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ORIGINAL PAPER

Direct and indirect fossil records of megachilid bees from the Paleogene of Central Europe (Hymenoptera: Megachilidae)

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Abstract Aside from pollen and nectar, bees of the subfamily Megachilinae are closely associated with plants as a source of materials for nest construction. Megachilines use resins, masticated leaves, trichomes and other plant materials sometimes along with mud to construct nests in cavities or in soil. Among these, the leafcutter bees (*Megachile* s.l.) are the most famous for their behaviour to line their brood cells with discs cut from various plants. We report on fossil records of one body fossil of a new non-leafcutting megachiline and of 12 leafcuttings from three European sites—Eckfeld and Messel, both in Germany (Eocene), and Menat, France (Paleocene). The excisions include the currently earliest record of probable *Megachile* activity and suggest the presence of such bees in the Paleocene European fauna. Comparison with extant leafcuttings permits the interpretation of a minimal number of species that produced these excisions. The wide range of size for the leafcuttings indirectly might suggest at least two species of *Megachile* for the fauna of Messel in addition to the other megachiline bee described here. The presence of several cuttings on most leaves from Eckfeld implies that the preferential foraging behaviour of extant *Megachile* arose early in megachiline evolution. These results demonstrate that combined investigation of body and trace fossils complement each other in understanding past biodiversity, the latter permitting the detection of taxa not otherwise directly sampled and inferences on behavioural evolution.

Keywords Insecta · Apoidea · Anthophila · Leafcutter bees · Ichnology · Biodiversity · Tertiary · Eckfeld · Messel · Menat

Introduction

Among hymenopteran insects, the bees (Apoidea: Anthophila) are perhaps the most popular group, followed closely by the ants (Formicidae). Most species of bees are solitary; that is, females each build and provision their own nests, while the more intensely investigated social species account for 5% or less of total bee diversity. Bees of the family Megachilidae comprise approximately 3,949 species of solitary or cleptoparasitic bees (Michener 2007; www.discoverlife.org (accessed 18 October 2008)). Megachilids are most noteworthy among bees for the transport of pollen in a ventral metasomal scopa rather than carrying such resources on their legs. The most frequently observed megachilids are the leafcutter bees, a name which obviously refers to the behaviour of many species of the genus *Megachile* to cut oblong or circular discs from leaves or petals with their mandibles (e.g. Michener 1953; Westrich

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1989; Kim 1992). These leaf fragments are then used as materials in nest construction, particularly for the brood cell chamber. A description of the leaf-cutting process is given by Michener (1953: 1716) and Hasenkamp (1974). Nests generally consist of a linear series of up to 15 cylindrical brood cells, which are built in a pre-existing or self-constructed tunnel. The burrows are situated in the soil or in cavities in wood, stems or other hollow objects (e.g. Michener 1953, 2007). Oblong or oval discs are used to line the walls of the brood cells which are longer than the cell's width. Rounded or circular discs are used to form distal and proximal structures in order to close the burrow. In some species, the rounded discs are additionally inserted between the brood cells where they form the cap and sometimes also the bottom of each cell arranged in a linear series (Hasenkamp 1974; Kim 1992, 2007). Several oval leaf discs are used to form a cup in which the provision of the brood cell is stored. The provision consists of nectar and pollen which the female collects and provides as food for the developing larva. After the egg is laid, the orifice of the cell is closed with circular discs to form the cell cap (e.g. Kim 1992). A possible function for lining the nests with leaf discs was given by Westrich (1989: p. 2006). Since the larval provisions of megachilid bees contains much nectar and is rather viscous, the use of leaf discs may prohibit desiccation of the bee-bread during the development of the larva. Larval development is impossible in open cells in which the contents become parched. Stephen and Torchio (1961: 88) assumed that wrapping the cells with leaf discs provides environmental stability within the cell, much in the same way that bees of other families use various chemical linings or other materials to line their cells to similarly prevent desiccation or infection.

While leaf-cutting behaviour is known for a derived clade of the genus *Megachile*, consisting of perhaps 870 modern species (*Megachile* s.l. has about 1,478 living species, or comprising nearly 37% of all megachilid diversity [www.discoverlife.org (2 February 2009)]), most other megachiline bees use masticated leaves, plant trichomes, mud or even resin as nesting materials (e.g. Roubik 1989; Michener 2007).

