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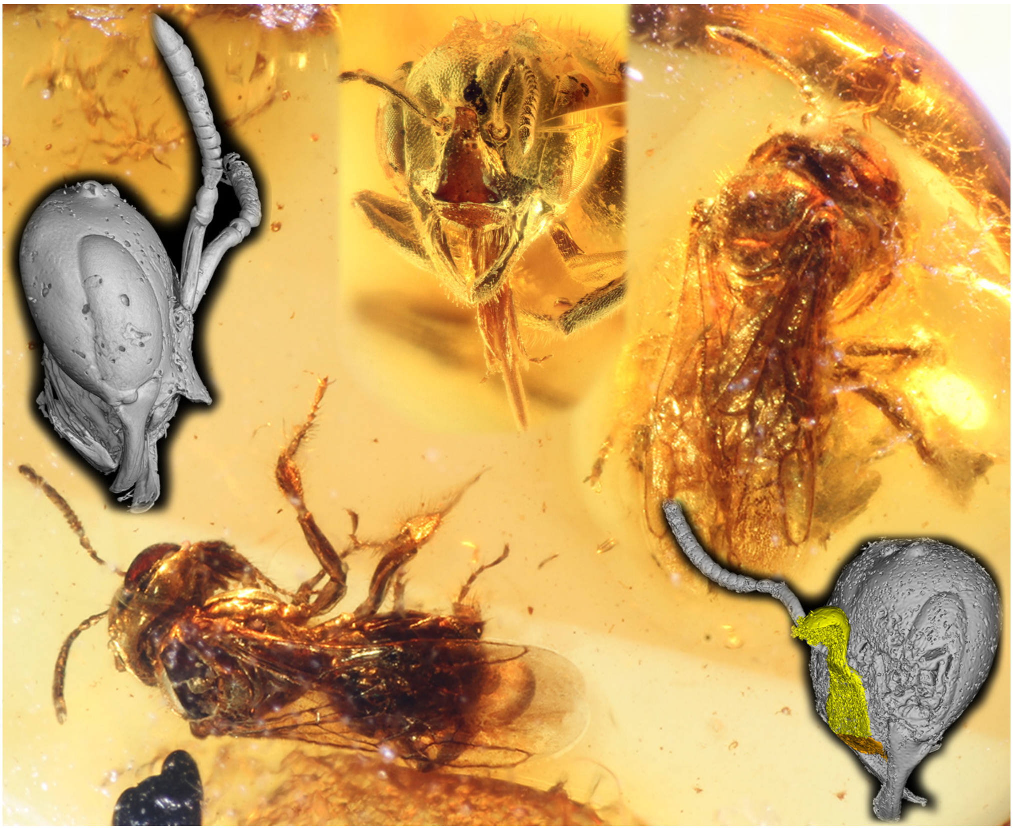

Journal *of* Melittology

No. 103 ISSN 2325-4467 6 July 2021

On the cover: A collage of photographs and μCT scans of melikertine bees in Eocene Baltic amber.

Journal *of* Melittology

Bee Biology, Ecology, Evolution, & Systematics *The latest buzz in bee biology*

No. 103, pp. 1–52 6 July 2021

New genera of melikertine bees with facial modifications in Baltic amber (Hymenoptera: Apidae)

Michael S. Engel[1,2] & Steven R. Davis[1]

Abstract. The tribe Melikertini (Apinae: Corbiculata) is an extinct group of highly eusocial bees presently known only from early to late Eocene deposits of Eurasia. Among melikertine diversity are a suite of species peculiar for their rather dramatic morphological specializations, at least in relation to modern corbiculate Apinae. Here we document two new species of Melikertini and utilize standard X-ray as well as propagation phase contrast synchrotron computed microtomography to further explore these and previously known species, revealing finer details not previously observable from melikertines. Accordingly, some species placed in the genera *Melikertes* Engel and *Succinapis* Engel are reëvaluated. Three new genera are characterized, as well as some further facial modifications not previously known for the tribe. New taxa and taxonomic changes presented are: ***Aethemelikertes emunctorii*** Engel, new genus and species; ***Haidomelikertes uraeus*** Engel, new genus and species; *H. proboscidea* (Engel), **new combination**; ***Amelikertotes*** Engel, new genus; *Amelikertotes clypeata* (Engel), **new combination**. Additionally, new records and taxonomic notes on other Baltic amber and Eocene bees are appended, with the following nomenclatural changes established: *Palaeomacropis* Michez & Nel is recognized as a megachiline rather than a melittid, and is transferred to Megachilinae where it is a new junior synonym of *Ctenoplectrella* Cockerell (**new synonymy**); *Ctenoplectrella eocenica* (Michez & Nel), **new combination**; a key is provided to species of *Ctenoplectrella*; **Thaumastobombina** Engel, new subtribe in Electrapini; ***Thnetobombus*** Engel, new subgenus in *Protobombus* Cockerell; ***Mesomelissa*** Engel, new subgenus in *Electrapis* Cockerell; *Electrapis* (*Euglossopteryx*) *biesmeijeri* (De Meulemeester *et al.*), new combination. A list of Eocene bees is appended.

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doi: http://dx.doi.org/10.17161/jom.i103.15655

ISSN 2325-4467

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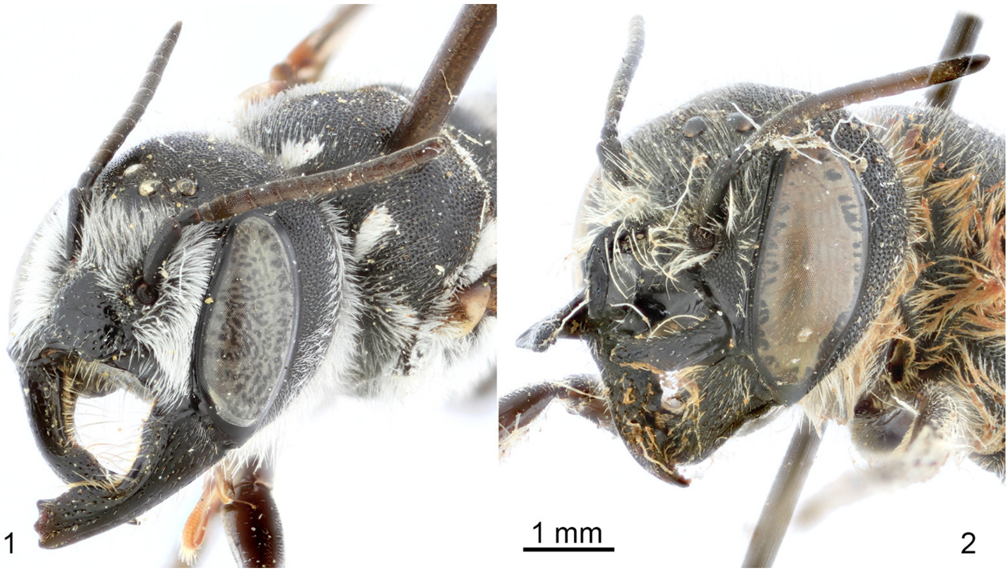
INTRODUCTION

Facial modifications of bees are not uncommon, particularly in lineages such as Megachilini where resin bees may have various contrivances in females (Figs. 1, 2), presumably for the manipulation and transport of masses of resin used in nest construction. While such morphological contrivances are seemingly commonplace in Megachilidae, among corbiculate bees such specializations are lacking with the exception of a series of fossil species in Eocene Baltic amber. All species of the genus *Succinapis* Engel, as previously circumscribed, are peculiar for upper extensions of the clypeal base that project upward between the antennae to varying degrees (Engel, 2001a) (Figs. 3, 4, 6). When first discovered the three variants were first interpreted as points along a continuum of variation within a single species, but when found as syninclusions no two forms have ever been found together, even when nearly a dozen workers are found in a single piece. Accordingly, as no intermediates have ever been discovered the three forms are considered as distinct species (Engel, 2001a). This pattern has continued as more and more syninclusions of these species have been discovered over the last 20 years. Moreover, the largest of protrusions do not correlate with individuals with allometrically larger heads or body sizes. Accordingly, there has been no evidence yet to surface suggesting that these various morphological varieties are anything other than distinct species, and hopefully future data will continue to corroborate such an interpretation.

More importantly, the advent of finer scales of resolution in micro-computed tomography (μCT) scans have permitted a new examination of details in these fossils, allowing for a fuller consideration of characters. These data now indicate that such bees are more different than previously surmised. Moreover, while visiting the Senckenberg Forschungsinstitut, Frankfurt in 2019, one of us (M.S.E.) sorted many new inclusions of *Succinapis* and other Baltic amber bees, adding various new records of specimens for these species and building upon earlier reports of additional material (*e.g.*, Engel, 2004; Patiny *et al.*, 2007; Appendix 1, *vide infra*). Among the material and in separate pieces were two new melikertine species exhibiting hitherto unknown morphological varieties of prominent facial modifications. These two bees also exhibited additional morphological differences from the various species of *Succinapis*, some in line with new μCT data from scans of the three previously recognized species, as well as a single species of *Melikertes* Engel that possessed a wholly different form of facial modification (that of the clypeal apex rather than the clypeal base). Accordingly, the aforementioned two new species are described here and, along with added information from μCT scans, this expanded diversity is organized into four genera, three of which are newly described. In addition, we have appended records of other Baltic amber bees (Appendix 1), notes to clarify the identity of an Eocene bee from Paris Basin (Oise) amber (Appendix 2), notes on Eocene electrapine bees (Appendix 3), and a general list of Eocene bees (Appendix 4).

MATERIAL AND METHODS

New and past material of Eocene amber bees was studied from the collections of the Senckenberg Forschungsinstitut, Frankfurt (SMF); Snow Entomological Collections, Division of Entomology, University of Kansas Natural History Museum, Lawrence (SEMC); and the Division of Invertebrate Zoology, American Museum of Natural History, New York (AMNH). Translingual symbols are used to specify the caste for



Figures 1–2. Examples of facial modifications in megachiline bees (Megachilinae: Megachilini), specifically examples of clypeal and supraclypeal structures. **1.** Oblique facial view of *Chelostomoides chilopsidis* (Cockerell). **2.** Oblique facial view of *C. armaticeps* (Cresson).

individuals of eusocial bees, and specifically ♀ for the worker caste (*e.g.*, Engel & Rasmussen, 2017; Rasmussen *et al*., 2017; Engel, 2019; Engel *et al*., 2019). Morphological terminology for the descriptive work was taken from Engel (2001a), Michener (2007), and Rasmussen *et al*. (2017), with specific terms for the protibial calcar of the strigilis adapted from Engel *et al*. (2017). Individual metrics of the specimens of the new species reported here were measured using the μCT scans. Standard light photographs were taken with a Canon EOS7 digital camera with various microscopic lens attachments, and illuminated by a Xenon flash.

Micro-CT scanning of amber specimens of *Haidomelikertes proboscidea* (Engel) (holotype), *H. uraeus* n. sp., *Succinapis goeleti* Engel (holotype and paratype), *S. micheneri* Engel (holotype), and *Aethemelikertes emunctorii* n. sp. (holotype) was done in 2019 at the AMNH using a GE Phoenix v|tome|x s240 equipped with a 180 kV X-ray source and a diamond target. Scanning parameters were as follows: voltage 80 kV, current 180 μA, number of projection images 1500, exposure 750 ms, averages 5, voxel sizes 3.0–4.3 μm. Reconstruction was performed using GE Phoenix datos|x 2.3.2 reconstruction software. Image segmentation was done using 3D Slicer 4.11. In general, μCT scans of certain insect inclusions have proven difficult with this platform, often resulting in low contrast between insect inclusion and amber matrix. The scans of *S. goeleti* were of sufficiently low contrast such that both the holotype and paratype here do not contribute additional information beyond traditional light microscopy and what was reported earlier (Engel, 2001a), and those poorly resolved, low-contrast results are therefore not presented.

The specimens of *Melikertes clypeatus* Engel (now classified below in *Amelikertotes*, n. gen.) were imaged in 2014 using propagation phase contrast X-ray synchrotron microtomography (afterwards PPC-SRμCT) at the Advanced Photon Source (APS) at Argonne National Laboratory, Chicago. The specimens were scanned following the protocols described in Soriano *et al*. (2010), with a monochromatic beam at 25 keV and 250 mm of distance between the camera and sample. Scan acquisition consisted of 1800 projections over 180°, with 0.3 s exposure time and 1.45 μm voxel size. Slices were reconstructed using a filtered back-projection algorithm adapted for local tomography applications (Tomopy software, APS: Gürsoy *et al.*, 2014). Subsequent three-dimensional processing was prepared using VGStudioMax 2.2 software (Volume Graphics, Heidelberg, Germany).

SYSTEMATIC PALEONTOLOGY

Tribe Melikertini Engel

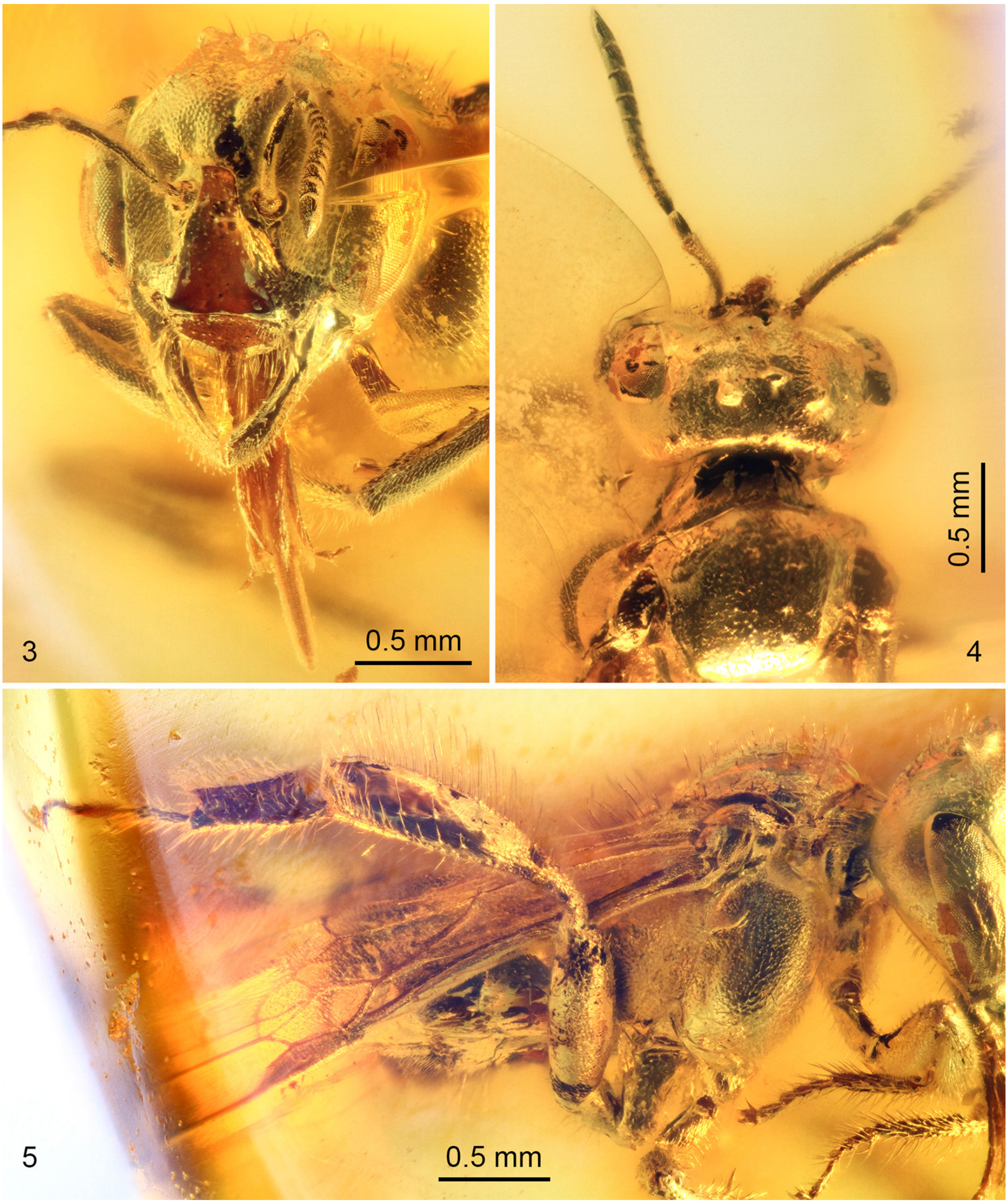
Melikertini Engel, 2001a: 112. Type genus: *Melikertes* Engel, 1998.

Melikertine bees superficially resemble stingless bees (Meliponini), with a general habitus similar to many small meliponine genera. However, Melikertini differ from Meliponini most noticeably by the complete wing venation (reduced in Meliponini), presence of a supraälar carina (absent in Meliponini), presence of an auricle (absent in Meliponini), absence of a penicillum (present in Meliponini), presence of a single metatibial spur (absent in Meliponini), toothed pretarsal claws (simple in Meliponini: nota bene, the inner ramus in Melikertini is minute and often difficult to see if not in the proper orientation), and presence of a well-developed sting (vestigial in Meliponini).

Several Melikertini have unusual morphological modifications. Aside from those taxa discussed herein with facial specializations, *Mochlomelikertes* Engel *et al.* has a uniquely modified mesoscutellum that bears a densely setose, elongate, medial extension of the posterior margin that extends caudally over the metanotum, propodeum, and beyond the apical margin of the second metasomal tergum (Engel *et al.*, 2014). More commonly, however, the unique specializations of melikertines are found in the workers and involve the clypeus, either along the apical margin or, more frequently, the base where it abuts the supraclypeal area (Figs. 3, 4, 6). In the latter instances the clypeus protrudes out and upward in various configurations, with the epistomal sulcus traversing behind the extension (visible also in μCT scans). These clypeal enhancements are elaborated on herein (*vide infra*).

Additional features of Melikertini include: Generally small- to moderate-sized (*ca.* 3–8.5 mm in length), with sparse body pubescence. The head is generally about as wide as or slightly wider than long, with a clypeus that is flat to gently convex and only weakly protrudent in profile, not considering the varied clypeal modifications discussed herein. The compound eyes are large, with comparatively straight inner ocular margins, at most with a faint concavity to the margin about midlength or above midlength, and the compound eyes are always bare (unlike Apini and some Meliponini).

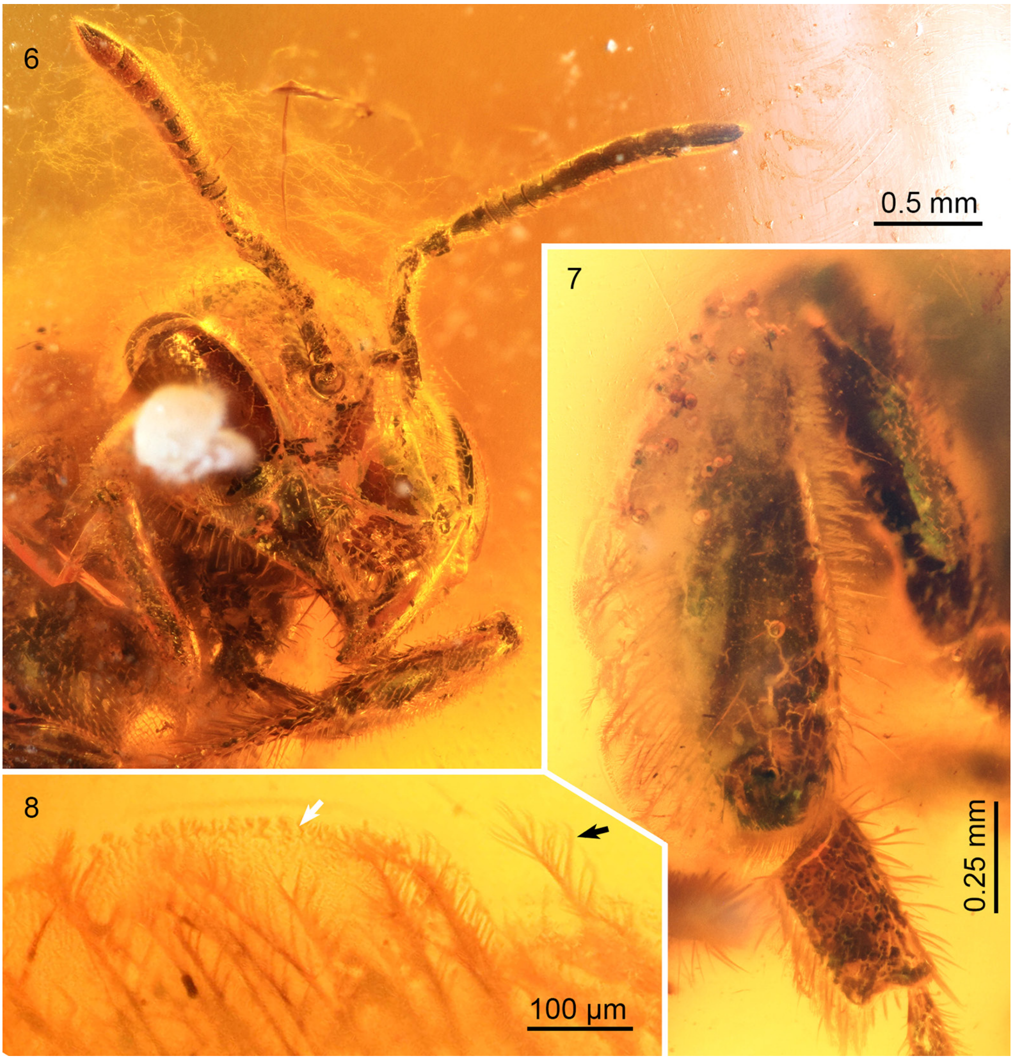
The mandibles are quite typical for Apini and Meliponini, that is they are elongate with a reduction of the outer mandibular grooves and with a distinctively wide rutellar cap that is largely indistinguishable from the remainder of the rutellum (Figs. 63–70). Like Meliponini there is a faint outer groove obliquely traversing the rutellum of the mandible, all other outer mandibular grooves and ridges lost or vestigial. Unlike Meliponini though, this groove gradually weakens further apically and disappears in a straight line with the lower corner of the apical margin, while in stingless bees this groove most frequently arches apically to terminate into the lower margin of the mandible (*e.g.*, Michener & Fraser, 1978; Rasmussen *et al.*, 2017: figs. 3C, 6D; Mi-



Figures 3–5. Worker of *Succinapis micheneri* Engel (SEMC B-018). **3.** Facial view. **4.** Dorsal view of head and mesoscutum. **5.** Right lateral view.

chener, 2007). There is a small narrow incision along upper part of the apical margin that defines a blunt tooth separate from the lower and much broader apical margin (Figs. 63–70), differing from many Meliponini in this regard who have more distinct teeth, albeit often small and shallowly incised. Some melikertines appear to have two incisions, thus suggesting two teeth along the upper portion of the apical margin, but this can often be difficult to observe, particularly if the mandibles are closed.

