhandlingar. 70 (2): 265–271.
https://doi.org/10.1080/11035894809454085

Friedman W.E. 2009. The meaning of Darwin's "abominable mystery". – Amer. J. Bot. 96 (1): 5–21.
https://doi.org/10.3732/ajb.0800150

Friis E.M., Pedersen K.R. 1996. *Eucommiitheca hirsuta*, a new pollen organ with *Eucommiidites* pollen from the Early Cretaceous of Portugal. – Grana. 35: 104–112.
https://doi.org/10.1080/00173139609429480

Friis E.M., Pedersen K.R., Crane P.R. 2004. Araceae from the Early Cretaceous of Portugal: evidence on the emergence of monocotyledons. – Proc. Natl. Acad. Sci. U.S.A. 101: 16565–16570.
https://doi.org/10.1073/pnas.0407174101

Friis E.M., Pedersen K.R., Crane P.R. 2006. Cretaceous angiosperm flowers: innovation and evolution in plant reproduction. – Palaeogeogr., palaeoclimatol., palaeoecol. 232 (2–4): 251–293.
https://doi.org/10.1016/j.palaeo.2005.07.006

Fu Q., Diez J.B., Pole M., Ávila M.G., Liu Z.J., Chu H., Hou Y., Yin P., Zhang G.Q., Du K., Wang X. 2018. An unexpected noncarpellate epigynous flower from the Jurassic of China. – Elife. 7: e38827.
https://doi.org/10.7554/eLife.38827

Gibbs P.E., Ferguson I.K. 1987. Correlations between pollen exine sculpturing and angiosperm self-incompatibility systems–a reply. – Plant Syst. Evol. 157 (3–4): 143–159.
https://doi.org/10.1007/BF00936194

Gomankov A.V., Meyen S.V. 1986. Tatarinovaya flora (sostav i rasprostranenie v pozdnei permi Evrazii). [Tatarina flora (composition and distribution in Late Permian of Eurasia)]. Moscow. 175 p. (In Russ.)

Grayum M.H. 1992. Comparative external pollen ultrastructure of the Araceae and putatively related taxa. – Monographs in Systematic Botany from the Missouri Botanical Garden. 43: 1–167.

Güebeli A.A., Hochuli P.A., Wildi W. 1984. Lower Cretaceous turbiditic sediments from the Rif chain (Northern Marocco)–palynology, stratigraphy and palaeogeographic setting. – Geologische Rundschau. 73 (3):

1081–1114.
https://doi.org/10.1007/BF01820889

Halbritter H., Ulrich S., Grímsson F., Weber M., Zetter R., Hesse M., Buchner R., Svojtka M., Frosch-Radivo A. 2018. Illustrated pollen terminology. Springer. 483 p.

Hesse M. 1984. Pollenkitt is lacking in Gnetatae: *Ephedra* and *Welwitschia*; further proof for its restriction to the angiosperms. – Pl. Syst. Evol. 144: 9–16.
https://doi.org/10.1007/BF00990796

Hesse M. 2000. Pollen wall stratification and pollination. – In: Pollen and pollination. Vienna. P. 1–17.
https://doi.org/10.1007/978-3-7091-6306-1_1

Hesse M., Zetter R. 2007. The fossil pollen record of Araceae. – Plant Syst. Evol. 263: 93–115.
https://doi.org/10.1007/s00606-006-0468-z

Hesse M., Weber M., Halbritter H.-M. 1999. Pollen walls of Araceae, with special reference to their fossilization potential. – Grana. 38: 203–209.
https://doi.org/10.1080/001731300750044582

Hesse M., Weber M., Halbritter H. 2000. A comparative study of the polyplicate pollen types in Arales, Laurales, Zingiberales and Gnetales. – In: Pollen and Spores: Morphology and Biology. Kew. P. 227–239.

Hluštík A., Konzalova M. 1976. *Frenelopsis alata* (K. Feistm.) Knobloch (Cupressaceae) from the Cenomanian of Bohemia, a new plant producing *Classopollis* pollen. – In: Evolutionary Biology. Prague. P. 125–131.

