Article

Transitional morphology and Afrotropical affinity of a bythinoplectine rove beetle from the early Eocene of India (Coleoptera: Staphylinidae: Pselaphinae)

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Abstract

Recently discovered Ypresian-age amber from Cambay, India, reveals an ancient arthropod assemblage on the Indian subcontinent during its collision with Asia. Despite the tectonic history of India, limited connections have been found between the Cambay palaeofauna and present-day Madagascan and mainland African faunas. Here, I describe a new fossil pselaphine rove beetle (Staphylinidae: Pselaphinae) recovered from the Cambay deposit that shows closest apparent phylogenetic affinity to modern Afrotropical genera. *Yprezethinus grimaldii* **gen. et sp. nov.** is placed in Bythinoplectini, subtribe Bythinoplectina. Based on antennal and maxillary palp morphology, *Yprezethinus* is a putative transitional stem lineage of the *Zethinus*-group of genera—an extant clade distributed across equatorial African rainforests. Although *Yprezethinus* shares with this clade the derived feature of ovoid antennal clubs formed by tight appression of the apical two segments, it differs from its putative extant relatives in its possession of the plesiomorphic complement of 11 antennomeres, without any fusions of segments. The fossil taxon signifies a biotic link between early Eocene India and continental Africa, and marks the Cenozoic emergence of a tropical leaf litter arthropod fauna approaching that of contemporary, ant-dominated rainforests.

Keywords: Pselaphinae, Staphylinidae, Cambay amber, Eocene, India, biogeography

Introduction

The well-documented faunal overlap between the Afrotropical and Indomalayan ecozones stems in part from the geological history of the Indian subcontinent, which drifted from Madagascar approximately ~88 Ma (Mega-annum) and sutured with Eurasian landmasses between ~60 and 45 Ma (Storey *et al.*, 1995; Hu *et al.*, 2016). Since that time, significant biotic exchange must have occurred between India and Eurasia, but prior to contact, India's long period of isolation may be expected to have given rise to a distinct fauna, phylogenetically closest to that of Madagascar and continental Africa. Despite this presumption, evidence of faunal associations with Africa in pre-contact India is surprisingly limited. Cretaceous and early Cenozoic vertebrate fossils from India show greatest affinity to Europe (Rose *et al.*, 2006; Kumar *et al.*, 2010; Mayr *et al.*, 2010), with a minority of Gondwanan connections (Smith *et al.,* 2016). Hypotheses for India's seeming lack of biogeographic insularity include possible land bridges to other landmasses, or island arcs, both of which might have channeled dispersal into and out of the drifting subcontinent (Briggs, 2003; Ali & Aitchison, 2008).

The apparent interconnectedness of the Indian palaeofauna extends to invertebrates, evident in the affinities of diverse arthropods in recently documented early Eocene amber from Cambay, India (Rust *et al.*, 2010). The age of Cambay amber has most recently been estimated at ~54.5 Ma (Ypresian), a determination based on dating fossil vertebrates between the two amber layers (Smith *et al.*, 2016). The amber therefore likely formed at approximately the time of India's collision with Eurasia. Thus far, the deposit has yielded a rich taxonomic assemblage, albeit with limited connection to Madagascar and continental Africa (Rust *et al.*, 2010; Wood *et al.*, 2021). Among taxa studied to date, the strongest link is perhaps to Laurasian groups, manifested in a number of taxa known from slightly younger (middle Eocene) Northern European Baltic amber. These include extinct genera of electrapine and melikertine bees (Apidae: Apinae) (Engel *et al.*, 2013), lygistorrhinid flies (now in Keroplatidae) (Stebner *et al.*, 2017), and several termite genera (Engel, 2011), among others (summarized recently in Wood *et al.*, 2021). The clearest indications of a Gondwanan component to the Cambay amber palaeofauna are fossil webspinners (Embiodea) belonging to Scelembiidae, found today in the Afrotropical and Neotropical regions

(Engel *et al.*, 2011), as well as a whipspider (Amblypygi) of the tribe Paleoamblypygi (Engel & Grimaldi, 2014), known today from West Africa and Colombia (Miranda *et al.*, 2022).

