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# Grana

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# The ultrastructure of some Rhaetian Circumpolles from southern England

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#### Abstract

The morphology and exine ultrastructure of *Classopollis torosus*, *C. meyeriana* and *Geopollis zwolinskae* are studied from the Cotham Member of the Lilstock Formation (Penarth Group) in southern England. The palynological assemblage that allows dating the deposits to the Rhaetian is outlined. Although the Circumpolles pollen grains under study show variations in the exine ultrastructure, some common characters support their origin from the same plant group, the Cheirolepidiaceae. An infratectum formed by large granulae arranged mostly in one row and sandwiched between the tectum and endexine is considered as the key character of the pollen grains under study. Ultrastructural transformations within Circumpolles are discussed. The origin of *Classopollis*-producing plants from any plant group with saccate pollen and alveolate ectexine is considered much less probable than from a group with non-saccate pollen with granular ectexine.

Keywords: Classopollis, Triassic, exine ultrastructure

The Cheirolepidiaceae are an extinct seed plant group that constituted an important element in many Mesozoic floras. The family is particularly well-represented in dispersed pollen floras by pollen of *Classopollis* and some related genera included in the morphological group Circumpolles occuring from the Late Triassic to the end of the Cretaceous (Watson, 1982; Petrosianz & Bondarenko, 1983). Much data on the morphology and ultrastructure of the pollen have accumulated over the years (see reviews in Pocock et al., 1990; Kedves, 1994), and the principal aim of this study is to investigate whether changes in exine ultrastructure in Circumpolles type pollen through time may contribute to the understanding of the origin of the Cheirolepidiaceae.

To reach this aim, we need a pool of fully comparable data on the exine ultrastructure of all specimens included in the analysis, which is not always the case of earlier published data, simply because other authors might have had different goals and paid more attention to other questions and less or no attention to details that we consider important. In addition, much less is known about the exine ultrastructure of the earliest Circumpolles; and the same is true for the latest representatives.

Our accumulation of ultrastructural data has resulted so far in studies of Circumpolles from the Carnian of Italy (Zavialova & Roghi, 2005) and *Classopollis* from the Callovian of Siberia (Zavialova, 2003), the Middle Jurassic of Kazakhstan (Zavialova & Tekleva, 2005) and the Albian–Cenomanian of Lebanon (Zavialova et al., 2008, in press). For the present paper, we looked for *Classopollis* pollen grains from well-dated deposits representing the earliest stages in the history of the group. Among several geological samples tested, only palynomorphs from the Rhaetian of England showed sufficient degree of preservation of ultrastructural details and provided information on the exine ultrastructure of *Classopollis torosus* (Reissinger) Couper, 1958,

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C. meyeriana (Klaus) Venkatachala & Góczán, 1964 and *Geopollis zwolinskae* (Lund) Brenner, 1986.

#### Materials and methods

All specimens come from the Upper Triassic Cotham Member of the Lilstock Formation (Penarth Group) sampled in the Manor Farm section near Aust (south Gloucestershire, southern England; Figure 1). This section was a temporary pit, excavated at the time of sampling (2001), to supply construction material for a new Severn crossing, completed several years ago. It is a geological site of international importance for the presence of Upper Triassic rocks containing plentiful fossils. It includes the top of the Mercia Mudstone Group (red-brown mudstones and the Blue Anchor Formation), the Penarth Group (Westbury Formation and Cotham Member of the Lilstock Formation) and the Lias Group (Pre-Planorbis Beds of the Blue Lias Formation) (Figure 2; Radley & Carpenter, 1998). The site has been subject to several studies, mainly focused on the Ceratodus Bone Bed, a fossiliferous bed occurring to the north of Bristol and around the Severn Estuary, being especially well developed at Aust. This vertebrate fossil-rich bed occurs at the base of the Westbury Formation as discontinuous lenses, occupying shallow depressions in the eroded top of the Blue Anchor Formation (Radley & Carpenter, 1998). There, the greyish-green levels of the Westbury Formation contain well-preserved bones, teeth, scales and coprolites mainly of fish and marine reptiles (Reynolds, 1947; Storrs, 1994;



Figure 1. Location map of west Somerset showing the position of the Manor Farm section, near Aust (*black star*).



Figure 2. Stratigraphic column of the Cotham Member of the Lilstock Formation.

Storrs et al., 1996), well-preserved ichnofossils and abundant bivalves. Vertebrate remains are common throughout the overlying Cotham Member and are mudstones, and lies about 7 m above the *Ceratodus* Bone Bed (Figure 2); it is devoid of vertebrate remains and occurs 1 m above a fossiliferous bed containing several bone fragments and coprolites. In this section, the Langport Member of the Lilstock Formation is absent and the Cotham Member is in contact with the shelly limestones and clays of the Pre-Planorbis Beds (Blue Lias Formation), which

Formation.

Clamys')

contain few vertebrate remains. The Aust section was sampled during the first field workshop of the IGCP Project 458 'Triassic– Jurassic Boundary Events' (September 2001). A palynological study of the section has revealed the presence of a diverse dinoflagellate cyst assemblage of Rhaetian age in the Cotham Member (Bucefalo Palliani & Buratti, 2006). The sample 'CO Clamys' corresponds to sample 'CO3' in Bucefalo Palliani and Buratti (2006) and is characterised by the presence of the dinoflagellate cyst *Rhaetogonyaulax rhaetica* (Sarjeant) Loeblich & Loeblich, 1968 (Figure 3P, R–T).

referable to the same species found in the Westbury

The bed sampled for this study (sample 'CO

consists of pale green-grey shelly

The sample was processed according to standard palynological techniques (Green, 2001; Wood et al., 2002; Riding & Kyffin-Hughes, 2004). It was treated with cold HCl and cold HF to remove carbonate and silicate minerals, respectively. The residue was washed with water until neutral pH was reached and sieved with a 10  $\mu$ m mesh. Finally, ZnCl<sub>2</sub> was applied to separate organic and inorganic residue. The organic residue was mounted to individual glass slides and prepared for light microscopy (LM) investigations. The slides are stored at the Department of Geosciences of the Padua University (Padua, Italy). LM was carried out using a Leica DMLB microscope and a Leica DFC 300 firewire camera for microphotography.

Specimens chosen for the morphological study were mounted in temporary water slides, and measured and photographed in transmitted light. Each pollen grain was treated consequently, using LM, scanning and transmission electron microscopy (SEM and TEM). We succeeded to treat six individual pollen grains this way. For SEM, cover glasses were removed, and the pollen grains were taken from the slides with a needle under a Leica DMLB stereomicroscope, mounted on SEM stubs, coated with platinum/palladium and examined under a Camscan MX 2500 SEM at the Department of Geosciences of the Padua University (Padua, Italy); accelerating voltage 20 kV. For TEM, pollen grains were removed from SEM stubs with a needle and embedded in epoxy resin (Meyer-Melikian & Telnova, 1991). The pollen grains were sectioned with a LKB 3 ultra-microtome using a diamond knife, and then examined unstained under Jeol 100B and Jeol 400 TEMs at the Laboratory of electron microscopy of the Biological Faculty, Lomonosov Moscow State University (Moscow, Russia); accelerating voltage 80 kV. Some ultra-micrographs (under low magnification) were made with an Olympus CO-770 digital camera, but the majority of ultra-micrographs (under higher magnification) were made on films and subsequently transformed to digital form via an Epson Perfection V700 Photo Scanner. Composite images were put together using the Photoshop 7.0 application. Resins containing the rest of sectioned pollen grains, grids with ultrathin sections and films with TEM images are kept at the Laboratory of Palaeobotany, A. A. Borissiak Palaeontological Institute of the Russian Academy of Sciences (PIN RAS, Moscow, Russia). LM, SEM and TEM digital images are stored as TIF-files at the Laboratory of Palaeobotany of the PIN RAS and at the Department of Geosciences of the Padua University (Padua, Italy).

