



Menatanthus mosbruggeri gen. nov. et sp. nov. – A flower with in situ pollen tetrads from the Paleocene maar lake of Menat (Puy-de-Dôme, France)

Dieter Uhl¹ · Khum N. Paudyal² · Sophie Hervet³ · Haytham El Atfy^{4,5}

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Abstract

The Paleocene Fossil-Lagerstätte Menat in France is well known for its wealth of outstandingly well preserved fossil insects and plants. Despite being known for more than a century, the palaeoflora, which is regarded as typical for the late Thanetian by some authors, has largely been neglected since the 1940s. New excavations and surveys yielded exceptionally well-preserved plant material, including a minute, heptamerous flower bearing in situ pollen tetrads, comparable to tetrads of the modern ericacean genus *Kalmia* L. in its anthers. The only known modern ericacean genus which is characterised by heptamerous flowers is *Bejaria* Mutis ex L., a basal relative of the tribe Phyllodoceae within Ericaceae, which also includes the genus *Kalmia* in a relatively basal position. However, heptamerous flowers also occur very rarely (mostly interpreted as teratologies) in a number of other modern Ericaceae, but also in various other modern angiosperm families. Due to the unique combination of a heptamerous flower with *Kalmia*-type pollen tetrads within the anthers, the new taxon *Menatanthus mosbruggeri* gen. nov. et sp. nov. is erected. The lack of morphological data from the flower itself and the fact that comparable pollen tetrads can be produced by a number of modern families, however, prevent an assignment of the new taxon to any known angiosperm family.

Keywords Fossil-Lagerstätte · *Kalmia*-type pollen · Heptamerous flower · *Bejaria* · *Ericipites ericius*

Introduction

The sedimentary deposition in many fossil maar lakes represents excellent archives for a diversity of continental biota. For macrofloras, well-known examples from the Paleogene of

Europe comprise the Paleocene maar lake of Menat (e.g. Wedmann et al. 2018), the Eocene maar lakes of Messel (e.g. Wilde 2018) and Eckfeld (e.g. Frankenhäuser and Wilde 1993; Wilde and Frankenhäuser 1993, 1998), as well as the late Oligocene maar lakes of Enspel (e.g. Köhler and Uhl 2014; Uhl 2015; Uhl and Poschmann 2018), Rott (e.g. Mosbrugger 1996; Winterscheid et al. 2018), and Kleinsaubernitz (e.g. Walther 1999).

The Paleocene deposits of Menat in France (Fig. 1) are of considerable interest for understanding the development of terrestrial ecosystems in Europe, as this maar lake provides one of the earliest European Fossil-Lagerstätten following the mass-extinction event at the Cretaceous-Paleogene boundary (e.g. Wappler et al. 2009; Wedmann et al. 2018). The locality is known for its unique wealth of excellently preserved fossil insects (e.g. Piton 1940; Wedmann et al. 2018 and citations therein) and its macroflora (e.g. Laurent 1912, 1919; Piton 1940), although the fossil flora is in a desperate need of a modern taxonomic revision (cf. Wedmann et al., 2018).

Here we describe a minute fossil flower with in situ pollen tetrads of unknown affinity as the new taxon *Menatanthus mosbruggeri* gen. nov. et sp. nov. and discuss its systematic

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✉ Dieter Uhl
dieter.uhl@senckenberg.de

¹ Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Senckenberganlage 25, 60325 Frankfurt am Main, Germany

² Central Department of Geology, Tribhuvan University, Kirtipur, Kathmandu, Nepal

³ Association Paléovergne, Musée de Menat, Mairie de Menat, 63560 Menat, France

⁴ Institut für Geowissenschaften, Eberhard Karls Universität Tübingen, Sigwartstraße 10, 72076 Tübingen, Germany

⁵ Department of Geology, Faculty of Science, Mansoura University, 35516 Mansoura, Egypt

significance. The flower is a significant addition to the flora known mostly from fossil leaves.

