

## Pollen morphotype edmundi and its significance for palaeoclimate reconstructions of the Neogene

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Pollen analysis has revealed the presence of the edmundi morphotype in the Paleogene and Neogene sediments of Central Europe. Its species, characterized by different morphologies, are mainly assigned to two families of extant plants – the Araliaceae and the Mastixiaceae – and compared to pollen of some genera (*Diplopanax* and *Mastixia* from the Mastixiaceae, and *Aralia*, *Fatsia* and *Schefflera* from the Araliaceae). The most significant genus for palaeoclimate reconstructions is the extant *Diplopanax*, whose seeds, similarly as the seeds of other representatives of the Mastixiaceae, appear in the warm phases of the Neogene. The type species of *Edmundipollis* (*E. edmundi*) has been compared to *Diplopanax* pollen. Based on similarities with extant plants, the CA (Coexistence Approach) was determined. The results indicate a very warm and humid subtropical climate (Cfa–Cwa) according to the Köppen classification.

Key words: Palynology, Neogene, climate, *Edmundipollis*, Araliaceae, Mastixiaceae.

### INTRODUCTION

Pollen grains with an unusual morphology have been encountered in terrestrial sediments spanning the Eocene to the Early Pliocene. They include dark brown forms with a hexagonal or rhomboidal outline in equatorial view and with meridionally arranged swellings of the exine, in which colpi with thick borders are incised. The brown colour is the effect of the exceptionally thick exine.

The morphotype was noted already in the first pollen studies conducted in Paleogene and Neogene sediments (Potonié, 1931) and referred to as *Pollenites edmundi*. In subsequent reports, Potonié (1951a, b) suggested that it resembles pollen of the Araliaceae family and created the genus *Araliaceoipollenites* for such pollen grains. Later, he noted differences in the structure of the established genus (Potonié, 1960) and distinguished two morphotypes: *Araliaceoipollenites* sp. (pl. 6, fig. 107) and *A. edmundi* (pl. 6, fig. 108). Both types were recognized in numerous pollen reports for the Neogene with their affinities with either the Araliaceae or the Cornaceae. In papers published in the 1980s or later (e.g., Thiele-Pfeiffer, 1980; Mohr, 1984; Nagy, 1985; Ashraf and Mosbrugger, 1996; Ferguson et al., 1998; Hofman and Zetter, 2001), the assumption prevailed that the edmundi morphotype is closest related to the pollen of extant *Mastixia*.

Presently, *Mastixia* (ca. 19 species) lives in subtropical or tropical climate zones. Its pollen regularly occurs in the Paleogene or Early Neogene of Central Europe, but is extremely rare in the Late Miocene except in the Inden Formation of the Lower Rhine Basin, and has not been found at all in continental Neogene pollen profiles of northern Europe (Denk et al., 2011).

When assuming the present-day climate requirements of *Mastixia* and the common appearance of the edmundi pollen from the Eocene to the Early Neogene, it seems that climate must have been very warm to subtropical at that time. This supposition is confirmed by carpological data (Mai, 1967, 1995, 2000; Czaja, 2003).

For determination of climate and palaeotemperatures based on fossil pollen, compared with pollen of living plants, a correct morphological description of fossil pollen and its precise comparison with the nearest living relatives (NLRs after Mosbrugger and Utescher, 1997) are indispensable.

The fossil edmundi morphotype has raised our particular attention. The morphotype includes forms with a variable morphology. We have thus attempted to compare this fossil pollen morphotype with a most similar structure observed in living plants.

### METHODS

The material for study was obtained from Neogene deposits of the Polish Lowlands, in which the edmundi morphotype was found (Stuchlik et al., 2014). The edmundi morphotype has been subdivided into morphospecies, encountered in two families: the Mastixiaceae (Cornaceae) and the Araliaceae, and

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compared with pollen of extant plants (NLRs). The modern climatic requirements of these plants are diverse. Numerous previous papers have considered that all the edmundi morphotype pollen grains represent the Mastixiaceae family (Thiele-Pfeiffer, 1980; Mohr, 1984; Ashraf and Mosbrugger, 1996).

This paper provides a graphical presentation of the mean annual temperature for the nearest living relatives (NLRs) of the edmundi morphotypes. According to the graph, the climatic requirements of plants with pollen corresponding to the edmundi morphotype are very wide, in the range of 5–28°C resulting from the wider range of temperatures for the Araliaceae family plants. The presence of Mastixiaceae pollen grains restricts the range to 15.5–28°C. For the NLRs of the edmundi morphotype this range is 16.5–20.5°C.

However, correct determination of the edmundi morphospecies is essential for climate reconstructions. If the edmundi morphotype from Late Miocene sediments is recognized as the equivalent of *Mastixia*, this would suggest that climate was very warm at that time, which is not indicated by the other taxa. The authors have not used the CA method in a classical way, but attempted to extend this method onto the possibility of climate interpretation. The botanical variability of the edmundi morphotype is essential for considerations of the Neogene climate.

