

Journal of Melittology

Bee Biology, Ecology, Evolution, & Systematics

The latest buzz in bee biology

No. 30, pp. 1–18

3 April 2014

The first male of the extinct bee tribe Melikertini (Hymenoptera: Apidae)

Michael S. Engel^{1,2}, Laura C.V. Breitkreuz², & Michael Ohl¹

Abstract. The first male bee of the extinct corbiculate tribe Melikertini Engel (Apinae) is described and figured. *Mochlomeelikertes hoffeinsorum* Engel, Breitkreuz, & Ohl, new genus and species, is easily distinguished from other groups within the tribe based on unique male modifications as well as a distinctive forewing venation. Some melikertines are famous for their peculiar modifications and processes, specifically the uniquely enlarged clypeal protrusions found in the genus *Succinapis* Engel. *Mochlomeelikertes hoffeinsorum* has its own singularly bizarre modifications, particularly an elongate, narrow extension of the mesoscutellum which projects posteriorly over the metanotum, propodeum, and part of the metasoma. The significance of these structures is briefly discussed.

INTRODUCTION

Fossil bees are uncommon. Although the group dates from the latter part of the Early Cretaceous (*e.g.*, Engel, 1996, 2000a, 2001a, 2004), there are comparatively few extinct species recorded from a numerically small number of individual specimens (*e.g.*, Michez *et al.*, 2012) — at least when the number of workers of the common *Proplebeia dominicana* (Wille & Chandler) and *P. silacea* (Wille) are excluded. Among this small diversity, an even smaller number are preserved as inclusions in amber, representing about 37% of all fossil bee species (Michez *et al.*, 2012; Wappler *et al.*, 2012; Engel & Michener, 2013a; Engel & Breitkreuz, 2013; Engel *et al.*, 2012, 2013). Among this scarcity of material, the vast majority are either ordinary females or workers of eusocial species

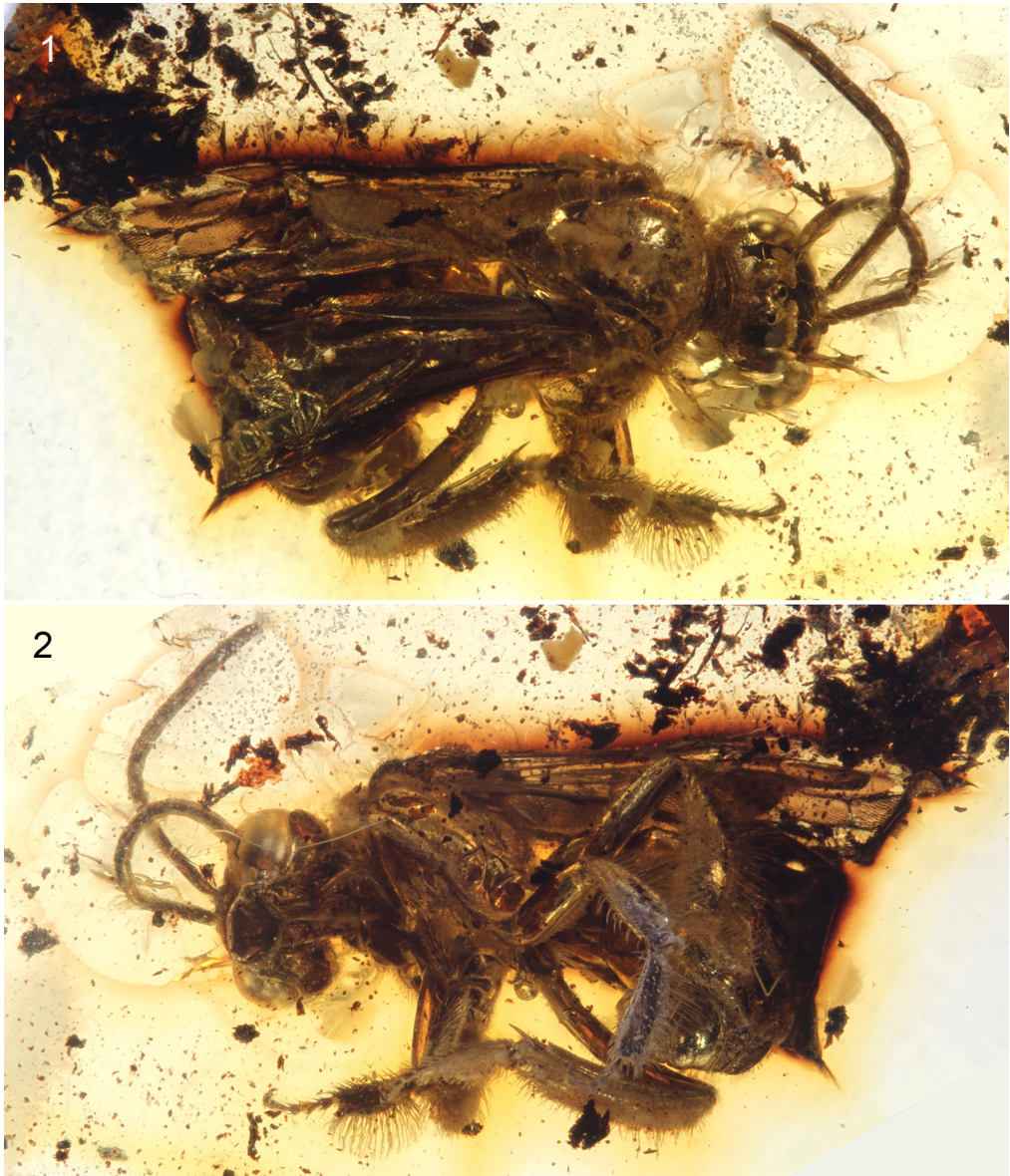
¹ Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024-5192 (mengel@amnh.org).

² Division of Entomology, Natural History Museum and Department of Ecology & Evolutionary Biology, 1501 Crestline Drive – Suite 140, University of Kansas, Lawrence, Kansas 66045 (msengel@ku.edu; l-breitkreuz@ku.edu).

³ Museum für Naturkunde, Invalidenstraße 43, 10115 Berlin, Germany (michael.ohl@mf-berlin.de).

Table 1. Species of fossil bees preserved as inclusions in amber for which males are known. For those marked with an asterisk (*) males are the only sex known. Higher classification follows that of Engel (2005).

