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## Taxonomic description of *in situ* bee pollen from the middle Eocene of Germany

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### Abstract

The middle Eocene Messel and Eckfeld localities are renowned for their excellently preserved faunas and diverse floras. Here we describe for the first time pollen from insect-pollinated plants found *in situ* on well-preserved ancient bees using light and scanning electron microscopy. There have been 140 pollen types reported from Messel and 162 pollen types from Eckfeld. Here we document 23 pollen types, six from Messel and 18 from Eckfeld (one is shared). The taxa reported here are all pollinated by insects and mostly not recovered in the previously studied dispersed fossil pollen records. Typically, a single or two pollen types are found on each fossil bee specimen, the maximum number of distinct pollen types on a single individual is five. Only five of the 23 pollen types obtained are angiosperms of unknown affinity, the remainder cover a broad taxonomic range of angiosperm trees and include members of several major clades: monocots (1 pollen type), fabids (7), malvids (4), asterids (5) and other core eudicots (1). Seven types each can be assigned to individual genera or infrafamilial clades. Since bees visit only flowers in the relative vicinity of their habitat, the recovered pollen provides a unique insight into the autochthonous palaeo-flora. The coexistence of taxa such as *Decodon*, *Elaeocarpus*, *Mortonioidendron* and other Tiliioideae, Mastixioideae, *Olax*, *Pouteria* and *Nyssa* confirms current views that diverse, thermophilic forests thrived at the Messel and Eckfeld localities, probably under a warm subtropical, fully humid climate. Our study calls for increased attention to pollen found *in situ* on pollen-harvesting insects such as bees, which can provide new insights on insect-pollinated plants and complement even detailed palaeo-palynological knowledge obtained mostly from pollen of wind-pollinated plants in the dispersed pollen record of sediments. In the case of *Elaeocarpus*, *Mortonioidendron*, *Olax* and *Pouteria* the pollen collected by the middle Eocene bees represent the earliest unambiguous records of their respective genera.

**Keywords:** *angiosperms, autochthonous pollen inventory, Eckfeld Maar, Electrapini, Messel Pit*

The Messel Pit (southern Hesse, near Darmstadt) and Eckfeld Maar (Eifel, Rhineland-Palatia) of central and western Germany (Figure 1) are among the most species-rich middle Eocene sites in Europe. In addition to their well-known fauna (e.g. Schaal & Ziegler 1992; Lutz 1993; Lutz et al. 2000; Wappler & Engel 2003) and macro-flora and meso-flora (e.g.

Wilde 1989; Wilde & Frankenhäuser 1998; Collinson et al. 2012), they harbour a highly diverse micro-flora with over 200 distinguished taxa of pollen and spores (Thiele-Pfeiffer 1988; Nickel 1994, 1996). In particular, the angiosperm pollen record documents diverse vegetation that was present in the middle Eocene of central Europe: A total of

114 pollen types with diagnostic features encompassing 38 families of angiosperms from 25 orders (Supplemental data File S1; Thiele-Pfeiffer 1988; Nickel 1996). Among many other insects, Messel and Eckfeld have yielded well-preserved fossils of bees, mostly of the extinct tribe Electrapini (Lutz 1993; Engel 2001a; Wappler & Engel 2003), although evidence for Megachilinae and a possible eucerine are also known (Wappler & Engel 2003; Wedmann et al. 2009). The Electrapini, are one of several highly eusocial corbiculate tribes among the Apinae, and one of several groups that form a grade leading to the more familiar tribes of honey bees and stingless bees (Lutz 1993; Schultz et al. 2001; Engel 2001a, 2001b; Wappler & Engel 2003). Given the presence of corbiculae (also known as metatibial ‘pollen baskets’, a specialised structure for the transport of moistened pollen back to the nest; Engel 2001a) and metatibial pollen presses among Electrapini (Engel 2001a), it is presumed that these taxa would have exhibited the same suite of behavioural repertoires necessary for collecting and manipulating pollen, and perhaps also similar harvesting preferences and strategies, as are known among their extant relatives. Fortunately, many of the bees from Messel and Eckfeld preserve on their bodies and particularly in their corbiculae the pollen they had collected and come into contact with during foraging bouts, thereby providing a means of inferring this aspect of their palaeo-biology. Naturally, before any such exploration of ancient bee pollen-collecting behaviour can be attempted, it is necessary to systematically survey the pollen of individual fossil bee specimens. Such an inventory provides an indication of the plants visited (either for nectar, pollen or oils) by the bee prior to death, and particularly those from which it actively collected pollen in its corbicula for transport to the nest and use as brood provisions. To date, there have been few studies aimed at retrieving and studying *in situ* pollen on fossils of pollen-harvesting/-feeding insects (Krassilov & Rasnitsyn 1982, 1996; Caldas et al. 1989; Ramírez et al. 2007). Here we document for the first time pollen found *in situ* on middle Eocene bees from the Messel and Eckfeld localities using a combination of light microscopy (LM) and scanning electron microscopy (SEM). The pollen grains recovered from these fossil insects are compared to those from earlier comprehensive LM studies of the sedimentary dispersed pollen record at Messel (Thiele-Pfeiffer 1988) and Eckfeld (Nickel 1996). Since insect-pollinated taxa commonly are not represented in the same way as wind-pollinated taxa in the dispersed pollen record, it can be assumed that

pollen adhering to bees reflect a different spectrum of plants as pollen dispersed in the sediment. Therefore, this kind of study can provide an entirely new angle of looking into the Messel and Eckfeld ecosystems.

## Material and methods

Fossil bees from two Eocene fossil Lagerstätten, the Grube Messel (‘Messel Pit’, maximum age  $47.8 \pm 0.2$  Ma, deposition lasted for 1.6 Ma; Mertz & Renne 2005) and Eckfelder Maar (‘Eckfeld Maar’,  $44.3 \pm 0.4$  Ma, 0.25 Ma of deposition; Mertz et al. 2000), were examined using a Leica MZ9.5 stereomicroscope equipped with standard incident ultraviolet (UV) illumination to detect pollen on the bees. Eleven bees, four from Messel and seven from Eckfeld, with pollen grains adhered to their bodies and representing species from two genera of Electrapini (Apidae: Apinae), *Electrapis* and *Protobombus* (Lutz 1993; Engel 2001a; Wappler & Engel 2003), were selected for study. For UV illumination, we used a 100 W high-pressure mercury burner in combination with a filter block consisting of an excitation filter (UV+ green: 425/60 nm), a dichromatic mirror (beam splitter, 470 nm) and a barrier (emission) filter (475 nm), providing a bright greenish fluorescence for the fluorescent material. The fossil pollen grains were extracted from the bee specimens with the help of wax sticky pads mounted at the end of a preparation needle. The wax was remobilised in 60 °C hot water and the pollen grains/clusters were fished out using a micromanipulator and placed into drops of glycerine. Using a micromanipulator, the grains and/or pollen clusters then were placed into drops of acetolysis liquid (9:1 mix of 99% acetic anhydride and 95–97% sulphuric acid) on new glass slides. These slides were heated over a candle flame for a short time to dissolve extra organic material and to stain the pollen grains, which was afterwards transferred in fresh drops of glycerine to new glass slides. The pollen grains were first photographed under LM and transferred to SEM stubs by use of a micromanipulator and washed with drops of absolute ethanol to remove any remaining glycerine. The stubs were sputter coated with gold and the pollen grains were photographed under a JEOL 6400 SEM. Heteropolar pollen grains were turned/rotated on the stub surfaces, recoated with gold, and again photographed under the scanning electron microscope. The bee fossils were photographed with a Leica MZ16 Stereomicroscope, using either a JVC (model KY-F70B) or a Nikon Coolpix 4500 digital camera.



Figure 1. Map of Germany indicating the positions of Eckfeld ( $50^{\circ} 6' 56''$  N,  $6^{\circ} 49' 7''$  E) and Messel ( $49^{\circ} 55' 3''$  N,  $8^{\circ} 45' 24''$  E).

### Systematic palaeontology

All pollen descriptions presented here include the most diagnostic features observed both in LM and SEM. The terminology follows mostly Punt et al. (2007) and Hesse et al. (2009). The classification (including informal clades) and author names of extant orders and families follow APG III (2009). Taxa *incertae sedis* are listed at the end of each larger taxonomic group. Pollen grains from the same bee or body part are figured together and not according to the systematic affiliation, hence, the irregular figure numbers in the systematic section. In total, we found 23 pollen types, representing 12 angiosperm families from 11 orders and including five eudicot pollen types of unknown affinity (Table I). Supplemental data File S2 includes a comprehensive list of the pollen obtained from the bee specimens and provides a summary of the taxonomic affinities (also provided in reduced form in Table I).

Clade Monocots  
Order Asparagales Link  
Family Iridaceae Juss.  
Subfamily Iridoideae Eaton

Iridoideae gen. et sp. indet.  
(Figures 8B–F, H, K–N, Q; 9A–E, G–I, S)

*Description.* — Pollen, oblate, elliptic in polar and equatorial view; equatorial diameter 28–34  $\mu$ m in LM, 24–30  $\mu$ m in SEM; sulcate, sulcus long, extending between apices; exine 1.1–1.8  $\mu$ m thick (LM), nexine thinner than sexine; semitectate; sculpturing reticulate in LM, and SEM, columellae are narrow and high, muri pluricolumellate, muri varying in width, lumina varying in size and form, lumina decrease in size towards apices and towards sulcus, muri fused around sulcus (SEM).

*Remarks.* — The LM and SEM pollen morphology of extant Iridoideae has been studied by Goldblatt and Le Thomas (1992). The thin columellae and smooth and flattened muri of the fossil pollen grains suggest affiliation to Iridoideae.

*Locality.* — Eckfeld.

*Previous records.* — This type was not reported by Nickel (1994, 1996) in the dispersed pollen flora from Eckfeld. This family was not reported by Wilde and Frankenhäuser (1998) in the macro-fossil record of Eckfeld.

*Bee specimen (and species).* — PE 2000/847.LS (*Electrapis prolata* Wappler et Engel); found on leg.

*Occurrence.* — In large groups along with Eudicot ord., fam., gen. et sp. indet. 2, Eudicot ord., fam., gen. et sp. indet. 3 and Anacardiaceae gen. et sp. indet. pollen types.

*Life form and pollination.* — Herbaceous perennial, evergreen or deciduous; entomophilous (can also be zoophilous).

Clade Fabids

Order Oxalidales Bercht. et J.Presl.

Family Elaeocarpaceae Juss. ex DC.

Genus *Elaeocarpus* L.

*Elaeocarpus* sp. 1

(Figure 7B–H)

*Description.* — Pollen, prolate, lobate in polar view, elliptic in equatorial view; polar axis 8–10  $\mu\text{m}$  long in LM, 8–9  $\mu\text{m}$  long in SEM, equatorial diameter 6–7  $\mu\text{m}$  in LM, 6–7  $\mu\text{m}$  in SEM; tricolporate; exine 0.7–0.8  $\mu\text{m}$  thick (LM), nexine thinner than sexine; tectate; sculpturing psilate in LM, psilate, perforate, granulate in SEM, colpus membrane microverrucate, sexine protruding in area of endoaperture forming a bridge (SEM).

Table I. List of pollen taxa documented in this study, their systematic placement, and from which bee specimen they were obtained.

Lineage/pollen taxon	Figure	Locality	Bee specimen
Monocots: Asparagales: Iridaceae			
Iridoideae gen. et .sp. indet.	8B–F, H, K–N, Q; 9A–E, G–L, S	Eckfeld	PE 2000/847.LS
Core eudicots: rosids: fabids (Fabidae): Oxalidales [ <b>Ox</b> ], Malpighiales [ <b>Ma</b> ], Fagales [ <b>Fa</b> ]			
[ <b>Ox</b> ] <i>Elaeocarpus</i> sp. 1	7B–H	Eckfeld	PE 2000/846a,b.LS
[ <b>Ox</b> ] <i>Elaeocarpus</i> sp. 2	15B–M	Eckfeld	PE 2000/846a,b.LS
[ <b>Ma</b> ] Euphorbiaceae gen. et .sp. indet. 1	7O–R	Eckfeld	PE 2000/846a,b.LS
[ <b>Ma</b> ] Euphorbiaceae gen. et .sp. indet. 2	13L–O; 14A–N	Eckfeld	PE 2000/852a,b.LS
[ <b>Ma</b> ] Euphorbiaceae gen. et .sp. indet. 3	15N–P	Eckfeld	PE 2000/863a,b.LS
[ <b>Fa</b> ] <i>Castanopsis</i> vel <i>Lithocarpus</i> sp.	5B–J; 7I, J, L, N	Eckfeld	PE 2000/846a,b.LS
		Messel	FIS MeI 10890
[ <b>Fa</b> ] Engelhardioideae gen. et .sp. indet.	14O–Q	Eckfeld	PE 2000/852a,b.LS
Core eudicots: rosids: malvids (Malvaceae): Myrtales [ <b>My</b> ], Malvales [ <b>Mv</b> ], Sapindales [ <b>Sa</b> ]			
[ <b>My</b> ] <i>Decodon</i> sp.	10O–Q	Eckfeld	PE 2000/849a,b.LS
[ <b>Mv</b> ] <i>Mortoniendron</i> sp.	5K–Q	Messel	FIS MeI 10890, FIS MeI 12151
[ <b>Mv</b> ] Tiliaceae gen. et .sp. indet.	3K; 4A–O	Messel	FIS MeI 6388
[ <b>Sa</b> ] Anacardiaceae gen. et .sp. indet.	9H–I	Eckfeld	PE 2000/847.LS
Core eudicots: Santalales			
<i>Olax</i> sp.	6H–O	Eckfeld	PE 1997/20.LS
Asterids: Cornales [ <b>Co</b> ], Ericales [ <b>Er</b> ], campanulids (Apiales [ <b>Ap</b> ])			
[ <b>Co</b> ] Mastixioideae gen. et .sp. indet.	16B–J	Eckfeld	PE 2014/1a,b.LS
[ <b>Co</b> ] <i>Nyssa</i> sp.	2B–N	Messel	FIS MeI 3300
[ <b>Er</b> ] <i>Pouteria</i> sp.	13A–K	Eckfeld	PE 2000/852a,b.LS
[ <b>Ap</b> ] Araliaceae gen. et .sp. indet. 1	3B–J	Messel	FIS MeI 6388
[ <b>Ap</b> ] Araliaceae gen. et .sp. indet. 2	6B–F	Messel	FIS MeI 12151
Eudicot ord., fam., gen. et sp. indet. 1	7I–M	Eckfeld	PE 2000/846a,b.LS
Eudicot ord., fam., gen. et sp. indet. 2	8B–G, I, K–M, O–Q; 9M–R; 10B–N; 11A–O	Eckfeld	PE 2000/847.LS, PE 2000/849a,b.LS
Eudicot ord., fam., gen. et sp. indet. 3	8D–F, J; 9A–B, D–F	Eckfeld	PE 2000/847.LS
Eudicot ord., fam., gen. et sp. indet. 4	12B–L	Eckfeld	PE 2000/852a,b.LS
Eudicot ord., fam., gen. et sp. indet. 5	12B, M–P	Eckfeld	PE 2000/852a,b.LS



*Remarks.* — The pollen morphology of extant Elaeocarpaceae has been studied using LM and SEM by Tang and Wu (1990). The small size vs. the wall thickness of these tricolporate grains in combination with the endoapertures forming a bridge and the psilate, perforate to granulate sculpturing clearly places these pollen grains in *Elaeocarpus*.

*Locality.* — Eckfeld.

*Previous records.* — This pollen type was not reported by Nickel (1994, 1996) in the dispersed pollen flora from Eckfeld. This family was not reported by Wilde and Frankenhäuser (1998) in the macro-fossil record of Eckfeld.

*Bee specimen and species.* — PE 2000/846a,b.LS (*Electrapis* sp.); found on thorax and leg.

*Occurrence.* — In large pure groups.

*Life form and pollination.* — Evergreen tree or shrub; entomophilous.

*Elaeocarpus* sp. 2  
(Figure 15B–M)

*Description.* — Pollen, prolate to spheroidal, lobate in polar view, elliptic in equatorial view; polar axis 13–16  $\mu\text{m}$  long in LM, 12–14  $\mu\text{m}$  long in SEM, equatorial diameter 11–14  $\mu\text{m}$  in LM, 10–12  $\mu\text{m}$  in SEM; tricolporate, endoapertures short lalongate, sexine protruding over pori forming a bridge; exine 0.8–1.1  $\mu\text{m}$  thick in LM, nexine thinner than sexine (LM); tectate, sculpturing psilate in LM, slightly microverrucate, perforate, granulate in SEM, colpus membrane microechinate to microverrucate (SEM).

*Locality.* — Eckfeld.

*Previous records.* — This type was not reported by Nickel (1994, 1996) in the dispersed pollen flora from Eckfeld.

*Bee specimen and species.* — PE 2000/863a,b.LS (*Electrapis* sp.); found on thorax, abdomen.

*Occurrence.* — In large pure groups, some groups with occasional grains of Euphorbiaceae gen. et sp. indet. 3 pollen type.

*Life form and pollination.* — Evergreen tree or shrub; entomophilous.

Order Malpighiales Juss. ex Bercht. et J.Presl.  
Family Euphorbiaceae Juss.

Euphorbiaceae gen. et sp. indet. 1  
(Figure 7O–R)

*Description.* — Pollen, prolate, lobate in polar view, elliptic in equatorial view; polar axis 17–19  $\mu\text{m}$  long in LM, 18–19  $\mu\text{m}$  long in SEM, equatorial diameter 12–13  $\mu\text{m}$  in LM, 12–13  $\mu\text{m}$  in SEM; tricolporate, endoapertures lalongate rectangular, nexine thickened along endopori and colpi (LM); exine 1.2–1.4  $\mu\text{m}$  thick, nexine thinner than sexine (LM); semitectate, sculpturing reticulate in LM and SEM, lumina funnel shaped, lumina decrease close to colpus (SEM).