The mesosoma is quite typical for corbiculate bees and particularly for Meliponini and Apini. Unlike Meliponini, there is a supraälar carina, in this regard plesiomorphi-



Figures 6–8. Worker of *Succinapis micheneri* Engel (SEMC B-017). **6.** Oblique facial view. **7.** Outer (prolateral) view of metatibia and metabasitarsus. **8.** Detail of fringe setae of metatibial posterior/upper margin; white arrow indicates a deceptive internal microfracture of resin trail with branched fractal pattern (such fracture planes and trails are a common taphonomic structure among or even running alongside many fine setae in amber inclusions, and can give such setae an artificially plumose appearance; accordingly, care must be taken before concluding whether or not amber-included setae are branched); black arrow highlights one of many truly plumose setae, separate from the internal microfracture planes.

cally similar to other corbiculates. The mesoscutellum is like many Meliponini (rather than the more bulbous mesoscutellum of Apini), with an apical margin that is broadly rounded and may or may not overhang the metanotum.

In general, the form of the protibial calcar that forms part of the strigilis (antennal cleaner) fits nicely into the general pattern of changes in the form of this modified spur across corbiculate bee tribes. While Apini, Bombini, and Euglossini have a secondary velum or pronounced lobe in its place (“anterior prong” or “anterior velum”)

(Schönitzer & Renner, 1980), Meliponini and Melikertini both lack the secondary velum and have only the primary velum that extends obliquely dorso-posteriorly from the rachis (Fig. 44) (orientation is assuming the leg is outstretched straight and orthogonal to the long axis of the body, meaning that the primary velum extends from the rachis upward and slightly inclined posteriorly). Euglossini and Bombini have serrate margins ("Zahnreihen" *sensu* Schönitzer & Renner, 1980) along the outer margin of the rachis as well as on the inner margin of the malus. Apini, Meliponini, and Melikertini lack these serrate margins (Fig. 44), potentially serving as another synapomorphy for this grouping of advanced eusocial tribes (Engel, 2001a, 2001b). Where observed, the malus of Melikertini is exceptionally short and simple to virtually absent.

Melikertine bees have a distinctive metatibia, the metatibia is consistently long and slender, scarcely expanding along its length for the corbicula (Figs. 5, 19–20, 46–50, 53, 54). In comparison to Meliponini, the metatibia in this regard is superficially similar to the legs of meliponine males, some *Lestrimelitta* Friese, or those *Trigona* Jurine of the *hypogea* species group, although melikertines were definitely pollen-collecting and probably also resin as it is not uncommon to find pollen or sometimes what seems to be resin in their corbiculae. While pollen is clear, potential resin masses in the corbiculae are more difficult to discern in some specimens owing to the resin being identical to the resin in which they are entombed. Nonetheless, a clear globular mass that looks like the surrounding resin but is typically faintly darker and distinguished by a subtle line demarcating it from the matrix resin may at times be found in the corbicula. The separation of these is analogous to those internal lines discernable between different resin flows. The subtle coloration differences could result from the resin in the corbicula having been partly processed by the bees during collection through the addition of specific enzymes. Alternatively, the color and faint line demarcating the surface of the mass in the corbicula from the resin matrix could reflect nothing more than the fact that the collected resin had already begun to harden relative to the subsequent resin flow that ensnared the bee. Bees collect resin that has already been exuded from tree wounds (sometimes inflicted by the bees themselves, with the resulting resin-secreting surfaces maintained and defended for days or weeks by repeated chewing: Schwarz, 1948; Howard, 1985) and begun hardening due to exposure to air (Leonhardt & Blüthgen, 2009), resulting in different stages of curing for the resin. Owing to the lack of metatibial expansion and the presence of an auricle on the metabasitarsal base, which thereby necessitates some corresponding surface on the apical margin of the metatibia with which to press, the posterior margin rounds down to a blunt posterior angle, the angle representing the outer rim of that surface facing the auricle. In this context, the metatibia of Melikertini is more similar to that of Apini or Bombini. The metatibia's posterior apical corner also differs in this context from the more typical apically broadened metatibia with an angulate, even sharply angled, posterior corner found in some Meliponini, or when the posterior border is broadly rounded it is almost always associated with a greatly expanded corbicular portion of the metatibia (*e.g.*, *Cephalotrigona* Schwarz: refer to images in Engel & Rasmussen, 2021). The corbicular surface is not depressed or even sometimes faintly convex, like much of the outer surface of the metatibia and again superficially resembling the hind legs of meliponine males or robber bees. The corbicula is often elongate and largely only demarcated by the pattern of setae on the outer surface, rather than a distinctly depressed surface typical of most corbiculate bees. As noted, the apex of the metatibia does have a slightly depressed, well-delimited surface defining the upper bounds of a pollen press and a distinct auricle is present proximally on the metabasitarsus to form the lower portion of the press

Table 1. Current classification of tribe Melikertini (Apinae: Corbiculata).

- Genus *Aethemelikertes* Engel, n. gen.
  - *A. emunctorii* Engel, n. sp.
- Genus *Amelikertotes* Engel, n. gen.
  - *A. clypeata* (Engel, 2001a), n. comb.
- Genus *Haidomelikertes* Engel, n. gen.
  - *H. proboscidea* (Engel, 2001a), n. comb.
  - *H. uraeus* Engel, n. sp.
- Genus *Melikertes* Engel, 1998
  - Subgenus *Melikertes* Engel, 1998
    - *M.* (*M.*) *kamboja* Engel & Ortega-Blanco in Engel *et al.*, 2013
    - *M.* (*M.*) *proavus* (Menge, 1856)
    - *M.* (*M.*) *stilbonotus* (Engel, 1998)
  - Subgenus *Paramelikertes* Engel & Ortega-Blanco in Engel *et al.*, 2013
    - *M.* (*P.*) *gujaratensis* Engel & Ortega-Blanco in Engel *et al.*, 2013
- Genus *Melissites* Engel, 2001a
  - *M. trigona* Engel, 2001a
- Genus *Mochlomelikertes* Engel, Breitkreuz, & Ohl, 2014
  - *M. hoffeinsorum* Engel, Breitkreuz, & Ohl, 2014
- Genus *Roussyana* Manning, 1960 [1961]
  - *R. palmnickenensis* (Roussy, 1937)
- Genus *Succinapis* Engel, 2001a
  - *S. goeleti* Engel, 2001a
  - *S. micheneri* Engel, 2001a

(Figs. 43, 53, 54). Unlike Meliponini there is no penicillum, although in *Amelikertotes* there is a small patch of long setae that extends apically from the outer, anterior, apical corner of the metatibia. These setae do not have the form of penicillum, instead having the form typical of most generally straight or slightly arched setae, but given their placement it is tempting to speculate such a patch as a precursor to an eventual penicillum. Overall, it is possible that the general form of the metatibia is a synapomorphy for Melikertini as it seems to be a derived condition relative to the general form of corbiculae and metatibiae of other corbiculate tribes.

Other leg features of the tribe include the presence of a well-developed mesotibial spur (variable, but many times greatly reduced and vestigial in Meliponini: Oliveira, 2002), a single metatibial spur (Figs. 19, 43), pretarsal claws with a minute inner ramus (often exceedingly difficult to see without the right orientation), and an arolium is always present and sometimes quite large.

The general pattern of wing venation is largely typical for those corbiculate bees with complete distal wing venation (distal wing venation reduced in Meliponini). The marginal cell is large and narrowly to broadly rounded apically, sometimes feebly appendiculate, and typically offset from the anterior wing margin to varying degrees. The marginal cell is always longer than the distance from its apex to the wing apex. The pterostigma is always well developed and of a moderate size, and typically around 2.5–3× longer than wide, with a minute prestigma, and with r-rs arising near the midpoint (sometimes slightly basad or distad) of the pterstigma. The second submarginal cell is always produced posteriorly where it meets 1m-cu, and 1m-cu is angulate apically where it meets 2M. The hind wing has a distinct jugal lobe that is broadly and deeply incised, and there are a reduced number of distal hamuli (relative to Euglossini, Bombini, Apini, Electrobombini, and Electrapini, with the exception of

Thaumastobombus Engel). The wing membranes lack alar papillae or infuscation patterns, always being hyaline.

The metasoma is quite like most Meliponini, although the sting apparatus is clearly not reduced, with many melikertines preserved with the simple sting everted and with the associated sheaths visible.

The diversity of melikertine bees as currently understood is summarized in table 1. The most commonly encountered melikertine has been *S. micheneri*, a distinctive species that can be found in comparatively larger numbers than other Melikertini. The growing number of well-preserved specimens has made it possible to make more extensive comparisons between this species and the newly discovered species reported herein. Conversely, some species are exceptionally rare, such as *Roussyana palmnickenensis* (Roussy) and *Melissites trigona* Engel (Engel, 2001a). Presently, all Melikertini are known only as inclusions in amber, while other extinct tribes from the same epoch are found as both inclusions and compressions (*e.g.*, Wappler & Engel, 2003; Wappler *et al.*, 2015; Wedmann *et al.*, 2009).

Key to Genera of Melikertini
(modified and expanded from that of Engel, 2001a, and Engel *et al.*, 2014)

As noted by Engel *et al.* (2014) it remains unknown to what degree some of the characters presented here are gender or caste specific. Accordingly, care should be taken when using the key in relation to new material of hitherto unknown castes or sexes.

1. Disc of clypeus comparatively flat, without distinct lateral carinae and without bell-like concavity 2
—. Clypeus with lateral carinae rising from apex to form margins of bell-like concavity arising from base of clypeus and overhanging disc (Figs. 10, 12, 14, 16) .... *Aethemelikertes* Engel, n. gen.
2(1). 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 obscuring supraclypeal area or even lowermost frons in facial view (Figs. 3, 4, 6, 23–26) 3
—. Clypeal protrusion absent 4
3(2). Apex of clypeal protrusion narrow, narrower than intertorular distance (Figs. 3, 4, 6) .... *Succinapis* Engel
—. Apex of clypeal protrusion broad, as wide as or slightly wider than intertorular distance (Figs. 23–26) .... *Haidomelikertes* Engel, n. gen.
4(2). Mesoscutellum without tongue-like medioapical extension [females: workers] 5
—. Mesoscutellum with prominent, tongue-like medioapical extension projecting over metanotum, propodeum, and portions of metasoma, dorsal surface of extension densely setose [males: drones] .... *Mochlomelikertes* Engel *et al.*
5(4). 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 6
—. Mesoscutellum not bulging, not overhanging metanotum or propodeum; metasomal terga uniformly colored; anterior and posterior margins of metabasitarsus approximately parallel 7

6(5). 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 below; second flagellomere distinctly shorter than third flagellomere, first flagellomere distinctly shorter than combined lengths of second and third flagellomeres .... *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 .... *Roussyana* Manning

7(5). Apical margin of clypeus straight, flat, not flared anteriorly and not projecting over plane of labrum (genus *Melikertes* Engel, *s.l.*) 8

—. Apical margin of clypeus flared and projecting anteriorly over plane with labrum, medioapically with shallow U-shaped emargination (Figs. 34–36, 38, 39, 57, 58, 60–62) .... *Amelikertotes* Engel, n. gen.

8(7). Forewing with two submarginal cells (1rs-m absent) .... *Paramelikertes* Engel & Ortega-Blanco

—. Forewing with three submarginal cells (1rs-m present) .... *Melikertes* Engel, *s.str.*

Aethemelikertes Engel, new genus

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Type species: *Aethemelikertes emunctorii* Engel, new species.

Diagnosis: This genus is immediately recognizable for the inverted clypeal basin that projects over the clypeal disc as a broadly concave surface, laterally demarcated by carinae that extend to the clypeal apical margin (Figs. 9–12, 14, 16). In addition, the labrum is trapezoidal with lateral margins converging apically, the slope in the apical half different from that proximally, laterally without a fringe of prominent setae, and the blunt apical margin with a shallow medial concavity.

Description: ♀: Small bee, *ca.* 3.9 mm in length; head wider than long, upper interorbital distance greater than compound eye length. Mandible with outer mandibular grooves reduced, faint impression of outer groove obliquely across apical half of mandible, vanishing well before apex; shallow indentation for single blunt preapical tooth along upper third of apical margin; axes of mandibular articulations converging anteriorly such that closed mandibles overlap at slightly obtuse angle and do not obscure or limit forward movement of labrum; malar space linear; labrum flat, slightly broader than medial length, lateral margins converging apically, with abrupt change in slope of convergence at about midlength, apical margin blunt, giving overall inverted trapezoidal appearance, apical margin with broad shallow concavity medially, surface with sparsely scattered suberect to erect setae, lateral margins without fringe of setae; clypeus with prominent basal modification, forming inverted basin overhanding clypeal disc, lateral margins of clypeal basin extending as longitudinal lateral carinae terminating at apical margin at juncture with labral basal angles; clypeal basin extending upward over supraclypeal area and between antennal toruli, as broad as intertorular space, upper apical margin seemingly slightly wavy or scalloped; disc of clypeus comparatively flat; epistomal sulcus laterally forming obtuse angle, medially sulcus obscured from view by clypeal basin; upper torular tangent slightly below head mid-

Figures 9–10. Holotype worker of *Aethemelikertes emunctorii*, new genus and species, in Eocene (Bartonian) Baltic amber (SMF Be 14262a). **9.** Ventral view. **10.** Slightly obliquely dorsal facial view emphasizing upper, slightly scalloped margin of clypeal basin.

length; intertorular distance about 2× torular diameter; scape shorter than torulocellar distance; first flagellomere slightly longer than wide, longer than second flagellomere, second and third flagellomeres equal in length, each wider than long; ocelli high on vertex, situated well above upper tangent of compound eyes; vertex unmodified (no depressions or ridges); preoccipital area rounded; gena slightly narrower than compound eye in profile. Mesoscutum with anterior border low, broadly rounded; tegula elongate-ovoid; mesoscutellum low, rounded, not greatly projecting over metanotum

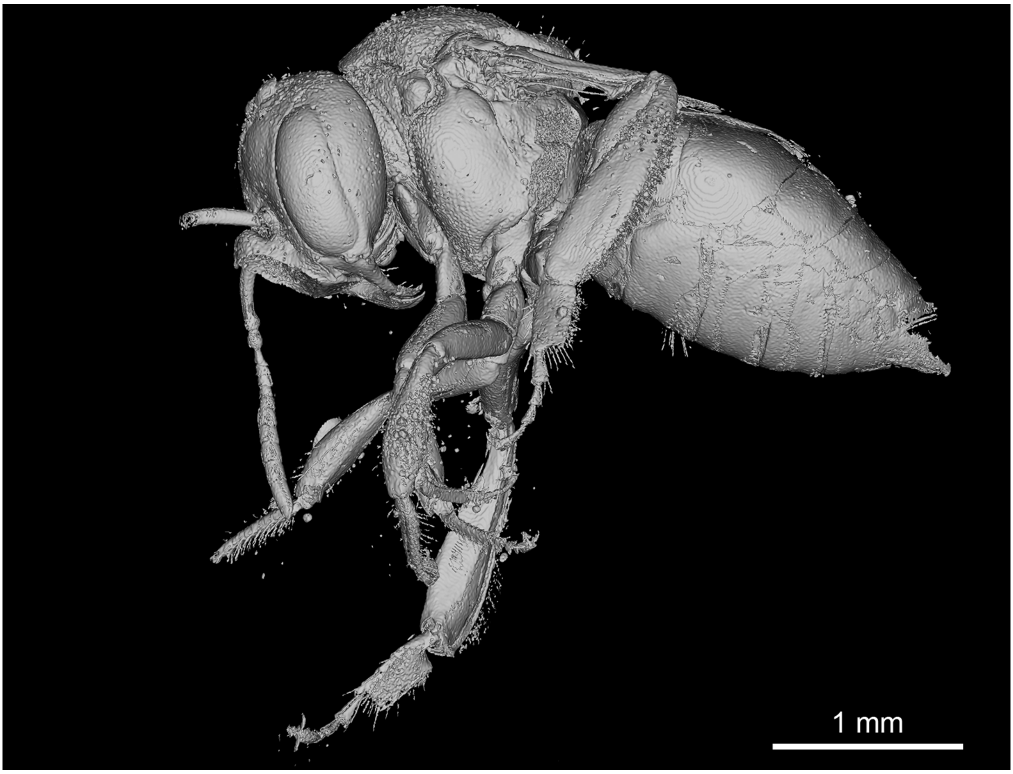


Figure 11. X-ray µCT scan of holotype worker of *Aethemelikertes emunctorii*, new genus and species (SMF Be 14262a), lateral view. Note that scan resolution was insufficient to resolve most setae.

and base of propodeum; propodeum with sloping basal area distinct from vertical posterior surface. Forewing with prominent, subtriangular pterostigma, pterostigma about 3× as long as maximum width, maximum width at about midlength, margin inside marginal cell sloping to costal margin; marginal cell acutely rounded apically, not appendiculate, apex offset from costal margin by about vein width; basal vein straight, confluent to overlapping slightly basad with 1cu-a; three submarginal cells present (1rs-m present), second submarginal cell trapezoidal, anterior border (3Rs) significantly shorter than r-rs, r-rs arising at about pterostigmal midlength (widest point); third submarginal cell broadest, but not broader than combined breadth of first and second submarginal cells; 1rs-m faintly arched, 2rs-m strongly arched, thus anterior border of third submarginal cell significantly shorter than posterior border of same cell; 1m-cu angulate at its extreme apex near second submarginal cell, entering second submarginal cell near cell midlength; anterior margin of hind wing with six distal hamuli arranged in an evenly spaced series; wing membranes hyaline clear; veins dark brown. Metatibia slender, elongate, length about 3.8× maximum width, posterior margin gently convex and slightly widening in apical two-thirds; surface of corbicula not depressed; posterior margin with fringe of elongate, plumose (branches minute and along length of setal rachis) setae, such setae as long as or longer than metatibial width, anterior margin with sparsely scattered simple setae and bristles, corbicular surface with sparsely scattered, erect, fine, simple setae, such setae long but not as long as those of posterior fringe; inner surface with keirotrichiate zone field covering most of surface except posterior, narrow, slightly depressed (*i.e.*, a weak clivulus present) glabrate zone and a broad, squarish apical glabrate zone (*sensu* Rasmussen *et al.*, 2017), apical glabrate zone slightly longer than apical width of metatibia; rastellum composed of stiff bristles along entire inner apical width of metatibia; single metatibial spur present, spur minutely ciliate along inner margin in apical half; metabasitarsus with auricle present on proximal surface facing apex of metatibia; metabasitarsus rectangular, longer than wide, length about 1.6× maximum width, margins roughly parallel, apical margin comparatively straight (*i.e.*, posterior angle not projecting), inner surface with abundant, elongate, suberect, simple bristles; pretarsal claws with minute inner subapical ramus; arolium present. Metasoma broad, ovoid, sparsely setose and largely smooth and shining, most setae minute, simple, and appressed to subappressed, more numerous (but still sparse) on more apical terga; metasomal sterna unmodified, with scattered, short, erect, fine, simple setae in apical quarter to third of sterna II–IV; sting present.

