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

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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).

Tribe Electrobombini Engel	**Tribe Melikertini Engel**
Genus *Electrobombus* Engel	Genus *Melikertes* Engel
E. samlandensis Engel	Subgenus *Melikertes* Engel
Tribe Electrapini Engel	*M. clypeatus* Engel
Genus *Electrapis* Cockerell	*M. kamboja*, n. sp.
E. krishnorum Engel	*M. proavus* (Menge)
E. martialis (Cockerell)	*M. stilbonotus* (Engel)
E. meliponoides (Buttel-Reepen)	Subgenus *Paramelikertes*, n. subgen.
E. tornquisti Cockerell	*M. gujaratensis*, n. sp.
Genus *Protobombus* Cockerell	Genus *Melissites* Engel
P. basilaris Engel	*M. trigona* Engel
P. fatalis (Cockerell)	Genus *Roussyana* Manning
P. hirsutus (Cockerell)	*R. palmnickenensis* (Roussy)
P. indecisus Cockerell	Genus *Succinapis* Engel
P. tristellus Cockerell	*S. goeleti* Engel
Genus *Thaumastobombus* Engel	*S. micheneri* Engel
T. andreniformis Engel	*S. proboscidea* Engel
	Tribe Meliponini Lepeletier de Saint Fargeau
	Genus *Exebotrigona* Engel & Michener
	E. velteni Engel & Michener
	Genus *Kelneriapis* Sakagami
	K. eocenica (Kelner-Pillault)
	Genus *Liotrigonopsis* Engel
	L. rozeni Engel

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 representation 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

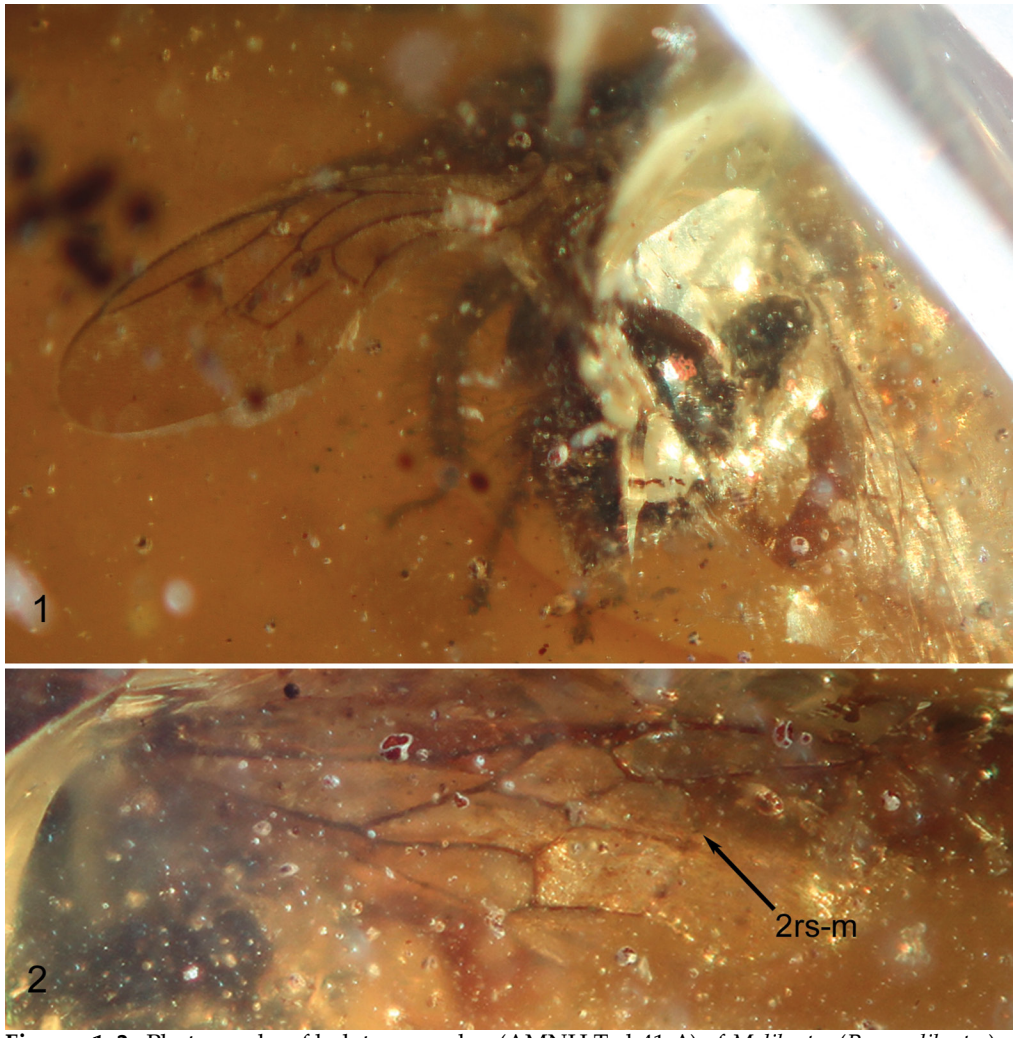
The present specimens were discovered during preparation of amber inclusions excavated from the Tarkeshwar (sometimes written Tadkeshwar) lignite mine in Gujarat, India. Amber from these deposits is of Early Eocene (Ypresian) origin. Rust *et al*. (2010) provide an overview of the age, botanical origin, 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 Paläontologie, 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 *Protobombus* 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 portions 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,