The fossil record and evolutionary history of megachilid bees have been outlined by Engel (1999, 2001, 2004) with a recent overview of the body fossil record for Megachilidae provided by Engel and Perkovsky (2006). The redescription of *Probombus hirsutus* Piton, 1940 by Nel and Petrulevicius (2003) noted megachiline affinities of this compression fossil from the Paleocene of Menat (France). Unfortunately, insufficiently preserved characters do not permit a more refined attribution of the species and it remains as Megachilinae *incertae sedis*. Other body fossils attributable to the Megachilidae are from Baltic amber which has an Eocene age. These Eocene fossils all belong to extinct subgroups of the Megachilidae as does the record of the body fossil from Messel described herein. Additional records from younger deposits are summarised by Engel (1999). With the exclusion of a single inclusion in Miocene Dominican amber (Engel 1999), most of these records are of Oligocene or Miocene compressions with little or no relief and their attribution as to genus requires serious revision (Engel 1999; Engel and Pervkosky 2006). It is noteworthy that the earliest records of leafcutter bees of the extant genus *Megachile* (e.g. Sarzetti et al. 2008), however, are not of body fossils but, instead, from fossil leafcuttings. The earliest find of leaf-cutting damage by *Megachile* is our possible new record from Menat. A synopsis of the hitherto known fossil records of probable leafcutter bee activity is given in Table 1, which is expanded by the new records provided herein (Table 2). Additional Eocene leaves with as of yet undescribed leafcutter bee damage were mentioned by Johnston (1993) and Labandeira (2002).

In this paper, we record a new body fossil of a non-leafcutting megachiline bee from the Fossillagerstätte Messel and several new megachilid leafcuttings from the Fossillagerstätten Eckfeld and Messel (both Germany) and Menat (France). All three fossil sites have their origin in former maar lakes and while Eckfeld and Messel have an Eocene age (Lutetian, 43 and 47 Ma ago, respectively, Mertz et al. 2000, Mertz and Renne 2005), Menat had its origin during the Paleocene (estimation of age varies: Thanetian, about 56 Ma ago: Russell 1982; Selandrian, about 60 to 61 Ma ago: pers. comm. P. Gingerich 2008 to TW).

The size range of the leaf excisions recorded for these Fossillagerstätten is quite wide, especially for Messel (Table 2). In comparison with extant leafcuttings we try to draw conclusions on the number of species which produced these trace remains.

Material and methods

The material discussed herein was obtained from the following institutions: Forschungsinstitut Senckenberg, Frankfurt/M (FIS); Hessisches Landesmuseum, Darmstadt (HLMD); National Museum d'Histoire Naturelle, Paris (NMHN); Naturhistorisches Museum Mainz (NHMM; coll. numbers beginning with PE or PB). Morphological terminology for the descriptions generally follows that of Engel (2001) and Michener (2007) for the body fossils. The line illustration of the wing venation was prepared using a camera lucida. Each fossil leaf was digitally photographed and extracted from the matrix by using Photoshop (Adobe). Measurements of the excisions were made using Image J (http://rsb.info.nih.gov/ij) and eccentricity of the leaf discs (see Table 2) was calculated using the protocol of Sarzetti et al. (2008). Each excision was measured repeatedly; there-

Table 1 Fossil records of leaf excisions likely produced by bees of the genus *Megachile* s.l. (exclusive of the new records presented herein)

Locality	Age	Collection no.	Plant taxon	Number of excisions	Length of megachilid excisions	Ichnospecies	References; comments
Dominican amber, Dominican Republic	Miocene	Private collection	not determined	1	Unknown		Grimaldi 1996: p. 110/111; megachilid origin unsure
Florissant, Colorado, USA	Upper Eocene	UCM-4543	not determined	3	3 to 3.2 mm	*Phagophytichnus pseudocircus* Sarzetti et al. 2008	Cockerell 1910, Meyer 2003; pers. comm. D. Smith and E. Leckey, 2007 to SW
Eckfeld Maar, Germany	Middle Eocene	PB2001/82 LS	not determined	3	4.5 mm	*P. pseudocircus*	Wappler and Engel 2002, 2003; Wappler 2003
Eckfeld Maar, Germany	Middle Eocene	PE1990/527 LS	not determined	2	3.6 to 3.7 mm		Wappler 2003
Río Pichileufú, Patagonia, Argentina	Middle Eocene	BAR 4740 a-b	not determined	2	ca. 8 mm[a]	*P. pseudocircus*	Sarzetti et al. 2008
Republic, Washington, USA	Lower Eocene	UWBM 57529A-B4131	Rosaceae, *Prunus* sp.	3	ca. 9 mm		Lewis 1994
Republic, Washington, USA	Lower Eocene	UWBM 95726, B4131	Ulmaceae, *Ulmus* sp.	2	both excisions together ca. 18.5 mm[a]		Labandeira 2002; pers. comm. C. Labandeira 2007 to SW
McAbee, Canada	Lower Eocene	UWBM 77597, B5757	Ginkgoaceae, *Ginkgo* sp.	1	18 mm		Labandeira 2002; pers. comm. C. Labandeira, 2007 to SW
Viola, Kentucky, USA	Eocene	not known	*Icacorea prepaniculata*	8	6 to 9 mm		Berry 1931
Puryear, Tennessee, USA	Eocene	not known	Lauraceae, *Nectandra pseudocoriacea*	4	5 to 6 mm	1 circular excision: *P. pseudocircus*	Brooks 1955

The lengths are measured as the maximum longitudinal length of the excision

[a] Calculation of the length of the excision from a given picture in the original paper

Table 2 Data of fossil plant leaves from Eckfeld, Messel and Menat with oblong or rounded excisions likely produced by species of *Megachile* s.l.

