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# Small and common: the oldest tropical Chrysomelidae (Insecta: Coleoptera) from the lower Eocene Cambay amber of India

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Three new genera and species of flea beetles (Chrysomelidae: Alticini) are described from the lowermost Eocene Cambay amber: *Cambaltica paleoindica* Nadein, gen. et sp. nov., *Protorthaltica setosella* Nadein, gen. et sp. nov., and *Davidaltica cambayensis* Nadein, gen. et sp. nov. These taxa share a zoogeographic affinity with extant Oriental and Afrotropical flea beetle faunas, with similarities to Afrotropical elements interpreted to be a result of Neogene migrations from Laurasia to Africa. The flea beetles within the Cambay amber are characterized by their small body size (1.2–1.9 mm), and the absence or rarity of larger flea beetles in the Cambay amber forest is assumed to be evidence for a progressive increase in the average body size of tropical flea beetles beginning in the early Eocene.

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Key words: Alticini, body size, fossil, new taxa.

LEAF BEETLES (Chrysomelidae) are relatively diverse in Eocene fossil resins worldwide, with 25 genera and 34 species described in the subfamilies Bruchinae, Chrysomelinae, Criocerinae, Cryptocephalinae, Eumolpinae, Galerucinae, Cassidinae and Lamprosomatinae (Santiago-Blay 1994, Nadein *et al.* 2016, Alekseev 2017, Kirejtshuk & Ponomarenko 2017, Nadein & Perkovsky 2018). Until recently, leaf beetle inclusions in Eocene ambers were restricted to extratropical European Lagerstätten such as the lowermost Eocene Oise amber (France), and the upper Eocene Baltic (Gdańsk Bay: Russia, Poland), Rovno (Ukraine), Danish (Denmark) and Bitterfeld (Germany) ambers. In general, Paleocene and early Eocene leaf beetles (Fig. 1, Table 1) are insufficiently investigated, despite being 1.5 times more diverse than Cretaceous records of the family (Nadein & Perkovsky 2018).

The lowermost Eocene Indian Cambay amber represents the only record of tropical Eocene Chrysomelidae worldwide; the first mention of this record was within a list of arthropods collected from Cambay (Rust *et al.* 2010), where ‘Chrysomelidae: Alticinae’ and Staphylinidae (two species of the latter being later

described by Ortega-Blanco *et al.* 2013 and Parker & Grimaldi 2014) were the only recorded beetles.

Cambay amber is found in a number of opencast lignite mines within the state of Gujarat, India, about 30 km northeast of the city of Surat (Fig. 2). The age of the Cambay amber has been estimated at 54.5 Ma based on the presence of age-diagnostic foraminiferans, dinoflagellate cysts and pollen, and chemostratigraphic analyses using dispersed organic carbon ( $\delta^{13}\text{C}$ ) signatures within the sediment and strontium isotopes measured from a variety of proxies (Smith *et al.* 2016 and references therein, Stebner *et al.* 2017a). This makes the Cambay amber 1.5 times older than known upper Eocene European ambers. The Cambay amber formed at a time of expanding modern diversity, at the beginning of the early Eocene climatic optimum (Zakrzewska *et al.* 2018). Before the discovery of the Cambay amber, the oldest insect assemblages closely resembling modern tropical forest faunas were recorded in the middle Miocene Dominican and Mexican ambers (Zherikhin 2002).

To date, most of the published work on the Cambay amber biota have related to the Diptera (Solórzano Kraemer & Evenhuis 2008, Solórzano Kraemer & Wagner 2009, Grimaldi & Singh 2012, Stebner *et al.* 2016, 2017a,b,c, Perkovsky 2017, Kania *et al.* 2018, Zakrzewska *et al.* 2018), although braconid wasps



Fig. 1. Danian–Ypresian (48.6–65.5 Ma) leaf beetle (Chrysomelidae) deposits: 1—Pascapoo Formation, Canada; 2—Okanagan, Canada and USA; 3—Green River Formation, USA; 4—Oise amber, France; 5—Menat, France; 6—Messel, Germany; 7—Arkhara, Russia; 8—Cambay amber, India. Map is modified from Scotese (2014).

(Ortega-Blanco *et al.* 2011), bees (Engel *et al.* 2013), termites (Engel *et al.* 2011a), dustywings (Grimaldi *et al.* 2013a), leptosaldine bugs (Grimaldi *et al.* 2013b), whipspiders (Engel & Grimaldi 2014), scale insects (Vea & Grimaldi 2015) and webspinners (Engel *et al.* 2011b) have also been described in separate papers.

Among the material at our disposal, we have identified four genera of the subfamily Galerucinae within the Cambay amber. One genus, belonging to the tribe Galerucini, is embedded in an amber piece of poor clarity and will be described later. In this paper, we describe three new genera of Alticini, which represent the oldest tropical leaf beetles in the fossil record, and the first fossil leaf beetles recorded from the Oriental region.

## Material and methods

This study is based on six specimens of Chrysomelidae from the lower Eocene Cambay amber. Amber specimens were all collected from the Tadkeshwar lignite mine in Gujarat State, India, and are sourced from the lower Ypresian Cambay Formation.

Specimen photographs were taken with a Leica M205C stereomicroscope and a Leica DFC 450 digital camera. Morphological terminology follows Nadein & Beždek (2014).

The type material described in the present paper was received from D. Grimaldi [American Museum of Natural History (AMNH), New York, USA], and will

be deposited in the amber collection of the Birbal Sahni Institute of Paleobotany, Lucknow, India.

## Systematic paleontology

Order COLEOPTERA Linnaeus, 1758  
 Suborder POLYPHAGA Emery, 1886  
 Family CHRYSOMELIDAE Latreille, 1802  
 Subfamily GALERUCINAE Latreille, 1802  
 Tribe ALTICINI Newman, 1834

**Cambaltica** Nadein, gen. nov.

*LSID.* urn:lsid:zoobank.org:act:3E201BFC-D288-4BF2-939A-B40E2E31143B

*Type species.* *Cambaltica paleoindica* Nadein, sp. nov.

*Etymology.* The genus name combines the name of the Cambay amber with *Altica*, the type genus of the tribe and a common suffix in a number of Alticini generic names. Gender feminine.

*Diagnosis.* The new genus is characterized by a modified metatibia with tarsal articulation shifted proximally from the tibial apex.

Few flea beetle genera have such modified metatibia (with medial or subapical position of metatarsus): the extant genera *Aphthonoides* Jacoby, 1885

Table 1. Paleocene and early Eocene leaf beetles (Chrysomelidae).