ETYMOLOGY: The new genus-group name is a combination of the Greek *aḗthēs* (ἀήθης), meaning, "unusual," and *Melikertes* Engel [itself a combination of *méli* (μέλῐ, "honey"), *keírô* (κείρω, "to cut"), and –*tḗs* (–τής, appended to verbs to form agent nouns; in the present case, making "honey cutter")], type genus of the tribe. The gender of the name is masculine.

Aethemelikertes emunctorii Engel, new species

ZooBank: urn:lsid:zoobank.org:act:8D128194-DD96-463E-93A9-442DEA649B74

(Figs. 9–12, 14, 16, 17–18, 20)

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

DESCRIPTION: ♀: Total body length (as preserved) 3.9 mm; forewing length (as preserved) 3.7 mm. Head slightly longer than wide, length (summit of vertex to clypeal apical margin) 1.20 mm, width (maximum width across compound eyes) 1.38 mm; compound eye length 0.82 mm; upper interorbital distance 0.95 mm, lower interorbital distance 0.84 mm; inner ocular margins largely straight, with faint arch about midlength, converging below; ocellar triangle broad, interocellar distance 0.40 mm. Scape length 0.50 mm, shorter than torulocellar distance. Mandible elongate, length 0.76 mm; labrum broader than long, basal width 0.44 mm, medial length 0.30 mm. Pronotum short, declivitous, without defined transverse dorsal ridge; pronotal lateral ridge absent; mesoscutum anterior border broadly rounded, anterior lip gently curving to meet posterior pronotal margin, not high over pronotal border; mesoscutum medial length 0.82 mm; intertegular distance 0.40 mm; mesoscutellum medial length 0.32 mm. Metatibia slender, length 1.40 mm, maximum width 0.37 mm; metabasitarsus longer than wide, length 0.43 mm, maximum width 0.27 mm. Forewing with basal vein (1M) basad 1cu-a, separated pterostigma longer than wide, maximum width at about midlength, margin inside marginal cell sloping to costal margin; marginal cell acutely rounded apically; basal vein (1M) straight; three submarginal cells (1rs-m present), second submarginal cell trapezoidal, posterior border strongly angled posteriorly (more strongly so than in Apini or many Meliponini); 2Rs straight (somewhat similar to Apini and some Meliponini); 3Rs shorter than r-rs, together about as long as 4Rs; 1rs-m weakly arched, 2rs-m strongly arched apicad in posterior half; wing membranes hyaline clear; veins dark brown.

Mandible smooth and shining; labrum smooth and shining; clypeus imbricate, coarsely so on disc and within clypeal basin, nearly granulose; face smooth to finely

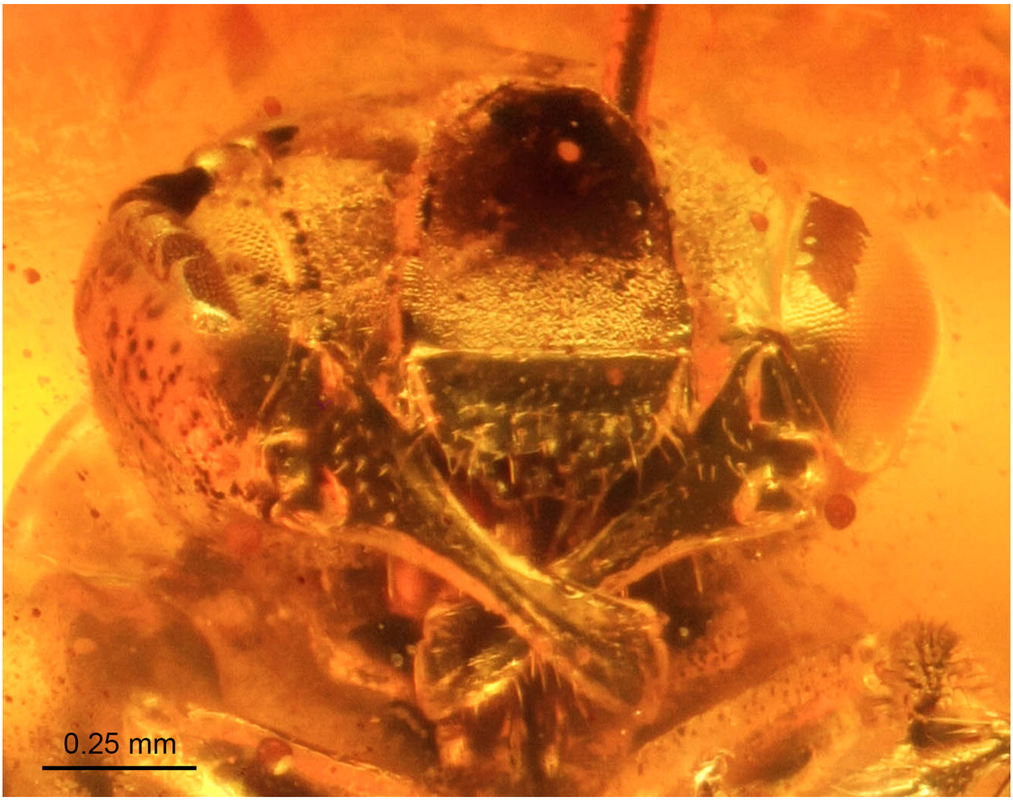
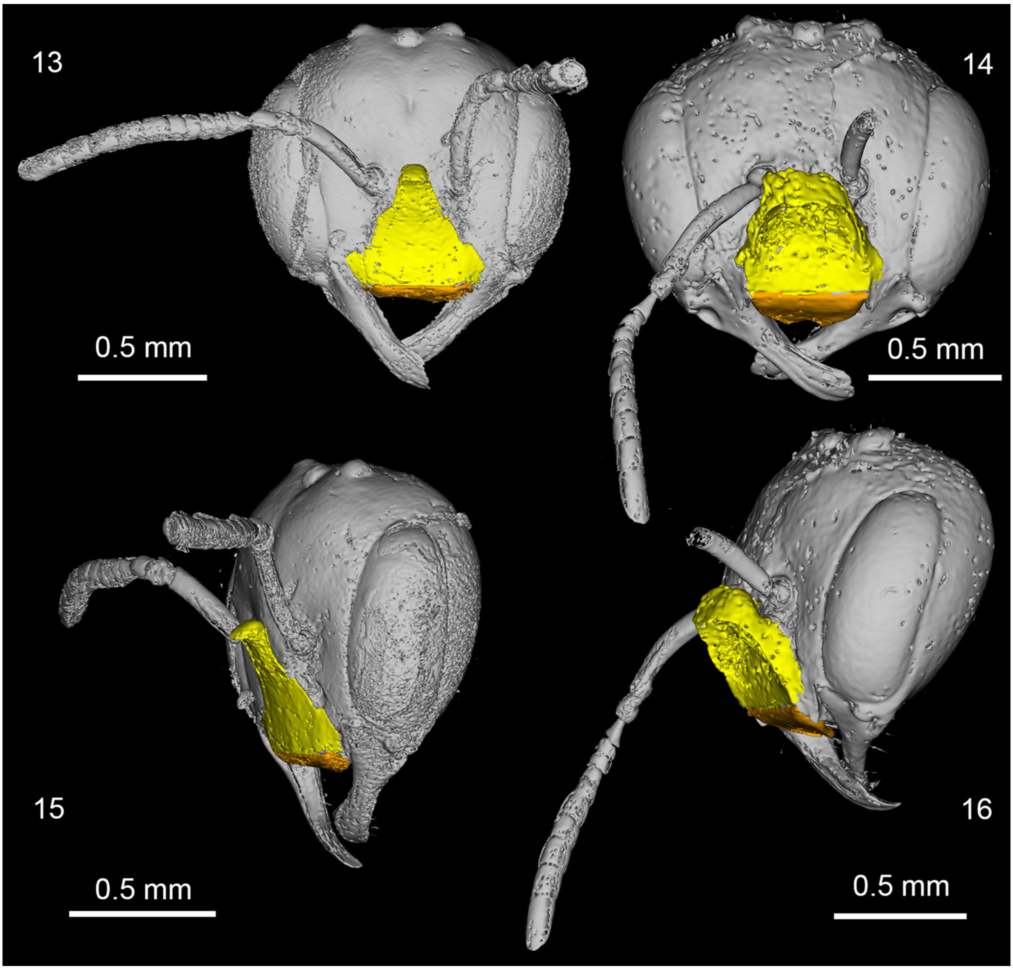


Figure 12. Ventral facial view of holotype worker of *Aethemelikertes emunctorii*, new genus and species (SMF Be 14262a). Note carinae demarcating lateral margins of basin extending to clypeal apex where clypeus extends laterally around base of labrum.

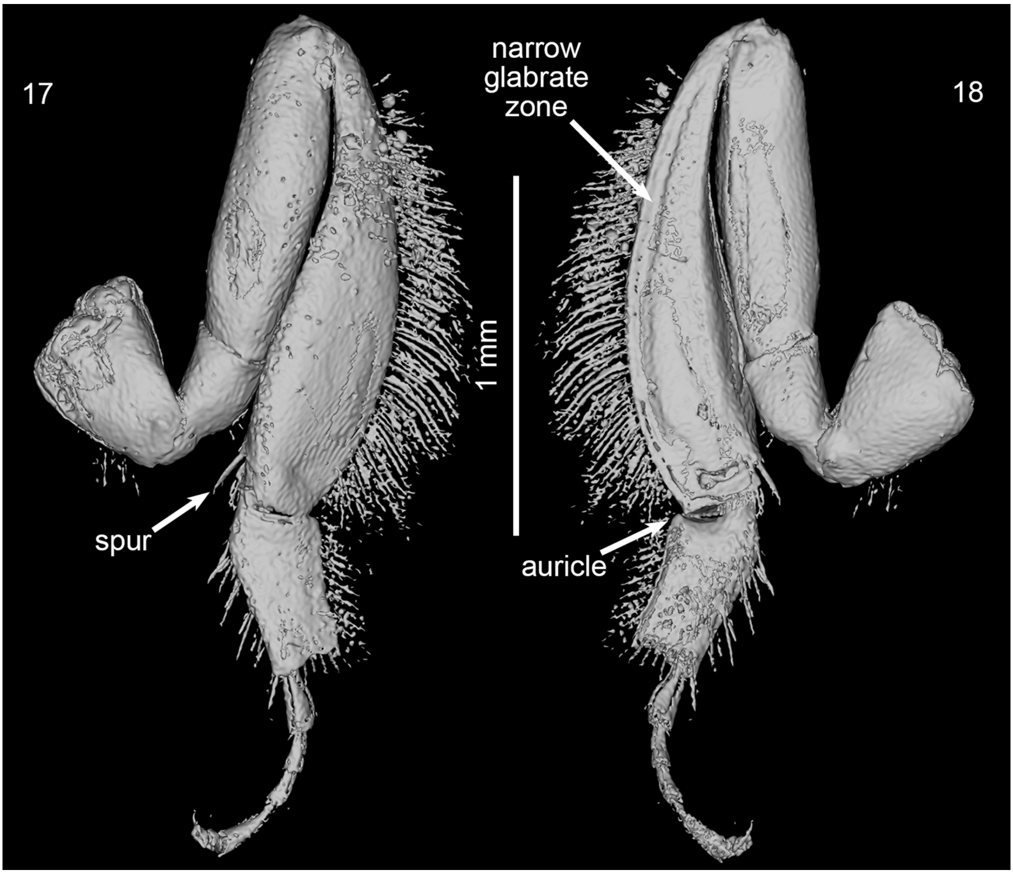
imbricate and shining (most of face poorly preserved and obscured by irregular surface material, but best view of integument along paraocular area of bee's left compound eye and seen obliquely from below); sculpturing of mesosomal dorsum obscured by irregular material in air layer (apexes of setae and bristles emerge from this layer and so can be discerned); pleura largely finely imbricate (best observed on left mesepisternum and ventrally on propleura, right pleuron obscured by large reflective air bubble), otherwise surfaces, particularly preëpisternal area with similar irregular material layer adhering to integument; legs generally smooth to faintly imbricate; metatibial corbicular surface smooth and shining; bases of wings covered with similar irregular material extending from mesosoma; metasomal terga smooth and shining, with minute punctures at setal bases; sterna faintly imbricate with setigerous punctures apically.

Pubescence generally sparse; mandible with sparse, minute, erect, simple setae on outer surface proximally, longer, erect, simple setae scattered along length of lower margin; labrum with sparsely scattered, short, suberect to erect setae; clypeus without setae, except perhaps a few minute, simple setae at upper apical margin of clypeal basin; face with sparsely scattered, short, erect, simple setae intermixed with some minutely branched setae (seemingly present on lower face and less so on upper face); scape with minute, appressed, simple setae scattered along length; vertex with similar setae as those on face emerging from irregular debris obscuring surface, some on ver-



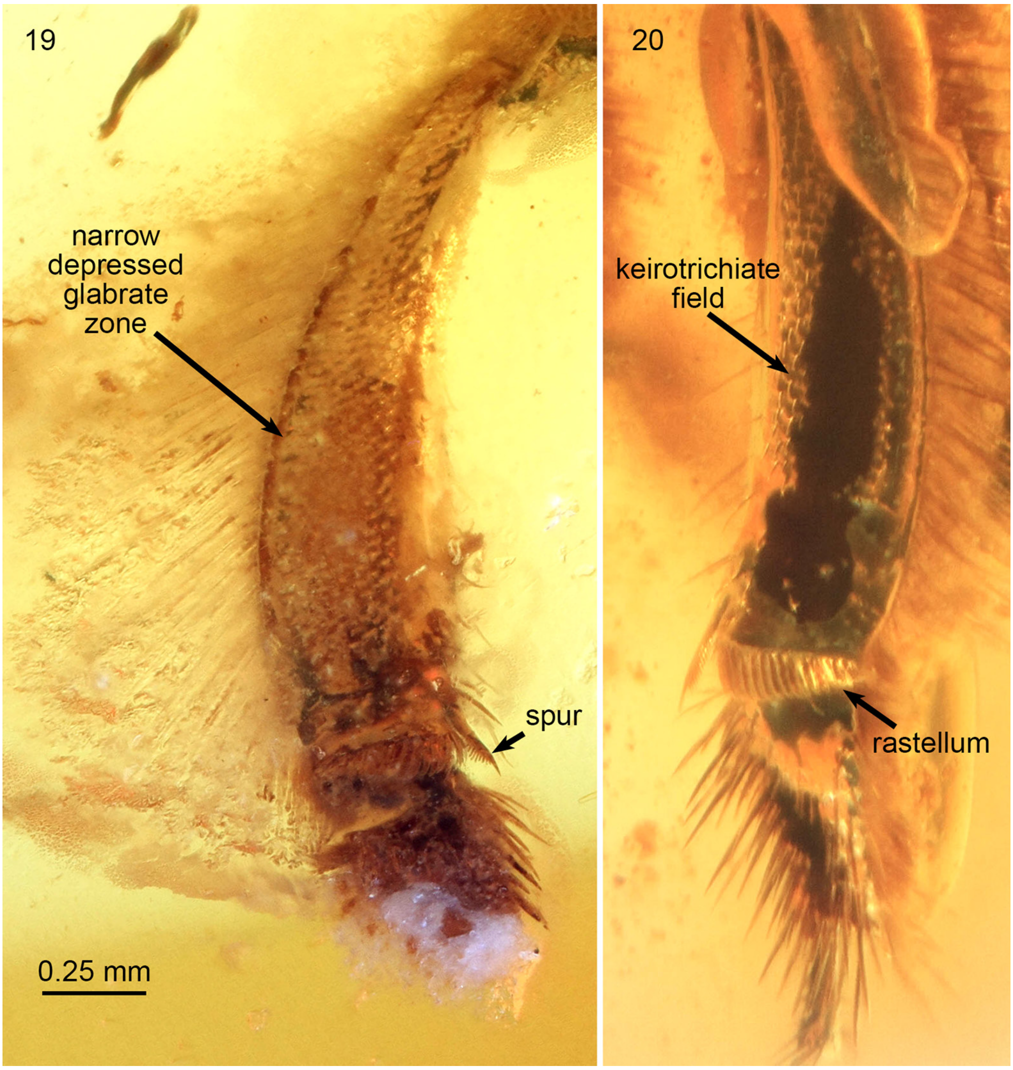
Figures 13–16. X-ray μCT scans of heads of holotype workers of *Succinapis micheneri* Engel (AMNH B-JH103) and *Aethemelikertes emunctorii*, new genus and species (SMF (Be 14262a), in Baltic amber; yellow highlights disc and modification of clypeus, orange highlights labrum. **13.** Facial view of *S. micheneri*. **14.** Facial view of *A. emunctorii*. **15.** Oblique profile of *S. micheneri*. **16.** Oblique profile of *A. emunctorii*. Note that scan resolution was insufficient to resolve most setae.

tex somewhat thicker and bristle like, but short, distinctly shorter than median ocellar diameter; mesosomal dorsum largely obscured but long, erect, simple bristles present along lateral and posterior margin of mesoscutellum, and more sparsely on mesoscutellar disc; mespisternum with sparse, short, simple setae; pro- and mesocoxae, pro- and mesotrochanters, and pro- and mesofemora with sparse, minute, largely appressed, simple setae; pro- and mesotibiae with some longer, erect, simple setae more apically, particular on inner margins and outer surface of mesotibia (left mesotibia with a mass of pollen amid such setae on outer surface, interesting as such material is clearly not in a position for subsequent transfer to the corbicula as it is the inner metabasitarsal bristles that are most often used to scrape pollen from the body and forelegs and then pack the accumulated material into the corbicula, or squeezed between the metabasitarsi and into the corbicula via a pollen press in those lineages that have



Figures 17–18. X-ray µCT scans of hindleg of *Aethemelikertes emunctorii*, new genus and species (SMF Be 14262a). **17.** Outer (prolateral) view. **18.** Inner (retrolateral) view. Note that scan resolution was insufficient to resolve most fine setae and setal details.

a metabasitarsal auricle: *e.g.*, Michener *et al.*, 1978); pro- and mesotarsi with abundant, longer, erect, simple bristles; metacoxa, metatrochanter, and metafemur similar to corresponding podites on midleg, except inner apical surface of metafemur with small ovoid patch of keirotrichia, finer and shorter than those of metatibia; metatibia with posterior margin with fringe of elongate, plumose (branches minute and along length of setal rachis) setae, setae as long as or longer than metatibial width, anterior margin with sparsely scattered simple setae and bristles, corbicular surface with sparsely scattered, erect, fine, long, simple setae; inner surface of metatibia with keirotrichiate zone covering most of surface except posterior, narrow, slightly depressed glabrate zone and broad, squarish, apical glabrate zone, apical glabrate zone slightly longer than apical width of metatibia; rastellum composed dense line of thick stiff bristles along entire inner apical margin of metatibia; metabasitarsus outer surface with sparse, fine, simple setae, inner surface and margins with abundant, elongate, erect to suberect, simple bristles; metasomal terga with sparse, minute, largely appressed, simple setae, such setae especially sparse on basal terga and becoming somewhat more numerous and slightly longer progressively on terga IV, V, and VI; sterna without setae except apically with erect, fine, simple setae on sterna II–IV, and more sparsely so on sterna V and VI.



Figures 19–20. Inner (retrolateral) surfaces of metatibiae of *Haidomelikertes*, new genus, and *Aethemelikertes*, new genus. **19.** *Haidomelikertes uraeus*, new species, holotype worker (SMF Be 14263a). **20.** *Aethemelikertes emunctorii*, new species, holotype worker (SMF Be 14262a).

Coloration largely not preserved or obscured, where evident seemingly brown to dark brown; otherwise microscopic separation of amber matrix from desiccated integument creating sufficient air space to form silver-looking reflection (common in many fossils, particularly from Baltic amber).

♀: *Latet*.

♂: *Latet*.

HOLOTYPE: ♀, SMF Be 14262a (SMF); Eocene (Bartonian–Priabonian: a recent lithological and palynological analysis of the Yantarny borehole indicated a potential late Bartonian or early Priabonian age for the amber-bearing Wild Earth and Upper Blue Earth Members of the Prussian Formation, although the former has far less dispersed amber than the latter, with the dinoflagellate and sporomorph assemblages largely indicating a late Bartonian age: Kasiński *et al*., 2020: 41, tables 1, 4) Baltic amber.