Coll. No., locality	Average length of excision (mm)	Average width of excision (mm)	Average eccentricity value, form	Host plant	No. of excisions
PE 1990-527, Eckfeld; Fig. 2i	3.43±0.02	2.34±0.01	0.73±0.00, oblong	Dicot. sp. indet.	2
PB 2001-82, Eckfeld, Fig. 2b	4.42±0.05	3.89±0.03	0.47±0.03, rounded	Fabaceae	3
PB 2003-991, Eckfeld, Fig. 2k	5.51±0.08	3.27±0.06	0.81±0.01, oblong	Fabaceae	1
PB 2005-67, Eckfeld, Fig. 2c	4.54±0.10	3.04±0.05	0.74±0.02, oblong, 1 rounded	Fabaceae	7
PB 2005-87, Eckfeld, Fig. 2a	4.01±0.04	2.57±0.02	0.77±0.01, oblong	Dicot. sp. indet.	3
PB 2005-264, Eckfeld, Fig. 2d	3.32±0.25	2.41±0.02	0.68±0.05, oblong	Dicot. sp. indet.	4
FIS Me 1472, Messel, Fig. 2h	4.19±0.18	3.17±0.05	0.65±0.05, rounded	*Laurophyllum hirsutum*	1
FIS Me 13360, Messel, Fig. 2j	2.96±0.02	1.63±0.03	0.83±0.01, oblong	Dicot. sp. indet.	1
FIS Me 21258, Messel, Fig. 2f	10.49±0.20	6.62±0.06	0.78±0.01, oblong	*Laurophyllum lanigeroides*	1
FIS Me 21259, Messel, Fig. 2g	12.49±0.44	6.02±0.02	0.88±0.01, oblong	*Laurophyllum* sp.	1
HLMD Me 13627, Messel, Fig. 2e	9.78±0.05	6.24±0.03	0.77±0.00, oblong	Juglandaceae sp.	1
NMHN 20576, Menat, Fig. 2l	7.16±0.03	4.70±0.10	0.75±0.01, oblong	*Salix* sp.	1

"Length of excision" corresponds to "max. chord length" of Sarzetti et al. (2008), "width of excision" corresponds to "min. chord length" of Sarzetti et al. (2008). A standard deviation (±SD) is indicated because each measurement was carried out repeatedly

fore, an error is indicated. In the case of more than one excision on the leaf the values are pooled together, this is indicated by the prefix "average" in the captions of Table 2. In Table 2 also the average eccentricity is given. Details for its calculation are explained by Sarzetti et al. (2008). When the eccentricity is 0, this is equivalent to a circle; when it is 1, it is equivalent to a line.

Systematic palaeontology

Family Megachilidae Latreille
Subfamily Megachilinae Latreille
Tribe Ctenoplectrellini Engel
Genus *Friccomelissa* gen. n.

Type species Friccomelissa schopowi sp. n.

Diagnosis Integument apparently without maculations; compound eye bare; compound eye apparently broader than gena; first flagellar article longer than second flagellar article; second flagellar article approximately as long as third flagellar article; preoccipital area sharply angled but apparently not carinate (gently rounded in *Ctenoplectrella* Cockerell). Mesosoma not coarsely sculptured; dorsal surface of pronotum long, length nearly as long as tangent from upper posterior border of compound eye to preoccipital ridge; mesoscutal anterior border broadly rounded; parapsidal lines linear; tegula oval; mesoscutellum apparently relatively low, not overhanging metanotum, anterior border without notches; metanotum apparently nearly horizontal; basal area of propodeum apparently not strongly declivitous; hind legs densely setose, without developed scopae; apparently without metabasitibial plate. Forewing with basal vein gently arcuate (strongly so in *Ctenoplectrella*); pterostigma longer than wide; marginal cell elongate, tapering to acute apex set along anterior wing margin; two submarginal cells present (i.e. 1rs-m absent); second free abscissa of Rs orthogonal to Rs+M; 2rs-m straight in anterior section, gently curved in posterior section (doubly arcuate in *Ctenoplectrella*), most likely confluent with 2 m-cu. Posterior margin of first metasomal tergum gently convex; sixth metasomal tergum without pygidial plate.

Etymology The new genus-group name is a combination of the old German name *Fricco* and *Melissa* (Greek, meaning "bee"). Fricco, also known as Frēo in Anglo-Saxon, was the goddess of love in western Germanic paganism.