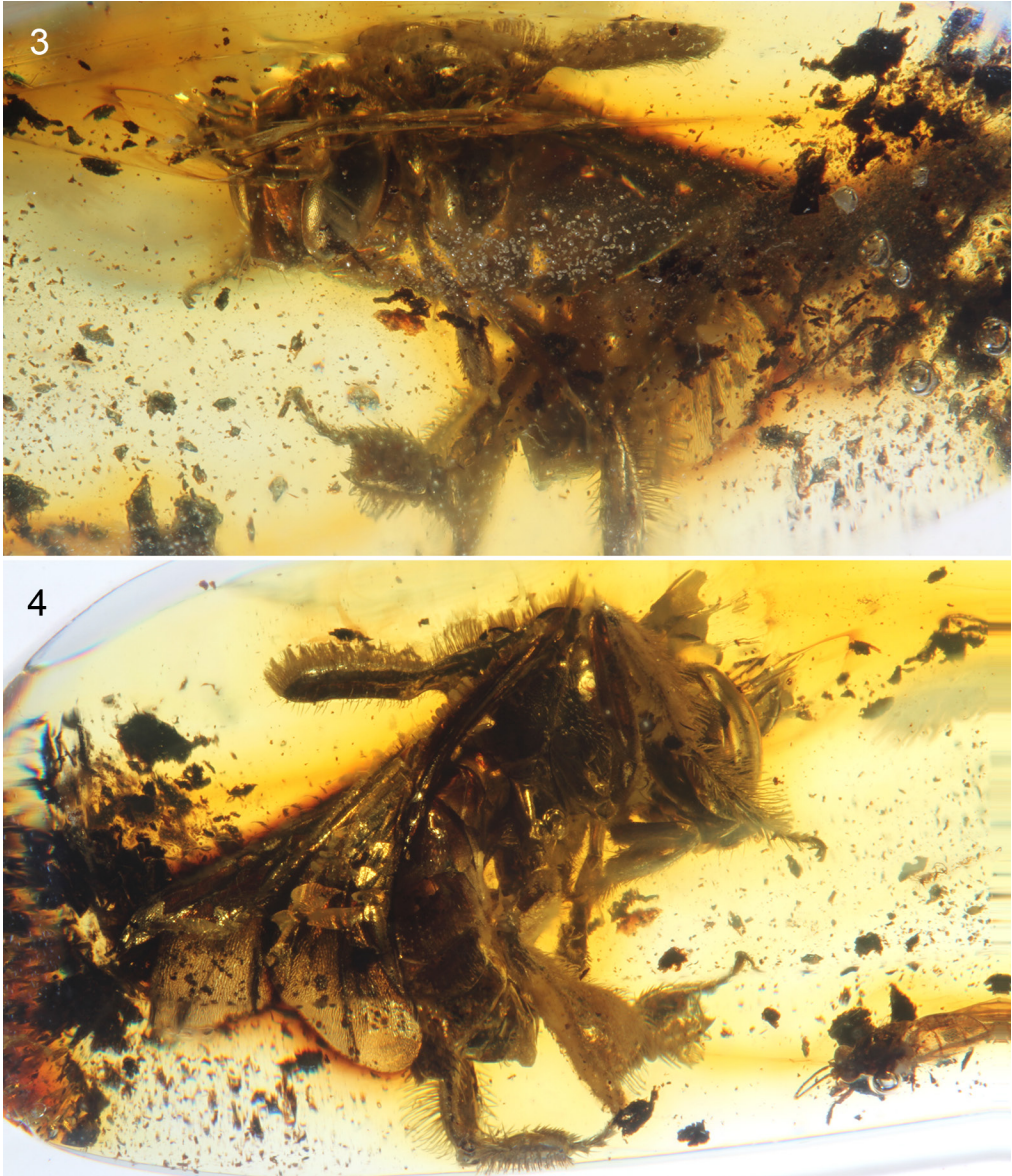
Taxon	Age	Locality	References
Apinae: Meliponini			
<i>Proplebeia dominicana</i> (Wille & Chandler, 1964)	Miocene	Dominican Republic	Michener & Poinar, 1996; Camargo <i>et al.</i> , 2000
<i>Proplebeia silacea</i> (Wille, 1959)	Miocene	Chiapas, Mexico	Engel, pers. obs.
<i>Proplebeia tantilla</i> Camargo <i>et al.</i> , 2000	Miocene	Dominican Republic	Camargo <i>et al.</i> , 2000
Apinae: Melikertini			
<i>Mochlomalikertes hoffensorsorum</i> n. gen., n. sp.*	Eocene	Baltic region	Herein
Megachilinae: Ctenoplectrellini			
<i>Ctenoplectrella viridiceps</i> Cockerell, 1909	Eocene	Baltic region	Engel, 2001a
Panurginae: Protandrenini			
<i>Heterosarus eickworti</i> Rozen, 1996*	Miocene	Dominican Republic	Rozen, 1996
Halictinae: Caenohalictini			
<i>Agapostemon luzzii</i> Engel & Breitung, 2013*	Miocene	Dominican Republic	Engel & Breitung, 2013
<i>Eickwortapis dominicana</i> Michener & Poinar, 1996*	Miocene	Dominican Republic	Michener & Poinar, 1996
Hylaeinae: Xeromelissini			
<i>Chiticola gracilis</i> Michener & Poinar, 1996*	Miocene	Dominican Republic	Michener & Poinar, 1996



Figures 1–2. Photographs of holotype (CCHH 1766-1) male of *Mochlomelikertes hoffeinsorum*, new genus and species. 1. Dorsal oblique view. 2. Ventral oblique view.

among the corbiculate bees, while males are virtually unknown as fossils. Hitherto eight species out of approximately 70 amber taxa are known from the male sex, and in the majority of these cases, they are the only gender thus far recorded for those particular taxa (Table 1). Obviously the limited paleontological evidence for bees is distinctly female-biased, and accordingly any information on male apoids in the fossil record is greatly welcomed.

In this context, the recent discovery of a male bee in Baltic amber is quite significant, particularly given that it represents an extinct tribe. Herein, we describe the second male bee from middle Eocene Baltic amber and the first of its kind for the



Figures 3–4. Photographs of holotype (CCHH 1766-1) male of *Mochlomelikertes hoffeinsorum*, new genus and species. 3. Left lateral view. 4. Right lateral oblique view.

Melikertini (Figs. 1–4). The first male was a single individual of the extinct megachil-ine tribe Ctenoplectrellini, *Ctenoplectrella viridiceps* Cockerell, and discussed by Engel (2001a). The present male certainly surpasses that of *C. viridiceps* in its spectacular morphologies and, in many ways, creates more mysteries surrounding it than any questions it resolves regarding melikertine males. Melikertine bees are already known to possess many peculiar anatomical features, the most spectacular being the unique facial projections of the genus *Succinapis* Engel, some of which could be quite large as in *Succinapis proboscidea* Engel (Engel, 2001a). The male described here lacks such facial features, but instead possesses its own unique projections, in this case from the

posterior of the mesoscutellum. Together, this paper along with Patiny *et al.* (2007), Engel (2004, 2008), and Gonzalez & Engel (2011), represent supplements to an earlier monographic treatment of bees in Baltic amber (Engel, 2001a).

MATERIAL AND METHODS

The single male specimen is excellently preserved within a relatively clear, light yellow piece of middle Eocene Baltic amber (Figs. 1–2), and the sample itself is embedded in GTS-polyester resin (Voss Chemie) (Hoffeins, 2001). The bee is virtually in tact, with minor damage to the apical portions of both forewings (Fig. 1). The piece also has a very partial fly near the lower surface but far enough removed from the bee so as not to obscure any views. There is scattered plant debris in the piece, in line with the bee, but it does not really detract from any view of the individual, except in some places near the apical portions of the body. The antennae are extended in front of the head and the flagella bent to the left, particularly the right antenna (Figs. 1, 2), and the mouthparts are folded into the proboscoidal fossa, but are not obscured from view by the legs. The legs are intact and mostly positioned alongside the body or bent underneath it (Figs. 1–4). The metasoma is curved ventrally, such that its apex points ventrally, and its apical segments are slightly distended, thus exposing the extreme apex of the genitalia. The wings are folded back over the body and their apical portions are bent downward along with the curvature of the metasoma, the left wing in particular is torn apical to the marginal cell (Fig. 1).

Photomicrographs were prepared with a Canon 7D digital camera attached to an Infinity K-2 long-distance microscope lens and illuminated by a Xenon-flash system. Measurements were taken with an ocular micrometer on an Olympus SZX-12 stereomicroscope and are approximate given that the optimal angle for some metrics was not achievable due to the orientation of the specimen relative to the polished planes of the amber piece. Morphological terminology generally follows that of Engel (2001a) & Michener (2007), and clear views of the forewing venation for various species in the tribe Melikertini were presented by the former as well as Engel *et al.* (2013). The origin, dating, and paleofauna of Baltic amber has been summarized by Weitschat & Wichard (2002, 2010), Engel (2001a), and Grimaldi & Engel (2005), while general paleontological summaries of bee evolution are provided by Engel (2001a, 2004), Ohl & Engel (2007), Michez *et al.* (2012), and Engel & Michener (2013b).