Figures 1–2. Photographs of holotype worker (AMNH Tad-41-A) of *Melikertes* (*Paramelikertes*) *gujaratensis*, new subgenus and species. **1.** Entire specimen as preserved in dorsal oblique view. **2.** Detail of forewing.

2003), 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

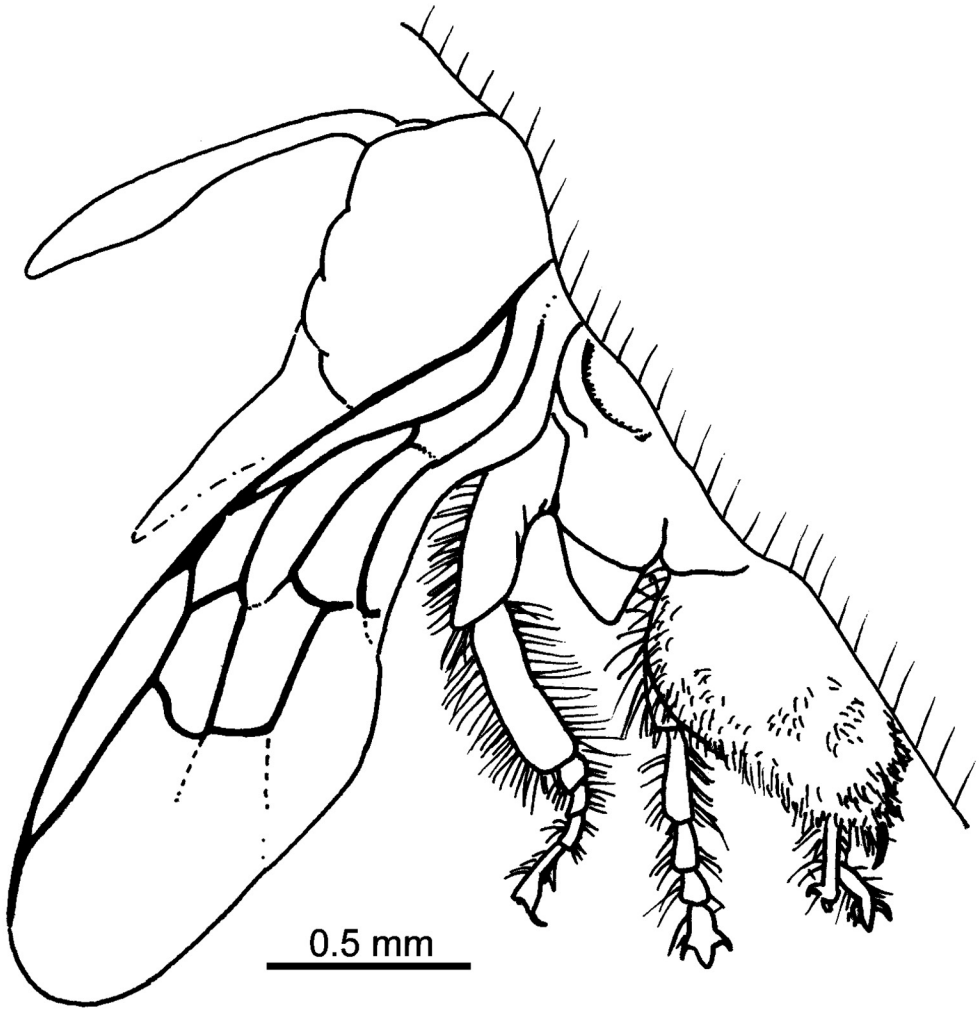