Comments The new genus is very similar to *Ctenoplectrella* but differs most notably by the more extensively developed pronotum. In the latter genus, the posterior pronotal dorsal-facing surface bordering the mesoscutum is very short, being significantly narrower than the shortest distance from the upper posterior border of the compound eye to the preoccipital ridge. In *Friccomelissa*, this same section of the pronotum is longer, its length being nearly as long as the tangent from the upper posterior border of the compound eye to the preoccipital ridge. In addition, 2rs-m is most likely confluent with 2 m-cu whereas this same vein is apical to 2 m-cu in *Ctenoplectrella*. Relationships of fossil Megachilinae relative to the modern lineages remain somewhat uncertain (e.g. Engel 2001). Given the number of plesiomorphic traits relative to Osmiini and Megachilini, the tribe Ctenoplectrellini may represent a stem group to Osmiini (which, when considering only modern species, may be monophyletic, including the subtribe Heriadina) or to both Osmiini + Megachilini. Among ctenoplectrellines, *Friccomelissa* shows a notably plesiomorphic condition in the confluent position of 2rs-m and 2 m-cu, a feature effectively intermediate between that seen in the Anthidiini (including the Dioxyina, which are basal to Anthidiina: *sensu* Engel 2005) and the group comprising Osmiini (including Heriadina), Megachilini, Ctenoplectrellini and Glyptapini (the latter two of which may be stem groups to the former two: Engel unpubl. data). Accordingly, *Friccomelissa* could represent a stem group to Ctenoplectrellini. A more refined placement for the genus must await the discovery of additional material and critical review of relationships among glyptapines and ctenoplectrellines, a study beyond the scope of the present contribution.

Additional differences between *Friccomelissa* and other ctenoplectrellines include the anteriorly straight 2rs-m (doubly arcuate in *Ctenoplectrella* and *Glaesosmia* Engel), the weakly arcuate basal vein (strongly arcuate in *Ctenoplectrella*) and the bordering of the marginal cell apex along the anterior wing margin (slightly separated from the wing margin in *Ctenoplectrella* and *Glaesosmia*). The overall size of the new genus and species is slightly larger than that recorded for *Ctenoplectrella* (i.e. from 4–6 mm in total body length), and about that recorded for *Glaesosmia* (i.e. more than 7 mm; Engel 2001, 2008; Engel and Perkovsky 2006).

Friccomelissa schopowi sp. n.

Holotype MeI 11036 (Fig. 1), deposited in the Messel insect collection of the Forschungsinstitut Senckenberg (FIS).

Etymology The specific epithet is a patronymic honouring Dr. Kosta Schopow, a great benefactor of the Forschungsinstitut Senckenberg.

Type locality and horizon Messel pit (latitude 49°55′ N, longitude 8°45′ E) near Darmstadt, Hesse, Germany; Messel Formation, lower mid-Eocene, Geiseltalian, ca. 47 Ma. The specimen was collected in the year 2002 in grid square E8/9, in strata 0.3–0.9 m above local stratigraphic marker level alpha.

Diagnosis As for the genus (*vide supra*).

Description As for genus, with the following minor additions: female total body length 7.2 mm; right forewing length 3.2 mm. Integument of mesosoma, where evident, rather smooth, with faint greenish hue on otherwise dark brown to black background. Wing membranes lightly infuscate except that between C and Sc+R and in anterior-basal corner of marginal cell more darkly fuscous; veins dark brown to black. Forewing with basal vein confluent with 1cu-a, slightly longer than first free abscissa of Rs; pterostigma longer than wide, border inside marginal cell relatively straight and about as long as border inside first submarginal cell; marginal cell long, tapering gently to acutely rounded apex, with R extending slightly beyond apex along anterior wing margin; first submarginal cell longer than second submarginal cell; second free abscissa Rs slightly basal to 1 m-cu, separated by approximately three times vein width; membrane with scattered minute setae, setae apparently positioned on minute, unpigmented alar papillae. Metasoma ovoid (as in other Ctenoplectrellini and many Osmiini), longer than combined lengths of head and mesosoma, about as wide as mesosoma.

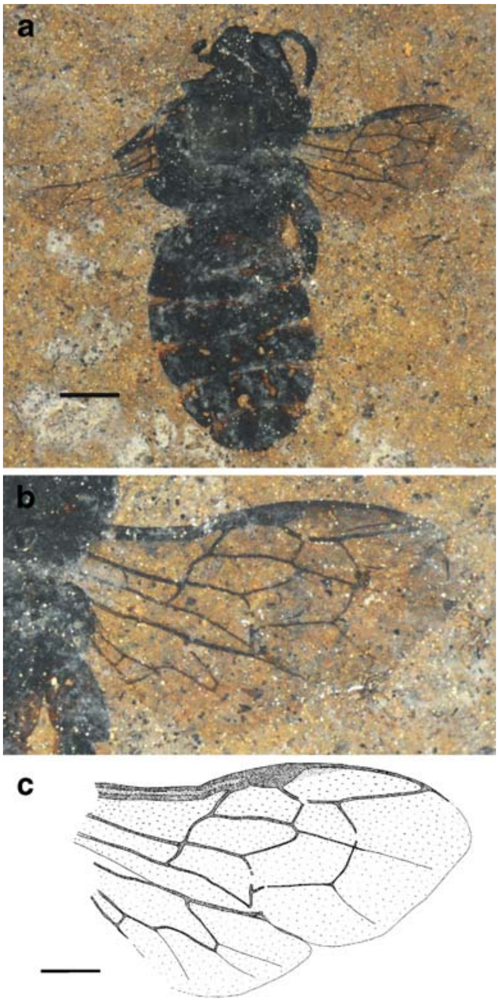

Fig. 1 *Friccomelissa schopowi* gen. et sp. n., holotype, MeI 11036. **a** Photograph of complete specimen. *Scale bar* equals 1 mm.**b** Photograph of right fore- and hind wing. **c** Camera lucida drawing of right fore- and hind wing. *Scale bar* equals 0.5 mm