*Remarks.* — The funnel shaped lumina of the reticulum is very typical for pollen of Euphorbiaceae. Several genera in the Euphorbiaceae share very similar pollen morphology. We therefore refrain from assigning this pollen type to a particular genus.

*Locality.* — Eckfeld.

*Previous records.* — This pollen type was not reported by Nickel (1994, 1996) in the dispersed pollen flora from Eckfeld. This family was not reported by Wilde and Frankenhäuser (1998) in the macro-fossil record of Eckfeld.

*Bee specimen and species.* — PE 2000/846a,b.LS (*Electrapis* sp.); found on leg.

*Occurrence.* — Single grains.

*Life form and pollination.* — From herb to succulent to shrub or tree; entomophilous (can also be zoophilous).

Euphorbiaceae gen. et sp. indet. 2  
(Figures 13L–O; 14A–N)

*Description.* — Pollen, prolate, lobate in polar view, elliptic in equatorial view; polar axis 20–25  $\mu\text{m}$  long in LM, 19–23  $\mu\text{m}$  long in SEM, equatorial diameter 15–19  $\mu\text{m}$  in LM, 13–18  $\mu\text{m}$  in SEM; tricolporate, endoapertures circular, nexine thickened around endopori forming a costa, nexine thickened along colpi (LM); exine 1.2–1.4  $\mu\text{m}$  thick in SEM, 1.5–1.7  $\mu\text{m}$  thick in LM, nexine thinner than sexine (LM); semitectate, sculpturing scabrate in LM, microreticulate in SEM, muri broad, muri decrease in size and become more numerous in the area around apertures (SEM).

*Locality.* — Eckfeld.

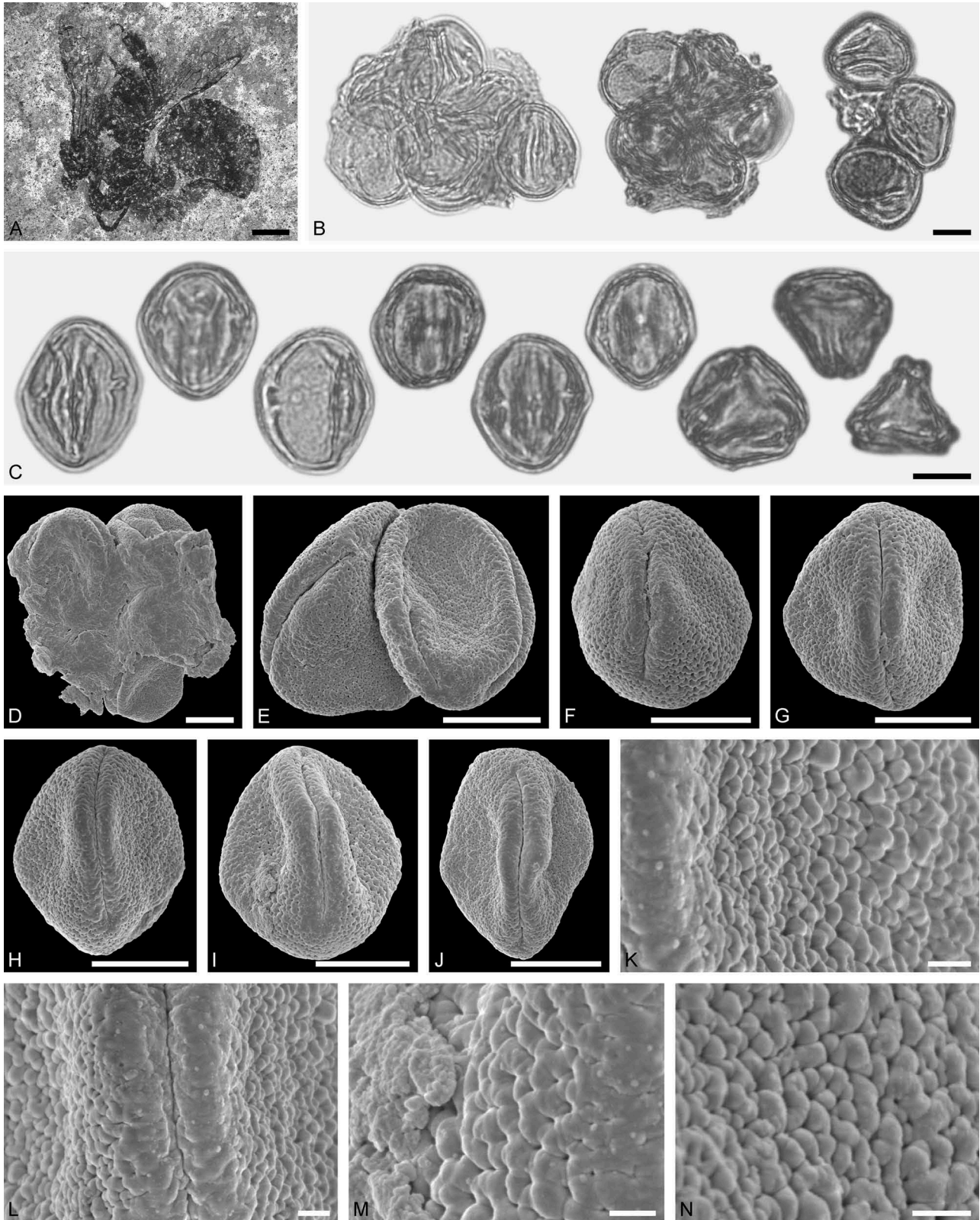


Figure 2. *Electrapis* sp. from Messel and associated pollen grains. **A.** Female (worker caste) FIS MeI 3300. **B, C.** LM micrographs. **D–N.** SEM micrographs. **B.** Clumps of *Nyssa* sp. pollen grains. **C.** *Nyssa* sp. grains in equatorial view (left) and polar view (right). **D, E.** Clumps of *Nyssa* sp. pollen grains. **F–J.** *Nyssa* sp. grains in equatorial view. **K–N.** *Nyssa* sp., details of tectum surface. Scale bars – 2 mm (A), 10  $\mu$ m (B–J), 1  $\mu$ m (K–N).

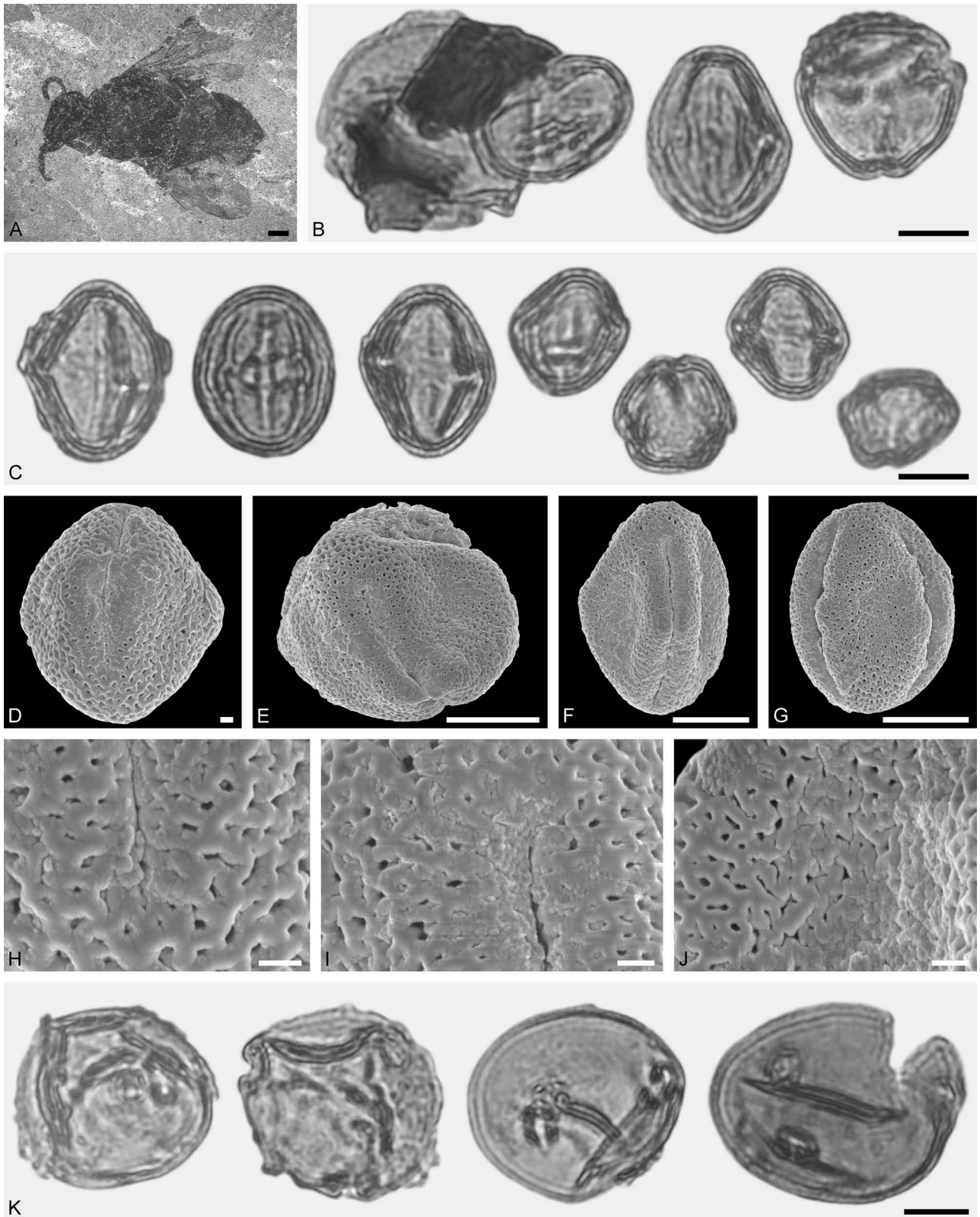


Figure 3. *Protobombus messelensis* Engel et Wappler from Messel and associated pollen grains. **A.** FIS MeI 6388, holotype, female. **B–C, K.** LM micrographs. **D–J.** SEM micrographs. **B.** Clump with Aralioideae gen. et sp. indet. 1 and Tilioideae gen. et sp. indet. pollen grains (left), Aralioideae gen. et sp. indet. 1 pollen in equatorial and polar view (right). **C.** Aralioideae gen. et sp. indet. 1 grains in equatorial view (left) and polar view (right). **D, F, G.** Aralioideae gen. et sp. indet. 1 grains in equatorial view. **E.** Aralioideae gen. et sp. indet. 1 grain in polar view. **H–J.** Aralioideae gen. et sp. indet. 1, details of tectum surface. **K.** Tilioideae gen. et sp. indet. pollen grains. Scale bars – 1 mm (A), 10  $\mu$ m (B–C, E–G, K), 1  $\mu$ m (D, H–J).



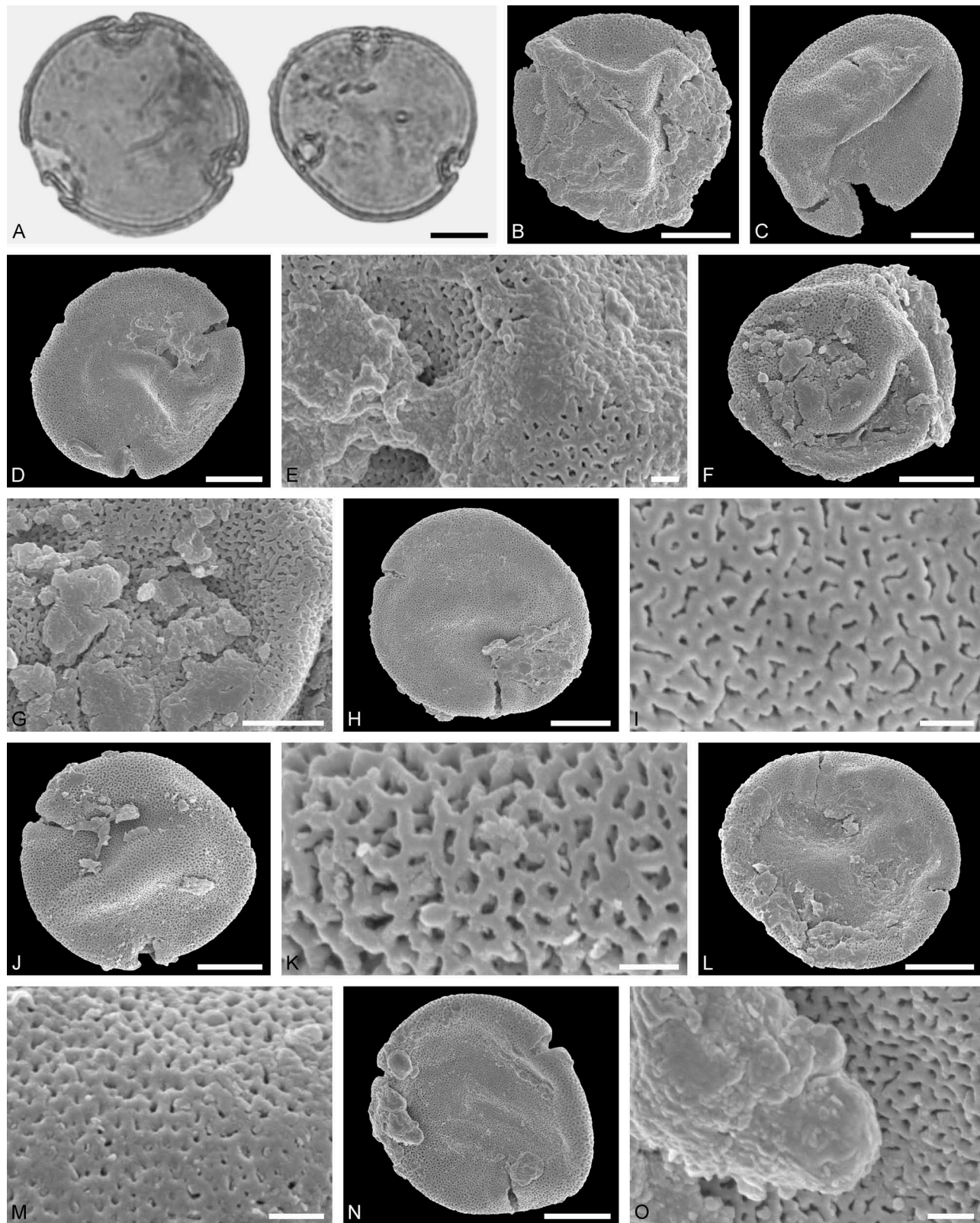


Figure 4. Associated pollen grains of *Protobombus messelensis* Engel et Wappler (FIS MeI 6388) from Messel. **A.** LM micrograph. **B–O.** SEM micrographs. **A.** Tilioideae gen. et sp. indet. pollen in polar view. **B–D, F, H, J, L, N.** Tilioideae gen. et sp. indet. pollen in polar view. **E, G, I, K, M, O.** Tilioideae gen. et sp. indet., details of tectum surface. **H–K.** Same pollen grain rotated. **H–I.** Proximal side. **J–K.** Distal side. **L–O.** Same pollen grain rotated. **L–M.** Proximal side. **N, O.** Distal side. Scale bars – 10  $\mu$ m (A–D, F, H, J, L, N), 1  $\mu$ m (E, G, I, K, M, O).

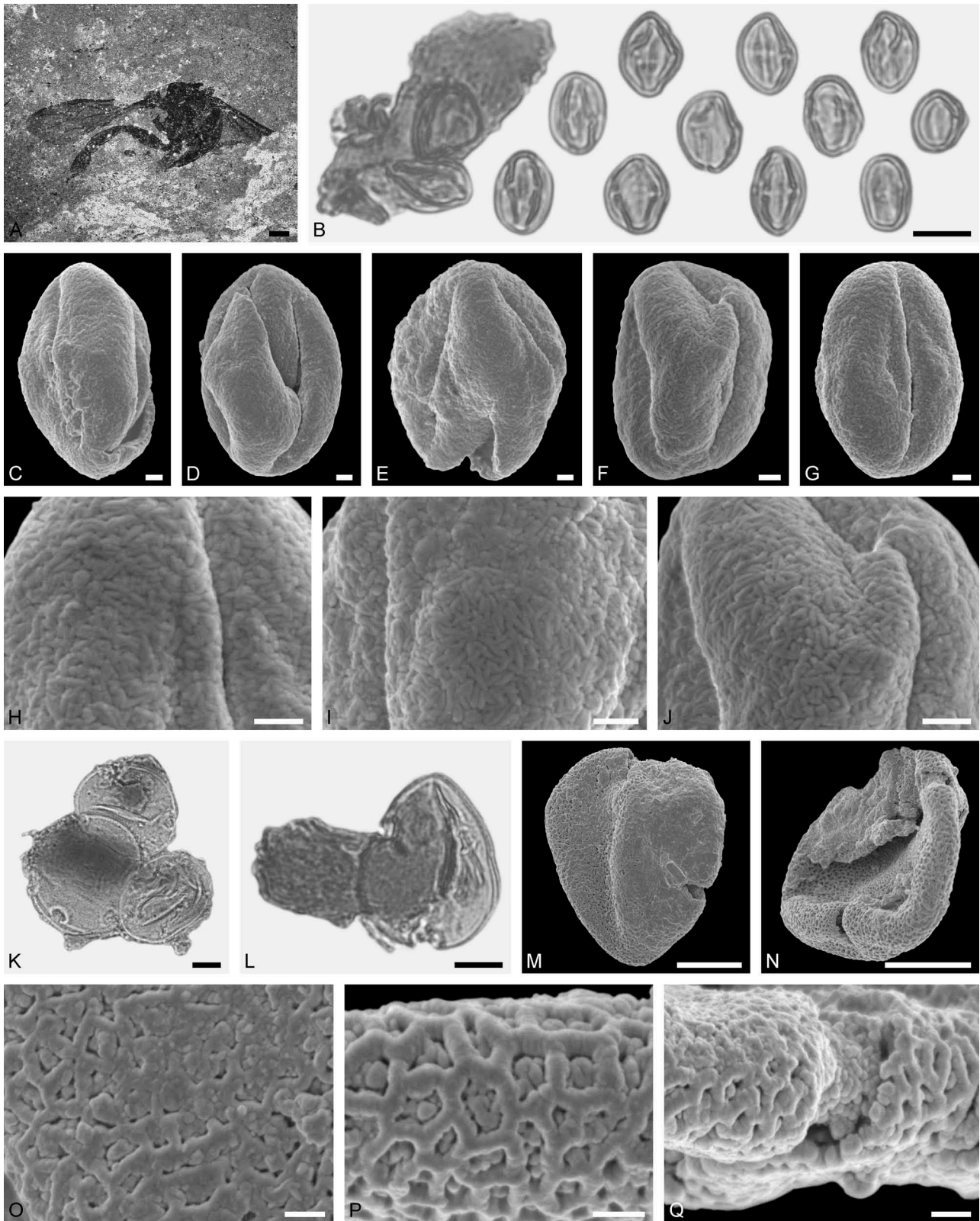


Figure 5. *Electrapis* sp. from Messel and associated pollen grains. **A.** Female (worker caste) FIS MeI 10890. **B, K-L.** LM micrographs. **C-J, M-Q.** SEM micrographs. **B.** Clump with *Castanopsis/Lithocarpus* sp. pollen grains (left), grains in equatorial view (right). **C-G.** *Castanopsis/Lithocarpus* sp. grains in equatorial view **H-J.** *Castanopsis/Lithocarpus* sp., details of tectum surface. **K.** Clump with *Mortoniendron* sp. pollen grains. **L.** *Mortoniendron* sp. pollen in polar view. **M, N.** *Mortoniendron* sp., same grain rotated. **O-Q.** *Mortoniendron* sp., details of tectum surface. Scale bars – 1 mm (A), 10  $\mu$ m (B, K-N), 1  $\mu$ m (C-J, O-Q).

