



A new Rovno amber termite genus (Isoptera, Rhinotermitidae) from Styr river basin

Evgeny E. Perkovsky and André Nel

ABSTRACT

Lukotermes milescaput gen. et sp. nov. is described on the basis of a dealate specimen from the Eocene amber of Vladimirets district of Rovno region (Ukraine). We provisionally attribute it to the family Rhinotermitidae, subfamily Heterotermitinae for its head shape. It is remarkable for its elongate head capsule with lateral sides parallel and its tibial spur formula 2:2:2. This last character is quite infrequent in this family, also present in the closely related family Serritermitidae, questioning its phylogenetic relationships. This point will be clarified only after the discovery of other specimens showing the wing venation and the mandibular dentition. It is also a very small termite, smallest fossil rhinotermitid, and the second smallest Paleogene termite after the Ypresian genus *Nanotermes* Engel and Grimaldi, 2011. It was supposed that initial weight of parents was more crucial in mesothermal climates with low seasonality of Priabonian European amber forests than in tropical climate of Ypresian Cambay forest. It could be the reason why miniaturization is very strong in Cambay termites and hardly seen in Priabonian ambers, rather than taphonomic biases.

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INTRODUCTION

Ukrainian Rovno amber (Priabonian stage, 33.9–37.8 Ma) is the southern coeval of notorious Baltic amber (Perkovsky et al., 2010). In the most studied order, Hymenoptera, 50% of recorded Rovno species are unknown from Baltic amber (Perkovsky, 2018; Simutnik and Perkovsky, 2020; Radchenko and Perkovsky, 2020). Nearly all Rovno amber material, scientifically studied before 2015, was mined in Klesov (Sarny district), but since 2015 most inclusions were found in the basins of Styr, Veselukha and Horyn (Vladimirets, Zarechnoje, and Dubrovitsa districts). Many taxa are unknown from Klesov, but recorded from Baltic amber, as well as first Rovno records of some Baltic amber species were reported from this area (Perkovsky and Olmi, 2018; Radchenko and Perkovsky, 2018; Perkovsky and Makarkin, 2019, 2020; Legalov et al., 2019; Martynova et al., 2019; Makarkin and Perkovsky, 2020; Mamontov et al., 2020; Lyubarsky and Perkovsky, 2020a; Radchenko and Khomich, 2020; Perkovsky et al., 2020; etc.).

Scientific study of Rovno amber inclusions started from *Electrotermes* von Rosen, 1913 (Kalotermitidae) syninclusions (Perkovsky, 2000), but termites of Rovno amber were not specially studied until 2020 (Perkovsky et al., 2010; Perkovsky and Vasilenko, 2020), while Baltic amber termites are well known with many described species (Engel et al., 2007; Engel, 2008; Krishna et al., 2013). Among these, the Rhinotermitidae are among the most frequently encountered, mainly by alate specimens of two species of *Reticulitermes* Holmgren, 1913. The extant representatives of this family are present under a wide variety of climates. Even if their maximal diversity is under warm tropical regions, the genus *Reticulitermes* is well present and diverse in the southern parts of the Holarctic empire. The fossil record of this family is currently reduced to the Cenozoic of North and Central America and Eurasia (including India) (see Fossilworks database). After Jouault et al. (personal commun., 2020), the family should originate in the Cretaceous. Here we describe a new rhinotermitid genus and species on the basis of a dealate adult that was glued in the fresh resin just after its mating swarm. This fossil is among the smallest known fossil or extant adult termites.

MATERIAL AND METHODS

The localities and composition of the Rovno amber fauna were recently characterized in a