Material and methods

The flower described here comes from finely laminated, bituminous, brownish to dark grey sediments exposed at the locality “stream site” (sensu Wedmann et al. 2018) within the village of Menat. It was collected during a palaeontological survey in 2014 and is curated at the Musée de Menat under collection numbers MNT-14-7537a-d.

The sediments exposed in this locality belong to the sedimentary infilling of a former maar lake (Vincent et al. 1977), which has been dated as being of (late) Paleocene age (cf. Wedmann et al. 2018). For further details on the source locality and strata, see Wedmann et al. (2018).

Macrophotographs of the flower were taken using a Leica M80 stereo microscope equipped with a Leica EC3 digital camera.

The studied samples were prepared following standard palynological extraction techniques (e.g. El Atfy et al. 2017). For this, an aliquot of 15–20 g of each sample was disintegrated to get rid of carbonates and silicates with treatment of 37% HCl and 45% HF, respectively. Thereafter, sieving was done to remove unwanted organic particles using a brass sieve (125 µm), followed by nylon mesh (mesh 10 µm). Generally, no oxidant acids were employed. The residues were routinely washed under plenty of distilled water until neutralized.

Afterwards, the single-grain technique (Ferguson et al. 2007) was applied, as follows: glycerine is added to the organic residue, with a pipette a drop of this mixture is transferred to a glass slide. Using a dissecting needle to which a nasal hair has been affixed, those grains which are of particular interest are brushed to the edge of the glycerine, where they can be located, adhered to the tip of the hair, and transferred to another glass slide with a fresh drop of glycerine for photography under a light microscope (LM). As no coverslip is used, it is possible to move the grains and thus to photograph individual grains in various orientations. LM microphotographs were taken using an Olympus BX41 microscope fitted with an Olympus SC50 digital camera. Thereafter, the palynomorphs were transferred to SEM stubs to which a drop of absolute ethanol has been added to remove all glycerine traces. Additionally, a small piece of one of the pollen bearing anthers was removed from the flower and mounted on a SEM stub. Subsequently, all the stubs were sputter-coated with gold-platinum and analysed with the aid of a JEOL JSM 6490 LV Scanning Electron Microscope (SEM; accelerator current 20 kV) at the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Germany.

Systematic palaeobotany

Angiospermae

Eudicots

Pentapetaleae

Incertae sedis

Menatanthus gen. nov. D.Uhl, Paudyal and El Atfy

Derivation of generic name: After the village of Menat, Puy-de-Dôme, France, where the holotype was discovered and the Greek *ανθος* (in the Latinised form *anthus*), meaning flower.

Generic and specific diagnosis: Heptamerous, actinomorphic flower, with seven lobed corolla (or calyx) and 14 stamens. Perianth lobes (petals or sepals) elliptic with slightly acute apices. Anthers elliptical, about 3 times longer than wide, containing two pollen sacs with permanent pollen tetrads of the *Kalmia*-type in situ.

Type species designated here: *Menatanthus mosbruggeri* sp. nov. D.Uhl, Paudyal and El Atfy

Menatanthus mosbruggeri sp. nov. D.Uhl, Paudyal and El Atfy (Figs. 2, 3, 4)

Derivation of specific name: Named after Prof. Dr. Volker Mosbrugger, a German palaeobotanist and former director general of the Senckenberg Gesellschaft für Naturforschung, Germany, in honour of his numerous contributions to Cenozoic palaeobotany and palaeoclimatology, as well as natural history in general.

Specific diagnosis: See combined generic and specific diagnosis.

Holotype: MNT-14-7537a; figured here in Fig 2a,c.

Type locality: “Stream site” sensu Wedmann et al. (2018) in the village of Menat, Puy-de-Dôme, France.

Type horizon and age: Paleocene (Thanetian) infill of the maar exposed at the village of Menat, Puy-de-Dôme, France.

Description

Macromorphology of the flower

Fig. 2a-c

Actinomorphic flower, heptamerous. Perianth lobes in a whorl of seven petals or sepals, free or only basally fused, elliptic with slightly acute apices, 1.5–1.6 mm wide and approx. 3–3.5-mm long. Perianth Androecium consisting of 14 stamens, probably arranged in two whorls. Filaments not seen but inferred by anther position to be free, and relatively short. Anthers elliptical, about 3 times longer than wide, dehiscent by slits (?) containing two pollen sacs, 1.5–1.6 mm long, bearing densely clustered, permanent pollen tetrads of yellow colour.