Species	Locality	Age	Reference
<i>Donacia anetae</i> Bieńkowski, 2015 (Donaciinae)	Arkharo, Amur Region, Russia	Early Paleocene	Bieńkowski 2015
<i>Donacia wightoni</i> Askevold, 1990 (Donaciinae)	Pascapoo Fm., Blackfalds, Alberta, Canada	Middle–Late Paleocene	Askevold 1990
' <i>Altica</i> ' <i>dryophyllorum</i> Piton, 1940 (Galerucinae)	Menat, France	Late Paleocene	Piton 1940
<i>Clytrina eocenica</i> Piton, 1940 (Clyrinae)	Menat, France	Late Paleocene	Piton 1940
<i>Cryptocephalus minusculus</i> Piton, 1940 (Clyrinae)	Menat, France	Late Paleocene	Piton 1940
Seed beetles (Bruchinae: Pachymerini), undescribed	Okanagan Highlands (Canada and USA)	Early Eocene	Archibald <i>et al.</i> 2014
<i>Chrysomela titana</i> (Meunier, 1921) [' <i>Lina</i> '] (Chrysomelinae)	Messel, Germany	Early Eocene	Meunier 1921
<i>Eosacantha delocranoides</i> Chaboo & Engel, 2009 (Cassidinae)	Green River Formation (Colorado, USA)	Early Eocene	Chaboo & Engel 2009
<i>Denaesaspis chelonopsis</i> Chaboo & Engel, 2009 (Cassidinae)	Green River Formation (Colorado, USA)	Early Eocene	Chaboo & Engel 2009
<i>Cryptocephalus vetustus</i> Scudder, 1878 (Cryptocephalinae)	Green River Formation (Wyoming, USA)	Early Eocene	Scudder 1878
<i>Aoriopsis eocenicus</i> Moseyko <i>et al.</i> , 2010 (Eumolpinae)	Oise amber, France	Early Eocene	Moseyko <i>et al.</i> 2010
<i>Acolaspoides longipes</i> Moseyko <i>et al.</i> , 2010 (Eumolpinae)	Oise amber, France	Early Eocene	Moseyko <i>et al.</i> 2010
<i>Crepidocnema yantarica</i> Moseyko <i>et al.</i> , 2010 (Galerucinae)	Oise amber, France	Early Eocene	Moseyko <i>et al.</i> 2010
<i>Cambaltica paleoindica</i> Nadein sp. nov. (Galerucinae)	Cambay amber, Gujarat, India	Early Eocene	Present paper
<i>Davidaltica cambayensis</i> Nadein sp. nov. (Galerucinae)	Cambay amber, Gujarat, India	Early Eocene	Present paper
<i>Protorthaltica setosella</i> Nadein sp. nov. (Galerucinae)	Cambay amber, Gujarat, India	Early Eocene	Present paper

(Oriental region), *Bechynella* Biondi & D'Alessandro, 2010 (Afrotropical region), *Chanealtica* Konstantinov, 2016 (Bolivia), *Metroserrapha* Bechyné, 1958 (Madagascar and the Mascarene Islands), *Serraphula* Jacoby, 1897 (Afrotropical region) and *Psylliodes* Berthold, 1827 (worldwide), and the extinct genus *Psyllototus* Nadein, 2010 from the Rovno, Danish and Baltic ambers. *Cambaltica* shares two key characters with all these genera except *Chanealtica*: shifted (pre-apical) metatarsal articulation and puncto-striate elytra. The new genus differs from *Psylliodes* in having 11 antennomeres and in the structure of metatarsomeres 1 and 2: in *Psylliodes*, metatarsomere 1 is long, thin and asetose, and metatarsomere 2 is half the length of metatarsomere 1, whereas in *Cambaltica* metatarsomere 1 evidently shorter, broader and densely setose, and metatarsomere 2 is 0.4 length of metatarsomere 1. The new genus differs from *Psyllototus* and *Metroserrapha* in the position of metatarsal articulation (closer to the apex), in metatarsomere 1 being shorter, thicker and ventrally densely setose, and in lacking an elongated metatarsomere 2. From *Chanealtica*, *Cambaltica* differs in its puncto-striate elytra, and in the metatarsal

attachment being closer to the metatibial apex. From *Serraphula* and *Aphthonoides*, *Cambaltica* differs in having a short, simple, unserrated apical spur, and shorter metatarsomere 1. The new genus differs from *Bechynella* in the shorter apical spur on the metatibia and much shorter metatarsomere 1.

**Description.** Body robust, moderately convex, cuticle glabrous. Head with vertex relatively narrow, frontal ridge present; antennal sockets located between eyes, close to both eye margin and frontal ridge; eyes large and strongly convex. Antennae more than half body length, with 11 filiform antennomeres.

Pronotum transverse, width 1.2 times length, pronotum width 0.91 of combined elytra at base, pronotum 0.42 of elytra length, lateral margins moderately rounded, distinctly explanate, anterior and posterior angles of pronotum each with one setiferous pore, pronotum surface punctate.

Elytra moderately elongate, length 1.6 times width, lateral margins explanate; elytral apices rounded; humeral calli developed and raised, elytron surface punctate, punctures arranged in partially confused rows.

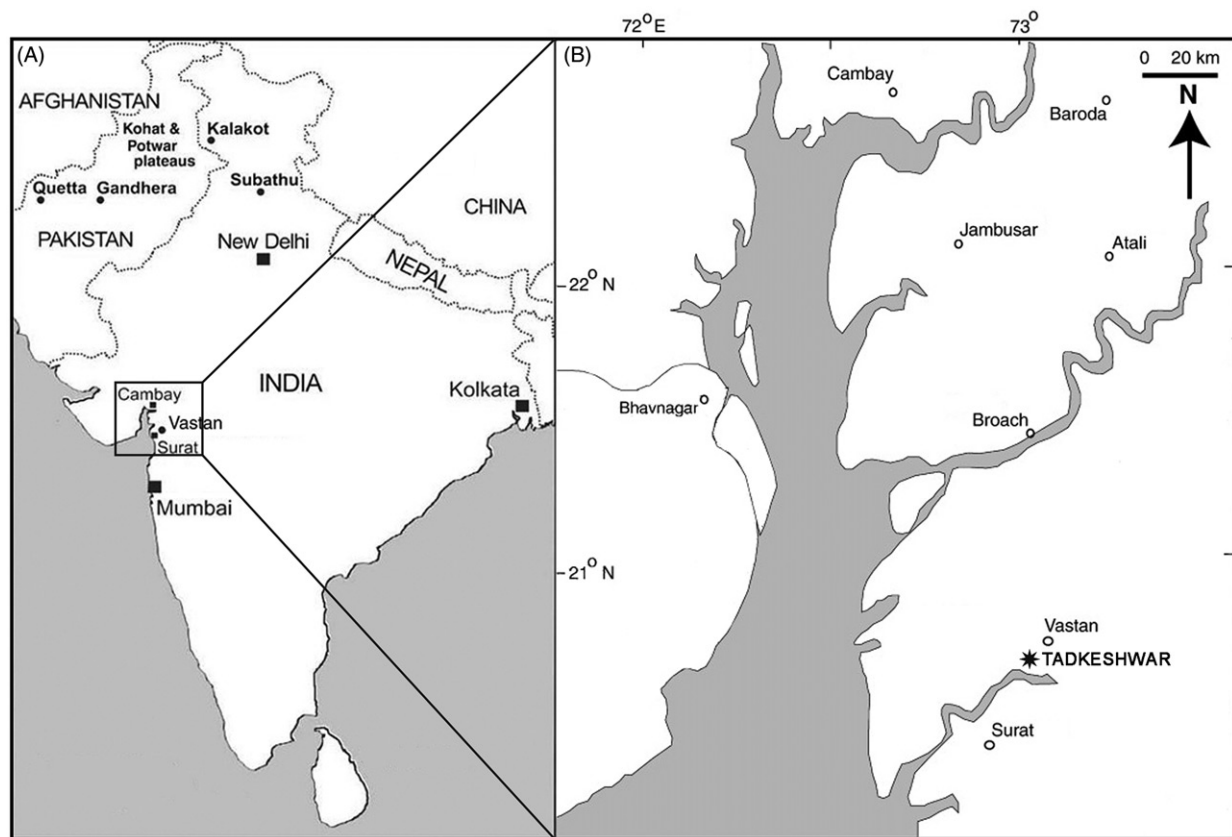


Fig. 2. Locality of the Cambay amber deposit (Tadkeshwar lignite mine): **A**, Within India as a whole; **B**, Within the Gulf of Cambay.

*Epipleura* broadest at base, gradually narrowing towards elytral apices, visible from lateral view. Hind wings fully developed.