series of reviews by Perkovsky et al. (2010), Jałoszyński and Perkovsky (2016), Perkovsky (2016, 2018), and Martynova et al. (2019). Nearly all studied Rovno amber inclusions from Rovno region were collected from Klesov and the Horyn River Basin (Perkovsky et al., 2010; Perkovsky, 2017) except new collections from the more western basins of the Styr and Stokhod rivers and especially the Veselukha River floodplain between them (Lyubarsky and Perkovsky, 2020b). These new collections (mostly from Voronki and Velyki Telkovichichi) revealed a number of new species of beetles, hymenopterans, neuropterans, and snakeflies (Jałoszyński and Perkovsky, 2019; Legalov et al., 2019; Perkovsky and Makarkin, 2019; Perkovsky et al., 2020) as well as some species described from Baltic amber (Simutnik et al., 2020 and references therein). Rovno amber, as many other succinites, is redeposited (Nadein et al., 2016). The amber piece with the holotype was collected between the Voronki Village and Lake Luko (ca. 35 km to south of Belorussia border) in the former Vladimirets district of Rovno region, together with holotype of the formicine ant *Cataglyphoides dluskyi* Radchenko and Khomich, 2020 (Radchenko and Khomich, 2020) and paratype of *Parastylotermes nathani* Perkovsky, 2020 in Perkovsky and Vasilenko (2020) (other syninclusions listed in Radchenko and Khomich, 2020). The type is deposited in the amber collection of I.I. Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine (Kiev, SIZK).

The amber piece was 130 mm long and 74 mm wide before cutting (N. Khomich, personal commun.); weight before primary treatment ca 310 g; weight after primary treatment 210 g (Radchenko and Khomich, 2020), clear but with some gas bubbles and ‘waves’ around the fossil termite. The piece was cut for *Cataglyphoides dluskyi* description with additional cutting to study the syninclusions, resulting in three samples (see Perkovsky et al., 2012). Photographs were taken using a Leica Z16 APO stereomicroscope with a Leica DFC 450 camera and processed with LAS V3.8 software. Morphological terminology follows Krishna et al. (2013).

SYSTEMATIC PALEONTOLOGY

Order Blattodea Brunner von Wattenwyl, 1882
 Infraorder Isoptera Brullé, 1832
 Family Rhinotermitidae Light, 1921
 ?Subfamily Heterotermitinae Froggatt, 1896
 Genus *Lukotermes* gen. nov.

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Type species. *Lukotermes milescaput* sp. nov.

Diagnosis. Imago characters only. Head distinctly longer than wide, with lateral sides parallel; a distinct bump above base of antenna; compound eyes and ocelli small; postclypeus short, without nose-like projection; pronotum not very transverse, with an anterior side straight and posterior margin strongly emarginated; forewing scale larger and longer than hind wing one, but only slightly overlapping its base; tibial spur formula 2:2:2; four tarsomeres; cerci two-segmented.

Etymology. Named after Lake Luko situated near the amber outcrop, and *termes*, common generic stem meaning termite. Neutral.

Lukotermes milescaput sp. nov.

Figures 1–3

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Type material. Holotype L-122 (well-preserved alate with body, legs, and wing scales preserved, mouthparts hidden by small bubbles), stored at SIZK.

Diagnosis. As for the genus; very small alate, body 3.3 mm long; 15 antennomeres; antennomeres 3 and 4 very small.

Etymology. Named after the Latin 'miles' for soldier, and 'caput' for head; because of the head similar to that of a soldier.

Age and outcrop. Priabonian, Eocene, Rovno amber, near Voronki Village and Lake Luko, Ukraine.

Description. Imago, female. Body 3.31 mm long, head length to apex of clypeus 0.80 mm, head width 0.70 mm, head elongate, longer than wide, with lateral sides parallel (Figure 1A–B, D); sparse short setae on head capsule (longest 0.05 mm long); right antenna with 15 antennomeres (antennomeres 3 and 4 very small); fontanelle weakly visible, situated in anterior part of head capsule with no groove between it and tip of labrum; postclypeus 0.10 mm long, convex but without nose-like projection; right ocellus more or less visible, 0.10 mm long; a pronounced bump above base of antenna; compound eye 0.21 mm long, 0.70 and 0.05 mm high; distance between middle of eye and posterior side of head/distance between middle of eye and anterior part of head = 1.60 (eye rather far from anterior part of head); distal labial palpomere much wider than distal maxillary palpomere. Thorax (Figure 1C) 1.0 mm long, ca. 0.6 mm wide; pronotum flat, 0.37 mm long, 0.53 mm wide, as broad as head with posterior margin strongly emarginate, posterior width along a line passing at median notch 2/3 width along anterior margin; sparse setae pronotum, more numerous on lateral side and pos-

terior half; setae are longer than on head, 0.08–0.09 mm long. Forewing scale 0.43 mm long, slightly overlapping base of hind wing scale; hind wing scale 0.36 mm long; forewing M and CuA apparently separated in scale; both fore- and hind wing scales covered with setae similar to those on pronotum (longest 0.1 mm), directed posteriorly. Four tarsomeres; tibial spur formula 2:2:2 (Figure 2B). Abdomen ca. 1.70 mm long, 0.70 mm wide; last sternite broad, 10th (last) tergite, cerci and paraprocts. Cerci two-segmented, with segments of similar lengths (Figure 3); styli and sternal glands not visible.