## PREVIOUS STUDY

Mamczar (1960) was the first to state that the differences in the structure of pollen grains assigned to *Pollenites edmundi* Potonié result from the derivation of these grains from two different plant families. Therefore, she distinguished a number of morphological forms among this fossil species, and then arranged them in two groups: *Pollenites edmundi* R. Pot – cf. *Cornus* L. and *Pollenites edmundi* R. Pot – cf. *Aralia* L. Comparative material from the *Cornus* genus included the species *C. alba* L., *C. amomum* Mill., *C. brachypoda* C.A. Mey, *C. sanguinea* L. and *C. stolonifera* Mchx. Extant species of the *Aralia* genus include *A. chinensis* L. and *A. spinosa* L. (Mamczar, 1962). Due to the very poor quality of the photographs and insufficient descriptions, the cited paper is at present only of historical significance. However, the idea that *Pollenites edmundi* grains with a hexagonal or rhomboidal outline in equatorial view and with meridionally arranged swellings of the exine, in which colpi with thick borders are incised, were produced by plants of two different families – the Araliaceae and the Cornaceae – was in fact revolutionary (Mamczar, 1962).

Forms close to the holotype of *Pollenites edmundi* and others with features corresponding to the edmundi morphotype but differing in minor morphological features, have been illustrated in various reports by other palynologists (e.g., Kremp, 1949; Potonié et al., 1950; Thomson and Pflug, 1953; Mamczar, 1960; Doktorowicz-Hrebicka, 1961; Thiele-Pfeiffer, 1980; Mohr, 1984). All of these pollen grains have been included in the species *Araliaceoipollenites edmundi* (Potonié) Potonié = *Tricolporopollenites edmundi* (Potonié) Thomson and Pflug. In order to emphasize the morphological variability of the pollen commonly assigned to the edmundi morphotype, Konzalová et al. (in Stuchlik et al., 2014) created the genus *Edmundipollis*. Its type species is *E. edmundi*, and the holotype specimen was illustrated by Potonié (1931: pl. 1, fig. V53a), and re-illustrated by Potonié (1951a, b).

Konzalová et al. (in Stuchlik et al., 2014) have assigned grains of variable morphology at species level to

the genus *Edmundipollis*. The diagnostic features of the species include differences in the layout of colpi and pores relative to each other, and variable thickness, structure and surface sculpture of the exine. Some of the distinguished types have been previously pointed out by Mamczar (1960) and Doktorowicz-Hrebicka (1961) as forms within the species *Pollenites edmundi*.

Detailed analysis of the similarities between the fossil pollen grains of the edmundi morphotype (*Edmundipollis*) and the pollen grains of living plants indicates, as mentioned earlier by Mamczar (1960, 1962), that they are most similar to pollen of plants from the Araliaceae and Cornaceae/Mastixiaceae families. Fossil pollen grains with a hexagonal outline, but with a completely different structure of colpi and pores, were also assigned to the edmundi morphotype by Doktorowicz-Hrebicka (1961). These grains are most probably related to the systematically distant Anacardiaceae family (Fig. 1).

## RESULTS

Following the primary concept of Mamczar (1962), the edmundi morphotype was also arranged in two groups. The first includes forms resembling pollen of the widely understood family Cornaceae (Fig. 2A), to which *Mastixia* was also assigned. These features are visible in light microscope (LM) as thinning of the exine along the colpi and alongate pores, forming an H-shaped unit in the equatorial area (Ferguson, 1977). Addi-

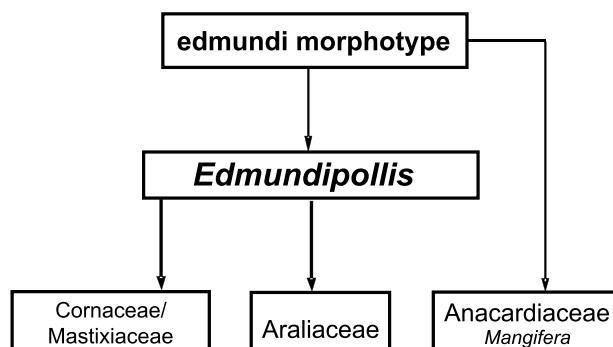


Fig. 1. Botanical relationships of the edmundi morphotype

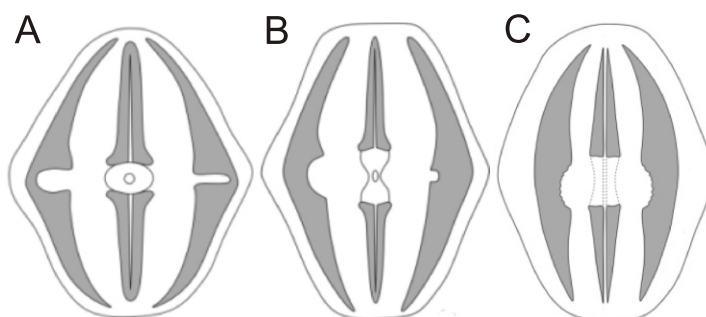


Fig. 2A – *Edmundipollis* – Cornaceae type, schematic outline of pollen grain and the H-shaped colpi-pores aperture unit at the equator; B – *Edmundipollis* – Araliaceae type, schematic outline of pollen grain and the double funnel-shaped colpus-pores aperture unit at the equator; C – *Tricolporopollenites mangiferoides* – schematic outline of pollen grain

tionally, the pollen of this family has a distinctly developed columella layer of the exine, of equal height on the equator and on the apocolpia. The exine surface visible in LM is scabrate. In SEM images, meridional swellings of the exine are visible, particularly in the equatorial area, and the surface is densely covered by irregularly shaped scabra of unequal width.

The second group includes forms displaying features of Araliaceae pollen, i.e. endo- and exopores incised in colpi in the equatorial area, which are the double funnel-shaped aperture unit (Fig. 2B). Additionally, the collumella layer of the exine in the apocolpium is evidently higher than in the equatorial area. The exine surface visible in LM is reticulate, and the lumina size increases towards the poles. On SEM images, meridional swellings of the exine with deeply incised colpi are visible, the exine surface is reticulate, the lumina sizes are fine and rather regular, and the muri are high and often wider than the lumina size.