*Previous records.* — This type was not reported by Nickel (1994, 1996) in the dispersed pollen flora from Eckfeld.

*Bee specimen and species.* — PE 2000/852a,b.LS (*Electrapis micheneri* Wappler et Engel); found on leg.

*Occurrence.* — In large pure groups.

*Life form and pollination.* — From herb to succulent to shrub or tree; entomophilous (can also be zoophilous).

Euphorbiaceae gen. et sp. indet. 3  
(Figure 15N–P)

*Description.* — Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 21–23 µm long in LM, 19–21 µm long in SEM, equatorial diameter 18–20 µm in LM, 14–17 µm in SEM; tricolporate, endoapertures alongate with a costa (LM); exine 1.7–1.9 µm thick in LM, nexine thinner than sexine (LM); semitectate, sculpturing scabrate in LM, microreticulate in SEM, lumen funnel-shaped (SEM).

*Locality.* — Eckfeld.

*Previous records.* — This type was not reported by Nickel (1994, 1996) in the dispersed pollen flora from Eckfeld.

*Bee specimen and species.* — PE 2000/863a,b.LS (*Protobombus pristinus* Wappler et Engel); found on body.

*Occurrence.* — Rare grains in clumps dominated by the *Elaeocarpus* sp. 2 pollen type.

*Life form and pollination.* — From herb to succulent to shrub or tree; entomophilous (can also be zoophilous).

Order Fagales Engl.  
Family Fagaceae Dumort.  
Subfamily Castaneoideae Orsted.

Genus *Castanopsis* (D.Don) Spach vel *Lithocarpus*  
Blume sp.  
(Figures 5B–J; 7I, J, L, N)

*Description.* — Pollen, prolate, lobate in polar view, elliptic in equatorial view; polar axis 11–16 µm long in LM, 10–13 µm long in SEM, equatorial diameter 9–11 µm in LM, 7–9 µm in SEM; tricolporate, endoapertures alongate slit-like; exine 0.8–1.0 µm thick (LM), nexine thinner than sexine; tectate;

sculpturing psilate in LM, microrugulate, perforate in SEM.

*Remarks.* — The pollen morphology of extant and extinct Fagaceae has been described in detail (e.g. Pragłowski 1982, 1984; Solomon 1983a, 1983b; Denk & Grimm 2009; Denk et al. 2012; Grímsson et al. 2015b). The similarities between pollen of *Castanopsis* and *Lithocarpus* (Pragłowski 1984) prevents assigning this pollen type to one of the two genera.

*Locality.* — Messel and Eckfeld.

*Previous records.* — This type corresponds to *Tricolporopollenites cingulum* ssp. *oviformis* (R.Potonié) Thomson et Pflug as figured by Thiele-Pfeiffer (1988, plate 11, figures 28–34) from the dispersed pollen flora of Messel, and by Nickel (1996, plate 9, figures 37–38) from the dispersed pollen flora of Eckfeld. Wilde (1989) and Collinson et al. (2012) did not report any Fagaceae fruits, seeds or leaves from Messel. This family was not reported by Wilde and Frankenhäuser (1998) in the macro-fossil record of Eckfeld.

*Bee specimen and species.* — FIS MeI 10890 (*Electrapis* sp.; Messel); PE 2000/846a,b.LS (*Electrapis* sp.; Eckfeld); found on thorax (Messel specimen), leg (Eckfeld specimen).

*Occurrence.* — In large pure groups and as single grains. Also found in small groups along with Eudicot ord., fam., gen. et sp. indet. 1 pollen type.

*Life form and pollination.* — Evergreen tree, entomophilous.

Family Juglandaceae DC. ex Perleb  
Subfamily Engelhardioideae Iljinskaya

Engelhardioideae gen. et sp. indet.  
(Figure 14O–Q)

*Description.* — Pollen, oblate, convex triangular in polar view, elliptic in equatorial view; equatorial diameter 23–25 µm in LM, 19–22 µm in SEM; triporate; exine 0.9–1.2 µm thick, nexine thinner than sexine, nexine linearly thickened from pori to polar areas forming endoplicae; tectate; sculpturing psilate to scabrate in LM, microechinate in SEM, microechini at regular intervals (SEM).

*Remarks.* — The LM and SEM pollen morphology of extant Juglandaceae genera have been studied by Stone and Broome (1975). Based on the morphology of the fossil pollen it represents an extinct taxon of the Engelhardioideae.

*Locality.* — Eckfeld.

*Previous records.* — This type may correspond to *Plicatopollis hungaricus* as figured by Nickel (1996, plate 6, figures 13–14). Wilde and Frankenhäuser (1998) reported several different Juglandaceae macro-fossils from Eckfeld. These include engelhardioid compound leaves and leaflets, engelhardioid fruits (*Palaecarya* sp.), *Hooleya*-like pterocaryoid fruits, and fragments of platycaryoid male inflorescences.

*Bee specimen and species.* — PE 2000/852a,b,LS (*Electrapis micheneri*); found on leg.

*Occurrence.* — Single grain.

*Life form and pollination.* — Deciduous or evergreen tree; anemophilous or possibly entomophilous. Among extant Juglandaceae, insect pollination has only been documented for *Platycarya* (Endress 1986). Since most Juglandaceae are wind-pollinated it cannot be ruled out that this pollen grain is a contamination from the sediment.

Clade Malvids

Order Myrtales Juss. ex Bercht. et J.Presl

Family Lythraceae J.St.-Hil.

Genus *Decodon* J.F.Gmel.

*Decodon* sp.

(Figure 100–Q)

*Description.* — Pollen, prolate, elliptic in equatorial view, circular in polar view, meridional ridges running down mid-mesocolpial areas, polar axis 18–19 µm long in LM, 14–16 µm in SEM, equatorial diameter 13–15 µm in LM, 11–13 µm in SEM; tricolporate, exine 0.9–1.1 µm thick, nexine thinner than sexine, sexine slightly thickened on meridional ridges and in polar regions; tectate, sculpturing psilate to scabrate in LM, microrugulate to rugulate, perforate, fossulate in SEM, sexine protruding forming a bridge in area of endopori (SEM).

*Remarks.* — The fossil record of *Decodon* and the pollen morphology of the genus has been described in detail by Grímsson et al. (2012). The meridional ridges observed on the fossil pollen clearly place it in genus *Decodon*.

*Locality.* — Eckfeld.

*Previous records.* — This pollen type was not reported by Nickel (1994, 1996) in the dispersed pollen flora from Eckfeld. This family was not

reported by Wilde and Frankenhäuser (1998) in the macro-fossil record of Eckfeld.

*Bee specimen and species.* — PE 2000/849a,b,LS (*Electrapis* sp.); found on thorax, abdomen.

*Occurrence.* — Rare grains in large clumps dominated by Eudicot ord., fam., gen. et sp. indet. 2 pollen type.

*Life form and pollination.* — Perennial shrub; entomophilous.

Order Malvales Juss. ex Bercht. et J.Presl

Family Malvaceae Juss.

Subfamily Tilioideae

Genus *Mortoniendendron* Standley et Steyerm.

*Mortoniendendron* sp.

(Figure 5K–Q)

*Description.* — Pollen, oblate, circular to convex-triangular in polar view, elliptic in equatorial view; equatorial diameter 37–44 µm in LM, 32–40 µm in SEM; brevitrilocporate, planaperturate, exine 1.3–1.6 µm thick, nexine thinner than sexine, nexine slightly thickened around endopori, thickenings semi-circular in outline; semitectate, sculpturing microreticulate in LM and SEM, lumina on distal polar area larger than those occurring on the proximal side, lumina with densely packed freestanding columellae, lumina slightly smaller close to colpi, colpus membrane microrugulate (SEM).

*Remarks.* — Extant pollen grains of various Malvaceae genera including *Mortoniendendron* have been described using LM and SEM by Perveen et al. (2004). The most characteristic feature of these fossil pollen grains are the lumina showing densely packed freestanding columellae that are not observed in this form in *Tilia* or *Craigia*.

*Locality.* — Messel.

*Previous records.* — This pollen type is not present in the dispersed pollen flora described by Thiele-Pfeiffer (1988). Wilde (1989) and Collinson et al. (2012) did not report any Malvaceae fruits, seeds or leaves from Messel.

*Bee specimen and species.* — FIS MeI 10890; FIS MeI 12151 (*Electrapis* sp.); found on leg (FIS MeI 10890), head (FIS MeI 12151).

*Occurrence.* — In pure clumps with few grains.



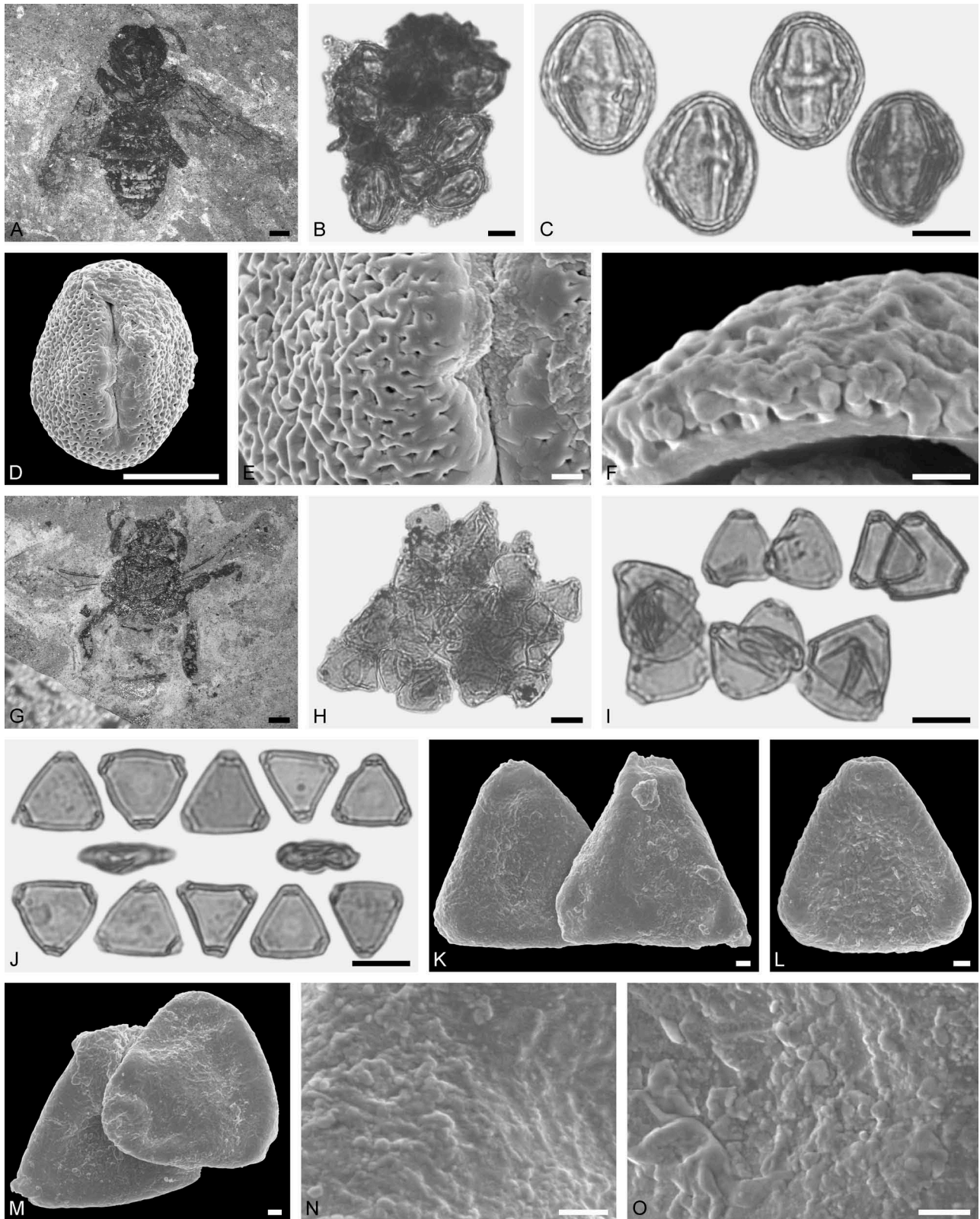


Figure 6. *Electrapis* sp. from Messel and *Electrapis electrapoides* Lutz from Eckfeld and associated pollen grains. **A**. Female (worker caste) FIS MeI 12151. **B**, **C**, **H–J**. LM micrographs. **D–F**, **K–O**. SEM micrographs. **B**. Clump with Aralioidae gen. et sp. indet. 2 pollen grains. **C**. Aralioidae gen. et sp. indet. 2 pollen in equatorial view. **D**. Aralioidae gen. et sp. indet. 2 pollen in equatorial view. **E**. Aralioidae gen. et sp. indet. 2, detail of tectum surface. **F**. Aralioidae gen. et sp. indet. 2, wall structure. **G**. Female (worker caste) PE 1997/20.LS. **H**, **I**. Large clump and smaller clumps with *Olax* sp. pollen grains. **J**. *Olax* sp. pollen in polar view (upper/lower) and equatorial view (middle). **K–M**. *Olax* sp. pollen in polar view. **N**, **O**. *Olax* sp., detail of tectum surface. Scale bars – 1 mm (A, G), 10  $\mu$ m (B–D, H–J), 1  $\mu$ m (E, F, K–O).



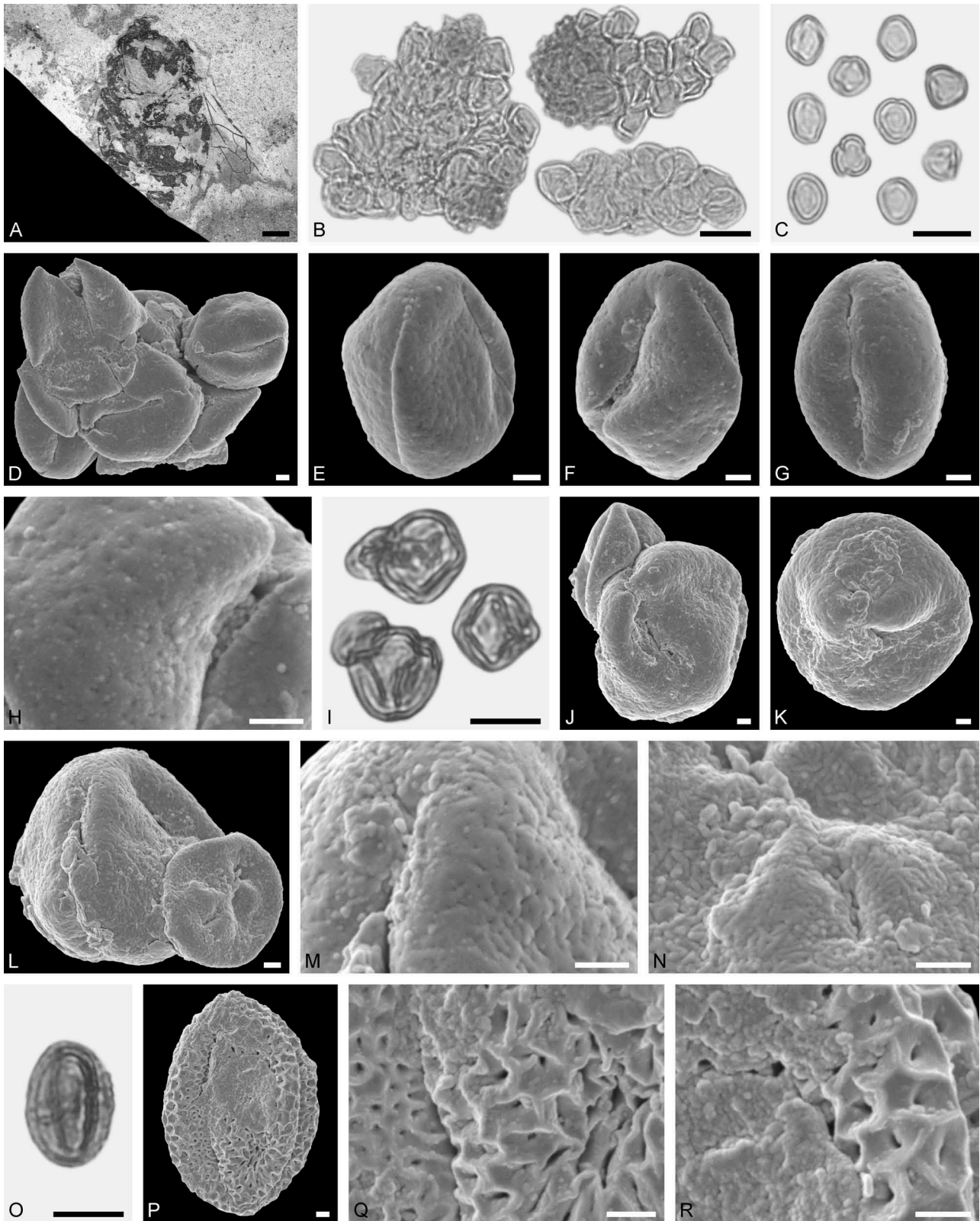


Figure 7. *Electrapis* sp. from Eckfeld and associated pollen grains. **A.** Female (worker caste) PE 2000/846a,b.LS. **B, C, I, O.** LM micrographs. **D, H, J-N, P-R.** SEM micrographs. **B.** Clumps dominated by *Elaeocarpus* sp. 1 pollen, also with Eudicot ord., fam., gen. et sp. indet. 1, Euphorbiaceae gen. et sp. indet. 1, and *Castanopsis/Lithocarpus* sp. pollen grains. **C.** *Elaeocarpus* sp. 1 pollen grains in equatorial and polar view. **D.** Clump with *Elaeocarpus* sp. 1 pollen grains. **E-G.** *Elaeocarpus* sp. 1 pollen in equatorial view. **H.** *Elaeocarpus* sp. 1, detail of tectum surface. **I-L.** Eudicot ord., fam. gen. et sp. indet. 1 pollen grains (large) and *Castanopsis/Lithocarpus* sp. (small, attached). **M.** Eudicot ord., fam., gen. et sp. indet. 1, detail of tectum surface. **N.** *Castanopsis/Lithocarpus* sp., detail of tectum surface. **O, P.** Euphorbiaceae gen. et sp. indet. 1 in equatorial view. **Q, R.** Euphorbiaceae gen. et sp. indet. 1, detail of tectum surface. Scale bars – 1 mm (A), 10  $\mu$ m (B, C, I, O), 1  $\mu$ m (D-H, J-N, P-R).