Preservation The specimen is a well-preserved female (ten flagellar articles, six exposed metasomal segments) who is largely dorsoventrally compressed, although the head is obliquely preserved. The head is slightly turned to the right and shifted anteriorly such that the depressed posterior surface is also somewhat exposed. The right antenna is visible from about the midlength of the scape onward and the normal complement of ten flagellar articles can be discerned. The head is fractured on the left side and several portions are missing. Given the orientation of the head and the partial damage of the cuticle to the left, the vertex can be seen only fragmentarily, with the section that would otherwise bear the ocelli obscured, although a small semicircular section of the damaged vertex cuticle may have been a part of the integument surrounding the posterior margin of a lateral ocellus. Small portions of the right fore and mid-legs can be observed pulled alongside the mesosoma and the same is true of the left hind leg, although no details of leg structure can be discerned. The right hind leg is slightly more extended and the metafemur, metatibia and metabasitarsus can be easily discerned, including their inner and outer surfaces as all three podites are anteriorly–posteriorly compressed. The fore and hind wings are extended out orthogonal to the longitudinal axis of the body. The right wings are preserved as if coupled by the hamuli, with the leading edge of the hind wing linked to the posterior border of the forewing. The left hind wing is similarly extended while the left forewing is folded proximally and crumpled under the left side of the mesosoma.

Systematic paleoichnology

As noted, derived species of the genus *Megachile* produce characteristic excisions in the margins of leaves. In Table 2 several new Paloegene leaf excisions most likely produced by species of *Megachile* are listed, with images of the excisions provided in Fig. 2. In the discussion, we elucidate why we assume a megachilid origin for these leafcuttings.

Ichnogenus *Phagophytichnus* van Ameron, 1966

Type ichnospecies Phagophytichnus ekowskii van Amerom, 1966, by monotypy.

Diagnosis Refer to Sarzetti et al. (2008).

Phagophytichnus pseudocircus Sarzetti et al. 2008

Additional material In Central Europe, the ichnospecies *P. pseudocircus* is represented by excisions in the fabacean leaf PB 2001-82, LS from the Eckfeld maar, as already described by Sarzetti et al. (2008). There are two new records of this ichnospecies, one from the Eckfeld maar, collection no. PB 2005-67, LS (NHMM; Fig. 2c) and one probable record from Messel, collection no. Me 1472 (FIS; Fig. 2h).

Remarks The fabacean leaf from the Eckfeld maar, coll. no. PB 2005-67, LS, bears seven excisions. Of these excisions, only one on the right side on the tip of the leaf exhibits well-preserved triangular projections, comprises an arc of about 270° and shows an eccentricity value of 0.63. The leaf from Messel, coll. no. Me 1472, bears only one excision with a slightly uneven margin which makes its ichnospecies assignment a bit uncertain. Nonetheless, this excision fits the ichnospecies diagnosis and has an eccentricity value of about 0.65.

Phagophytichnus isp. indet.

Material examined PE 1990-527, LS (NHMM); PB 2003-991, LS (NHMM); PB 2005-67, LS (NHMM); PB 2005-87, LS (NHMM); PB 2005-264 (NHMM); Me 13209 (FIS); Me 13360 (FIS); Me 21258 (FIS); Me 21259 (FIS); HLMD Me 13629 (HLMD); 20576 (NMHN).

Diagnosis Oblong to rounded leaf-margin excision, showing eccentricity values from 0.68 to 0.88. All vein orders, except the midrib, are removed. Triangular projections along the margin of the leaf are lacking or the arc of the excision comprises less than 270°.

Remarks Along the cuspate margin are some parts showing distinctive dark areas, with a moderate rim of reaction tissue.