Due to the compression of the organic substance, no details of the gynoecium are distinguishable. Also, it is not possible to decide whether the perianth is valvate or imbricate.

Remarks: Due to the preservation of the specimen, it is not clear whether the perianth lobes seen in this flower represent petals or sepals. In the authors' opinion, they likely represent petals, as the organic layer is rather thin, and no trace of these organs can be seen on the counterpart MNT-14-7537b of the holotype (not shown here). Under this interpretation, we infer that the sepals may be much smaller and hidden in the featureless organic mass in the centre of the flower. Also, in comparison to fossil flowers from Lagerstätten with a comparable preservation like Messel or Enspel (cf. Schaarschmidt 1984; Uhl 2015), it would be expected that the sepals would appear more solid consisting of a more robust organic layer. But as it is, there is no definitive proof for an interpretation as petals. Although it is not possible to observe where the filaments of the anthers originate, it seems likely that they are diplostemonous (or obdiplostemonous), as 14 anthers and 7 petals or sepals can be observed.

Pollen morphology

Fig. 2d–e, Fig. 3a–f, Fig. 4a–d

LM: Pollen are arranged in permanent tetrads; tetrahedral and rarely decussate and slightly lobed in outline; tetrad size (maximum diameter) ranges between 25 and 30 μm ($N = 50$); pollen tricolporoidate/tricolporate; scabrate.

SEM: Exine sculpture moderately to coarsely rugulate with distinct fossulae, rugulate pattern less pronounced (less and shallower fossulae) around the colpi, rugulae smooth. Margo tectate.

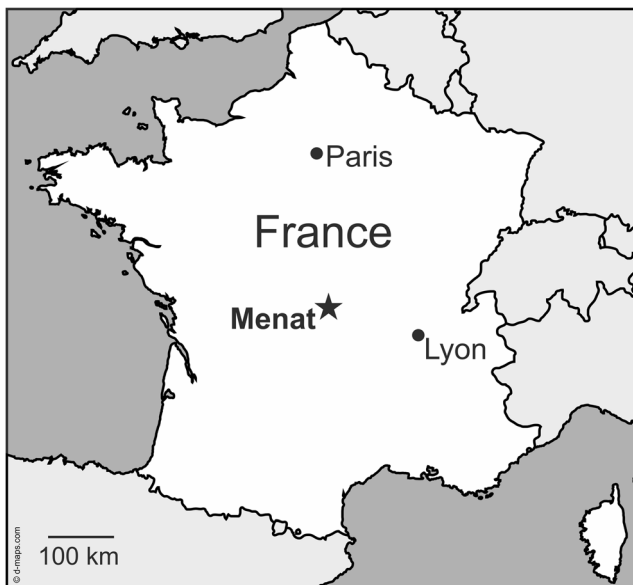


Fig. 1 Map of France showing the geographic position of Menat (source: <http://d-maps.com/m/europa/france/france/france09.gif>)

Remarks: The morphological details of the retrieved pollen that can be observed with LM and SEM are very similar to the pollen of several modern species of the Ericacean genus *Kalmia* L., especially *K. angustifolia* L. and *K. polifolia* Wengen. (Sarwar and Takahashi 2012), as well as to fossil pollen tetrads from the Eocene of the Borken coal field in Germany described as *Kalmia*-type by Hofmann and Gregor (2018) as well as Hofmann (2018). Although a tectate margo has not been described or illustrated in these studies, it is known from pollen of modern *Kalmia procumbens* (L.) Gift, Kron and P.F. Stevens ex Galasso, Banfi and F. Conti (Halbritter and Berger 2018). Viscin threads, which are present in some modern species of *Kalmia* (Sarwar and Takahashi 2012; Halbritter and Berger 2018), have not been observed in the fossil tetrads from Menat.