Figure 3. Holotype worker (AMNH Tad-41-A) of *Melikertes* (*Paramelikertes*) *gujaratensis*, new subgenus and species.

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*.

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 *Protobombus* (*vide supra*).

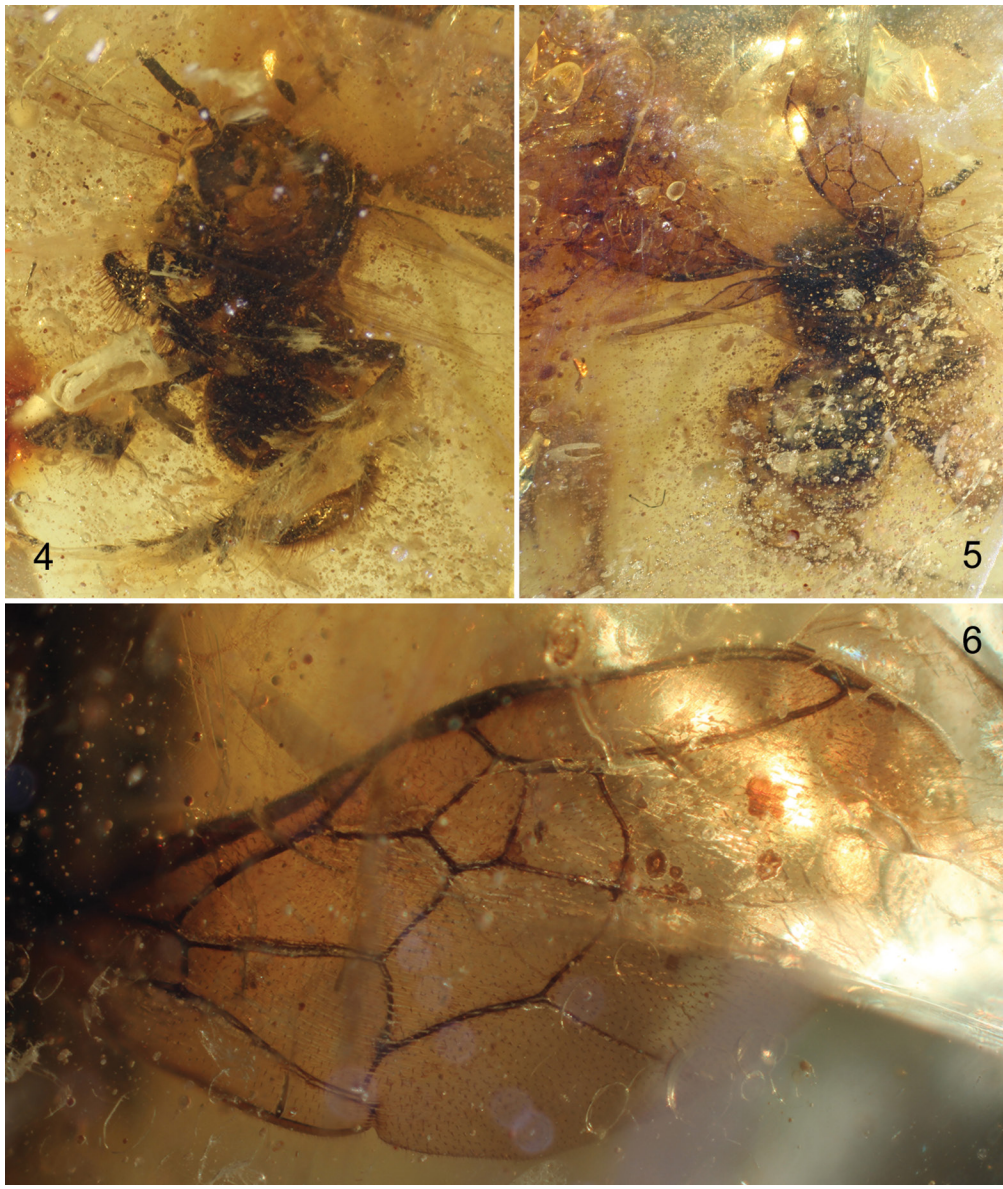
ETYMOLOGY: The specific epithet refers to the Indian State of Gujarat, from which the amber originates.