Discussion

The tracemaker

We assume that bees of the genus *Megachile* produced the oval excisions presented herein. Our approach is based on comparison with excisions made by extant *Megachile* and similar damages produced by other extant insect taxa. Generally, leaf margin feeding is found in a very wide range of insects. But margin feeding of, for example, lepidopteran caterpillars and leaf margin “chewing” from other insects can be excluded with reasonable certainty because this type of feeding results in excisions which have a very irregular margin. Oblong or circular excisions which have a smooth margin are not found very often, because

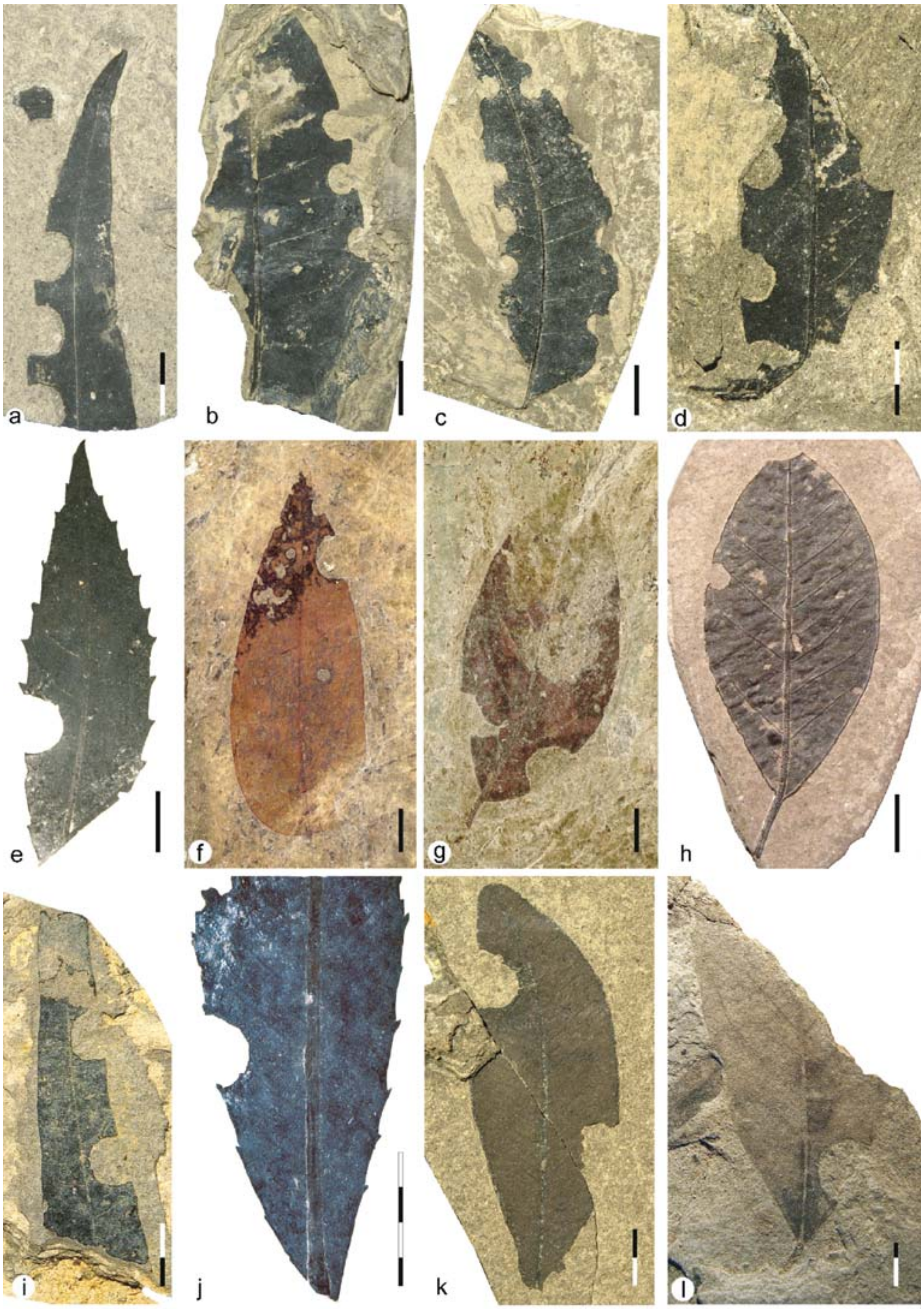

Fig. 2 Dicotyledonous leaves showing typical margin excisions most likely produced by megachilid bees from the localities Eckfeld maar, Messel and Menat. **a** Unidentifiable dicot (PB 2005-87, LS, NHMM). **b** Dicot sp. (PB 2001-82, LS, NHMM; Fabaceae). **c** Dicot sp. (PB 2005-67, LS, NHMM; Fabaceae). **d** Unidentifiable dicot (PB 2005-264, LS, NHMM). **e** Dicot sp. (Me 13627, HLMD; Juglandaceae). **f** *Laurophyllum lanigeroides* (Me 21258, FIS; Lauraceae). **g** *Laurophyllum* sp. (Me 21259, FIS; Lauraceae). **h** *Laurophyllum hirsutum* (Me 1472, FIS; Lauraceae). **i** unidentifiable dicot (PB 1990-527, LS, NHMM). **j** Dicot sp. (Me 13360, FIS; Juglandaceae). **k** Dicot sp. (PB 2003-991, NHMM; Fabaceae). **l** *Salix* sp. (20576, NMHN; Salicaceae). **b, c, h** representing typical damage of the ichnospecies *P. pseudocircus*. *Striped scale bars* equal 5 mm, *black scale bars* equal 10 mm