Etymology: The specific epithet is taken from the Latin *emunctorium*, an acolyte's candle snuffer, as an allusion to the bell- or scoop-like appearance of the clypeus.

Haidomelikertes Engel, new genus

ZooBank: urn:lsid:zoobank.org:act:8C4FFC1B-AD66-431C-96DD-96AA7A98CC6C

Type species: *Haidomelikertes uraeus* Engel, new species.

Diagnosis: This genus includes those species with broad clypeal basal protrusions that are as wide as the intertorular distance and therefore completely cover the entire supraclypeal area in facial view (Figs. 23–26) (when viewed from above the clypeal protrusion fills the entire intertorular space, versus being distinctly narrower, typically about one half, the intertorular space in *Succinapis*). The clypeal protrusion in *Haidomelikertes* superficially resembles a rearing cobra, and does not form an inverted convex basin with lateral carinae as is present in *Aethemelikertes* (*vide supra*). In addition, the labrum is subtriangular, with a prominent lateral fringe of stiff, erect, elongate setae arising from the labral surface (Fig. 28); the apical margin is narrowly blunt and not concave medially; and the convergence of the lateral margins does not change slope at midlength (contrast with that of *Aethemelikertes*, *supra*). Lastly, the apical glabrate zone on the inner surface of the metatibia is shorter than the apical metatibial width (Fig. 19) (versus longer in *Aethemelikertes*).

Description: ♀: Small bees, *ca*. 3.3–4.2 mm in length; head as wide as or slight wider than long, upper interorbital distance greater than compound eye length. Mandible with outer mandibular grooves reduced, faint impression of outer groove obliquely across apical half of mandible, vanishing well before apex; shallow indentation for single blunt preapical tooth along upper third to upper quarter of apical margin; axes of mandibular articulations converging anteriorly such that closed mandibles overlap at slightly obtuse angle and do not obscure or limit forward movement of labrum; malar space linear; labrum flat, slightly broader than medial length, lateral margins converging apically, without change in slope of convergence, apical margin narrowly blunt, therefore surface of inverted trapezoidal shape, surface with sparsely scattered suberect to erect short setae, laterally with fringe of stiff, elongate, erect setae; clypeus with prominent, broad basal protrusion dorsally extending over supraclypeal area and between antennal toruli, as broad as intertorular space, without carinae laterally extending to clypeal apical margin, apex slightly to greatly above upper torular tangent, apex orthogonally angled forward and projecting anteriorly as a shelf of variable expanse, apical margin of shelf gently convex; disc of clypeus flat; epistomal sulcus laterally forming obtuse angle, medially sulcus obscured from view by clypeal protrusion; upper torular tangent at about head midlength; intertorular distance about 2× torular diameter; scape shorter than torulocellar distance; first flagellomere about as long as wide, slightly longer than second flagellomere, second and third flagellomeres equal in length, each wider than long; ocelli high on vertex, situated well above upper tangent of compound eyes; vertex unmodified (no depressions or ridges); preoccipital area rounded; gena narrower than compound eye in profile. Mesoscutum with anterior border low, broadly rounded; tegula elongate-ovoid; mesoscutellum low, rounded, not greatly projecting over metanotum and base of propodeum; propodeum with sloping basal area distinct from vertical posterior surface. Forewing with prominent, subtriangular pterostigma, pterostigma about 2.5× as long as maximum width, maximum width slightly basad midlength, margin inside marginal cell sloping to costal margin; marginal cell acutely rounded api-

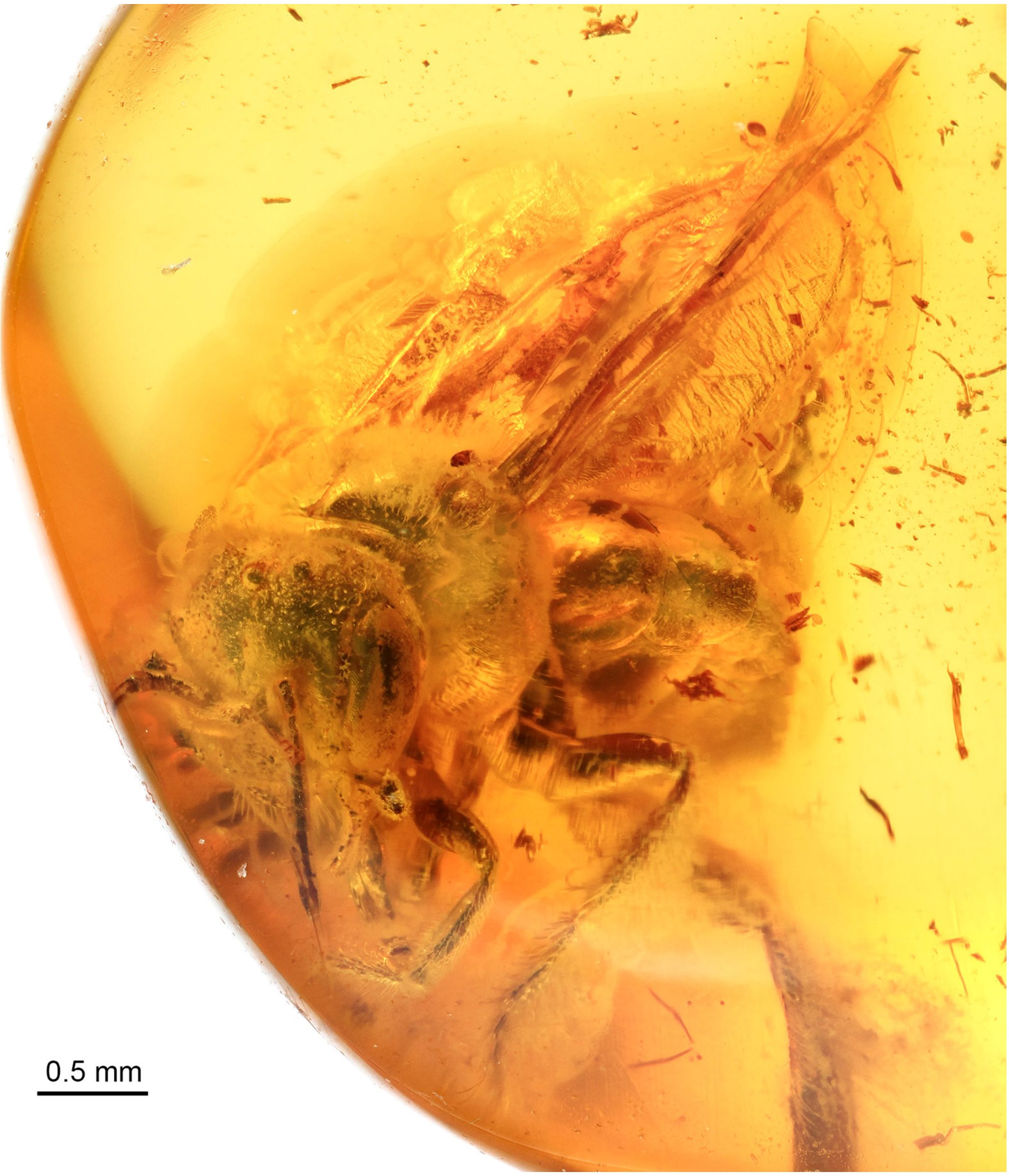


Figure 21. Holotype worker of *Haidomelikertes uraeus*, new genus and species, in Eocene (Bartonian) Baltic amber (SMF Be 14263a).

cally, not appendiculate, apex offset from costal margin by about vein width; basal vein straight, confluent with 1cu-a; three submarginal cells present (1rs-m present), second submarginal cell trapezoidal, anterior border (3Rs) significantly shorter than r-rs, r-rs at widest point of pterostigma; third submarginal cell about as broad as first submarginal cell; 1rs-m faintly arched, 2rs-m strongly arched, thus anterior border of third submarginal cell significantly shorter than posterior border of same cell, anterior border of third submarginal cell (4Rs) slightly shorter than combined lengths of r-rs and 3Rs; 1m-cu angulate in apical third near second submarginal cell, entering second submarginal cell distad cell midlength; anterior margin of hind wing with 5–6 distal hamuli arranged in an evenly spaced series; wing membranes hyaline

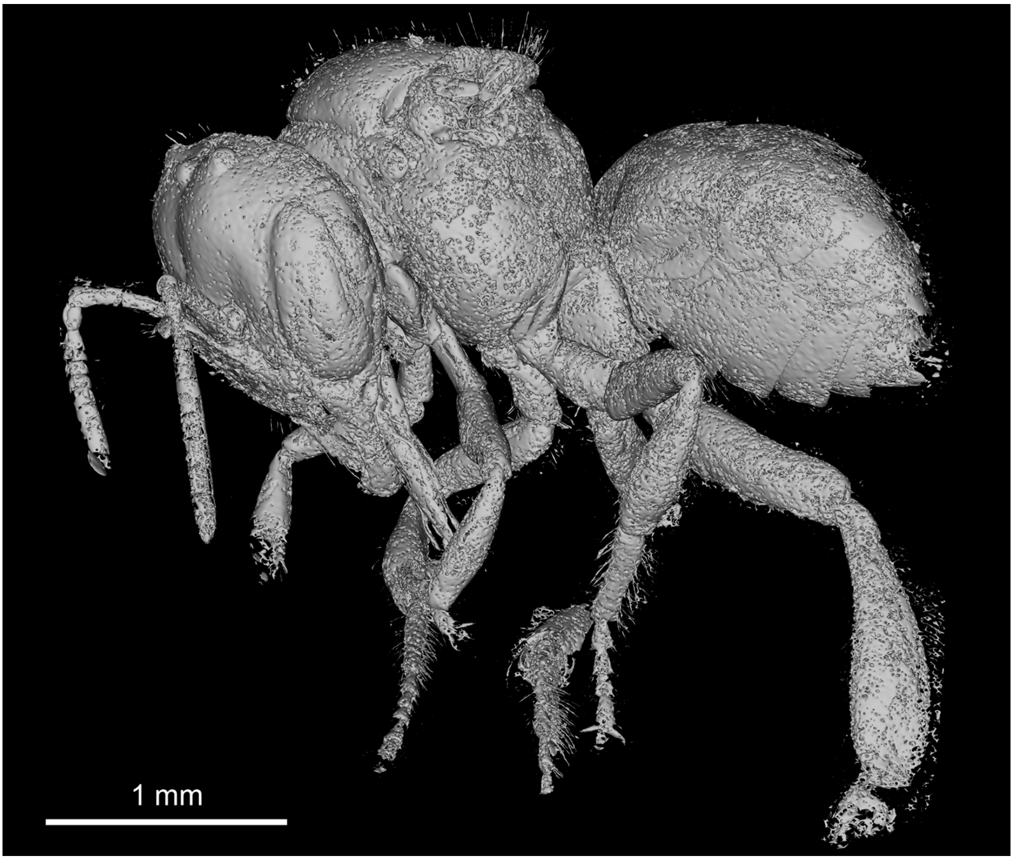


Figure 22. X-ray µCT scan of holotype worker of *Haidomelikertes uraeus*, new genus and species (SMF Be 14263a), oblique frontolateral view. Note that scan resolution was insufficient to resolve most setae.

clear; veins dark brown. Metatibia slender, elongate, length about 3.5× maximum width, posterior margin gently convex and slightly widening in apical two-thirds; surface of corbicula not depressed; posterior margin with fringe of elongate, plumose (branches minute and along length of setal rachis) setae, such setae longer than metatibial width, anterior margin with sparsely scattered simple setae and bristles, corbicular surface with sparsely scattered, erect, fine, simple setae; inner surface with keirotrichiate zone field covering most of surface except exceedingly narrow, posterior, slightly depressed (*i.e.*, a weak clivulus present) glabrate zone and a rectangular apical glabrate zone, length of apical glabrate zone slightly less than apical width of metatibia; rastellum composed of stiff bristles along entire inner apical width of metatibia; single metatibial spur present, spur minutely ciliate along inner margin in apical half; metabasitarsus with auricle present on proximal surface facing apex of metatibia; metabasitarsus roughly quadrate, longer than wide (only observed for *H. proboscidea* as metabasitari damaged in *H. uraeus*), margins roughly parallel, apical margin comparatively straight, inner surface with abundant, elongate, suberect, simple bristles; pretarsal claws with minute inner subapical ramus; arolium present. Metasoma broad, ovoid, sparsely setose and largely smooth and shining, most setae minute, simple, and appressed to subappressed; metasomal sterna unmodified, with scattered, short, erect, fine, simple setae on sterna II–V; sting present.

ETYMOLOGY: The new genus-group name is a combination of the Ancient Greek *Hā̆idēs* [*Ἅιδης*, genitive singular, *Hā̆idou* (*Ἅιδου*)], the god of the underworld and realm of the shades, and *Melikertes*, type genus of the tribe. The name is an allusion to the haidomyrmecine ants who are famed for their peculiar and often extreme facial and mandibular modifications (*e.g.*, McKellar *et al.*, 2013; Perrichot *et al.*, 2016, 2020; Barden *et al.*, 2020). The gender of the name is masculine.

Key to Species of *Haidomelikertes*

1. Clypeal protrusion extending well above upper torular tangent, apex angled anteriorly and extending forward as prominent shelf (Figs. 23, 25), with dorsal-facing surface about 2× torular diameter, neck of clypeal protrusion between antennal toruli slightly narrower than apex (Fig. 23); slightly larger species, length *ca.* 4.1 mm .... *H. proboscidea* (Engel)

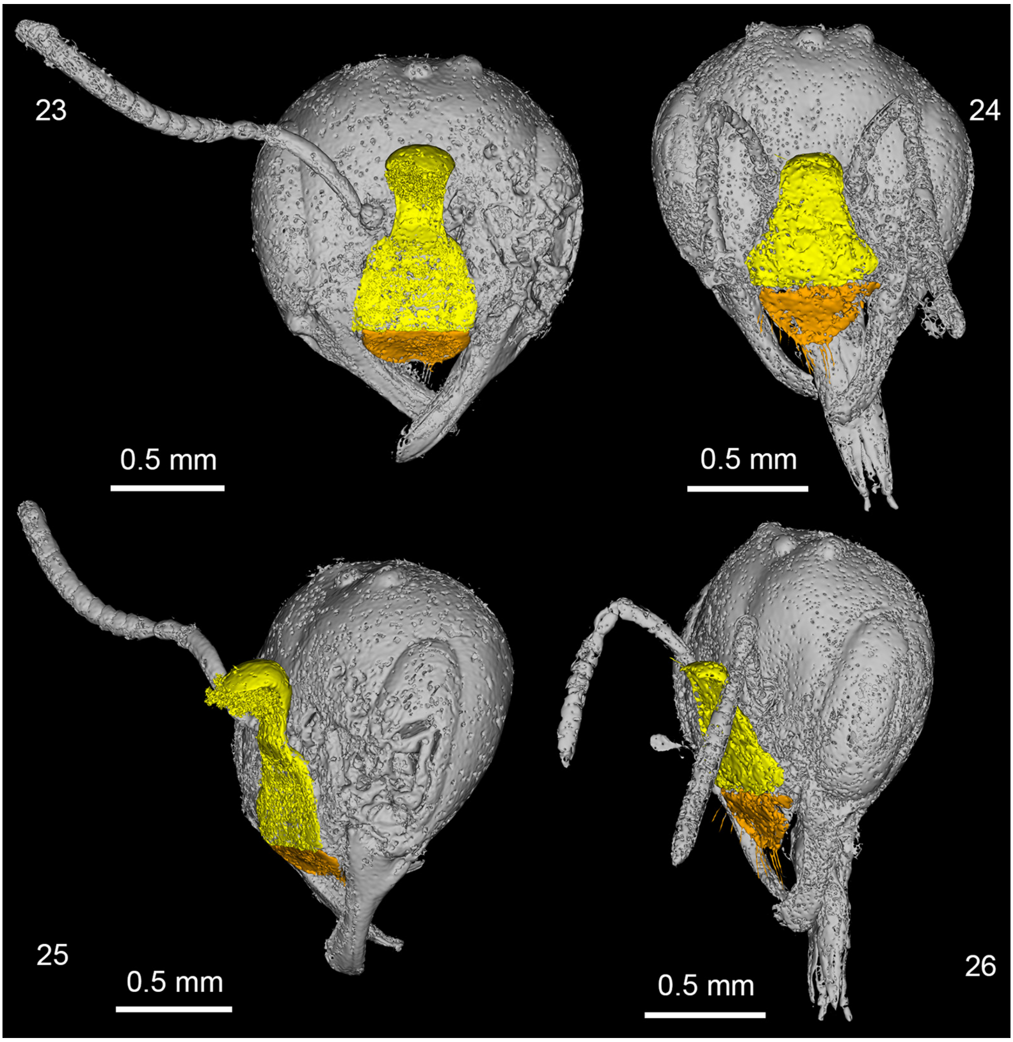
—. Clypeal protrusion only slightly extending above upper torular tangent, apex angled anteriorly and extending forward as thin, lamellate shelf (Figs. 24, 26–28), dorsal-facing surface about a torular diameter or slightly less in length; neck of clypeal protrusion not narrowed relative to apex (Fig. 24); slightly smaller species, length *ca.* 3.3 mm .... *H. uraeus* Engel, n. sp.

Haidomelikertes uraeus Engel, new species

ZooBank: urn:lsid:zoobank.org:act:74265917-E6B4-44B4-8F45-93D269B0D810
(Figs. 19, 21, 22, 24, 26–28)

DIAGNOSIS: This species is distinguished from its congener by the form of the clypeal protrusion, which extends only slightly above the upper torular tangent, and its forward-projecting surface only extends as a lamella, no longer than a torular diameter (Figs. 24, 26–28). The neck of the clypeal protrusion is also not narrowed above the supraclypeal area and between the antennal toruli relative to its apical width (Fig. 24). Additionally, this species is about a full 20% shorter than *H. proboscidea*.

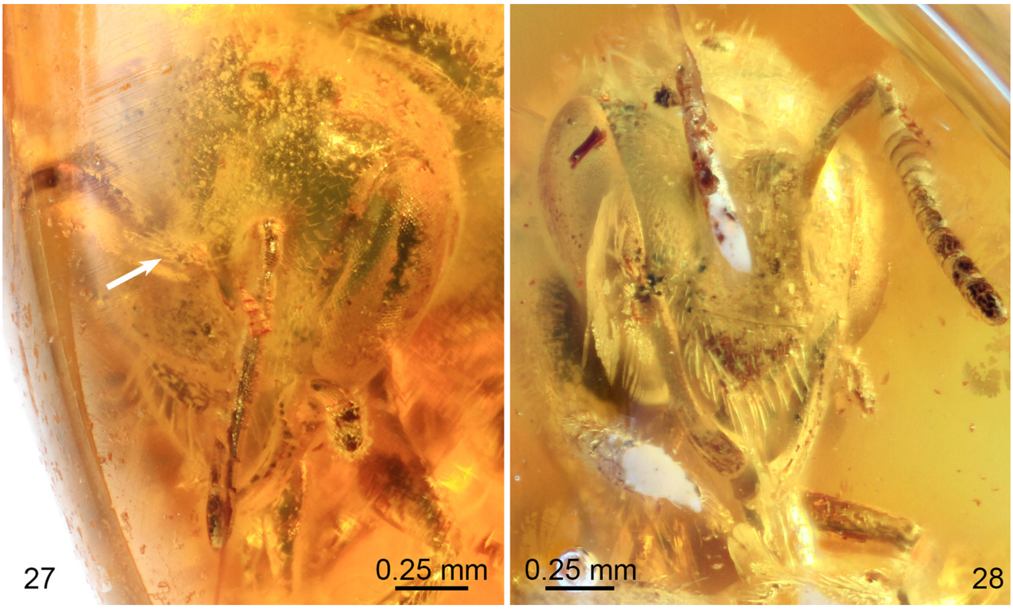
DESCRIPTION: ♀: Total body length (as preserved) 3.3 mm; forewing length (as preserved) 3.5 mm. Head as long as wide, length (summit of vertex to clypeal apical margin) 1.30 mm, width (maximum width across compound eyes) 1.30 mm; compound eye length 0.80 mm; upper interorbital distance 0.94 mm, lower interorbital distance 0.80 mm; inner ocular margins largely straight, with faint arch slightly above midlength, converging below; ocellar triangle broad, interocellar distance 0.40 mm. Scape length 0.50 mm, shorter than torulocellar distance. Mandible elongate, length 0.65 mm; labrum broader than long, basal width 0.46 mm, medial length 0.27 mm. Pronotum short, declivitous, without defined transverse dorsal ridge, therefore sloping continuously from mesoscutal border; pronotal lateral ridge absent; mesoscutum anterior border broadly rounded, anterior lip gently curving to meet posterior pronotal margin, not overhanging pronotal border; mesoscutum medial length 0.77 mm; intertegular distance 0.37 mm; mesoscutellum medial length 0.31 mm. Metatibia slender, length 1.20 mm, maximum width 0.34 mm. Forewing with basal vein (1M) confluent with 1cu-a, pterostigma longer than wide, maximum width just basad midlength, margin inside marginal cell sloping to costal margin; marginal cell acutely rounded apically; basal vein (1M) straight; three submarginal cells (1rs-m present), second submarginal cell trapezoidal, posterior border strongly angled posteriorly;



Figures 23–26. X-ray μCT scans of heads of holotype workers of *Haidomelikertes proboscidea* (Engel), new combination (AMNH B-JH96), and *H. uraeus*, new genus and species (SMF (Be 14263a), in Baltic amber; yellow highlights disc and modification of clypeus, orange highlights labrum. **23.** Facial view of *H. proboscidea*. **24.** Facial view of *H. uraeus*. **25.** Oblique profile of *H. proboscidea*. **26.** Oblique profile of *H. uraeus*. Note that scan resolution was insufficient to resolve most setae.