Legs relatively short and thick, fore and middle tibiae distinctly thickened towards apex, tarsal claws appendiculate. Metafemur swollen; articulation of metatarsi shifted proximally, about 0.25 tibia length from apex; length of metatarsomere 1 is 0.3 metatibia length, not longer than following tarsomeres combined, moderately broad, ventrally densely setose; metatarsomere 2 about 0.4 length of metatarsomere 1, apical spur of metatibia simple, unserrated.

**Cambaltica paleoindica** Nadein, sp. nov. (Fig. 3)

*LSID.* urn:lsid:zoobank.org:act:5D26F742-1700-4315-ADB8-A5F1339A45D1

*Etymology.* The species name combines the prefix ‘paleo-’ (from Greek: *palaios*, *palaeo-*, meaning ‘ancient’) and India, the country of origin of the Cambay amber.

*Holotype.* Amber specimen triangular in shape, light yellowish-brown, transparent; specimen no. Tad-265, label data: ‘Amber: India: Gujarat, Tadkeshwar lignite mine, Cambay Form. (Paleo–Eocene), 21°21.400’N 73°4.532’E, Jan 17–22, 2010 Grimaldi/Nascimbene/

Singh/Luzzi/Rana/Sarkar’, ‘Tad-265: \* Coleoptera Chrysomelidae’.

*Paratype.* Amber specimen irregularly rectangular in shape, yellowish-brown, transparent; specimen no. Tad-370, otherwise same label information as for the holotype.

*Diagnosis.* Body glabrous, frontal ridge narrow, eyes large, antennae filiform, pronotum weakly convex, setae on pronotal angles equal length to lateral margin, punctures on pronotal surface large, elytra convex, elytral punctures organized in rows, metatibia broadened distally in lateral view.

*Description.* Body glabrous, blackish with strong lustre, body length 1.7–1.9 mm, width 0.9 mm. Head nearly as broad as pronotum; head vertex short and narrow, apparently convex; frontal ridge narrow and raised. Antennomere 1 narrow, same length as following two antennomeres combined; antennomere 2 about 0.5 length of antennomere 1; antennomeres 3–10 thin, length about 2.0–2.5 times width; antennomere 11 longer than preceding segments, comparatively narrow, pointed apically.

Pronotum weakly convex, lateral margins smooth, anterior and posterior angles neither swollen nor extended beyond lateral margins; setae on pronotal

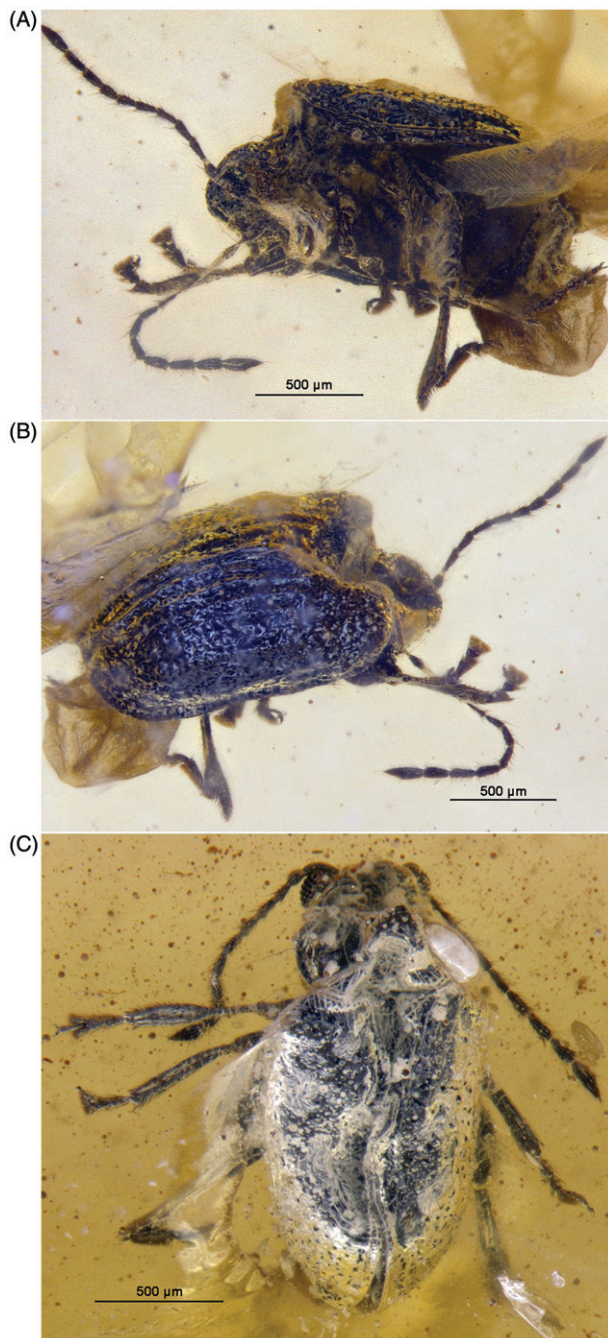


Fig. 3. *Cambaltica paleoindica* Nadein gen. et sp. nov. **A**, **B**, Holotype, specimen no. Tad-265: **A**, ventrolateral view; **B**, Dorsolateral view. **C**, Paratype, specimen no. Tad-370, dorsal view.

angles equal length to lateral margin, punctures on pronotal surface large, deep and dense, equal in size to those developed on the elytra, distance between punctures variable.

Elytra convex, lateral margins subparallel, not rounded; punctures on surface large and deep, comparatively dense, well organized into rows, distance between punctures variable, surface between punctures apparently smooth; seven visible interstices between rows of punctures, interstices convex and with confused punctuation.

Metatibia straight, distinctly broadened distally in lateral view, coinciding with point of tarsal articulation; tibia narrowed apically, lateral margins of dorsal surface with a row of long, acute, thick and dense bristles reaching tarsal articulation in apical third, apical spur small. Metatarsomere 1 straight, length about 4 times width, and gradually widening apically.

**Protorthaltica** Nadein, gen. nov.

*LSID.* Urn:lsid:zoobank.org:act:39488DD4-C014-4D7D-926C-0977B4009703

*Type species.* *Protorthaltica setosella* Nadein, sp. nov.

*Etymology.* The genus name combines the Ancient Greek prefix ‘prōto-’, meaning ‘foremost’ or ‘earliest form of’, with the genus name *Orthaltica*, which the new genus resembles. Gender feminine.

*Diagnosis.* The new genus is similar to the extant genera *Orthaltica* Crotch, 1873 (Palearctic, Nearctic, Oriental, Australian regions), *Hirtiaphthona* Kimoto, 2000 (Thailand) and *Epitrix* Foudras, 1860 (world-wide), and the extinct genus *Sucinolivolia* Bukejs *et al.*, 2015 from the upper Eocene Baltic amber. It differs from all these genera in its narrower and more transverse pronotum, the possibly confused elytron punctures, and the very long seta set in the angles of the pronotum. *Protorthaltica* also differs from *Epitrix* in the apparently sparser but longer pubescence of the elytra. It differs from *Orthaltica* in the supposed absence of long setae on the head vertex, and from *Hirtiaphthona* in the confused elytron punctures. It differs from *Sucinolivolia* in the pointed last palpomere of the maxillary palpi, apparently confused elytron punctures, more narrow antennomeres, and in having tarsomere 3 of the pro- and mesotarsi not bilobed.

*Description.* Body slender, not convex. Base of head slightly narrower than pronotum width, eyes large. Antennae less than half body length, with 11 unmodified, filiform antennomeres. Last maxillary palpomere large and pointed.