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
ZooBank: urn:lsid:zoobank.org:act:696E7ECF-DBFF-42A3-BF99-E2B44CC4D13A
(Figs. 4–11)

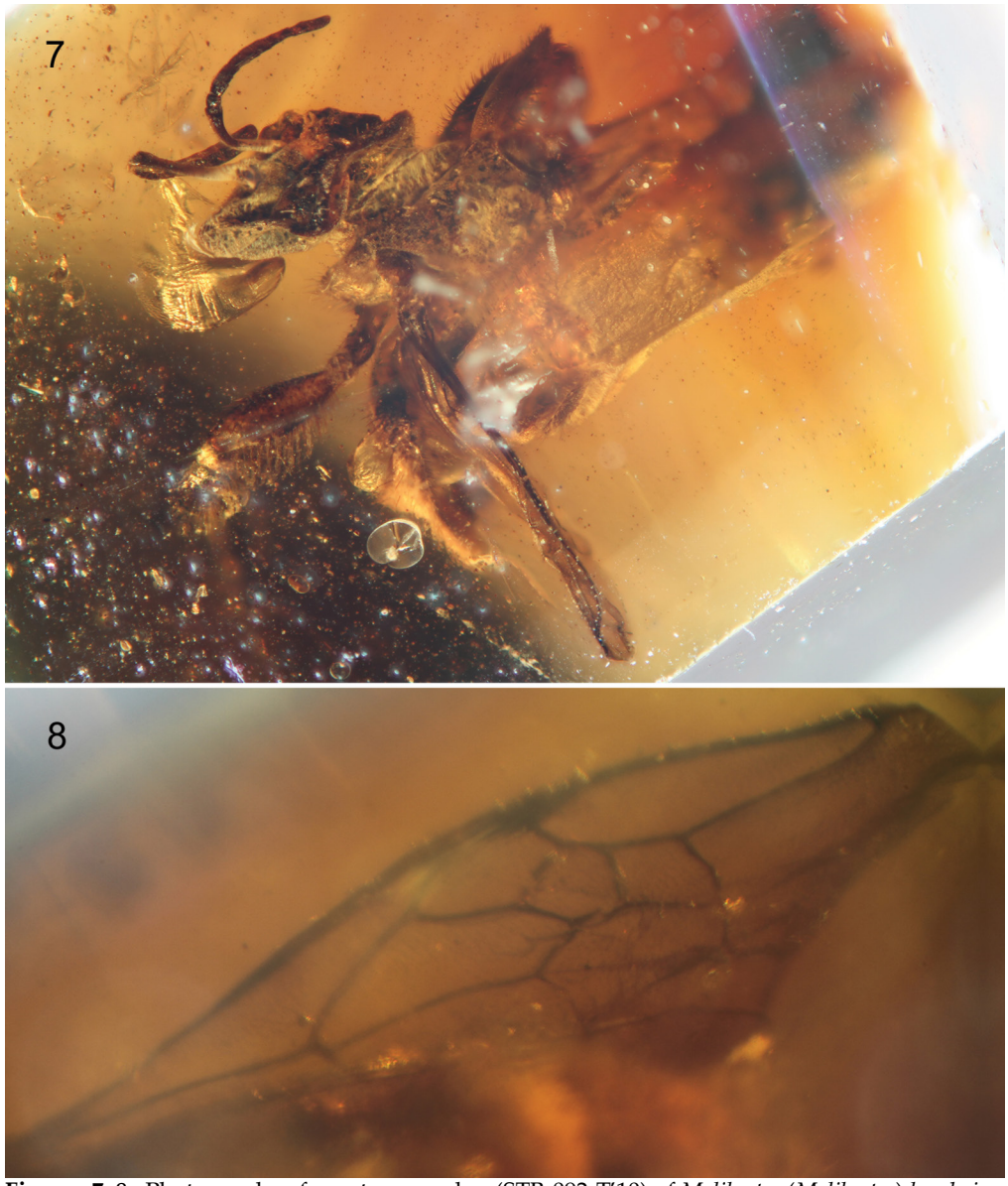
DIAGNOSIS: Differs from *M. gujaratensis* in having shorter mandibles, presence of 1rs-m (absent in *M. gujaratensis*); marginal cell broader and not tapering along its length; discal and subdiscal cells somewhat longer than high (around 1.6 times).

