

Evolution of tropical termites in early Paleogene with description of a new species of Stylotermitidae (Isoptera) from Rovno amber (late Eocene of Ukraine)

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ABSTRACT. The first Rovno amber stylotermitid *Parastylotermes nathani* Perkovsky sp.n. is described. It is the fourth amber stylotermitid and the second Priabonian one. Two non-Priabonian amber stylotermitids are known from the tropical Ypresian Cambay amber. In Cambay amber stylotermitids compose half of the species, and all termites with trimerous tarsi extraordinary 75% of Cambay termites. Another peculiarity of the Cambay amber isopteran community is the small body size: Cambay termites are 2.3–2.6 times smaller than Aptian Crato and Cenomanian Burmese termites and two times smaller than Ypresian Oise amber termites. The dominance of small termites with trimerous tarsi in Cambay amber is likely because of a change in the nature of predation pressure in the tropics during the earliest Cenozoic. The only known Cretaceous arboreal birds belonged to Enantiornithes (opposite birds). These opposite birds are known to have low cranial kinesis and thus would have difficulty catching small insects. At the K-Pg boundary, the extinction of Enantiornithes occurred. Concurrent with this event there was a rapid radiation of crown birds and their expansion in the low latitudes, increasing pressure from predation. The smallest (2 mm) isopteran, *Nanotermes* (earliest termitid), was found in Cambay amber. The strong miniaturization of the earliest termitids would be instrumental in the loss of obligate intestinal protozoa symbionts. These protists were too big to become fully established in the narrow gut of small third instar of the earliest termitids. The loss of dependence on protists resulted in the loss of most larval instars in termitids and irreversible separation of neuter and sexual lines, paving the way to their ecological dominance in the tropics. How to cite this paper: Perkovsky E.E., Vasilenko D.V. 2020. Evolution of tropical termites in early Paleogene with description of a new species of Stylotermitidae (Isoptera) from Rovno amber (late Eocene of Ukraine) // Invert. Zool. Vol.17. No.3. P.231–246. doi: 10.15298/invertzool.17.3.03

KEY WORDS. *Parastylotermes nathani* sp.n., *Nanotermes*, Enantiornithes, miniaturization, Termitidae, loss of the obligate symbiosis with intestinal protozoa, ecological domination.

Эволюция тропических термитов в раннем палеогене с описанием нового вида *Stylotermitidae* (Isoptera) из ровенского янтаря (поздний эоцен Украины)

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РЕЗЮМЕ. Описан первый вид стилотермитид из ровенского янтаря, *Parastylotermes nathani* Perkovsky sp.n. Это четвертый янтарный и второй приабонский вид стилотермитид; два других вида янтарных стилотермитид известны из тропического ипрского камбейского янтаря. В камбейском янтаре стилотермитиды составляют половину видов, а все термиты с трехчлениковыми лапками даже три четверти всех видов термитов. Другой особенностью камбейских термитов являются мелкие размеры: камбейские термиты в 2,3–2,5 раза мельче аптских термитов Сантаны и сеноманских термитов бирманского янтаря и в 2 раза мельче ипрских термитов из янтаря Уазы. Доминирование мелких термитов с трехчлениковыми лапками в камбейском янтаре может быть обусловлено изменением характера пресса хищников в тропиках начала кайнозоя, вызванного вымиранием энантиорнисовых («противоположных птиц») с низким кинетизмом черепа, которые не могли охотиться за мелкими насекомыми, и быстрой радиацией неогнат в низких широтах. В камбейском янтаре найден самый мелкий (2 мм) термит *Nanotermes* (древнейшая термитида). Сильная миниатюризация древнейших термитид могла быть причиной потери ими облигатного симбиоза с простейшими, населяющими кишечник низших термитов. Эти протисты оказались слишком крупны для узкого кишечника мелких рабочих древнейших термитид. Независимость от симбиоза с простейшими привела к потере термитидами большинства личиночных стадий и необратимому обособлению касты рабочих, которое обоусловило их экологическое доминирование в тропиках.

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КЛЮЧЕВЫЕ СЛОВА. *Parastylotermes nathani* sp.n., *Nanotermes*, Enantiornithes, миниатюризация, Termitidae, потеря облигатного симбиоза с кишечными простейшими, экологическое доминирование.

Introduction

Until recently, only one termite species with trimerous tarsi, Baltic *Parastylotermes robustus* (Rosen, 1913) was known from amber, it was described in details by Emerson (1971). Wings of this species were reported by Emerson (1971) from Danish amber as well. Finding the second Priabonian species of the genus is especially interesting, because the recently resurrected family of Stylotermitidae (Engel, 2009) now contains three genera with trimerous tarsi — Ypresian *Prostylotermes* Engel et Grimaldi, 2011, Miocene-Ypresian *Parastylotermes* Snyder et Emerson, 1949 (both with tibial spur formula 2-2-2) and extant *Stylotermes* Holmgren et Holmgren, 1917 (Oriental, reaching the southern borders of Palearctic, tibial spur formula 3-2-2). Trimerous tarsi, wing venation, forewing scale setation and tibial spur formula 2-2-2 (Fig. 2C) attribute the new species to the genus *Parastylotermes*.

The fauna of Priabonian amber forests is a mix of the temperate and tropical elements, while the temperate elements strongly prevail (Archibald, Farrell, 2003; Perkovsky, 2013, 2016, 2017; Ivanov *et al.*, 2016). In Rovno amber forest, the tropical elements are represented better (Perkovsky, 2018; Lyubarsky, Perkovsky, 2019; Perkovsky *et al.*, 2020 and references therein) than in Baltic amber forest. The temperate elements in Priabonian amber fauna of termites are represented by rhinotermitid *Reticulitermes* Holmgren, 1913 (Emerson, 1971) and Archotermopsidae. The tropical elements are represented by Mastotermitidae, *Heterotermes* Froggatt, 1897 (Emerson, 1971; Engel, 2008), *Proelectrotermes* Rosen, 1913 that is most diverse in Burmese amber (Engel *et al.*, 2007a) and *Electrotermes* Rosen, 1913 (known from Oise amber; closely related extant *Postelectrotermes* Krishna, 1961 is known outside of tropics only from Baluchistan and Madeira); the distribution of extinct and extant stylotermitids in Old World allows adding them to this group.

