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by Michael S. Engel et al.

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The bees of Early Eocene Cambay amber
(Hymenoptera: Apidae)

Michael S. Engel1,2, Jaime Ortega-Blanco1, 
Paul C. Nascimbene2, & Hukam Singh3

Abstract. The fauna of bees known from Early Eocene (Ypresian) Cambay amber are reviewed. Presently only three species have been recovered, all from among the corbiculate Apinae and representing the extinct tribes Electrapini and Melikertini, and all from genera known from the slightly younger middle Eocene Baltic amber. A single, poorly-preserved and fragmentary female of an unidentifiable species of Protobombus Cockerell is recorded. Two new species of the genus Melikertes Engel are documented, one representing a new subgenus, Paramelikertes Engel & Ortega-Blanco, as is a third, fragmentary melikertine of uncertain identity. The new species are Melikertes (Paramelikertes) gujaratensis Engel & Ortega-Blanco, new species, and M. (Melikertes) kamboja Engel & Ortega-Blanco, new species.

INTRODUCTION

The Eocene is the first geological epoch from which there is a rich and diverse fauna of bees preserved. Unfortunately, most of these are from a single formation, namely the extensive deposits of middle Eocene (Lutetian) Baltic amber and its related resins such as the Rovno amber of the Ukraine (Engel, 1998, 2001a, 2001b, 2004, 2008; Engel & Perkovsky, 2006; Gonzalez & Engel, 2011; Michez et al., 2012; Ohl & Engel, 2007; Patiny et al., 2007). Eocene bees are known from elsewhere including two species

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Table 1. Currently described Eocene amber Apinae (all are preserved in Baltic amber except the two new species from Cambay amber reported herein and *Exebotrigona velteni* Engel & Michener in Fushan amber).

<table>
<thead>
<tr>
<th>Tribe Electrobombini Engel</th>
<th>Tribe Melikertini Engel</th>
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<tbody>
<tr>
<td>Genus <em>Electrobombus</em> Engel</td>
<td>Genus <em>Melikertes</em> Engel</td>
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<tr>
<td><em>E. samlandensis</em> Engel</td>
<td>Subgenus <em>Melikertes</em> Engel</td>
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<tr>
<td>Genus <em>Electrapis</em> Cockerell</td>
<td>Genus <em>Melissites</em> Engel</td>
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<tr>
<td><em>E. khrishnorum</em> Engel</td>
<td><em>M. clypeatus</em> Engel</td>
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<tr>
<td><em>E. martialis</em> (Cockerell)</td>
<td><em>M. kamboja</em>, n. sp.</td>
</tr>
<tr>
<td><em>E. meliponoides</em> (Buttel-Reepen)</td>
<td><em>M. proavus</em> (Menge)</td>
</tr>
<tr>
<td><em>E. tornquisti</em> Cockerell</td>
<td><em>M. stilbonotus</em> Engel</td>
</tr>
<tr>
<td>Genus <em>Protobombus</em> Cockerell</td>
<td>Subgenus <em>Paramelikertes</em>, n. subgen.</td>
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<tr>
<td><em>P. basilaris</em> Engel</td>
<td><em>M. gujaratensis</em>, n. sp.</td>
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<tr>
<td><em>P. fatalis</em> (Cockerell)</td>
<td>Genus <em>Roussyana</em> Manning</td>
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<tr>
<td><em>P. hirsutus</em> (Cockerell)</td>
<td><em>R. palmnickenensis</em> (Roussy)</td>
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<tr>
<td><em>P. indecisus</em> Cockerell</td>
<td>Genus <em>Succinapis</em> Engel</td>
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<tr>
<td><em>P. tristellus</em> Cockerell</td>
<td><em>S. goeleiti</em> Engel</td>
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<tr>
<td>Genus <em>Thaumastobombus</em> Engel</td>
<td><em>S. micheneri</em> Engel</td>
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<tr>
<td><em>T. andreniformis</em> Engel</td>
<td><em>S. probosidea</em> Engel</td>
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in Early Eocene Oise and Fushan ambers (Michez et al., 2007; Engel & Michener, 2013) and various compressions or traces from Eckfeld and Messel in Germany (Lutz, 1993; Wappler & Engel, 2003; Wedmann et al., 2009), Quilchena in British Columbia (Engel & Archibald, 2003), MacBee in British Columbia and Republic in Washington State (Labandeira, 2002), Claron Formation in southwestern Utah (Sarzetti et al., in press), Rio Pichi-Leufú in Patagonia, Argentina (Sarzetti et al., 2008), and Puryear in Tennessee State (Brooks, 1955; Wedmann et al., 2009), and Viola in Kentucky State (Berry, 1931; Wedmann et al., 2009). The Eocene is also the last of the rather ‘unfamiliar’ faunas of bees, where many of the taxa are not easily attributable to modern tribes and the genera are more distinctively different from modern forms. Given this, not surprisingly the composition of these faunas is in more dramatic contrast with that of the present than are those of the Oligocene and most certainly the Miocene (e.g., Engel, 2004; Engel et al., 2012; Kotthoff et al., 2011; Michez et al., 2012; Ohl & Engel, 2007; Wappler et al., 2012; Zeuner & Manning, 1976). While the relative abundance of material from the Eocene might indicate a robust understanding of bee life and diversity during this epoch,
there is a noticeable bias in the record toward the eusocial bees and more importantly a
hitherto biogeographic restriction to North America and Europe, with a few records of
ichnospecies from southern South America. Accordingly, our knowledge of the global
diversity of bees at this time is somewhat speculative.