Pronotum transverse, width about 1.5 length, setose; pronotum width about 0.71 of combined elytra at their base and about 0.27 elytra length; anterolateral and posterolateral callosities weakly projecting, each bearing a very long seta.

Elytra moderately elongate (length 1.3 times width), not strongly convex, broadest distal of mid-length; lateral margins nearly vertical, surface setose; humeral calli well developed and projecting beyond elytra extent, punctuation apparently confused. Hind wings fully developed. Scutellum small.

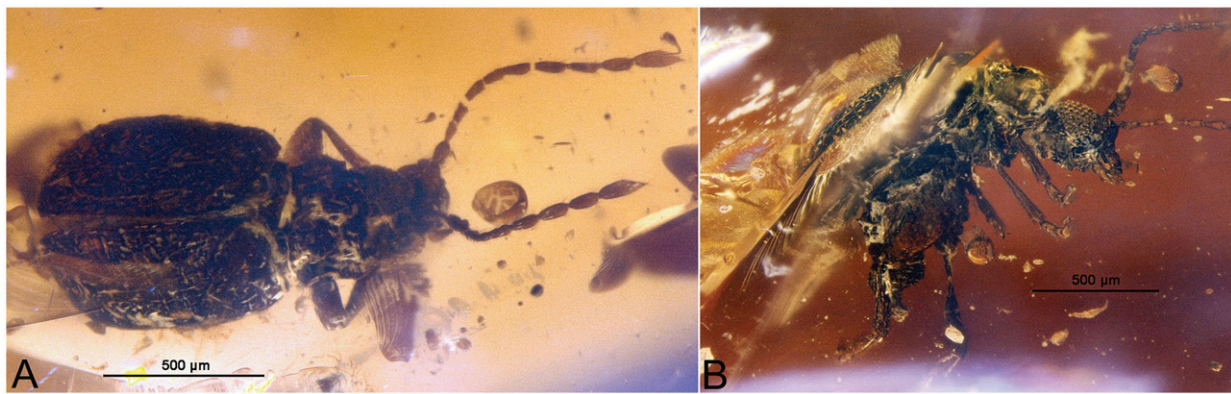


Fig. 4. *Protorthaltica setosella* Nadein gen. et sp. nov., holotype, specimen no. Tad-89: **A**, Dorsal view; **B**, Lateral view.

Profemora weakly broadened, metafemora strongly swollen. Pro- and mesotibiae thin, gradually and very weakly widening towards apex, dorsal surface of pro- and mesotibiae distinctly setose, without visible carinae or grooves along entire flank; tibial apices simple, rounded, without denticles, setae, excavations or ridges; tibial spur small and simple; tarsal claws appendiculate. Metatibia straight, gradually widened towards apices, apex with external row of short, dense bristles; tarsomere 3 of fore and middle legs not bilobed; metatarsomere 1 broad, shorter than following tarsomeres combined, ventral side densely setose.

***Protorthaltica setosella*** Nadein, sp. nov. (Fig. 4)

*LSID.* Urn:lsid:zoobank.org:act:614F311B-637B-4268-84B2-A22046D792DA

*Etymology.* The specific epithet refers to the setose dorsum of the new species.

*Holotype.* Amber specimen rectangular, brownish-yellow, moderately transparent; specimen no. Tad-89, label data: ‘Amber: India: Gujarat, Tadkeshwar lignite mine, Cambay Form. (Paleo–Eocene), 21°21.400’N 73°4.532’E, I/7–12/09 Grimaldi & Nascimbene’.

*Diagnosis.* Body slender, eyes large, pronotum covered with short and sparse setae, pronotal anterolateral and posterolateral callosities each bearing a long seta, elytra covered with medium-length, semi-erect setae, elytral punctures apparently confused, hind wings developed, metafemora strongly swollen, metatibial apex with external row of short and dense bristles.

*Description.* Dorsum blackish, legs and antennae yellowish-brown; length 1.2 mm, width 0.6 mm. Antennomere 1 moderately broadened, shorter than the following two antennomeres combined; antennomere 2 slightly broadened, shorter and narrower than antennomere 1; antennomeres 3–10 narrow, about 2.0–2.5

times longer than wide; antennomere 11 comparatively large, about 3 times longer than wide, pointed apically.

Pronotal surface covered with short and sparse setae, surface of pronotum strongly deformed, probably punctate.

Elytral surface deformed, probably densely punctate, lateral margin of elytra moderately rounded, elytral surface covered with moderately sparse and medium-length, semi-erect setae; punctures apparently not organized into striae.

Metafemora swollen, length 1.6 times width; tarsomere 1 of fore- and mid-legs somewhat broader and longer than following tarsomeres.

***Davidaltica*** Nadein, gen. nov.

*LSID.* urn:lsid:zoobank.org:act:0EEA10E1-FBE0-4BAF-8F8C-0A493226DCA4

*Type species.* *Davidaltica cambayensis* Nadein, sp. nov.

*Etymology.* The genus name combines the proper name ‘David’ (the name of the amber’s collector David Grimaldi (AMNH), renowned specialist on flea beetles David Furth (Smithsonian Institution), and the son of the junior author) with the genus name *Altica*. Gender feminine.

*Diagnosis.* The new genus differs from the extant *Tegyrius* Jacoby, 1887 (South India and Sri Lanka) in having larger and denser punctures on both the elytra and pronotum, more regular rows of elytral punctures and convex intervals between these rows, straight metatibia, and setose elytral apices. It differs from *Bikasha* Maulik, 1931 (Oriental, Afrotropical and southeastern Palearctic regions) in the much larger punctures on the pronotum, setose elytral apex, narrower metatibial apex and the much broader metatarsomere 1. It differs from *Pratima* Maulik, 1931 (Seychelles and Mascarene Islands) in having more regular rows of punctures on the elytra with convex intervals between the rows, in

its longer and broader metatarsomere 1, and setose elytral apices.

*Description.* Body short, elongate, not convex, mostly glabrous. Head with frontal ridge; head width including eyes about equal to pronotal width; antennal sockets placed between eyes; maxillary palpi large, long. Eyes large, round, strongly convex. Antennae with 11 filiform antennomeres, half body length.

Pronotum transverse, distinctly narrower than combined width of the elytra at their base; anterior and posterior margins straight, anterior half of pronotum broader than posterior, lateral margin sinuate with lateral edge smooth; anterior and posterior angles of pronotum each with setiferous pore forming small callosity; punctate pronotal surface.

Elytra weakly convex, moderately elongate, punctures on elytra arranged in partially confused rows, elytral apices setose. Humeral calli well developed. Hind wings fully developed.

Legs comparatively thin; pro- and mesotibiae straight; metafemora distinctly swollen, metatibia straight, outer margin of apex with a row of long, dense bristles; metatibial apical spur small and pointed. Metatarsomere 1 long, about half of tibia length on this leg, ventral side densely setose, tarsal claws appendiculate.

**Davidaltica cambayensis** Nadein, sp. nov. (Fig. 5)

*LSID.* urn:lsid:zoobank.org:act:53579849-1578-4221-88E4-4A2E7DCCD99D

*Etymology.* The species epithet refers to the name of the amber deposit.

*Holotype.* Amber specimen rectangular, light yellowish-brown, transparent; specimen no. Tad-342, label data: ‘Amber: India: Gujarat, Tadkeshwar lignite mine, Cambay Form. (Paleo–Eocene), 21°21.400’N 73°4.532’E, Jan 17–22, 2010 Grimaldi/Nascimbene/Singh/Luzzi/Rana/Sarkar’, ‘Tad-342: \*1 Coleoptera: Alticinae (Chrys.)’.

*Paratype 1.* Specimen no. Tad-258, otherwise same label data as for the holotype.