Holotype of the new species was collected in Rovno region. Paratype K-8878 was mined in

Pugach quarry (Klesov) in 2009. Paratype L-139 was collected near Voronki village (see Martynova *et al.*, 2019), Vladimirets district of Rovno region, in the same piece with holotype of formicine ant *Cataglyphoides dluskyi* Radchenko et Khomich, 2020 (Radchenko, Khomich, 2020). All studied material is deposited in the collection of the Schmalhausen Institute of Zoology (SIZK) in Kiev.

Parastylotermes nathani Perkovsky **sp.n.**

Figs 1, 2.

Material. Holotype: SIZK UA-5704, Rovno amber, late Eocene; syninclusion: Hemiptera, Drepanosiphidae. Paratypes: SIZK K-8878, Klesov, Rovno amber, late Eocene, syninclusions: Hybotidae, Isoptera wing; SIZK L-139, Voronki, Vladimirets district, Rovno amber, late Eocene (syninclusions listed in Radchenko, Khomich, 2020).

DIAGNOSIS: New species differs from the other representatives of the genus, except Cambay amber *Parastylotermes krishnai* Engel et Grimaldi, 2011, by the short (length of forewing of the other species — 9.4–10.7 mm) and narrow (Fig. 1A, B, F) wings (forewing of the other species 1.8–2.6 times as long as wide), from bigger Baltic *Parastylotermes robustus* also by 18-segmented antennae of holotype and Klesov specimen (*P. robustus* have 16–17-segmented antennae, in new species 16-segmented antennae known only for the small specimen from Voronki) and CuA with 11 primary branches reaching to posterior wing margin (*P. robustus* by Engel *et al.*, 2011 have 7–8); *P. krishnai* differs from both new species and *P. robustus* by 14-segmented antennae and the apical branching of the medial vein in the forewing.

DESCRIPTION. Body brown. Head and pronotum with strong setae, with maximal setae length 0.19 mm (Figs 1C, 2A, E, G), more dark on the head and light brown on wing scales and abdomen.

Head dark brown. Postclypeus (Fig. 1C, D) convex, short, 4.3 times as wide as long, with shallow impression in middle (Fig. 2A). Anterior margin of postclypeus not emarginated. Fon-

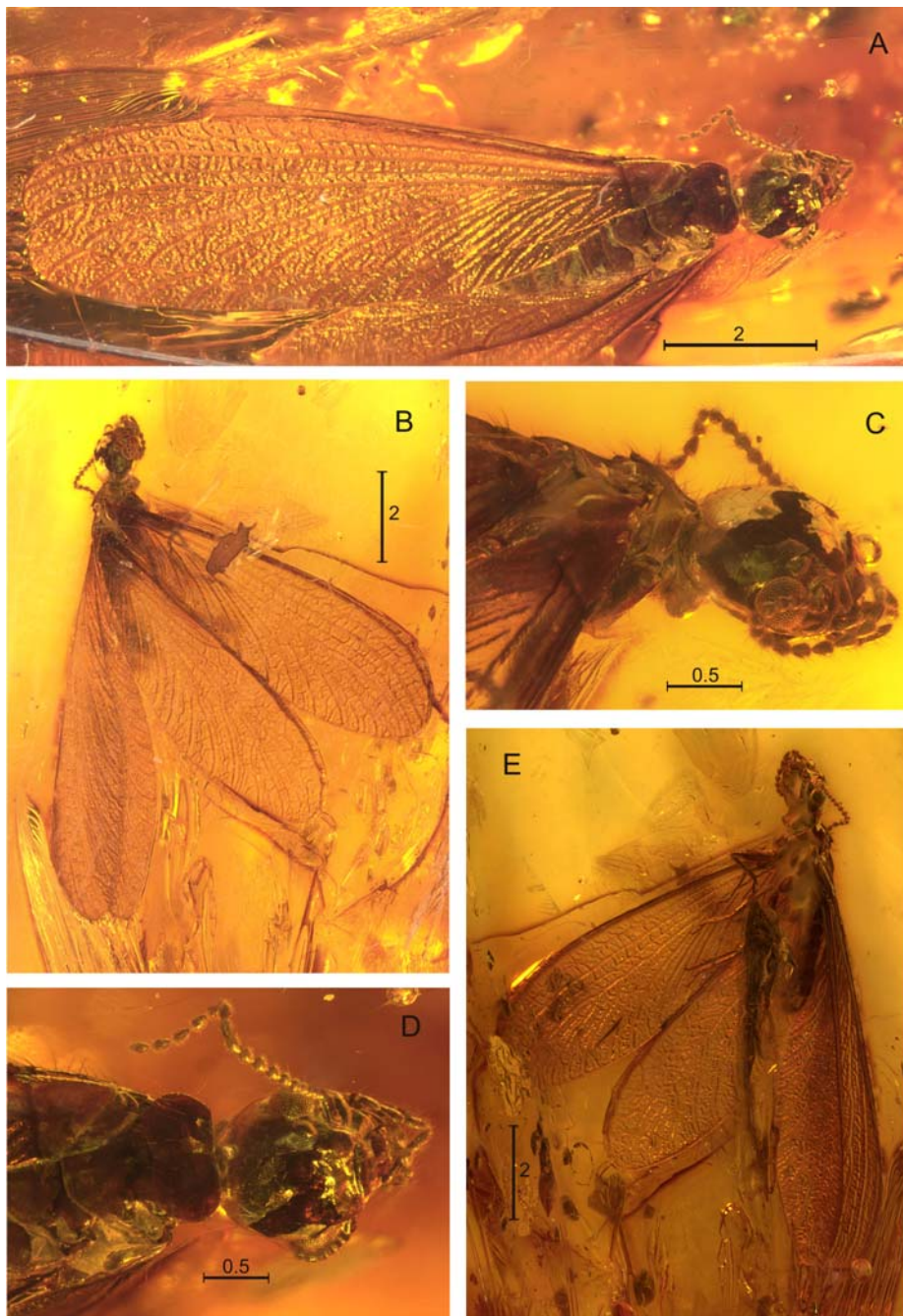


Fig. 1. General view and details of structures of *Parastylotermes nathani* sp.n., holotype A — left wings; B — general view, dorsal; C — head and antennae, dorsolateral; D — proximal part of body, dorsal; E — general view, ventrolateral.