Hochuli P.A., Feist-Burkhardt S. 2004. A boreal early cradle of angiosperms? Angiosperm-like pollen from the Middle Triassic of the Barents Sea (Norway). – Journal of Micropalaeontology. 23 (2): 97–104.
https://doi.org/10.1144/jm.23.2.97

Hochuli P.A., Feist-Burkhardt S. 2013. Angiosperm-like pollen and *Afropollis* from the Middle Triassic (Anisian) of the Germanic Basin (northern Switzerland). – Frontiers in plant science. 4: 344.
https://doi.org/10.3389/fpls.2013.00344

Hofmann C.C., Zetter R. 2010. Upper Cretaceous sulcate pollen from the Timerdyakh Formation, Vilui Basin (Siberia). – Grana 49 (3): 170–193.
https://doi.org/10.1080/00173134.2010.512364
https://paleobotany.ru/palynodata

Hughes N.F. 1961. Further interpretation of *Eucommiidites* Erdtman 1948. – Palaeontology. 4 (2): 292–299.

Hughes N.F. 1994. The enigma of angiosperm origins. Cambridge. 303 p.

Hughes N.F., McDougall A.B. 1994. Search for antecedents of Early Cretaceous monosulcate columellate pollen. – Rev. Palaeobot. Palynol. 83 (1–3): 175–183.
https://doi.org/10.1016/0034-6667(94)90067-1

Information system of plant morphology and anatomy, 2021. http://botany-collection.bio.msu.ru/

Kawahara A.Y., Plotkin D., Espeland M., Meusemann K., Toussaint E.F., Donath A., Gimnich F., Fransen P.B., Zwick A., Reis M., Barber J.R., Peters R.S., Liu S., Zhou X., Mayer C., Podsiadlowski L., Storer C., Yack J.E., Misof B., Breinholt J.W. 2019. Phylogenomics reveals the evolutionary timing and pattern of butterflies and moths. – Proceedings of the National Academy of Sciences. 116 (45): 22657–22663.
https://doi.org/10.1073/pnas.1907847116

Koloda N.A. 1996. Novoe v sistematike permskoj kvazimonosakkatnoj pyl'cy. [New in systematics of Permian quasimonosaccate pollen]. – Trudy Geol. instituta Komi RAN. 89: 49–59 (In Russ.).

Krassilov V.A. 1989. Proiskhozhdenie i rannyaya evolutsiya tsvetkovykh rastenii. [Origin and early evolution of angiosperms]. Moscow: Nauka Press. 262 p. (In Russ.).

Krassilov V.A., Tekleva M.V., Meyer-Melikian N.R., Rasnitsyn A.P. 2003. New pollen morphotype from gut compression of a Cretaceous insect, and its bearing on palynomorphological evolution and palaeoecology. – Cret. Res. 24: 149–156.
https://doi.org/10.1016/S0195-6671(03)00029-6

Kurmann M.H., Zavada M.S. 1994. Pollen morphological diversity in extant and fossil gymnosperms. – In: Ultrastructure of fossil spores and pollen. Kew. P. 123–137.

Kuyl O.S., Muller J., Waterbolk H.T. 1955. The application of palynology to oil geology, with special reference to western Venezuela – Geologie en Mijnbouw. New series. 17 (3): 49–76.

Kvaček J., Doyle J.A., Endress P.K., Daviero-Gomez V., Gomez B., Tekleva M. 2016. *Pseudoasterophyllites cretaceus* from the Cenomanian (Cretaceous) of the Czech Republic: A possible link between Chloranthaceae and *Ceratophyllum*. Taxon. 65 (6): 1345–1373.

Kvaček J., Pacltová B. 2001. *Bayeritheca hughesii* gen. et sp. nov., a new *Eucommiidites*-bearing pollen organ from the Cenomanian of Bohemia. – Cret. Res. 22: 695–704. https://doi.org/10.1006/cres.2001.0285

Le Thomas A., Lugardon B. 1976. De la structure grenue à la structure columellaire dans le pollen des Annonacées. – Adansonia. Ser. 2. 15 (4): 543–572.

Li H.T., Yi T.S., Gao L.M., Ma P.F., Zhang T., Yang J.B., Gitzendanner M.A., Fritsch P.W., Cai J., Luo Y., Wang H. 2019. Origin of angiosperms and the puzzle of the Jurassic gap. – Nature Plants. 5 (5): 461.
https://doi.org/10.1038/s41477-019-0421-0

Magallón S., Gómez-Acevedo S., Sánchez-Reyes L.L., Hernández-Hernández T., 2015. A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. – New Phytol. 207 (2): 437–453. https://doi.org/10.1111/nph.13264

Malyavkina V.S. 1949. Opredelitel' spor i pyl'cy. Jura-mel. [Guide of spores and pollen. Jurassic-Cretaceous]. – Trudy VNIGRI. Novaja serija. 33: 1–137 (In Russ.).