Here, I present evidence for the Afrotropical derivation of components of the Cambay amber palaeofauna with the description of a new genus and species of rove beetle (Staphylinidae) belonging to the subfamily Pselaphinae. Pselaphines comprise a speciose clade of small-bodied (~1–3 mm-long), predatory, soil- and litter-inhabitants (Chandler, 1990, 2001), many of which are guests of social insects (Parker, 2016b). The new fossil taxon appears to be a transitional stem group of a Recent pselaphine clade known today from the equatorial rainforests of Africa, providing a bona fide connection between the fauna of early Eocene India and Africa. The limited dispersal abilities of small-bodied litter-inhabiting invertebrates, such as many pselaphines, may render them vicariance-prone, and thus potential indicators of ancient biotic assemblages.

Material and methods

Fossil preparation
The new fossil taxon described herein was found in ~20 kg of raw Cambay amber. The raw amber piece was trimmed using a 4" diameter diamond-edged, water-fed trim saw and embedded in EpoTek 301B synthetic resin. The piece was further reduced in size to maximize views of the beetle, and then polished with wet emery paper of decreasing grit size (400; 600; 800; 1,200; 2,400).

Specimen imaging
Photomicrographs of amber were taken with a Zeiss compound microscope with the flat amber face coated with glycerol and a cover slip, and top lighting provided by an LED light source. Montage images were constructed from stacks using Helicon Focus or Zerene Stacker. For confocal imaging of museum loan material of the *Zethinus*-group, specimens were left uncleaned aside from a superficial brushing of large dust particles, and imaged directly on their original card mounts, which were held firmly in the chosen orientation using Blu-Tack on a glass slide. A Leica SP5 confocal microscope with a 488 nm laser was used to obtain image stacks, using a 1 μm step size between Z-sections taken through the specimen. Image stacks were maximally projected in LAS AF.

Taxonomic description and comparative morphology
For morphological description, the amber specimen was examined under a Leica M205 microscope. The terminology used follows Park (1942) as modified by

Chandler (2001), except that the terms "mesoventral" and "metaventral" are used in place of "mesosternal" and "metasternal" following Herman (Herman, 2013).

For comparative study of fossil and Recent morphology, extant *Zethinus*-group specimens were borrowed from the collection of the Royal Museum for Central Africa, Tervuren, Belgium (M. de Meyer, curator).

Material examined:
Zethinus leleupi Jeannel: ♂ holotype; 2♀ paratypes; 2 further ♂ specimens (det. R. Jeannel).
Zethinus **sp. nov.** ("*inopinatus*" det. G. Coulon, 1983): unpublished ♂ holotype; unpublished 1♂ 1♀ paratypes.
Zethinus **sp. nov.** ("*confusus*"; det. G. Coulon; all specimens previously determined as *Z. leleupi* by R. Jeannel, 1963): unpublished ♂ holotype; unpublished 2♂ paratypes.
Dichozethinus nigripennis (Jeannel): ♀ holotype.
Dichozethinus angolanus Coulon: ♂ holotype; 2♀ paratypes.
Pseudozethinus curtipennis (Jeannel): ♂ holotype ; 1 paratype.

Systematic palaeontology

Family Staphylinidae Latreille, 1802
Subfamily Pselaphinae Latreille, 1802
Tribe Bythinoplectini Schaufuss, 1890

Yprezethinus gen. nov.
urn:lsid:zoobank.org:act:2DEC8AE3-3EBA-4791-A08E-AFDAD243E43A

Type species. *Yprezethinus grimaldii* **sp. nov.** here designated.

Etymology. The generic name is a combination of "Ypresian" and *Zethinus* Raffray, a Recent bythinoplectine genus to which the new taxon is phylogenetically close.