A variety of synonymous terms are applied to describe Classopollis morphology and ultrastructure, thoroughly discussed and diagrammed by Pocock et al. (1990) and Kedves (1994). We apply the terms pseudopore, rimula and trilete scar to the distal, subequatorial and proximal (correspondingly) supposedly apertural thinnings of the exine. The general subdivision of the exine into ectexine and endexine is used. A tectum and an infratectum are distinguished in the ectexine. The former is rather generally used, encompassing the tectum with supratectal elements, columellae and ectonexine 1 of Pettitt and Chaloner (1964) or supratectal elements and tectum of Lugardon (1985).

## Palynological assemblage

The palynological assemblage recovered from the sample 'CO Clamys' is largely dominated by *Classopollis torosus, Rhaetipollis germanicus* Schulz, 1967, *Ricciisporites tuberculatus* Lundblad, 1954, *Ovalipollis pseudoalatus* (Thiergart) Schuurman, 1976 and *Vesicaspora fuscus* (Pautsch) Morbey, 1975. *Classopollis meyeriana, Granuloperculatipollis rudis* (Venkatachala & Góczán) Scheuring, 1978 and *Geopollis zwolinskae* also occur together with a diverse group of accessory elements (Figures 2, 3; Table I). The marine organic-walled micro-plankton is a quantitatively important portion of the assemblage and is represented by the dinoflagellate cysts of *Rhaetogonyaulax rhaetica*.

This microfloral assemblage could be referred to the Rhaetian *Rhaetipollis-Limbosporites* Zone



Figure 3. Stratigraphically important species found in the Cotham Member of the Lilstock Formation from Manor Farm section near Aust. A-C. Rhaetipollis germanicus. D. Camarozonosporites laevigatus. E. Classopollis meyeriana. F. Limbosporites lundbladii. G. Ovalipollis pseudoalatus. H. Microreticulatisporites fuscus. I, J. Geopollis zwolinskae. K. Densosporites sp. L. Osmundacidites wellmanii. M. Vesicaspora fuscus. N, O. Ricciisporites tuberculatus. P, R-T. Rhaetogonyaulax rhaetica. Q. Camerosporites pseudomassulae. Scale bars – 10 μm.

POLLEN	Circumpolles
	Classopollis meyeriana (Klaus) Venkatachala &
	Goczan, 1964
	Classopours torosus (Reissinger) Couper, 1958
	Geopollis zwolinskae (Lund) Brenner, 1986
	Granuloperculatipollis rudis (Venkatachala &
	Goczán) Scheuring, 1978
	Rhaetipollis germanicus Schulz, 1967
	Monosulcates
	Cycadopites spp.
	Monosaccites
	Camerosporites pseudomassulae Mädler, 1964
	Bisaccates
	Alisporites spp.
	Lunatisporites rhaeticus (Schulz)
	Warrington, 1974
	Ovalipollis pseudoalatus (Thiergart)
	Schuurman, 1976
	Platysaccus papilionis Potonié & Klaus, 1954
	Vesicaspora fuscus (Pautsch) Morbey, 1975
SPORES	Triletes
	Aratrisporites spp.
	Baculatisporites spp.
	Calamospora mesozoica Couper, 1958
	Camarozonosporites laevigatus Schulz, 1967
	Camarozonosporites rudis (Leschik)
	Klaus, 1960
	Carnisporites spp.
	Cingulizonates rhaeticus (Reinhardt)
	Schulz, 1967
	Conbaculatisporites spp.
	Concavisporites spp.
	Deltoidospora spp.
	Densosporites fissus (Reinhardt) Schulz, 1967
	Kraeuselisporites reissingeri (Harris)
	Morbey, 1975
	Leptoledipites argentaeformis (Bolchovitina)
	Limbosporites hundhladii Nilsoon 1058
	Micromatical atists and a function (Nilson)
	Morbey, 1975
	Osmundacidites wellmanii Couper, 1953
	Retitriletes austroclavatidites (Cookson) Döring,
	Krutzsch, Mai & Schulz, 1963
	Todisporites spp.
	Aletes
	Ricciisporites tuberculatus Lundblad, 1954
DINOCYSTS	Rhaetogonyaulax rhaetica (Sarjeant) Loeblich
	& Loeblich, 1968

(Kuerschner et al., 2007). The group of dominant taxa and accessory taxa are characterised by Rhaetian elements, such as *Rhaetipollis germanicus*, *Ricciisporites tuberculatus*, *Camerosporites pseudomassulae* Mädler, 1964, *Limbosporites lundbladii* Nilsson, 1958, *Camarozonosporites laevigatus* Schulz, 1967, *Camarozonosporites rudis* (Leschik) Klaus, 1960, *Cingulizonates rhaeticus* (Reinhardt) Schulz, 1967, and *Leptoledipites argentaeformis* (Bolchovitina) Morbey, 1975 (Morbey, 1975; Bjærke & Manum, 1977; Lund, 1977; Schuurman, 1977, 1979; Visscher et al., 1980). A Rhaetian age is also supported by the presence of the dinoflagellate cyst Rhaetogonyaulax rhaetica, which is the index fossil of the Rhaetogonyaulax rhaetica (Rrh) interval biozone (Powell, 1992; Riding & Thomas, 1992; Kuerschner et al., 2007). The assemblage is well comparable with the one documented from the Cotham Member elsewhere in southern Great Britain (Warrington et al., 2008). A close similarity is observable to the palynoflora documented within that unit from the St Audrie's Bay-Doniford Bay section (Somerset), which was referred to as the Rhaetian (Hounslow et al., 2004; Warrington et al., 2008). However, at St Audrie's Bay, the members of Circumpolles (i.e. Granuloperculatipollis rudis and Geopollis zwolinskae) only occur below the Cotham Member and Leptolepidites argenteaeformis ranges until the base of the Westbury Formation (Hounslow et al., 2004; Warrington et al., 2008).

In the present study, *Geopollis zwolinskae*, which has not been definitely recorded in the literature above the Blue Anchor Formation (Hounslow et al., 2004), is found within the Cotham Member in association with *Granuloperculatipollis rudis* and *Leptolepidites argentaeformis*.

# Descriptions and comments on pollen morphology and ultrastructure

# Classopollis torosus

(Figures 4A–C, 5A–C, 6A–H; Table II)

Two specimens of Classopollis torosus (CO 98 and CO 105, Figure 4A, B) and one specimen (CO 108, Figure 4C) determined as C. torosus(?) have been studied. The specimens are more or less rounded-oval, flattened in obliquely equatorial (CO 98, Figure 4B), obliquely polar (CO 105, Figure 4A) or polar (CO 108, Figure 4C) position. Their dimensions are 26.0  $\mu$ m  $\times$  30.4  $\mu$ m (CO 98), 24.8  $\mu$ m  $\times$  30.8  $\mu$ m (CO 105) and 28.6  $\mu$ m  $\times$  31.4  $\mu$ m (CO 108). In transmitted light, the proximal scar is visible only in CO 108 (Figure 4C). The scar is small, with the rays 2.1-2.8µm long. No definite pseudopore was detected, but a significantly large area of lighter (=thinner) exine is present in the polar region in CO 98 and CO 105 (Figure 4A, B). Some short striations are visible (CO 98, Figure 4A). In optical sections of the equatorial margin the exine seems columellate (CO 98, CO 108, Figure 4A, C). Several folds of the exine (distal exine as understood by comparison between LM and SEM images) that are present in CO 105 and a few interrupted lines (CO 108) may be an underdeveloped rimula or remnants of an insufficiently preserved rimula.