Herein we provide an overview of the bee fauna of Cambay amber (Gujarat, India) as it is presently understood. Bees are as of yet still rare in the deposits and so our perspective is quite limited but these do significantly expand the biogeographic repre-
sentation of bees during the Eocene. To date only a handful of fragmentary specimens have been recovered and these all come from among the eusocial corbiculate Apinae (Table 1). Descriptions and notes on these taxa are hoped to bring these to the attention of melittologists and to inspire future collections to intensively seek more specimens.

MATERIAL AND METHODS

The present specimens were discovered during preparation of amber inclusions excavated from the Tarkeshwar (sometimes written Tadkeshwar) lignite mine in Gu-
jarat, India. Amber from these deposits is of Early Eocene (Ypresian) origin. Rust et
al. (2010) provide an overview of the age, botanical origin, and known fauna of the
amber. The amber was embedded in epoxy resin and polished following the method of Nascimbene & Silverstein (2000). Morphological terminology follows Engel (2001a) and Michener (2007). Observations were made using Olympus SZ-60 and SZX-12 stereomicroscopes and an Olympus BX-41 compound microscope with reflected and transmitted light. Photomicrographs were taken with a Canon EOS 7D digital camera attached to an Infinity K-2 long-distance microscope lens illuminated by a Xenon flash. Type material is presently in the American Museum of Natural History, New York, USA (AMNH) and the Steinmann Institut für Geologie, Mineralogie, und Paläontolo-
gie, Bonn, Germany (SIPB), but primary types will eventually be transferred to the amber collection of the Birbal Sahni Institute of Palaeobotany, Lucknow, India.

SYSTEMATIC PALEONTOLOGY

Subfamily Apinae Latreille
Tribe Electrapini Engel
Genus *Protobombus* Cockerell

*Protobombus*? species indeterminate

**Material:** AMNH Tad-41-A; India: Gujurat, Tadkeshwar lignite mine; Cambay Formation (Paleo-Eocene), 7–12 January 2009 (AMNH).

**Comments:** A poorly preserved female worker (length approximately 7.5 mm, forewing length approximately 6.7 mm) putatively of the electrapine genus *Proto-
bombus* Cockerell as indicated by the shape of the metabasitarsus. The specimen is poorly preserved with the wings outstretched from the body, the mesosoma of which is largely opened ventrally and cleared. The head is also only partially preserved, most of the right side and ventral portions being incomplete at the amber surface, with only the scape, pedicel, and basalmost flagellomeres preserved from the bee’s left side. The wings themselves are also somewhat partial with the anterior-apical por-
tions of the bee’s right forewing missing and the left forewing largely crumpled and obscured. Given the diversity of these bees in the somewhat contemporaneous amber of the Baltic region (Engel, 2001a, 2004) as well as other deposits (Wappler & Engel,
it is perhaps not surprising that such similar species should be discovered in Cambay amber. It is greatly hoped that more complete and well-preserved specimens will eventually be recovered.