Рис. 1. Общий вид и детали строения голотипа *Parastylotermes nathani* sp.n. А — левые крылья; В — общий вид, сверху; С — голова и антенны, в верхнебоковом положении; D — голова и проксимальная часть крыла, сверху; E — общий вид, в нижнебоковом положении.

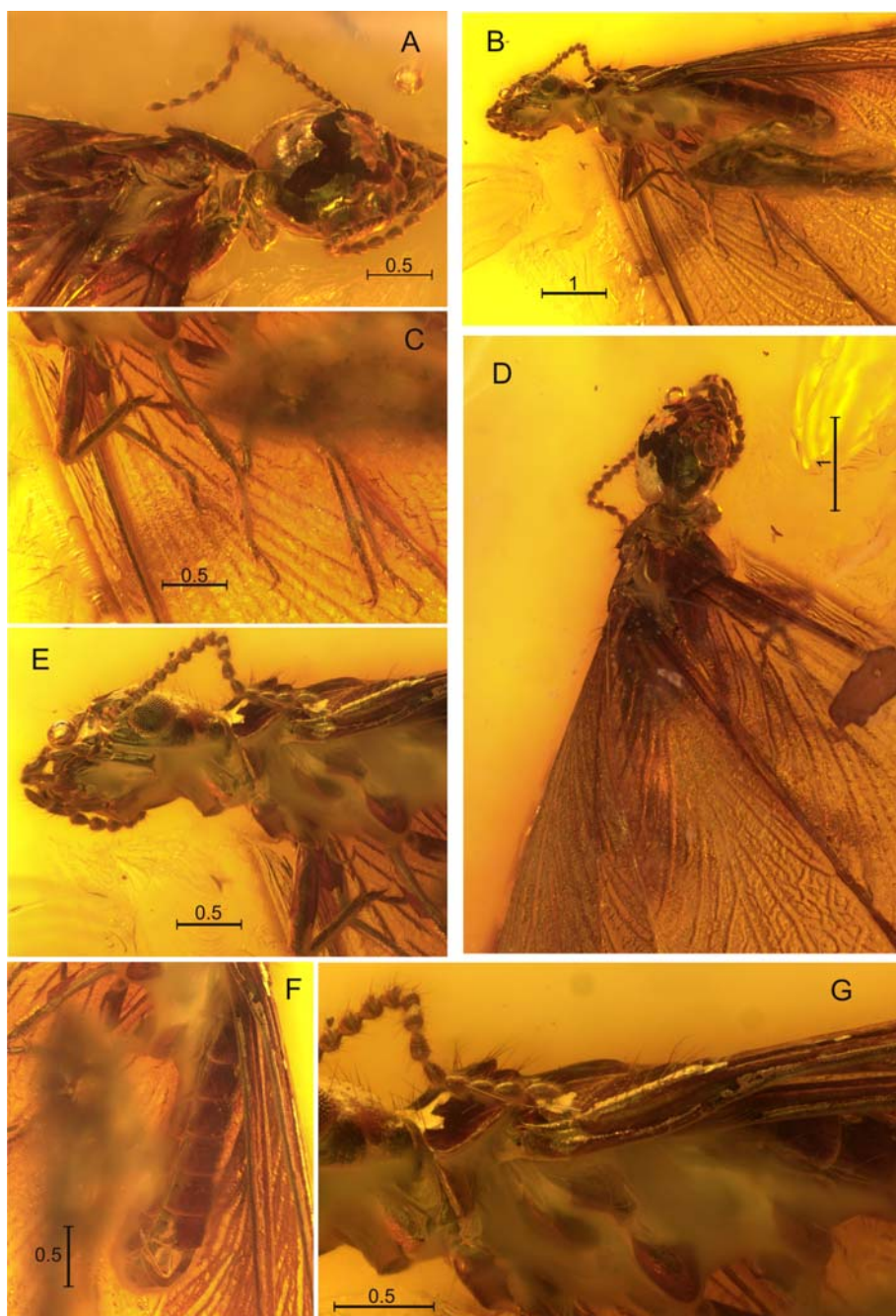


Fig. 2. Microphotographs of details of structures of *Parastylotermes nathani* sp.n, holotype. A — head, dorsolateral; B — body, lateral; C — legs, D — proximal parts of right wings; E — head and thorax, ventrolateral; F — abdomen; G — pronotum and left forewing scale, lateral

Рис. 2. Микрофотографии деталей строения голотипа *Parastylotermes nathani* sp.n. А — голова в верхнебоковом положении; В — тело, сбоку; С — ноги; D — проксимальная часть правых крыльев; E — голова и грудь, в нижнебоковом положении; F — брюшко; G — пронотум и левая переднекрыловая чешуйка, сбоку.

tanelle small, its front margin situated on the level of hind margin of eyes (Fig. 1C); four maxillary palpomeres, three labial palpomeres. Antennae of holotype (Fig. 2E). and paratype K-8878 18-segmented, antennae of paratype L-139 16-segmented.

Pronotum wide and flat, shallow longitudinal groove in middle (Fig. 1D); front margin with slight indentation in middle. Pronotum widest before middle. anterior and posterior angles widely rounded, hind margin distinctly emarginate with a shallow angle in middle.

Legs light brown; tibial spur formula 2-2-2, additional spines on tibiae absent. Tarsi trimerous, apical tarsomere longer than combined lengths of basitarsus and second tarsomere (Fig. 2C), second tarsomere projecting apically beneath base of apical tarsomere (Fig. 2C, E); pretarsal claws simple, arolium absent.