there are few insects capable of making this kind of trace. Very similar leaf damages could be produced by, for example, leafcutting ants (Formicidae, myrmicine tribe Attini). Although leafcutting ants cannot be completely ruled out as producers, it seems very unlikely, especially since most of the plants attacked end up with very severe cutting damages where often only the main leaf chords are left (see plates 12 to 13 in Wirth et al. (2003)), and the Attini are an exclusively New World lineage. The presence of scar tissue at the margin of several excisions demonstrates that cutting activity took place while the leaf was still attached to the living plant, thereby excluding caddisfly larvae as the tracemaker, as was noted by Berry (1931). An argument in favour of megachiline bees as producers of these excisions is the presence of both circular cuts whose megachiline origin was demonstrated by Sarzetti et al. (2008) and oblong cuts on several leaves.

Disc sizes in extant and fossil species of Megachile and possible implications for past biodiversity

In order to estimate the number of megachiline species which could have produced the observed size range of leaf excisions, it is essential to compile as much data as possible from extant species of *Megachile* s.l. These data can then serve as a baseline upon which inferences regarding the number of species producing the observed fossil cuttings can be made.

A positive relationship between the size of discs to the size of the bees and to the diameter of the constructed burrow was suggested early on by Bischoff (1927: p. 242) and later by Stephen and Torchio (1961). Altevogt (1955: 160) more strongly advocated that for some megachilid species, there should be a direct correlation between body length of the bee and the average length of the oval discs. Kim (2007) observed that disc size has a positive relationship with the bees' head widths, indicating that larger bees cut larger discs than smaller individuals of the same species. All of this is intuitive given that many bees typically fix themselves in a set position and then move their head in a semi-circular fashion when cutting the leaf disc, thereby resulting in a fragment of approximately similar proportion.

However, it has been also observed that many species of *Megachile* remove leafcuttings that range from one half to the full length of the body, while other species also can remove cuttings larger than the individual (Horne 1995: 868).

The observed variability of the sizes of oval discs has been assumed previously to be due to inaccurate cutting in the last section of the cutting process (Altevogt 1955; Hasenkamp 1974). This hypothesis has been amended by more recent investigations. Kim (1992: 87; 2007: Fig.1) demonstrated that the lengths of oval discs within a cell vary strongly. The size of the oval leaf discs decreased from the outer cell wall layer towards the inner cell wall layer, an observation similarly made by Michener (1953: 1707). Additionally, the average oval disc length decreased along the sequence of brood cells towards the nest entrance which was significantly related to sex allocation (Kim 1992: 88). An overview on observed minimal and maximal lengths of oblong discs cut by different extant *Megachile* species is given in Table 3. The diameters of bottom discs also show a positive relationship to the number of cell wall layers, that is, their mean widths decrease toward the inner layers of the cell wall. For example, in *M. gentilis* the mean widths of bottom discs varied between 4.9 and 5.8 mm. Recently, the disc-size regulation in *Megachile* brood cell building behaviour was investigated more closely (Kim 2007). Interestingly, the diameter of the used burrow did not influence the disc length, but did influence the disc width.

With these factors in mind, it seems possible to use the observed metrics from our fossil leaf excisions to infer a minimal number of species that could have produced this broad range of variation. The length of the oblong leaf discs (belonging to indeterminate ichnospecies) recorded from leaves from Eckfeld ranges from about 3 mm to a maximum length of 5.5 mm (Table 2). Compared with the size ranges of oblong discs from extant species of *Megachile* (Table 3), the size range from Eckfeld could have been produced easily by a single species. However, the recorded length range of the oblong leafcuttings from Messel consists of a spectrum from about 3 to about

Table 3 Synopsis of the observed minimal and maximal lengths of oblong and rounded discs cut by different extant *Megachile* species

Megachile species	Oblong discs: minimum length (mm)	Oblong discs: maximum length (mm)	Rounded discs: minimum width (mm)	Rounded discs: maximum width (mm)	References
M. bicolor	16	22	8	11	Altevogt (1955)[a]
M. brevis	7	15			Michener (1953) (values for firm leaves)
M. gentilis	7	15	4.9±0.47	5.8±0.53	Kim (1992)
M. inermis	17	20	ca. 7	ca. 7	Medler (1958)
M. integra	13.3±1.7	16.9±1.3	5.3±0.8	9.1±0.9	Williams et al. (1986)
M. maritima	12	22	8	12	Altevogt (1955)[a]
M. mendica mendica	9.1±1.1	11.6±1.4	6.1±1.2	7.6±0.7	Williams et al. (1986)
M. pacifica	9	13			Hasenkamp (1974)[a]
M. rotundata	6	>8			Stephen and Torchio (1961)
M. timberlakei	7.5	12.5			Kim (1992)
M. tsurugensis	10	19			Kim (2007)
M. umatillensis	16	19			Bohart and Youssef (1972) (values for petals)

[a] Calculation of the diameter of the leaf disc from a given picture in the original paper. In the oval discs, only the longest diameter of the disc is measured. Where applicable, a standard deviation (±SD) is indicated.