Figure 4. General morphology of the studied specimens, LM. A. Classopollis torosus, CO 98. B. C. torosus, CO 105. C. C. torosus(?) CO 108. D. C. meyeriana, CO 84. E. C. meyeriana, CO 102. F. Geopollis zwolinskae, CO 87. Scale bars – 10 μm.

The surface is without prominent sculptural elements, nearly smooth or scabrate (Figure 5A–C). Images, taken at a higher magnification, show very small pits of about 0.1  $\mu$ m in diameter, elevations of about 0.2  $\mu$ m high (Figure 5B) and granulae of about 0.25  $\mu$ m in diameter (Figure 5A). The proximal scar of CO 105 is open, with the sides of this triangle being about 8.9–10.8  $\mu$ m long; and there are short proximal filaments about 0.5–0.9  $\mu$ m wide (Figure 5A). The proximal scar of CO 108 is closed (Figure 5B).

The studied specimens are not completely identical in their exine ultrastructure (Figure 6A–H). CO 108 is supposed to be less well preserved than the two other specimens; therefore the description will be mostly based on sections of CO 98 and CO 105.

The exine is about  $1.3-1.5 \ \mu m$  thick and consists of ectexine and endexine (Figure 6A–F). The tectum is 0.5–0.6  $\mu m$  thick. It consists of two parts: the upper one, microgranular, is about 0.25  $\mu m$  thick, and the lower one, homogeneous, is about 0.3  $\mu m$  thick (Figure 6F). The minute granulae of the outer part are about 0.03–0.09  $\mu$ m in diameter. Although the inner part of the tectum is solid and continuous, its internal finely undulating contour implies that ontogenetically it was formed of the same elements as the overlying sub-layer. In CO 105 (Figure 6C, D), the gradation of the tectum in two parts is less distinct than in CO 98 (Figure 6A, B, E, F), but in some regions, a narrow gap (parallel to the surface) is present at about the mid-depth of the tectum, which can be an index that the tectum consists of two sub-layers (Figure 6C, white arrow).

The tectum is underlain by a layer of large and rather widely spaced granulae. The smaller ones are 0.2-0.3 µm in diameter, while larger ones have a diameter from 0.5–1.34 µm. The smaller granulae are completely rounded, the larger granulae are wider than higher. The distances between the granulae vary from 0.3 to 0.9 µm. In most places, the granulae are predominantly arranged in one row (Figure 6B, C). The granulae can fuse forming a structure up to 5 μm long and 0.6 μm thick (Figure 6E, white arrow). This regular arrangement of the infratectum seems very peculiar and easily distinguishable from other types of granular infratectum, e.g., the infratectum of many small and irregularly distributed granulae of Duplicisporites granulatus (Leschik) Scheuring, 1970 (Zavialova & Roghi, 2005).

In some sections (Figure 6B, D), short areas within the ectexine lack the layer of large granulae and the tectum is in contact with the endexine. We suppose that such regions represent a cut through the rimula. The ultrastructure of the polar apertures is not revealed, since the sections are not situated centrally enough (judging by the comparison between the length of the sections and the diameter of the pollen grain).

The endexine is continuous, about 0.4  $\mu$ m thick throughout the perimeter of the pollen grain, slightly more electron-dense than the ectexine or of approximately the same electron density. The studied specimens vary in the ultrastructure (and even the presence) of the endexine. It seems that in CO 105 the endexine is composed of minute granulae (easily discernible on the outer and inner surface of this layer; Figure 6C), which are pressed in layers, separated by an intermittent line of minute lacunae filled with electron-dense matter. These lines are interrupted, so it is difficult to count the exact number of the layers (about ten layers).

The endexine in CO 98 is very similar, but is not identical to that of CO 105. The lamellae of CO 98 are also indicated by intermittent lines of lacunae with electron-dense matter, but no indices of granular units are detected (Figure 6E).

No inner hollow is detected in the sections of CO 108 (Figure 6G, H). Although they are situated in



Figure 5. Surface patterns in studied pollen grains, SEM. A. *Classopollis torosus*, CO 105, proximal surface, proximal filaments are visible. **B**, **C**. *C. torosus*, CO 108: **B**. Proximal pole; **C**. Proximal view. **D**–**F**. *C. meyeriana*, CO 102: **D**. Proximal pole; **E**. Proximal view; **F**. Blow-up situated closer to equatorial area. **G**. *Geopollis zwolinskae*, CO 87, note the presence of two rimulae. Scale bars – 10  $\mu$ m (A, C, E, G), 3  $\mu$ m (B, D, F).



peripheral areas, they are long enough  $(16-18 \ \mu m)$ to pass through the inner hollow, not only to touch the outer layer of the sporoderm; at least, smaller sections of CO 98 of about 12 µm long already reveal two-layered exine (Figure 6A). Therefore, we suppose that the hollow is present in these sections, but not detectable since the exine suffered from strong pressure and because a continuous endexine (in such cases usually indicating the position of the hollow which once contained the gametophyte) is lacking. We suggest that the endexine is not preserved rather than not developed, in other words, that this specimen is more probably insufficiently preserved rather than immature. Taylor and Alvin (1984), who studied the development of *Classopollis* exine, suggested that the endexine and ectexine developed simultaneously. If the specimen in question were immature, the two layers should have been underdeveloped in the same degree. Besides, judging from illustrations in Taylor and Alvin (1984), immature pollen grains are smaller than mature pollen grains, which is not the case in CO 108; it does not differ in size from the other, supposedly mature specimens. If we are right, the total thickness of the ectexine should be about 0.7-1.0 um. The ectexine includes a continuous tectum  $(0.3-0.4 \ \mu m \text{ thick})$  with a finely undulating external contour, which corresponds to the minute elevations and pits visible under SEM (Figure 5B). Since such a contour is developed over the whole perimeter of the exine, the distal surface (unstudied in SEM) does not differ from the proximal surface. The underlying layer of the ectexine is constituted of granulae comparable in size with analogous granulae of CO 98 and CO 105. Unlike other specimens, regular arrangement of infratectal granulae mostly in one row is not evident in this specimen, but we relate this to preservation. As far as it is possible to judge by peripheral sections, larger granulae occur in the proximal ectexine.

In sum, two sub-layers of the tectum are distinct in CO 98, and vague indication of the presence of two sub-layers of the tectum is evidenced in CO 105. The tecta in all three specimens have undulating

external and internal contours that allow us to suppose that they were formed of minute granulae in one and the same way and all had two sub-layers, which now look more or less evident dependent on maturity and/or preservation. The infratectum is formed of large granulae situated mostly in one row. The columellate appearance observed in transmitted light is probably due to relatively wide spaces between these granulae. Preservation of CO 108 prevents detecting this regular arrangement of granulae in its ectexine, but it is visible clearly enough in CO 98 and CO 105. The absence of the endexine in CO 108 is probably preservational, but the differences between the multi-lamellate endexine of CO 98 and the multi-lamellate endexine consisting of minute granulae of CO 105 are more probably due to a slightly more mature state of the former specimen.