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



Figures 4–6. Photographs of holotype worker (AMNH Tad-272-A) of *Melikertes* (*Melikertes*) *kamboja*, new species. **4.** Frontal view of specimen as preserved. **5.** Dorsal oblique view. **6.** Detail of forewing.

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,

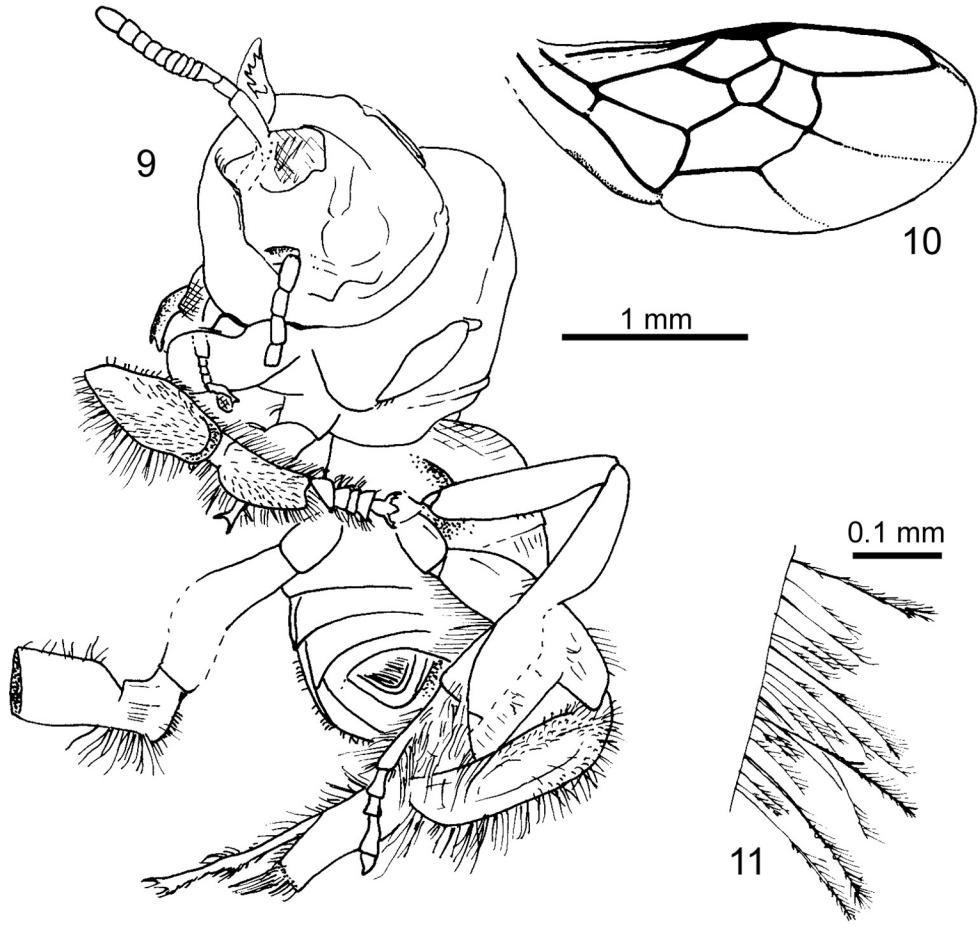


Figures 7–8. Photographs of paratype worker (STB-092-T'10) of *Melikertes* (*Melikertes*) *kamboja*, new species. **7.** Dorsal view of specimen as preserved. **8.** Detail of forewing.

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).



Figures 9–11. Holotype worker (AMNH Tad-272-A) of *Melikertes* (*Melikertes*) *kamboja*, new species. **9.** Sketch of specimen as preserved. **10.** Detail of forewing. **11.** Detail of metabasitarsal setae.

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-Arayan 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: Gujurat, 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

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 eusocial 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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REFERENCES

Berry, E.W. 1931. An insect-cut leaf from the Lower Eocene. *American Journal of Science, Series 5* 21(124): 301–304.

Brooks, H.K. 1955. Healed wounds and galls on fossil leaves from the Wilcox deposits (Eocene) of western Tennessee. *Psyche* 62(1): 1–9.

Engel, M.S. 1998. A new species of the Baltic amber bee genus *Electrapis* (Hymenoptera: Apidae). *Journal of Hymenoptera Research* 7(1): 94–101.

Engel, M.S. 2001a. A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). *Bulletin of the American Museum of Natural History* 259: 1–192.