Meyen S.V. 1997. Permian conifers of Western Angaralands. – Rev. Palaeobot. Palynol. 96: 351–447.
https://doi.org/10.1016/S0034-6667(96)00046-2

Meyer-Melikian N.R., Afonin S.A., Gomankov A.V. 1998. Pollen ultrastructure of some conifers from Permian deposits of Russian platform. – Bot. Zhurn. 83 (3): 1–8 (In Russ.).

Nathorst A.G. 1878. Beiträge zur fossilen Flora Schwedens. Stuttgart. p. 1–78.

Osborn J.M., Taylor T.N., de Lima M.R. 1993. The ultrastructure of fossil ephedroid pollen with gnetalean affinities from the Lower Cretaceous of Brazil. – Rev. Palaeobot. Palynol. 77: 171–184.
https://doi.org/10.1016/0034-6667(93)90003-D

Pedersen K.R., Crane P.R., Friis E.M. 1989. Pollen organs and seeds with *Eucommiidites* pollen. – Grana. 28:

279–294.
https://doi.org/10.1080/00173138909427441

Petrosyants M.A., Bondarenko N.M. 1983. Kharakternye i korreljativnye taksony pyl'cy golosemennyh (pozdnij mel – paleogen). Pyl'ca hejrolepidievyh. Sinopsis. [Characteristic and correlative taxa of gymnosperm pollen (late Cretaceous – Paleogene). Cheirolepidiaceae pollen. Synopsis]. Moscow. 80 p. (In Russ.)

Pettitt J.M., Chaloner W.G. 1964. The ultrastructure of the Mesozoic pollen *Classopollis*. – Pollen et spores. 6 (2): 611–620.

Pflug H.D. 1953. Zur Entstehung und Entwicklung des angiospermiden Pollens in der Erdgeschichte. – Palaeontographica. B 95 (4–6): 60–171.

Pocock S.A.J., Vasanthy G., Venkatachala B.S. 1990. Pollen of Circumpolles – an enigma or morphotrends showing evolutionary adaptation. – Rev. Palaeobot. Palynol. 65: 179–193.
https://doi.org/10.1016/0034-6667(90)90069-U

Pocock S.A.J., Vasanthy G. 1988. *Cornetipollis reticulata*, a new pollen with angiospermid features from Upper Triassic (Carnian) sediments of Arizona (U.S.A.), with notes on *Equisetosporites*. – Rev. Palaeobot. Palynol. 55: 337–356.
https://doi.org/10.1016/0034-6667(88)90092-9

Pott C., McLoughlin S. 2009. Bennettitalean foliage in the Rhaetian–Bajocian (latest Triassic–Middle Jurassic) floras of Scania, southern Sweden. – Rev. Palaeobot. Palynol. 158(1–2): 117–166.
https://doi.org/10.1016/j.revpalbo.2009.08.004

Reymanówna M. 1968. On seeds containing *Eucommiidites troedssonii* pollen from the Jurassic of Grójec, Poland. – Bot. J. Linn. Soc. 61: 147–152.
https://doi.org/10.1111/j.1095-8339.1968.tb00112.x

Rowley J.R., Skvarla J.J., Pettitt J.M. 1992. Pollen wall development in *Eucommia ulmoides* (Eucommiaceae). – Rev. Palaeobot. Palynol. 70 (4): 297–323.
https://doi.org/10.1016/0034-6667(92)90069-S

Sannier J., Baker W.J., Anstett M.C., Nadot S. 2009. A comparative analysis of pollinator type and pollen ornamentation in the Araceae and the Arecaceae, two unrelated families of the monocots. – BMC research notes. 2 (1): 1–11.

Silvestro D., Bacon C.D., Ding W., Zhang Q., Donoghue P.C., Antonelli A., Xing Y. 2021. Fossil data support a pre-Cretaceous origin of flowering plants. Nature Ecology and Evolution, 1–9.
https://doi.org/10.1038/s41559-020-01387-8

Sokoloff D.D., Remizowa M.V., El E.S., Rudall P.J., Bateman R.M. 2019. Supposed Jurassic angiosperms lack pentamery, an important angiosperm-specific feature. – New Phytol. 228 (2): 420–426.
https://doi.org/10.1111/nph.15974

Sun G., Dilcher D.L., Zheng S., Zhou Z. 1998. In search of the first flower: a Jurassic angiosperm, *Archaefructus*, from northeast China. – Science. 282 (5394): 1692–1695.
https://doi.org/10.1126/science.282.5394.1692

Tarasevich V.F. 2002. Morfologija i ul'trastruktura pyl'cy triby Spathiphylleae v svjazi s ejo polozheniem v semejstve Araceae. [Pollen morphology and ultrastructure of the tribe Spathiphylleae in connection to its position in the Araceae] – In: Materialy X Vserossijskoj palinologicheskoj konferencii "Metodicheskie aspekty palinologii". Moscow. P. 246–248 (In Russ.).