SYSTEMATIC PALEONTOLOGY

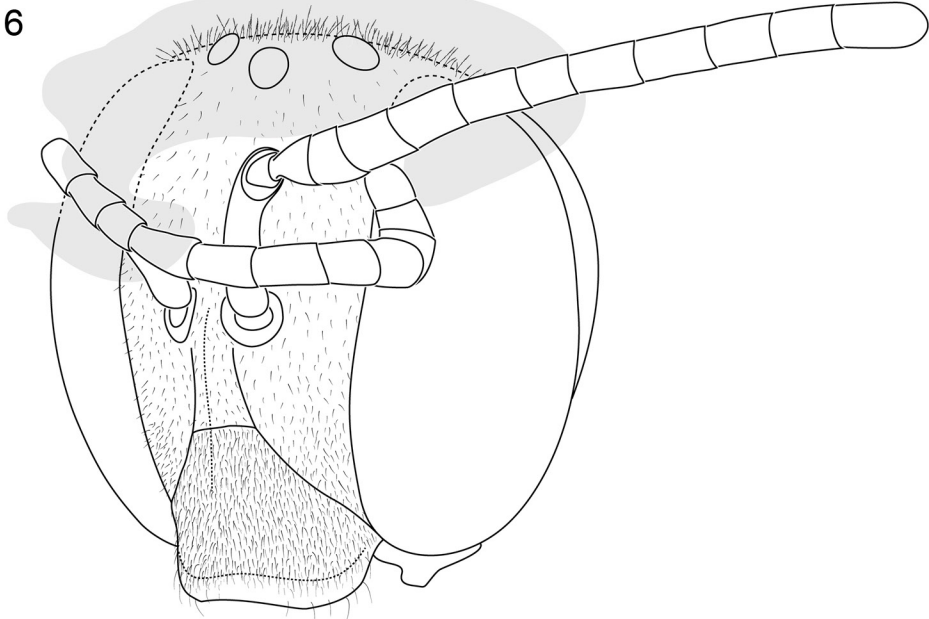
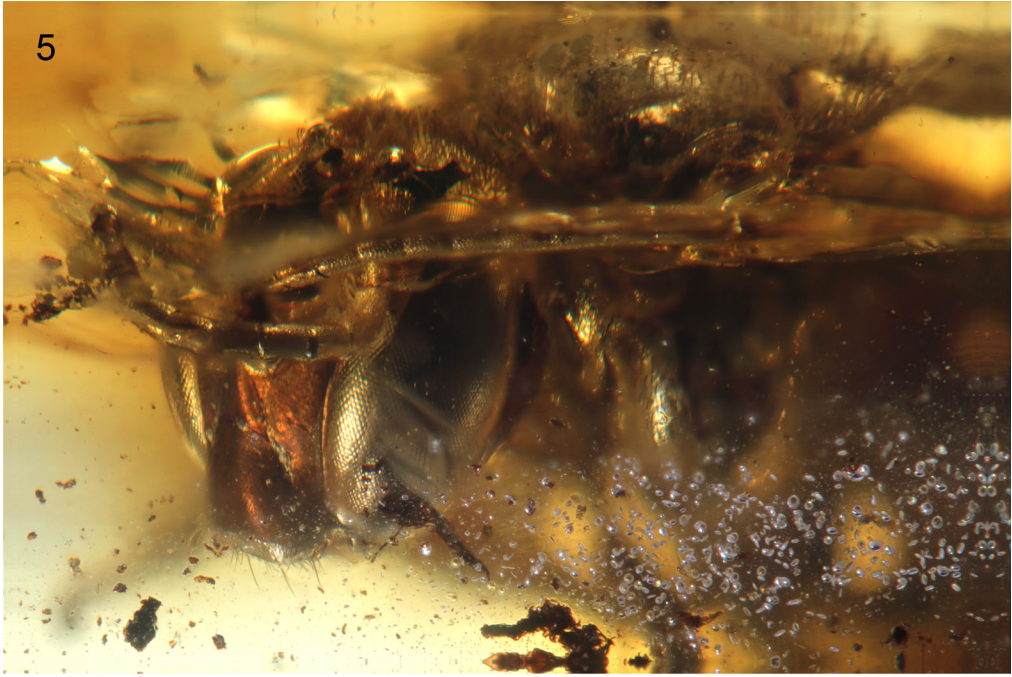
Tribe Melikertini Engel

Mochlomelikertes Engel, Breitzkreuz, & Ohl, new genus

ZooBank: urn:lsid:zoobank.org:act:D766BE9A-2AB7-4CF4-87FC-B78572B56C3B

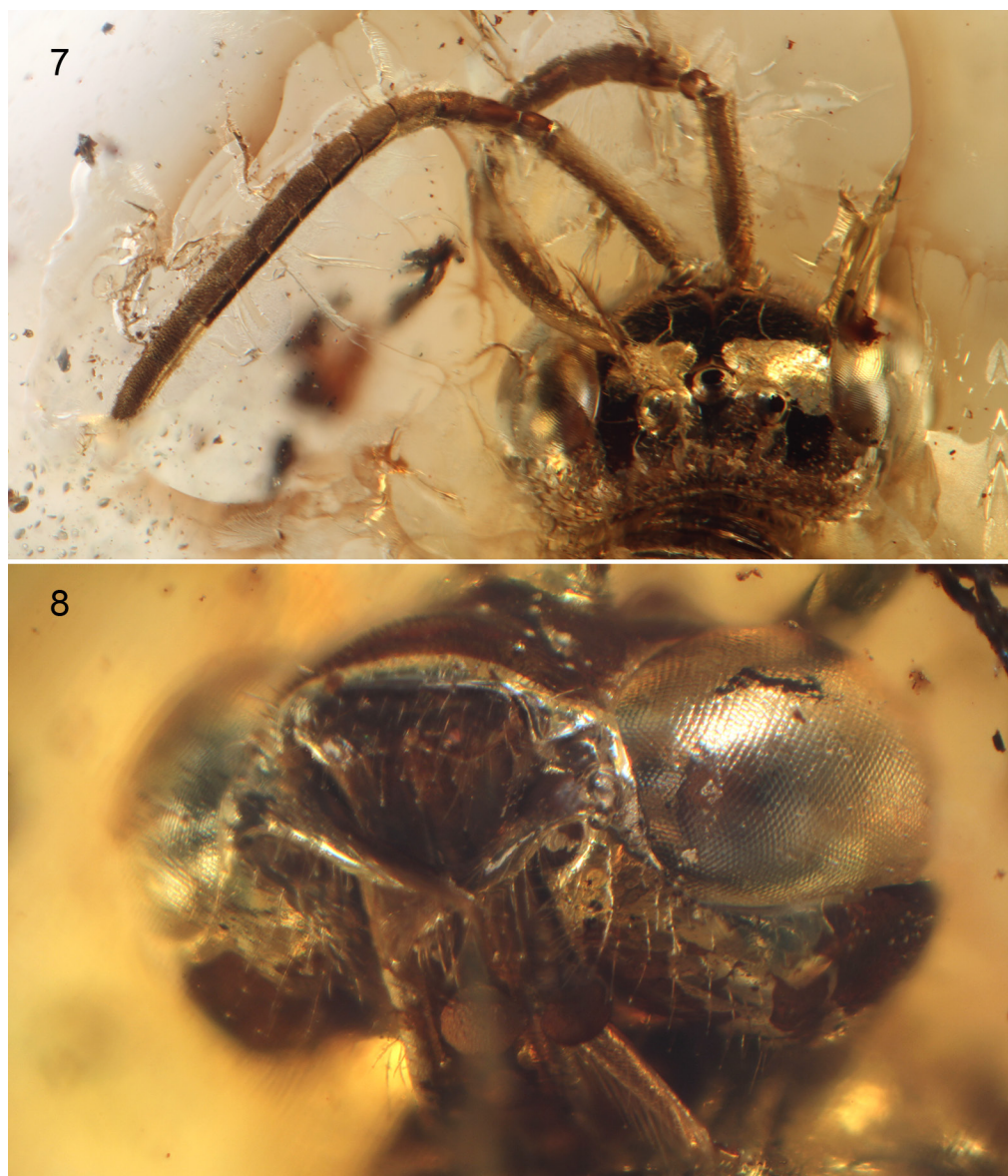
TYPE SPECIES: *Mochlomelikertes hoffeinsorum* Engel, Breitzkreuz, & Ohl, new species.

DIAGNOSIS: ♂: Medium-sized bee, *ca.* 8 mm in length. Mandibles simple, elongate; axes of mandibular articulations converging anteriorly such that closed mandibles overlap at slightly obtuse angle (Fig. 8); clypeus with apical margin pale, contrasting with brown integument of remainder of head (Figs. 5, 8); clypeus without basal prominence or protrusion; epistomal sulcus forming broadly obtuse angle. Pronotal lobe densely setose; mesoscutum with anterior border low, broadly rounded; tegula elongate-ovoid; mesoscutellum with elongate medial extension of posterior margin