Diagnosis. The new genus, *Yprezethinus*, and its single species, *Y. grimaldii*, can be distinguished from all other Pselaphinae by the following combination of characters: (1) Head laterally excavate, with fossae extending from clypeus to anterior margin of eye; capable of holding retracted maxillary palpi; (2) antenna 11-segmented with enlarged ovular club formed from tightly appressed antennomeres 10 and 11; (3) maxillary palpomere 3 approximately twice as long as wide, ~2/3 palpomere 2 length, bearing narrow, elongate, apically globose tubercle; (4) maxillary palpomere 4 shorter than 3, rounded-conical, bearing narrow, apically globose tubercle (similar to that of palpomere 3), as well as prominent apical
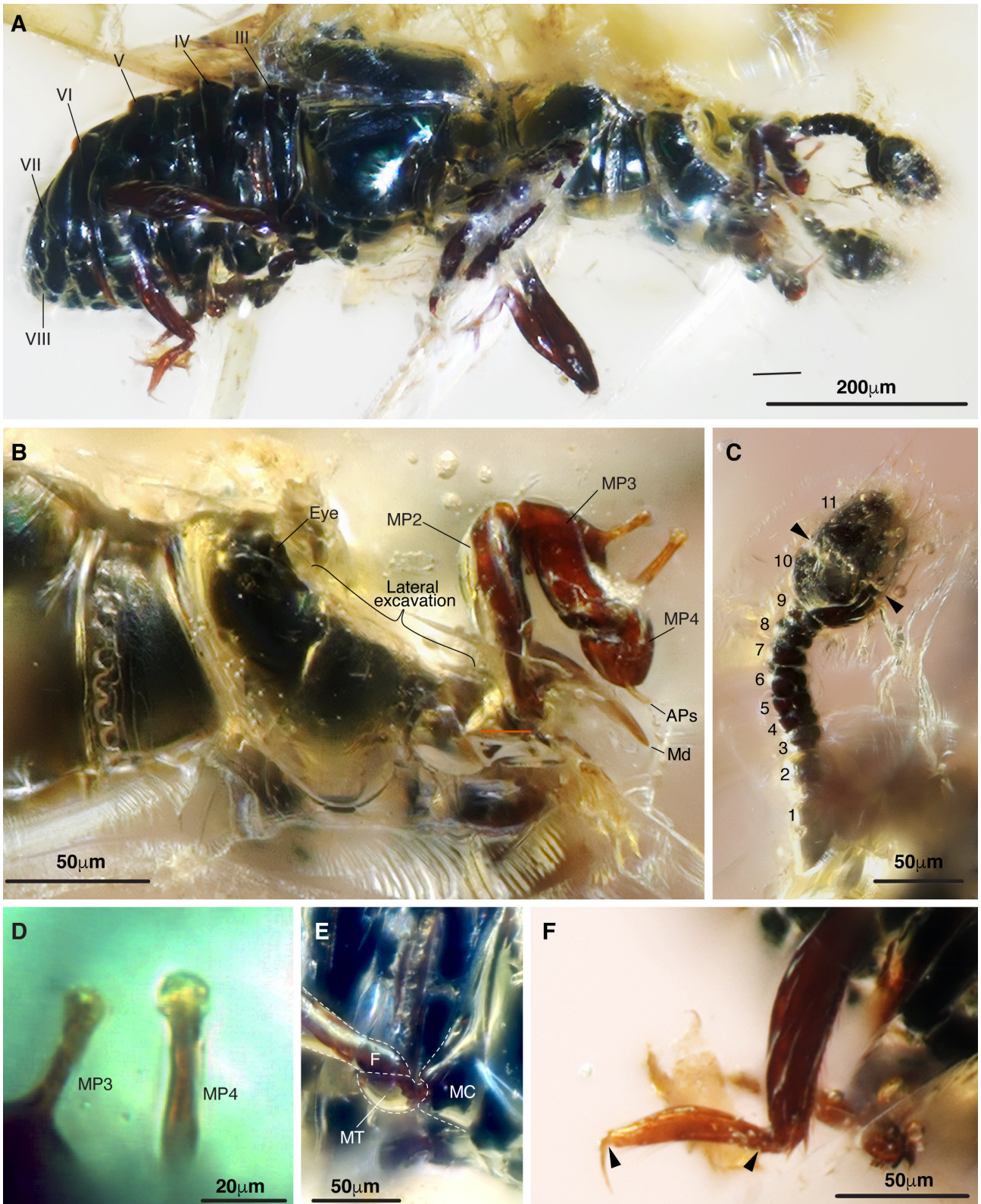
FIGURE 1. *Yprezethinus grimaldii* Holotype AMNH Tad-130. **A**, Habitus with visible abdominal sternites labelled. **B**, Head and pronotum with segments of maxillary palpomeres numbered (MP2–MP4). Bythinoplectina-type lateral excavation, eye, apical pseudosegment of maxillary palp (APs) and mandible (Md) indicated. **C**, Right antenna with antennomeres numbered. Note the club formed from tightly appressed, hemisphere-shaped antennomeres 10 and 11. **D**, Close-up view of apically globose tubercles of maxillary palpomeres 3 and 4. **E**, Proximal leg articulation, showing conically projecting metacoxa (MC), short metatrochanter (MT) and femur (F). **F**, Right metatarsus (F) with bythinoplectine-type enlarged third tarsomere spanning distance between arrowheads, and minute first visible tarsomere.

pseudosegment; (5) procoxae and metacoxae contiguous; (6) tarsi seemingly 2-segmented, with short first visible segment (probable composite of tarsomeres 1 and 2) and long second visible segment (probable tarsomere 3); and (7) all tarsi with single claws.