Apart from the classical edmundi morphotype (*Edmundipollis*), often yield pollen with a similar morphology, were described by Doktorowicz-Hrebnička (1961) as *Pollenites edmundi* forma tenuis. This type of pollen grains with a hexagonal outline slightly resembles the edmundi morphotype, but differs in the lack of meridionally arranged exine swellings and a completely different development of colpi and pores. In Stuchlik et al. (2014), the pollen was described as *Tricolporopollenites mangiferoides* Słodkowska and compared to pollen of the extant *Mangifera* of the Anacardiaceae family (Fig. 2C).

Features resembling those in pollen of the Araliaceae and Cornaceae can easily be identified in the fossil edmundi morphotype. Fossil pollen grains usually do not have clear properties of the pollen of extant plants, such as the presence of meridional swellings of the exine, a hexagonal or rhomboidal

outline, and a very thick exine. The genus *Edmundipollis* is a typical morphogenus, without reference in the name of the botanical affinity. Smaller units were established within it, regarded as morphospecies, which have been compared to the pollen of genera and species of extant plants.

A comparative table has been prepared for the distinguished species of *Edmundipollis* in order to present the morphological differences between them (Table 1).

*Cornaceapollis satzveyensis* (Fig. 3A) is compared to the pollen of some species of *Mastixia* (Thiele-Pfeiffer, 1980), but does not represent the edmundi morphotype and is considered as the fossil representative of the Cornaceae, because it has features characteristic of this family. Despite the lack of similarity to the edmundi morphotype, it has been included in the comparative table of the species of *Edmundipollis* assigned to the family Mastixiaceae.

The species *Edmundipollis edmundi* (Fig. 4A, B) and *E. mastixioides* (see Fig. 6A), which have classical features of the edmundi morphotype, have been assigned to the family Mastixiaceae.

*Diplopanax* Hand.-Mazz. with two extant species (*D. stachyanthus* – Fig. 4C, D and *D. vietnamensis*) inhabit the wet tropical mountains of Vietnam and southern China. These are broad-leaved evergreen trees with woody fruits. It was originally described as only a single species of *D. stachyanthus* included in the family Araliaceae. *Diplopanax* was later discovered to be congeneric with *Mastixicarpum* Chandler, a genus known only from fossil seeds and included in the family Mastixiaceae (Eyde and Xiang, 1990). *Mastixicarpum* are found in the Northern Hemisphere from the uppermost Cretaceous to the Middle Miocene (Mai, 2000), and were an integral component of the

Table 1

**A comparative table for the species of *Cornaceapollis satzveyensis*, *Edmundipollis*, *Araliaceipollenites amplus* and *Tricolporopollenites mangiferoides* in order to present the morphological differences between them**

Species	Size polar/equatorial diameter	Outline and shape by P/E	Apocolpium	Colpi	Pores	Colpi/pores aperture unit	Sculpture
<i>Cornaceapollis satzveyensis</i> (Pflug) Ziemińska-Tworzydło	43–54 /28–40 µm	oval prolate	narrowly rounded	deep, arcuate, not bent at equator, lack of meridional swellings	lalongate	H shaped colpi/pores aperture unit	scabrate
<i>Edmundipollis edmundi</i> (Potonié) Słodkowska and Ziemińska-Tworzydło	40–50 /28–42 µm	hexagonal-rhomboidal subprolate to prolate	flat	long, deep incised into meridional swellings	lalongate, oval 10/5 µm	H shaped colpi/pores aperture unit	scabrate
<i>E. mastixioides</i> Słodkowska and Ziemińska-Tworzydło	40–50 /22–47 µm	rhomboidal, nearly circular oblate/spheroidal to prolate /spheroidal	broadly rounded	meridional swellings with deep-incised long colpi parallel to the outline	lalongate, oval 12/5 µm	H shaped colpi/pores aperture unit	scabrate
<i>Araliaceipollenites amplus</i> Słodkowska	45–60 /36–47 µm	broadly oval subprolate	small, narrow rounded	long, deep, arcuate, lack of meridional swellings	circular 5–10 µm in diameter	double funnel-shaped aperture unit	reticulate
<i>E. megagranatus</i> (Mamczar) Słodkowska and Ziemińska-Tworzydło	45–58 /38–42 µm	oval – rhomboidal subprolate to prolate	broadly rounded	arcuate, deep incised into meridional swellings	lalongate, nearly circular 5–7 µm in diameter	double funnel-shaped aperture unit	rugulate-reticulate
<i>E. grossularius</i> (Potonié) Słodkowska and Ziemińska-Tworzydło	35–45 /27–35 µm	hexagonal – rhomboidal subprolate to prolate	flat to slightly rounded	deep incised into meridional swellings	nearly circular 5–8 µm in diameter	double funnel-shaped aperture unit	reticulate
<i>E. vitiosus</i> (Mamczar) Słodkowska and Ziemińska-Tworzydło	37–44 /30–37 µm	hexagonal – rhomboidal subprolate	flat to slightly pointed	arcuate, deep incised into meridional swellings	nearly circular up to 5 µm in diameter	double funnel-shaped aperture unit	microreticulate
<i>Tricolporopollenites mangiferoides</i> Słodkowska	36–52 /26–32 µm	hexagonal – rhomboidal prolate to perprolate	flat to broadly rounded	arcuate, parallel to outline, lack of meridional swellings	lalongate, oval 5/12 µm	lack of specific design of aperture unit	scabrate