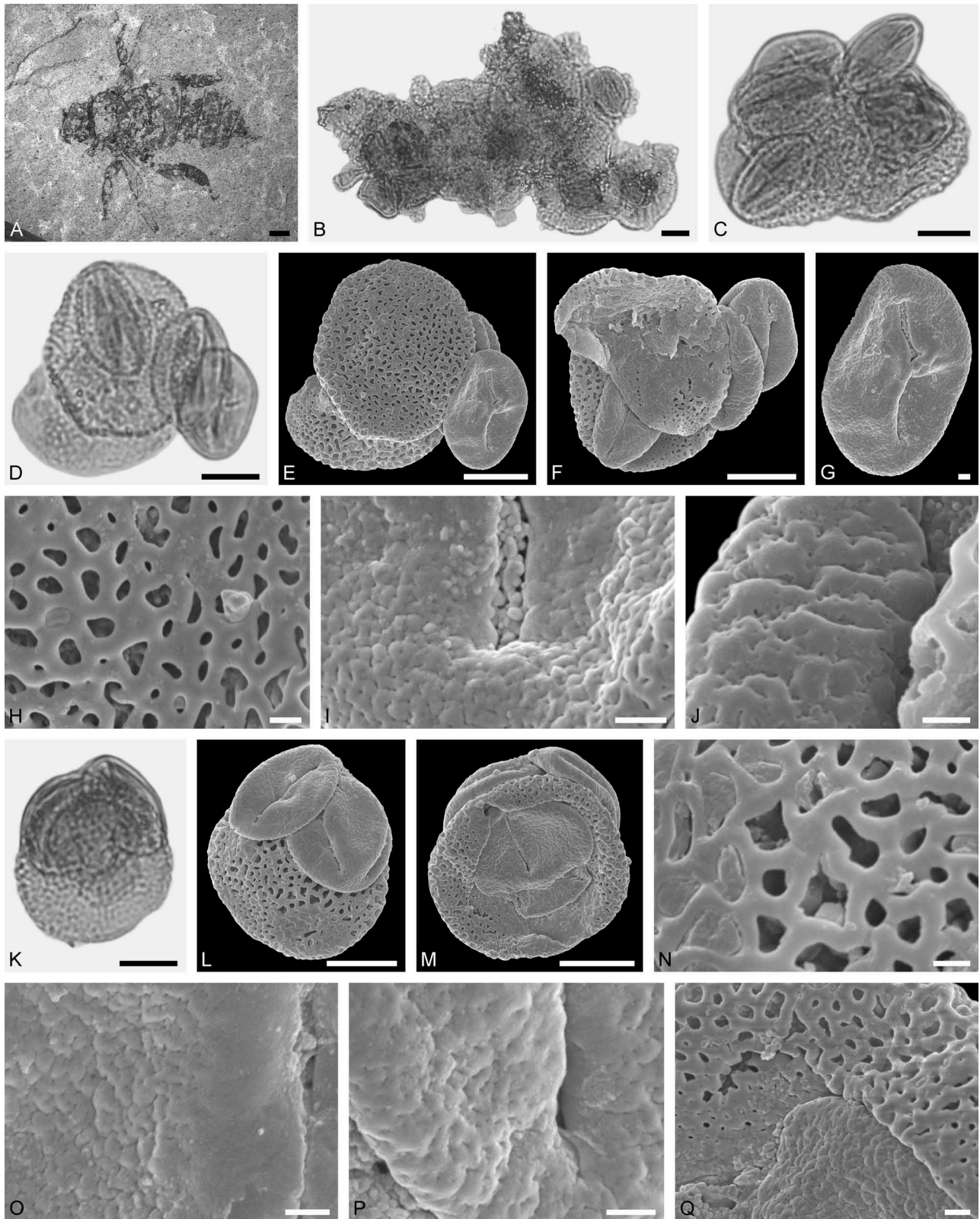


Figure 8. *Electrapis prolata* Wappler et Engel from Eckfeld and associated pollen grains. **A**. Female (worker caste) PE 2000/847a,b,LS. **B–D**, **K**. LM micrographs. **E–J**, **L–Q**. SEM micrographs. **B–D**. Clumps dominated by Iridoideae gen. et sp. indet. and Eudicot ord., fam., gen. et sp. indet. 2 pollen grains, also with pollen of Eudicot ord., fam., gen. et sp. indet. 3, and rare Anacardiaceae gen. et sp. indet. pollen grains. **D–J**. Same clump rotated. **G**. Eudicot ord., fam., gen. et sp. indet. 2 pollen in equatorial view. **H**. Iridoideae gen. et sp. indet., detail of tectum surface. **I**. Eudicot ord., fam., gen. et sp. indet. 2, detail of tectum surface. **J**. Eudicot ord., fam., gen. et sp. indet. 3, detail of tectum surface. **K–Q**. Same clump rotated. **N**. Iridoideae gen. et sp. indet., detail of tectum surface. **O**, **P**. Eudicot ord., fam., gen. et sp. indet. 3, detail of tectum surface. **Q**. Iridoideae gen. et sp. indet., detail of tectum surface. Scale bars – 1 mm (A), 10  $\mu$ m (B–F, K–M), 1  $\mu$ m (G–J, N–Q).

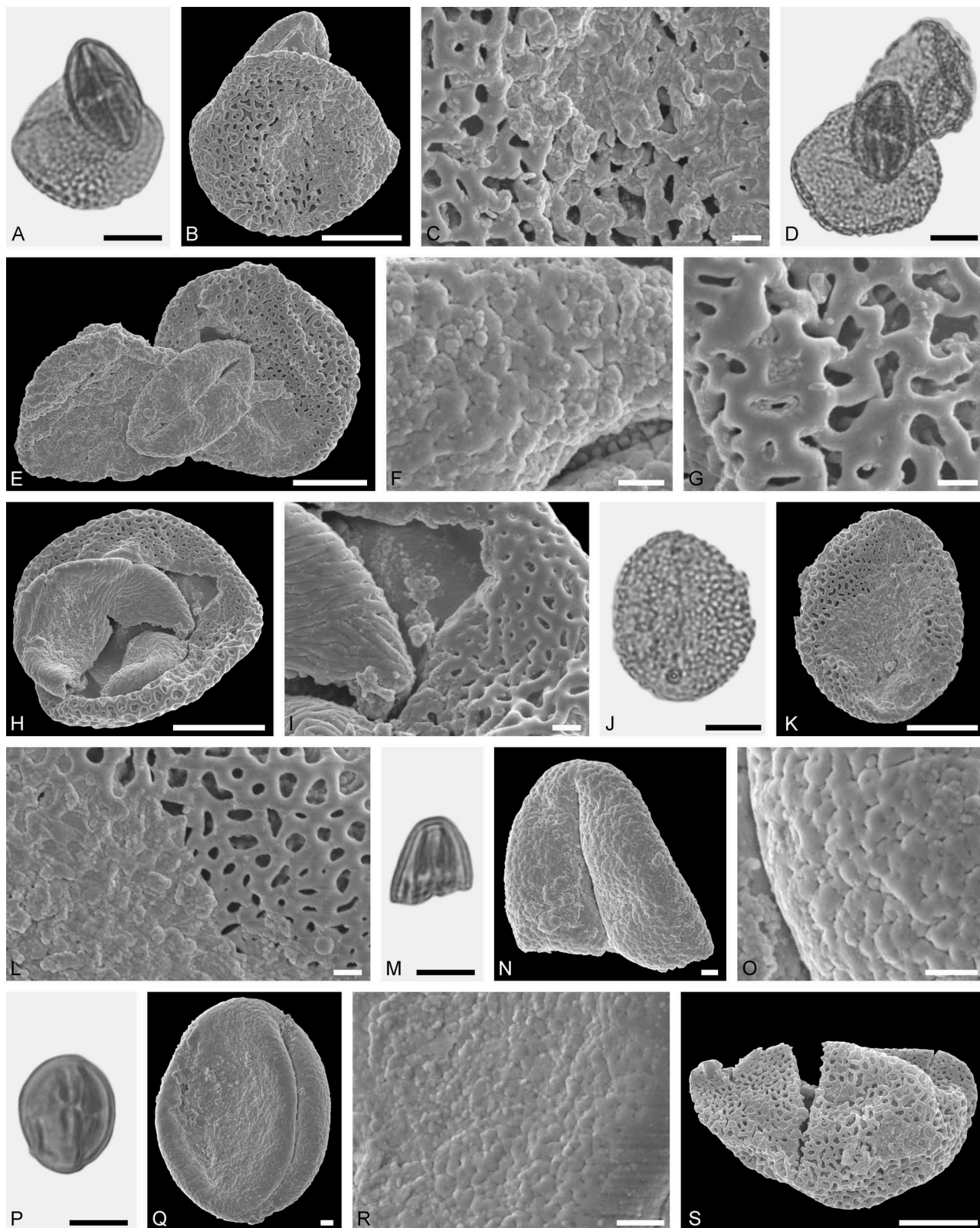


Figure 9. Pollen grains on *Electrapis prolata* Wappler et Engel (PE 2000/847a,b,LS) from Eckfeld. **A, D, J, M, P.** LM micrographs. **B, C, E-I, K, L, N, O, Q-S.** SEM micrographs. **A-C.** Clump with Iridoideae gen. et sp. indet. and Eudicot ord., fam., gen. et sp. indet. 3 pollen grains. **C.** Iridaceae gen. et sp. indet., detail of tectum surface. **D-G.** Clump with Iridaceae gen. et sp. indet. and Eudicot ord., fam., gen. et sp. indet. 3 pollen grains. **F.** Eudicot ord., fam., gen. et sp. indet. 2, detail of tectum surface. **G.** Iridoideae, detail of tectum surface. **H, I.** Clump with Iridoideae gen. et sp. indet. and Anacardiaceae gen. et sp. indet. pollen grains. **I.** Iridoideae gen. et sp. indet. (right) and Anacardiaceae gen. et sp. indet. (left), detail of tectum surface. **J-L.** Iridoideae gen. et sp. indet. **L.** Iridoideae gen. et sp. indet., detail of tectum surface. **M-O.** Eudicot ord., fam., gen. et sp. indet. 2. **O.** Eudicot ord., fam., gen. et sp. indet. 2, detail of tectum surface. **P-R.** Eudicot ord., fam., gen. et sp. indet. 2. **R.** Eudicot ord., fam., gen. et sp. indet. 2, detail of tectum surface. **S.** Iridoideae gen. et sp. indet. Scale bars – 10  $\mu\text{m}$  (A, B, D, E, H, J, K, M, P, S), 1  $\mu\text{m}$  (C, F, G, I, L, N, O, Q, R).

*Life form and pollination.* — Shrub or tree, evergreen; entomophilous.

Tilioideae gen. et sp. indet.  
(Figures 3K; 4A–O)

*Description.* — Pollen, oblate, circular in polar view, elliptic in equatorial view; equatorial diameter 37–41 µm in LM, 34–39 µm in SEM; brevitricolporate, planaperturate, endoaperture 6–7 µm wide, colpi 9–10 µm long (LM); exine 1.4–1.7 µm thick, nexine thinner than sexine, nexine thickened around endopori, thickenings semi-circular in outline; semitectate, sculpturing microreticulate in LM and SEM, lumina on distal polar area larger than those occurring on the proximal side, muri are fused around apertures (SEM).

*Remarks.* — Even though we are unable to affiliate this fossil pollen type to a particular extant genus it does resembles *in situ* grains of the fossil species *Cragia bronni* (Unger) Z.Kvaček, Bůžek et Manchester (Kvaček et al. 2002), as well as extant pollen of *Craigia* and *Tilia* (cf. Perveen et al. 2004).

*Locality.* — Messel.

*Previous records.* — Reported as *Intratriporepollenites* cf. *I. maxoides* Krutzsch in Thiele-Pfeiffer (1988, plate 8, figures 35–36).

*Bee specimen and species.* — FIS MeI 6388 (*Protobombus messelensis* Engel et Wappler); found on leg, thorax, abdomen.

*Occurrence.* — As single grains and in large groups along with Aralioidae gen. et sp. indet. pollen type.

*Life form and pollination.* — Small to large tree, possibly deciduous; entomophilous (possibly also anemophilous).

Order Sapindales Juss. ex Bercht. et J.Presl  
Family Anacardiaceae R.Br.

Anacardiaceae gen. et sp. indet.  
(Figure 9H–I)

*Description.* — Pollen, spheroidal to prolate, circular to lobate in polar view, elliptic in equatorial view, tricolporate; exine 0.9–1.0 µm thick, nexine thinner than sexine (LM); tectate, sculpturing striate in SEM, numerous perforations in grooves between striae, perforations in groups and/or rows, distal ends of colpi truncated to round, colpus membrane microverrucate to microechinate (SEM).

*Remarks.* — The typical striate sculpturing including the grouped perforations and the way the colpi terminate suggest that this pollen type belongs in Anacardiaceae. This pollen is also superficially similar to pollen of *Landeenia*, an extinct Sapindales from the Eocene of Wyoming, USA (Manchester & Hermsen 2000). The *Landeenia* pollen is tricolpate, has much longer striae, and is considerably larger than the Anacardiaceae type pollen, and is therefore not comparable.

*Locality.* — Eckfeld.

*Previous records.* — This pollen type might be the same as reported by Nickel (1996, plate 9, figures 31–32) as *Aceripollenites striatus* (Pflug) Thiele-Pfeiffer from the dispersed pollen flora of Eckfeld. Wilde and Frankenhäuser (1998) reported a possible Anacardiaceae fruit, cf. *Pentoperculum*, from the macro-fossil record of Eckfeld.

*Bee specimen and species.* — PE 2000/847.LS (*Electrapis prolata*); found on leg.

*Occurrence.* — In large groups along with Iridaceae gen. et sp. indet., Eudicot ord., fam., gen. et sp. indet. 2 and Eudicot ord., fam., gen. et sp. indet. 3 pollen types.

*Life form and pollination.* — Leaves evergreen or deciduous; trees or shrubs; entomophilous.

Order Santalales R.Br. ex Bercht. et J.Presl  
Family Olacaceae R.Br.

Genus *Olax* L.

*Olax* sp.  
(Figure 6H–O)

*Description.* — Pollen, oblate, triangular in polar view, elliptic in equatorial view; polar axis 6–7 µm long in LM, equatorial diameter 12–15 µm in LM, 11–13 µm wide in SEM; triporate, sexine protruding over pori forming an atrium; exine 0.8–1.1 µm thick (LM), nexine thinner than sexine; tectate; sculpturing psilate in LM, psilate, irregularly granulate, slightly microrugulate in SEM.

*Remarks.* — The pollen morphology of Olacaceae has been studied by Maguire et al. (1974) from specimens in North America, and by the Institute of Botany and South China Institute of Botany (1982), from south-eastern Asian material. The generally small, extremely oblate (almost flat), triangular and triporate pollen grains are characteristic for the genus *Olax*. The inconspicuous sculpturing seen



under SEM on these small type of pollen grains is also typical for this genus.

*Locality.* — Eckfeld.

*Previous records.* — This type corresponds to *Oloxipollis matthesi* ssp. *minor* Krutzsch as figured by Nickel (1996, plate 7, figure 34). This family was not reported by Wilde and Frankenhäuser (1998) in the macro-fossil record of Eckfeld.

*Bee specimen and species.* — PE 1997/20.LS (*Electrapis electrapoides* Lutz); found on thorax.