Similar tetrads have also been found in palynological samples prepared from the surrounding sediment of the same slab, as well as from other samples above and below the layer containing the flower at the locality “stream site” (sensu Wedmann et al. 2018) in the village of Menat.

Discussion

Although fossil flowers are rare as compared to fossil leaves, wood and carpological remains (e.g. Collinson 2011), remains of flowers (i.e. compressions and impressions) are well known from a number of Paleogene and Neogene lake deposits. Examples of such lake deposits with flowers preserved from Central Europe include Messel (Eocene: Schaarschmidt 1984; Schaarschmidt and Wilde 1986), Eckfeld (Eocene: Frankenhäuser and Wilde 1993), Enspel (Oligocene: Uhl 2015), Rott (Oligocene: Weyland 1937, 1938; Mosbrugger 1996), and Öhningen (Miocene: Heer 1855, 1856, 1859; Teodoridis and Kvaček 2005). Fossil flowers from the Paleocene deposits of Menat have previously been mentioned and illustrated by Laurent (1912) and Piton (1940), but so far no detailed descriptions and in-depth analyses of the taxonomy or systematics of these remains have been provided.

The in situ pollen tetrads, isolated from the anthers, show great similarities with tetrads of the modern Ericacean genus *Kalmia* L., which has a modern distribution mainly in North America (Southall and Hardin 1974). The pollen morphology of a number of modern *Kalmia* species was analysed by means of LM and SEM by Sarwar and Takahashi (2012) and Halbritter and Berger (2018). According to these authors, the analysed species are stenopalynous, with medium-sized, 3-colpor(oid)ate, oblate pollen with a rugulate exine sculpture. Like in many other Ericaceae, pollen is released in tetrahedral tetrads. Viscin threads, a typical feature of many Ericaceae, are present in some, but not all, species of *Kalmia* (Halbritter and Berger 2018; Sarwar and Takahashi 2012). This fits