Forewing scale large, overlapping the two thirds of hind wing scale, humeral margin slightly convex, apical margin straight. CuP (claval fissure) strongly curved in the lower fifth of its length, scale with numerous long, erect setae, particularly along humeral margin, without short setae (Figs 1C, 2G). C and R more darkly pigmented than remaining veins; M in middle of wing more close to CuA than to R, CuA with 11 primary branches reaching posterior wing margin. Forewing 3–3.2 times as long as wide. Hind wing scale with straight apical margin (suture). Abdomen brown (Fig. 2F), tergites and sternites with long setae.

Measurements (in mm). Total length with wings 8.6–11, total length without wings 4.3–5.5, length of head to hind margin of postclypeus 1, length of head to front margin of clypeus 1.2; width of head with eyes 1.15–1.3 (holotype 1.3), length of postclypeus 0.07, width of postclypeus 0.3, maximum diameter of eye 0.38–0.4 (holotype 0.4), eye height 0.35, length of ocellus 0.18, width of ocellus 0.09, ocellus from eye 0.04, distance between eye and lower head margin 0.05–0.1 (holotype 0.05), length of pronotum 0.5, width of pronotum 0.82–1.05, length of hind tibia 1.2, length of forewing from costal suture 6.3–7.8; forewing width 1.95–2.6; distance between C and R on forewing 0.2,

distance between R and M in the middle of forewing 0.5, distance between M and Cu in the middle of forewing 0.4; length of forewing scale 0.9–1; length of hind wing 6.2; width of hind wing 1.8–2.5; length of hind wing scale 0.6–0.69.

ETYMOLOGY. The new species is named for Nathan E. Perkovsky (1988–2020).

Discussion

Stylotermitidae is the sister group of all remaining Neoisoptera (Krishna *et al.*, 2013; Wu *et al.*, 2018). Stylotermitid colonies are small, without discrete nests, found in living and partially dead trees (Krishna *et al.*, 2013; Liang *et al.*, 2017). The species described is the second Priabonian termite with trimerous tarsi, and thus 15% of Priabonian amber termite species have trimerous tarsi (Engel *et al.*, 2007b; Engel, 2008; this paper). In Ypresian resins, termites with trimerous tarsi compose half of all species, and they compose 75% in Cambay amber (Nel, Bourguet, 2006; Engel *et al.*, 2011); half of the Cambay species are stylotermitids. The statistic on the proportion of trimerous vs. tetramerous and pentamerous termites in Ypresian resins are based on too few specimens to be absolutely accurate, but we can indicate that 42% of Cambay specimens (26% of all known Ypresian specimens) belong to genera with trimerous tarsi. Trimerous tarsi are uncommon among the extant termites, as shown by the global fauna, in which only 2.3% have trimerous tarsi: Of 2937 extant species, only 45 *Stylotermes* Holmgren et Holmgren, 1917 (Stylotermitidae), 12 *Speculitermes* Wasmann, 1902 (Termitidae) species and 10 *Indotermes* Roonwal et Sen-Sarma, 1958 (Termitidae) species (Krishna *et al.*, 2013) have trimerous tarsi. All these three extant genera are distributed in the Oriental Realm. Even on the Indian subcontinent and Burma where species with trimerous tarsi are relatively common and diverse, they compose just 6% of termite species (Roonwal, Chhotani, 1989; Chhotani, 1997).

In addition to their abundance (see below), Cambay termites are also very small (Table 1). Ypresian stylotermitids are much smaller (imagoes are 4.0 mm long [*Parastylotermes* *krish-*

Table 1. Body length of Burmese and Cambay amber termites.
Таблица 1. Длина тела термитов из бирманского и камбейского янтаря.

No	Species	Body length of alate without wings (mm)	Deposit and age	Reference
1	<i>Mylacrotermes cordatus</i>	5.95	Burmese amber, Cenomanian	Engel <i>et al.</i> , 2007a, Fig. 6
2	<i>Dharmatermes avernalis</i>	5.3	Burmese amber, Cenomanian	Engel <i>et al.</i> , 2007a, Fig. 7
3	<i>Tanytermes anawrahtai</i>	5.3	Burmese amber, Cenomanian	Engel <i>et al.</i> , 2007a
4	<i>Kachinitermes tristis</i>	3.95	Burmese amber, Cenomanian	Emerson, 1969
5	<i>Ginormotermes rex</i>	ca 24	Burmese amber, Cenomanian	Engel <i>et al.</i> , 2016
6	<i>Krishnatermes yoddha</i>	10.04	Burmese amber, Cenomanian	Engel <i>et al.</i> , 2016
7	<i>Anisotermes xiai</i>	12.6	Burmese amber, Cenomanian	Zhao <i>et al.</i> , 2019
8	<i>Kachinitermopsis burmensis</i>	3.3	Burmese amber, Cenomanian	Poinar, 2009
9	<i>Cosmotermes opacus</i>	5.9	Burmese amber, Cenomanian	Zhao <i>et al.</i> , 2020
Average body length of Burmese species*		8.5		Our data
10	<i>Parastylotermes krishnai</i>	4	Cambay amber, Ypresian	Engel <i>et al.</i> , 2011
11	<i>Prostylotermes kamboja</i>	4.4	Cambay amber, Ypresian	Engel <i>et al.</i> , 2011
12	<i>Zophotermes ashoki</i>	4.9	Cambay amber, Ypresian	Engel <i>et al.</i> , 2011
13	<i>Nanotermes isaacae</i>	ca 2	Cambay amber, Ypresian	Engel <i>et al.</i> , 2011
Average body length of Cambay species		3.7		Our data

*Only one representative of genus is counted.

nai Engel et Grimaldi, 2011] and 3.8 or 5.0 mm [male, female *Prostylotermes kamboja* Engel et Grimaldi, 2011]) than extant Indian *Stylotermes* (medium body length 7.6 mm) (Roonwal, Chhotani, 1989). Cambay isopteran (Table 1) are 2.3 times smaller than the ‘mid’-Cretaceous Burmese amber isopteran; termites from Albian Spanish amber are even larger than termites from Burmite: *Ithytermes montoyai* Sánchez-García, Peñalver, Delclòs et Engel, 2020 is 9.6

mm (Sánchez-García *et al.*, 2020), and the head and pronotum of *Morazatermes krishnai* Engel et Delclòs, 2010 is 6 mm long (Engel, Delclòs, 2010). Aptian Crato species are mostly large-bodied (Grimaldi *et al.*, 2008), 2.6 times larger than Cambay species, with the length of the Aptian Siberian *Baissatermes lapideus* Engel, Grimaldi et Krishna, 2007 ca. 10 mm (Engel *et al.*, 2007a, fig. 1), near the medium length of Crato species (9.5 mm). Finally, Cambay ter-

mites are two times smaller than Ypresian Oise isopterans (see details below).