*Occurrence.* — In large pure clumps.

*Life form and pollination.* — Evergreen shrub or small tree; entomophilous.

Clade Asterids

Order Cornales Link.

Family Cornaceae Bercht. et J.Presl

Subfamily Mastixioideae Harms

Mastixioideae gen. et sp. indet.

(Figure 16B–J)

*Description.* — Pollen, prolate, lobate in polar view, elliptic in equatorial view; polar axis 34–42 µm long in LM, 31–37 µm long in SEM, equatorial diameter 29–38 µm in LM, 28–33 µm in SEM; tricolporate, nexine markedly thickened along colpi, sexine sometimes protruding over pori forming a bridge; exine 2.0–2.2 µm thick in LM, nexine thinner than sexine (LM); tectate, sculpturing scabrate in LM, verrucate, rugulate, perforate, fossulate in SEM, verrucae often with central positioned perforation, colpus membrane verrucate to microverrucate, rugulate (SEM).

*Remarks.* — The pollen morphology of Cornaceae has been studied using LM and SEM by Ferguson (1997). The fossil pollen clearly belongs in the subfamily Mastixioideae in which there are two modern genera and several extinct ones known from fruits (Mai 1995). We are unable to assign this pollen type to a particular extant genus, but the morphology of the fossil pollen suggests it is close to *Mastixia*.

*Locality.* — Eckfeld.

*Previous records.* — This type was not reported by Nickel (1994, 1996) in the dispersed pollen flora from Eckfeld. Wilde and Frankenhäuser (1998) reported Mastixiaceae fruits from the macro-fossil record of Eckfeld.

*Bee specimen and species.* — PE 2014/1a,b.LS (*Protobombus* sp.); found on thorax, abdomen.

*Occurrence.* — In large pure clumps.

*Life form and pollination.* — Evergreen tree; entomophilous.

Subfamily Nyssioideae Arn.

Genus *Nyssa* L.

*Nyssa* sp.

(Figure 2B–N)

*Description.* — Pollen, prolate, triangular in polar view, elliptic in equatorial view; polar axis 25–27 µm long in LM, 22–24 µm long in SEM, equatorial diameter 21–23 µm in LM, 19–20 µm in SEM; tricolporate, nexine thickened along colpi and endopori (costa; LM); exine 1.8–2.2 µm thick, nexine slightly thinner or as thick as sexine (LM); tectate, sculpturing scabrate in LM, microverrucate, micro-rugulate, fossulate, perforate in SEM, sculpture elements are more dense in area of mesocolpium, sculpture elements more fused along colpi forming a margo (SEM).

*Remarks.* — Pollen of several extant species of *Nyssa* has been described using LM and SEM by Göschl (2008). The fossil pollen grains described here clearly fall within the morphological range of extant *Nyssa* pollen grains. The arrangement and form of the apertures as well as the sculpturing type seen under SEM undoubtedly associates these pollen grains with *Nyssa*.

*Locality.* — Messel.

*Previous records.* — It is possible that this type corresponds to *Nyssapollenites kruschi* ssp. *analepticus* in Thiele-Pfeiffer (1988, plate 15, figures 28–29). Collinson et al. (2012) described *Nyssa disseminata* (R. Ludw.) Kirchheimer endocarps from Messel. Wilde (1989) also reported *Nyssa* sp. leaves from this locality.

*Bee specimen and species.* — FIS MeI 3300 (*Electrapis* sp.); found on leg.

*Occurrence.* — Large clumps with numerous pollen grains. All grains in clumps of same type.

*Life form and pollination.* — Small to large evergreen tree (possibly deciduous); entomophilous (perhaps also anemophilous).

Order Ericales Bercht. et J.Presl



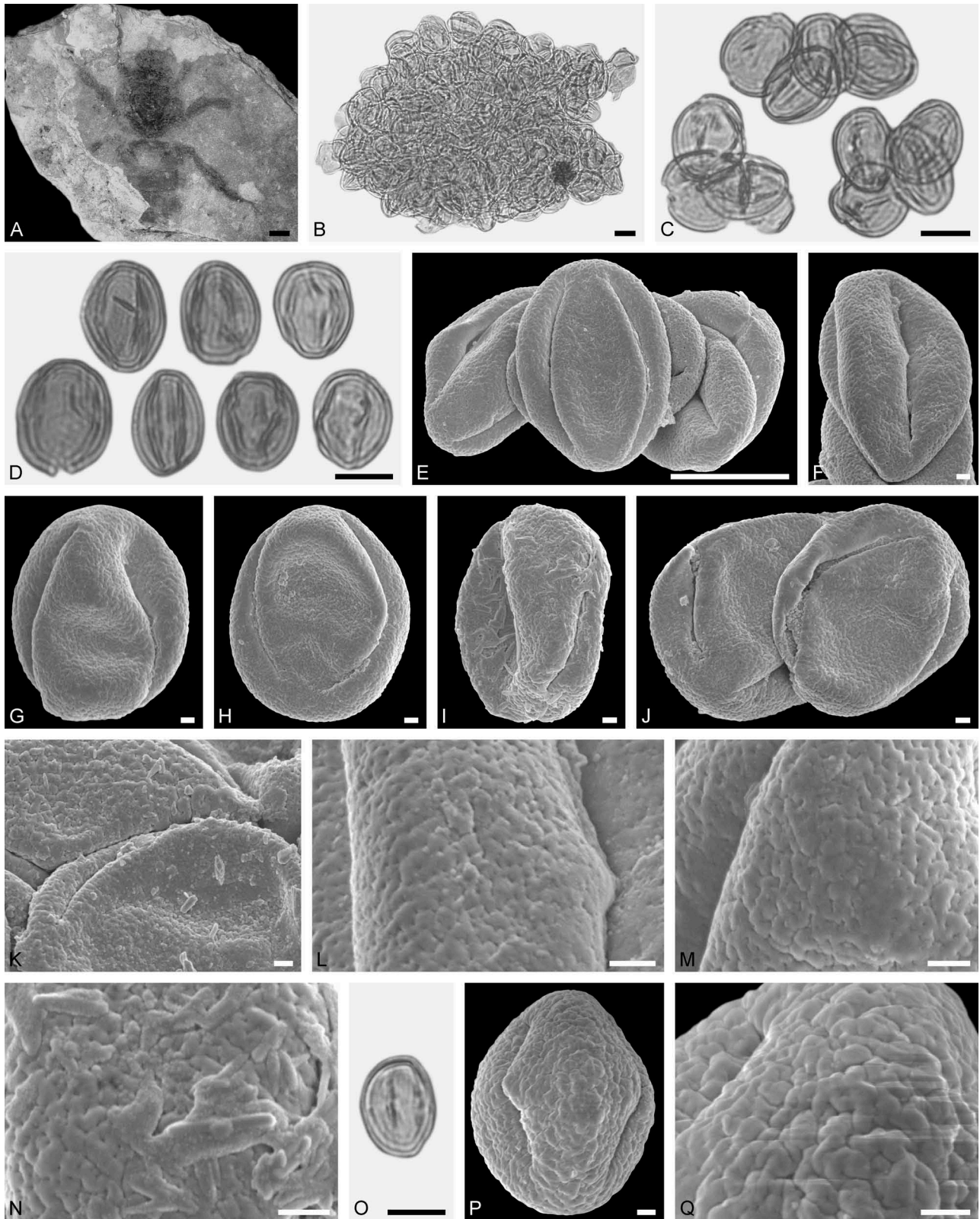


Figure 10. *Electrapis* sp. from Eckfeld and associated pollen grains. **A**. Female (worker caste) PE 2000/849a,b.LS. **B–D**, **O**. LM micrographs. **E–N**, **P**, **Q**. SEM micrographs. **B**, **C**. Clumps dominated by Eudicot ord., fam., gen. et sp. indet. 2 pollen grains, also rare *Decodon* sp. pollen. **E**, **F**, **J**. Clumps with Eudicot ord., fam., gen. et sp. indet. 2 pollen grains. **G–I**. Eudicot ord., fam., gen. et sp. indet. 2 pollen grains in equatorial view. **K–N**. Eudicot ord., fam., gen. et sp. indet. 2, detail of tectum surface. **O–Q**. *Decodon* sp. pollen. **Q**. *Decodon* sp., detail of tectum surface. Scale bars – 1 mm (A), 10  $\mu$ m (B–D, O), 1  $\mu$ m (F–N, P, Q).

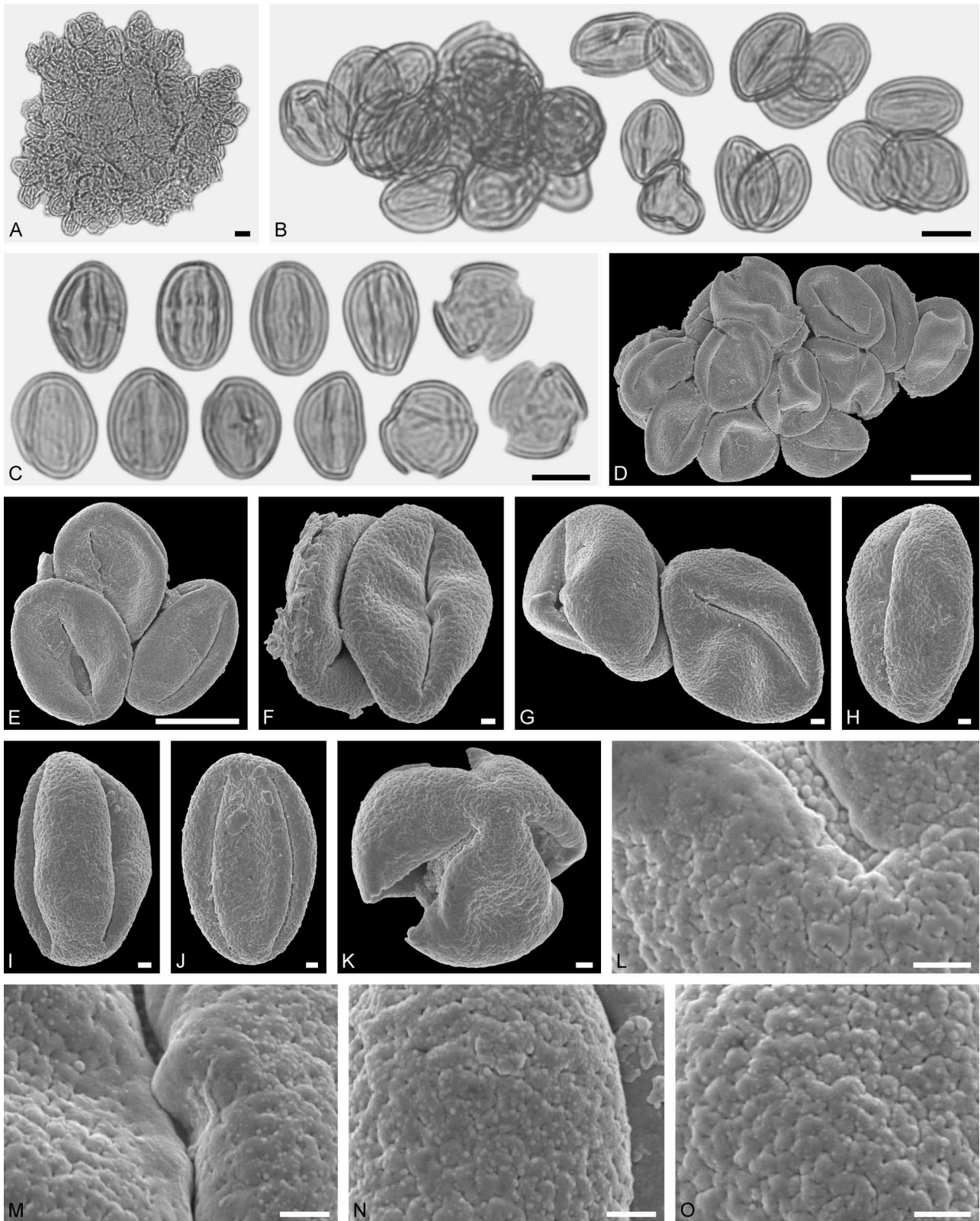


Figure 11. Pollen grains on *Electrapis* sp. (PE 2000/849a,b,LS) from Eckfeld. **A–C.** LM micrographs. **D–O.** SEM micrographs. **A, B.** Clumps with Eudicot ord., fam., gen. et sp. indet. 2. **C.** Eudicot ord., fam., gen. et sp. indet. 2 pollen grains in equatorial view (left) and polar view (right). **D–G.** Clumps with Eudicot ord., fam., gen. et sp. indet. 2 pollen grains. **H–J.** Eudicot ord., fam., gen. et sp. indet. 2 pollen grains in equatorial view. **K.** Eudicot ord., fam., gen. et sp. indet. 2 pollen grain in polar view. **L–O.** Eudicot ord., fam., gen. et sp. indet. 2, detail of tectum surface. Scale bars – 10  $\mu\text{m}$  (A–E), 1  $\mu\text{m}$  (F–O).

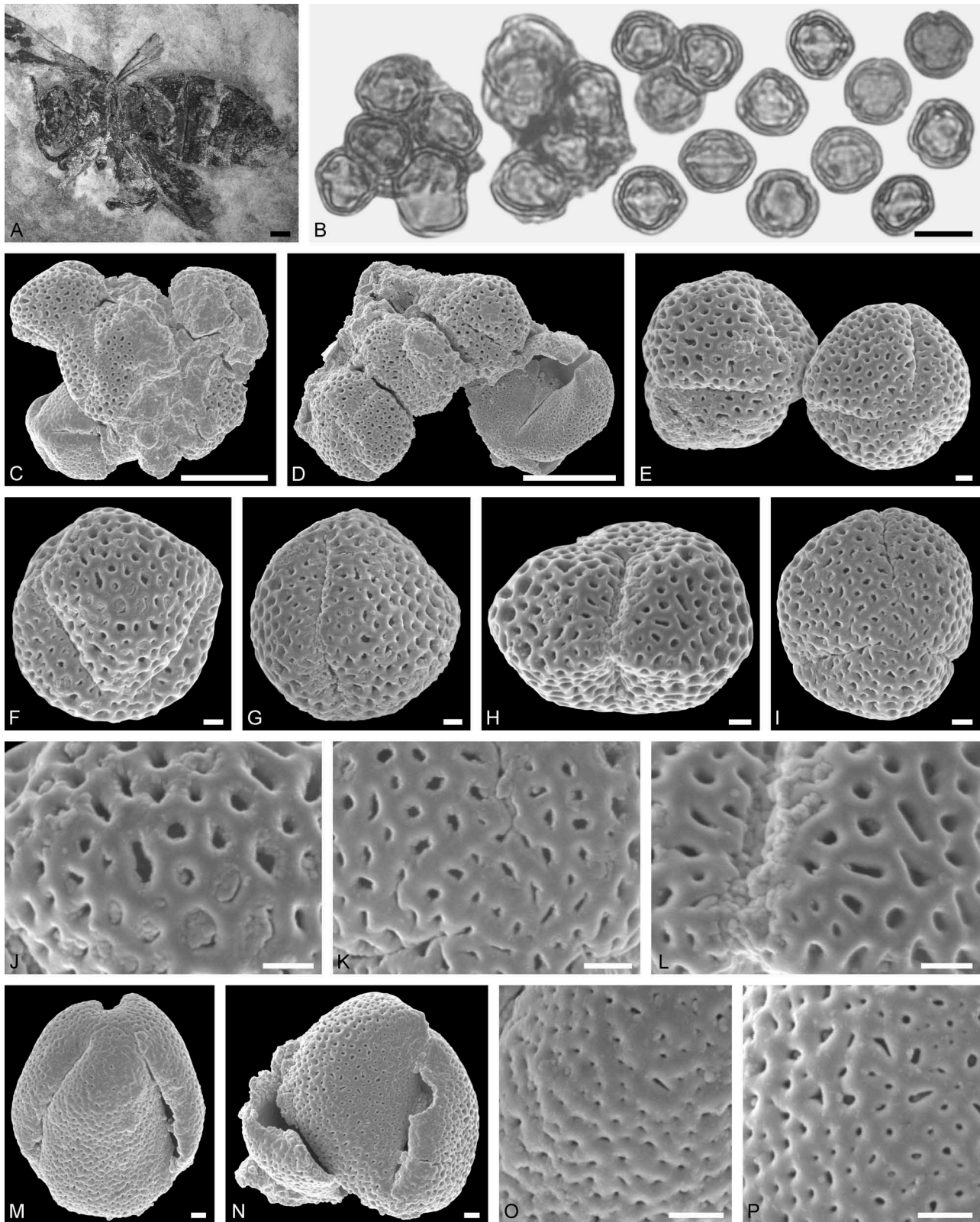


Figure 12. *Electrapis micheneri* Wappler et Engel from Eckfeld and associated pollen grains. **A.** Female (worker caste) PE 2000/852a,b.LS. **B.** LM micrograph. **C–P.** SEM micrographs. **B.** Groups with Eudicot ord., fam., gen. et sp. indet. 4 and Eudicot ord., fam., gen. et sp. indet. 5 pollen grains (left), and pollen of Eudicot ord., fam., gen. et sp. indet. 4 in equatorial and polar view (right). **C–E.** Clumps with Eudicot ord., fam., gen. et sp. indet. 4 pollen grains. **F–H.** Eudicot ord., fam., gen. et sp. indet. 4 pollen grains in equatorial view. **I.** Eudicot ord., fam., gen. et sp. indet. 4 pollen in polar view. **J–L.** Eudicot ord., fam., gen. et sp. indet. 4, detail of tectum surface. **M, N.** Eudicot ord., fam., gen. et sp. indet. 5 pollen grains in equatorial view. **O, P.** Eudicot ord., fam., gen. et sp. indet. 5, detail of tectum surface. Scale bars – 1 mm (A), 10  $\mu$ m (B–D), 1  $\mu$ m (E–P).