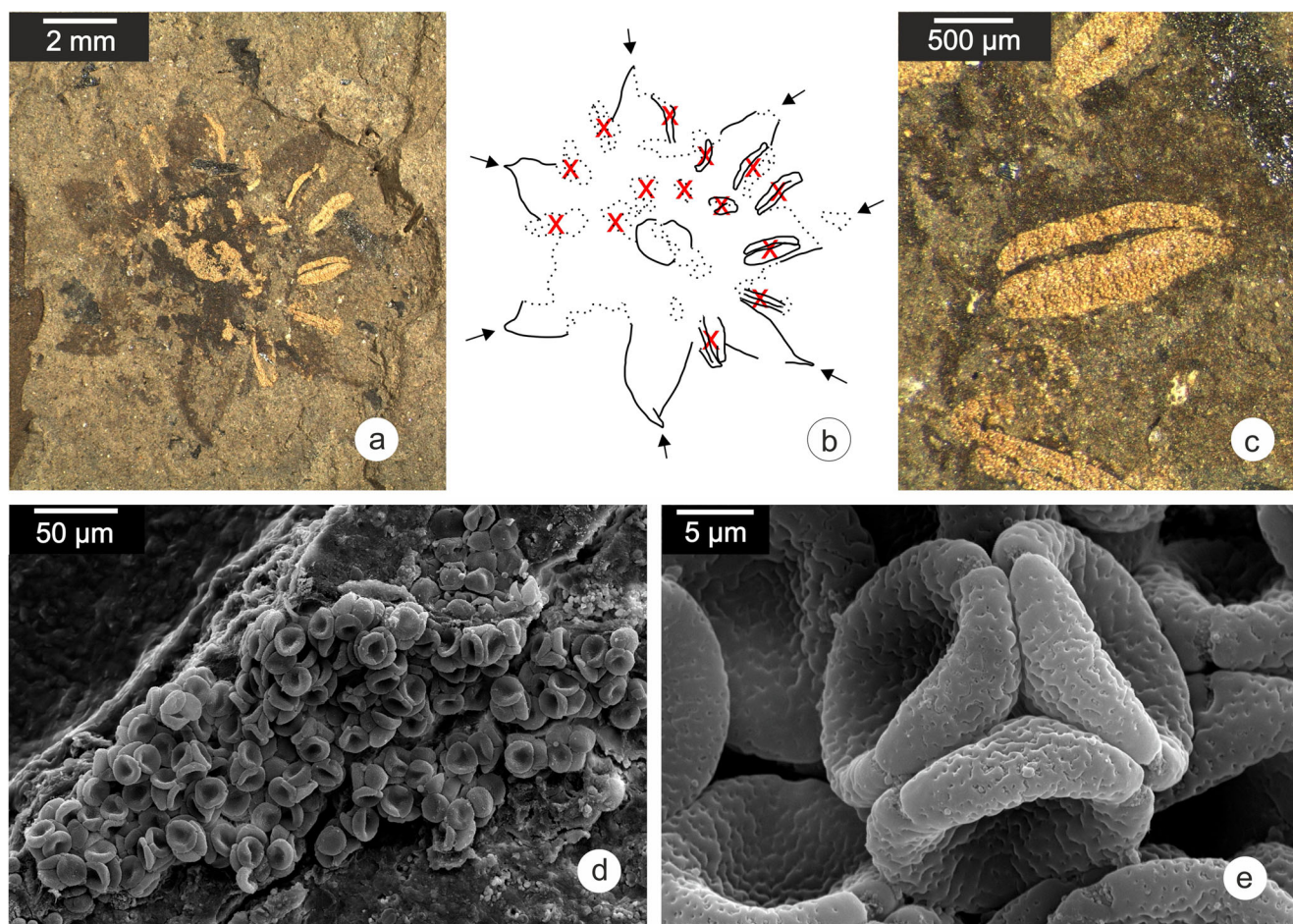


Fig. 2 *Menatanthus mosbruggeri* nov. gen. et nov. sp. flower with in situ pollen from Menat. **a** Overview of the heptamerous flower (holotype MNT-14-7537a). **b** Sketch drawing of the flower showing the most conspicuous morphological characters. **c** Enlargement of a single

anther, with in situ pollen. **d** SEM images of in situ pollen tetrads within an anther (MNT-14-7537c). **e** Enlargement of an individual tetrad from (c)

exactly to the pollen tetrads, isolated from the anthers of the here described flower from Menat.

The genus *Kalmia* L. consists of seven to eleven extant species, endemic to Northern America and Cuba (e.g. Ebinger 1974; Southall and Hardin 1974; Judd 1995; Stevens et al. 2004). Ebinger (1974) regarded *Kalmia* as “a relatively primitive member of the Ericaceae”. It is placed in the tribe Phyllodoceae Drude, whose members are usually evergreen plants with buxoid or ericoid leaves (Ebinger 1974). Like many other Ericaceae, the genus is characterised by pentamerous flowers, with a sympetalous corolla and a synsepalous calyx.

So far only few macrofossils have been related to *Kalmia*, and all of these records originate from Central Europe, i.e. from early to middle Miocene coal seams in Lusatia, Germany (Litke 1966; Mai 1995). The hitherto oldest known record of *Kalmia*-type pollen tetrads was described from the Eocene of the Borken coalfield in Hesse, Germany (Hofmann 2018). From this locality, this pollen type had previously been identified as *?Ericipites callidus* based only on LM (Hottenrott et al. 2010), whereas a combined LM and SEM

study revealed close similarities to pollen tetrads of modern *Kalmia* (Hofmann and Gregor 2018; Hofmann 2018).

The LM investigation shows that the pollen tetrads from Menat correspond to the genus *Ericipites* Woodhouse 1933 and particularly resemble *Ericipites ericius* (R. Potonié 1931) R. Potonié 1960, a taxon which was mentioned and illustrated earlier by Kedves (1982) from the Paleocene deposits of Menat. A palynological sample taken from the edge of the flower bearing rock specimen, some centimetres away from the flower, as well as samples from rock specimens originating from positions well above and below the layer from which the flower originates, yielded morphologically similar pollen tetrads assignable also to *Ericipites ericius*. Thus it seems unlikely that the occurrence of pollen tetrads within the anthers reflects immature tetrads.