Description. Body length: ~0.8 mm. Body form relatively flattened and elongate ("euplectite body form" *sensu* Parker, 2016a) (Fig. 1A).

Head
Head transverse, with prominent frontal rostrum extending from clypeus to anterior margins of eyes (rostrum challenging to visualize in the holotype Tad-130 but discernable with specimen in dorsal view). Lateral margins of head deeply excavate, with large dorsal fossae that extend either side of frontal rostrum to anterior margins of eyes (Fig. 1B). Antennae mounted on underside of frontal rostrum. Antennae composed of 11 antennomeres; antennal clubs formed from tightly appressed antennomeres 10 and 11, separation of these segments observable as a narrow groove encircling the club (Fig. 1C; "*sillon annulaire*" *sensu* Coulon, 1989). Maxillary palpi 4-segmented with conspicuous additional 5th apical pseudosegment (Fig. 1B, APs). Maxillary palpomere 3 enlarged, longer than palpomere 4. Both palpomeres 3 and 4 bearing narrow, elongate, apically globose tubercles on dorsal faces (Fig. 1B, D). Maxillary palpi capable of retracting into lateral excavations of head. Head venter with median gular sulcus.

Thorax
Prothorax approximately as wide as long; subequal in width to head. Prothoracic morphology largely occluded. Pterothorax ~1.7× longer and ~1.3× wider than prothorax. Dorsal and ventral fovea are mostly indiscernible in Tad-130, but mesoventrite bearing possible lateral mesocoxal fovea (LMCF) following the foveal system of Pselaphinae from Chandler (2001). Apparent carina extending from mesocoxal cavity to lateral margin of mesoventrite.

Abdomen
Abdomen approximately equal in width to pterothorax and ~1.3× pterothorax length. Dorsal view of abdomen occluded, but five tergites (IV–VIII) visible. Tergites IV–VI subequal in length and width; VII ~ 1.2× longer than VI, narrowing posteriad; VIII ~ 0.5× shorter than VII, narrowing to abdominal apex. Distinct paratergites present on at least tergites V–VII (those on IV likely present but occluded). Six sternites clearly visible (III–VIII) (Fig. 1A); entire apical margin of sternite III visible between and laterally to metacoxae.

Legs
Procoxae and mesocoxae projecting ventrally, contiguous at midline. Metacoxae relatively flat and broadly conical, contiguous at midline, projecting posteriorly (Fig. 1E). Trochanters of all legs short such that apex of coxa sits adjacent to base of femur. Tarsi with two visible tarsomeres; first visible tarsomeres very short (Fig. 1F).

Elytra and flight wings
Taxonomic characters of the elytra are mostly occluded in Tad-130, but putative humeral carina present. Flight wings present.

Remarks. *Yprezethinus* belongs to the tribe Bythinoplectini based on its possession of the following combination of characters: (1) head with prominent frontal rostrum; (2) margins of head anterior to eyes deeply excavate, capable of accommodating the retracted maxillary palpi (Fig. 1B); (3) complex maxillary palpi, with palpomere 3 subequal to or longer than 4 (3 longer than 4 in *Yprezethinus*) (Fig. 1B); (4) contiguous metacoxae (Fig. 1E), a plesiomorphic state in Pselaphinae, seen in the supertribes Faronitae and Euplectitae (the latter including Bythinoplectini); (5) tarsi composed of 2 visible segments (Fig. 1F; Coulon 1989) argued that the first visible tarsomere is actually composed of the dorsum of morphological tarsomere 1 and the venter of morphological tarsomere 2); (6) tarsi with single claws (Fig. 1F). Within Bythinoplectini, *Yprezethinus* is placed within the subtribe Bythinoplectina on account of the lateral margins of the head being completely excavate, from clypeus (below the antennal insertions of the frontal rostrum), extending posteriorly to the eyes (Coulon, 1989; Chandler, 2001).