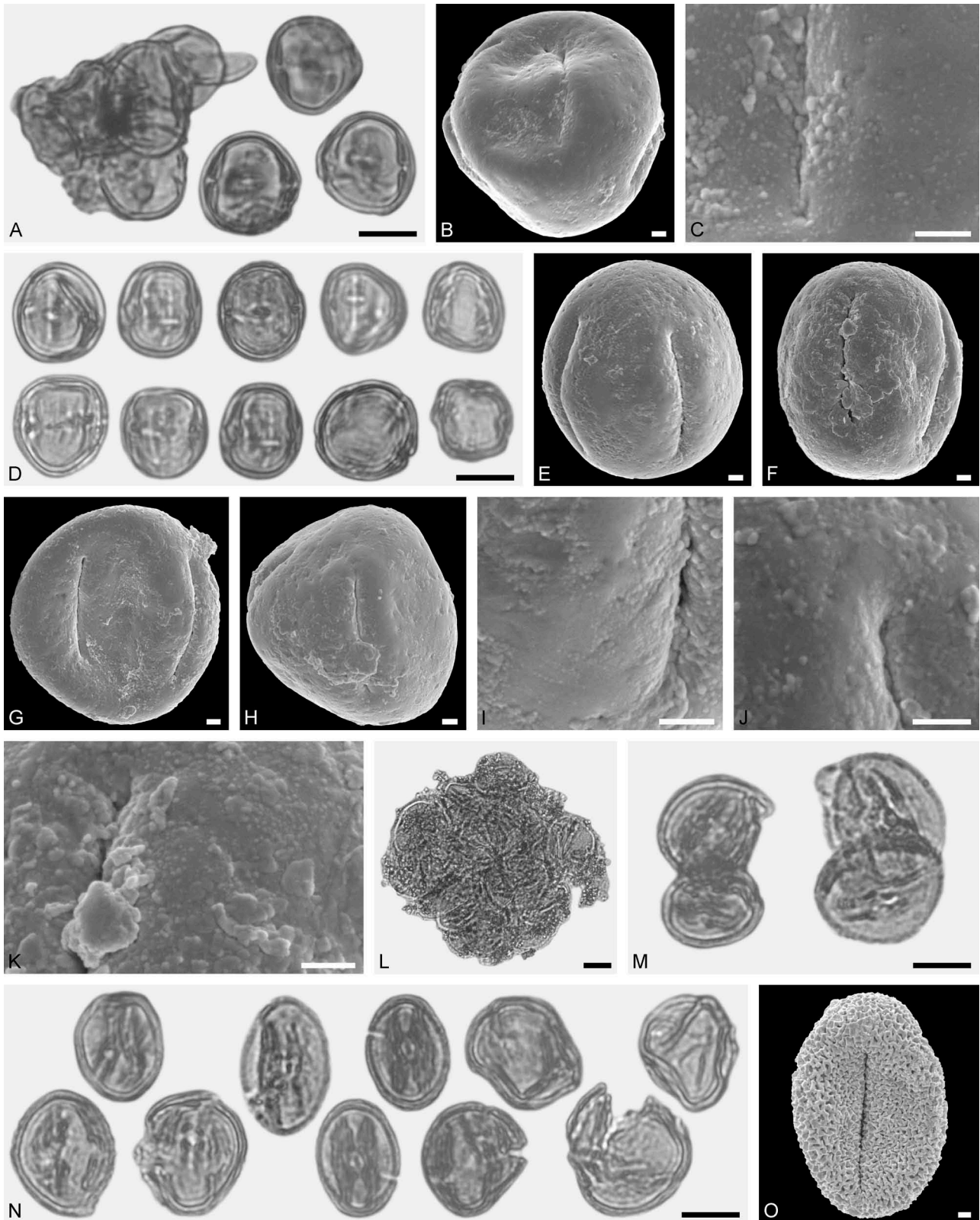


Figure 13. Pollen grains on *Electrapis micheneri* Wappler et Engel (PE 2000/852a,b,LS) from Eckfeld. **A, D, L–N.** LM micrographs. **B–C, E–K, O.** SEM micrographs. **A.** Group with *Pouteria* sp. pollen grains and single grains in equatorial view. **B.** *Pouteria* sp. pollen in equatorial view. **C.** *Pouteria* sp., detail of tectum surface. **D.** *Pouteria* sp. pollen grains in equatorial (left) and polar view (right). **E–H.** *Pouteria* sp. pollen in equatorial view. **I–K.** *Pouteria* sp., detail of tectum surface. **L, M.** Clumps with Euphorbiaceae gen. et sp. indet. 2 pollen grains. **N.** Euphorbiaceae gen. et sp. indet. 2 pollen grains in equatorial view. **O.** Euphorbiaceae gen. et sp. indet. 2 pollen in equatorial view. Scale bars – 10  $\mu\text{m}$  (A, D, L–N), 1  $\mu\text{m}$  (B, C, E–K, O).



## Family Sapotaceae Juss.

Genus *Pouteria* Aubl.*Pouteria* sp.  
(Figure 13A–K)

*Description.* — Pollen, prolate, circular in polar view, elliptic in equatorial view; polar axis 18–19  $\mu\text{m}$  long in LM, 17–18  $\mu\text{m}$  long in SEM, equatorial diameter 15–18  $\mu\text{m}$  in LM, 13–17  $\mu\text{m}$  in SEM; stephano(4,5)colporate, endoapertures lalongate elliptic, endoapertures with costa, colpi often short, narrow with broad round to truncated distal ends, nexine in area of colpi thickened; exine 1.2–1.4  $\mu\text{m}$  thick, nexine thinner than sexine (LM); tectate, sculpturing psilate in LM, psilate, perforate in SEM, with irregularly distributed sporopollenin granules (SEM).

*Remarks.* — Pollen of the Sapotaceae (including genus *Pouteria*) have been described in detail using LM and SEM by Harley (1991). The shape and outline of the fossil pollen grains in combination with the number, arrangement and form of the apertures clearly associate these pollen grains with Sapotaceae. The size and sculpturing seen under SEM further suggests that they belong to genus *Pouteria* (cf. Harley 1991).

*Locality.* — Eckfeld.

*Previous records.* — This type corresponds to *Tetracolporopollenites* sp. 3 figured by Nickel (1996, plate 13, figures 34–36). This family was not reported by Wilde and Frankenhäuser (1998) in the macro-fossil record of Eckfeld.

*Bee specimen and species.* — PE 2000/852a,b.LS (*Electrapis micheneri*); found on head, leg.

*Occurrence.* — Large pure clumps.

*Life form and pollination.* — Small to large evergreen tree; entomophilous.

Clade Campanulids  
Order Apiales Nakai  
Family Araliaceae Juss.  
Subfamily Aralioideae Eaton  
Aralioideae gen. et sp. indet. 1  
(Figure 3B–J)

*Description.* — Pollen, prolate, convex-triangular in polar view, elliptic in equatorial view; polar axis 19–27  $\mu\text{m}$  long in LM, 15–27  $\mu\text{m}$  long in SEM, equatorial diameter 17–21  $\mu\text{m}$  in LM, 17–21  $\mu\text{m}$  in SEM;

tricolporate, endopori lalongate rectangular, nexine thickened along polar sides of endoapertures, nexine slightly thickened along colpi; exine 1.6–1.9  $\mu\text{m}$  thick, nexine thinner than sexine (LM), sexine sometimes protruding in area of endoapertures forming a bridge; semitectate, sculpturing scabrate in LM, microreticulate to perforate in SEM, muri denser with slit-like lumen in central mesocolpium area, muri more fused along colpi (SEM).

*Remarks.* — The morphology of this pollen type places it within the Aralioideae. Many genera of the Aralioideae have pollen of similar morphology. There are few detailed generic accounts on the pollen morphology of extant Aralioideae, and we therefore refrain from assigning this to a particular extinct/extant genus, but point out the similarities of this pollen to those from many of the so-called *panax*-type pollen (including *Acanthopanax*, *Dendropanax*, *Heteropanax*, *Kalopanax*, *Oplopanax* and *Panax*; e.g. IBSCIB-CAS 1982; Miyoshi et al. 2011).

*Locality.* — Messel.

*Previous records.* — It is possible that this type corresponds to *Tricolporopollenites* sp. 18 in Thiele-Pfeiffer (1988, plate 14, figures 69–72), but difficult to confirm because the specimen was not investigated by SEM. Collinson et al. (2012) did not report any Araliaceae fruits or seeds from Messel. Wilde (1989) described two different types of Araliaceae leaves (*Hedera* sp., ?cf. *Fatsia*) from Messel.

*Bee specimen and species.* — FIS MeI 6388 (*Protobombus messelensis*); found on leg, thorax, abdomen.

*Occurrence.* — As single grains and in large clumps along with Tilioideae gen. et sp. indet. pollen type.

*Life form and pollination.* — Most likely an evergreen tree or shrub; entomophilous.

Aralioideae gen. et sp. indet. 2  
(Figure 6B–F)

*Description.* — Pollen, prolate, lobate in polar view, elliptic in equatorial view; polar axis 23–25  $\mu\text{m}$  long in LM, 21–23  $\mu\text{m}$  long in SEM, equatorial diameter 19–20  $\mu\text{m}$  in LM, 17–19  $\mu\text{m}$  in SEM; tricolporate, endoapertures lalongate rectangular, nexine thickened along endopori and colpi (LM); exine 1.3–1.5  $\mu\text{m}$  thick, nexine thinner than sexine (LM); semitectate, sculpturing scabrate in LM, microreticulate in SEM, lumina funnel shaped, muri varying in height, muri fused along colpus forming a margo,



sexine protruding over endoaperture forming a bridge (SEM).

*Locality.* — Messel.

*Previous records.* — This pollen type was not found in the dispersed pollen flora described by Thiele-Pfeiffer (1988).

*Bee specimen and species.* — FIS MeI 12151 (*Electrapis* sp.); found on abdomen.

*Occurrence.* — In large pure groups.

*Life form and pollination.* — Most likely an evergreen tree or shrub; entomophilous.

#### Eudicots

*Remarks.* — We are unable to affiliate the following five pollen types from Eckfeld to any extinct or extant Eudicot family. All five types were not reported by Nickel (1994, 1996) in the dispersed pollen flora from Eckfeld.

Eudicot ord., fam., gen. et sp. indet. 1  
(Figure 7I–M)

*Description.* — Pollen, prolate, lobate in polar view, elliptic in equatorial view; polar axis 13–16  $\mu\text{m}$  long in LM, 12–14  $\mu\text{m}$  long in SEM, equatorial diameter 12–13  $\mu\text{m}$  in LM, 11–12  $\mu\text{m}$  in SEM; tricolporate; exine 1.0–1.3  $\mu\text{m}$  thick (LM), nexine thinner than sexine; tectate; sculpturing scabrate in LM, micro-rugulate, perforate in SEM, sexine protruding markedly in area of endoaperture forming a conspicuous bridge (SEM).

*Bee specimen and species.* — PE 2000/846a,b,LS (*Electrapis* sp.); found on leg.

*Occurrence.* — As single grains or in small clumps along with the *Castanopsis/Lithocarpus* sp. pollen type.

*Life form and pollination.* — Unknown; probably entomophilous.

Eudicot ord., fam., gen. et sp. indet. 2  
(Figures 8B–G, I, K–M, O–Q, 9M–R, 10B–N, 11A–O)

*Description.* — Pollen, prolate, lobate in polar view, elliptic in equatorial view; polar axis 18–21  $\mu\text{m}$  long in LM, 18–20  $\mu\text{m}$  long in SEM, equatorial diameter 12–17  $\mu\text{m}$  in LM, 12–16  $\mu\text{m}$  in SEM; tricolporate, endoapertures lalongate slit-like; exine 0.7–1.0  $\mu\text{m}$

thick, nexine thinner than sexine (LM); tectate, sculpturing scabrate in LM, microrugulate, perforate in SEM, microrugulae fused around colpi forming a psilate broad margo, sexine often protruding around endoapertures forming a bridge, distal ends of colpi truncated to round, colpus membrane microverrucate to microechinate, surface often overlain by irregularly distributed granular sporopollenin particles (SEM).

*Bee specimen and species.* — PE 2000/847.LS (*Electrapis prolata*); PE 2000/849a,b,LS (*Electrapis* sp.); found on leg (both specimens).

*Occurrence.* — In large groups along with Iridaceae gen. et sp. indet., Eudicot ord., fam., gen. et sp. indet. 3 and Anacardiaceae gen. et sp. indet. pollen types.

*Life form and pollination.* — Unknown; probably entomophilous.

Eudicot ord., fam., gen. et sp. indet. 3  
(Figures 8D–F, J; 9A–B, D–F)

*Description.* — Pollen, prolate, lobate in polar view, elliptic in equatorial view; polar axis 20–23  $\mu\text{m}$  long in LM, 18–22  $\mu\text{m}$  long in SEM, equatorial diameter 12–14  $\mu\text{m}$  in LM, 11–12  $\mu\text{m}$  in SEM; tricolporate; exine 0.9–1.2  $\mu\text{m}$  thick, nexine thinner than sexine (LM); tectate, sculpturing scabrate in LM, rugulate, perforate in SEM, numerous perforations in grooves between rugulae, perforations in groups and/or rows, distal ends of colpi truncated to round, colpus membrane microverrucate to microechinate (SEM).

*Bee specimen and species.* — PE 2000/847.LS (*Electrapis prolata*); found on leg.

*Occurrence.* — In large groups along with Iridaceae gen. et sp. indet., Eudicot ord., fam., gen. et sp. indet. 2 and Anacardiaceae gen. et sp. indet. pollen types.

*Life form and pollination.* — Unknown; probably entomophilous.

Eudicot ord., fam., gen. et sp. indet. 4  
(Figure 12B–L)

*Description.* — Pollen, oblate to spheroidal, circular to lobate in polar view, elliptic in equatorial view; polar axis 11–13  $\mu\text{m}$  long in LM, 9–13  $\mu\text{m}$  long in SEM, equatorial diameter 12–14  $\mu\text{m}$  in LM, 11–14  $\mu\text{m}$  in SEM; tricolporate, endoapertures long, lalongate rectangular to slit-like, forming an endocingulum; exine 1.8–2.0  $\mu\text{m}$  thick, nexine thinner

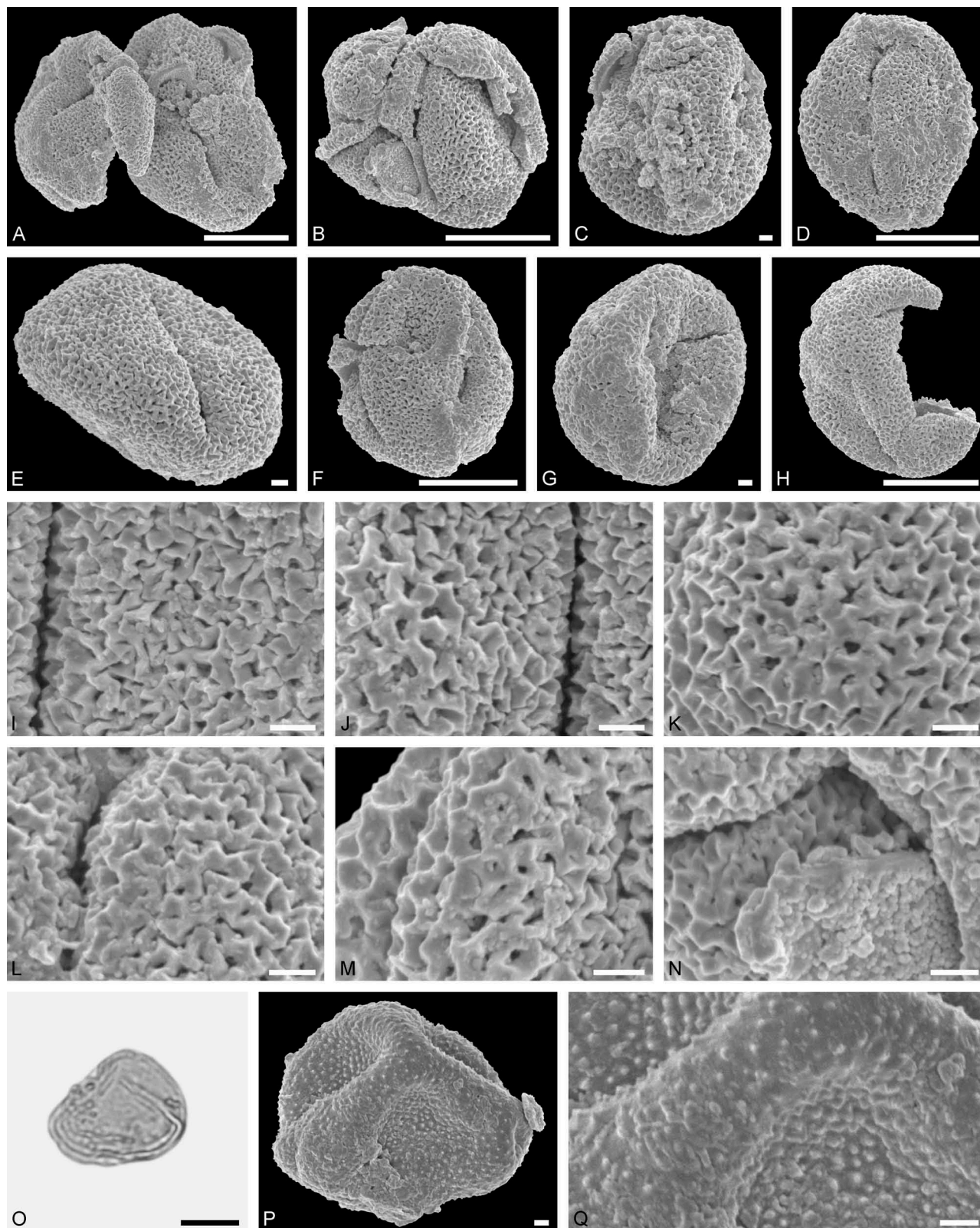


Figure 14. Pollen grains on *Electrapis micheneri* Wappler et Engel (PE 2000/852a,b,LS) from Eckfeld. **A–N, P, Q.** SEM micrographs. **O.** LM micrograph. **A, B.** Clumps with Euphorbiaceae gen. et sp. indet. 2 pollen grains. **C–H.** Euphorbiaceae gen. et sp. indet. 2 pollen grains in equatorial view. **I–N.** Euphorbiaceae gen. et sp. indet. 2, detail of tectum surface. **O, P.** Engelhardioideae gen. et sp. indet. pollen grain in polar view. **Q.** Engelhardioideae gen. et sp. indet., detail of tectum surface. Scale bars – 10  $\mu\text{m}$  (A, B, D, F, O), 1  $\mu\text{m}$  (C, E, G, I–N, P, Q).