2Rs straight; 3Rs shorter than r-rs, together slightly longer than 4Rs; 1rs-m faintly arched, 2rs-m arched apicad in posterior half; wing membranes hyaline clear; veins dark brown.

Mandible smooth and shining; labrum smooth; clypeal disc finely imbricate; face smooth and shining; mesoscutum and mesoscutellum smooth and shining; mespisternum largely smooth to finely imbricate; basal area of propodeum glabrous, smooth, shining; legs generally smooth; metatibial corbicular surface smooth and shining; metasomal terga smooth and shining, with minute punctures at setal bases; sterna faintly imbricate.



Figures 27–28. Oblique facial views of holotype worker of *Haidomelikertes uraeus*, new genus and species (SMF Be 14263a). **27.** Slightly dorsal left oblique; white arrow points to apex of facial protuberance. **28.** Slightly ventral right oblique.

Pubescence generally sparse; mandible with sparse, minute, suberect, simple setae on outer surface proximally, longer, erect, simple setae scattered along length of lower margin; labrum with sparsely scattered, short, suberect to erect setae on disc, laterally with numerous, elongate, erect, simple setae forming fringe along margins; clypeus largely without setae on disc, some short, fine, suberect setae in apicolateral areas lateral to and in angled area lateral to labrum; clypeal extension some scattered, short, fine, erect, simple setae on the upper and lower surfaces of the anterior extension; face with sparsely scattered, short, erect, simple setae intermixed with some minutely branched setae; scape with minute, appressed, simple setae scattered along length; vertex with similar setae as those on face along with bristle-like setae that are about as long as median ocellar diameter or often slightly shorter; mesoscutum with sparsely scattered, erect, simple bristles intermixed with finer, erect, plumose setae, such plumose setae more numerous and particularly so anteriorly; mesoscutellum as on mesoscutum except lateral and posterior margins with more abundant erect bristles and numerous plumose setae; mespisternum with scattered, short, decumbent, simple setae; pro- and mesocoxae, pro- and mesotrochanters, and pro- and mesofemora with sparse, minute, largely appressed, simple setae; pro- and mesotibiae with some longer, erect, simple or branched setae, particularly apically, and more so on outer surface of mesotibia; pro- and mesotarsi with abundant, longer, erect, simple bristles; metacoxa, metatrochanter, and metafemur similar to corresponding podites on midleg, except inner apical surface of metafemur with small ovoid patch of keirotrichia, finer and shorter than those of metatibia; metatibia with posterior margin with fringe of elongate, plumose (branches minute and along length of setal rachis) setae, setae longer than metatibial width, anterior margin with sparsely scattered simple setae and bristles, corbicular surface with sparsely scattered, erect, fine, simple setae; inner surface with keirotrichiate zone covering most of surface except exceedingly

Figure 29. Two workers of *Amelikertotes clypeata* (Engel), new combination, in Eocene Baltic amber (SEMC B-147).

narrow, posterior, slightly depressed glabrate zone and rectangular apical glabrate zone, length of apical glabrate zone slightly less than apical width of metatibia; rastellum composed of stiff bristles along entire inner apical width of metatibia; metabasitarsus with sparse, simple setae on outer surface, inner surface and margins with abundant, elongate, erect to suberect, simple bristles; metasomal terga with sparse, minute, largely appressed, simple setae, such setae especially sparse on basal terga and becoming progressively more numerous on terga IV–VI; sterna with fine, erect, simple setae on apical half to third of sterna II–IV, and somewhat shorter on sterna V and VI.

Coloration not preserved, where evident seemingly brown to dark brown.

♀: *Latet*.

♂: *Latet*.

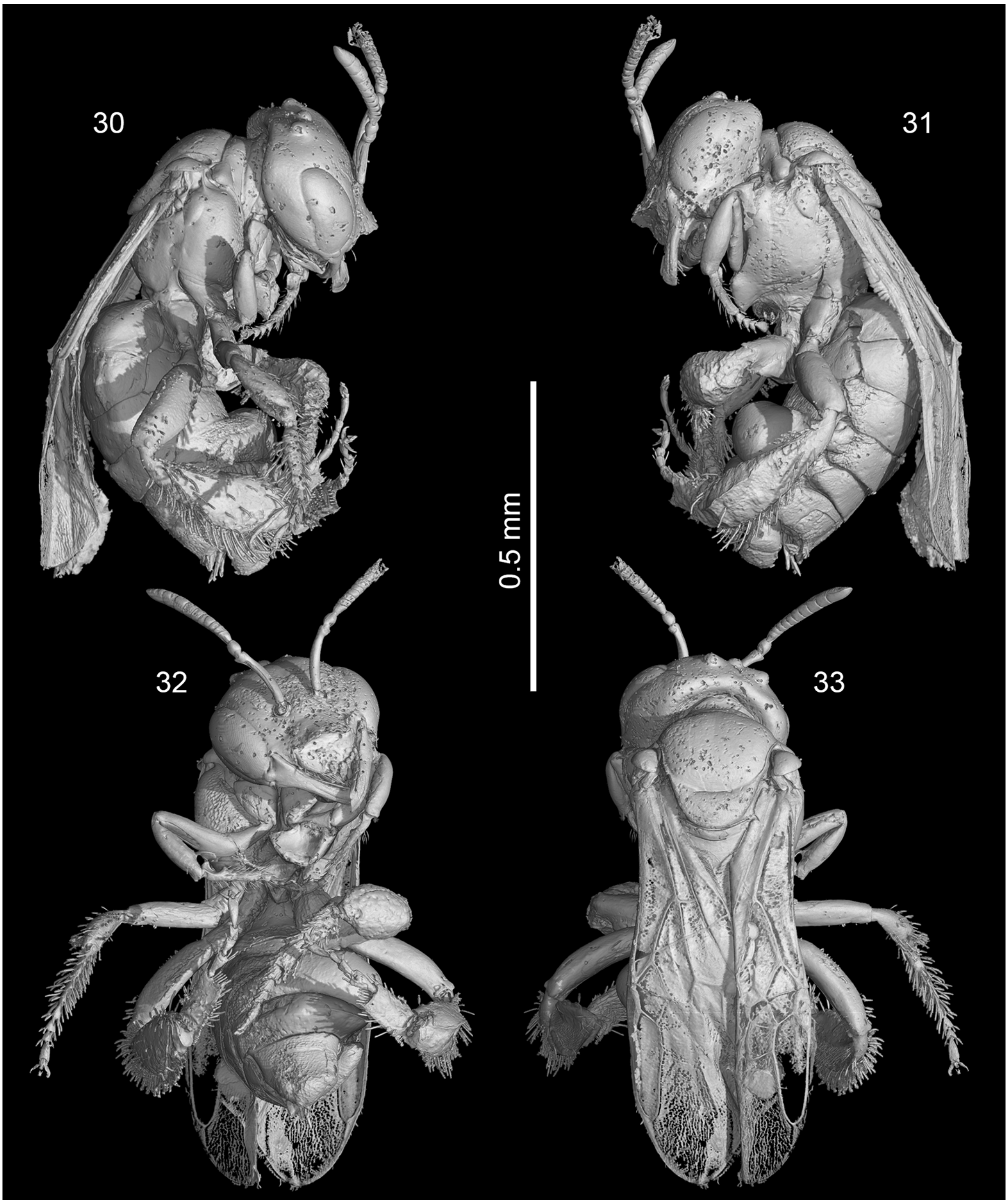
Holotype: ♀, SMF Be 14263a (SMF); Eocene (Bartonian–Priabonian: refer to note for holotype of *Aethemelikertes emunctorii*, *vide supra*) Baltic amber.

Etymology: The specific epithet is taken from the Ancient Greek *ouraîos* (*οὐραῖος*, uraeus), the stylized, upright rearing cobra used as a symbol of divine authority (symbol of the goddess Wadjet, *wꜣḏyt*) in Ancient Egypt.

Haidomelikertes proboscidea (Engel), new combination
(Figs. 23, 25)

Succinapis proboscidea Engel, 2001a: 121. Holotype ♀, AMNH (*visum*).

This species is described in full by Engel (2001a) and together with the above generic description and associated images there is sufficient detail to provide for its identification. Accordingly, a thorough description is not repeated here.



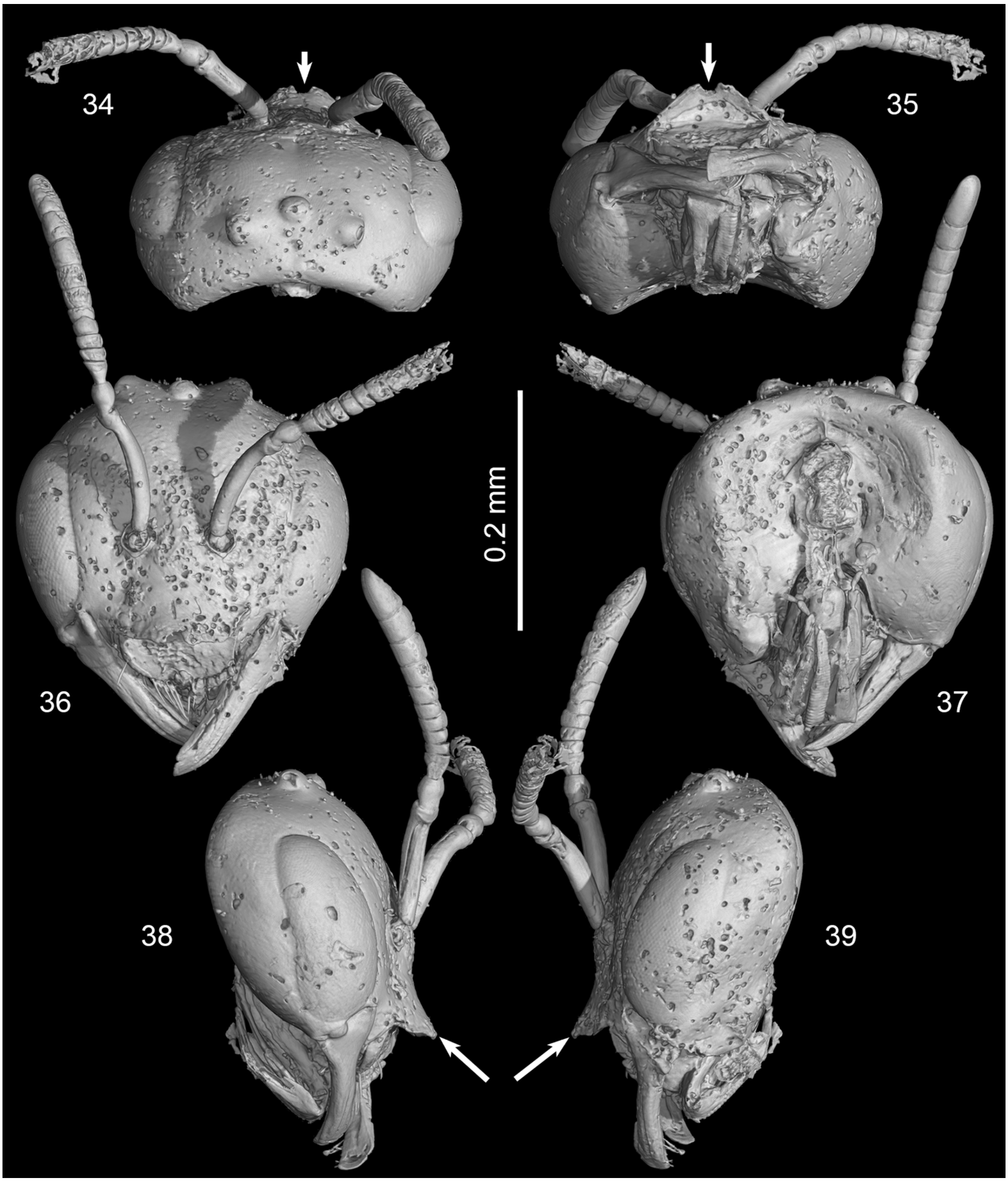
Figures 30–33. PPC-SRμCT scan of worker of *Amelikertotes clypeata* (Engel), new combination; upper right worker from figure 29. **30.** Right lateral view. **31.** Left lateral view. **32.** Ventral view. **33.** Dorsal view. Note that scan resolution was insufficient to resolve most fine setae.

Amelikertotes Engel, new genus

ZooBank: urn:lsid:zoobank.org:act:C88F964D-190C-4588-8C06-E4A93650CEAF

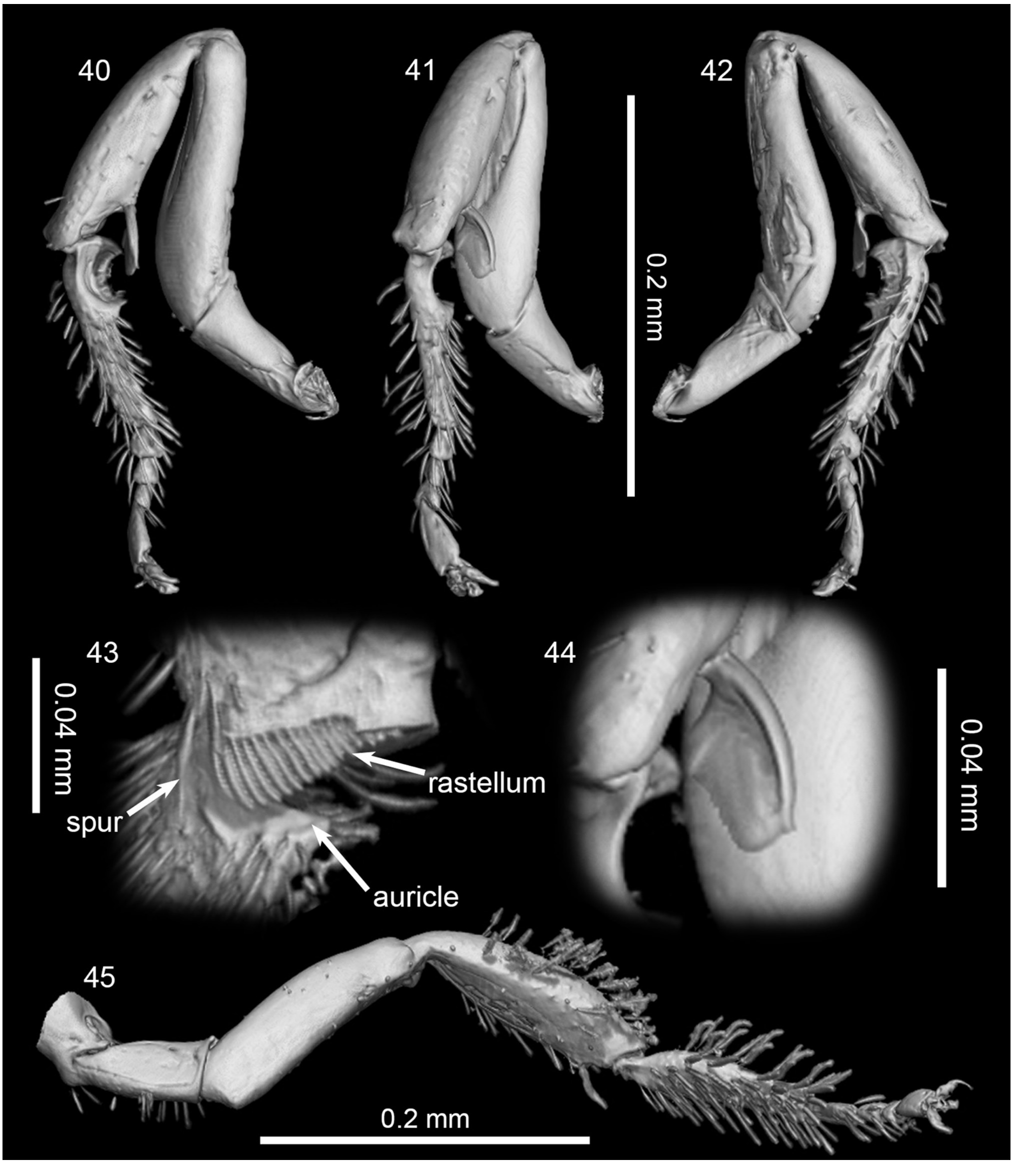
TYPE SPECIES: *Melikertes clypeatus* Engel, 2001a.

DIAGNOSIS: This genus is most similar to *Melikertes* but can be readily distinguished by the flared and medially cleft apical margin to the clypeus (Figs. 30–39, 51–62). In addition, the fringe of setae on the posterior margin of the metatibia is shorter than those in *Aethemelikertes* or *Haidomelikertes*.



Figures 34–39. PPC-SRμCT scan of worker head of *Amelikertotes clypeata* (Engel), new combination; upper right worker from figure 29. **34.** Dorsal view. **35.** Ventral view. **36.** Facial view. **37.** Posterior view. **37.** Right lateral view. **38.** Left lateral view. Arrows point to flared and cleft clypeus. Note that scan resolution was insufficient to resolve most fine setae.