To my knowledge, *Yprezethinus* is the first described fossil representative of Bythinoplectini. According to Coulon's (1989) generic revision of Bythinoplectini, *Yprezethinus* belongs within informal "Section V" of this tribe, a group of eight genera distributed in the Neotropical and Afrotropical ecozones that all possess maxillary palpomeres 3 and 4 with narrow, elongate, apically globose tubercles—a putative synapomorphy (Fig. 1B, D). Within Section V, *Yprezethinus* appears to be extremely close to a putatively monophyletic group of similar genera centered on *Zethinus* Raffray (herein the "*Zethinus*-group"). For comparison to extant *Zethinus*-group character states, confocal images of the cephalic morphology of two species of *Zethinus* are shown in Figure 2. *Zethinus* illustrates clearly the laterally excavate head of the subtribe Bythinoplectina, in which the antennae are mounted on a frontal rostrum, below which the maxillary palpi can be fully retracted into large fossae (Fig. 2A–C). *Zethinus* also exemplifies the characteristic Section V maxillary palp morphology, with palpomeres 3 and 4 bearing elongate tubercles (Fig. 2D). Genera within the *Zethinus*-group are distinguished from the remaining Section V Bythinoplectini genera by the morphology
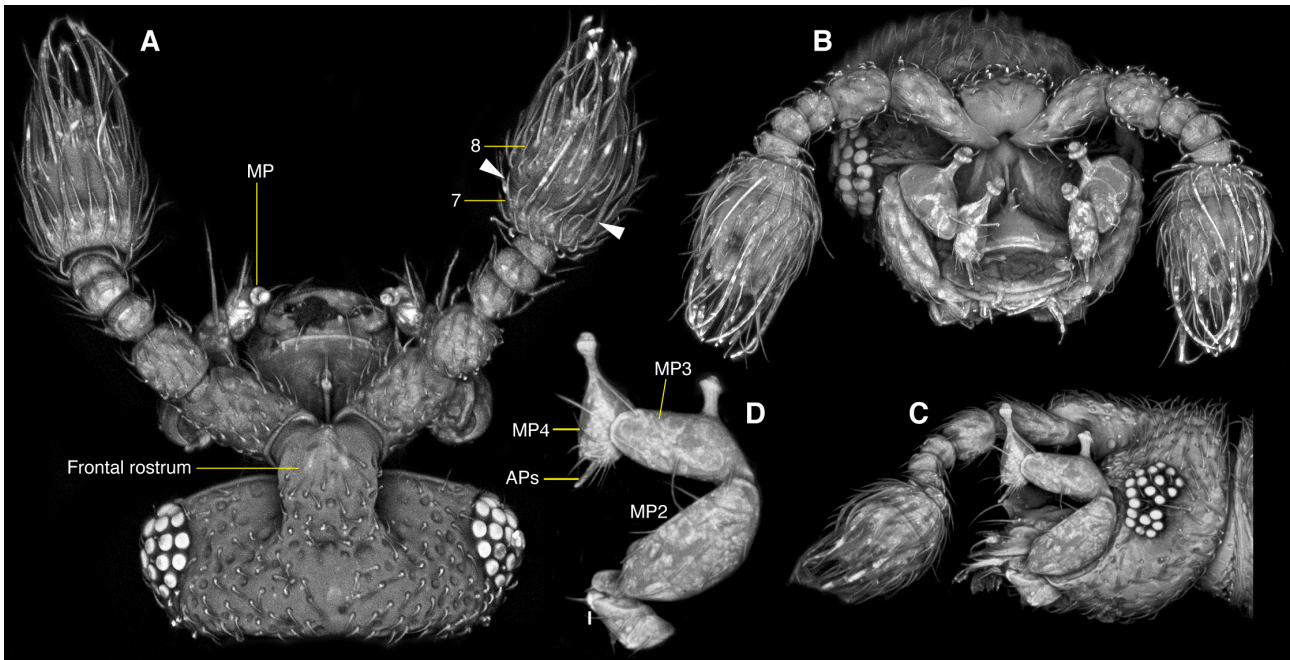
FIGURE 2. Cephalic morphology of *Zethinus*-group Bythinoplectini. **A**, **B**, *Zethinus leleupi* males (Democratic Republic of Congo: Mabali). **C**, **D**, *Zethinus* **sp. nov.** male (Democratic Republic of Congo: Kinshasa). **A**, Dorsal head and cephalic appendages of *Zethinus* showing antennae mounted under the frontal rostrum, either side of which are large excavations that extend posteriorly to the anterior margins of the eyes. Tightly appressed antennomeres 7 and 8 together form an ovoid antennal club; arrowheads indicate the boundary between these antennomeres—the "*sillon annulaire*" *sensu* Coulon, 1989. MP: left maxillary palp. **B**, Frontal view of *Zethinus* head showing retracted maxillary palpi inside excavations lateral to frontal rostrum. **C**, Head of *Zethinus* in lateral view with maxillary palp retracted into excavation. **D**, Maxillary palp of *Zethinus* showing diagnostic Bythinoplectini Section V morphology with narrow, elongate, apically globose tubercles on palpomeres III and IV. Prominent apical pseudosegment (APs) is indicated.