All Cambay amber termites belong to Neoisoptera. All known Ypresian and the single Cretaceous Neoisoptera *Archeorhinotermes rossi* Krishna et Grimaldi, 2003 are small; it reflects unidirectional decrease in size as general pattern of termite evolution (Nalepa, 2011). *Amitermes parvus* (Hill, 1922), the smallest from 120 termites, used in work of Nalepa (2011), have median adult head width of 0.67 mm and was indicated as undoubtedly miniaturized species. Head width of *Archeorhinotermes rossi* is 0.69 mm (Krishna, Grimaldi, 2003), so it is not less miniaturized. With the development of the fontanelle (possession of fontanelle defines Neoisoptera), termites evolved a highly effective new defense mechanism — the frontal weapon. Ants are undoubtedly the most important termite invertebrate predators (Deligne *et al.*, 1981) now-a-day, and probably also in the Cenozoic. The frontal weapon appears particularly useful to protect against numerous ant species in the tropics, such as individually foraging small-colony ponerines, including the arboreal *Platythyrea* Roger, 1863, known from the Early Eocene of Europe. Neoisopterans are not recorded in Oise amber and middle Eocene Eckfeld, and rare in the latest Eocene Bembridge Marls. In succinites (Priabonian ambers), more ‘basal’ termite groups are very strongly represented, whereas only a third of Baltic amber species belong to Neoisoptera (Engel *et al.*, 2007b; Engel, 2008). In the late Oligocene lacustrine outcrops of Aix-en-Provence and Camoins-les-Bains (France), Neoisoptera are also quite rare (only two alate specimens) while the Mastotermitidae are frequent (ca. 20 alates) (Nel, pers. com). In the diverse Miocene termite fauna of New Zealand (six genera), neoisopterans are completely absent (Engel, Kaulfuss, 2017). The absolute dominance of Neoisoptera at the species level has been documented from the large samples found only in Miocene tropical ambers (Krishna *et al.*, 2013), and even in Dominican amber, the number of kalotermitid and mastotermitid specimens among the named species is comparable to the

number of neoisopterans. The reasons for the absence of ‘lower’ termites in Cambay amber may be because of diverse and relatively numerous ants (6% of all inclusions: Parker, Grimaldi, 2014), but the tropical ant fauna of this amber (Rust *et al.*, 2010) remains undescribed. In coeval Oise amber, ants represent 2.5% of all insects (Parker, Grimaldi, 2014), and neoisopterans are absent. Krishna & Grimaldi (2009: 43–44) noted that “kalotermitids feed and nest in sound wood, and so would be expected to have been living in close proximity to copious resin... the scarcity of kalotermitids in Dominican amber may reflect a genuine absence of these termites in the amber forest, and not just an absence of data”. In our opinion, this statement is also true for the absence of kalotermitids in Cambay amber.

Roisin (2000) indicated that a correlation can be drawn between the “one-piece” life type termites (OPT), that is, living within a piece of wood serving simultaneously as a nest and as a food source, and a *Kalotermes* Hagen, 1853-like caste pattern, characterized by the presence of pseudergates (pseudoworkers) and the absence of workers. The only Ypresian termite that is larger than the Priabonian congeners and Cretaceous representatives of a closely related genus, and indeed the largest of all Ypresian termites, is the kalotermitid *Electotermes flecki* Nel et Bourguet, 2006 from Oise amber, an OPT species. Paradoxically, it is even larger than *Mastotermes minutus* Nel et Bourguet, 2006 from Oise amber, while in all other faunas where kalotermitids and Mastotermitidae Froggatt, 1897 occur together (from the earliest Cenomanian till the present), mastotermitids are 2–2.5 times larger than kalotermitids.

Separate life-type species (ST), *sensu* Korb & Thorne (Korb, Thorne, 2017), have a nest that is separate from their multiple food sites. All known Neoisoptera are ST type species. ST here comprises “intermediate-type” termites nesting in and feeding on wood but able to expand their colonies by exploiting several pieces of wood through subterranean tunnels (Roisin, 2000) as well as the true “separate life” nesting termites where colonies are found in the

soil. Of the “intermediate-type” Ypresian amber termites, we can include *Mastotermes*, who by this time had real workers, and *Zophotermes* Engel, 2011, with their supposed *Prorhinotermes*-like pseudergates. “Intermediate-type” species also include *Reticulitermes*, a typical example, as well as some Termitidae, such as *Microcerotermes parvus* (Haviland, 1898) (Roisin, 2000), and others. Cambay amber termites, e.g. small stylotermitids and very small termitids, were probably all ST species (“intermediate-type” or true “separate-life”). The stylotermitid caste system remains unknown (Wu *et al.*, 2018); however, soldiers are known, and the worker caste is always mentioned and deserves additional investigation (Liang *et al.*, 2017). Miniaturization was accompanied by a decrease in the number of tarsomeres (to 3) and antennomeres (to 12 in *Nanotermes* Engel et Grimaldi, 2011) and a loss of a third foretibial spur in all Cambay termites.