DISCUSSION

Following the key of Krishna et al. (2013: 69–71), *Lukotermes* gen. nov. would fall in the group of families Serritermitidae Westwood, 1840 + Rhinotermitidae because of the following characters: antenna with 15 antennomeres; fontanelle present, situated in anterior part of head capsule; forewing scale weakly overlapping base of hind wing scale; pronotum flat, not saddle-shaped; and four tarsomeres. Unfortunately, the shape of the mandible teeth of *Lukotermes* gen. nov. is unknown, thus the choice between the two options 'each mandible with a long apical tooth, left with 1–2 marginal teeth, right without a subsidiary tooth' (Serritermitidae) vs. 'each mandible with a short apical tooth, left with three marginal teeth, right with a subsidiary tooth' (Rhinotermitidae) cannot be decided (see also Canello and De Souza, 2005: 4).

In recent molecular phylogenetic analysis (Bucek et al., 2019), Rhinotermitidae appear paraphyletic in respect to Termitidae and Serritermitidae fit inside the Rhinotermitidae. Thus a new morphological phylogenetic analysis is necessary to better evaluate the value of the characters that are currently used to define these two families. This situation renders somewhat uncertain the attribution to the Rhinotermitidae of any fossil genus.

Nevertheless, we shall discriminate our fossil from the described serritermitid or rhinotermitid genera.

The family Serritermitidae only comprises the two extant genera *Serritermes* Wasmann, 1897 and *Glossotermes* Emerson, 1950. Both have a tibial spur formula 2:2:2 while it is 3:2:2 in the extant Rhinotermitidae and the Cretaceous subfamily Archeorhinotermitinae (Krishna and Grimaldi, 2003; Maiti, 2006). Only the extant Termitogetoninae Holmgren, 1910 (*Termitogeton* Desneux, 1904) and the Ypresian genus *Zophoter-*