Tarasevich V.F. 2008. Ob jevoljucionnyh urovnjah v semejstve Araceae po palinologicheskim dannym [On evolutionary levels in the family Araceae based on palynological data]. – In: Palinologija: Stratigrafija i Geojekologija. Vol. 1. Saint-Petersburg. P. 115–121 (In Russ.).

Tarasevich V.F., Zhilin S.G. 1999. On monosulcate and disulcate pollen grains from the Albian-Turonian Kazakhstan. – Acta Palaeobot. Suppl. 2: 211–217.

Taylor T.N., Zavada M.S. 1986. Developmental and Functional aspects of fossil pollen. – In: Pollen and Spores: Form and Function. London. P. 165–178.

Taylor E.L., Taylor T.N., Krings M. 2009. Paleobotany: the biology and evolution of fossil plants. New York. 1230 p.

Tekleva M.V., Krassilov V.A. 2009. Comparative pollen morphology and ultrastructure of modern and fossil gnetophytes – Rev. Palaeobot. Palynol. 156 (1–2): 130–138.
https://doi.org/10.1016/j.revpalbo.2008.12.007

Tekleva M.V., Roghi G. 2018. *Lagenella martini* from the Triassic of Austria – exine structure and relationships with other striate palynomorphs. – Rev. Palaeobot. Palynol. 258: 13–21.
https://doi.org/10.1016/j.revpalbo.2018.06.011

Tekleva M.V., Krassilov V.A., Kvaček J., van Konijnenburg-van Cittert J.H.A. 2006. Pollen genus *Eucommiidites*: ultrastructure and affinities. – Acta Palaeobot. 46 (2): 137–155.

Tekleva M.V., Polevova S.V., Zavialova N.E. 2007. On some peculiarities of sporoderm structure in members of the Cycadales and Ginkgoales. – Paleontological Journal. 41 (11): 1162–1178.
https://doi.org/10.1134/S0031030107110159

Tekleva M.V., Stephenson M.H., Zavialova N.E. 2019. The exine ultrastructure of *Pretricolpipollenites bharadwajii* from the Permian of Jordan. – Rev. Palaeobot. Palynol. 268: 19–28.
https://doi.org/10.1016/j.revpalbo.2019.05.003

Traverse A. 2004. Proposal to conserve the fossil pollen morphogeneric name *Classopollis* against *Corollina* and *Circulina*. – Taxon. 53: 847–848.
https://doi.org/10.2307/4135468

Traverse A. 2007. Paleopalynology. Dordrecht. 813 p.
https://doi.org/10.1007/978-1-4020-5610-9

Traverse A., Cornet B., Ames H.T. 1975. A new look at the "*Classopollis–Circulina*" taxonomic – nomenclatural problem. Geosci. Man. 11: 159–160.

Trevisan L. 1988. Angiosperm pollen (monosulcate–trichotomosulcate phase) from very early Lower Cretaceous rocks of Southern Tuscany, Italy. – In: Abstr 7 Int Palynol Congr. Brisbane. P. 165.

Utting J. 1994. Palynostratigraphy of Permian and Lower Triassic rocks, Sverdrup Basin, Canadian Arctic Archipelago (Vol. 478). Geological Survey of Canada Bulletin. Ottawa. 107 p. https://doi.org/10.4095/194811

Van Erve A.W. 1982. Nomenclatural note on *Corollina* Malyavkina, 1949 (fossil-pollen dispersae) – Taxon.

31 (3): 546–548.
https://doi.org/10.1002/j.1996-8175.1982.tb03553.x

Van der Merwe J.J.M., Van Wyk A.E., Kok P.D.F. 1990. Pollen types in the Lauraceae. – Grana. 29: 185–196.
https://doi.org/10.1080/00173139009427751

Vasanthy G., Cornet B., Pocock S.A.J. 2004. Evolution of proangiosperms during Late Triassic: pre-Cretaceous pollen trends towards mono-and dicotyledonous taxa diversification. – Geophytology. 33 (1–2): 99–113.