Ericipites ericius has been recorded from Paleocene up to Pliocene deposits and is regarded as an arctotertiary floristic element (Ziemińska Tworzydło 1996), whereas other species assigned to the genus *Ericipites* were already widespread in the Northern Hemisphere during the Late Cretaceous (Kedves 1988).

Fig. 3 Pollen tetrads of *Menatanthus mosbruggeri* nov. gen. et nov. sp., isolated from anthers (MNT-14-7537d). **a** SEM image of a cluster of tetrads isolated by single-grain technique. **b** LM image of the same cluster of tetrads as shown in (a). **c** SEM image of an individual tetrahedral pollen tetrad isolated by single-grain technique. **d** LM image of the same cluster of tetrads as shown in (c). **e** SEM image of an individual decussate and slightly lobed pollen tetrad isolated by single-grain technique. **f** LM image of the same cluster of tetrads as shown in (e)

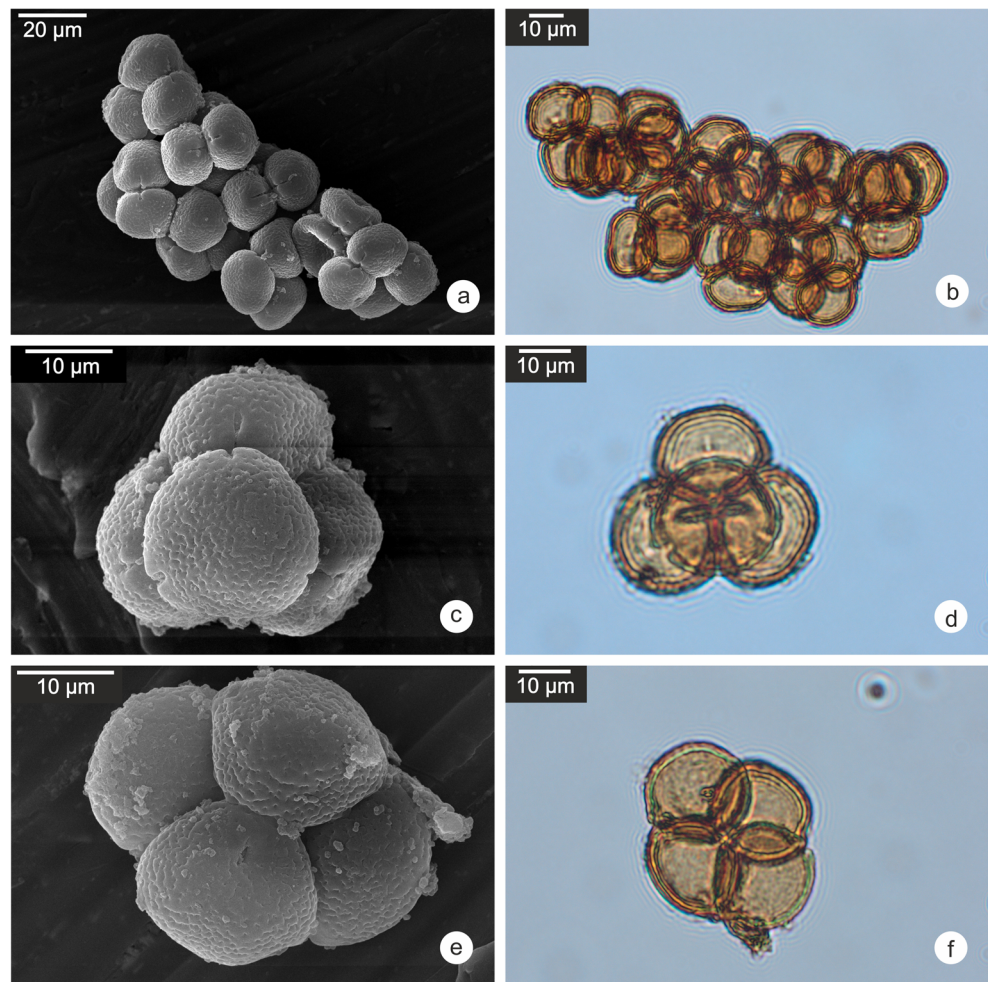
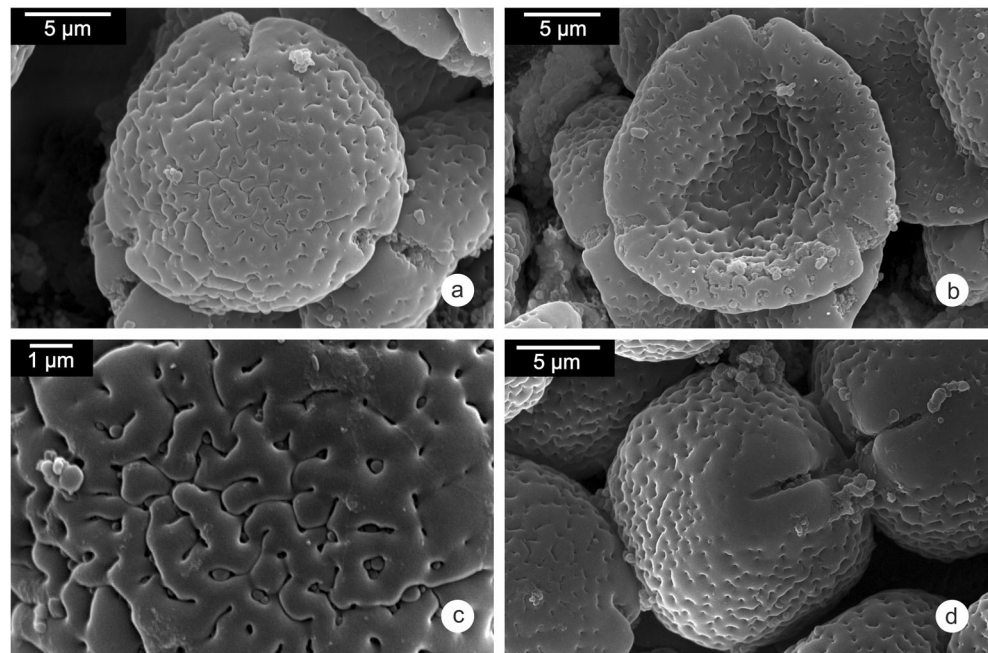