of the antennal club, which is spherical or ovoid and composed of the apical-most two antennomeres that are tightly appressed hemispheres (Fig. 2A; note that in *Zethinus* species, the apical two antennomeres are 7 and 8). *Yprezethinus* possesses similar antennal club morphology (Fig. 1C). *Yprezethinus* is therefore placed into crown-group Bythinoplectini, and the *Zethinus*-group of Section V specifically.

Importantly, *Zethinus*-group genera possess a maximum of nine antennomeres (*Dichozethinus* Jeannel has eight antennomeres; *Zethinus* Raffray and *Pseudozethinus* Coulon both have nine). *Yprezethinus* is therefore distinguished from these other genera by its possession of 11 antennomeres—the plesiomorphic condition in Pselaphinae (Chandler, 2001; Parker, 2016a). Hence, I hypothesize that although *Yprezethinus* sits within the bythinoplectine crown, it is a stem-lineage of the *Zethinus*-group, which has not undergone any of the antennomere fusions or losses characteristic of crown-group members of this putative clade. If Section V bythinoplectines as a whole form a monophyletic group, then the genus *Hendecameros* Comellini may represent an early-branching lineage: this taxon possesses the

plesiomorphic character states of 11-segmented antennae and distinct (non-appressed) antennomeres 10 and 11 (Coulon, 1989). I speculate that *Yprezethinus* may capture a transitional form between a *Hendecameros*-like ancestor and Recent *Zethinus*-group genera, in which antennomeres 10 and 11 show the derived state of appression, but no reduction in antennomere number has yet occurred.

Yprezethinus grimaldii sp. nov.
urn:lsid:zoobank.org:act:6657B0A8-4BF3-4A3A-88DD-F943C01A9967

Holotype. Sex unknown. 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 / No. Tad-130"

"Tad-130: / 1 Coleoptera: Scydmaenidae?"
Specimen in AMNH.

Etymology. The specific name honors entomologist Dr David Grimaldi—friend, mentor, colleague and collaborator—on his 65th birthday, and in recognition of his wide-ranging contributions to the study of fossilized insects (including pioneering the investigation of Cambay amber).

Diagnosis. As for genus.

Type locality and horizon. Cambay amber preserving *Yprezethinus* was collected from outcrops inside lignite mines in Gujarat state, western India, Tadkeshwar (21°21.400′N, 73°4.532′E). The horizon is estimated to be Early Ypresian (*ca.* 54.5 Ma; see Smith *et al.*, 2016).

Description. Body length: ~0.8 mm (Fig. 1A). Body largely glabrous, with smooth, shiny integument. Body color of Tad-130 dark, almost black; antennae also dark, brown-black; other appendages somewhat dark reddish brown.