*Paratype 2.* Specimen no. Tad-87, label data: ‘Amber: India: Gujarat, Tadkeshwar lignite mine, Cambay Form. (Paleo–Eocene), 21°21.400’N 73°4.532’E, 1/7–12/09 Grimaldi & Nascimbene’.

*Syninclusions.* An adult fulguroid (Hemiptera), ca 4 mm length, is embedded in the same piece of amber as paratype 2.

*Diagnosis.* Body short, not convex, glabrous, head small, frontal ridge narrow and raised, pronotum

densely punctate, pronotal callosities each with a long setae, elytral punctures large, arranged in rows, elytral apices covered with sparse and erect setae, hind wings fully developed, metatibial outer margin of apex with a row of long, dense bristles.

*Description.* Body blackish with metallic lustre dorsally, ventral side blackish, legs and antennae brownish; length of holotype 1.5 mm, width 0.5 mm. Head (Fig. 5D) small, vertex narrow, frontal ridge narrow and raised; penultimate maxillary palpomere large and thick, last palpomere large and apically pointed. Antennomere 1 thick, length about 3 times width; antennomere 2 swollen, as broad as antennomere 1 but 0.4–0.5 length; antennomeres 3–10 narrow and long, length about 2–3 times width; antennomere 11 length 3 times width, apex elongate to pointed (Fig. 5D).

Pronotum weakly convex, length about 0.38 of elytra; densely punctate, with pronotal punctures large and deep, nearly as large as elytral punctures, distance between punctures smaller than puncture diameter; anterolateral and posterolateral callosities not protruding, each callosity with a long seta, setal length equal to that of pronotal lateral margin.

Elytral punctures dense, large and deep, arranged in rows (Fig. 5C); intervals between puncture rows convex, distance between rows about equal to puncture diameter; margin of elytral apices rounded, elytral apices covered with rather sparse, moderately long, erect setae.

Pro- and mesotibiae gradually and weakly widening apically, densely setose. Metafemur length about 2.5 times width, hind tibia (Fig. 5E) thickened and gradually widening towards apex; apical spur small and pointed, metatarsomere 1 broad, length about 3 times width, metatarsomere 2 about 0.3 length of metatarsomere 1.

## Discussion

### *Zoogeographic connections*

Stebner *et al.* (2017c) indicated that, of the arthropods within the Cambay amber, the whipspiders (Amblypygi: Paracharontidae) and webspinners (Embioptera) show biogeographic affinities to Africa and Africa and South America, respectively. However, a representative of the Paracharontidae is also known from the Late Carboniferous of USA (Mazon Creek, Cape Breton, Coseley localities; Engel & Grimaldi 2014), and the single extant species—*Paracharon caecus* Hansen, 1921, an enigmatic, blind taxon living in termite nests within Guinea-Bissau (Engel & Grimaldi 2014)—can not be used as evidence for the family’s Gondwanan origin.

Within the Embioptera, the genus *Kumarembia* Engel *et al.*, 2011b of the family Scelembiidae was considered a Gondwanan element within the Indian



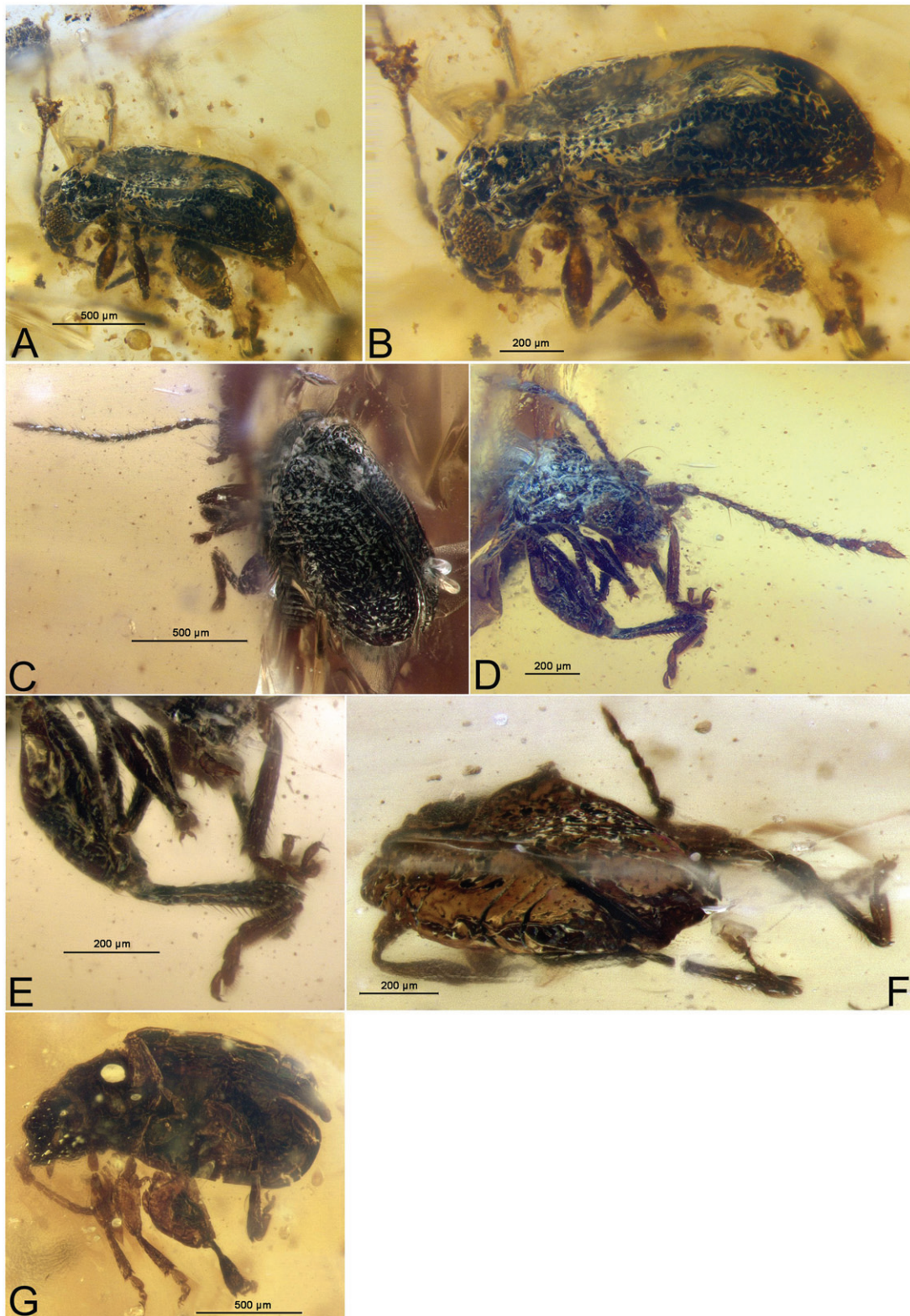


Fig. 5. *Davidaltica cambayensis* Nadein gen. et sp. nov. A, B, Holotype, specimen no. Tad-342, lateral view. C–E, Paratype, specimen no. Tad-258: C, Dorsolateral view; D, Anterolateral view; E, Middle and hind legs. F, G, Paratype 2, specimen no. Tad-87: F, Posterior view; G, Ventrolateral view.

amber fauna based on the current distribution of this family in Central and East Africa and South America (Engel *et al.* 2011b). However, we disagree with this interpretation based on two reasons: first, Scelembiidae

and Pachylembiidae were recently synonymized (Miller *et al.* 2012), and fossil members of the latter family (and specifically of the genus *Sorellembia* Engel & Grimaldi, 2006) were previously recorded from the

Burmese amber (Engel *et al.* 2011b) and the mid-Cretaceous of Laurasia (Sevastjanova *et al.* 2016, Metcalfe 2017), with representatives of the modern genus *Pachylembia* Ross, 1984 inhabiting the pine–oak zone of Jalisco and Guerrero (Mexico). Second, the Indian continent separated from Madagascar, where only introduced webspinners are known, about 90 million years ago (Ross 2003). Of course, all Cretaceous Madagascar's webspinners could have become extinct, but we consider this highly unlikely, and instead suggest that the dispersal of webspinners to Gondwana took place after the supercontinent split into its eastern and western parts (see details in Martynova *et al.* 2019). As a result, it appears the Scelembiidae should be added to the extensive list of families presently known only from the southern continents, but having had a Laurasian or worldwide distribution in the Cretaceous (see discussion in Gumovsky *et al.* 2018).