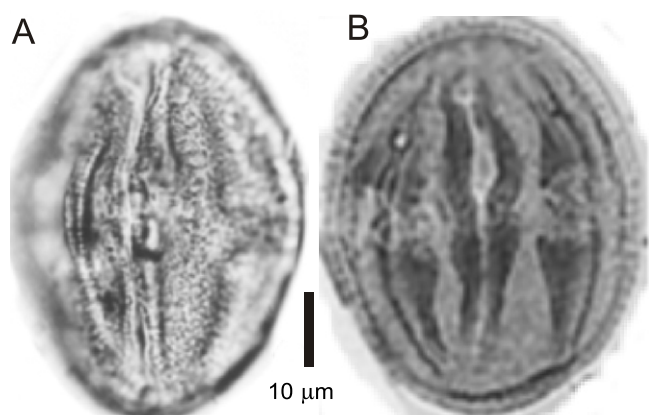


Fig. 3A – *Cornaceaepollis satzveyensis* fossil pollen; B – *Mastixia* sp., extant pollen; C – *Mastixia arborea* (Wight) C.B. Clarke extant flowers (<http://florakarnataka.ces.iisc.ernet.in/>)

*Mastixia*-like paratropical broad-leaved evergreen vegetation, about 65 to 15 Ma.

*Diplopanax stachyanthus* (see Fig. 6C) evergreen trees, up to 25 m tall, often grows in warm and moist evergreen broad-leaved forests on mountain slopes or in valleys (1300–1900 m a.s.l.) in Chinese provinces (Hunan, Guangdong, Guangxi, Yunnan and Guizhou) and northern Vietnam. Its distribution area is characterized by relatively high elevations in warm and moist climate.

*D. vietnamensis* is discovered in southern Vietnam as co-dominant in wet, evergreen broad-leaved tropical mountain forest (Averyanov and Hiep, 2002).

Fossil seeds of *Diplopanax limnophilus* (Unger) Czaja = *Mastixicarpum limnophilus* (Ung.) Kirh. (Fig. 5) are known from Middle Miocene localities in Europe, e.g. Wiesa in Germany (Mai, 1967), South Bohemia in the Czech Republic (Ševčík et al., 2007), and Turów (coll. Museum of the Earth PAS) and Wieliczka (Łańcucka-Środoniowa and Zastawniak, 1997) in Poland.

*Mastixia* Blume (Fig. 6B, C) is a genus of about 19 species of evergreen trees. Nowadays often grows in evergreen broad-leaved forest. Its range extends from India through south-east Asia and New Guinea to the Solomon Islands (Kubitzki, 2004).

*Mastixia arborea* (Fig. 6C) is found in India and Sri Lanka. Trees up to 20 m tall. Often grows in evergreen broad-leaved forests, up to 1900 m a.s.l. *M. tetrandra* (Fig. 6B) is endemic to Sri Lanka. The trees form sub-canopy level in evergreen lowland forests (Premathilake and Nilsson, 2001).

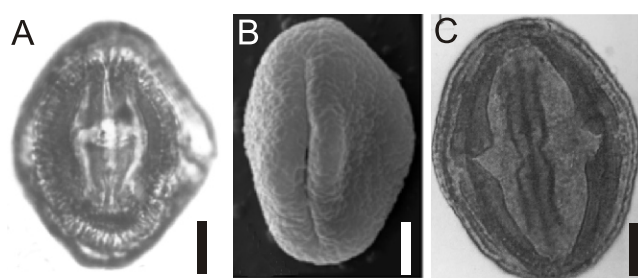


Fig. 4A, B – *Edmundipollis edmundi* fossil pollen (A – LM, B – SEM); C, D – *Diplopanax stachyanthus* Hand.-Mazz. [C – extant pollen LM (Wang et al., 1995: pl. 23, fig. 1); D – extant plant, twig with fruits (<http://especies.ac.cn/pages/1919#media-images>); scale bar – 10 µm



Fig. 5. Fossil seeds of *Mastixicarpum limnophilum* (Ung.) Kirh. = *Diplopanax limnophilus* (Ung.) Czaja

“Turów” open pit – Museum of the Earth PAS collection

A classical fossil representative of the Araliaceae family that does not represent the edmundi morphotype is *Araliaceoipollenites amplus* (Fig. 7A) compared with *Dendropanax morbifer* H.Lév pollen.

*Dendropanax* Decne and Planch is a genus consisting of 92 species of evergreen trees and shrubs. They are native to Central and South America, eastern Asia and the Malay Peninsula. *Dendropanax morbiferus* H.Lév. (Fig. 7B, C) – evergreen trees up to 15 m tall, an endemic species found at the sea shore and islands in the southwestern region of South Korea (Eyde and Xiang, 1990).