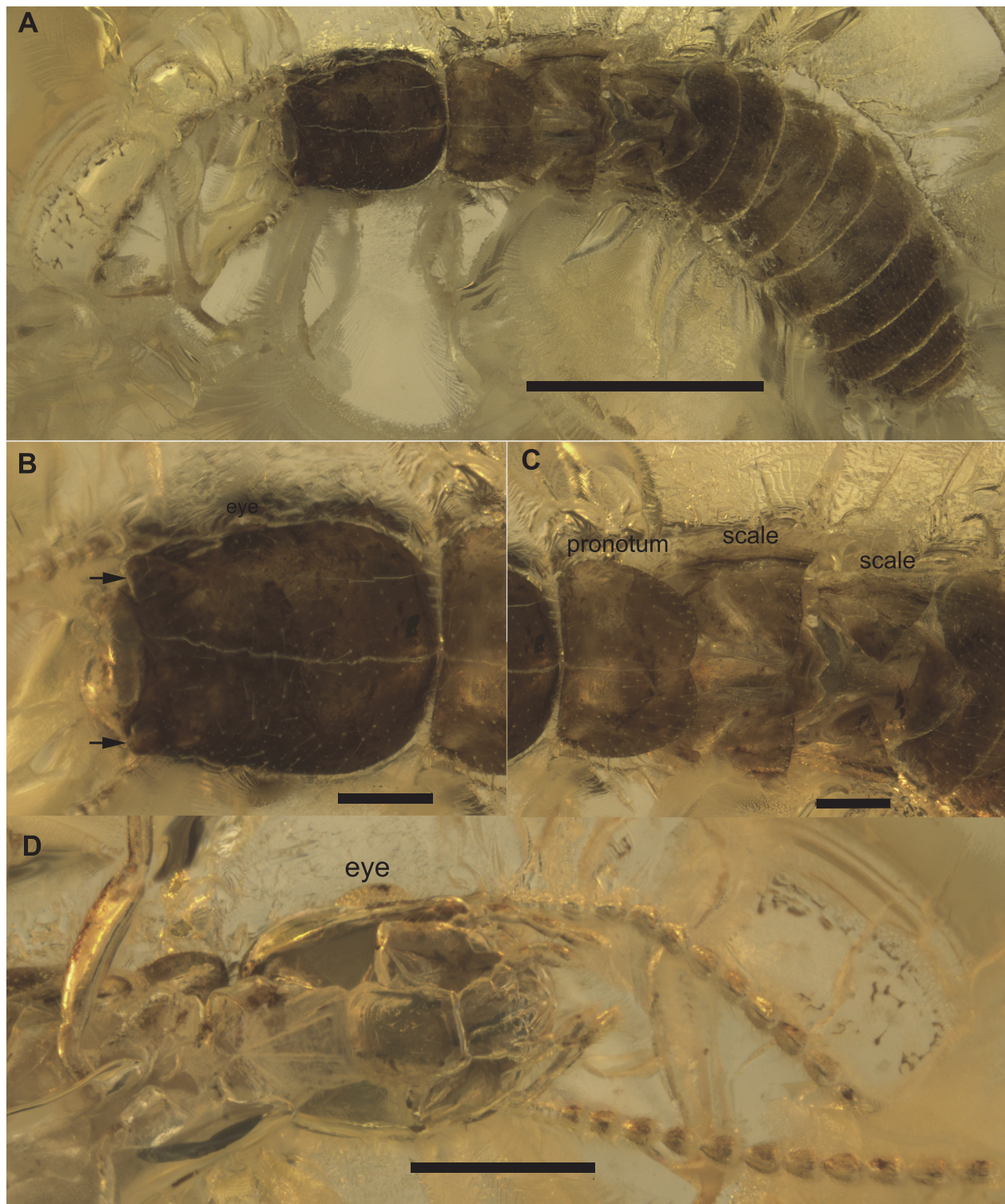


FIGURE 1. *Lukotermes milescaput* gen. et sp. nov., holotype L-122, female. General habitus (A), head from above, arrows: bumps (B), thorax from above (C), head from below (D). Scale bars equal 1 mm in A, 0.2 mm in B–C, 0.5 mm in D.