The flea beetles (subfamily Galerucinae: Alticini) recorded here from the Cambay amber demonstrate some affinity with modern Oriental and Afrotropical faunas, which themselves share a high number of genera (27% according to Biondi & D'Alessandro 2012). *Cambaltica* is morphologically similar to *Bechynella* and *Metroserrapha* from the Afrotropical region (Biondi & D'Alessandro 2010), whereas *Protorthaltica* is similar to *Hirtiaphthona* (of the Oriental region) and *Orthaltica* (of the Afrotropical, Australian and Nearctic regions, with a majority of species in the Oriental region), and *Davidaltica* most closely resembles *Tegyrius* (South India, Sri Lanka), *Bikasha* (from the southeastern Palearctic, Oriental and Afrotropical regions) and *Pratima* (Seychelles and Mascarene Islands). No connections to flea beetles from modern Neotropical faunas or European Eocene ambers were found in this assemblage.

Although Africa was originally part of Gondwana and remained south of the Tethys Sea after the supercontinent's break-up, its paleobiogeographical history appears to have been distinct from that of both Gondwana and Laurasia as early as the earliest Cretaceous, with its isolation broken intermittently by discontinuous filter routes linking the continent to Laurasia (Gheerbrant & Rage 2006). It appears that the Alticini originated much later than the Early Jurassic separation of Gondwana and Laurasia, and the only Cretaceous record of the Alticini (and the only other galerucine record) is from Laurasia (Nadein & Perkovsky 2018). The hypothesis of a Gondwanan origin for the Alticini, as suggested by Scherer (1988), therefore contradicts the paleontological data and creates difficulties in explaining aspects of the modern fauna, such as the scarcity of the Alticini in Australia (Scherer 1988). Although the Afrotropical region shares the highest number of flea beetle genera with the Oriental region (26 of 102 genera; Biondi & D'Alessandro 2012), we strongly disagree with the

hypothesis of a Gondwanan origin for these shared genera (as stated in Biondi & D'Alessandro 2012, p. 80). We instead suppose that the similarity of the Afrotropical and Oriental flea beetle faunas is a result of Miocene dispersal from Laurasia to Africa, thereby making the Alticini within the Cambay amber of Laurasian origin.

Both Cretaceous galerucines (*Taimyraltica* Nadein, 2018 from Russia, and an undescribed form from the Canadian amber; R. McKellar, pers. comm. 2017) are from the northern hemisphere ('*Baeomorpha* realm', as proposed by Gumovsky *et al.* 2018); we suppose a northern origin for the tribe based on the distinctly Laurasian distribution of these Cretaceous galerucines.

#### *Why are alticines so common in the Cambay amber?*

The Cambay amber differs strongly from upper Eocene European ambers in both the abundance and diversity of alticines, with six alticine specimens in 700 Cambay amber arthropods (Rust *et al.* 2010). Meanwhile, a representative Rovno amber collection at the Schmalhausen Institute of Zoology (Kyiv) contains seven alticines within the 36 000 arthropods determined to the ordinal level (as of September, 2018); in the Copenhagen University's representative collection of Danish amber there is one alticine among a total of 7609 arthropods (Larsson 1978); in Giecwicz representative collection of Baltic amber (housed in Muzeum Ziemi, Warszawa) contains one alticine among 7954 arthropods (Kosmowska-Ceranowicz 2001), and in the large representative Baltic amber collection of the Borissiak Paleontological Institute (Moscow), no alticines are found (unpublished data). All in all, alticines are at least 44–68 times more common in the Cambay amber than in upper Eocene ambers, which we believe is due to a combination of two factors: paleoecological implications and size biases.

*Paleoecological implications.* The first factor is trophic and spatial localization, which appears to have increased the probability of capture and preservation. The source of the Cambay amber resin is considered to be a member of the Dipterocarpaceae, an important forest-forming family of mainly tropical, lowland rainforest trees (Rust *et al.* 2010), which likely formed part of an angiosperm-dominated Indian amber forest (Singh *et al.* 2015). Extant leaf beetles are reported to be associated trophically with the Dipterocarpaceae (Momose 2005, Willmer 2011, Kishimoto-Yamada *et al.* 2013), and although it is theoretically possible the Cambay Alticini were feeding on leaves of the resin's source, their abundance is incomparable with the abundance of ambrosia beetles in *Hymenaea* resins (see below) and a direct association is highly unlikely. There may be a consortial link between the Cambay Alticini and the

resin-producing plant if the beetles were feeding on epiphytes growing on the source plant, rather than on the source plant itself.

This idea can be indirectly supported by the relative abundance of flea beetles in the Cambay amber, where more than one species has two or three specimens. This is disproportionately large in comparison with, for example, the Baltic amber, where most leaf beetle species are represented by a single specimen (the recorded exceptions being the eumolpine *Taphioporos carsteni* Bukejs & Moseyko, 2015, and the flea beetles *Psyllototus doeberli* Bukejs & Nadein, 2013, *Crepidodera decolorata* Nadein & Perkovsky, 2010 and *Crepidodera tertiotertiaria* Bukejs *et al.*, 2016). Although it is possible that additional specimens are present, but were not published, it should be remembered that the Baltic amber has an order of magnitude greater taxa diversity and abundance than the Cambay amber fauna. In the Rovno (with more than 40 000 studied inclusions; i.e., at least 55 times more than recorded in the Cambay amber) and Danish amber faunas (see above), all leaf beetle species are represented by single specimens.

Interestingly, no examples of damage attributable to leaf beetles was found among photographs of damaged leaves from the Vastan mine (provided to us by H. Singh, Birbal Sahni Institute of Paleobotany, Lucknow, India); however, no dipterocarp leaves have yet been reported from this site (Singh *et al.* 2015).

Although some small Lepidoptera have been found in the Cambay amber, these might be leaf-mining taxa, based on the discovery of a rhyssipoline braconid, a typical parasitoid of leaf-mining Lepidoptera, in the same amber (Ortega-Blanco *et al.* 2011). Further, Zherikhin (2002, p. 379) stated that: ‘Even when the high level of incompleteness of the lepidopteran fossil record is taken into account, it seems that before the Oligocene the share of endophytic and detritivorous moth taxa were disproportionately large in comparison with the present-day situation, and accordingly the diversification of the families with ectophytic caterpillars occurred mainly in the Oligocene and Miocene’. We consider that if the ectophytic Lepidoptera are indeed rare prior to the Oligocene, as suggested by Zherikhin, the Alticini might have been one of the most important folivorous insects in the early Eocene Cambay amber forest.