Engel, M.S. 2001b. Monophyly and extensive extinction of advanced eusocial bees: Insights from an unexpected Eocene diversity. *Proceedings of the National Academy of Sciences, U.S.A.* 98(4): 1661–1664.

Engel, M.S. 2004. Geological history of the bees (Hymenoptera: Apoidea). *Revista de Tecnologia e Ambiente* 10(2): 9–33.

Engel, M.S. 2008. A new species of *Ctenoplectrella* in Baltic amber (Hymenoptera: Megachilidae). *Acta Zoologica Academiae Scientiarum Hungaricae* 54(4): 319–324.

Engel, M.S., & S.B. Archibald. 2003. An Early Eocene bee (Hymenoptera: Halictidae) from Quilchena, British Columbia. *Canadian Entomologist* 135(1): 63–69.

Engel, M.S., & C.D. Michener. 2013. A minute stingless bee in Eocene Fushan amber from northeastern China (Hymenoptera: Apidae). *Journal of Melittology* 14: 1–10.

Engel, M.S., & E.E. Perkovsky. 2006. An Eocene bee in Rovno amber, Ukraine (Hymenoptera: Megachilidae). *American Museum Novitates* 3506: 1–12.

Engel, M.S., I.A. Hinojosa-Diaz, & A.P. Rasnitsyn. 2009. A honey bee from the Miocene of Nevada and the biogeography of *Apis* (Hymenoptera: Apidae: Apini). *Proceedings of the California Academy of Sciences, Series 4* 60(3): 23–38.

Engel, M.S., D.A. Grimaldi, V.H. Gonzalez, I.A. Hinojosa-Díaz, & C.D. Michener. 2012. An exomalopsine bee in Early Miocene amber from the Dominican Republic (Hymenoptera: Apidae). *American Museum Novitates* 3758: 1–16.

Engel, M.S., A.D. Pan, & B.F. Jacobs. 2013. A termite from the Late Oligocene of northern Ethiopia. *Acta Palaeontologica Polonica* 58(2): 331–334.

Gonzalez, V.H., & M.S. Engel. 2011. A new species of the bee genus *Ctenoplectrella* in middle Eocene Baltic amber (Hymenoptera, Megachilidae). *ZooKeys* 111: 41–49.