Termites in Cambay amber compose 1.7% all insect inclusions. Their colonies were small in size (the size of foragers is discussed in detail below), and therefore would not have attracted the attention of specialized predators; e.g. extant stylotermitids (see above) is the most cryptic Taiwan isopterans (Liang *et al.*, 2017). *Zophotermes* belongs to Prorhinotermitinae (Krishna *et al.*, 2013), which differ from most neoisopterans by having pseudergate workers. Pseudergate workers are favored when termites live in small, short-lived, unstable societies under highly uncertain environmental conditions (Thompson *et al.*, 2000).

Compared to social Hymenoptera, termites appear to be very vulnerable insects; there is strong pressure favoring adaptations that minimize their predation (Noirot, 1985). Miniaturization of Cambay termites could be associated with changes in predation pressure from generalists in the Paleocene tropics, resulting in a decrease in size of tropical termites by the early Eocene.

Pressure from a generalist predator would be especially important because the existence of specialized termite predators in the Cambay amber forest is highly doubtful. After reapprais-

ing the Sakhalinian amber age (Baranov *et al.*, 2015; Radchenko, Perkovsky, 2016), only ‘basal’ aneuretine ants from Paskapoo (LaPolla, Barden, 2018), and, possibly, ant from Menat, described as a member of the Eumenidae (Archibald *et al.*, 2018 and references therein) of the Paleocene are known. The Paleocene – Eocene was the most important time in the diversification of ants (LaPolla *et al.*, 2013), but it is believed that the widespread distribution of ants with large colonies which would be able to launch raids on termites occurred much later than the beginning of the Eocene (Perkovsky, Wegierek, 2018 and references therein). Famous fossil pangolins, such as *Eurotamandua* Storch, 1981, *Eomanis* Storch, 1978 and *Euromanis* Storch et Martin, 1994 from Messel (Germany), are much younger than the age of Cambay amber (Lenz *et al.*, 2015). We do not agree with Bourguignon *et al.* (2017) that ant and termite specialists began by preying on termites, adding ants to their diet later, because the arrival of termites predates mammalian myrmecophagy. Most myrmecophages eat both termites and ants, and in all Paleogene faunas, ants were much more numerous and diverse than termites. Mammals that specialize on termites do not appear until the Miocene, when termitids were very common. In the rich vertebrate fauna of the Tadkeshwar lignite mine, where all Cambay termites have been mined, even Insectivora are absent (Smith *et al.*, 2016), and the primitive primates present were definitely not entomophagous (Bajpai *et al.*, 2008).

The most important termite predators among lizards are the Scincidae (Deligne *et al.*, 1981; Feylininae (ex. Feylinidae) now included in Scincidae), but all named Cretaceous scincids are described from the Santonian-Campanian of Alberta; Canadian amber yields only a single unnamed termite. Fauna of Canadian amber belong not to Isoptera realm, but to *Baeomorpha* realm, where termites are very uncommon (Gumovsky *et al.*, 2018). After this time and until the Priabonian, a single named scincid is known from the late Paleocene of France, and its specialization on termites is highly unlikely. Other more common and important termite pred-

ators among lizards, listed by Deligne *et al.* (1981), are Pygopodidae and Dibamidae, that have not been found as fossils until Oligocene (Dibamidae) or Miocene (Pygopodidae) (Hutchinson, 1997; Čerňanský, 2019). Snakes that regularly predate termites (Typhlopidae and Colubridae: Calamarinae) are unknown as fossils or absent until the late Oligocene.

One of the End Cretaceous extinctions could have been especially important for increasing selection pressure on the earliest Paleogene Indian termites, i.e. the extinction of opposite birds (Enantiornithes) that dominated the low latitudes during the Cretaceous (Mayr, 2017; Perkovsky *et al.*, 2018 and references therein) and supposed explosive radiation of crown birds (Neornithes; Field *et al.*, 2020b). Fossils of Cretaceous arboreal crown birds are unknown. Thus far, only Maastrichtian diving and littoral crown birds have been described (Mayr *et al.*, 2018; Field *et al.*, 2020a). Birds are important, well-known termite predators, but opposite birds with limited cranial kinesis could not catch small insects (ca 10 mm and less) (Perkovsky *et al.*, 2019, 2020 and references therein). Therefore, workers and soldiers of most Kachin amber termites were probably free from avian pressure, as were the workers and soldiers (ca 5–6 mm) of the most common Crato termite, *Meiatermes araripena* Krishna, 1990 (more than 70% of all Crato termites, Grimaldi *et al.*, 2008), and the single Barremian Spanish *Meiatermes* worker which is slightly bigger (7.2 mm: Martínez-Delclòs, Martinell, 1995). Most crown birds belong to Neognathae, with advanced cranial kinesis permitting the swallowing of insects do not need to toss them in the air as opposite birds, and therefore they were able to easily feed on insects less than 1 cm in length (Perkovsky *et al.*, 2020). However, it seems that most of the regular avian predators of wingless termites were absent in the Ypresian tropics, at least in the Cambay amber forest. The most important extant arboreal avian predators of wingless termites are woodpeckers (Vasconcelos *et al.*, 2015), but advanced Eucavitaves were not present in the Ypresian, although there were arboreal birds that could hunt for small insects,

such as the small, thin-beaked Upupiformes (Zelenkov, pers. comm.). Now common termite predators include Phasianidae, Numididae, Otididae, Motacillidae and certain small Ploceidae (Deligne *et al.*, 1981), none of which were present in the Ypresian.