*Size biases and leaf beetle abundances in Cenozoic resins.* Solórzano Kraemer *et al.* (2018) indicated that arboreal beetles, particularly the Chrysomelidae, are well represented in recent and fossil resins, as they are attracted to yellow sticky traps and are abundant high up on the trees. Solórzano Kraemer *et al.* (2018) statistically compared natural entrapment in *Hymenaea verrucosa* Gaertner, 1791 (Angiospermae: Fabales: Caesalpinioideae) tree resin in Madagascar with the

assemblage of arthropods trapped by standardized entomological traps around the same tree species at the same localities. Overall, the share of leaf beetles was only 3.6% among all beetles collected in *H. verrucosa* resin, whereas their share of all beetles captured in the yellow sticky traps was 8% (they represent 13% of beetles collected in yellow sticky traps at a height of 1 m; Solórzano Kraemer *et al.* 2018). Similarly, although the leaf beetles are quite diverse in European upper Eocene ambers (Nadein *et al.* 2016, Alekseev 2017, Kirejtshuk & Ponomarenko 2017, Nadein & Perkovsky 2018), they are numerically nearly invisible in terms of the overall fauna (Zherikhin *et al.* 2009). We suppose that one of the reasons for this is a size bias in amber trapping, with this idea corroborated by both the Mexican amber faunal composition and actual paleontological data.

More than 75% of arthropod specimens in the Mexican amber are less than 2 mm long (Solórzano Kraemer *et al.* 2015), with the majority of arthropod specimens between 1 and 2 mm in size (Solórzano Kraemer *et al.* 2015); insects caught in sticky traps within Mexican tropical forests do not differ strongly from this size distribution. Presumably then, the strong underrepresentation of leaf beetles in Madagascar resin can be explained by size biases, as the majority of Madagascar flea beetles are 3.0–8.5 mm in length; only one flea beetle genus (*Metroserrapha*) among the 40 genera known in Madagascar is represented by smaller species of about 1.5 mm length, although the Madagascar species of this genus are not yet described (Biondi & D’Alessandro 2012) and it is unknown whether they occur at the site of this actual paleontological study.

An apparent contradiction to this assumed size bias is the abundance of Platypodinae (ambrosia beetles) in both modern *Hymenaea* resin from Madagascar (82.7% of all beetles captured in the resin; Solórzano Kraemer *et al.* 2018) and Dominican amber (Zherikhin *et al.* 2009). These highly elongate Madagascar ambrosia beetles, identified as belonging to the genus *Mitosoma* Chapuis, 1865, are 3.7–4.0 mm in length (Wood 1993), which is far larger than the average insect captured in the Mexican amber. However, Solórzano Kraemer *et al.* (2018) suggested that *Mitosoma* may have been involved in the production of resin, thereby explaining their high rates of entrapment.

Therefore, we can surmise that the presence of numerous and very small (see below) flea beetles actively moving through the resin trees was very favourable for their entrapment in Cambay amber.

#### *Cambay amber leaf beetles appear very small*

Leaf beetles from a number of amber deposits (excluding Cambay) have average body sizes of 2.1–5.3 mm (Table 2), although the full range of sizes is much wider (Fig. 6). For the taxa-rich upper Eocene (Baltic, Rovno and Danish) ambers, the average leaf beetle is

Table 2. Diversity and body sizes of leaf beetles in major Cenozoic ambers.

Amber	No. of taxa	Size range (mm) (minimum–maximum)	Average size (mm)	Standard deviation
Cambay	4	1.2–1.9	1.55	0.29
Oise	3	2.3–3.6	3.07	0.68
Rovno	6	1.8–2.8	2.15	0.34
Danish	4	2.3–3.5	3.03	0.53
Baltic	22	1.3–7.5	3.65	1.73
Dominican	9	1.5–10.2	5.34	2.65
Rovno–Danish–Baltic (combined)	32	1.3–7.5	3.29	1.56

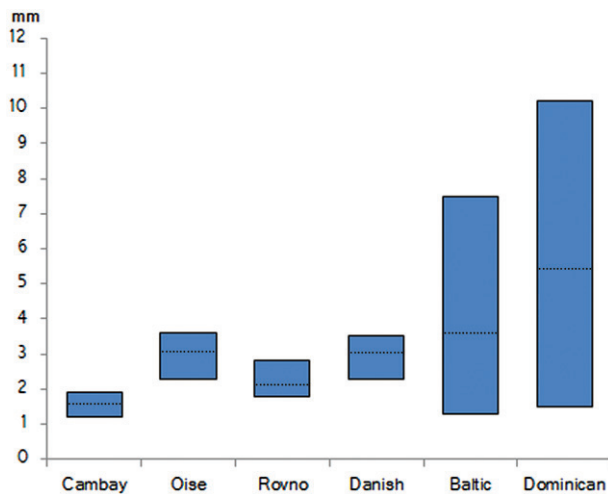


Fig. 6. Comparison of leaf beetle (Chrysomelidae) body lengths (from minimum to maximum) for important Cenozoic ambers; average size marked with dotted line; the species numbers and average specimen sizes for each site are listed in Table 2.

3.29 mm long, which is twice the average length of leaf beetles from the Cambay amber (1.55 mm) and 1.5 times the average length of leaf beetles from the Oise and Cambay ambers (2.2 mm). The normal distribution curve of leaf beetle sizes from the Baltic, Rovno and Danish ambers (Fig. 7) demonstrates that most specimens fall within a relatively narrow range around 2.5–3.5 mm. The shift towards larger sizes in these three younger ambers is also noticeable and generally agrees well with modern size distributions.

Looking more specifically at the subfamily Galerucinae, only two representatives are known from the Cretaceous and none from Paleocene. Although a large (up to 5.5 mm long) flea beetle, '*Altica* *dryophylorum*' (Piton, 1940), has been described from the Paleocene of France (Menat), attribution to this genus appears to be erroneous based on the description and illustration (Piton 1940, pp. 212–213, fig. 79), which shows the presence of puncto-striate elytra and the absence of a longitudinal basal groove on the pronotum. Further, none of the characters in the description allow its reliable classification to the tribe Alticini; however, re-examination of the type material was not possible since the specimen is apparently lost (A. Nel and G. Doitseau, Muséum National d'Histoire Naturelle, Paris, pers. comm. 2018). Both Cretaceous

galerucines (*Taimyraltica* Nadein, 2018 from Russia, and an undescribed form from the Canadian amber; R. McKellar, pers. comm. 2017) are small, with the oldest of these two (the Santonian *Taimyraltica*) only 2 mm long (Nadein & Perkovsky 2018). Like the Cambay galerucines, the only other early Eocene galerucine, *Crepidocnema yantarica* Moseyko *et al.*, 2010 from the Oise amber, is also small at 2.3 mm length. In the late Eocene, the length of the largest flea beetle (*Crepidodera svetlanae* Bukejs, 2014) is only 3.4 mm, and seven of 14 Galerucinae from upper Eocene ambers are 1.35–2.00 mm long. This is similar to the recent northern (high altitude) and montane faunas, which have a higher share of smaller flea beetles compared with the tropics, and no specimen is greater than 8 mm long (Warchalowski 2010). The size of Alticini in the recent tropics is strikingly different: for example, in Buon Loi, South Vietnam, at least 44 species from 24 genera are known, but only five species from four genera (*Aphthona* Chevrolat, 1836, *Longitarsus* Berthold, 1827, *Phyllotreta* Chevrolat, 1836, *Sphaeroderma* Stephens, 1831) are smaller than 2 mm (Medvedev 2009), and all these genera are also known from the Palearctic. It is noteworthy that two of those species have a minimum length of 1.8 mm, whereas the minimum length is 1.9 mm for the other three species. Only 44 Indochinese alticine species in 11 genera (from a total of 504 species and 90 genera known) are smaller than 1.8 mm (Medvedev 2009), whereas the largest Indochinese flea beetles are up to 16.5 mm long; i.e., more than twice the length of the largest Palearctic species. The average size of Alticini species from Buon Loi (3.4 mm) is larger than that of an unbiased (representative) sample of flea beetles from any Eocene amber (average size 2.1 mm; Fig. 8).