Tribe Melikertini Engel  
Genus Melikertes Engel  

**Paramelikertes** Engel & Ortega-Blanco, new subgenus  
ZooBank: urn:lsid:zoobank.org:act:08DFB6FD-5DC6-4EBF-ABEE-F19E1E031A2C

**Type species:** *Melikertes (Paramelikertes) gujaratensis* Engel & Ortega-Blanco, new species.

**Diagnosis:** This new group can be differentiated from *Melikertes s.str.* (Engel, 2001a) by the presence of only two submarginal cells (Figs. 2, 3), the confluence of...
2rs-m with 2m-cu, the more elongate and narrow marginal cell, the marginal cell apex acutely pointed on the wing margin, the more densely setose metasoma, and the more strongly developed and dense stout bristles of the mid- and hind legs. Like Melikertes the malar space is apparently short, the clypeus lacks the clypeal protrusion typical of Succinapis Engel, the mesoscutellum apparently does not project over the metanotum, and the metasomal terga are not banded.

**Etymology:** The new subgeneric name is a combination of the Greek prefix para (meaning, “near”) and Melikertes, type genus of the tribe. The name is masculine.

**Comments:** The genus Melikertes Engel was previously known from three species in Baltic amber – Melikertes proavus (Menge), M. stilbonotus (Engel), and M. clypeatus Engel (Table 1). Two new species are added here, one in the new subgenus, and the remainder classified in Melikertes s.str.

**Figure 3.** Holotype worker (AMNH Tad-41-A) of Melikertes (Paramelikertes) gujaratensis, new subgenus and species.
Melikertes (Paramelikertes) gujaratensis Engel & Ortega-Blanco, new species
ZooBank: urn:lsid:zoobank.org:act:6F377DAD-AA95-4FF1-AABB-FAB4F4A1F5D1 (Figs. 1–3)

Diagnosis: As for the subgenus (vide supra).

Description: ♀ (worker): Total body length (as preserved) approximately 3 mm; forewing length 2.28 mm. Mandible elongate and narrow (though not entirely clear in possible views). Scape long and narrow, slightly widened apically; pedicel narrow; flagellomeres wider than scape and pedicel. Mesoscutellum damaged but apparently not covering metanotum or propodeum. Legs covered by apparently long, largely simple setae; metabasitarsus moderately expanded, with parallel sides, covered by distinctly branched setae, setae longer than metabasitarsal width; pretarsal claws widened basally, apparently simple. Forewing with basal vein straight, basad cu-a by slightly less than length of cu-a; M angled posteriorly after separating from Rs; r-rs slightly more than three-quarters length second abscissa of Rs; second abscissa Rs straight; 1rs-m absent; second submarginal cell; 1m-cu meeting second submarginal cell near base, distad second abscissa Rs by about one-half length of 1m-cu; 2rs-m confluent with 2m-cu; 2rs-m slightly arched apically in posterior half; discal and subdiscal cells much longer than high (around 3.8 times); marginal cell elongate. Metasoma densely covered by setae, without evidence bands of coloration or setae; tip of sting discernible.

Holotype: ♀, AMNH Tad-41-A (Fig. 1, 3); India: Gujarat, Tadkeshwar lignite mine; Cambay Formation (Paleo-Eocene), 72–12 January 2009 (AMNH). Syninclusions include an aphelinid (Chalcidoidea), spider, and the aforementioned specimen of Proto-bombus (vide supra).

Etymology: The specific epithet refers to the Indian State of Gujarat, from which the amber originates.

Comments: Although the body of the holotype is not ideally preserved, the structure of the legs, mesoscutellum, metasomal terga, and absence of a clypeal protrusion (such protrusions are present in Succinapis) all indicate this to be a species of Melikertes (Engel, 2001a), a genus of the extinct tribe Melikertini otherwise known only from the Eocene of Europe.

Subgenus Melikertes Engel

Melikertes (Melikertes) kamboja Engel & Ortega-Blanco, new species

Diagnosis: Differs from M. gujaratensis in having shorter mandibles, presence of 1rs-m (absent in M. gujaratensis); marginal cell broader and not tapering along its length; discal and subdiscal cells somewhat longer than high (around 1.6 times).