The avian material from the Vastan lignite mine (one of the Cambay amber mining locations) is dominated by *Vastanavis*-like coracoids, of which 25 were found (Mayr *et al.*, 2010, 2013). No other type of coracoid is known from the locality (Mayr *et al.*, 2010). *Vastanavis* Mayr *et al.*, 2007 have also been reported from the Tadkeshwar lignite mine (Smith *et al.*, 2016). *Vastanavis* is assigned to Vastanavidae (Psittaciformes). They are not small and are unlikely to have had a small, thin bill. Most primitive termites had small colonies, and small size of alates could limit at least the number of first-brood eggs. The apparent absence of specialized avian ant and termite predators suggests that a decrease in the size of workers and soldiers reduced the attractiveness of termites as prey for generalist birds. Stylotermitid workers were 2.3–4 mm long (Engel *et al.*, 2016, Table S3), and *Zophotermes* pseudergates were 2–4 mm long. *Nanotermes* workers should be less than 1.5 mm (possibly much less: in the smallest known extant Termitinae from India and Sri Lanka [e.g. *Pericapritermes ceylonicus* (Holmgren, 1911) and *Krishnacapritermes maitii* Chhotani, 1997], workers are only 0.6–0.7 mm length of alates]. We do not know the size of *Nanotermes* colonies, but the size of its sterile castes would be too small for generalist avian predators. A decrease of termite size in Cambay amber could be one of the reasons that they reached their maximum relative abundance in the Paleogene, 1.7% of all Cambay insects. For comparison, termite inclusions from the nearly contemporary Oise amber (neoisopterans absent) make up less than 0.05%. Miniaturization may also explain the eponymous small size of imagines of *Mastotermes minutus* from Oise amber (7 mm, Nel, pers. comm.). The species is two times smaller than Miocene *M. electrodominicus* Krishna et Grimaldi, 1991, who was the smallest mastotermitid till the description of

M. minutus. Other species of the genus are up to three times larger than *M. minutus*. Large protist symbionts (up to 0.55 mm in extant *Mastotermes*) are damaged and digested in a small termite's gut, so for *Mastotermes*, the possibility of size reduction is even more limited than in other lower termites (see below). *M. minutus* head width is 1.9 mm, it is not far from head width of third instar of subsocial cockroach *Cryptocercus punctulatus* Scudder, 1862 averages 1.28 mm (by Nalepa, 2011); it narrows the gap between Mastotermidae and all other termite families (by Nalepa, 2011 at least some termite species from these families may be described as miniaturized). Smaller foragers (4–5.7 mm; 0.6–0.8 length of alates, see Engel *et al.*, 2016, Table S3) would attract less attention from generalist predators, but their symbiosis with protists would be not very effective. Co-habitation of *Mastotermes* of *minutus* size with any ST type termite (including neoisopteran) is unknown. With the appearance of specialized ant and termite predators among mammals, as well as ants with large colonies attacking termites in the late Early Eocene (LaPolla *et al.*, 2013; Perkovsky, Wegierek, 2018), the predators became less selective, and the adaptive reasons of termite miniaturization drastically decreased.

The smallest and most interesting Cambay termite is the most ancient termitid, *Nanotermes*. It is the world's smallest termite, with the body length of alates at 2 mm, and also has trimerous tarsi. Termitidae is the isopteran family that ecologically dominates extant tropical forests. Almost certainly, "the origin and early diversification of the Termitidae was within sub-Saharan Africa" (Krischna *et al.*, 2013: 168). They were already present in the early Ypresian in insular India, and the estimation of their divergence from rhinotermitids (Bucek *et al.*, 2019) in the earliest Paleocene is reasonable. Miniaturization of termitids appears to be a pre-adaptation that seems important for their future diversification. The size of termitid colonies can reach millions of individuals, although some 'primitive' soil feeders retain relatively smaller colonies (Krischna *et al.*, 2013). Termiti-

dae have a worker caste that is strictly sterile. They constitute the vast majority of extant termite species (80%) and are the ecologically dominant taxa in tropics (Bourguignon *et al.*, 2017). Moving forward in time, the next undoubtable termitid from the terminal Oligocene of France is not large (body length of alate is 5 mm; Nel, 1984). Only in Dominican amber do some amber termitids reach 8 mm.

Very small termites (such as *Nanotermes*, workers of Ypresian stylotermitids and small pseudergates of *Zophotermes*) would not attract significant attention from birds. Modern small-sized insectivorous birds try to catch a larger prey and do not forage on small creatures (Zelenkov, pers. comm.) according to observations. Cambay amber flea beetles appear very small compared to extant tropical Alticini (Nadein, Perkovsky, 2019), probably for the same reason. Miniaturization experienced by ancient termitids influenced the simplification of their venation as well.

Thus, the dominance of small termites with trimerous tarsi in Cambay amber is likely related to changes in the nature of predatory pressure in the tropics of the earliest Cenozoic caused by the extinction of opposite birds and rapid radiation of crown birds at low latitudes. In turn, the small sizes of early Neoisoptera facilitated the appearance of a sterile worker caste. The developmental pathway of all Termitidae bifurcates at the first molt after the first externally undifferentiated larval instar (Noirot, 1969). The irreversible separation of neuter and sexual lines in higher termites, apparent after the first molt, is not surprising given that in the course of their evolution, termitids achieved a degree of miniaturization observed in *Nanotermes*. In 1.5 mm long *Nanotermes* workers, or 2.4 mm extant Indian workers, the presence of more than two larval instars and one worker instar is unnecessary, since molting requires energy, and the workers of oldest termitids would be small. In more 'basal' (and larger) lower termites, there are three larval instars and up to eight worker instars (Roisin, 2000), partly influenced by their symbiosis with protists (see below). Small workers are known among extant termitids from

different subfamilies; thus, on the Indian subcontinent, only workers of 2.4–3.5 mm are known for 28 species (15% of all Indian termitids for which the length of workers is known), among which there are even two species with dimorphic workers. For another 79 species (43%), at least some of the workers are smaller than 4 mm (Roonwal, Chhotani, 1989; Chhotani, 1997). For lower termites, workers of 2.74–3.5 mm are known in only three species (two of these are insular or known only from the type locality), which comprises 4% of the total Indian subcontinent lower termites for which the lengths of workers or pseudergates are known. For another 18 species (23% of lower termites), at least some workers are smaller than 4 mm, and all except two of them belong to Neoisoptera (Roonwal, Chhotani, 1989). The small size of Paleogene termitids may be especially important because many termitids forage in the open (Engel *et al.*, 2009), making them more conspicuous to predators. Interestingly, the mentioned single named Oligocene Termitidae (from Southern France; Nel, 1984) is also miniaturized. The length of its body without wings is 5 mm. Eighty-seven percent of extant Indian termitid species for which the body lengths without wings are reported are larger, while all Indian workers (with one exclusion) from species with imaginal body lengths shorter than 5 mm have body lengths between 2.7–4.6 mm (Roonwal, Chhotani, 1989; Chhotani, 1997).