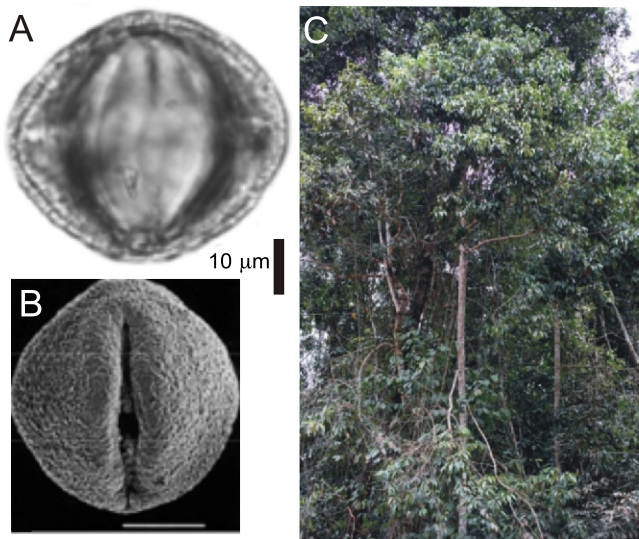


Fig. 6A – *Edmundipollis mastixioides* fossil pollen; B – *Mastixia tetrandra* (Wight) Clarke extant pollen SEM (Premathilake and Nilsson, 2001); C – *M. arborea* (Wight) Clarke – extant plant ([http://www.biotik.org/laos/species/m/maspe/maspe\\_en.html](http://www.biotik.org/laos/species/m/maspe/maspe_en.html))

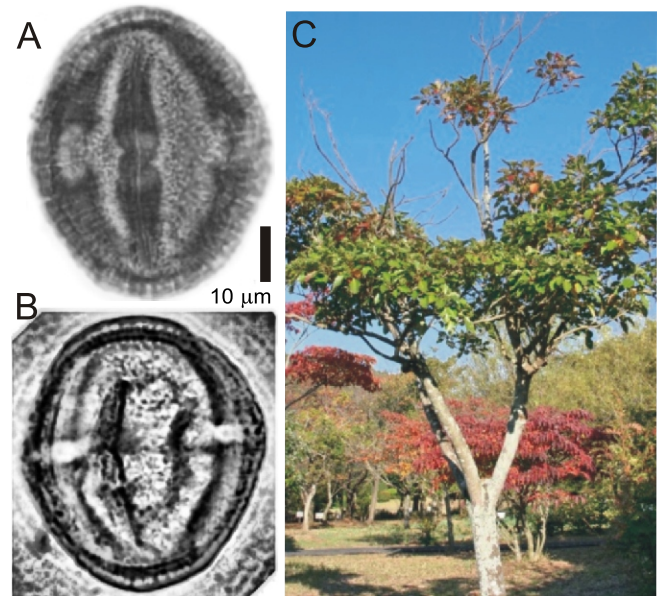


Fig. 7A – *Araliaceipollenites amplus* fossil pollen; B, C – *Dendropanax morbiferus* H.Lév (B – extant pollen, C – extant plant, <http://www.doopedia.co.kr/photobox/comm/community.do?>)

The species *Edmundipollis megagranatus* (Fig. 8A, B), *E. grossularius* (Fig. 9A, B) and *E. vitiosus* (Fig. 10A, B), which have features typical of the edmundi morphotype, have been assigned to the Araliaceae family.

*Aralia* L. is a genus consisting of 71 species, shrubs and small trees, distributed in eastern and southeastern Asia and the Americas. *A. elata* (Fig. 8C) is an upright deciduous small tree or erect large shrub growing up to 10 m in height on rich well-moistened slopes, 900–2000 m a.s.l. Native to far eastern Russia (Sakhalin, Manchuria and the Kuriles), East Asia – China, Korea, and Japan (Hokkaido, Honshu, Shikoku, Kyushu – Wikipedia, the free encyclopedia 11.02.2016).

*Schefflera* Forst. Evergreen trees, shrubs and lianas, sometimes epiphytic, growing 1–30 m tall, a pantropical genus of over 700 species, widely distributed in tropics and subtropics of both hemispheres. *Schefflera rhododendrifolia* (Fig. 9C, D), evergreen trees and shrubs that originate from high elevations of 2500–3200 m a.s.l., cold deciduous forests of India, Bhutan and Nepal ([http://www.efloras.org/florataxon.aspx?flora\\_id=2&taxon\\_id=250073459](http://www.efloras.org/florataxon.aspx?flora_id=2&taxon_id=250073459)).

*Fatsia* Dec. and Planch. – evergreen shrubs, up to 5 m in height, or small trees. Few species are native to the coastal forests of southern Japan, Taiwan and South Korea. *Fatsia japonica* (Fig. 10C, D) evergreen shrubs up to 5 m tall, native to Japan (Honshu, Shikoku and Kyushu islands).

*Tricolporopollenites mangiferoides* (Fig. 11A) slightly resembles the edmundi morphotype with respect to the hexagonal outline, but differs in all other morphological features (Fig. 2C). It is most similar to pollen of *Mangifera indica* from the Anacardiaceae family and this is likely its most probable botanical affinity.

*Mangifera* L. comprises 45 species; evergreen trees distributed in India and Indochina.

*Mangifera indica* L. (Fig. 11B–D) predominates in tropical lowland areas north and south of the equator, in southern Asia, especially eastern India, Burma and the Andaman Islands (<https://npgsweb.ars-grin.gov/gringlobal/taxonomydetail.aspx?23351>).