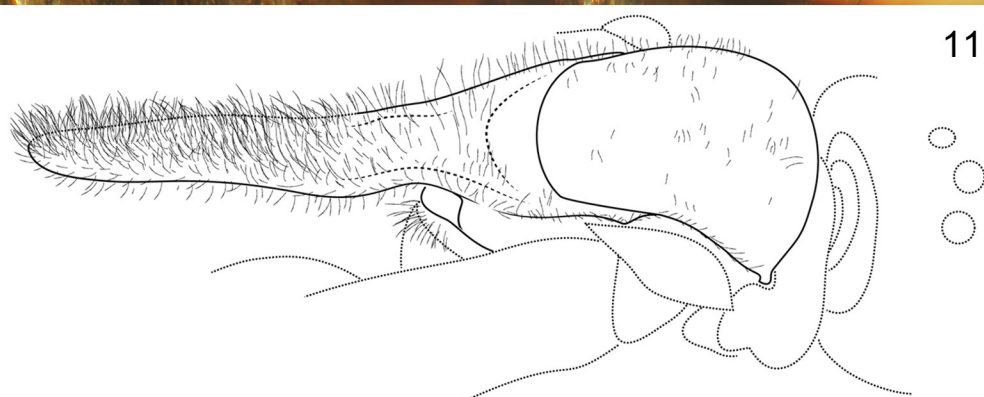
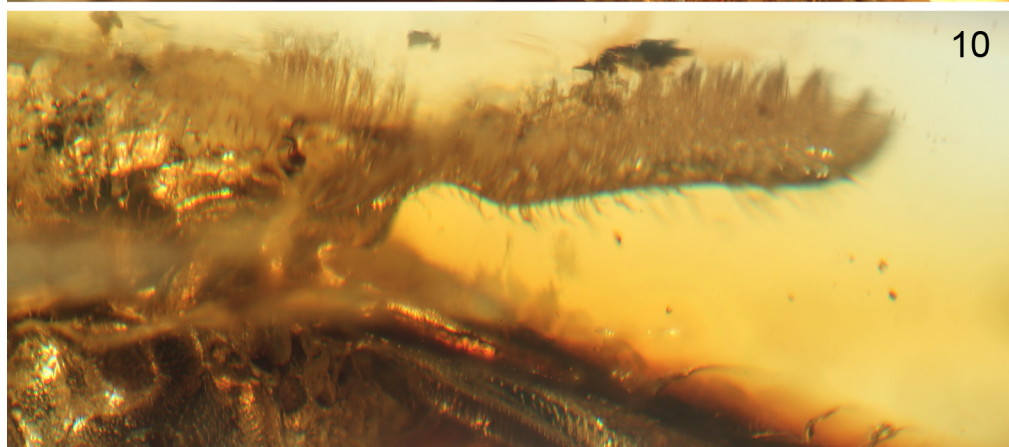
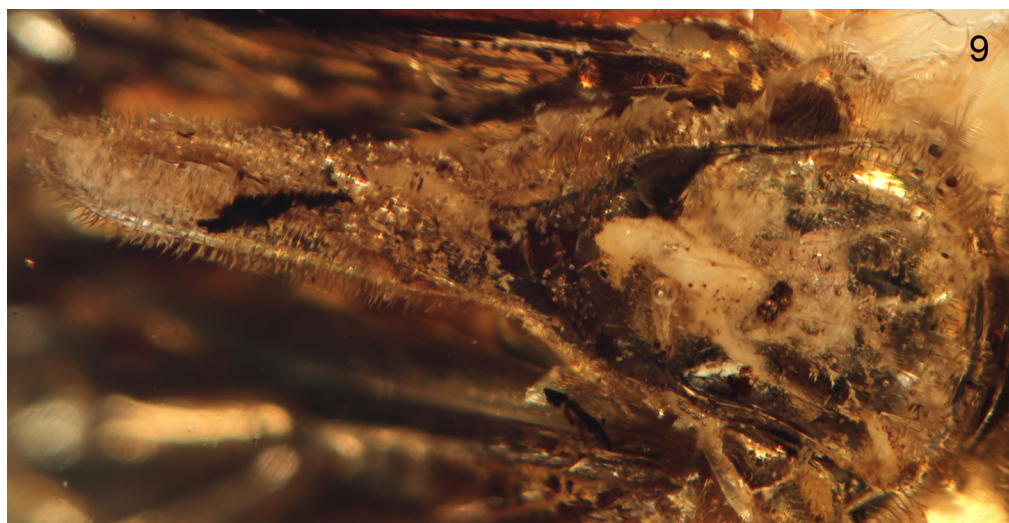
Figures 5–6. Photograph and illustration of head of holotype (CCHH 1766-1) male of *Mochlommelikes hoffeinsorum*, new genus and species. 5. Left oblique view. 6. Illustration of head as preserved.

(Figs. 3, 4, 9–11), with process greatly elongate and projecting over metanotum, propodeum, and anterior portions of metasoma (at least extending beyond apical margin of second metasomal tergum), and with projection slightly longer than remainder of mesosoma and densely setose on dorsal surface (Figs. 9–11). Forewing with prominent pterostigma; two submarginal cells present (1rs-m absent); second submarginal cell



Figures 7–8. Photographs of head of holotype (CCHH 1766-1) male of *Mochlomelikertes hoffeinorum*, new genus and species. 7. Dorsal view. 8. Ventral apical oblique view showing mouthparts.

greatly elongate, length 3.5 times width (resulting from absence of 1rs-m and thereby representing equivalent length of what would otherwise be the second and long third submarginal cells); first submarginal cell angled, horsehead-shaped (resulting from strongly angled second abscissa Rs); r-rs relatively long, meeting pterostigma near midpoint; 1m-cu short, relatively straight; basal vein basad cu-a. Mesobasitarsus elongate, nearly as long as mesotibia (Fig. 12), both podites slightly swollen with numerous elongate setae along outer and posterior surfaces, such setae minutely branched in apical quarters; metatibia without corbicula (true for all males), with outer surface slightly swollen, outer and posterior surfaces of metatibia and metabasitarsus with numerous, elongate setae (Fig. 13), such setae minutely branched in apical thirds to



Figures 9–11. Holotype (CCHH 1766-1) male of *Mochlomelikertes hoffeinsorum*, new genus and species. **9.** Photograph of dorsal view of mesosoma. **10.** Photograph of left lateral view of mesoscutellum and its posterior extension. **11.** Illustration of mesosomal dorsum.

quarters; inner surface of metatibia with keirotrichia; keirotrichiate zone not elevated, running from base to near apex, separated from posterior border by distance less than

one-third width of keirotrichiate zone; single metatibial spur present, spur minutely serrate; metabasitarsus subquadrate, slightly longer than wide, inner surface with dense, stiff, simple setae forming loose comb rows (typical among higher corbiculate bees); pretarsal claws cleft. Metasoma sparsely setose, most setae minute, simple, and appressed to subappressed; visible metasomal sterna unmodified; gonostyli relatively broad, thumb-like, apically rounded, with a few distinct setae along outer apical borders.

ETYMOLOGY: The new genus-group name is a combination of the *mochlos* (Greek, "lever", a reference to large mesoscutellar extension which resembles an extended lever) and *Melikertes*, type genus of the tribe Melikertini. The name is masculine.

Key to Genera of Melikertini
(modified from Engel, 2001a)

Note that this key is somewhat artificial and merely meant as a heuristic tool given that only males are known for the new taxon, while only female workers are known for the remainder. Thus, it is unknown to what degree some of the unique features are gender specific.

1. Clypeal protrusion absent 2
- Clypeal protrusion present, *i.e.*, base of clypeus produced into variously modified facial prominences, prominence bending upward over fronto-clypeal portion of epistomal sulcus and supraclypeal area, ending between antennal toruli and sometimes projecting strongly forward at that point (only workers known) *Succinapis* Engel
- 2(1). Mesoscutellum without tongue-like medioapical extension 3
- Mesoscutellum with prominent, tongue-like medioapical extension projecting over metanotum, propodeum, and portions of metasoma (Figs. 1, 3, 4, 9–11), dorsal surface of extension densely setose (Figs. 9–11) (only male known) *Mochlomelikertes*, n. gen.
- 3(2). Mesoscutellum bulging, overhanging metanotum and propodeum; apical margins of metasomal terga distinctly lighter than remainder of metasoma, thus metasoma appears banded; anterior and posterior margins of metabasitarus distinctly converging toward apex 4
- Mesoscutellum not bulging, not overhanging metanotum or propodeum; metasomal terga uniformly colored; anterior and posterior margins of metabasitarus approximately parallel (genus *Melikertes* Engel, *s.l.*) 5
- 4(3). Forewing with anterior margin of first submarginal cell approximately equal to length of anterior margin of second submarginal (*i.e.*, r-rs as long as immediately succeeding abscissa of Rs); compound eyes converging ventrally; second flagellomere distinctly shorter than third flagellomere, first flagellomere distinctly shorter than combined lengths of second and third flagellomeres (only workers known) *Melissites* Engel
- Forewing with anterior margin of first submarginal cell many times longer than length of anterior margin of second submarginal cell (*i.e.*, r-rs many times longer than immediately succeeding abscissa of Rs); compound eyes approximately parallel; second and third flagellomeres approximately equal in length, first flagellomere approximately equal to combined lengths of second and third flagellomeres (only workers known) *Roussyana* Manning

- 5(3). Forewing with two submarginal cells (1rs-m absent) (only workers known)
 *Paramelikertes* Engel & Ortega-Blanco
 —. Forewing with three submarginal cells (1rs-m present) (only workers known) ...
 *Melikertes* Engel, *s.str.*