An orphan group of *Stylotermes halumicus* Liang *et al.*, 2017 with fewer than 50 workers and soldiers that was kept in the laboratory started producing replacement reproductives within 6 months (Wu *et al.*, 2018). These data suggest that *Stylotermes* has a linear developmental pathway similar to that of the *Prorhinotermes* Silvestri, 1909 (Wu *et al.*, 2018), *Psammotermes* Desneux, 1902 and *Termitogeton* Desneux, 1904. The mesonotum and metanotum of *Stylotermes* workers, in contrast to those of termitids, can bear long pleural processes (Roonwal, Chhotani, 1989). Colonies of *Stylotermes* are likely composed of no more than a few hundred individuals (Wu *et al.*, 2018: small to medium nests in the referenced Tsai *et al.*,

1978). Symbiotic protists in lower termites can be transmitted only by anal trophallaxis, and it strongly influences its caste system. Reasons for the extinction of most stylotermitids are discussed below.

A feature of social evolution in the most basal termites is that the resources of the colony are inherited by neotenuics (secondary reproductives with juvenile morphological characters). In the most ‘basal’ families (Mastotermitidae, Archotermopsidae, Stolotermitidae), all genera produce neotenuics, while the percentage of termitid genera producing neotenuics does not exceed 16% (Higashi *et al.*, 2000). This is a strong argument for retaining the flexibility of developmental pathways in lower termites that tend not to nest in ephemeral dead branches of living trees (Higashi *et al.*, 2000). An indicator of eusociality is reproductive skew, defined as the probability that workers and soldiers forego direct reproduction (0, all colony members reproduce; 1, all colony members except a single colony breeder forego direct reproduction) (Higashi *et al.*, 2000). Reproductive skew equals 0–0.25 in Architermopsidae and Stolotermitidae and close to 1 in most Termitidae (Higashi *et al.*, 2000).

Contrary to Engel *et al.* (2009), we cannot judge whether Termitidae were abundant during the Eocene in Africa or even other tropical regions based on their absence in Baltic amber because the Baltic amber forest climate was equable (Nadein *et al.*, 2016 and references therein). Extant lower termites with protist symbionts are much better adapted to life outside of the tropics than higher termites (termitids) that originated in the African tropics with their complex of bacterial symbionts. Termite species richness drops very rapidly from roughly 10° north and south of the equator. Species richness at 48°N and S is only 1–4% of the richness at the Equator (Eggleton, 2000). Because the age of succinites is Priabonian (Perkovsky *et al.*, 2007) (contra Engel *et al.*, 2009), termite abundance in ambers was 0.2–0.3% at 48°N in the Priabonian but already nearly 2% in the tropics in the Ypresian. Regarding that the first spike in abundance is due not only to the diversification of the Termitidae (Engel *et al.*, 2009) and Rhinoter-

mitidae but also to the diversification of Stylotermitidae, it is evident that at least in the early Paleogene of tropical Asia, the role of Stylotermitidae was much more significant than in the extant fauna. Three species have been named from the Miocene of California and Washington as well (Krishna *et al.*, 2013). The inability to compete with termitids resulted in stylotermitids becoming a relict group.

Future studies of termite-symbiont coevolution can profoundly change our understanding of their geographical distribution (cf. Perkovsky, Wegierek, 2018). The single successful temperate rhinotermid genus *Reticulitermes* has protist symbionts in common with East Asian archotermopsids, absent in all other rhinotermitids (Gile *et al.*, 2018 and references therein). The absence of neoisopterans from the Miocene of New Zealand is meaningful as well.

Engel *et al.* (2009) suggested that social evolution is like any other highly adaptive feature, such as the evolution of flight in dinosaurs, and thus may take tens of millions of years to refine. It appears it took much longer for termites to reach ecological dominance compared to ants (Engel *et al.*, 2009). The reasons why lower termites that appear in the geological record of the earliest Cretaceous (Vršanský, Aristov, 2014) are nowhere near reaching ecological dominance are understandable now: there are limitations imposed by protist symbionts, requiring more time for the evolution of ecological dominance.

As indicated by Engel *et al.* (2009: 13), “eusociality *per se* does not result in ecological success, but living in very large colonies with extreme division of labor does”. Gut prokaryotes replaced gut protozoa as the key digestive symbionts in the still mostly wood-eating most recent common ancestor of Termitidae (Bucek *et al.*, 2019). For higher termites, the loss of the obligate symbiosis with intestinal Protozoa is of the same importance as ants having a close symbiosis with hemipterans. Honeydew gathering dolichoderines and formicines developed a characteristic proventriculus that allows the crop to carry large amounts of liquid (Perkovsky, Wegierek, 2018 and references therein). The association of lower termites with protists pre-

vented their ecological dominance, and to reach it, termites required much more time.

Termites have their own cellulases, but the loss of key digestive symbionts would be induced by the very strong selective pressure for miniaturization. The extreme miniaturization of the termitid ancestor (the average head width of *Nanotermes* equals 6% of that of *Cryptocercus punctulatus*) was influenced by the rapid diversification of crown birds and their expansion in the low latitudes following the extinction of opposite birds, and this very well corresponds to the estimated age of divergence between Termitidae and their sister clade at 64.9 Ma (Bucek *et al.*, 2019). The hindgut symbionts of lower termites are not fully established until the third or fourth instar (Nalepa, 2011 and references therein). The third instar of the oldest termitids was too small to allow the establishment of hindgut symbionts. Later, the third instar was lost. It leads to the irreversible separation of neuter and sexual lines. Obtaining new gut biota and switching to soil feeding or acquiring external symbionts by the many termitid lineages (Bucek *et al.*, 2019) were just consequences of extreme miniaturization of their common ancestors.

Compliance with ethical standards

CONFLICT OF INTEREST: The authors declare that they have no conflict of interest.

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