#### Classopollis meyeriana

#### (Figures 4D, E, 5D-F, 7A-G)

Two specimens (CO 84, CO 102) were studied, showing some variation in the exine ultrastructure. The specimens are rounded or rounded oval (Figure 4D, E). CO 84 is 31 µm in diameter (Figure 4D) and CO 102 is about 32.3  $\mu$ m  $\times$  28.6  $\mu m$  (Figure 4E). The texture is punctuate. The proximal scar is visible in CO 102. It is open; each side of the triangle is about 9 µm. No definite pseudopore was detected. Columellate appearance is seen in optical sections of CO 84 (Figure 4D). CO 102 shows a distinct rimula, which separates an area of the distal surface of about 26.3  $\mu$ m  $\times$  21.8 µm (Figure 4E). The exine of this specimen is much lighter (=thinner) than the other. The surface is scabrate, with small granulae of about 0.1  $\mu m$  in diameter (Figure 5D–F).

The exine of CO 84 is two-layered and 0.8-1.2 µm thick (Figure 7A–F). The tectum is about 0.27 µm thick. It is hard to detect the two sub-layers in the tectum; however, in some places they are traceable (Figure 7C): the upper sub-layer is about 0.13 µm

Figure 6. The exine ultrastructure of *Classopollis torosus*, TEM. **A**, **B**, **E**, **F**. Specimen CO 98: **A**. Section situated close to the surface; granular nature of the infratectum is clearly visible; **B**. Section in the central area of the pollen grain, note large granulae of the infratectum arranged predominantly in one row; **E**. Some granulae of the infratectum are fused, lamellae of the endexine are indicated by intermittent lines of lacunae filled with electron-dense matter. Thick white arrow points to a black contour representing metal coating for SEM, remnants of such coating are also visible in all other figures. Thin white arrow indicates several granulae fused in one structure; **F**. Note the undulating (because of minute granulae) contour of the outer and inner perimeters of the tectum and large granulae of the infratectum. The outer portion of the tectum is shown with a white line. **C**, **D**. Specimen CO 105: **C**. Enlargement of (**D**), note that the endexine in this specimen seems to be composed of small granulae pressed in layers, thin white arrow points to the supposed boundary between the upper and lower portions of the tectum; **D**. Entire section of the pollen grain. **G**, **H**. Specimen CO 108: **G**. Enlargement of (**H**); **H**. Entire section of the pollen grain, the endexine is lacking. Abbreviations: t = tectum, i.gr. = granule of the infratectum, end = endexine, \* = flattened inner hollow of the pollen grain. Scale bars – 1  $\mu$ m (A–D, G, H), 0.67  $\mu$ m (E), 0.4  $\mu$ m (F).

Table II. Taxa studied and n	umber of the specimen.					
Characters	Classopollis torosus CO 98	Classopollis torosus CO 105	Classopollis torosus? CO 108	Classopollis meyeriana CO 84	Classopollis meyeriana CO 102	Geopollis zwolinskae CO 87
Sizes Scar	26.0  imes 30.4	$24.8 \times 30.8$ Small. open	28.6 × 31.4 Small. close	31	32.3 × 28.6 Small. open	$25 \times 29$
Rays, length			2.8-3.1		<b>A</b>	
Sides of open scar		8.9 - 10.8			6	
Rimula	۵.	Unclear	Unclear	Unclear	One distinct	Two distinct
Exine total thickness	1.5	1.3	0.	0.8 - 1.2	۵.	1.57 - 1.7
Ectexine, thickness	1.1	0.8	0.7-1.0 (?)	0.7 - 0.8	0.6 - 1.4	0.92 - 1.0
Endexine, thickness	0.4	0.4	<u>ი</u> .	0.4 - 0.46		0.65 - 0.7
Tectum, total thickness	0.55	0.5 - 0.6	0.3 - 0.4	0.27	0.3	0.46
Upper tectum	0.25			0.13	0.1	
Lower tectum	0.3			0.14	0.2	
Minute granulae	0.09	0.03 - 0.06				
Infratectum, thickness	0.57 - 0.64	0.5 - 0.75	0.37 - 0.45?	0.4 - 0.46	0.5 - 0.7	0.35 - 0.5
Large granulae, diameter	From 0.2–0.3 up to 0.9	From 0.25, 0.5–0.7,	From $0.2-0.4$ ,	0.3-0.4, up to $0.7$	Pillars rather than	0.3–0.35, up to 0.6
		up to 1.34	up to 0.8–1.2		granulae, 0.3–0.6 wide	
Fused granulae	up to 5 long and 0.6 high				1.25 long	0.92 long
Distance between granulae	0.3, 0.5, 0.7	0.1–0.25, up to 0.9	0.14 - 0.18	0.08 - 0.39	0.1 - 0.5	0.04 - 0.15
Endexine	Multilamellate,	Multilamellate,		Multilamellate, no granular	۵.	Multilamellate, no
	no granular units	with granular units		units, but undulated		granular units
				outer contour		



Figure 7. The exine ultrastructure of *Classopollis meyeriana*. **A–F.** Specimen CO 84: **A.** Montage of an entire section, an arrow indicates the position of rimula; **B.** One row of infratectal granulae sandwiched between the tectum and endexine; **C.** Tectum is to the left, its upper portion is marked with a white line, endexine is visible in the lower right corner; **D**, **F.** Multilamellate endexines of two sides of the pollen grain closely pressed to each other, rounded endings of infratectal units to the left; **E.** Granulae of infratectum; thick black arrow indicates a layer of metal coating, which is also visible in other figures. **G.** Specimen CO 102, the endexine is nearly lacking, the granular structure of the infratectum is less obvious. Black arrows indicate the position of rimula, white arrow points to supposed endexine remnants. Abbreviations: t = tectum, i.gr. = granule of the infratectum, end = endexine, \* = flattened inner hollow of the pollen grain. Scale bars – 1 µm (A, B), 0.5 µm (C, D, F), 0.4 µm (E), 1.25 µm.

thick and the lower sub-layer is about  $0.14 \,\mu\text{m}$  thick. The external and internal contours of the tectum are undulating implying that it was formed of minute granulae, similarly to the earlier described tectum of *Classopollis torosus*.

The infratectum looks columellate-like (Figure 7A); however, some infratectal units show rounded outlines (Figure 7A, 7B) suggesting that the infratectum is formed by large granulae arranged in one row and sandwiched between the tectum and endexine, similarly as in the earlier described specimens of Classopollis torosus. The outlines of the same individual elements in serial sections transform (from a section to an adjacent section) from a small circle to a larger circle, then to a columella-like element, then again to a large circle and, finally, to a small circle. This allows us to suggest that the individual elements are granulae. The endexine is welldeveloped, of constant thickness (0.4-0.46 µm), appears homogeneous at low magnification (Figure 7A, B) and multi-lamellate at higher magnification (Figure 7D–F). Although no minute granulae like those in the endexine of C. torosus (CO 105) were detected, the undulating outer contour of the endexine (visible e.g. in Figure 7C) suggests that this layer was formed in a similar way as in C. torosus (CO 105). In the area of the rimula, the infratectum becomes abruptly thinner (Figure 7A, arrow).

The exine of CO 102 shows a well-developed ectexine and some material that may represent endexine remnants (Figure 7G). The total thickness of the proximal exine is 0.6-0.8 µm. The distal exine is about 1 µm. The section has passed through the rimula where the exine reduces up to 0.2 µm thick (Figure 7G, black arrow). In contrast, in the areas of the girdle, the thickness of the exine increases up to 1.4 µm. The uppermost portion of the tectum forming a scabrate surface pattern visible in SEM (Figure 5F) is 0.1 µm thick, slightly more electron-dense than the underlying sub-layer, which is homogeneous and about 0.2 µm thick. It is fused with the infratectum  $(0.5-0.7 \ \mu m \ thick)$  in such a way that main constructing elements of the latter look like pillars rather than granulae (resembling ectexine 2 of Classopollis torosus; Pettitt & Chaloner, 1964). Judging from the outlines of lacunae between the pillars (wider outward, narrow centrally, and wider inward) and from the presence of a few granulae, we suspect that ontogenetically this infratectal layer was formed by large granulae, arranged mostly in one row. However, this granular nature of the layer is not clearly evident. In the area of the rimula, only tectum is visible. Some material with a greater electron density is present between the proximal and distal exine, supposedly representing remnants of the endexine (Figure 7G, white arrow).