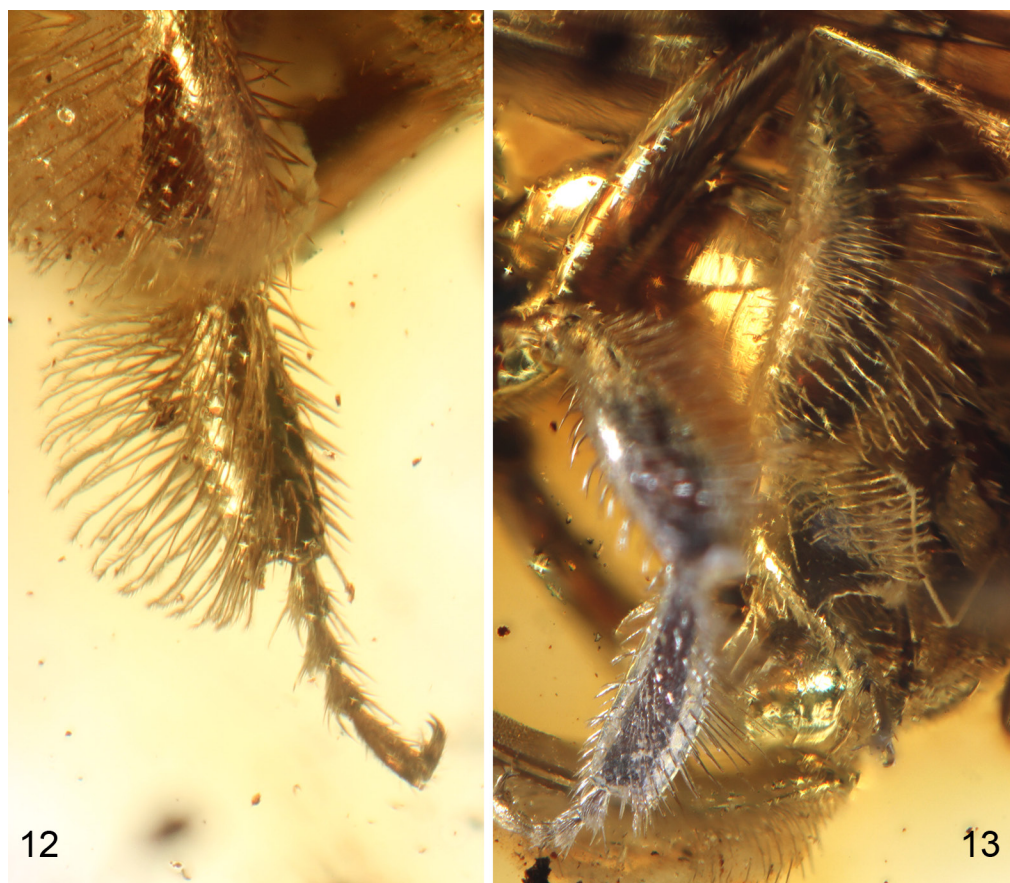
Mochlomelikertes hoffeinsorum Engel, Breitzkreuz, & Ohl, new species

ZooBank: urn:lsid:zoobank.org:act:AF3449F2-26B9-4545-8697-F7427337D6AF

(Figs. 1–13)

DIAGNOSIS: As for the genus (*vide supra*).

DESCRIPTION: ♂: Total body length (as preserved) 8.0 mm; forewing length (as preserved) 6.75 mm. Head slightly wider than long, length 2.10 mm, width 2.18 mm. Mouthparts generally typical for corbiculate Apinae; labial palpomeres I and II elongate, somewhat flattened (Fig. 8), palpomere I longest; palpomeres III and IV minute. Mandibles simple, slender, length 0.70 mm, apexes acute, axes of articulations converging anteriorly, closed mandibles crossing at slightly greater than a right-angle (Fig. 8). Malar area virtually absent anteriorly, and only slightly present posteriorly (resulting from anterior convergence of axes of mandibular articulations). Labrum wider than long, medial length 0.18 mm, width 0.58 mm, surface flat, apical margin weakly concave medially (Fig. 8). Clypeus low in profile (Figs. 5, 6, 8), weakly convex, only slightly extending beyond lower tangent of compound eyes (Figs. 5, 6), without basal prominence or protrusion; fronto-clypeal sulcus very weakly arched apically, dorsal portion of clypeo-facial sulcus (*i.e.*, that portion of epistomal sulcus between the fronto-clypeal sulcus and the anterior mandibular articulation) relatively straight until near anterior mandibular articulation, then angled laterally; anterior tentorial pit in upper half of clypeo-facial sulcus; epistomal sulcus laterally forming broadly obtuse angle. Supraclypeal area slightly longer than wide, low in profile; subantennal sulci slightly longer than antennal torular diameter, meeting epistomal sulcus at angle between frontoclypeal sulcus and upper portion of clypeo-facial sulcus. Antennal toruli separated by less than an individual torular diameter; distance from antennal torulus to compound eye greater than an individual torular diameter; scape long, length 0.90 mm, apical width 0.18 mm; pedicel length 0.17 mm, width 0.17 mm; flagellum with 11 flagellomeres (Figs. 5–7); individual flagellomeres slightly longer than wide except apicalmost flagellomere which is much longer than wide; first flagellomere length 0.23 mm, width 0.15 mm; second flagellomere length 0.23 mm, width 0.15 mm; third flagellomere length 0.23 mm, width 0.15 mm; fourth flagellomere length 0.22 mm, width 0.15 mm; fifth flagellomere length 0.20 mm, width 0.15 mm; sixth flagellomere length 0.20 mm, width 0.15 mm; seventh flagellomere length 0.20 mm, width 0.15 mm; eighth flagellomere length 0.20 mm, width 0.15 mm; ninth flagellomere length 0.23 mm, width 0.17 mm; tenth flagellomere length 0.27 mm, width 0.17 mm; eleventh flagellomere length 0.33 mm, width 0.17 mm. Compound eye slightly wider than gena in lateral profile; compound eye length 1.67 mm, width 0.80 mm; median ocellus at upper tangent of compound eyes, diameter 0.20 mm; distance from median ocellus to lateral ocellus 0.08 mm, lateral ocellus to compound eye 0.22 mm, between lateral ocelli 0.33 mm, ocellar triangle to preoccipital ridge 0.28 mm; preoccipital area rounded (Fig. 7). Pronotum short, declivitous, without defined transverse, dorsal ridge or well-defined posterior, dorsal-facing surface along mesoscutal border; pronotal lateral ridge absent; mesoscutum anterior border broadly rounded, anterior lip gently curving to meet posterior pronotal margin, not high or overhanging pronotal border, median and parap-



Figures 12–13. Photographs of legs of holotype (CCHH 1766-1) male of *Mochlomelikertes hof-feinsorum*, new genus and species. **12.** Apex of mesotibia and entire mesotarsus and mesopretarsus. **13.** Metafemur, metatibia, metatarsus, and metapretarsus (with portions of left mesotibia and mesotarsus in foreground).

sidal lines scarcely impressed; mesoscutum length 1.50 mm; tegula large, elongate-ovoid, anteriorly broadly rounded, posteriorly elongate and acutely rounded, nearly two-thirds length of mesoscutum; intertegular distance 1.33 mm; mesoscutellum with axillae large, axillar medial corners separated by slightly less than axillar width; transcutal articulation deeply impressed (*i.e.*, mesoscutal-mesoscutellar sulcus deeply impressed); laterally from axilla, mesoscutellar margin weakly arches medioposteriorly before posterior margin projects posteriad into elongate extension (Figs. 3, 4, 9–11), with depressed area in line with lateral margin before extension apparently demarcating more typical area of posterior margin (Figs. 10, 11); mesoscutellar posterior margin medially elongate to form tongue- or lever-like extension, process greatly elongate and projecting over metanotum, propodeum, and anterior portions of metasoma (projecting over at least basal three metasomal segments), with projection slightly longer than remainder of mesosoma (Figs. 3, 4, 9), and apex of extension broadly rounded; mesoscutellum length to beginning of depressed area 0.47 mm, projection length 2.20 mm, width 0.50 mm, total mesoscutellum length (mesoscutellar disc and entire length of extension) 2.67 mm; metanotum unmodified; propodeum strongly declivitous, basal area longer than metanotum; pleura generally unmodified, hypopimeral area small.