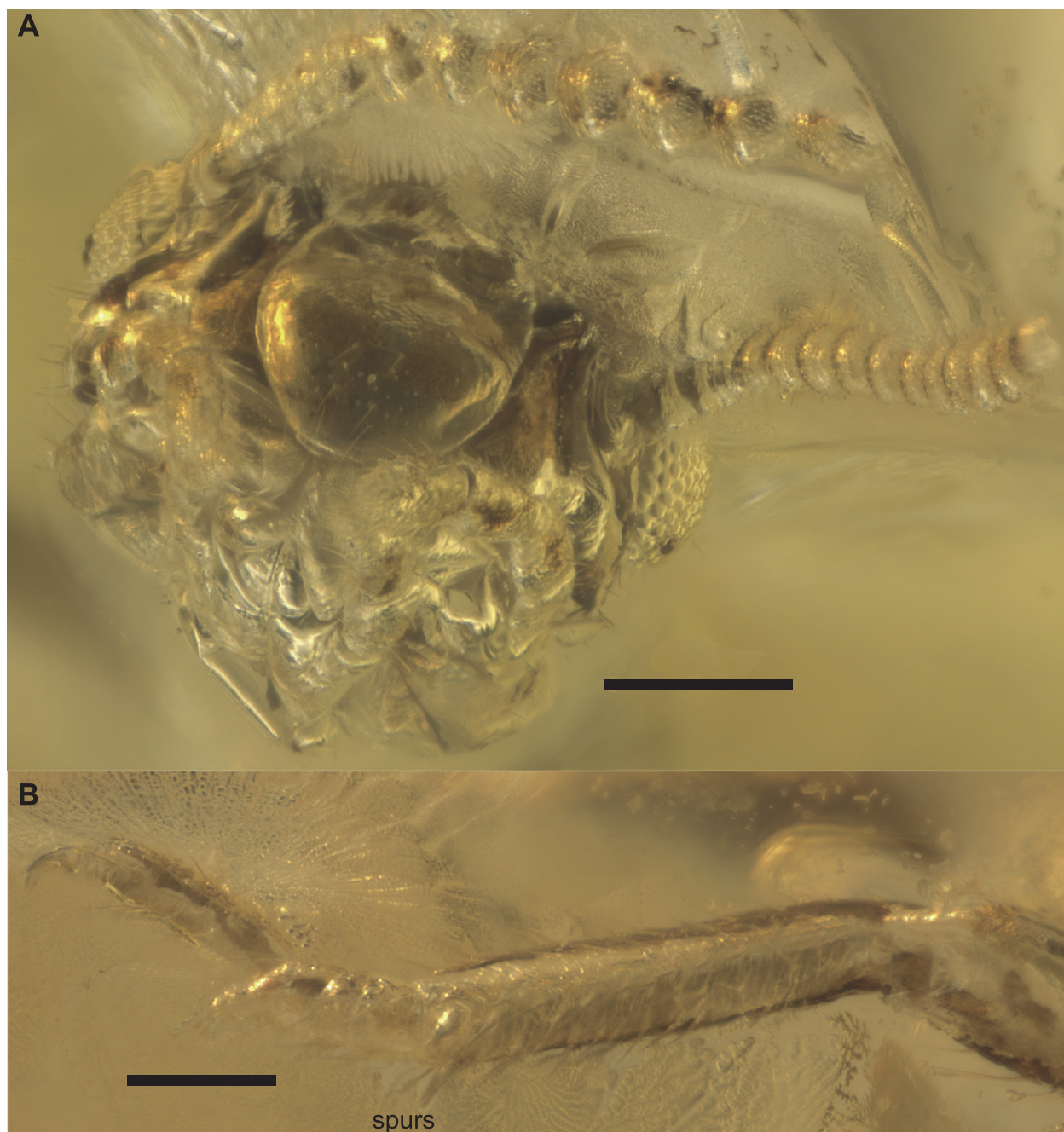


FIGURE 2. *Lukotermes milescaput* gen. et sp. nov., holotype L-122, female. Head frontal view (A), fore leg (B). Scale bars equal to 0.2 mm in A, 0.1 mm in B.

mes Engel (in Engel et al., 2011), currently attributed to the rhinotermitid subfamily Prorhinotermitinae Quennedey and Deligne, 1975, have a tibial spur formula 2:2:2. Maiti (2006: 149) indicated that the unique extant prorhinotermitine genus *Prorhinotermes* Silvestri, 1909 has a spur formula 3:2:2, but Krishna and Grimaldi (2003: 3) supposed that it is 2:2:2; while it is 3:2:2 for Engel et al. (2011: 114, 120). Silvestri (1909: 287, figures

49, 61, 63) indicated 'Tibiae primi paris (figure 49) spinis tribus apicalibus, secundi et tertii paris spinis duabus armatae' and figured three spurs for the fore tibia of alate, soldier and worker. Thus 3:2:2 seems to be the correct issue for *Prorhinotermes*. Engel et al. (2011: 120) added that 'the distribution of the 3-2-2 tibial spur formula across Rhinotermitidae, and even Neoisoptera as a whole, suggests that it is a plesiomorphic condition for these sub-