### Geopollis zwolinskae

(Figures 3J, K, 4F, 5G, 8A–D)

One specimen (CO 87) was studied. The pollen grain is  $25 \ \mu m \times 29 \ \mu m$  in size, preserved in equatorial position. Two rimulae are visible (Figure 4F). The surface is scabrate; the presence of two rimulae is confirmed by SEM (Figure 5G).

The exine is bi-layered (Figure 8A-D). The ectexine consists of tectum and infratectum (Figure 8B). We found no indicators of the presence of two sub-layers in the tectum, which is, nonetheless, rather thick  $(0.46 \ \mu\text{m})$ . The infratectum  $(0.35-0.5 \ \mu\text{m}$  thick) is formed by one row of distinct large granulae of about 0.35 µm in diameter. Interestingly, much smaller granulae (about 0.09 µm) are scattered between the large granulae (Figure 8B, D, white arrow). The endexine is multi-lamellate; the lamellae being clearly visible under higher magnification (Figure 8D). Outer lamellae are more distinct than inner lamellae. No traces of minute granulae were detected in the endexine. In the rimular area, the ectexine becomes abruptly thinner at the expense of the infratectum, making about 0.5 µm (Figure 7A, black arrows).

## Discussion

The studied specimens are quite diverse in exine ultrastructure (Table II), but specimens similar in some ultrastructural characters correspond to the diagnoses of different species. Specimens lacking or nearly completely lacking an endexine are present in Classopollis torosus(?) and C. meyeriana. This is probably due to preservation. In addition, a multi-lamellate type of the endexine also shows variations: it can be without or with granular units in C. torosus, without granular units or with undulating contour implying the existence of granular units in C. meyeriana (Figure 7C), and without granular units in Geopollis zwolinskae. Probably, these differences do not have taxonomic significance but reflect slightly different stages of maturity of well-preserved pollen grains: the endexine without any traces of granular units is supposed to be observed in mature specimens, and the endexine with granular units is present in slightly less mature specimens.

The same two specimens that almost lack endexine show much less confident regular arrangement of infratectal large granulae. We suppose [at least for *Classopollis torosus*(?)] that this is a preservational alteration of the ultrastructure, since the large granulae of infratectum freely rest on the endexine (as it is seen in better preserved specimens) and, if this underlying layer was destroyed, their regular



Figure 8. The exine ultrastructure of *Geopollis zwolinskae*, CO 87. **A.** Entire section, the ectexine sharply decreases in thickness in the areas of rimulas, indicated by black arrows. **B.** Blow-up of (**A**), note large granulae of the infratectum and much smaller granulae between them (*white arrow*). **C.** Portion of the section showing that the endexine is more distinctly lamellate in its outer regions. Thick black arrow indicates a layer of metal coating, which is also visible in other figures. **D.** Lamellae of the endexine. White arrow points to one of small granulae situated between large granulae of the infratectum. Abbreviations: t = tectum, i.gr. = granule of the infratectum, end = endexine, \* = flattened inner hollow of the pollen grain. Scale bars  $-1 \mu m$  (A, B),  $0.4 \mu m$  (C),  $0.25 \mu m$  (D).

arrangement can easily be broken. We believe that all the studied specimens originally had an infratectum formed by large granulae that were regularly arranged, mostly in one row, and this regular arrangement of large granulae is a key ultrastructural characteristic of the pollen included in this study, allowing confident differentiation from other types of granular ectexine. Lugardon (1985) hypothesised that a granular infratectum characterised all or nearly all members of Circumpolles. The present work confirms this hypothesis for Rhaetian members of the group. The studied pollen grains show enough differences in general morphology to be defined as members of three taxa. For example, *Geopollis zwolinskae* is characterised by two rimulae. However, Pocock et al. (1990, fig. 13) showed a *Classopollis meyeriana* with two rimulae and cited several published cases of Circumpolles. The pollen grains under study also vary in ultrastructural characteristics. These variations do not correlate with the affiliation of the specimens to the three particular taxa. Similarities between the specimens strongly suggest that they were produced by related plants of the same group. We suggest that originally all pollen grains under study shared several ultrastructural characters, which now are either clearly visible or their presence can be drawn from certain indirect indices or are lost (in some specimens). Among them are a double layered tectum and an infratectum composed of large regularly arranged granulae freely resting on a multi-lamellate endexine. The infratectum becomes thinner or disappears in apertural areas.

The present study has contributed to the data pool on the exine ultrastructure of the Circumpolles group. A considerable bulk of information was already accumulated about the exine ultrastructure of unequivocal cheirolepidiaceous pollen of different age and geography. If any directed changes took place in the exine ultrastructure during the existence of the family they should therefore be traceable in this material.

Pollen grains of *Classopollis* are shown to be ultrastructurally diverse during the geological history of the genus (Figure 9, Table III). The tectum definitely consists of two sub-layers in some members; in others, it bears only supratectal elements or it may be simply composed of a single layer. No temporal trend is detectable in the ultrastructure of this layer; and consequently, this feature was probably rather constant. A multi-lamellate endexine occurs in both early and late members, such as Rhaetian Classopollis meyeriana and Classopollis torosus (this study), Rhaetian-Liassic Classopollis torosus (Pettitt & Chaloner, 1964) and Barremian Classopollis torosus (Taylor & Alvin, 1984). The same is true for a homogeneous endexine and a filamentous endexine. Results of the present study show that the type of the endexine may vary within the same species from the same geological sample. The ultrastructure of apertural areas was investigated in some studies, but disregarded in others; therefore, more information is needed before adequate comparison can be accomplished. Unlike the tectum and endexine, the infratectum appears to show an evolutionary trend through geological time. Older members most probably had a regularly arranged infratectum formed by large granulae. Such an infratectum gave rise to the columellate-like infratectum. Both columellate-like and granular infratectum are known in species from the Jurassic (e.g., Classopollis torosus with a columellate-like infratectum and Classopollis meyeriana with a granular infratectum; Zavialova, 2003; Zavialova & Tekleva, 2005; Tekleva & Krassilov, 2009), whereas the granular infratectum is unknown in Cretaceous members of the group (both Barremian Classopollis torosus and Albian-?Cenomanian Classopollis martinottii Reyre, 1970 have columellate-like infratectum; Taylor & Alvin, 1984; Zavialova et al., in



Figure 9. Stratigraphic position of members of Circumpolles studied with help of TEM. Letters in circles refer to Table III.

press). Finally, the columellate-like elements evolved into branching elements (*Classoidites glandis* Van Ameron, 1965; Médus, 1977; Kedves, 1994). There is a possibility that these changes accompanied transformations, which took place in other organs of the family.

Other questions that arise after reviewing the ultrastructure of various Circumpolles concern the predecessors of *Classopollis*. What type of pollen grains could have allowed morphological transformation/s that led to *Classopollis*? Or, in other words, what plant group could have been the ancestor of the Cheirolepidiaceae? What place did early members of the Circumpolles group occupy in this transformation? Do they represent pollen grains of early members of the Cheirolepidiaceae and their predecessors? Were

all of them produced by the Cheirolepidiaceae or only one particular morphotype among these several types?