Forewing with basal vein (*i.e.*, first free abscissa of M) basad cu-a, separated by four times vein width; basal vein relatively straight; first free abscissa Rs originating near apex of prestigma, distinctly less than one-half length of basal vein; pterostigma relatively large, trapezoidal, apical width 1.5 times basal width, length slightly more than four times basal width, apically tapering within marginal cell, border within marginal cell relatively straight; r-rs meeting pterostigma near midpoint, r-rs long, about as long as maximum width of pterostigma; only two submarginal cells present, owing to loss of 1rs-m; first submarginal cell much smaller than second submarginal cell, strongly arched in shape, appearing horsehead-shaped; Rs+M angled posteriorly, with second free abscissa Rs originating such that Rs+M subequal to second abscissa M (*i.e.*, free abscissa of M beyond Rs+M), abscissa of Rs strongly angulate in basal third (much like in many first submarginal cells among corbiculate apines: *e.g.*, *Thaumastobombus andreniformis* Engel, *Melissites trigona* Engel, *Bombus randeckensis* Wappler & Engel: Engel, 2001a; Wappler *et al.*, 2012); 1m-cu relatively straight, short, about as long as first free abscissa Rs, thus first medial greatly narrowed apically; Rs+M and second free abscissa of M (*i.e.*, between Rs+M and 1m-cu), forming a relatively straight line, angled posteriorly; M at point of 1m-cu extending straight toward wing apical margin and parallel with longitudinal axis of wing; second submarginal cell elongate, length 3.5 times width; 2rs-m relatively straight; 2m-cu relatively straight, meeting second submarginal cell near apex, basad 2rs-m by seven times vein width; marginal cell long, broad basally, tapering gently along length to acutely rounded apex, apex offset from anterior wing margin by vein width, apex minutely appendiculate; wing membrane not papillate, with uniform distribution of microtrichia; hind wing with normal complement of veins; six distal hamuli arranged in a regularly-spaced series; well-developed jugal lobe present. Malus of protibial strigilis arched, with broad velum, apical rachis short and simple; mesotibia only slightly longer than mesobasitarsus, slightly swollen; mesobasitarsus length 2.75 times width, slightly swollen like mesotibia (Fig. 12); metatibia without corbicula (Fig. 13), broadened apically, with outer surface slightly swollen (Fig. 13) with scattered setae over entire surface (rather than depressed and with distinctly broad asetose area as in female workers), inner surface with keirotrichia, with keirotrichiate zone not elevated, running from base to near apex, separated from posterior border by distance less than one-third width of keirotrichiate zone; apical polished area beyond keirotrichiate zone with subapical, transverse row of four, short, apically-blunt peg-like setae; metatibia length 2.07 mm, maximum width 0.73 mm; single metatibial spur present, spur minutely serrate; metabasitarsus roughly subquadrate (Fig. 13), slightly longer than wide, length 0.73 mm, width 0.57 mm, length about 1.3 times width, not distinctly swollen, apical margin weakly concave; pretarsal claws of all legs cleft. Metasoma generally unmodified, seven exposed terga; sterna with apical margins straight; gonostyli broadly rounded apically.

Pubescence generally pale in appearance; head with short to minute, simple setae largely appressed on face, slightly longer around clypeal apex; setae more numerous on clypeus than on remainder of face; setae becoming slightly longer and more erect on vertex posterior to ocelli (Figs. 5–7); postgena with scattered setae similar to those on vertex (Fig. 8); mandible with few simple, erect setae, mostly along ventral margin; labrum with scattered, long, simple, suberect setae; labial palpomere II with long, simple, posteriorly-directed setae along lateral and apical borders, surface otherwise with minute, appressed, simple setae (Fig. 8). Mesosoma with generally sparse, short pubescence; pronotal lobe with dense, short, erect setae; mesoscutum with sparse, erect setae with minute apical branches, such setae slightly longer and more numerous

anteriorly, particularly anterolaterally (Fig. 9); tegula with minute, fine, appressed to suberect setae scattered over surface; mesoscutum with long, erect, apically minutely-branched setae borne laterally and anterior to depressed area at base of extension, with dorsal surface of extension bearing dense, long, apically-branched setae (Figs. 9–11), such setae present laterally albeit less numerous, and similar setae present on ventral surface of extension although more sparsely scattered and shorter than comparable setae on dorsal surface (Fig. 10); metanotum with scattered, short, simple, erect setae; propodeum with basal area glabrous, lateral surfaces with scattered, short, simple, erect setae; pleura with sparsely scattered, erect to suberect, long, simple setae — except hypoepimeral area with minute, simple, appressed setae; pubescence of legs generally sparsely scattered and erect to suberect, except as follows: setae of protibia and protarsus distinctly more numerous than profemur, individual setae simple, suberect, stiff, and longer than width of associated podite; mesotrochanter with narrow band of dense, short setae on ventral surface; mesofemur with sparse, simple, suberect setae on most surfaces, except similar narrow band of short, dense setae on posteroventral border; mesotibia outer surface with numerous elongate, simple setae (Fig. 12), such setae longer than width of mesotibia, other surfaces with distinctly shorter, erect, somewhat blunt, simple setae; mesobasitarsus similar to mesotibia except simple elongate setae along posterior border and posterior portion of outer surface, and remainder of surface with shorter, simple, erect setae (Fig. 12); metatrochanter with ventral, narrow brush of dense, short setae; metafemur with ventral surface glabrous, remaining surfaces with sparse, suberect, short, simple setae; metatibia outer surface with scattered erect, elongate setae (Fig. 13), individual setae with exceedingly minute branches in apical third to quarter of length, inner surface glabrous except for zone of keirotichia (vide supra); metabasitarsus with outer surface bearing setae similar to outer surface of metatibia over its posterior half (Fig. 13), with anterior half largely devoid of setae, and inner surface with comb rows composed of stiff, apically-directed, simple setae. Metasoma with sparse, short to minute, simple, appressed to suberect setae; terga IV through VII apically also with scattered, erect, short setae; gonostyli with minute, simple setae apicolaterally.

Integument generally faintly and minutely imbricate or smooth throughout; brown to dark brown where evident, otherwise integument microscopically separated from amber to form reflective, silvery metallic sheen common in Baltic amber inclusions; integument of head apparently brown except antenna and mouthparts lighter, no evidence of areas with possible maculation during life with exception of extreme clypeal apical margin distinctly white (either white or perhaps yellow in life); mesosoma apparently dark brown with legs somewhat lighter; metasoma apparently brown throughout; wing membranes hyaline and without areas of infuscation, veins dark brown to black.

♀: Unknown.

♂: Unknown.

HOLOTYPE: ♂, Baltic amber [succinite], middle Eocene (Lutetian), Blaue Erde; in the Hoffeins Collection (coll. No. CCHH 1766-1) to be deposited in the Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany.

ETYMOLOGY: The specific epithet honors Christel and Hans Werner Hoffeins, collectors of this and many other spectacular inclusions and who initially recognized its significance and drew it to our attention.

DISCUSSION

The significance of the present find is twofold, 1) male bees are exceedingly rare in the fossil record and up to the present no male melikertine was known, and 2) melikertines are famous for their bizarre modifications and the present individual is certainly among the most dramatic in exhibiting morphologies utterly peculiar relative to corbiculate bees today. Bees of the tribe Melikertini comprise a suite of higher corbiculate bees of the advanced eusocial behavioral grade and are the closest relatives of the stingless bees (Meliponini) (Engel, 2001a, 2001b). Melikertines are among the more common of bees found in Eocene amber (e.g., Engel, 2001a, 2004; Engel *et al.*, 2013; Michez *et al.*, 2012), along with those representatives of the Electrapini and Ctenoplectrellini (Engel, 2001a, 2004, 2008; Gonzalez & Engel, 2011; Patiny *et al.*, 2007). Given this frequency relative to other apoid tribes, it is perhaps most natural that a male melikertine would be discovered in time. Fossils of male bees are known from compressions (e.g., Michez *et al.*, 2012), but have to date been of limited value either owing to a lack of sufficiently preserved details or a need for a thoroughly modern revision. Thus, it is presently those males in amber that are the most valued owing to the fidelity of their preservation. So far, nine species in amber, including the one described herein, are known from males either exclusively or in association with their female counterparts (Table 1), and these are distributed across five families of bees and roughly equally so among short- and long-tongued bees. Among the long-tongued bees, there is a bias toward the Meliponini, and a single genus therein, and so there is a relatively smaller diversity known relative to the short-tongued bees. With the great diversity of halictines, particularly Augochlorini, known from Dominican amber (Engel, 1995, 1996, 1997, 2000b, 2009; Engel & Rightmyer, 2000), it is surprising that among the males known from this deposit that the only two would be of the Caenohalictini (Michener & Poinar, 1996; Engel & Breitzkreuz, 2013). The Dominican amber fauna is rather diverse (Engel *et al.*, 2012), and the known males are spread across the tribes Xeromelissini, Protandrenini, Caenohalictini, and Meliponini (Table 1), making it the richest source of male bees in the fossil record. Despite this, the relatively young age of the Dominican amber means that those bees discovered are somewhat modern in character, and even the extinct genera recovered are quite similar to their living relatives. The same is true of the males of *P. silacea* found in Mexican amber (Engel, pers. obs.). Thus, *M. hoffeinsorum* is of great interest due to its age: it is from the Paleogene and more than twice the age of species from Dominican or Mexican amber. *Mochlome-likertes* is also representative of an extinct tribe of corbiculate bees and exhibits some rather peculiar traits not presently known among the living fauna.