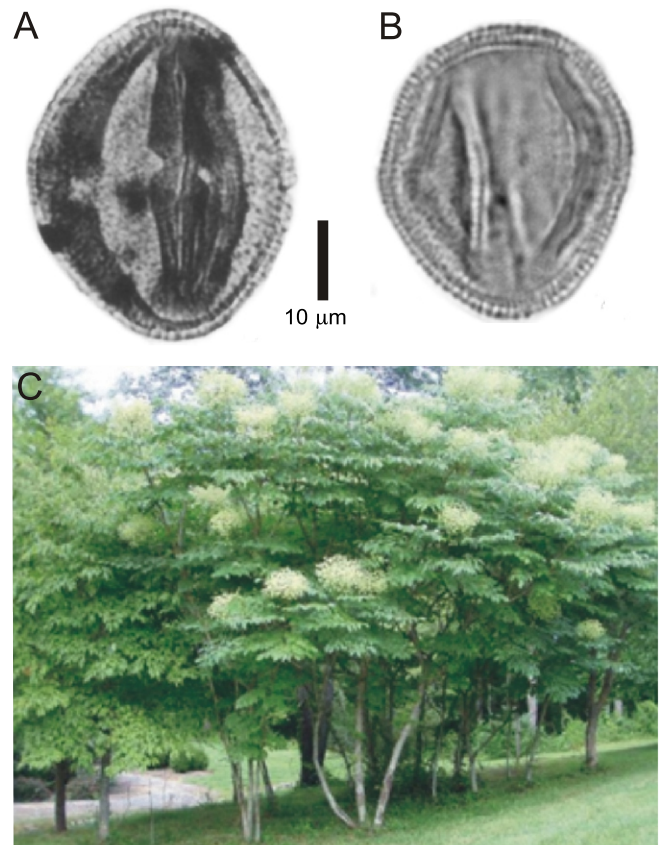


Fig. 8A – *Edmundipollis megagranatus* fossil pollen; B, C – *Aralia elata* (Miq.) Seem.; B – extant pollen; C – extant plant (Wikipedia, the free encyclopedia 11.02.2016)

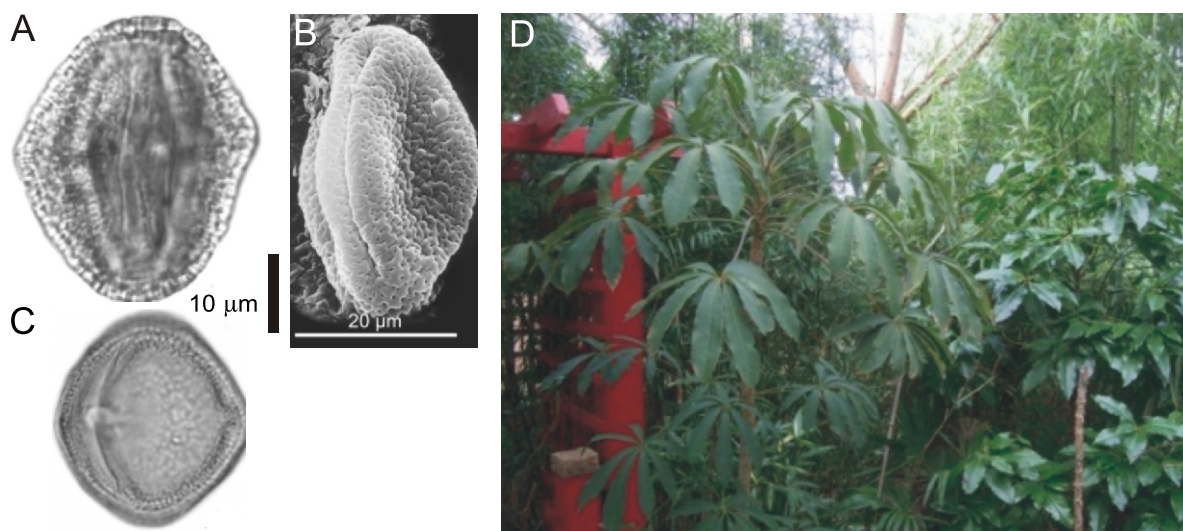


Fig. 9A, B – *Edmundipollis grossularius* fossil pollen (A – LM, B – SEM); C, D – *Schefflera rhododendrifolia* (Griff.) Frodin (C – extant pollen, D – extant plant, <http://1.bp.blogspot.com/>-)

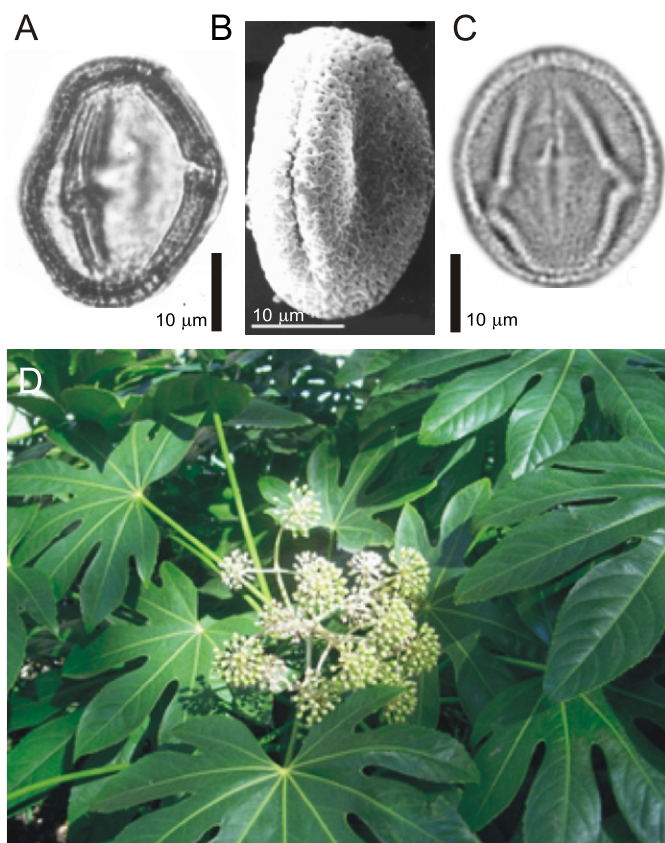


Fig. 10A, B – *Edmundipollis vitiosus*, fossil pollen (A – LM, B – SEM); C, D – *Fatsia japonica* (Thunb.) Dec. and Planch. (C – extant pollen; D – extant flowers, <http://1.bp.blogspot.com/>-)