Walker J.W., Walker A.G. 1984. Ultrastructure of Lower Cretaceous angiosperm pollen and the origin and early evolution of flowering plants. – Ann. Mo. Bot. Gard. 71: 464–521.
https://doi.org/10.2307/2399035

Yang W., Li S., Jiang B. 2007. New evidence for Cretaceous age of the feathered dinosaurs of Liaoning: zircon U-Pb SHRIMP dating of the Yixian Formation in Sihetun, northeast China. – Cret. Res. 28 (2): 177–182.
https://doi.org/10.1016/j.cretres.2006.05.011

Zavada M.S. 1984. The relation between pollen exine sculpturing and self-incompatibility mechanisms. – Plant Syst. Evol. 147 (1–2): 63–78.
https://doi.org/10.1007/BF00984580

Zavada M.S. 2004. The earliest occurrence of angiosperms in southern Africa. – South African Journal of Botany. 70 (4): 646–653.
https://doi.org/10.1016/S0254-6299(15)30205-2

Zavialova N.E. 2015. Evolutionary transformations of sporoderm ultrastructure in certain monophyletic lineages of higher plants. – Botanica Pacifica. 4 (2): 49–57.
https://doi.org/10.17581/bp.2015.04213

Zavialova N., Blomenkemper P., Kerp, H., Hamad A.A., Bomfleur B. 2020. A lyginopterid pollen organ from the upper Permian of the Dead Sea region. Grana, 1–16.
https://doi.org/10.1080/00173134.2020.1772360

Zavialova N., Buratti N., Roghi G. 2010a. The ultrastructure of some Rhaetian Circumpolles from southern England. – Grana. 49 (4): 281–299.
https://doi.org/10.1080/00173134.2010.522253

Zavialova N.E., Gomankov A.V. 2009. Occurrence of angiosperm-like ultrastructural features in gymnosperm pollen from the Permian of Russia. – Rev. Palaeobot. Palynol. 156 (1–2): 79–89.
https://doi.org/10.1016/j.revpalbo.2009.02.002

Zavialova N.E., Markevich V.S., Bugdaeva E.V., Polevova S.V. 2011.The ultrastructure of fossil dispersed monosulcate pollen from the Early Cretaceous of Transbaikalia, Russia – Grana. 50: 182–201.
https://doi.org/10.1080/00173134.2011.611530

Zavialova N., Meyer-Melikian N.R., Gomankov A.V. 2001. Ultrastructure of some Permian pollen grains from the Russian Platform. – In: Proceedings of the IX International Palynological Congress, Houston, Texas, USA. p. 99–114.

Zavialova N.E., Polevova S.V., Moiseenko A.V., Orlova O.A. 2019. Vozmozhnost' primenenija TEM-tomografii dlja izuchenija ul'trastruktury iskopaemyh sporoderm [Possibilities of the application of TEM-tomography for study of fossil sporoderm ultrastructure]. – In: Tezisy X chtenij pamjati A.N. Krishtofovicha. Saint-Petesburg. P. 26 (In Russ.).

Zavialova N.E., Roghi G. 2005. Exine morphology and ultrastructure of *Duplicisporites* from the Triassic of Italy. – Grana. 44 (4): 337–342.
https://doi.org/10.1080/00173130500354523

Zavialova N.E., Tekleva M.V., Smirnova S.B., Mroueh M. 2010b. Exine ultrastructure in pollen grains of *Classopollis* Pflug from the Cretaceous of Lebanon – Paleontological Journal. 44 (10): 1353–1367.
https://doi.org/10.1134/S0031030110100126

Zavialova N., Tekleva M., Stephenson M. 2019. The Permian through the eyes of pollen morphologists. Permophiles. N 67: 9–11.

Zavialova, N., van Konijnenburg-van Cittert J.H. 2011. Exine ultrastructure of in situ peltasperm pollen from the Rhaetian of Germany and its implications. – Rev. Palaeobot. Palynol. 168: 7–20.
https://doi.org/10.1016/j.revpalbo.2011.09.007

Zavialova N., van Konijnenburg-van Cittert J.H. A. 2016. Exine ultrastructure of in situ pollen from the cycadalean cone *Androstrobus manis* Harris, 1941 from the Jurassic of England – Rev. Palaeobot. Palynol. 225: 33–42.
https://doi.org/10.1016/j.revpalbo.2015.11.003

Zavialova N., van Konijnenburg-van Cittert J., Zavada M. 2009. The pollen ultrastructure of *Williamsoniella coronata* Thomas (Bennettitales) from the Bajocian of Yorkshire. Int. J. Plant Sci. 170 (9): 1195–1200.
https://doi.org/10.1086/605873