Fig. 4 Pollen of *Menatanthus mosbruggeri* nov. gen. et nov. sp. from anthers (MNT-14-7537c). **a** SEM-image of a single in situ pollen. **b** SEM image of a single in situ pollen. **c** Detail of surface structure (enlargement from (a)). **d** Detail of isolated cluster of pollen tetrads (shown in Fig. 3a) showing details of the rather smooth colpi and the tectate margo



Thiele-Pfeiffer (1980) suggested the modern genera *Arctous* Niedenzu, *Calluna* Salisb., *Erica* L., *Gaultheria* L., *Ledum* L., *Lyonia* Nutt., *Rhododendron* L., *Vaccinium* L., and other genera within Ericaceae as potential source taxa of *E. ericius*; nonetheless, an origin from a totally extinct ericacean genus also cannot be excluded. However, according to Erdtman (1971), morphologically comparable tetrads occur also within different taxa included in Empetraceae, Epacridaceae, and Pyrolaceae. Additionally, Geeraerts et al. (2009) reported the occurrence of permanent tetrads in Ebenaceae (i.e. *Diospyros mannii* and *D. longifolia*). As stated above the morphology of the recorded pollen tetrads from Menat corresponds very closely to pollen of modern *Kalmia*. Therefore, an assignment of the flower to Ericaceae seems possible, but an unequivocal assignment is not possible based on the pollen tetrads alone. It is also not possible to conclude that other occurrences of *Ericipites ericius* (and *Ericipites callidus*) can be correlated to *Kalmia*-type pollen or even to *Kalmia* and related ericacean taxa.