## DISCUSSION

The pollen grains of the living species of *Mastixia* and the species of the Araliaceae, cited as comparative taxa, usually do not have a well-marked hexagonal outline, meridionally arranged swellings and a thick exine. Only the pollen of *Diplo-*

*panax*, to which *Edmundipollis edmundi* is compared, has most features of the *edmundi* morphotype. Based on this, their close similarity is assumed. Moreover, this similarity is emphasized by the presence of fossil seeds of *Mastixcarpum* in Cenozoic sediments, which are considered as seeds of the extant genus *Diplopanax* (Eyde and Xiang, 1990; Czaja, 2003).

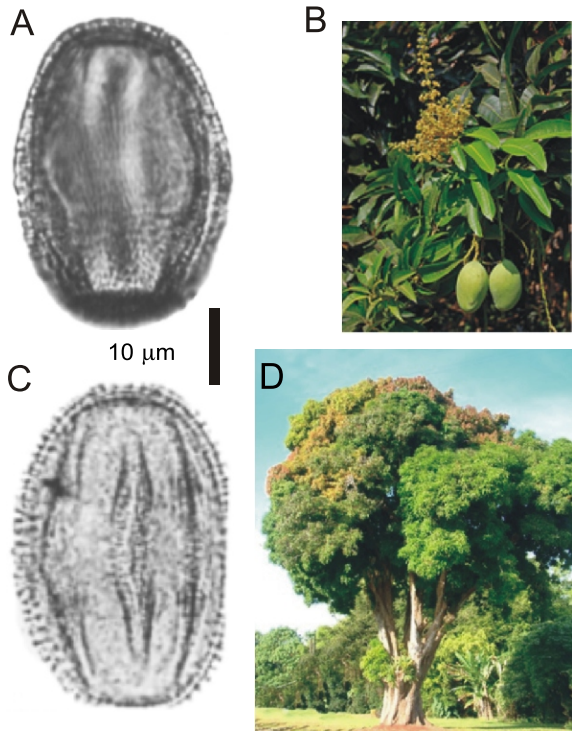
The study of pollen grains of the entire *Edmundipollis* genus is significant due to the affinities of only some of its species with *Mastixia*, as suggested in this paper.

Kirchheimer (1957), based on Mastixiaceae seeds in the brown coal sediments from Saxony, introduced the term “mastixia flora” as an indicator of particularly warm periods in the Neogene. This concept was developed by Mai (1967), who established Neogene floral zones, and confirmed them later (Mai, 1995) by indicating the presence of various species of *Mastixia* seeds. Other extinct genera related to *Mastixia*, e.g. *Eomastixia*, *Retinomastixia* and *Tectocarya*, also occur in the Miocene “mastixia flora”. The knowledge on their pollen is incomplete and they may be assigned to fossil species within the Cornaceae/Mastixiaceae.

All these extinct genera, determined based on fossil seeds, appear in the warm periods of the Paleogene and Neogene, but not later than in the Middle Miocene. Only the seeds of *Mastixia thomsonii* Mai are known from the earliest Pliocene (Mai, 1995, 2000). The plants described on the basis of fossil seeds from the Paleogene and Neogene, and including both extinct genera and the extant *Mastixia*, are considered to have been an integral component of the *Mastixia*-like paratropical broad-leaved evergreen vegetation of the Northern Hemisphere from the latest Cretaceous to the Pliocene (Mai, 1995).

Based on the comparison of the *Edmundipollis* species with the pollen of living genera from the Araliaceae and Mastixiaceae families, a relationship was constructed using the coexistence approach (Mosbrugger and Utescher, 1997; Utescher et al., 2014).

The chart (Fig. 12) was compiled using data from the NECLIME database on the mean annual temperatures for the genera and species of living plants, to the pollen of which the *Edmundipollis* was compared (Figs. 3B, 4C, 8B, 9C, 10C, 11C). The boundaries of the annual average temperature characteris-



**Fig. 11A – *Tricolporopollenites mangiferoides* fossil pollen; B–D – *Mangifera indica* L. [B – flowers and twig with fruits (Bekalo et al., 1996), C – extant pollen, D – extant plant]**

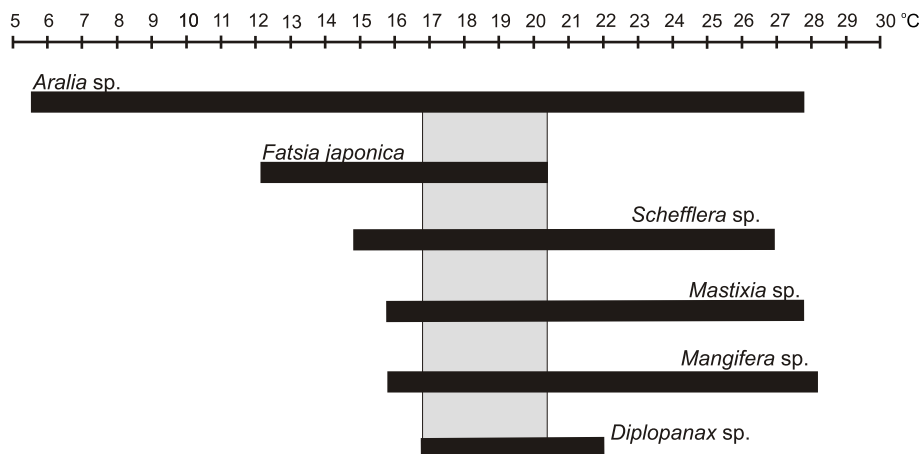
tic for discussed plants determine the range their co-existence of 16.5–20.5°C.