Let us suppose how a hypothetical ancestral pollen type could have looked like. First of all, we believe that it should have a trilete scar. This is an unequivocal primitive feature, in fact, the only primitive feature in *Classopollis*; therefore, it most probably should have been inherited from earlier forms. One more important thing is that, even in early members of the group, the trilete scar, if present, is always small. Therefore, most probably, the pollen grains of the ancestor should also be characterised by a vestigial proximal scar.

The presence of a trilete scar was mentioned in the evolutionary scheme for the group drawn by de Jersey (1973), who hypothesised a transformation from the Early Triassic *Grebespora concentrica* Jansonius, 1962, through Late Triassic *Discisporites psilatus* (de Jersey) Raine et al., 1988 to *Classopollis meyeriana*. However, later this idea was abandoned (Raine et al., 1988): *Discisporites psilatus* was re-interpreted and transferred to *Densoisporites psilatus* (de Jersey) Raine et al., 1988 of supposed lycopsid affinity. Indeed, de Jersey's (1973) hypothesis is unconvincing both considering the conceivability of the structural transformation and keeping in mind the possible botanical affinity.

Pollen grains with a small proximal trilete scar were produced by several groups of gymnosperms. Scheuring (1976) proposed a transition from *Triadispora* to *Classopollis*, based on pollen-morphological data and keeping in mind the possible origin of the Cheirolepidiaceae from the Voltziaceae. On the basis of data about macrofossils, Clement-Westerhof and Van Konijnenburg-van Cittert (1991) supposed that the Cheirolepidiaceae descended from the Majonicaceae, characterised by the *Lueckisporites* type of palynomorphs, which represents, similarly to *Triadispora*, a pollen grain with two protosacci and a small trilete scar.

Our data on early Classopollis do not support either hypothetical line. Although the specimens studied from the Rhaetian deposits of England show a certain degree of variability, an infratectum formed by one layer of large and rather widely spaced granulae is either clearly visible or can be supposed for all studied specimens. Such an infratectum fits very well to the position of the primitive type within the group: it appears in the oldest members of the group [such as the Rhaetian Classopollis and Geopollis under study and the Upper Triassic Circulina sp. form 1 and the Rhaetian-Liassic Classopollis harrisii Muir & Van Konijnenburg-Van Cittert, 1970 (Médus, 1977), is probably present in some younger members (Upper Jurassic Classopollis torosus and Classopollis meyeriana; Rowley & Srivastava, 1986; Krassilov et al., 1997; Zavialova & Tekleva, 2005; Tekleva & Krassilov, 2009], and the more columellate-like infratectum and the infratectum with elongated rods of some other members of the group (e.g., Barremian *Classopollis torosus* and Albian–?Cenomanian *Classopollis martinottii*; Taylor & Alvin, 1984; Zavialova et al., in press) are easily derivable from it (Table III).

However, the transition from Triadispora or Lueckisporites implies a transformation from a protosaccate structure of the ectexine. Triadispora has a protosaccus with regular ectexinal partitions, many of those are situated perpendicularly to the surface; the protosaccus of Lueckisporites is filled with numerous thin undulating partitions, and nonsaccate regions are composed of the similar, but shorter units (Scheuring, 1974; Zavialova, 2001). In our opinion, the transformation from either of these types would lead to an ectexine with, at least occasionally, branching units, which is not the case for the Rhaetian Classopollis and Geopollis. An ectexine with branching columellate-like elements is only known in a younger member of the group, *Classoidites* glandis (Table III). In addition, unlike protosaccate exines, the tectum and infratectum appear as two distinct layers in Circumpolles and supposedly were formed in different stages and/or modes during the ontogenesis. Therefore, it is difficult to use the Rhaetian Classopollis and Geopollis as a transitional link in either scheme. The same problem will remain if any saccate pollen grain (with alveolate ectexine) will be involved in a scheme.

Currently, it is difficult to reconcile the conclusions based on macro-remains and those on the exine ultrastructure, because it would imply an evolution of the regular granular infratectum from the drastically different alveolate infratectum. Based on merely ultrastructural data it is possible to evolve the regular granular infratectum from an irregularly granular structure. For instance, species of Duplicisporites that are Carnian members of the Circumpolles group (Zavialova & Roghi, 2005) show a less pronounced but, nonetheless, granular ectexine. The Upper Triassic Circulina sp. form 3 seems to show irregularly arranged granulae in the infratectum (Médus, 1977). Members of the same formal morphological group are much more similar to Classopollis in general morphology than monosaccate supposedly teratological forms that were used by Scheuring (1976) as an example of the supposed link toward Classopollis. They are much more conceivable to occupy a penultimate, closest to Classopollis, place in the chain of transformations from the pollen grain of a hypothetical ancestor to the typical cheirolepidiaceous pollen grain.

One more thing can be pointed out: in the case of a saccate ancestral type, the presence of a distinctly

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Table III. Comparis	on between members of Circur	npolles studied with the help of TEM sh	owing some ultrastructural characteristics o	f the exines.			
Taxon	Double layered tectum	Infratectum	Endexine	Age	Geography	Reference	Fig. 9
Duplicisporites pranulatus	Lacking	Numerous fine granulae	Appears homogeneous	Carnian	Italy	Zavialova & Roghi, 2005	A
Duplicisporites vervucosus	Lacking	Numerous fine granulae	Appears homogeneous	Carnian	Italy	Zavialova & Roghi, 2005	A
Circulina sp. form 1	Present	Large granulae (cross sections are needed to decide if they are regularly arranged)	Thick, indistinctly lamellate	Upper Triassic	France	Médus, 1977	в
<i>Circulina</i> sp. form 2	More probably double (unclear from illustrations)	Irregularly arranged granulae (trapezoidal rods, described by Médus, probably represent a result of meservational damage)	Appears homogeneous (micrographs under greater magnification are needed)	Upper Triassic	France	Médus, 1977	а
<i>Circulina</i> sp. form 3	Lacking	Numerous, densely packed and irregularly arranged granulae	Thick, indistinctly lamellate	Upper Triassic	France	Médus, 1977	в
Classopollis meyeriana	Supposedly present	Regularly arranged large granulae mostly in one row	Multilamellate (no minute granulae are visible, but the contour is undulating) or nearly lacking	Rhaetian	England	This work	C
Geopollis zwolinskai	Thick, but no indices of two sub-layers	Regularly arranged large granulae mostly in one row	Multilamellate, no minute granulae are present	Rhaetian	England	This work	U
Classopollis torosus	Present	Regularly arranged large granulae mostly in one row	Multilamellate (minute granulae can be present) or lacking	Rhaetian	England	This work	U
Classopollis torosus Classopollis harrisii	Present Present	Columellate-like Probably composed of regularly	Multilamellate Thick, appear homogeneous	Rhaetian-Liassic Rhaetian-Liassic	England France	Pettitt & Chaloner, 1964 Médus, 1977	D B
O'acconollie alaccoidae	Summerced alamante	arranged large granulae (serial sections are needed)	(micrographs under greater magnification are needed)		Hundowy Formt	Vadvas 1004	ц
Classopouis cuissouces	are possibly present	Unctual	homogeneous (poorly preserved) Secondarily homogeneous		Hungary, Egypt Hungary Fount	Kedves 1994	ц ц
			(poorly preserved)		rur		a p
Classopours torosus Classopollis torosus	rresent Supratectal elements are present	Columenate-like Elongated columellate-like elements in the region of the	Appears nomogeneous A thin filament in some regions, a thickened sheet in some other	Callovian Oxfordian	w estern Siberia England	zavialova, 2005 Rowley & Srivastava, 1986	чĢ
		band, but circular elements that in our opinion can be granulae in other regions	regions, or lacking in the areas of the pseudopore and proximal scar				

(Continued)