Following a hypothetical assignment of the new taxon to Ericaceae, based on the resemblance of the fossil pollen from Menat to pollen of modern *Kalmia*, the question remains, whether flower morphology can point in the same direction or not. Flowers with heptamerous symmetry are rare in modern Ericaceae (which are mostly pentamerous) but occur more or less frequently in a number of taxa (e.g. some species of *Rhododendron* and many of *Hymenantes*), although flowers of these taxa are usually synpetalous and synsepalous (Copeland 1943). The only modern Ericaceae genus which is characterised by heptamerous, actinomorphic flowers is *Bejaria* Mutis ex. L. (Copeland 1943). This genus includes 15 species occurring in South and Central America as well as the Caribbean with only one species, *B. racemosa* Vent., occurring in the southeast USA (Clemants 1995).

The flowers of *Bejaria* are actinomorphic with a ± choripetalous corolla and a somewhat synsepalous calyx which is rather small but thick and massive, and the genus is characterised by heptamerous flowers with (ob)diplostemonous anthers (like most other Ericaceae), although in some species pentamery occurs (Copeland 1943; Palser and Murty 1967; Stevens 1971; Ronse De Craene and Bull-Hereñu 2016). Owing to these features, the genus was long treated as a basal member of Ericaceae, which typically have a basally fused corolla and pentamerous flowers (Camp 1941). However, recent molecular phylogenetic studies placed *Bejaria* at the base of tribe Phyllodoceae within Ericaceae, as a sister group to all other taxa (including *Kalmia*) included in this tribe (Gillespie and Kron 2013).

Despite the morphological similarities to the genus *Bejaria*, it is clear that the heptamerous symmetry of the flower, together with the (ob)diplostemonous anthers, cannot be used for an assignment of this flower to *Bejaria*. The pollen morphology of four modern *Bejaria* species has been analysed by

means of LM and SEM by Sarwar and Takahashi (2014), who reported that all analysed species have a somewhat flat pollen surface, an indistinct primary apocolpial exine structure and finely gemmate-pilate secondary structure, pollen are 3-colpor(oid)ate and costae are indistinct. This differs markedly from the *Kalmia*-type pollen of *Menatanthus* gen. nov.

Although there are some similarities of the new taxon with a few taxa belonging to the Ericaceae, especially *Kalmia* and *Bejaria*, there are also some features that point against an affiliation of the new taxon with Ericaceae. The anthers in most modern Ericaceae are dorsifixed and dehiscence via terminal pores, whereas in *Menatanthus mosbruggeri*, they are probably basifixed and dehiscent via slits. Nevertheless, some modern taxa exhibit basifixed anthers and some dehisce via longitudinal slits (e.g. *Epigaea*, *Loiseleuria*, *Leiophyllum*) (Watson and Dallwitz 1992 onwards). Viscin threads, a typical feature of many Ericaceae, are missing in all tetrads analysed so far from Menat, even in unprocessed specimens taken directly from the anthers for SEM. Although Sarwar and Takahashi (2012) reported that such threads occur only in some of the modern species of *Kalmia*, it seems possible that the lack of this feature in some of the specimens analysed by these authors is primarily an artefact of preparation.

All in all, a number of morphological features occur in the flower described here from Menat that would not contradict an assignment of the flower to Ericaceae, but these features can also occur in other families. None of the visible morphological characters is exclusive for Ericaceae, and thus it is not possible to assign the flower to this family beyond any doubt.

As a heptamerous flower with *Kalmia*-type pollen tetrads has (at least to our knowledge) so far never been described in the (palaeo-)botanical literature, we are convinced that it is reasonable to describe this flower as the new genus and species *Menatanthus mosbruggeri*, even if a systematic assignment is not possible at the moment. The finding of this new taxon in the Paleocene maar deposits of Menat highlights the so far largely unexplored large palaeobotanical potential of this Lagerstätte, and it is suspected that future studies on fossil plants from this locality will significantly add to our knowledge about the Paleocene vegetation in Europe.

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Compliance with ethical standards

Conflict of interests The authors declare that they have no conflict of interest.

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