It is obviously an open question as to whether or not the male holotype described here is associated with one of the previously described species of Melikertini. Admittedly, there is a lack of certainty given that we do not have male-female associations among any of the known Melikertini. Furthermore, unique traits among other melikertines are only known from workers, which may not necessarily exclude a male from lacking such features. For example, the peculiar clypeal prominences of species of *Succinapis* might be gender-specific and therefore their absence in males might be of little taxonomic value. From a practical standpoint, one could argue that the establishment of a new genus is warranted until such a time as males and females are found together, but this is unlikely given the rarity of male apoids in amber. Despite these difficulties, we nonetheless believe that there is sufficient evidence for the erection of a new genus. Firstly, the new male is quite large, nearly twice the size of most species of Melikertini.

For example, total body lengths among species of *Succinapis* range from 3.5–4.2 mm, and most *Melikertes* are between 3.0 and 3.8 mm, while *M. trigona* and *Roussyana palm-nickenensis* (Roussy) are 4.2 mm and 3.1 mm, respectively (Engel, 2001a; Engel et al., 2013). It is therefore inconceivable that the holotype of *M. hoffsessorum* (at 8.0 mm in length) is conspecific with one of these taxa. There is a single melikertine, *M. proavus* (Menge), which is of a comparable size (8.3 mm in length), but the wing venation is dramatically different, and the form of the tegula also differs notably between these taxa (*vide* Engel, 2001a), and neither of these features is sexually dimorphic in other corbiculate apine taxa. Thus, there is nothing to suggest that *M. hoffsessorum* should be considered the male of *M. proavus* nor can the species be accommodated within the genus *Melikertes* s.l. It will be exciting to discover the female of *M. hoffsessorum* and to learn to what degree the characters observed in the male are shared.

Some Melikertini exhibit rather bizarre morphological traits. The aforementioned clypeal prominences of species of *Succinapis* are unique among the corbiculate Apinae and in some ways reminiscent of similar facial modifications among the Lithurginae or Centridini (e.g., Michener, 1983, 1988; Snelling, 1983; Moure, 2003; Vélez & Vivallo, 2012; Gonzalez et al., 2013). Whereas in these other groups the facial prominences are typically supraclypeal, those in *Succinapis* are entirely clypeal in origin. The functions of these facial modifications in workers of a eusocial species are entirely unknown. Interestingly, *M. hoffsessorum* also has a structure wholly unknown among the corbiculate Apinae, and unique within the Anthophila. The mesoscutellar extension is a feature *sui generis*. Certainly modified mesoscutella are diverse among bees, ranging from simple paired tubercles among many lineages, to the flattened, shield-like structure of *Thyreus* Panzer (Lieftinck, 1962; Straka & Engel, 2012), or the short, flattened, bifid, medial extensions of *Crocisaspidia* Ashmead (Ashmead, 1899; Pauly, 1990). Nonetheless, no elongate extension such as that observed in *M. hoffsessorum* is known among bees, nor do any of the mesoscutellar modifications among living Anthophila reach back to the third metasomal segment. The function of the densely setose, tongue-like process of *M. hoffsessorum* defies imagination and most certainly would have limited the movement of the metasoma in life. Given that the mesoscutellar extension is not articulated, it would have impeded any upward movement of the metasoma, and its posterior orientation on the dorsum of the individual would have rendered it useless in terms of manipulating females or other tactile events during copulation (assuming it was a secondary sexual trait in the same manner as modified tarsi, tibiae, or femora in several groups). While some mesoscutellar modifications are easily understood in terms of defense, such as protecting the dorsum of the mesosoma-metasoma articulation, these are often found in cleptoparasitic groups where there is more likely to be antagonistic interactions between a cuckoo encountering the host female within or near a nest. Again, the mesoscutellar process in *M. hoffsessorum* does not seem to be for defense: it is relatively narrow, and although extending posteriorly quite a long distance, it does not reach laterally to block the movements of a potentially broad-jawed aggressor, or any assailant attacking from a lateral or dorsally oblique direction. Moreover, cleptoparasites are unknown among the Melikertini and to assume that this is the male of a cuckoo or socially-parasitic bee is beyond speculative. For the moment, the purpose of such a structure remains elusive but does highlight how different the biology of these bees must have been from groups living today. Such a structure must have been associated with aspects of biology, behavior (e.g., metasomal movements relative to the mesosoma, leg movements over the body, grooming movements), and development (e.g., pupation and eclosion, formation of the extension) which are now lost. Evolu-

tionary developmental work among bees is greatly needed (Engel, 2011), precisely for understanding the origins of exaggerated morphologies such as the expression of male traits among cuckoo bees, the production of the modified metatibiae of orchid bees, the modified mandibles and faces of many Megachilini, and the independently elongate proboscides of some xeromelissines, halictines, and augochlorines, among many others. Such work may ultimately permit a more thorough understanding of the underlying mechanisms permitting the formation of a feature such as the mesoscutellar extension observed in *M. hoffeinsorum* and perhaps therein insights into its use.

ACKNOWLEDGEMENTS

We are deeply grateful to Christel and Hans Werner Hoffeins for bringing the present material to our attention and permitting its study and eventual deposition in the Senckenberg Deutsches Entomologisches Institut. Reviews by Victor H. Gonzalez and Ryan C. McKellar were particularly helpful and significantly improved the final paper. Participation of L.C.V.B. was supported by U.S. National Science Foundation grant DEB-1144162 (to M.S.E.), while additional support was provided by DBI-1304957 (to M.S.E.). This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

REFERENCES

- Ashmead, W.H. 1899. Classification of the bees, or the superfamily Apoidea. *Transactions of the American Entomological Society* 26: 49–100.
- Camargo, J.M.F., D.A. Grimaldi, & S.R.M. Pedro. 2000. The extinct fauna of stingless bees (Hymenoptera: Apidae: Meliponini) in Dominican amber: Two new species and redescription of the male of *Proplebeia dominicana* (Wille and Chandler). *American Museum Novitates* 3293: 1–24.
- Cockerell, T.D.A. 1909. Some European fossil bees. *Entomologist* 42(559): 313–317.
- Engel, M.S. 1995 [1996]. *Neocorynura electra*, a new fossil bee species from Dominican amber (Hymenoptera: Halictidae). *Journal of the New York Entomological Society* 103(3): 317–323.
- Engel, M.S. 1996 [1997]. New augochlorine bees (Hymenoptera: Halictidae) in Dominican amber, with a brief review of fossil Halictidae. *Journal of the Kansas Entomological Society, Supplement* 69(4): 334–345.
- Engel, M.S. 1997. A new fossil bee from the Oligo-Miocene Dominican amber (Hymenoptera: Halictidae). *Apidologie* 28(2): 97–102.
- Engel, M.S. 2000a. A new interpretation of the oldest fossil bee (Hymenoptera: Apidae). *American Museum Novitates* 3296: 1–11.
- Engel, M.S. 2000b. Classification of the bee tribe Augochlorini (Hymenoptera: Halictidae). *Bulletin of the American Museum of Natural History* 250: 1–89.
- Engel, M.S. 2001a. A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). *Bulletin of the American Museum of Natural History* 259: 1–192.
- Engel, M.S. 2001b. Monophyly and extensive extinction of advanced eusocial bees: Insights from an unexpected Eocene diversity. *Proceedings of the National Academy of Sciences, U.S.A.* 98(4): 1661–1664.
- Engel, M.S. 2004. Geological history of the bees (Hymenoptera: Apoidea). *Revista de Tecnologia e Ambiente* 10(2): 9–33.
- Engel, M.S. 2005. Family-group names for bees (Hymenoptera: Apoidea). *American Museum Novitates* 3476: 1–33.
- Engel, M.S. 2008. A new species of *Ctenoplectrella* in Baltic amber (Hymenoptera: Megachilidae). *Acta Zoologica Academiae Scientiarum Hungaricae* 54(4): 319–324.
- Engel, M.S. 2009. Two new halictine bees in Miocene amber from the Dominican Republic (Hymenoptera, Halictidae). *ZooKeys* 29: 1–12.
- Engel, M.S. 2011. Systematic melittology: Where to from here? *Systematic Entomology* 36(1): 2–15.