Table III. (Continue	ed).						
Taxon	Double layered tectum	Infratectum	Endexine	Age	Geography	Reference	Fig. 9
Classopollis meyeriana	Present	Supposedly of large granulae	Supposedly poorly preserved	Upper Jurassic	Kazakhstan	Krassilov et al., 1997; Zavialova & Tekleva, 2005; Tekleva & Krassilov, 2009	H; I; J
Classopollis torosus	Present	Columellate-like	Multilamellate in mature pollen grains, reconstructed as homoge-	Barremian	England	Taylor & Alvin, 1984	К
Classopollis martinottii	Present	Columellate-like	neous in immature pollen grains Only filamentous remnants were detected	Albian- ?Cenomanian	Lebanon	Zavialova et al., in press	Г
Classoidites glandis	Present	Numerous, irregular, probably anastomosing granulae	Lamellate	Upper Cretaceous	Portugal	Kedves, 1994	Е
Classoidites glandis	Present	Branching columellate-like elements	Appears homogenous, there is a possibility that it is lamellate (unclear from the illustrations)	Turonian	France	Médus, 1977	в

delineated girdle (transformed from the saccus) should be very probable in the pollen of early Cheirolepidiaceae. That is not the case of the early members of the Circumpolles group, which often have an interrupted rimula and a weakly developed girdle. However, if the ancestral type lacked sacci, the early members of the Circumpolles group fit much better to the role of the intermediate chain towards advanced members of the Circumpolles and, at the same type, to the role of pollen grains of early Cheirolepidiaceae. There are also some other indications of cheirolepidaceous affinity of early Circumpolles. Roghi et al. (2006) found in the Carnian deposits of the Julian Alps cheirolepidiaceous shoots accompanied by a high percentage of Praecirculina, Camerosporites and Duplicisporites species in the palynological assemblage. This co-occurrence supports the affinity of the pollen to the same plant group, though in situ finds in generative organs are strongly needed to test our hypothesis. As to the ancestor of the family, in our opinion, it should have produced pollen with finely granulate rather than alveolate ectexine.

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# References

- Bjærke, T. & Manum, S. B. (1977). Mesozoic palynology of Svalbard. The Rhaetian of Hopen, with a preliminary report on the Rhaetian and Jurassic of Kong Karls Land. *Norsk Polarinstitut, Skrifter*, 165, 1–48.
- Brenner, W. (1986). Bemerkungen zur Palynostratigraphie der Rhät-Lias-Grenze in SW-Deutschland. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 173, 131–166.
- Bucefalo Palliani, R. & Buratti, N. (2006). High diversity dinoflagellate cyst assemblages from the Late Triassic of southern England: new information on early dinoflagellate evolution and palaeogeography. *Lethaia*, 39, 305–312.

- Clement-Westerhof, J. A. & Van Konijnenburg-van Cittert, J. H. A. (1991). *Hirmeriella muensteri*: new data on the fertile organs leading to a revised concept of the Cheirolepidiaceae. *Review* of Palaeobotany and Palynology, 68, 147–179.
- Couper, R. A. (1953). Upper Mesozoic and Cainozoic spores and pollen grains from New Zealand. New Zealand Geological Survey, Paleontological Bulletin, 22, 5–77.
- Couper, R. A. (1958). British Mesozoic microspores and pollen grains, a systematic and stratigraphic study. *Palaeontographica Abt. B*, 103, 75–179.
- de Jersey, N. J. (1973). Rimulate pollen grains from the Lower Mesozoic of Queensland. In J. E. Glover & G. Playford (Eds), Mesozoic and Cainozoic palynology: essays in honour of Isabel Cookson (pp. 127–140). Sydney: Special Publication of the Geological Society of Australia.
- Green, O. R. (2001). A manual of practical laboratory and field techniques in palaeobiology. Dordrecht: Kluwer Academic Publishers.
- Hounslow, M. W., Posen, P. E. & Warrington, G. (2004). Magnetostratigraphy and biostratigraphy of the Upper Triassic and lowermost Jurassic succession, St Audrie's Bay, UK. *Palaeogeography, Palaeoclimatology, Palaeoecology, 213*, 331–358.
- Kedves, M. (1994). Transmission electron microscopy of the fossil gymnosperm exines. Szeged: J. Nyomda.
- Klaus, W. (1960). Sporen der karnischen Stufe der ostalpinen Trias. Jahrbuch der Geologischen Bundesanstalt, 5, 107–184.
- Krassilov, V. A., Zherikhin, V. V. & Rasnitsyn, A. P. (1997) *Classopollis* in the guts of Jurassic insects. *Palaeontology*, 40, 1095–1101.
- Kuerschner, W. M., Bonis, N. R. & Krystyn, L. (2007). Carbonisotope stratigraphy and palynostratigraphy of the Triassic– Jurassic transition in the Tiefengraben section, Northern Calcareous Alps (Austria). *Palaeogeography, Palaeoclimalogy, Palaeoecology, 244, 257–280.*
- Loeblich, A. R. Jr & Loeblich, A. R. III. (1968). Index to the genera, subgenera, and sections of the Pyrrophyta, II. *Journal* of Paleontology, 42, 210–213.
- Lugardon, B. (1985). Observations nouvelles sur l'ultrastructure des Circumpolles. IX. Symposium de l'association des palynologues de langue française (A.P.L.F.), Montpellier, Abstract volume, 21.
- Lund, J. J. (1977). Rhaetic to lower Liassic palynology of the onshore south-eastern North Sea Basin. *Geological Survey of Denmark II*, 109, 1–103.
- Lundblad, B. (1954). Contribution to the geological history of the Hepaticae. *Svensk Botanisk Tidskrift*, 48, 381–416.
- Mädler, K. (1964). Bemerkenswerte Sporenformen aus dem Keuper und unteren Lias. Fortschritte in der Geologie von Rheinland und Westfalen, 12, 169–200.
- Médus, J. (1977). The ultrastructure of some Circumpolles. Grana, 16, 23–29.
- Meyer-Melikian, N. R. & Telnova, O. P. (1991). On the method of study of fossil spores and pollen using light, scanning electron and transmission electron microscopes. In *Palynological taxa in biostratigraphy*. Proceedings of the 5th Soviet Union Palynology Conference, Moscow, 1990 (pp. 8–9). Moscow: USSR Academy of Sciences (in Russian).
- Morbey, S. J. (1975). The palynostratigraphy of the Rhaetian Stage, Upper Triassic, in the Kendelbachgraben, Austria. *Pal-aeontographica Abt. B*, 152, 1–75.
- Muir, M. & Van Konijnenburg-van Cittert, J. H. A. (1970). A rhaetoliassic flora from Airel, northern France. *Palaeontol*ogy, 13, 433–442.
- Nilsson, T. (1958). Über das Vorkommen eines mesozoischen Sapropelgesteins in Schonen. Acta Universitatis Lundensis, 53, 1–112.
- Petrosianz, M. A. & Bondarenko, N. M. (1983). Characteristic and correlative gymnosperm pollen taxa (Late Cretaceous-

Paleogene): pollen of Cheirolepidiaceae, a synopsis. Moscow: Nauka (in Russian).