Description: ♀: Small bees, *ca.* 3.1–3.4 mm in length; head wider than long, upper interorbital distance greater than compound eye length. Mandible with shallow incision for single blunt preapical tooth along upper quarter of apical margin; axes of mandibular articulations converging anteriorly such that closed mandibles overlap at slightly obtuse angle and do not obscure or limit forward movement of labrum; malar space linear; labrum flat, slightly broader than medial length, broadly U-shaped, margins forming a continuous arc between basolateral corners, margin entire (*i.e.*, not

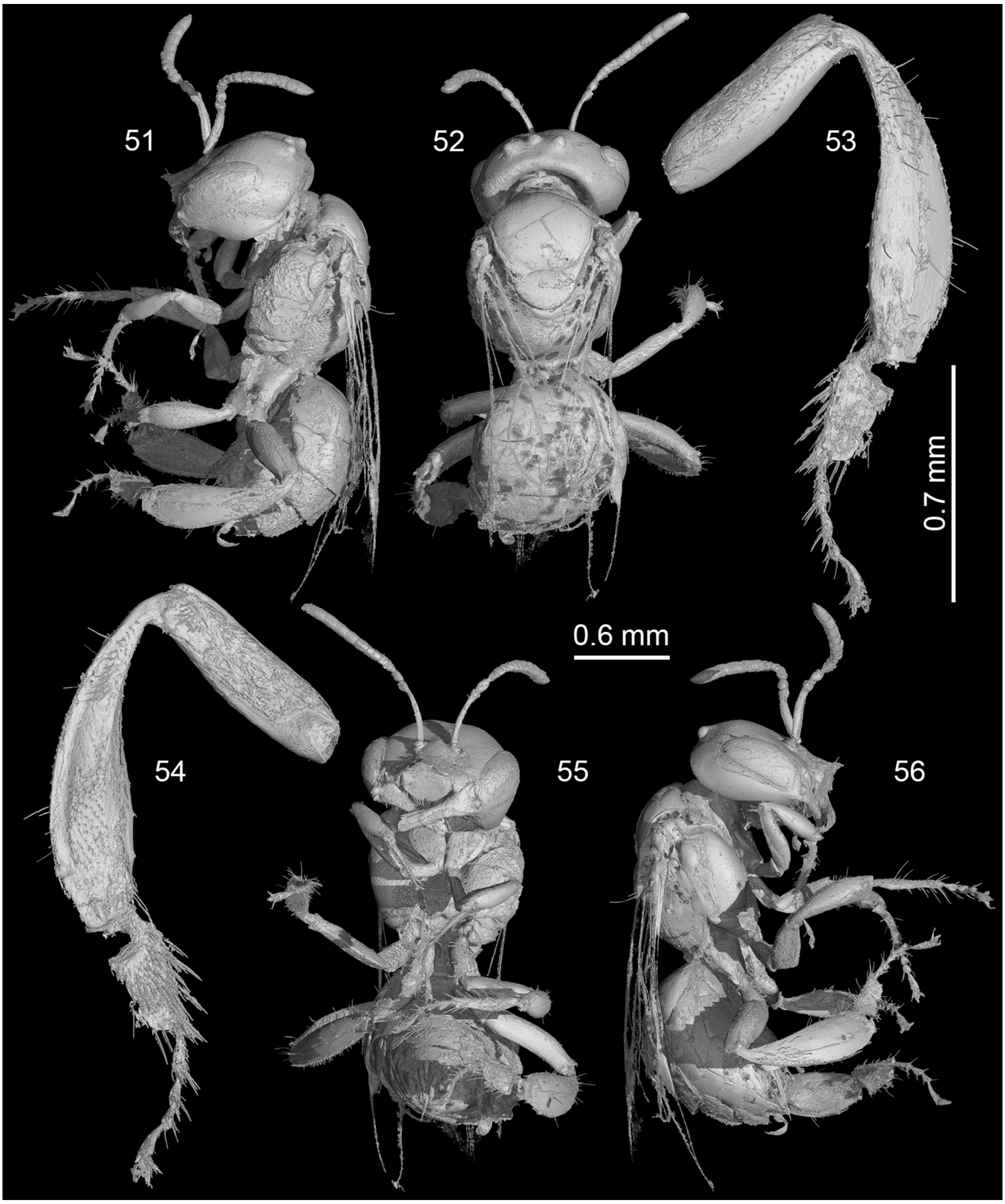


Figures 40–45. PPC-SRμCT scan of fore- and midleg structures of worker of *Amelikertotes clypeata* (Engel), new combination; upper right worker from figure 29. **40.** Foreleg, outer (prolateral) view. **41.** Foreleg, anterior view. **42.** Foreleg, inner (retrolateral) view. **43.** Magnified view of metatibial-metabasitarsal joint showing auricle and rastellum. **44.** Magnified view of protibial calcar. **45.** Midleg. Note that scan resolution was insufficient to resolve most fine setae.

emarginate or concave), surface with sparsely scattered suberect to erect setae, without lateral with fringe; clypeus without basal protrusion, disc weakly convex, apical margin flared anteriorly and projecting obliquely over labral articulation, extending forward by about 1.75× median ocellar diameter, apical margin with deep, U-shaped medial concavity; epistomal sulcus laterally forming obtuse angle; upper torular tangent slightly below head midlength; intertorular distance about 1.65× torular diameter; scape shorter than torulocellar distance; first flagellomere about as long as wide,

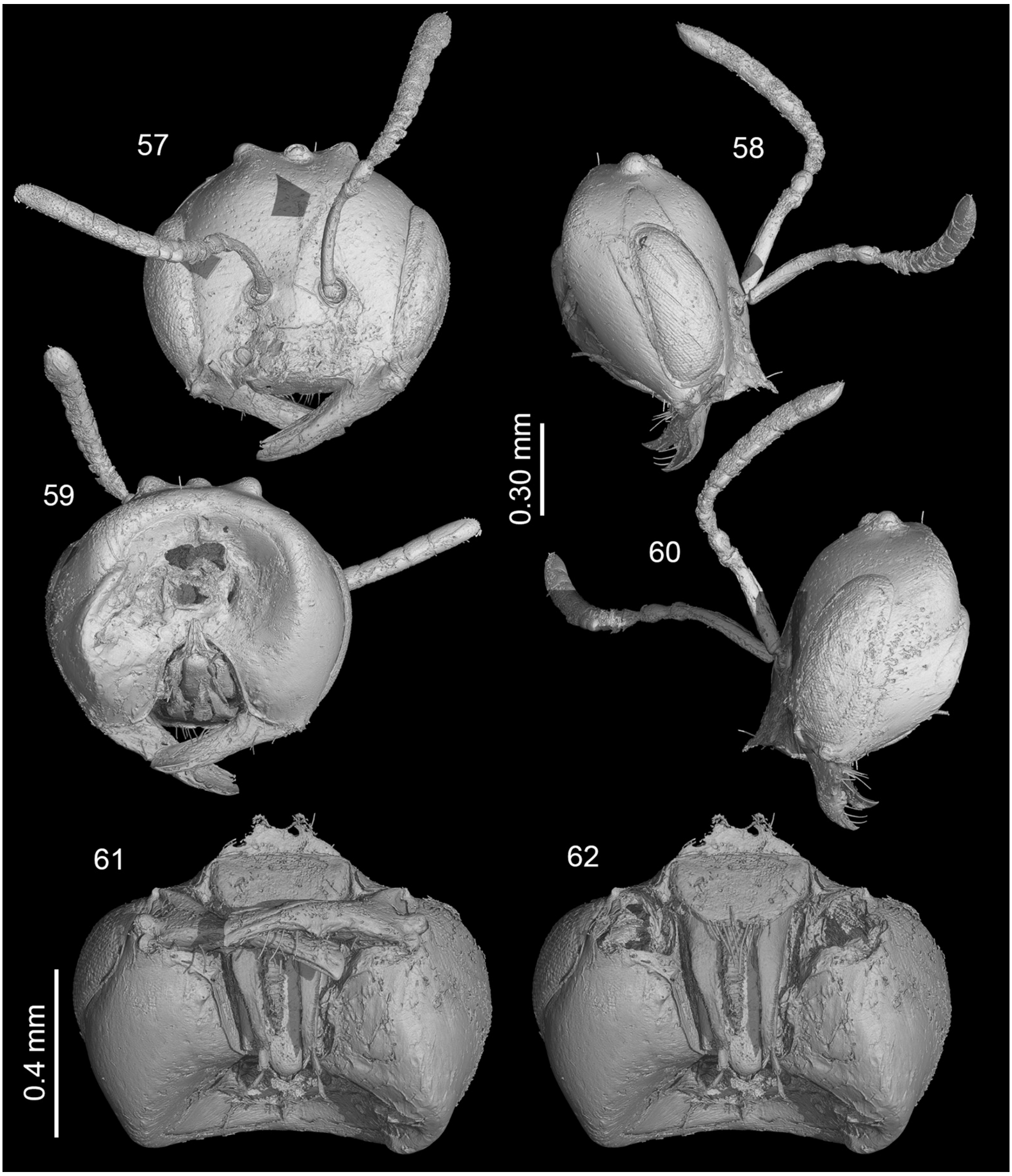
Figures 46–50. PPC-SRμCT scan of hind leg structures of worker of *Amelikertotes clypeata* (Engel), new combination; upper right worker from figure 29. **46.** Right hind leg, outer (prolateral) view. **47.** Right hind leg, inner (retrolateral) view. **48.** Left metatibia, view along posterior edge. **49.** Left hind leg, inner (retrolateral) view. **50.** Left hind leg, outer (prolateral) view, note debris packed into surface of corbicula. Note that scan resolution was insufficient to resolve most fine setae.

slightly longer than second flagellomere, second and third flagellomeres equal in length, each wider than long; ocelli high on vertex, situated well above upper tangent of compound eyes; vertex unmodified (no depressions or ridges); preoccipital area rounded; gena slightly narrower than compound eye in profile. Mesoscutum with anterior border low, broadly rounded; tegula elongate-ovoid; mesoscutellum low, rounded, not projecting over metanotum and base of propodeum; propodeum with sloping basal area distinct from vertical posterior surface. Forewing with prominent, subtriangular pterostigma, pterostigma about 2.5× as long as maximum width, margin inside marginal cell sloping to costal margin; marginal cell broad along entire length, broadly rounded apically, appendiculate, apex offset from costal margin by about 3–4× vein width; basal vein straight, slightly basad 1cu-a; three submarginal cells present (1rs-m present), second submarginal cell trapezoidal, anterior border (3Rs) significantly shorter than r-rs, r-rs distad widest point and midlength of pterostigma; third submarginal cell about as broad as first submarginal cell; 1rs-m faintly arched, 2rs-m weakly arched in posterior half, thus anterior border of third submarginal cell shorter than posterior border of same cell, anterior border of third submarginal cell (4Rs) shorter than combined lengths of r-rs and 3Rs; 1m-cu angulate apically near second submarginal cell, entering second submarginal cell near cell midlength; anterior margin of hind wing with five distal hamuli arranged in an evenly spaced series; wing membranes hyaline clear; veins dark brown. Metatibia slender, elongate, posterior margin gently convex and slightly widening in apical two-thirds; surface of corbicula not depressed; posterior margin with fringe of long, plumose (minute branches



Figures 51–56. PPC-SRμCT scan of worker of *Amelikertotes clypeata* (Engel), new combination; lower left worker from figure 29. **51.** Left lateral view. **52.** Dorsal view. **53.** Outer (prolateral) view of hind leg. **54.** Inner (retrolateral) view of hind leg. **55.** Ventral view. **56.** Right lateral view. Scale bar at right for 53 and 54, scale bar in center for 51, 52, 55, and 56. Note that scan resolution was insufficient to resolve most setae of the body and legs (*e.g.*, posterior fringe of fine setae on metatibia is not resolved).

along length of setal rachis) setae, such setae slightly shorter than to about as long as metatibial width, anterior margin with few simple setae and bristles, largely apically, corbicular surface with sparsely scattered, erect, fine, simple setae; inner surface with keirotrichiate zone covering most of surface except exceedingly narrow, posterior, slightly depressed glabrate zone and a rectangular apical glabrate zone, length of



Figures 57–62. PPC-SRμCT scan of worker head of *Amelikertotes clypeata* (Engel), new combination; lower left worker from figure 29. **57.** Facial view. **58.** Right lateral view. **59.** Posterior view. **60.** Left lateral view. **61.** Ventral view. **62.** Ventral view with mandibles removed to reveal labrum. Scale bar in center for 57–60, scale bar at bottom left for 61 and 62. Note that scan resolution was insufficient to resolve most fine setae.

apical glabrate zone slightly less than apical width of metatibia; rastellum composed of stiff bristles along nearly entire inner apical width of metatibia; single metatibial spur present; metabasitarsus with auricle present on proximal surface facing apex of metatibia; metabasitarsus rectangular, longer than wide, margins roughly parallel, apical margin slightly concave, inner surface with abundant, elongate, suberect, simple bristles; pretarsal claws with minute inner subapical ramus; arolium present. Metasoma broad, ovoid, sparsely setose; metasomal sterna unmodified; sting present.

Etymology: The new genus-group name is a combination of the Greek *a*– (ᾰ̓–, alpha privativum), meaning, "not"; *Melikertes*, type genus of the tribe; and the feminine suffix –*tēs* [–της, denoting a "quality of" or "state of being of", genitive –τητος; related to feminine –*ótita* (–ότητα), forming abstract nouns, derived from –*tēta* (–τητᾰ)]. The gender of the name is feminine.

Amelikertotes clypeata (Engel), new combination
(Figs. 29–70)

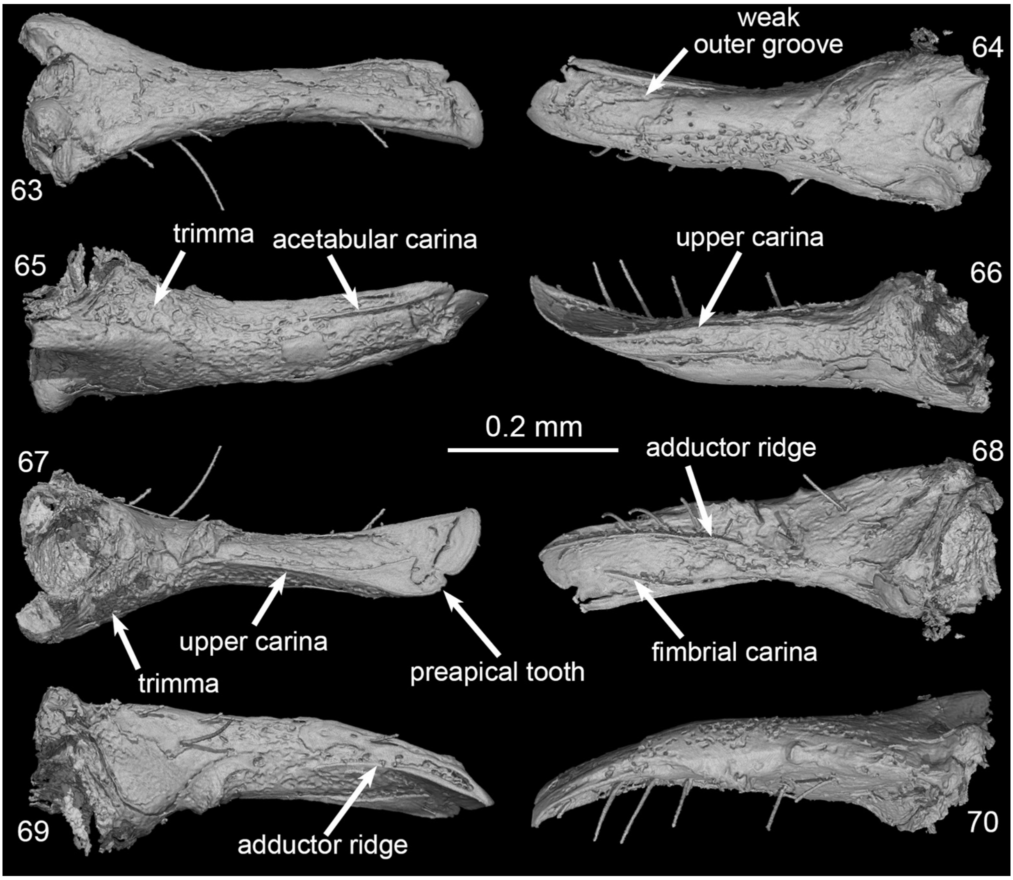
Melikertes clypeatus Engel, 2001a: 128. Holotype ♀, AMNH (*visum*).

This species is described in full in Engel (2001a) and is further imaged here using PPC-SRμCT from two new specimens (Fig. 29). Therefore a full description is not repeated here.

Additional material: 2♀♀, B-147, Baltic amber (SEMC); 1♀, Bitterfeld amber (Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, Hamburg, Germany).

DISCUSSION

Species of Melikertini are a distinctive element of the Eocene bee fauna, and were apparently widespread as species are also known from Ypresian amber from the Cambay Basin (Engel *et al.*, 2013). As further documented here, a subset of species possessed some unique and fascinating morphological specializations otherwise unknown among eusocial bees. A definitive purpose for the various facial modifications observed among melikertine bees remains elusive. Nonetheless, it seems a good working hypothesis that these somehow relate to the collection and manipulation of resin. There are melikertine individuals that seem to have resin masses in their corbiculae (although this is not definitive), while others more clearly are carrying pollen. Furthermore, the mandibles are quite similar to those of Meliponini and Apini, and these mandibular forms have been attributed to their working with wax and/or resin (*e.g.*, Michener & Fraser, 1978). Add to this the observation that large, flat labra and sometimes facial alterations in resin-collecting megachiline bees (Figs. 1, 2) are potentially also related to resin collection and transport (Messer, 1984; Snelling, 1990), and it further suggests working with resin as a potential function. However, megachilines carry resin back with their mandibles, and supported at least from behind by the elongate labrum (which sometimes has a ridged apex potentially to support a resin mass), and perhaps above by clypeal alterations, if present. By contrast, meliponines use their mandibles to collect resin, but then gradually transfer bits to the metatibia for transport, thus not requiring facial alterations to help stabilize a resin mass in flight. It is this placement of resin in the corbicula that has been attributed to the loss of the auricle in Meliponini (Michener, 2013; Engel & Rasmussen, 2021). Nonetheless, it also tantalizing that Melikertini have been recovered as an extinct sister group to Meliponini (Engel, 2001a, 2001b; Schultz *et al.*, 2001; Cardinal & Packer, 2007), a group that uses resins extensively in nest construction and as a defense against fungi (Schwarz, 1948; Wille & Michener, 1973; Michener, 1974; Roubik, 2006; Leonhardt & Blüthgen, 2009). It would be nice in the future to find melikertines clearly with resin elsewhere than their corbiculae, even amid the mandibles and on the lower face, suggesting a bee was ensnared while working resin. It could be that melikertines, still possessing an



Figures 63–70. PPC-SRμCT scan of mandibles of worker of *Amelikertotes clypeata* (Engel), new combination; lower left worker from figure 29. Right mandible rotated axially in left column, left mandible rotated axially in right column. **63.** Outer (slightly ventral oblique) view of right mandible. **64.** Outer (slightly ventral oblique) view of left mandible. **65.** Dorsal view of right mandible. **66.** Dorsal view of left mandible. **67.** Inner view of right mandible. **68.** Inner view of left mandible. **69.** Ventral view of right mandible. **70.** Ventral view of left mandible.

auricle, did not actually carry resin in their corbiculae (although current observations seem to contradict this) and instead transported this material in a fashion analogous to that of megachilines. If not functioning in relation to resin, these facial modifications are an enigma. They do not seem to be suitable as defensive structures nor would they seem to be specializations for particular floral associations, particularly as the clade to which Melikertini belongs is dominated by polylectic lineages (*e.g.*, Michener, 1974, 1990, 2007; Wappler *et al.*, 2015), and the same would seemingly apply to them as well. Similarly, it seems implausible, or at least exceptionally improbable, that these relate to some aspect of pollen manipulation within the nest, such as shaping pollen masses within brood cells, or for working wax and other materials specifically for nest architectural specializations. Lastly, the fact that Melikertini are solely found in fossiliferous resins, while the other abundant group of Eocene corbiculate bees, the Electrapini, are known from both amber as well as compressions in roughly contemporaneous and geographically coincident deposits (*e.g.*, Wappler & Engel, 2003; Wappler *et al.*, 2015), tends to favor the resin-associated hypothesis. Organisms that are more actively living in or in a closer biological association (physical or behavioral) with the resin-producing tree have a higher probability of becoming captured and entombed in the resin and therefore ultimately preserved in amber (Solórzano Kraemer *et al*., 2018). Thus, for the time being resin collection is a suitable null hypothesis. As to the peculiar modifications observed in the sole male melikertine known (*i.e*., the massively elongate mesoscutellar process: Engel *et al*., 2014), even a satisfactory working hypothesis evades us.

It would be interesting to find a sufficient number of individuals of each species of Melikertini with wings outstretched, flat, and unobstructed from which landmarks could be properly measured for geometric morphometrics. Certainly *S. micheneri*, *S. goeleti*, *Melikertes stilbonotus* (Engel), and *A. clypeata* are good candidates, particularly the first species, as the number of specimens is greatest for these four, and it seems that future inclusions shall only continue to expand their numbers. Such an analysis might provide further data for properly clustering the species when taken in combination with other morphological characters. Naturally, it is tempting to compare the wings of these species with modern corbiculate bees, particularly the eusocial tribes Bombini and Apini, as well as the extinct Electrapini. Such an attempt, however, should be undertaken with caution as it is well documented that the morphospace occupied by lineages changes through time and perhaps in relation to the evolution of specific changes in ecology or biology (*e.g*., Barden & Grimaldi, 2016). Morphospace for Eocene representatives of the modern tribes, whether stem- or crown-group representatives, may not correspond to the morphospace observed among living species alone from the same clade. If this were the case, then morphometrics from wings taken in isolation from other data might place a fossil well outside of the cluster of modern species, regardless of whether the two truly form a monophyletic group. Shifting morphospace resulting from the extinction of species defining the total morphospace for the lineage can significantly shift the clustering of species. For example, in ants morphospace has significantly expanded since the Cretaceous (Barden & Grimaldi, 2016). Conversely, in snakeflies morphospace has contracted and shifted considerably from the Cretaceous, to the Eocene, and ultimately to our present fauna (Haug *et al*., in review). The morphospace of, for example, Bombini and its constituent subgenera as circumscribed based on living species may not be representative of the total morphospace occupied by these same units over the last 10–30 million years. The diversity of extinct species from these clades may well have occupied, like ants or snakeflies, areas of morphospace outside of the space circumscribed by living species alone. Morphospace for a group such as Bombini or any of its constituent subgenera may have been far greater, far narrower, or been shifted in any given dimension of morphospace during the Miocene. The total morphospace through time and certainly during any given slice of time may be considerably different than that outlined by extant species alone, despite the species belonging to the same monophyletic group. When a fossil wing falls within the space occupied by a modern group it can perhaps be considered tentative evidence for a placement of that species within that particular clade (although the morphospace of unrelated extinct groups could have overlapped with modern clades!), pending further character evidence. But, if a fossil wing falls outside of the cluster of modern species, it does not necessarily follow that this is positive evidence for placing that species into a different group, at least not without corroborating evidence. Additionally, it can be difficult to determine whether a shape pattern is plesiomorphic or apomorphic, and in the absence of evidence for polarity such morphometric data is merely a phenetic measure, potentially outlining a paraphyletic group sharing a common, but plesiomorphic, shape pattern. Such evolutionary changes in morphospace are known among corbiculate bees. Honey bees have one of the more robust fossil records and morphometrics of wings of living and fossil Apini demonstrate that the expanse of this morphological variation within the clade has narrowed and shifted since the Oligocene (Kotthoff *et al*., 2013). Accordingly, it may not be a wholly valid comparison to use extant morphospace to place isolated fossils from distant epochs in the absence of other character data to help place those extinct taxa, although one of us (M.S.E.) and others have relied on such evidence in the recent past (*e.g*., Kotthoff *et al*., 2011; Wappler *et al*., 2012; Dehon *et al*., 2014, 2017, 2019; Dewulf *et al*., 2014; Prokop *et al*., 2017). Certainly, such analyses are of considerable heuristic value or as a powerful tool within a given fauna, living or extant, but the results from these must be tempered by other data when comparing between temporal faunas.