However, although greater numbers (in comparison with the modern tropics) of small flea beetles seems quite plausible for the early Eocene Cambay amber, larger flea beetles should somehow be reflected in the Cambay amber inclusions. As an example, nearly one-quarter of all arthropods in the Mexican amber are larger than 2 mm (Solórzano Kraemer *et al.* 2015), and comparatively large insects, up to 7.5 mm long, are also known from the Cambay amber (Rust *et al.* 2010, Engel *et al.* 2011b, 2013). This concept is also supported by a comparison of the extant fauna of Hispaniola to the insects recorded in the Miocene

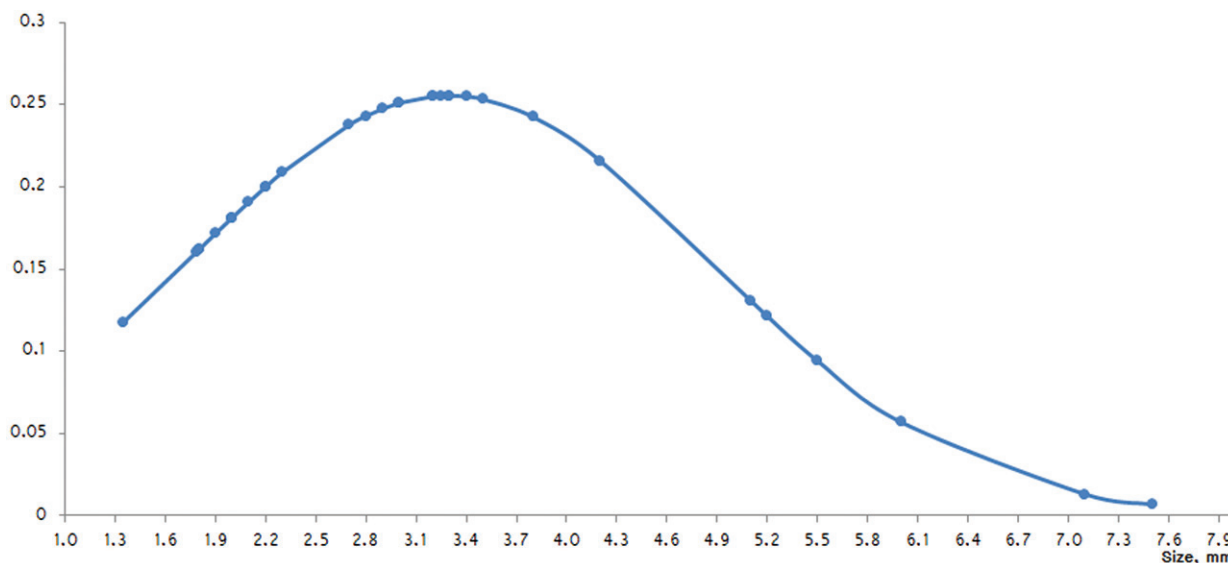


Fig. 7. Sizes of fossil leaf beetles (Chrysomelidae) for the combined Baltic, Rovno and Danish ambers, normal distribution curve.

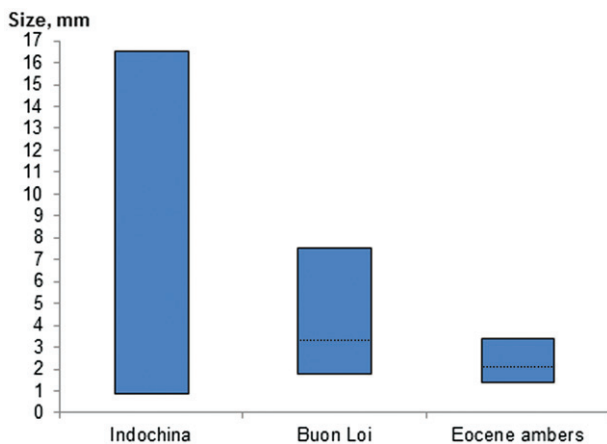


Fig. 8. Comparison of body length (from minimum to maximum) for Alticinae from modern-day Indochina, modern-day Buon Loi (South Vietnam) and European Eocene (Baltic, Rovno, Danish, Oise) ambers; average size marked with a dotted line.

Dominican amber (Perez-Gelabert 2008): although small flea beetles (such as two 1.1 mm long, bryophilous species of the genus *Kiskeya* Konstantinov & Chamorro-Lacayo, 2006) are represented in the recent Hispaniolan fauna, many angiosperm-hosted alticinae are comparatively large (Perez-Gelabert 2008), including *Alagoasa megalopia* Blake, 1939 (4.2 mm), *Pseudodisonycha hispaniolae* Blake, 1954 (up to 5 mm), *Hirtasphaera hirsuta* Medvedev, 2004 (6.4 mm), and *Disonycha comma* White, 1990 (up to 7.5 mm). Therefore, it is not unexpected that the only flea beetle described from the Dominican amber, *Wanderbiltiana wawasita* Santiago-Blay *et al.*, 2004, is also large (4.5 mm). Further, large leaf beetles are common in the Paleogene, known from the Paleocene of Canada (Paskapoo Formation, Alberta, at least 7 mm long), France (Menat, Auvergne, 4.5–6.5 mm long) and Russia (Arkharu, Amur Region, at least 11 mm long), and the early Eocene of Green River, USA (length

3.1–5.0 mm; Chaboo & Engel 2009) and Okanagan, Canada and USA (length 6–12 mm; Archibald *et al.* 2014); *Lina titana* (Meunier, 1921) from the early Eocene of Messel, Germany, was 25 mm long (until recently, this latter site was considered to be of middle Eocene age, but see Lenz *et al.* 2015) and large flea beetles, as large as 5 mm length, are known from the middle Eocene Eckfeld paratropical rainforest (Wappler 2003, pp. 107–109, fig. 74, table 13c–g).

In summary, these data suggest that large flea beetles were absent or at least rare in the Cambay amber forest, with a sharp increase in the size of tropical Alticinae feeding on woody plants in the middle Eocene, although additional data will be needed to confirm this hypothesis.

## Conclusions

We agree with Stebner *et al.* (2017b) that, considering the scarcity of early Eocene amber deposits, the Cambay amber is of great significance. In particular, the site fills a gap in the Oriental fossil record of the Paleogene, provides information on the phylogenetic relationships, divergence estimates, and biogeographic patterns of certain groups, and adds information on the early Eocene palaeoenvironment.

The discovery of a diverse assemblage of extinct alticinae in the Cambay amber highlights climatic differences between the tropical Cambay amber forest, and the Baltic, Rovno and Scandinavian amber forests, which were located distinctly further north and nearly 15 million years after the peak of Eocene global warming (Perkovsky *et al.* 2007, Perkovsky 2016, 2017, 2018, Sokoloff *et al.* 2018). We strongly doubt that any of the described alticinae were trophically connected with the Cambay amber tree, based on comparisons with platypodine abundance in Miocene and

extant *Hymaenea* resins (Zherikhin *et al.* 2009, Solórzano Kraemer *et al.* 2018), but they could have been associated with the resin-producing tree; for example, living on epiphytes and lianas on dipterocarps and other tree species of the Cambay amber forest. The numbers and diversity of Cambay Alticini indicate a possibility that the Alticini were of great importance within the Asian tropical folivorous guild in the early Eocene.

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## Disclosure statement

No potential conflict of interest was reported by the authors.

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