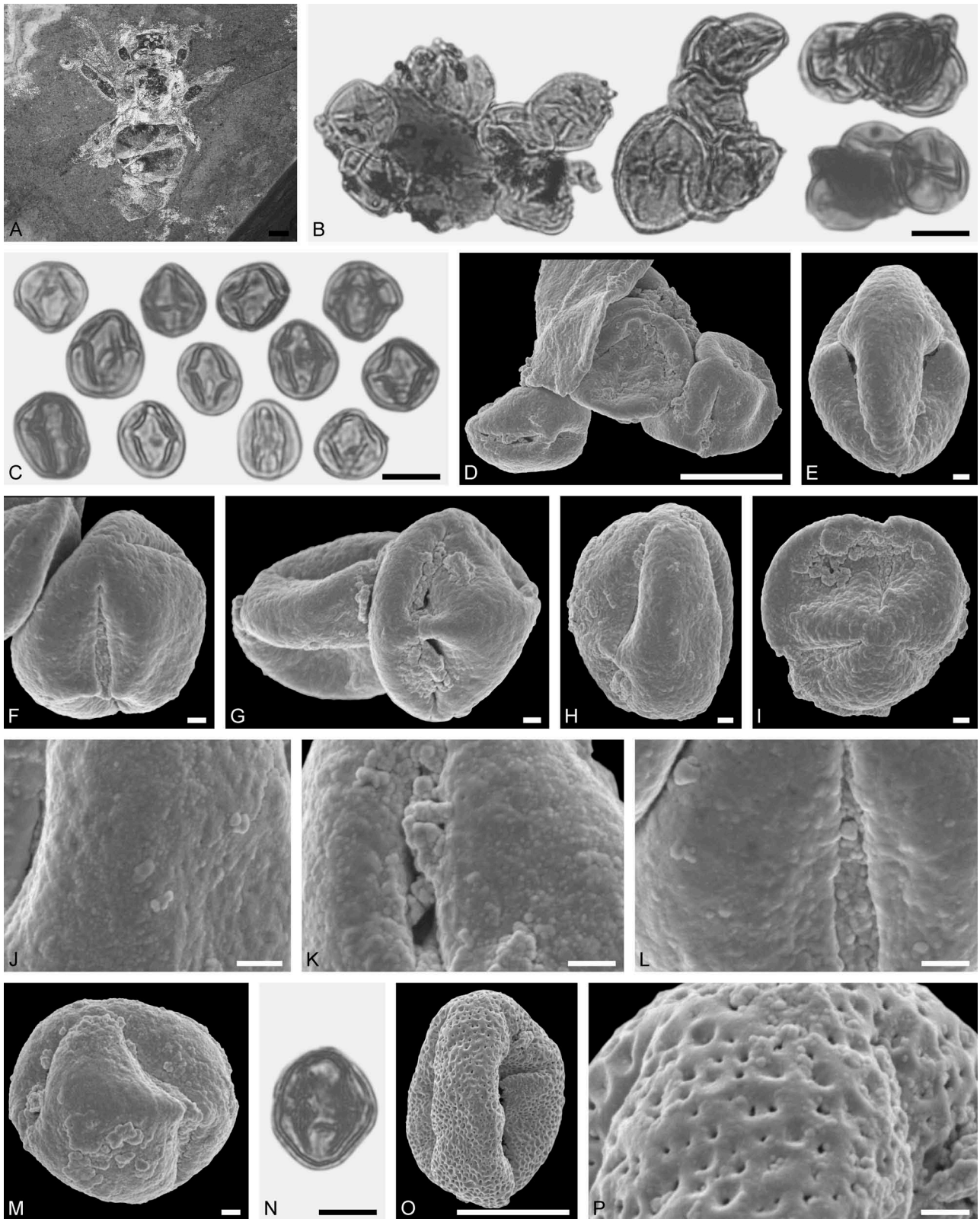


Figure 15. *Protobombus pristinus* Wappler et Engel from Eckfeld and associated pollen grains. **A.** Female (worker caste) PE 2000/863a,b.LS. **B, C, N.** LM micrographs. **D–M, O, P.** SEM micrographs. **B.** Clumps dominated by *Elaeocarpus* sp. 2 pollen grains, with rare Euphorbiaceae gen. et sp. indet. 3 pollen grains. **C.** *Elaeocarpus* sp. 2 pollen grains in equatorial view. **D, F, G.** Clumps of *Elaeocarpus* sp. 2 pollen grains. **E, H, M.** *Elaeocarpus* sp. 2 pollen in equatorial view. **I.** *Elaeocarpus* sp. 2 pollen in polar view. **J–L.** *Elaeocarpus* sp. 2, detail of tectum surface. **N, O.** Euphorbiaceae gen. et sp. indet. 3 pollen in equatorial view. **P.** Euphorbiaceae gen. et sp. indet. 3, detail of tectum surface. Scale bars – 1 mm (A), 10  $\mu$ m (B–D, N–O), 1  $\mu$ m (E–M, P).

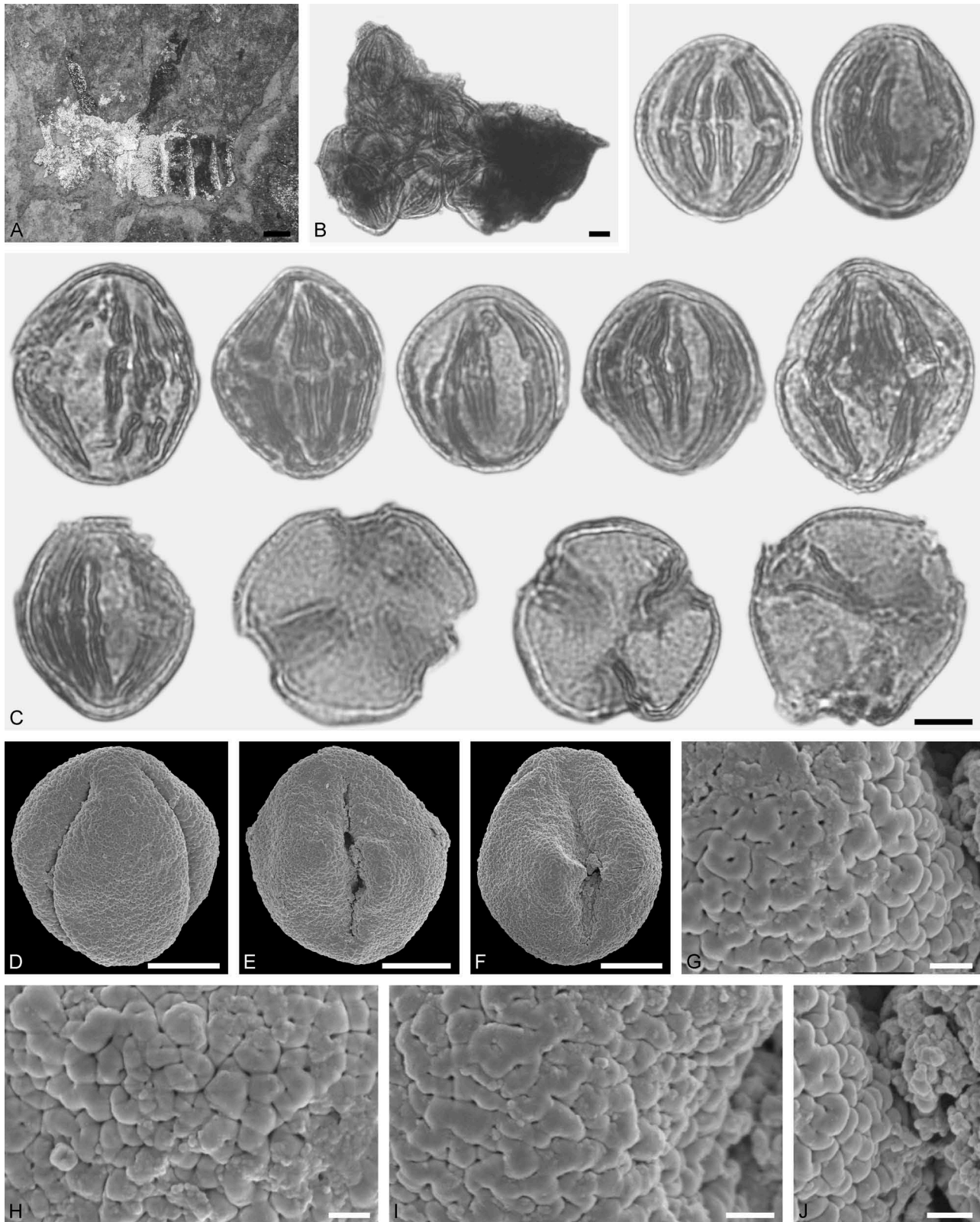


Figure 16. *Protobombus* sp. from Eckfeld and associated pollen grains. **A.** Female (worker caste) PE 2014/1a,b.LS. **B, C.** LM micrographs. **D–J.** SEM micrographs. **B.** Clump with Mastixioideae gen. et sp. indet. pollen grains. **C.** Mastixioideae gen. et sp. indet. pollen grains in equatorial view (upper left) and polar view (lower right). **D–F.** Mastixioideae gen. et sp. indet. pollen grains in equatorial view. **G–J.** Mastixioideae gen. et sp. indet., detail of tectum surface. Scale bars – 1 mm (A), 10  $\mu$ m (B–F), 1  $\mu$ m (G–J).



than sexine (LM); semitectate, sculpturing scabrate in LM, microreticulate in SEM, lumina decreasing in polar areas, sexine slightly protruding over endoapertures forming a bridge, colpus membrane microverrucate to microrugulate (SEM).

*Bee specimen and species.* — PE 2000/852a.b,LS (*Electrapis micheneri*); found on thorax, abdomen.

*Occurrence.* — In large groups along with Eudicot ord., fam., gen. et sp. indet. 5 pollen type.

*Life form and pollination.* — Unknown; probably entomophilous.

Eudicot ord., fam., gen. et sp. indet. 5  
(Figure 12B, M–P)

*Description.* — Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 15–17 µm long in LM, 15–17 µm long in SEM, equatorial diameter 13–15 µm in LM, 13–15 µm in SEM; tricolporate; exine 0.9–1.1 µm thick, nexine thinner than sexine (LM); tectate, sculpturing psilate in LM, perforate to microreticulate in SEM, perforations decreasing in size towards colpi (SEM).

*Bee specimen and species.* — PE 2000/852a.b,LS (*Electrapis micheneri*); found on thorax, abdomen.

*Occurrence.* — In large groups along with the Eudicot ord., fam., gen. et sp. indet. 4 pollen type.

*Life form and pollination.* — Unknown; probably entomophilous.

## Discussion

*Comparison of in situ bee pollen inventory with that of the sediments*

Despite the relatively low number of distinct pollen types (23 types from 12 families of 11 angiosperm orders), the *in situ* pollen cover a substantial taxonomic range of eudicots and one representative of the monocots (Figure 17, Table I). Nine of the types described here may refer to dispersed pollen described earlier (Thiele-Pfeiffer 1988; Nickel 1994, 1996); the other 15 (including five eudicot pollen of unknown affinity) are new for the two localities Messel and Eckfeld (Table II). The maximum number of pollen types found on a single bee is five (specimen PE 2000/846a,b,LS; *Electrapis* sp. from Eckfeld); the median amount is two (Figure 18; Table II). The LM studies by Thiele-Pfeiffer (1988)

Table II. Pollen diversity (in number of distinguished types) at Messel and Eckfeld localities with respect to the bee specimen on which the pollen types were found. Number for dispersed pollen types refer to the studies of Thiele-Pfeiffer (1988) and Nickel (1996).

Locality/bee specimen <sup>a</sup>	Number of distinct pollen types						
	Total	Asterids	Fabids	Malvids	Other core eudicots	Monocots	Eudicot, aff. indet.
<b>Messel</b>							
FIS MeI 3300 ( <i>Electrapis</i> sp.)	1	1					
FIS MeI 12151 ( <i>Electrapis</i> sp.)	2	1		1 <sup>c</sup>			
FIS MeI 6388 ( <i>Protobombus messelensis</i> )	2	1		1			
FIS MeI 10890 ( <i>Electrapis</i> sp.)	2		1	1 <sup>c</sup>			
Types <i>in situ</i>	6	3	1	2 <sup>c</sup>	0	0	0
With possible dispersed analogues	5	1	1	3	0	0	0
Total number of dispersed pollen types	140 <sup>b</sup>	18	32	9	5	7	66
<b>Eckfeld</b>							
PE 2014/1a,b,LS ( <i>Protobombus</i> sp.)	1	1					
PE 2000/846a,b,LS ( <i>Electrapis</i> sp.)	5		4				1
PE 2000/863a,b,LS ( <i>Protobombus pristinus</i> )	1		1				
PE 2000/847.LS ( <i>Electrapis prolata</i> )	4			1		1	2
PE 2000/849a,b,LS ( <i>Electrapis</i> sp.)	2			1			1
PE 1997/20.LS ( <i>Electrapis electrapoides</i> )	1				1		
PE 2000/852a.b,LS ( <i>Electrapis micheneri</i> )	5	1	2				2
Types <i>in situ</i>	19	2	7	2	1	1	6
With possible dispersed analogues	5	1	2	1	1	0	0
Total number of dispersed pollen types	161 <sup>b</sup>	26	27	11	7	10	77

<sup>a</sup>Palaeozoological taxonomy follows Wappler and Engel (2003). <sup>b</sup>Including pollen assigned to not listed angiosperm groups (basal angiosperms, magnoliids, basal eudicots). <sup>c</sup>Same type on both bee specimens.



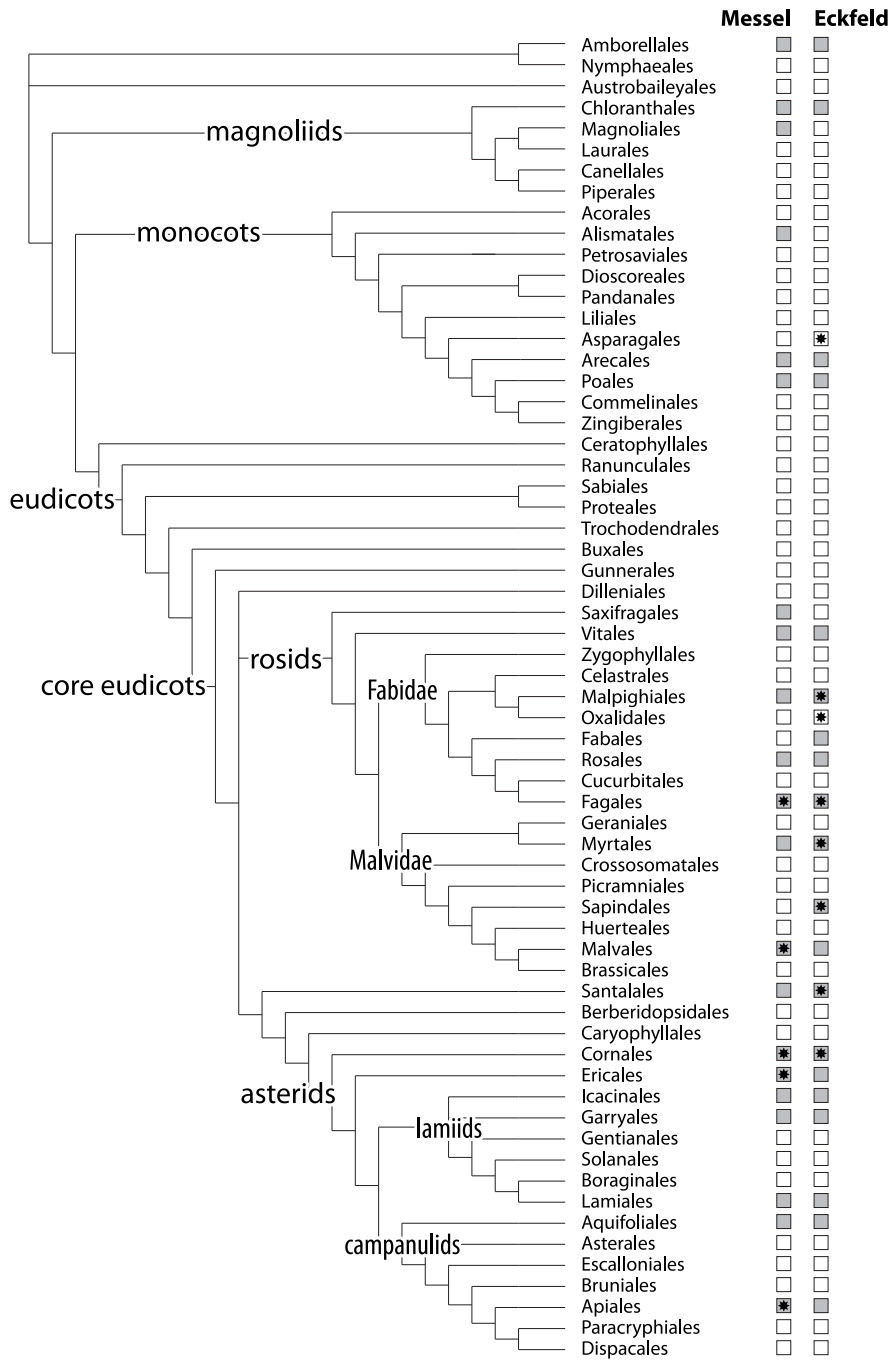


Figure 17. Angiosperm pollen diversity at the Eocene Messel and Eckfeld localities mapped on currently accepted angiosperm phylogeny (Stevens 2001+; APG III 2009), deep relationships modified after (Goremykin et al. 2015). Grey filled boxes indicate orders present in the LM studied sedimentary pollen record of Messel and Eckfeld, black stars highlight angiosperm orders documented here from bee fossils originating from both localities.

and Nickel (1994, 1996) list in total 240 pollen types (including 125 of unknown or uncertain systematic affinity). The remaining 114 pollen types are assigned to 38 families of angiosperms from 25 orders (File S1). The total numbers of distinguished pollen types cannot be straightforwardly compared between our study and the earlier LM studies. Pollen types distinguished under LM may represent the same SEM-defined pollen taxon and vice versa. A one-to-one comparison would necessitate studying

dispersed pollen obtained from sediment samples at both localities using SEM. Nevertheless, taxonomic control is typically poorer in LM than in SEM studies. As far as known, SEM studies of the same dispersed pollen flora reveal usually higher biodiversity and taxonomic resolution than LM studies (Grímsson & Zetter 2011; Grímsson et al. 2011, 2015a, 2016; Bouchal et al. 2016). Thus, it could be expected that a comprehensive SEM study of the dispersed pollen at Messel and Eckfeld would pro-

Table III. Further information for taxa found on Messel and Eckfeld bees compiled from various resources.