Mai (1995) suggested that the large number of thermophilic evergreen taxa in the warm phases of the Neogene indicates a mean annual temperature of 15–20°C. Such large amount of thermophilic plants in Neogene forests is observed until the Middle Miocene, whereas in the Late Miocene and Pliocene their number distinctly falls. According to the classical climate subdivision by de Candolle, referred to by Mai (1995: p. 433), this is the mesotherm zone with a subtropical and warm-temperate climate. According to contemporary data on climate zones the mean annual air temperature in the subtropical zone is within 20–24°C (<http://www.neclime.de/definitions.html>). This range of

mean annual temperature according to the chart by Utescher et al. (2009: fig. 3 and supplementary online materials 3) corresponds to Cfa–Cwa climate types existing in Central Europe throughout most of the time-span from the Late Eocene to Middle Miocene, and during a short-term phase in the later Tortonian in the Lower Rhine Basin (Utescher et al., 2000). Pollen flora described from the middle Eocene is characteristic of the Cfa–Cwa climate (Grímsson et al., 2016). According to the climate subdivision of Köppen, such values of the mean annual temperature are within C-type climates. This is a very warm and humid subtropical climate of the Cfa–Cwa subgroup (Kottek et al., 2006).

Chart, which include also the plants of lower temperature requirements in comparison to the above-mentioned ones (Fig. 12) from the Middle Miocene localities, point to a mean annual temperature around 17.5°C and indicate a warm-temperate group climate (Utescher et al., 2006). The above-presented differences between the mean annual temperature calculated only from the highly thermophilic components of Neogene forests (Fig. 12) and all its components show that, during their Neogene wide geographic range reaching Central Europe, both the extinct genera and the extant *Mastixia* and *Diplopanax* of the Mastixiaceae could have been slightly more tolerant to the mean annual temperature than at present. The current range of the two living genera of *Mastixia* and *Diplopanax* is a relict range and does not allow concluding on the common presence of very warm climate in the Miocene of Central Europe. Term of Central Europe is used within the meaning the Miocene palaeogeographic province located north of the Carpathians, where the climate was warm-temperate with average annual temperatures of 15–16°C. At the same time, south of the Carpathians, average annual temperatures ranged from 17 to 20°C (Jiménez-Moreno et al., 2008).

The occurrence of *Edmundipollis* and the distribution of its species indicate that the type species *E. edmundi* (comparable with *Diplopanax*) ended its range in the Middle Miocene of Central Europe. In Poland, its latest occurrence is at the Konin site (Mamczar, 1960), i.e. the first Mid-Polish lignite seam. From the Middle Miocene of Germany (Wackersdorf brown coal), Thiele-Pfeiffer (1980) described grains of *Tricolporopollenites edmundi* (pl. 12, figs. 11–15) and *Tricolporopollenites satzveyensis* = *Cornaceapollis satzveyensis* (pl. 12, figs. 16–21), comparable with *Mastixia* pollen. From the 2. Lausitz lignite seam, Sontag (1966) presented numerous photographs of *Tricolporopollenites ex gr. edmundi*, of which only four can be referred to the pollen of *Diplopanax* (*Edmundipollis edmundi* – pl. 48, fig. 4c, pl.



**Fig. 12. Mean annual temperature of NLRs of the edmundi morphotype based on <http://www.palaeoflora.de/>**

49, figs. 2a, 2b, 2c), one to *Mastixia* (*E. mastixioides* – pl. 48, fig. 4b), and the remaining pollen grains are representatives of the Araliaceae. [Konzalová \(1976\)](#) determined *E. edmundi* as *Araliaceipollenites edmundi* (pl. 16, figs. 1–3) from the Lower Miocene of the North Bohemian coal basin. Numerous sites of this type can be mentioned for Central Europe, but none of them is younger than Middle Miocene. This means that pollen of *E. edmundi* has its last occurrence in the Middle Miocene in terrestrial sediments of Central Europe. Representatives of the Mastixiaceae are not recorded in the Neogene of northern Europe ([Denk et al., 2011](#)).

## CONCLUSIONS

The morphological species *Edmundipollis edmundi* suggests a warm climate of subtropical Cfa–Cwa type. Correct as-

signment of *E. edmundi* is thus of basic significance for palaeoclimate reconstruction. Incorrect assignment leads to inappropriate climate conclusions. Various morphological forms of *Tricolporopollenites edmundi*, recovered from the Upper Miocene Inden Formation, have been compared to the modern reference taxa *Mastixia* (*Aralia*?) ([Ashraf and Mosbrugger, 1996: p. 86, tab. 2c](#)), and assigned to a palaeotropical element occurring between the Oligocene and Pliocene. All illustrated forms of this species ([Ashraf and Mosbrugger, 1996: pl. 6, figs. 14–19](#)) can be assigned to species of *Edmundipollis* belonging to the Araliaceae.

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