Assuredly, the opportunities for extracting new information from old specimens remain numerous. The application of technologies such as the μCT scans presented here will undoubtedly expand and revise our present understanding of these species, as will the discovery of further material through future exploration. Unlike most other bee lineages, there is a comparatively large abundance of material of the eusocial corbiculate bee tribes preserved as both compressions and inclusions in amber (*e.g*., Michez *et al*., 2012; Kothoff *et al*., 2013; Barden & Engel, 2021), and so future paleomelittological investigations are poised to capitalize on greater varieties of data from a continually expanding swath of available material.

ACKNOWLEDGEMENTS

We are thankful to Jörg Wunderlich for bringing the two new specimens, described here as *A. emunctorii* and *H. uraeus*, to the attention of M.S.E. and permitting their study and deposition in the Senckenberg Forschungsinstitut, Frankfurt. M.S.E. is grateful to Mónica M. Solórzano Kraemer for making his visit to Frankfurt in October 2019 possible through support of the German VolkswagenStiftung (Project Nr. 90946). PPC-SRμCT was supported by Argonne National Laboratory Advanced Photo Source grant GUP-39093 (to M.S.E.). Jennifer C. Thomas expertly and generously assisted with microphotographs. Additional thanks are owed André Nel and Olivier Béthoux for kindly making it possible for us to study detailed images of the holotype of *Palaeomacropis eocenica*, and to Valerie Ngô-Muller for expertly producing the photographs of figures 24 and 25. Lastly, two anonymous reviewers provided important input that helped improve the final version of the manuscript prior to publication. This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

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ZooBank: urn:lsid:zoobank.org:pub:9B971CED-5718-4F52-8B06-233EBF188AC7

APPENDIX 1

New records of Baltic amber bees

Given the importance of being able to examine series of specimens for bee species and the uncommon nature of fossil bees (Michez *et al.*, 2012), it seems prudent to put on record sundry new specimens, building on earlier accounts documenting such new material (Engel, 2004; Patiny *et al.*, 2007). By documenting this material it should aid future investigators in pulling together data from progressively larger series of specimens.

Family Megachilidae Latreille
Subfamily Megachilinae Latreille
Tribe Glyptapini Cockerell
Genus *Glyptapis* Cockerell
Glyptapis disareolata Engel

New record: 1♀, SMF Be 9327.

Tribe Ctenoplectrellini Engel
Genus *Ctenoplectrella* Cockerell
Ctenoplectrella sp.

New record: 1♀, SMF Be 413.

Family Apidae Latreille
Subfamily Xylocopinae Latreille
Tribe Boreallodapini Engel
Genus *Boreallodape* Engel
Boreallodape baltica Engel

New record: 1♀, SMF Be 9325.

Subfamily Apinae Latreille
Corbiculata Engel
Tribe Electrapini Engel
Genus *Protobombus* Cockerell
Subgenus *Protobombus* Cockerell, *s.str.*
Protobombus (*Protobombus*) *hirsutus* (Cockerell)

New record: 1.5♀♀, SMF Be 9326.

Protobombus (*Protobombus*) sp.

New record: 1♀, SMF Be9332.

Tribe Melikertini Engel
Genus *Melikertes* Engel
Subgenus *Melikertes* Engel, *s.str.*
Melikertes (*Melikertes*) *stilbonotus* (Engel)

NEW RECORDS: 1♀, SMF Be 359; 2♀♀, SMF Be 9328.

Genus *Succinapis* Engel
Succinapis goeleti Engel

NEW RECORDS: 1♀, SMF Be 12410; 2♀♀, SMF Be 12411; 5.5♀♀, SMF Be 9330.

Succinapis micheneri Engel

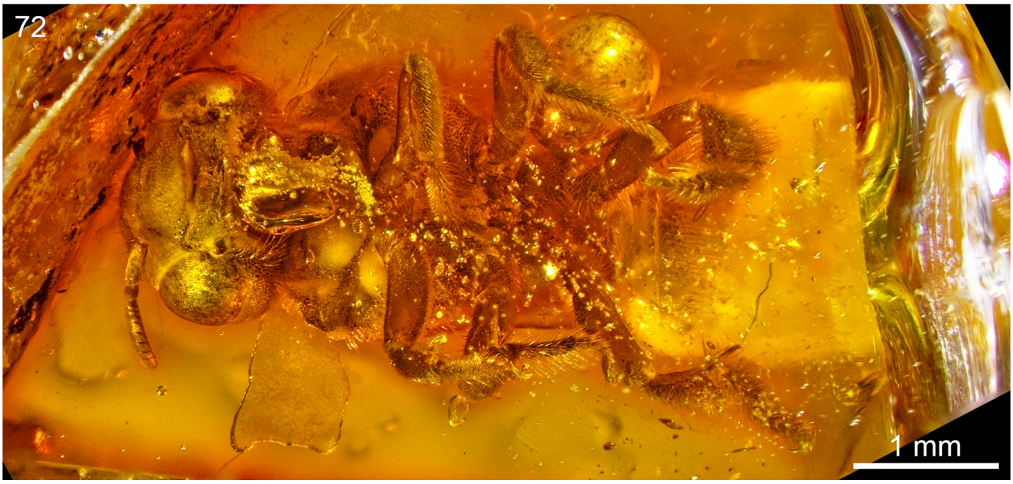
NEW RECORDS: 1♀, B-018 (SEMC); 1♀, B-015 (SEMC); 1♀, B-017 (SEMC).

APPENDIX 2

On the identity of *Palaeomacropis eocenica* (Megachilinae: Ctenoplectrellini)

Fossils of the short-tongued bee family Melittidae are few and some of those that had long been attributed to the family have been subsequently removed to other lineages based on a more critical review of type material (*e.g.*, Dewulf *et al.*, 2014, removed *Melitta willardi* Cockerell; Engel, 2001a, removed *Glyptapis* Cockerell and *Ctenoplectrella* Cockerell, which were placed in Melittidae by Zeuner & Manning, 1976). Melittid fossils are critical as important calibration points in estimations of phylogenetic divergences, and accordingly proper identifications are vital to successful interpretations. In 2015 one of us (M.S.E.) made a reëvaluation of the forewing venation of the putative fossil macropidine *Palaeomacropis eocenica* Michez & Nel (established as *eocenicus*, but the gender of *Palaeomacropis* is feminine and the adjectival specific epithet must therefore be emended to match) from Eocene amber of Oise, France (Michez *et al.*, 2007), and noted that the venation was typical for the megachiline tribe Ctenoplectrellini. Similarly, several features of the description also matched megachilids (*vide infra*), leading to some uncertainty in the proper placement of this fossil. In 2019 and 2020 we were finally able to examine aspects of the holotype of *P. eocenica* in detail thanks to the efforts of A. Nel and O. Béthoux (Paris) (Figs. 71–76), and to confirm and correct various character-state attributions (*vide infra*). *Palaeomacropis* is actually a megachiline bee and must be removed from the fossil record of Melittidae and transferred to Megachilidae.

At the time of its description it was noted that *P. eocenica* had a poorly developed metatibial and metabasitarsal scopa (typical for Ctenoplectrellini) and that instead there was a distinct metasomal scopa (typical for Megachilidae), characters that made the fossil stand out among Melittidae (Michez *et al.*, 2007). These traits are, however, typical for Megachilinae and Megachilidae, respectively (Michener, 2007). An excellent synapomorphy for Megachilinae is the point of contact between the subantennal sulcus and the antennal torulus. In Megachilidae the subantennal sulcus is angled or arches laterally to meet the antennal torulus along its lower, outer margin (Roig-Alsina & Michener, 1993; Engel, 2001a). This character is clearly visible in the holotype of *P. eocenica* (Figs. 74, 75). Additionally, the first and second labial palpomeres (LP_1 and LP_2) are flattened and much longer than wide (partly visible in holotype), and contrast starkly from the typically short and cylindrical more apical palpomeres (LP_3 and LP_4). In fact, even though parts of LP_1 and LP_2 are obscured from a lower oblique facial view, their length could also be deduced by the distant position of LP_3 and LP_4 from the head and other mouthparts (Fig. 76), indicating that the preceding palpomeres must be more elongate, even when the labiomaxillary complex is partially exerted, in order to account for such a projected position (if LP_1 and LP_2 were similarly short and cylindrical, the apex of the labial palpus would be far more proximal with the labiomaxillary complex in its current position). This form of labial palpus structure is a hallmark trait of Megachilidae and Apidae (*e.g.*, Roig-Alsina & Michener, 1993; Michener, 2007). The bee is therefore a long-tongued bee. Consistent with this, the preëpisternal sulcus is absent, as in other long-tongued bees. The wing venation is typical for Megachilinae and specifically the Ctenoplectrellini (Fig. 73) (Engel, 2001a), and the specimen is, in fact, a species of *Ctenoplectrella*, a genus of megachiline bees not uncommon in Eocene amber. Lastly, the outer mandible ridges of *P. eocenica* are those of a megachiline bee and not that of a melittid. Melittidae have a more typical long mandible as most



Figures 71–72. Holotype female of *Ctenoplectrella eocenica* (Michez & Nel), new combination, in Eocene Oise amber (PA 3190 1/17). **71.** Lateral view. **72.** Ventral view. Photographs courtesy of Muséum National d'Histoire Naturelle (*accepit a* A. Nel and O. Béthoux).

other short-tongued bees, with a relatively complete compliment of outer ridges and grooves (Michener & Fraser, 1978: fig. 11), although that of *Dasypoda* Latreille is an outlier among the family. Conversely, in general, Ctenoplectrellini have mandibles similar to those among many Osmiini or even some Anthidiini. In particular, the outer and condylar ridges are exceptionally narrow and closely positioned in the lower half of the mandible's width, and they merge near the apical tooth of the lower apical margin, forming a shallow rutellar cap (*e.g.*, Michener & Fraser, 1978: fig. 30), the point of fusion between these ridges is in line with the first preapical tooth or margin. This pattern of outer and condylar ridges is easily observable in the holotype of *P. eocenica* (Fig. 76).

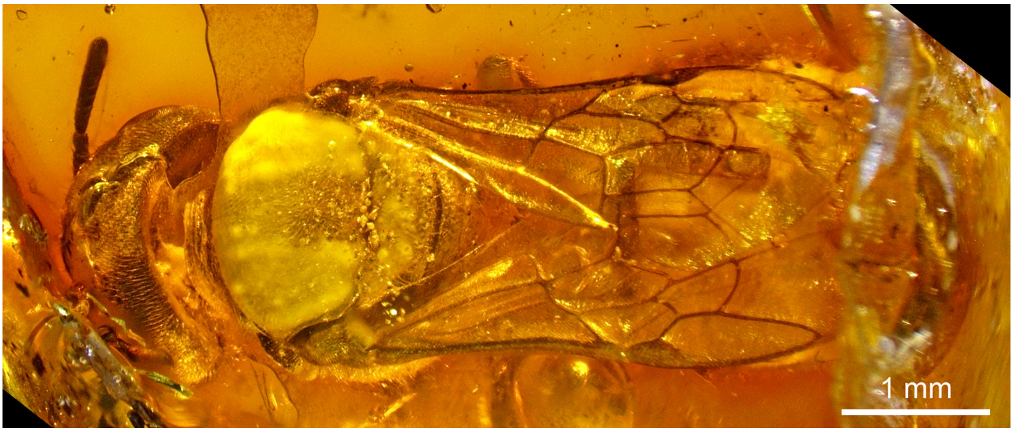


Figure 73. Dorsal view of holotype female of *Ctenoplectrella eocenica* (Michez & Nel), new combination, in Eocene Oise amber (PA 3190 1/17). Photograph courtesy of Muséum National d'Histoire Naturelle (*accepit a* A. Nel and O. Béthoux).

The phylogenetic placement of *Ctenoplectrella* and Ctenoplectrellini has been explored by Gonzalez *et al*. (2012, 2019), where it is considered an extinct sister group to the extant sub-Saharan genus *Aspidosmia* Brauns, and with *Glaesosmia* Engel putatively diverging more basal relative to these two genera. The phylogenetic placement of *Friccomelissa* Wedmann *et al*. preserved in middle Eocene oil shale from Grube Messel (Wedmann *et al*., 2009) is more uncertain but has the characteristic form of wing venation of other ctenoplectrellines.

Hitherto there have been six species in the genus, with specimens found in Baltic, Bitterfeld (reworked Baltic amber), and Rovno ambers (Engel, 2001a, 2008; Engel & Perkovsky, 2006; Gonzalez & Engel, 2011). The Oise amber species fits nicely within this diversity and has most features superficially similar to *C. gorskii* Engel, and in general habitus to the slightly larger *C. phaeton* Gonzalez & Engel (Gonzalez & Engel, 2011).

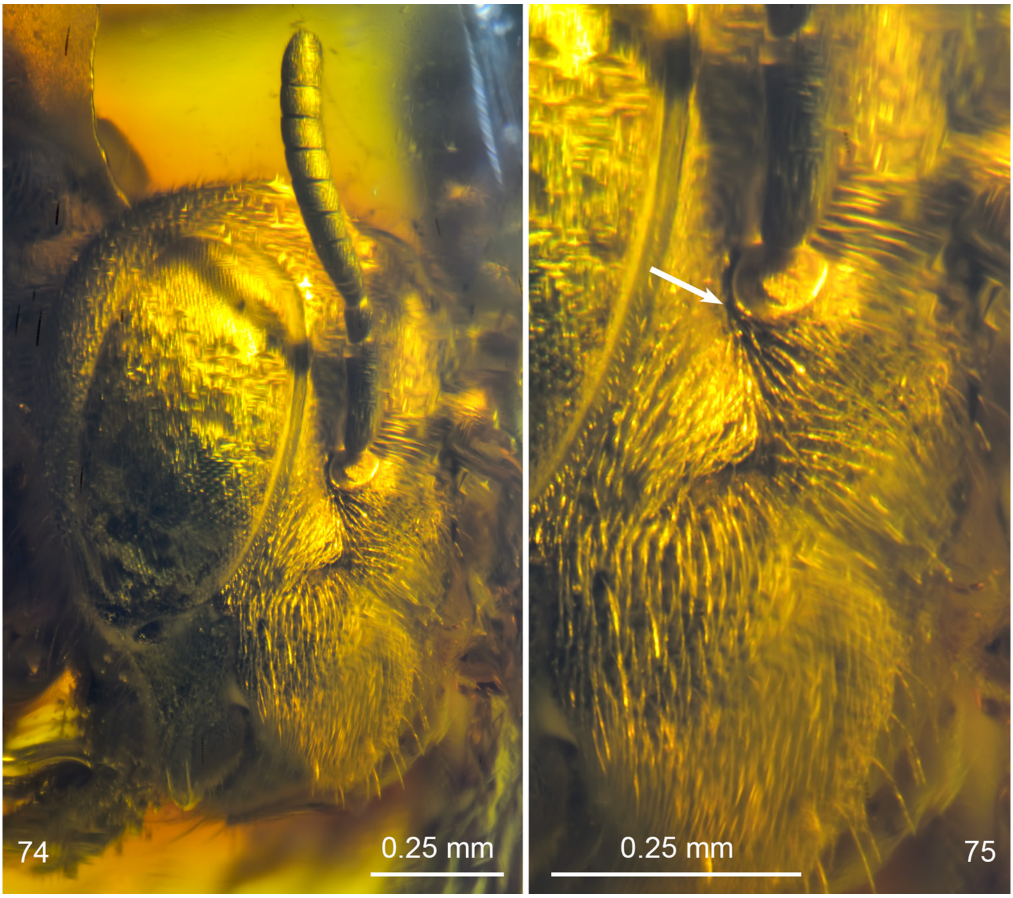
Given this reassessment of the identity of *P. eocenica*, the following nomenclatural changes are necessitated:

Family Megachilidae Latreille
Subfamily Megachilinae Latreille
Tribe Ctenoplectrellini Engel
Genus *Ctenoplectrella* Cockerell

Ctenoplectrella Cockerell, 1909a: 19. Type species: *Ctenoplectrella viridiceps* Cockerell, 1909a, by monotypy. Cockerell, 1909b: 314; Zeuner & Manning, 1976: 172; Engel, 2001a: 68.

Palaeomacropis Michez & Nel in Michez *et al*., 2007: 703. Type species: *Palaeomacropis eocenicus* Michez & Nel in Michez *et al*., 2007, by original designation. **New synonymy.**

Engel (2001a) reported the original description of *Ctenoplectrella* as Cockerell (1909b), following the precedent established by Zeuner & Manning (1976). However, a recent examination of the dates of publication for Cockerell's two papers in which *Ctenoplectrella* is described (Cockerell, 1909a, 1909b), reveals that the situation is actually reversed. Cockerell's paper in *Schriften der physikalisch-ökonomischen Gesellschaft zu Königsberg in Prussia* (Cockerell, 1909a) appeared 20 September 1909, while the other



Figures 74–75. Oblique facial view of holotype female of *Ctenoplectrella eocenica* (Michez & Nel), new combination (PA 3190 1/17). **74.** Head in right oblique profile. **75.** Magnified view of 74, with arrow noting juncture of subantennal sulcus at outer margin of antennal torulus. Photographs courtesy V. Ngô-Muller.

paper did not appear until December 1909 (Cockerell, 1909b). Thus, *Ctenoplectrella* and *C. viridiceps* Cockerell date from 20 September of that year and not December.

Ctenoplectrella eocenica (Michez & Nel), new combination
Figures 22–25

Palaeomacropis eocenicus Michez & Nel in Michez *et al.*, 2007, *nomen imperfectum* [*recte*: *eocenica*]: 704. Holotype ♀, Muséum National d'Histoire Naturelle, Paris (*visum*).