Description: ♀ (worker): Total body length (as preserved) ca. 3.64 mm; forewing length 2.77 mm. Mandible elongate, curved, with at least two apical rounded teeth. Clypeus damaged but clearly without medial cleft or protuberances. Scape elongate and narrow; pedicel compressed and drawn out as preserved; flagellum distinctly wider than scape and pedicel. Mesosoma and legs covered by thin branched setae (particularly well visible on tibiae and basitarsi); mesoscutellum apparently not bulging nor covering metanotum or propodeum. Metabasitarsus slightly widened with
parallel sides; setae distinctly branched (Fig. 11). Forewing with basal vein straight, basad cu-a by about one-half length of cu-a; M angled posteriorly after separating from Rs; r-rs slightly more than three-quarters length second abscissa of Rs; second abscissa Rs straight; 1rs-m present (thus three submarginal cells) (Figs. 6, 8, 10); second submarginal cell narrow, narrowed anteriorly, anterior border along Rs shorter than r-rs; third submarginal cell larger than second, with anterior border along Rs about three times longer than anterior border of second submarginal cell; 1m-cu meeting second submarginal cell near midpoint; 2rs-m weakly arched apically in posterior half,
confluent with 2m-cu; discal and subdiscal cells somewhat longer than high (around 1.6 times); marginal cell elongate, broadly tubular (i.e., not tapering in width along its length), apex broadly rounded and truncate and appendiculate. Hind wing with six distinct hamuli on anterior margin. Metasoma with reddish aspect as preserved, apparently not banded and without fasciae; sting short and straight.

**Holotype**: AMNH Tad-272-A (Figs. 4, 5, 9); India: Gujarat, Tadkeshwar lignite mine; Cambay Fm. (Paleo-Eocene), 7–12 January 2009 (AMNH).

**Paratype**: STB-092-T’10 (Fig. 7); India: Gujarat, Tadkeshwar lignite mine; Cambay Fm. (Paleo-Eocene) (SIPB).

Etymology: The name Kamboja refers to the Indo-Iranian Kshatriya tribe who are referred to in ancient Indian texts such as the Mahabharata. In the 2nd Century B.C. the Kambojas invaded northern India and wrestled control of various Indo-Aryan territories including Gujarat, eventually settling and giving their name to the area (Khambat or Cambay). The name is treated as a noun in apposition.

Genus & species indeterminate

Material: AMNH Tad-179; India: Gujarat, Tadkeshwar lignite mine; Cambay Formation (Paleo-Eocene), 17–22 January 2010 (AMNH).

Comments: A partial female worker (preserved length approximately 5.3 mm, consisting of head to about start of metasoma, remainder of bee missing at amber surface) of a melikertine of indeterminate generic position. The head and mesosoma superficially resemble Melissites Engel but more complete material is needed to make
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a positive identification and description possible. The specimen consists of a complete head, and most of the mesosoma, although the dorsum is slightly caved inward on the mesoscutellum and mesoscutum. The wings, folded over the body, are largely missing beyond the basal vein. The metasoma is not preserved and the legs are fragmentary and curled beneath the body. Debris and other inclusions (e.g., a beautiful ant) within the piece obscure several important views of the bee.

DISCUSSION

Although the material currently available of bees in Cambay amber is not well preserved, the rarity of bees in general and the biogeographic location and age of the specimens are of sufficient significance to warrant a brief account. We therefore offer these preliminary observations highlighting what is known at this time. Interestingly, the taxa recovered are of genera already well characterized in the slightly younger ambers of the Baltic region (Engel, 2001a). All of the taxa discussed herein are of eu-social lineages and these genera obviously had wide distributions during the Eocene, extending from nuclear Europe (i.e., the Baltic deposits) across the Turgai Strait and Asia and into India, and spanning a period that saw the beginning of subduction for the northern Indian Plate, the eventual disappearance of the Kohistan-Ladakh archipelagos, and closure of the Neotethys Seaway. It is likely that since electrapines and melikertines are known in the Baltic and Indian ambers, that they will eventually be discovered in the roughly contemporaneous Fushan amber deposits of northeastern China (Wang et al., in prep.), and indeed species certainly extended into northern Africa and may have occupied parts of North America owing to connections extant at the time. Indeed, it is not unusual for putatively ‘Old World’ groups to be discovered as fossils in the Tertiary of North America (e.g., Engel et al., 2009; Kotthoff et al., 2013). Continued exploration of the Cambay deposits are needed to determine what, if any, other of those lineages known from European ambers may be found there, or more interestingly any potentially unique genera and tribes for the region. It seems likely that at least the Boreallodapini would have been present in this biogeographic region at the time (Engel, 2001a), and they should be sought from the Cambay amber. There is also needed greater exploration of fossiliferous deposits in Africa and Tertiary deposits such as those in Ethiopia (e.g., Engel et al., 2013) may prove of great importance for further understanding of Paleogene biogeography.
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