12.5 mm, with a sizeable gap between these extremes (Table 2). One could argue for a bimodal distribution of oblong excisions from Messel in regard to their length, with one species making oblong excisions with a length around 3 mm and another species making excisions ranging from 9.8 to 12.5 mm, but in effect, the sample size is rather small and so should be considered somewhat tenuous. The difference from the minimum- to the maximum-sized excision is 9.53 mm among the Messel material. A comparably large size range is found in only four out of 12 extant *Megachile* species (Table 3). This might indicate that at least two species with distinctly different body sizes produced the excisions in the fossil leaves from Messel. In summary, not only does the existence of the trace fossils indicate the presence of *Megachile* s.l. among the European Eocene bee fauna but the range of variation of the leafcuttings also indirectly suggests that more than one species of tracemaker was active at Messel. As such, the paleobotanical record and the excisions produced on them may permit us to detect additional levels of insect diversity, especially if more traces are available (i.e. a larger sample size) upon which to allow more reliable conclusions.

Another interesting aspect among the traces is the unusual diminutiveness of some excisions. If these excisions were really produced by bees, then the producing bee species must have been very small. Even when a quite large size spectrum of oblong leaf excisions is assumed, diameters of leafcuttings of about 3 mm can only be produced by bees with a rather small body size. Today some of the smallest leafcutting bees are of the subgenus *Eutricharaea* and can be about 5 mm in total length. Naturally, it is possible that some extinct species were even smaller or that diminutive species similar in size to the smallest modern taxa were capable of producing these 3 mm discs.

Plants used for cutting leaf discs in extant and fossil Megachile species

Megachilid bees have been known for a long time to use a wide range of plant species for cutting leaf discs. For example, Friese (1923) mentioned various kinds of leaves cut by different megachilid bee species and Michener (1953: Table 7) listed a wide range of plants cut by *M. brevis*. Most often, plant species belonging to the Rosaceae were used, but also recorded were species of Polygonaceae, Polemoniaceae, Solonaceae, Cassiaceae, Fabaceae, Lythraceae, Crassulaceae, Oenotheraceae, Aceraceae, Caprifoliaceae and Compositae (Asteraceae).

Conversely, Horne (1995) noted that there are many selective foraging megachiline species which consistently use only a few plant species. Horne (1995) demonstrated that many of the leaves used for disc cutting were selected nonrandomly by *M. rotundata*. For both *M. rotundata* and *M. brevis* a special kind of selective behaviour was observed which can be referred to as trap-lining (Horne 1995; Michener 1953). Michener (1953: p. 1714–1715) noted that a nesting megachilid bee did most of the cutting of leaves in a small area. An advantage of this tendency to return to a single place for cutting leaf discs might be that it is possible to gather these materials rapidly without the need to search on each trip. Horne (1995) demonstrated for *M. rotundata* that on many plant species, this bee often makes a single excision per leaf, but on plants with larger leafs prefers to make more than one excision per leaf. There is little information on how far from the nest bees will fly to obtain leaves and petals, but given the diversity of available plants that can be used, leaf discs are probably usually obtained from localities near to the nesting site (Michener 1953: 1719), a behaviour that may help result also in uniformity of plant material in some nests.

The fossil leaves from Eckfeld and Messel with probable *Megachile* excisions can only be partly determined and for those the material comes from only three plant families. For Messel, Lauraceae and Juglandaceae are recorded with *Megachile* damage, while from Eckfeld only Fabaceae were found with such damage (Table 2). Owing to the small sample size, interpretation of this material is limited. There are several cuttings on most of the fossil leaves from the Eckfeld Maar (Table 2, Fig. 2). This is in accordance with the aforementioned observation that modern species will frequently prefer to make a series of excisions from the same leaf, indicating that this preferential behaviour was selected for early in megachiline evolution. However, it is not yet clear why all the leaves from Messel are cut only a single time. This may be an artefact owing to the small sample size (most likely) or reflect a peculiar behaviour on the part of the trace maker. Horne (1995) showed that for extant *M. rotundata* preference or avoidance responses concerning cutting activity were strongly dependent on plant species.

Regardless, given their interesting relationship with plants as nesting resources, the diversity of megachiline bees (*Megachile* and related genera and tribes) in past epochs can be ascertained from not only the remains of actual bee specimens but also from the record of their activities on the surrounding flora. As such, the diversity of plant damage made by modern osmiines, anthidiines and other *Megachile* lineages should be critically examined for any evidence (e.g. masticated leaves, shaved trichomes, etc.) that might be useful in studying the paleobotanical record and for providing minimum ages for the origin of particular behaviours. Such evidence may further help to expand our current understanding of the diversity of these tribes in the past despite the usual paucity of bee specimens in the fossil record.

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