Kotthoff, U., T. Wappler, & M.S. Engel. 2011. Miocene honey bees from the Randeck Maar of southwestern Germany (Hymenoptera, Apidae). *ZooKeys* 96: 11–37.

Kotthoff, U., T. Wappler, & M.S. Engel. 2013. Greater past disparity and diversity hints at ancient migrations of European honey bee lineages into Africa and Asia. *Journal of Biogeography* 40(10): 1832–1838.

Labandeira, C.C. 2002. Paleobiology of middle Eocene plant-insect associations from the Pacific Northwest: A preliminary report. *Rocky Mountain Geology* 37: 31–59.

Michener, C.D. 2007. *The Bees of the World* [2nd Edition]. Johns Hopkins University Press; Baltimore, MD; xvi+[i]+953 pp., +20 pls.

Michez, D., A. Nel, J.-J. Menier, & P. Rasmont. 2007. The oldest fossil of a melittid bee (Hymenoptera: Apiformes) from the Early Eocene of Oise (France). *Zoological Journal of the Linnean Society* 150(4): 701–709.

Michez, D., M. Vanderplanck, & M.S. Engel. 2012. Fossil bees and their plant associates. In: Patiny, S. (Ed.), *Evolution of Plant-Pollinator Relationships*: 103–164. Cambridge University Press; Cambridge, UK; xv+477+[6] pp.

Nascimbene, P., & H. Silverstein. 2000. The preparation of fragile Cretaceous ambers for conservation and study of organismal inclusions. In: Grimaldi, D. (Ed.), *Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey*: 93–102. Backhuys Publishers; Leiden, The Netherlands; viii+498 pp.

Ohl, M., & M.S. Engel. 2007. Die Fossilgeschichte der Bienen und ihrer nächsten Verwandten (Hymenoptera: Apoidea). *Denisia* 20: 687–700.

Patiny, S., M.S. Engel, P. Vanmarsenille, & D. Michez. 2007. A new record of *Thaumastobombus andreniformis* Engel 2001 in Eocene amber (Hymenoptera: Apidae). *Annales de la Société Entomologique de France* 43(4): 505–508.

Rust, J., H. Singh, R.S. Rana, T. McCann, L. Singh, K. Anderson, N. Sarkar, P.C. Nascimbene, F. Stebner, J.C. Thomas, M. Solórzano-Kraemer, C.J. Williams, M.S. Engel, A. Sahni, & D. Grimaldi. 2010. Biogeographic and evolutionary implications of a diverse paleobiota in amber from the Early Eocene of India. *Proceedings of the National Academy of Sciences, U.S.A.* 107(43): 18360–18365.

Sarzetti, L.C., C.C. Labandeira, & J.F. Genise. 2008. A leafcutter bee trace fossil from the middle Eocene of Patagonia, Argentina, and a review of megachilid (Hymenoptera) ichnology. *Palaeontology* 51(4): 933–941.

Sarzetti, L.C., P.A. Dinghi, J.F. Genise, E. Bedatou, & M. Verde. In press. Curved fossil bee cells as tools for reconstructing the evolutionary history and palaeogeographical distribution of Diphaglossinae (Apoidea, Colletidae). *Palaeontology*

Wappler, T., & M.S. Engel. 2003. The middle Eocene bee faunas of Eckfeld and Messel, Germany (Hymenoptera: Apoidea). *Journal of Paleontology* 77(5): 908–921.

Wappler, T., T. De Meulemeester, A.M. Aytekin, D. Michez, & M.S. Engel. 2012. Geometric morphometric analysis of a new Miocene bumble bee from the Randeck Maar of southwestern Germany (Hymenoptera: Apidae). *Systematic Entomology* 37(4): 784–792.

Wedmann, S., T. Wappler, & M.S. Engel. 2009. Direct and indirect fossil records of megachilid bees from the Paleogene of central Europe (Hymenoptera: Megachilidae). *Naturwissenschaften* 96(6): 703–712.

Zeuner, F.E., & F.J. Manning. 1976. A monograph on fossil bees (Hymenoptera: Apoidea). *Bulletin of the British Museum (Natural History), Geology* 27(3): 149–268.

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