- Engel, M.S., & L.C.V. Breikreuz. 2013. A male of the bee genus *Agapostemon* in Dominican amber (Hymenoptera: Halictidae). *Journal of Melittology* 16: 1–9.
- Engel, M.S., & C.D. Michener. 2013a. A minute stingless bee in Eocene Fushan amber from northeastern China (Hymenoptera: Apidae). *Journal of Melittology* 14: 1–10.
- Engel, M.S., & C.D. Michener. 2013b. Geological history of the stingless bees (Apidae: Meliponini). In: Vit, P., & D.W. Roubik (Eds.), *Stingless Bees Process Honey and Pollen in Cerumen Pots*: 1–7. Facultad de Farmacia y Bioanálisis, Universidad de Los Andes; Mérida, Venezuela; ix+156 pp. [<http://www.saber.ula.ve/handle/123456789/37108>]
- Engel, M.S., & M.G. Rightmyer. 2000. A new augochlorine bee species in Tertiary amber from the Dominican Republic (Hymenoptera: Halictidae). *Apidologie* 31(3): 431–436.
- Engel, M.S., D.A. Grimaldi, V.H. Gonzalez, I.A. Hinojosa-Díaz, & C.D. Michener. 2012. An exomalopsine bee in Early Miocene amber from the Dominican Republic (Hymenoptera: Apidae). *American Museum Novitates* 3758: 1–16.
- Engel, M.S., J. Ortega-Blanco, P.C. Nascimbene, & H. Singh. 2013. The bees of Early Eocene Cambay amber (Hymenoptera: Apidae). *Journal of Melittology* 25: 1–12.
- Gonzalez, V.H., & M.S. Engel. 2011. A new species of the bee genus *Ctenoplectrella* in middle Eocene Baltic amber (Hymenoptera, Megachilidae). *ZooKeys* 111: 41–49.
- Gonzalez, V.H., M.S. Engel, & T.L. Griswold. 2013. The lithurgine bees of Australia (Hymenoptera: Megachilidae), with a note on *Megachile rotundipennis*. *Journal of Melittology* 11: 1–19.
- Grimaldi, D., & M.S. Engel. 2005. *Evolution of the Insects*. Cambridge University Press; Cambridge, UK; xv+755 pp.
- Hoffeins, H.W. 2001. On the preparation and conservation of amber inclusions in artificial resin. *Polskie Pismo Entomologiczne* 70(3): 215–219.
- Lieftinck, M.A. 1962. Revision of the Indo-Australian species of the genus *Thyreus* Panzer (= *Crocisa* Jurine) (Hym., Apoidea, Anthophoridae) Part 3. Oriental and Australian species. *Zoologische Verhandlungen* 53: 1–212, +3 pls.
- Michener, C.D. 1983. The classification of the Lithurginae (Hymenoptera: Megachilidae). *Pan-Pacific Entomologist* 59(1–4): 176–187.
- Michener, C.D. 1988 [1989]. The genus *Lithurge* in the Antilles (Hymenoptera, Megachilidae). *Folia Entomológica Mexicana* 76: 159–164.
- Michener, C.D. 2007. *The Bees of the World* [2nd Edition]. John Hopkins University Press; Baltimore, MD; xvi+[i]+953 pp., +20 pls.
- Michener, C.D., & G. Poinar, Jr. 1996 [1997]. The known bee fauna of the Dominican amber. *Journal of the Kansas Entomological Society, Supplement* 69(4): 353–361.
- Michez, D., M. Vanderplanck, & M.S. Engel. 2012. Fossil bees and their plant associates. In: Patiny, S. (Ed.), *Evolution of Plant-Pollinator Relationships*: 103–164. Cambridge University Press; Cambridge, UK; xv+477 pp.
- Moure, J.S. 2003. Duas espécies novas de *Centris* (*Heterocentris*) Cockerell, da região Amazônica e do Brasil Central (Hymenoptera, Apoidea). *Revista Brasileira de Zoologia* 20(2): 265–268.
- Ohl, M., & M.S. Engel. 2007. Die Fossilgeschichte der Bienen und ihrer nächsten Verwandten (Hymenoptera: Apoidea). *Denisia* 20: 687–700.
- Patiny, S., M.S. Engel, P. Vanmarsenille, & D. Michez. 2007. A new record of *Thaumastobombus andreniformis* Engel 2001 in Eocene amber (Hymenoptera: Apidae). *Annales de la Société de Entomologique de France* 43(4): 505–508.
- Pauly, A. 1990. Classification des Nomiinae Africains (Hymenoptera Apoidea Halictidae). *Koninklijk Museum voor Midden-Afrika Terouren België, Annalen Zoologische Wetenschappen* 261: 1–206.
- Rozen, J.G., Jr. 1996 [1997]. A new species of the bee *Heterosarus* from Dominican amber (Hymenoptera: Andrenidae; Panurginae). *Journal of the Kansas Entomological Society, Supplement* 69(4): 346–352.
- Snelling, R.R. 1983. The North American species of the bee genus *Lithurge* (Hymenoptera: Megachilidae). *Contributions in Science* 343: 1–11.
- Straka, J., & M.S. Engel. 2012. The apid cuckoo bees of the Cape Verde Islands (Hymenoptera, Apidae). *ZooKeys* 218: 77–109.

- Vélez, D., & F. Vivallo. 2012. A new South American species of *Centris* (*Heterocentris*) Cockerell, 1899 with a key to the species with horn-like projections on the clypeus (Hymenoptera: Apidae: Centridini). *Zootaxa* 3357: 49–55.
- Wappler, T., T. De Meulemeester, A.M. Aytakin, D. Michez, & M.S. Engel. 2012. Geometric morphometric analysis of a new Miocene bumble bee from the Randeck Maar of southwestern Germany (Hymenoptera: Apidae). *Systematic Entomology* 37(4): 784–792.
- Weitschat, W., & W. Wichard. 2002. *Atlas of Plants and Animals in Baltic Amber*. Verlag Friedrich Pfeil; München, Germany; 256 pp.
- Weitschat, W., & W. Wichard. 2010. Baltic amber. In: Penney, D. (Ed.), *Biodiversity of Fossils in Amber from the Major World Deposits*: 80–115. Siri Scientific Press; Manchester, UK; 304 pp.
- Wille, A. 1959. A new fossil stingless bee (Meliponini) from the amber of Chiapas, Mexico. *Journal of Paleontology* 33(5): 849–852, +1 pl.
- Wille, A., & L.C. Chandler. 1964. A new stingless bee from the Tertiary amber of the Dominican Republic (Hymenoptera; Meliponini). *Revista de Biología Tropical* 12(2): 187–195.

ZooBank: urn:lsid:zoobank.org:pub:D3E9ABEE-FC97-4D2F-8834-E6D1F6C81D55



Journal of JM Melittology

A Journal of Bee Biology, Ecology, Evolution, & Systematics

The *Journal of Melittology* is an international, open access journal that seeks to rapidly disseminate the results of research conducted on bees (Apoidea: Anthophila) in their broadest sense. Our mission is to promote the understanding and conservation of wild and managed bees and to facilitate communication and collaboration among researchers and the public worldwide. The *Journal* covers all aspects of bee research including but not limited to: anatomy, behavioral ecology, biodiversity, biogeography, chemical ecology, comparative morphology, conservation, cultural aspects, cytogenetics, ecology, ethnobiology, history, identification (keys), invasion ecology, management, melittopalynology, molecular ecology, neurobiology, occurrence data, paleontology, parasitism, phenology, phylogeny, physiology, pollination biology, sociobiology, systematics, and taxonomy.

The *Journal of Melittology* was established at the University of Kansas through the efforts of Michael S. Engel, Victor H. Gonzalez, Ismael A. Hinojosa-Díaz, and Charles D. Michener in 2013 and each article is published as its own number, with issues appearing online as soon as they are ready. Papers are composed using Microsoft Word® and Adobe InDesign® in Lawrence, Kansas, USA.

Editor-in-Chief

Michael S. Engel
University of Kansas

Assistant Editors

Victor H. Gonzalez
Southwestern Oklahoma State University

Charles D. Michener
University of Kansas

Journal of Melittology is registered in ZooBank (www.zoobank.org), archived at the University of Kansas and in Portico (www.portico.org), and printed on demand by Southwestern Oklahoma State University Press.

<http://journals.ku.edu/melittology>
ISSN 2325-4467