Head
Head length ~0.13 mm (Fig. 1A); estimated width across eyes ~0.18 mm. Frontal rostrum medially sulcate. Head constricted sharply behind eyes, narrowing to occiput. Gular region of head strongly convex to occipital constriction. Eye with approximately 10 facets. Antennomere 1 partially obscured but appears to be cylindrical-conical, and longer than wide, similar in width to antennomere 2. Antennomere 2 spherical, ~1.3× wider than antennomere 1. Antennomeres 3–9 subequal in width but varied in length and shape (Fig. 1C). Antennomeres 3–6 subequal in length, twice as wide as long; antennomere 1 transverse obconical with distinct pedicel, 4–6 transverse cylindrical with concealed pedicels. Antennomeres 7–9 subequal in length, 1.5× as wide as long; antennomere 7 rounded-cylindrical, 8 and 9 weakly obconical. Ovoid club formed by antennomeres 10 and 11 (Fig. 1C); club at maximum width 3× wider than antennomeres 3–9. Antennomere 11 approximately 1.5× as long as 10. Segments of antennal club, especially antennomere 11, decorated in long, dense sensory setae (preceding antennal segments without discernable setation) (Fig. 1C). Estimated length of antenna 0.19 mm. Maxillary palpi (Fig. 1B) with short palpomere 1 and enlarged, clavate palpomere 2. Palpomere 3 broadly triangular in lateral view, twice as long as wide and approximately two thirds palpomere 2 length, with narrow, elongate, apically globose tubercle emerging dorsally at ~2/5 palpomere length (Fig. 1B, D). Palpomere 4 rounded-conical in shape, ~0.5× palpomere 3 length, dorsally bearing narrow, elongate, apically globose tubercle similar to that emerging from palpomere 3 (Fig. 1B, D). Apex of palpomere 4 bearing prominent 5th apical pseudosegment (Fig. 1B). Estimated length of extended maxillary palpus 0.18 mm. Mandibles prominent, narrow, sickle-shaped, apparently raptorial (Fig. 1B).

Thorax
Pronotum with rounded margins, widest in apical half. Pronotum 0.14 mm long, approximate width at widest point 0.2 mm.

Abdomen
Ventral abdomen length along midline 0.29 mm (Fig. 1A). Width at widest point (along apical margin of tergite IV) 0.27 mm. Tergites and sternites largely glabrous, but basal sulcus of sternite IV with apparent patch of dense, short (possibly squamous) setae.

Legs
Femora and tibiae of all legs thickened in apical half; lacking cuticular modifications. Tibiae apically setose on ventral face, most prominent on protibia. Tarsi ventrally with sparse, long mechanosensory setae. Lengths of leg segments: profemur 0.18 mm, protibia 0.13 mm, protarsus 0.07 mm, mesofemur 0.16 mm, mesotibia 0.14 mm, mesotarsus 0.06 mm, metafemur 0.16 mm, metatibia 0.16 mm, metatarsus 0.07 mm.

Elytra
Elytral length along margin 0.23 mm (Fig. 1A). Elytra apparently glabrous.

Discussion

Bythinoplectini comprise a pantropical clade that occurs primarily in lowland rainforest leaf litter. Discovery of a fossilized member of this tribe in Cambay amber is consistent with the wet tropical broadleaf forest palaeoenvironment in which this amber is posited to have formed (Rust *et al.*, 2010). A previously described pselaphine from Cambay amber, *Protoclaviger trichodens* Parker & Grimaldi (Protoclavigerini), was an obligate myrmecophile (Hlaváč *et al.*, 2021; Parker & Grimaldi, 2014). While some bythinoplectines are thought to be myrmecophilous (Coulon, 1989), this lifestyle is relatively uncommon within the tribe, and *Yprezethinus* exhibits no morphological specializations that indicate a close association with ants. Nevertheless, free-living pselaphines such as Bythinoplectini attain peak abundance in modern, ant-dominated tropical leaf litter (Parker, 2016a, b). The relatively high frequency of ants belonging to crown-group subfamilies in Cambay amber (Rust *et al.*, 2010), along with the presence of free-living pselaphines belonging to crown-groups of extant tribes, indicate that the early Eocene rainforest floor insect community had a modern aspect. This inference is in stark contrast to that drawn from investigations of mid-Cretaceous Burmese amber, where both of these faunal components are scarce or absent (Barden, 2016; Parker, 2016a). The Cambay amber palaeofauna may thus embody an early phase in the Cenozoic "rise of modern ants" and concomitant radiations of litter-dwelling groups like pselaphines, which abound throughout contemporary, ant-dominated tropical forest floors globally (Parker & Kronauer, 2021).

The inferred close phylogenetic relationship between *Yprezethinus* and the *Zethinus*-group of Recent Bythinoplectini reveals a component of the Cambay Palaeofauna that is Afrotropical by association. All *Zethinus*-group taxa described thus far have originated from the equatorial forests of the Guineo-Congolian region, with records from Angola, Côte d'Ivoire, Democratic Republic of Congo and Gabon (Coulon, 1989 and G. Coulon, pers. comm.). *Yprezethinus* may therefore represent a breakaway lineage within the otherwise Afrotropical stem of the *Zethinus*-group, which persisted on the drifting Indian subcontinent until at least the early Eocene. To my knowledge, no other *Zethinus*-group or Section V bythinoplectines, either Recent or fossil, have so far been found in Indomalaya, supporting the conclusion that this breakaway lineage became extinct.