Pollen taxa	Constituent <sup>a</sup> taxa	Modern distribution	Köppen signature
<b>Eckfeld</b>			
Iridoideae	30 genera, 820 spp. (APW)	Worldwide, with focus on Central and South America (APW)	<i>A-, B-, C-</i> and warmest <i>D</i> -climates
<i>Elaeocarpus</i>	<i>c.</i> 360 spp. (FoC)	Mainly Old World Tropics; extending into subtropics in East Asia and into temperate SE Australia, New Zealand and mountains of eastern Madagascar (GBIF, > 32 000 records)	<i>A, Cfa, Cwa, Cfb</i>
Euphorbiaceae	218 genera, > 6500 spp. (APW)	Worldwide, except (sub-)arctic-alpine environments	<i>A-, B-, C-</i> and <i>D</i> -climates
<i>Decodon</i>	Monotypic	Subtropical to temperate eastern North America (FoNA)	<i>Cfa, Cfb, Dfa, Dfb</i>
Anacardiaceae	80 genera, 873 spp. (APW)	Mostly tropical, some genera extending far into the temperate zone (APW)	<i>A-, B-, and C-</i> climates, <i>D</i> -climates with hot or warm summers
<i>Olax</i>	<i>c.</i> 40 species (FoC)	Tropical Africa and Southeast Asia, tropical and subtropical Australasia (GBIF, >5800 records)	<i>A, Cfa, Cfb, Csa, Csb</i>
<i>Pouteria</i>	<i>c.</i> 50 species (FoC)	Tropical Americas (until S Florida), Africa, Southeast Asia and Australasia (here extending into coast lands of subtropical Australia and northernmost New Zealand; GBIF >20 000 records)	<i>A, (Cfa)</i>
Mastixioideae	2 genera, 27 species (FoC)	South, Southeast and East Asia ( <i>Diplopanax, Mastixia</i> ; FoC; GBIF ~400 records)	<i>A, (Cwa)</i>
<b>Eckfeld and Messel</b>			
Evergreen castanoids	4 genera, >420 spp. (FoC; three in North America, FoNA)	Tropical to subtropical East and Southeast Asia, and New Guinea ( <i>Castanopsis, Lithocarpus</i> ; GBIF, >22 000 records); subtropical to temperate western North America ( <i>Chyrsolepis, Notholithocarpus</i> ; FoNA)	<i>A, Cfa, Cwa</i> [ <i>Cast., Lith.</i> ] <i>Csb, Dsb</i> [ <i>Noth., Chr.</i> ]
<b>Messel</b>			
<i>Mortoniendron</i>	18 spp. (Tropicos)	Central America, sea level to high montane forests (GBIF, >1000 records; CRBP, 559 records)	<i>A, Cfa, Cwa</i>
Other Tilioideae	2 genera <sup>a</sup> , up to 40 spp. (FoC)	Subtropical to temperate parts of the Northern Hemisphere, in Canada and Scandinavia into snow climates ( <i>Tilia</i> ; GBIF >82 000 records), <i>Craigia</i> restricted to south-central China, N Vietnam (FoC)	<i>Cfa, Cfb, Cwa, Cwb, (Dfa, Dfb)</i>
<i>Nyssa</i>	<i>c.</i> 12 species (FoC, FoNA)	Subtropical to temperate eastern North America, southern half of China (mostly subtropical climates; GBIF, >1200 records), one species distributed from India to Malaysia (FoC)	<i>Cfa, Cfb, Dfa, Cwa</i>
Aralioideae	41 genera, 1275 spp. (APW)	Mostly tropical, but a few extending deep into the temperate zone (APW)	<i>A-, C-</i> and warmer <i>D</i> -climates

Abbreviations of data sources (online data bases, accessed 20 August 2015): APW, Angiosperm Phylogeny Website (Stevens 2001+); GBIF, Global Biodiversity Information Facility, [www.gbif.org](http://www.gbif.org); CRBP, Costa Rica Biodiversity Portal, <http://crbio.cr/portalCRBio>; FoC, e-Flora of China (eFlora 2008); FoNA, e-Flora of North America (eFloras 2008), Tropicos, Tropicos® database (Tropicos.org). <sup>a</sup>*Craigia, Tilia*, not including *Mortoniendron*.

vide a large number of distinct taxa (genera, groups of genera).

It is clear that the *in situ* pollen on the bees only cover a relatively small fraction of the actual middle Eocene floral diversity in and around the Messel and Eckfeld localities. There are several explanations for the low diversity of pollen attached to the bee fossils. The most important elements at both localities – regarding the number of distinguished pollen taxa in the dispersed pollen record – are the fabids. Fabids at Messel and Eckfeld account for 43% and 32%, respectively, of pollen taxa listed with unambiguous systematic affinity, followed by asterids of the orders Cornales and Ericales (14% and 21%,

respectively). Both angiosperm groups include many wind-pollinated modern genera and species, and, in the case of Fagales, which account for over 20% of the LM-diagnosed pollen taxa at both localities, are predominately or partly wind-pollinated. In addition, eusocial bees harvest pollen within a limited range of their dwellings, and the extinct species may have had collection preferences similar to some of their modern-day relatives (Wappler et al. 2015), almost all of whom are polylectic (e.g. Apini, Meliponini, Bombini). Furthermore, insect-pollinated taxa are typically underrepresented in the dispersed pollen record because of their much lower pollen yield, and many groups are easily overlooked,

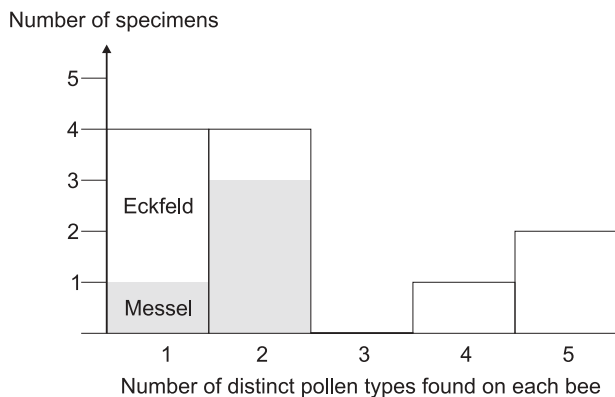


Figure 18. Bar chart visualising the number of pollen types found on individual bee specimens (cf. Table I).

particularly when the dispersed pollen flora is studied using LM only. This is highlighted by our results.

Despite the fact that the pollen obtained *in situ* from the 12 bee fossils cover only one-third of the families found in the dispersed pollen inventories, we have discovered for the first time evidence of the monocot order Aspergales (Iridoideae gen. et sp. indet.), the fabid order Oxidales (*Elaeocarpus* sp. 1, sp. 2; Figures 7, 15) and the family Euphorbiaceae (three pollen types; a member of the Malpighiales) in the Eocene of Eckfeld. Previously, the Malpighiales were represented by only a single pollen taxon (*Tricolpopollenites retiformis* P.W.Thomson et Pfug) with affinity to *Salix* and reported from both localities (File S2; Thiele-Pfeiffer 1988; Nickel 1996). Also new is the discovery of *Decodon* (Lythraceae) at Eckfeld. Lythraceae pollen types with putative affinity to *Ammannia*, *Lawsonia*, *Rotala* and *Woodfordia* have been described so far only from Messel (File S2; Thiele-Pfeiffer 1988). However, the new type of Mastixioideae pollen confirms prior LM studies that distinguished one or two taxa at both localities (File S2; Thiele-Pfeiffer 1988; Nickel 1994, 1996). In the case of Messel, our *Mortoni dendron* pollen adds to the known Tilioideae diversity (two taxa described by Thiele-Pfeiffer 1988). In conclusion, our investigation of pollen adherent to bee fossils shows that these natural ‘pollen traps’ can provide new insights and complement our knowledge on the broader palaeo-palynological assemblages.

#### *Pollen-collecting/-feeding insects as natural ‘pollen traps’*

There are only a few studies, which diagnosed pollen in or on insect fossils. This is surprising given the considerable interest in insect–plant interactions and coevolution, and that such pollen is perhaps the best

direct evidence for such associations. Probably the oldest record of insects feeding on pollen (with affinities to conifer, glossopterid and peltasperm pollen) is from the Cisuralian (Krassilov & Rasnitsyn 1996). In addition, the same authors described conifer pollen and pollen of unknown affinity from the intestines of Lower Cretaceous sawflies (Krassilov & Rasnitsyn 1982). Pollen with potential affinity to angiosperms (*Afropollis* sp.) has been cited to occur also in the intestines of mid-Cretaceous wasps (Caldas et al. 1989). A spectacular find was a taxonomically identifiable orchid pollinium attached to a worker of the fossil stingless bee *Proplebeia dominicana* (Wille et Chandler) in early Miocene (19–15 Ma) amber from the Dominican Republic (Ramírez et al. 2007). Prior to this, orchid fossils had not been found from the Dominican Republic, although their presence was predicted by the occurrence of orchid bees (Euglossini) in the same Miocene deposits (Engel 1999) and the same is true for Mexican amber (Engel 2014). Many fossil bees preserved in amber, not only corbiculate bees, have pollen preserved in their scopae or corbiculae (e.g. Engel 1995, 1998, 2006, 2009), but it is often not possible to observe sufficient details owing to an inability to prepare the material close to the individual grains without destroying the bee. Unfortunately, the oldest definitive bee, *Cretotrigona prisca* (Michener et Grimaldi) in Maastrichtian amber from New Jersey, is not preserved with its pollen (Engel 2000) and meaningful evidence from the Cretaceous record of bee–plant interactions is challenging to ascertain (Michez et al. 2012).

Naturally, bees are not the only pollinating insects and fossil pollen is also preserved on the bodies of other such insect groups (e.g. amber inclusions of fig wasps; Peñalver et al. 2006). Even though known to exist for quite a long time, at least for the Eckfeld locality (Lutz 1993), pollen clumps contained in the corbiculae of ancient bees had not previously been examined. Whereas the *in situ* pollen in flowers embedded in coeval Baltic amber has been studied to some degree (Weitschat & Wichard 2002), pollen on those bees reported from the same fossil resins (Engel 2001a) have yet to be explored.

The pollen documented here provides the oldest unambiguous (pollen) record of *Elaeocarpus* (Oxidales: Elaeocarpaceae), *Mortoni dendron* (Malvales: Malvaceae: Tilioideae), *Olax* (Santalales: Olacaceae) and *Pouteria* (Ericales: Sapotaceae). Today, *Elaeocarpus* and *Olax* are found mainly in the Old World Tropics (sub-Saharan Africa, Madagascar, south and southeast Asia, tropical Australasia; Table III), and add two more examples of early Northern Hemisphere occurrences of lineages today restricted to the tropics and extra-tropical Southern Hemi-

sphere (Grímsson et al. 2014). These same records may provide new minimum age priors for calibrating molecular-only estimates of clade divergence times. For instance, in their dating of the Elaeocarpaceae, Crayn et al. (2006) fixed the crown clade of *Elaeocarpus* to 30 Ma based on Oligocene mesocarps from Australia (Dettmann & Clifford 2001), which they considered the earliest attributable fossils for the genus and at the same time reflecting an initial radiation for the group. They estimated a late Eocene (*c.* 39 Ma) age for the divergence of *Elaeocarpus* from its sister group, and their value is about 5 Ma younger than the pollen carried by the ancient bees at Eckfeld Maar in the Northern Hemisphere. Intrafamilial relationships among Santalales have been investigated using molecular data (e.g. Malécot & Nickrent 2008), but the phylogenies were not dated due to a lack of suitable fossils. The same applies to the asterid family Sapotaceae (Manchester et al. 2015). Hence, our pollen of *Olax* and *Pouteria* may serve as the first available ingroup dating constraints for Olacaceae and Sapotaceae.

*Mortonioidendron* is a tropical-subtropical New World relative of the widespread lindens (*Tilia*), today found only in Central America. To our knowledge, there has been no effort to date the divergences among or within the three genera included in the subfamily Tilioideae (*Craigia*, *Mortonioidendron* and *Tilia*). The Eckfeld bees also carry the oldest European evidence of the genus *Decodon*; pollen coeval to the oldest pollen described from the Princeton Chert, British Columbia, Canada (Grímsson et al. 2012). *Decodon* is known from the Late Cretaceous and Paleogene of the Americas (Graham 2013), hence providing further proof that this New World taxon expanded to continental Europe by the middle Eocene (Grímsson et al. 2012). These discoveries highlight the importance of studying pollen found on fossil insects and that dispersed pollen from sediments should also be studied using SEM to more accurately reveal the total ‘true’ diversity of a given palaeo-flora, which is often underestimated by the LM based pollen/sedimentary record, as well as elucidate the interactions of the plants with their pollinators.

#### *Ecological and palaeo-climatic framework of Messel and Eckfeld*

Wilde and Frankenhäuser (1998) refrained from an explicit climatic interpretation based on the palaeo-floristic assemblage (macro-, meso- and micro-fossils) found at Eckfeld. They noted that many of the macro- and meso-fossils cannot be

assigned to modern taxa with any degree of confidence, and highlighted the special taphonomic composition around the maar lake. Major floristic elements around the palaeo-lake were Juglandaceae with affinities to *Platycarya* as well as Engelhardioideae; a high abundance of wind-pollinated Engelhardioideae explains the recovery of this pollen type (single grains) from one of the bees (Table I). In addition, palms were present but may not have been abundant (Wilde & Frankenhäuser 1998). Palms, *Platycarya* and Engelhardioideae thrive in tropical as well as subtropical and temperate habitats without frost or snow in winter.

The pollen found on the bees indicate the presence of several more modern genera (*Decodon*, *Elaeocarpus*, *Olax*, *Pouteria*) and three additional groups (evergreen Castaneoideae, Iridoideae, Mastixioideae), and since the bees can be considered to have harvested pollen directly from flowers of plants within a limited area, they most likely originate from the immediate vicinity of the palaeo-lake. Hence, these records in association with the bees provide a limited but localised impression about the climate, but also evidence for Eocene distributional areas in contrast to modern ranges. In the case of Messel, Aralioideae coexisted with evergreen Castaneoideae, Tilioideae (including *Mortonioidendron*) and *Nyssa*. The geographical distribution of potential modern analogues of the plants producing the *in situ* bee pollen as well as their ‘Köppen signatures’, which indicate the general climate zones occupied by a certain taxon (cf. Denk et al. 2013; Grímsson et al. 2016), also suggest that a warm humid climate prevailed at Eckfeld and Messel during the middle Eocene (Table III). The distribution range of all taxa that coexisted at Messel cover subtropical, fully humid and winter-dry climates (*Cfa*-, *Cw*-climates according to the Köppen classification). Previous accounts on the Messel macro-flora have also suggested a very warm and humid, tropical to subtropical climate (Wilde 1989, p. 119–120; Collinson et al. 2012, p. 13).

Nearly all Eckfeld taxa are found today also in the Tropics except for *Decodon*. However, this genus is today only represented by a single species in eastern North America, but had a much wider distribution in the past encompassing low latitudes (Graham 2013). Analogously, the Mastixioideae, the only taxon in Eckfeld absent from today’s *Cfa*-climates, had a wider distribution in the past. Overall, a warm, humid, subtropical *Cfa*-climate transient to a tropical climate could have provided the environment for the Eckfeld locality (*c.* 2 Ma years younger than Messel), whereas a distinctly subtropical climate, either fully humid (*Cfa*) or with more summer than winter



precipitation (*Cwa*), is favoured for Messel owing to the autochthonous pollen community collected by the bee populations.

## Conclusion

Despite the intensive effort required and limited taxonomic coverage, the study of pollen actively or passively collected by insects can provide valuable new insights and contribute to a more holistic understanding of the floristic components of past ecosystems. One advantage in studying fossil pollen adhered to fossil insects is that insect-pollinated plant taxa that are rare or otherwise hard or even impossible to find in the dispersed pollen (sedimentary) record can be revealed. Such information is vital for neontological research that aims at correlating angiosperm and insect distribution patterns, exploring the evolution of plant–insect interactions and coevolution, or appropriately calibrating molecular estimates of divergence times. Another advantage is the autochthony of pollen found *in situ* on (or in) bees, reflecting a potentially informative fragment of a highly localised flora.

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No potential conflict of interest was reported by the authors.

## Supplemental data

Supplemental data for this article can be accessed [here](#).

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