Key to Species of *Ctenoplectrella*
(modified from Gonzalez & Engel, 2011)

1. Forewing 2rs-m arched apically in posterior half, thus second submarginal cell more strongly produced toward wing apex along posterior margin; medioapical margin of clypeus straight (shape of clypeus unknown in *C. phaeton*) 2

—. Forewing 2rs-m relatively straight and therefore second submarginal cell not

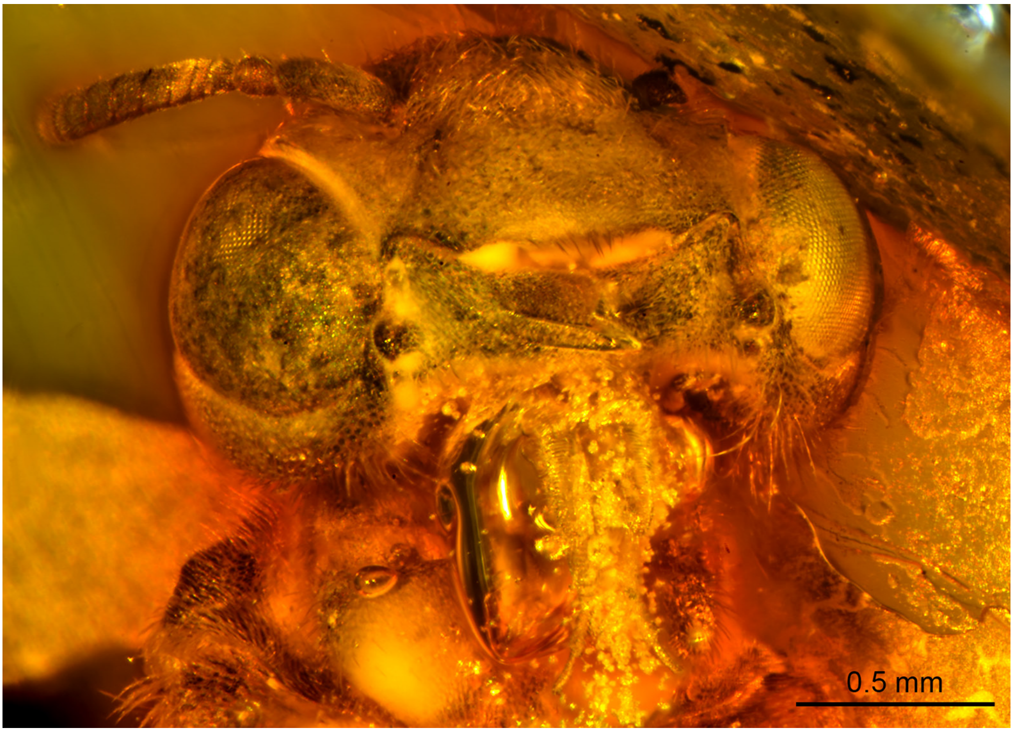


Figure 76. Lower view of head of holotype female of *Ctenoplectrella eocenica* (Michez & Nel), new combination (PA 3190 1/17). Photograph courtesy V. Ngô-Muller.

more strongly produced toward wing apex along posterior margin; medioapical margin of clypeus gently convex [Baltic amber] .... *C. viridiceps* Cockerell

2(1). Forewing basal vein confluent with cu-a; first submarginal cell shorter than second submarginal cell 3

—. Forewing basal vein distad cu-a; first submarginal cell as long as or longer than second submarginal cell 6

3(2). Mesepisternum impunctate laterally; metasomal terga faintly imbricate 4

—. Mesepisternum with coarse, faint punctures laterally; metasomal terga with small, scattered punctures 5

4(3). Propodeal setae long, erect, and branched; tarsal setae fuscous; gena tapering in width from widest above to narrower below [Rovno amber] .... *C. zherikhini* Engel & Perkovsky

—. Propodeal setae scattered, short, and simple; tarsal setae white or off-white; gena of relatively equal width along its length [Baltic amber] .... *C. grimaldii* Engel

5(3). Metepisternum punctate; body pubescence distinctly short and sparse [Baltic amber] .... *C. phaeton* Gonzalez & Engel

—. Metepisternum impunctate; body pubescence of moderate length, not distinctly short and sparse [Baltic amber] .... *C. cockerelli* Engel

6(2). First submarginal cell as long as second submarginal cell; pleura punctate [Oise amber] .... *C. eocenica* (Michez & Nel)

—. First submarginal cell longer than second submarginal cell; pleura impunctate [Baltic amber] .... *C. gorskii* Engel

APPENDIX 3

Classificatory notes on Eocene bees of the tribe Electrapini (Apidae: Apinae)

The bee tribe Electrapini includes some of the more robust bees found in Eocene deposits, although several exceptions do exist. Species are found as both inclusions in amber as well as in sedimentary deposits and have a generally apine- or bombine-like habitus. Presented here are some notes on the classification of these bees in the hopes of further clarifying their affiliations.

Tribe Electrapini Engel

Key to Genera of Electrapini

1. Metabasitarsus quadrangular, about as long as maximum width 2
—. Metabasitarsus elongate, 1.5–2× as long as maximum width .... *Electrapis* Cockerell
2(1). Lateral margins of clypeus strongly concave, epistomal sulcus forming an obtuse angle opening toward compound eye; 10 or more distal hamuli; inner metatibial spur minutely ciliate or serrate .... *Protobombus* Cockerell
—. Lateral margins of clypeus nearly linear, epistomal sulcus therefore comparatively straight; 7 distal hamuli; inner metatibial spur densely pectinate, with numerous branches along rachis .... *Thaumastobombus* Engel

Thaumastobombina Engel, new subtribe

ZooBank: urn:lsid:zoobank.org:act:837B20B9-BF39-4EE9-9CDA-A0C2E8E55A56

Type genus: *Thaumastobombus* Engel, 2001a.

Diagnosis: This subgroup of electrapines are the most similar to Apini and Meliponini, and inclusion in Electrapini may render the tribe paraphyletic, but that remains to be demonstrated. The subtribe is distinctive for the reduced number of distal hamuli (7 versus the 10 or more in other genera), and the densely pectinate inner metatibial spur (ciliate to serrate in other genera). The reduced number of hamuli is most similar to Melikertini and Meliponini among other corbiculate tribes.

Included genera: The subtribe includes only the type genus, which is known only from Baltic amber.

Subtribe Electrapina Engel

Genus *Protobombus* Cockerell

The genus *Protobombus* Cockerell is a group of modestly robust, small to medium-sized bees, superficially similar to *Electrapis* Cockerell except in the form of the metabasitarsus, more consistently sinuate 2Rs (variable in *Electrapis*), and typically smaller body size (the smallest of the currently described species of *Electrapis* are about the size of the largest described species of *Protobombus*). Species of *Protobombus* are known as inclusions in Baltic and Cambay ambers, and also as compressions from the Eckfeld Maar and Grube Messel.

Key to Subgenera of *Protobombus*

1. Forewing basal vein (1M) proximad 1cu-a 2
—. Forewing basal vein (1M) confluent with 1cu-a ...... *Protobombus* Cockerell, *s.str.*
2(1). Forewing with three submarginal cells (1rs-m present) .... *Thnetobombus* Engel, n. subgen.
—. Forewing with two submarginal cells (1rs-m absent) ... *Sophrobombus* Cockerell

Subgenus *Protobombus* Cockerell, *s.str.*

The subgenus presently includes four named species, three in Bartonian Baltic amber (Engel, 2001a) and one from the Ypresian of Grube Messel (Wappler & Engel, 2003), along with one undescribed species in Ypresian Cambay amber (Engel *et al.*, 2013).

Subgenus *Sophrobombus* Cockerell, new status

The subgenus includes only the type species, *P.* (*Sophrobombus*) *fatalis* (Cockerell) in Bartonian Baltic amber (Engel, 2001a).

Thnetobombus Engel, new subgenus

ZooBank: urn:lsid:zoobank.org:act:3D2791AE-5C3B-476F-9A99-740E99A6CED1

Type species: *Protobombus basilaris* Engel, 2001a.

Diagnosis: The subgenus is distinctive among species of *Protobombus* for the combination of three submarginal cells and a basal vein proximal to 1cu-a.

Etymology: The new subgeneric name is a combination of the Greek words *thnētós* (*θνητός*, "mortal") and *bómbos* (*βόμβος*, "humming"). The gender of the name is masculine.

Included species: The subgenus presently includes two species, *P.* (*Thnetobombus*) *basilaris* Engel in Bartonian Baltic amber and *P.* (*T.*) *pristinus* Wappler & Engel from the Lutetian Eckfeld Maar (Engel, 2001a; Wappler & Engel, 2003).

Genus *Electrapis* Cockerell

The genus *Electrapis* Cockerell as currently circumscribed is likely paraphyletic, encompassing a breadth of disparate morphologies. Accordingly, names are applied here to the most readily distinctive groups. Relationships of these taxa to other *Electrapis* or other electrapine genera are murky, and for this reason these entities are retained as subgenera pending further work and more completely preserved material.

Key to Subgenera of *Electrapis*

1. Forewing r-rs well separated from 1Rs; basal vein (1Rs+M) straight or weakly bowed 2
—. Forewing r-rs close to 1Rs; basal vein (1Rs+M) prominently bowed .... *Eckfeldapis* Lutz

2. Forewing pterostigma longer than wide 3
—. Forewing pterostigma greatly reduced, as long as wide .... *Electrapis* Cockerell, *s.str.*
3. Forewing basal vein (1M) proximad 1cu-a; 1m-cu entering second submarginal cell medially or at 2/3 length .... *Mesomelissa* Engel, n. subgen.
—. Forewing basal vein (1M) confluent with 1cu-a; 1m-cu entering second submarginal cell near apex .... *Euglossopteryx* Dehon & Engel

Subgenus *Eckfeldapis* Lutz, new status

The subgenus includes *Electrapis* (*Eckfeldapis*) *electrapoides* (Lutz) and *E.* (*E.*) *prolata* Wappler & Engel from the Lutetian Eckfeld Maar, and at least one undescribed species from the Green River Formation (Engel, pers. obs.).

Subgenus *Electrapis* Cockerell, *s.str.*

The subgenus includes only the type species *E.* (*Electrapis*) *meliponoides* (Buttel-Reepen) from Baltic amber.

Subgenus *Euglossopteryx* Dehon & Engel, new status

The subgenus includes only *E.* (*Euglossopteryx*) *biesmeijeri* (De Meulemeester *et al.*), new combination, from the Green River Formation.

Mesomelissa Engel, new subgenus

ZooBank: urn:lsid:zoobank.org:act:BA59CDBC-93CC-4176-9468-18CCE8F2C0A3

TYPE SPECIES: *Chalcobombus martialis* Cockerell, 1908 (*sensu* Engel, 2001a).

DIAGNOSIS: This subgenus includes those species in which the basal vein (1M) is comparatively straight (distinctly arched in *Eckfeldapis*) and is proximal to 1cu-a, while r-rs is well separated from 1Rs and with a normally developed pterostigma (pterostigma significantly reduced in *Electrapis s.str.*, r-rs and 1Rs close together on pterostigma in *Eckfeldapis*), and 1m-cu meets the second submarginal cell at midlength or about 2/3 length. In addition, 2Rs is comparatively straight (rather than sinuate) and 2rs-m is comparatively close to 2m-cu, either confluent or separated by about 1–3× a vein width (except in *E. tornquisti* Cockerell where the separation is great, about 6–10× a vein width).

ETYMOLOGY: The new subgeneric name is a combination of the Greek words *mésos* (*μέσος*, "middle") and *mélissa* (*μέλισσᾰ*, "bee"). The gender of the name is feminne.

INCLUDED SPECIES: Aside from the type species in Baltic amber, the subgenus includes *E.* (*Mesomelissa*) *krishnorum* Engel and *E.* (*M.*) *tornquisti* in Baltic amber, *E.* (*M.*) *micheneri* Wappler & Engel from the Eckfeld Maar, and one undescribed species from Green River.

APPENDIX 4

A checklist of Eocene bees (Apoidea: Anthophila)

The following list gives a general idea of those bees currently known from Eocene (56–33.9 Ma) deposits. The following abbreviations are used for deposits: BA = Baltic amber (including Bitterfeld amber) (Bartonian, 39–40 Ma); Bembridge Marls (Priabonian, 36 Ma); CA = Cambay amber (Ypresian, 50–52 Ma); EM = Eckfeld Maar (Lutetian, 44.3 Ma); FS = Florissant shale (Priabonian, 34 Ma); GM = Grube Messel (Ypresian, 49 Ma); GR = Green River (Ypresian, 48–52 Ma, precise age of any given specimen is dependent on specific subunit within the geological member); OA = Oise amber (Ypresian, 49–50 Ma); RA = Rovno amber (Priabonian, 36–37 Ma). Note that most species from Florissant are currently *incertae sedis* at various levels pending a thorough revision of their identities. A few have been critically reviewed and are included in the list where they seem to belong systematically, but caution should be used for those attributed to extant genera.

Family ANDRENIDAE Latreille	
Subfamily Andreninae Latreille	
Tribe Andrenini Latreille	
'*Andrena*' *clavula* Cockerell	FS (34 Ma)
'*Andrena*' *grandipes* Cockerell	FS (34 Ma)
'*Andrena*' *hypolitha* Cockerell	FS (34 Ma)
'*Andrena*' *percontusa* Cockerell	FS (34 Ma)
'*Andrena*' *septula* Cockerell	FS (34 Ma)
Genus *Andrenopteryx* Dewulf & Engel	
A. willardi (Cockerell)	FS (34 Ma)
Genus *Lithandrena* Cockerell	
L. saxorum Cockerell	FS (34 Ma)
Genus *Pelandrena* Cockerell	
P. reducta Cockerell	FS (34 Ma)
N. gen. & sp. (Engel, unpubl. data)	GR (48–52 Ma)
Subfamily Panurginae Leach	
Tribe *Incertae sedis*	
Genus *Libellulapis* Cockerell	
L. antiquorum Cockerell	FS (34 Ma)
L. wilmattae Cockerell	FS (34 Ma)
Family HALICTIDAE Thomson	
Subfamily Halictinae Thomson	
Tribe Halictini Thomson	
Genus *Cyrtapis* Cockerell	
C. anomala Cockerell	FS (34 Ma)
Genus *Electrolictus* Engel	
E. antiquus Engel	BA (39–40 Ma)
Genus *Kronolictus* Engel	
K. scudderiellus (Cockerell)	FS (34 Ma)
K. scudderiellus (Cockerell)	FS (34 Ma)
Genus *Ocymoromelitta* Engel	
O. florissantella (Cockerell)	FS (34 Ma)
O. miocenica (Cockerell)	FS (34 Ma)
O. sorella Engel	FS (34 Ma)

Family PALEOMELITTIDAE Engel	
Genus *Paleomelitta* Engel	
P. nigripennis Engel	BA (39–40 Ma)
N. gen. & sp. (Engel, unpubl. data)	RA (36–37 Ma)
Family MELITTIDAE Kawall	
Subfamily Melittinae Kawall	
Tribe Eomacropidini Engel	
Genus *Eomacropis* Engel	
E. glaesaria Engel	BA (39–40 Ma)
Family MEGACHILIDAE Latreille	
Subfamily Lithurginae Newman	
Tribe Protolithurgini Engel	
Genus *Protolithurgus* Engel	
P. ditomeus Engel	BA (39–40 Ma)
Subfamily Megachilinae Latreille	
Tribe Glyptapini Cockerell	
Genus *Glyptapis* Cockerell	
G. densopunctata Engel	BA (39–40 Ma)
G. disareolata Engel	BA (39–40 Ma)
G. fuscula Cockerell	BA (39–40 Ma)
G. mirabilis Cockerell	BA (39–40 Ma)
G. n. sp. (Engel, unpubl. data)	BA (39–40 Ma)
G. n. sp. (Engel, unpubl. data)	RA (36–37 Ma)
Tribe Ctenoplectrellini Engel	
Genus *Ctenoplectrella* Cockerell	
C. cockerelli Engel	BA (39–40 Ma)
C. eocenica (Michez & Nel)	OA (49–50 Ma)
C. gorskii Engel	BA (39–40 Ma)
C. grimaldii Engel	BA (39–40 Ma)
C. phaeton Gonzalez & Engel	BA (39–40 Ma)
C. viridiceps Cockerell	BA (39–40 Ma)
C. zherikhini Engel & Perkovsky	RA (36–37 Ma)
C. n. sp. (Engel, unpubl. data)	GR (48–52 Ma)
Genus *Glaesosmia* Engel	
G. genalis Engel	BA (39–40 Ma)
Genus *Friccomelissa* Wedmann *et al.*	
F. schopowi Wedmann *et al.*	GM (49 Ma)
N. gen. & sp. (Engel, unpubl. data)	GR (48–52 Ma)
Tribe *Incertae sedis*	
'*Anthidium*' *exhumatum* Cockerell	FS (34 Ma)
'*Anthidium*' *scudderi* Cockerell	FS (34 Ma)
'*Dianthidium*' *tertiarium* Cockerell	FS (34 Ma)
Lithanthidium pertriste Cockerell	FS (34 Ma)
'*Megachile*' *praedicta* Cockerell	FS (34 Ma)
'*Heriades*' *bowditchi* Cockerell	FS (34 Ma)
'*Heriades*' *halictinus* Cockerell	FS (34 Ma)
'*Heriades*' *mersatus* Cockerell	FS (34 Ma)
'*Heriades*' *mildredae* Cockerell	FS (34 Ma)
'*Heriades*' *priscus* Cockerell	FS (34 Ma)
'*Heriades*' *saxosus* Cockerell	FS (34 Ma)

Family APIDAE Latreille	
Subfamily Xylocopinae Latreille	
Tribe Xylocopini Latreille	
Genus *Xylocopa* Latreille	
Subgenus *Incertae sedis*	
X. gabrielae Engel	FS (34 Ma)
Tribe Boreallodapini Engel	
Genus *Boreallodape* Engel	
B. baltica Engel	BA (39–40 Ma)
B. mollyae Engel	BA (39–40 Ma)
B. striebichi Engel	BA (39–40 Ma)
Subfamily Apinae Latreille	
Tribe *Incertae sedis*	
'*Anthophora*' *melfordi* Cockerell	FS (34 Ma)
Genus *Pygomelissa* Engel & Wappler (perhaps Eucerini)	
P. lutetia Engel & Wappler	GM (49 Ma)
Tribe Melectini Westwood	
Genus *Protomelecta* Cockerell	
P. brevipennis Cockerell	FS (34 Ma)
Clade Corbiculata Engel	
Tribe Bombini Latreille	
Genus *Calyptapis* Cockerell	
C. florissantensis Cockerell	FS (34 Ma)
Genus *Oligobombus* Antropov	
O. cuspidatus Antropov	BM (36 Ma)
Tribe Electrobombini Engel	
Genus *Electrobombus* Engel	
E. samlandensis Engel	BA (39–40 Ma)
Tribe Electrapini Engel	
Subtribe Electrapina Engel	
Genus *Electrapis* Cockerell, *s.l.*	
Subgenus *Eckfeldapis* Lutz	
E. electrapoides (Lutz)	EM (44.3 Ma)
E. prolata Wappler & Engel	EM (44.3 Ma)
E. n. sp. (Engel, unpubl. data)	GR (48–52 Ma)
Subgenus *Electrapis* Cockerell, *s.str.*	
E. meliponoides (Buttel-Reepen)	BA (39–40 Ma)
Subgenus *Euglossopteryx* Dehon & Engel	
E. biesmeijeri (De Meulemeester *et al.*)	GR (48–52 Ma)
Subgenus *Mesomelissa* Engel	
E. krishnorum Engel	BA (39–40 Ma)
E. martialis (Cockerell)	BA (39–40 Ma)
E. micheneri Wappler & Engel	EM (44.3 Ma)
E. tornquisti Cockerell	BA (39–40 Ma)
E. n. sp. (Engel, unpubl. data)	GR (48–52 Ma)
N. subgen. & sp. (Engel, unpubl. data)	GR (48–52 Ma)
Genus *Protobombus* Cockerell, *s.l.*	
Subgenus *Protobombus* Cockerell, *s.str.*	
P. hirsutus Cockerell	BA (39–40 Ma)
P. indecisus Cockerell	BA (39–40 Ma)
P. messelensis Engel & Wappler	GM (49 Ma)
P. tristellus Cockerell	BA (39–40 Ma)
P. sp. (Engel *et al.*, 2013)	CA (50–52 Ma)

Subgenus *Sophrobombus* Cockerell	
P. fatalis (Cockerell)	BA (39–40 Ma)
Subgenus *Thnetobombus* Engel	
P. basilaris Engel	BA (39–40 Ma)
P. pristinus Wappler & Engel	EM (44.3 Ma)
Subtribe Thaumastobombina Engel	
Genus *Thaumastobombus* Engel	
T. andreniformis Engel	BA (39–40 Ma)
Tribe Melikertini Engel	
Genus *Aethemelikertes* Engel	
A. emunctorii Engel	BA (39–40 Ma)
Genus *Amelikertotes* Engel	
A. clypeata (Engel)	BA (39–40 Ma)
Genus *Haidomelikertes* Engel	
H. proboscidea (Engel)	BA (39–40 Ma)
H. uraeus Engel	BA (39–40 Ma)
Genus *Melikertes* Engel, *s.l.*	
Subgenus *Melikertes* Engel, *s.str.*	
M. kamboja Engel & Ortega-Blanco	CA (50–52 Ma)
M. proavus (Menge)	BA (39–40 Ma)
M. stilbonotus (Engel)	BA (39–40 Ma)
Subgenus *Paramelikertes* Engel & Ortega-Blanco	
M. gujaratensis Engel & Ortega-Blanco	CA (50–52 Ma)
Genus *Melissites* Engel	
M. trigona Engel	BA (39–40 Ma)
Genus *Mochlomelikertes* Engel *et al.*	
M. hoffeinsorum Engel *et al.*	BA (39–40 Ma)
Genus *Roussyana* Manning	
R. palmnickenensis (Roussy)	BA (39–40 Ma)
Genus *Succinapis* Engel	
S. goeleti Engel	BA (39–40 Ma)
S. micheneri Engel	BA (39–40 Ma)
Tribe Meliponini Lepeletier de Saint Fargeau	
Genus *Exebotrigona* Engel & Michener	
E. velteni Engel & Michener	BA (39–40 Ma)
Genus *Kelneriapis* Sakagami	
K. eocenica (Kelner-Pillault)	BA (39–40 Ma)
Genus *Liotrigonopsis* Engel	
L. rozeni Engel	BA (39–40 Ma)
Subfamily *Incertae sedis*	
'*Ceratina*' *disrupta* Cockerell	FS (34 Ma)
Family *Incertae sedis*	
'Megachilinae' sp. Antropov	BM (36 Ma)

JM Journal of Melittology

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

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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.

Journal of Melittology is registered in ZooBank (www.zoobank.org), and archived at the University of Kansas and in Portico (www.portico.org).

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