The discovery of *Yprezethinus* contrasts with most other Cambay arthropods thus far studied, which show largely Laurasian or even New World affinities (Rust *et al.*, 2010; Wood *et al.*, 2021). Pselaphines tend to frequent narrow ranges and exhibit high endemicity at the genus and species levels, most likely due to their minute size and potential for extreme habitat specificity, which limits their capacity for long distance dispersal (Reichle, 1966, 1967, 1969). The reduced vagility of pselaphines relative to many other arthropod groups is a property of sedentary litter/soil-dwelling organisms that has been posited to foster vicariance (Noonan, 1988; Carlton, 1990). The land bridges or volcanic island arcs hypothesized to explain the apparent lack of endemism on India prior to contact with Eurasia may have provided sufficient access for mobile taxa such as vertebrates and some flying insects (including foundresses of social insect colonies). They may have been less effective for trafficking litter- and soil-inhabiting arthropods such as pselaphines, however. The relative spatial fixity of pselaphines, combined with the group's high diversity and ubiquity, suggests that the subfamily may have general utility for biogeographic studies (Carlton, 1990).

As noted by Jeannel (1961, 1964), a biotic link between India and the Afrotropics is also strongly supported by the distribution of recent pselaphine taxa. While the Pselaphinae fauna of India is extremely poorly known, evidence comes from a variety of taxa shared by Indomalaya, Madagascar and/or the Afrotropics, but not elsewhere. The *Batrisocenus* genus-complex of the tribe Batrisini is one such example (Nomura, 1991), with a range principally spanning Indomalaya and the Afrotropics (including Madagascar), but extending to South Africa, and with one species of *Batrisocenus* Jeannel reaching the tropical Northern tip of Australia (Chandler, 2001). Such a distribution of closely allied (and in some cases potentially synonymous) genera could have arisen from India acting as a biotic "ferry" to seed the Indomalayan ecozone with taxa from Eastern Gondwana (with subsequent, limited dispersal southward through Indomalaya to Australia). My own observation of the otherwise Indomalayan batrisine genus *Mnia* Newton & Chandler in litter samples from Madagascar (J. Parker, pers. observ.) also supports this scenario, as does the discovery in Sri Lanka (to which India was historically joined) of *Batrisiotes* Jeannel and *Coryphomus* Jeannel (Löbl & Kurbatov, 2001)—two additional batrisine genera previously known only from the Afrotropics (Newton & Chandler, 1989). Similarly, within Trichonychini, the genera *Asymoplectus* Raffray and *Chaetorhopalus* Raffray are shared by both Afrotropical and Indomalayan regions, and in Pselaphini, *Pselaphotrichus* Besuchet is known only from the Afrotropics and India.

Conversely, the contribution from Eurasia to the Indomalayan pselaphine fauna appears to have been more limited: the large Holarctic/Palearctic tribes Tychini and Bythinini, both of which are likely of Laurasian origin, are fully absent from the Afrotropics, and generally absent from the Indomalayan region, with only *Atychodea* Reitter of Tychini occurring there (Chandler, 1988; Kurbatov & Sabella, 2008). These conspicuous absences may be taken to indicate an ecological or climatic constraint in the southward spread of these primarily temperate tribes into tropical areas. However, putative stem-group bythinines occur in mid-Cretaceous amber from Myanmar (Parker, 2016a; Yin *et al.*, 2018), which formed in tropical conditions (Grimaldi *et al.*, 2002), suggesting a more complex scenario involving the extinction (perhaps competitive displacement) of this tribe in Indomalaya, and its exclusion to more northern latitudes.

In summary, affinities of the fossil pselaphine described here and those of Recent Indomalayan taxa are not with Eurasia, but with the Afrotropics and other Gondwanan regions. Additional examples of an "out-of-India" origin of Indomalayan pselaphines may exist. Their discovery will depend on further collecting efforts, especially in India, the unravelling of genus-level synonymies among pselaphines from Africa, Madagascar and the Indomalayan countries, and, perhaps most of all, from resolution of supraspecific phylogenetic relationships within this vast staphylinid subfamily.

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