- Pettitt, J. M. & Chaloner, W. G. (1964). The ultrastructure of the Mesozoic pollen Classopollis. Pollen et Spores, 6, 611–620.
- Pocock, S. A. J., Vasanthy, G. & Venkatachala, B. S. (1990). Pollen of Circumpolles – an enigma or morphotrends showing evolutionary adaptations. *Review of Palaeobotany and Palynology*, 65, 179–193.
- Powell, A. (1992). Dinoflagellate cysts of the Triassic System. In A. Powell (Ed.), A stratigraphic index of dinoflagellate cysts (pp. 1– 6). London: Chapman & Hall.
- Radley, J. D. & Carpenter, S. C. (1998). The Late Triassic strata of Manor Farm, Aust, South Gloucestershire. *Proceedings of* the Bristol Naturalists' Society, 58, 57–68.
- Raine, J. I., de Jersey, N. J. & Ryan, K. G. (1988). Ultrastructure and lycopsid affinity of *Densosporites psilatus* (de Jersey) comb. nov. from the Triassic of New Zealand and Queensland. *Memoirs of the Association of Australasian Palaeontologists*, 5, 79–88.
- Reynolds, S. H. (1947). The Aust section. Proceedings of the Cotteswold Naturalists' Field Club, 29, 29–39.
- Reyre, Y. (1970). Stereoscan observations on the pollen genus Classopollis Pflug, 1953. *Palaeontology*, 13, 303–322.
- Riding, J. B. & Kyffin-Hughes, J. E. (2004). A review of the laboratory preparation of palynomorphs with a description of an effective non-acid technique. *Revista Brasileira de Paleontologia*, 7, 13–44.
- Riding, B. & Thomas, J. E. (1992). Dinoflagellate cysts of the Jurassic System. In A. Powell (Ed.), A stratigraphic index of dinoflagellate cysts (pp. 7–97). London: Chapman & Hall.
- Roghi, G., Ragazzi, E. & Gianolla, P. (2006). Triassic amber of the Southern Alps (Italy). *Palaios*, 21, 143–154.
- Rowley, J. R. & Srivastava, S. K. (1986). Fine structure of *Classopollis* exines. *Canadian Journal of Botany*, 64, 3059–3074.
- Scheuring, B. (1970). Palynologische und palynostratigraphische Untersuchungen des Keupers im Boelchentunnel (Solothurner Jura). Schweizer Paläontologische Abhandlungen, 88, 1–119.
- Scheuring, B. W. (1974). Protosaccate Strukturen, ein weitverbreitetes Pollenmerkmal zur frühen und mittleren Gymnospermenzeit. Geologische und paläontologische Mitteilungen Innsbruck, 4, 1–30.
- Scheuring, B. W. (1976). Proximal exine filaments, a widespread feature among Triassic *Protosaccites* and Circumpolles to secure the dispersal of entire tetrads. *Pollen et Spores*, 18, 611–639.
- Scheuring, B. W. (1978). Microfloren aus den Meridekalken des Mte San Giorgio (Kanton Tessin). Schweizerische paläontologische Abhandlungen, 100, 1–205.
- Schulz, E. (1967). Sporenpaläontologische Untersuchungen rhäto-liassischer Schichten im Zentralteil des germanischen Beckens. *Paläontologische Abhandlungen*, B 2, 543–633.
- Schuurman, W. M. L. (1976). Aspects of late Triassic palynology. 1. On the morphology, taxonomy and stratigraphical/geographical distribution of the form genus *Ovalipollis. Review of Palaeobotany* and Palynology, 21, 241–266.
- Schuurman, W. M. L. (1977). Aspects of Late Triassic palynology. 2. Palynology of the "Grès et Schiste à Avicula contorta" and "Argiles de Levallois" (Rhaetian) of north-eastern France and southern Luxemburg. *Review of Palaeobotany and Palynology*, 23, 159–253.
- Schuurman, W. M. L. (1979). Aspects of Late Triassic Palynology. 3. Palynology of latest Triassic and earliest Jurassic deposits of the Northern Limestone Alps in Austria and southern Germany, with special reference to a palynological classification of the Rhaetian Stage in Europe. *Review of Palaeobotany and Palynology*, 27, 33–75.

- Storrs, G. W. (1994). Fossil vertebrate faunas of the British Rhaetian (latest Triassic). Zoological Journal of the Linnaean Society, 112, 217–259.
- Storrs, G. W., Gower, D. J. & Large, N. F. (1996). The diapsid reptile, *Pachystropheus rhaeticus*, a probable choristodere from the Rhaetian of Europe. *Palaeontology*, 39, 323–349.
- Taylor, T. N. & Alvin, K. L. (1984). Ultrastructure and development of Mesozoic pollen: *Classopollis. American Journal of Botany*, 71, 575–587.
- Tekleva, M. V. & Krassilov, V. A. (2009). Modern Gnetales and fossil gnetophytes: comparative pollen morphology and ultrastructure. *Review of Palaeobotany and Palynology*, 156, 130–138.
- Van Ameron, H. W. J. (1965). Upper Cretaceous pollen and spores assemblages from the so-called 'Wealden' of the province of Leon (northern Spain). *Pollen et Spores*, 7, 93–134.
- Venkatachala, B. S. & Góczán, F. (1964). The spore-pollen flora of the Hungarian 'Kössen Facies'. Acta Geologica Hungarica, 8, 203–228.
- Visscher, H., Schuurman, W. M. L. & Van Erve, A. W. (1980). Aspects of a palynological characterization of Late Triassic and Early Jurassic "Standard" units of chronostratigraphical classification in Europe. *Proceedings of the IV International Palynology Conference, Lucknow (1976–1977)*, 2, 281–287.
- Warrington, G. (1974). Studies in the palynological biostratigraphy of the British Trias. I. Reference sections in west Lancashire and north Somerset. *Review of Palaeobotany and Palynology*, 17, 133–147.
- Warrington, G., Cope, J. C. W. & Ivimey-Cook, H. C. (2008). The St Audrie's Bay-Doniford Bay section, Somerset, England: updated proposal for a candidate Global Stratotype Section and Point for the base of the Hettangian Stage, and of the Jurassic System. *ISJS Newsletter*, 35, 2–68.

- Watson, J. (1982). The Cheirolepidiaceae: In C. B. Beck (Ed.), Origin and evolution of Gymnosperms (pp. 265–273). New York: Columbia University Press.
- Wood, G. D., Gabriel, A. M. & Lawson, J. C. (2002). Palynological techniques – processing and microscopy. In J. Jansonius & D. C. McGregor (Eds), *Palynology: principles and applications* (pp. 29–50). Toronto: American Association of Stratigraphic Palynologists Foundation.
- Zavialova, N. E. (2001). L'ultrastructure du pollen saccules de gymnospermes fossiles en relation avec les implications systematiques. XVII. Symposium de l'association des palynologues de langue française (A.P.L.F.), Arles, Abstract volume XVII, 95.
- Zavialova, N. E. (2003). On the ultrastructure of *Classopollis* exine: a tetrad from the Jurassic of Siberia. *Acta Palaeontologica Sinica*, 42, 1–7.
- Zavialova, N. E. & Roghi, G. (2005). Exine morphology and ultrastructure of *Duplicisporites* from the Triassic of Italy. *Grana*, 44, 337–342.
- Zavialova, N. E. & Tekleva, M. V. (2005). Exine ultrastructure of pollen grains of the genus *Classopollis* extracted from guts of Jurassic insects. *Proceedings of the XI. All-Russia Palynological Conference "Palynology: theory and practice"*, Moscow, 86–87 (in Russian).
- Zavialova, N. E., Tekleva, M. V. & Smirnova, S. B. (2008). New data on the ultrastructure of *Classopollis* Pflug. Proceedings of the XII. All-Russia Palynological Conference "Palynology: stratigraphy and geoecology", St. Petersburg, 1, 64-68 (in Russian).
- Zavialova, N. E., Tekleva, M. V. & Smirnova, S. B. & Mroueh, M. (in press). Exine ultrastructure in pollen grains of *Classopollis* Pflug from the Cretaceous of Lebanon. *Russian Paleontological Journal*, 44.