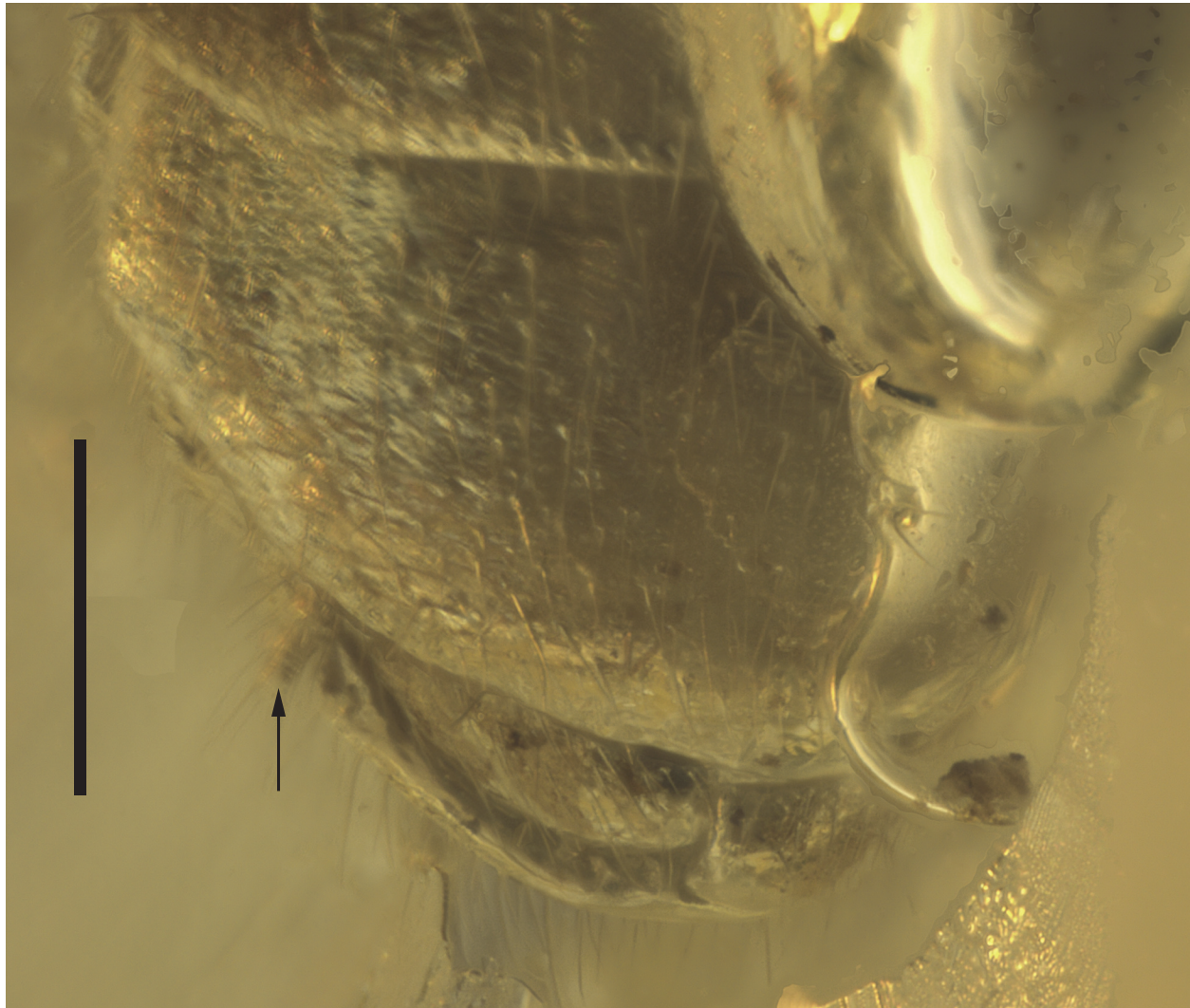


FIGURE 3. *Lukotermes milescaput* gen. et sp. nov., holotype L-122, female. Abdomen apex, arrow: cercus. Scale bar equals 0.2 mm.

families, in which case the 2-2-2 tibial formula in *Zophotermes* is apomorphic'. Engel et al. (2011) did not discuss the possible affinities of *Zophotermes* with the Serritermitidae, but indicated (page 120) that *Zophotermes* 'shares with Prohinoitermitinae and Psammotermitinae the unique branching of the forewing M from CuA outside of the scale (figure 5), otherwise unknown among the Rhinotermitidae', that is M and CuA are basally coalescent and separate just distal of the scale. In *Lukotermes* gen. nov., M and CuA seem to be separated in the scale. In *Glossotermes*, M and CuA are currently supposed to be coalescent (Canello and De Souza, 2005: 10, figure 12), while in *Serritermes*, M is basally fused with R (Emerson and Krishna, 1975: 6, figure 3). Thus the venation characters are

homoplastic and not really sufficient for a family attribution.

It remains that the tibial spur formula 2:2:2 is likely a specialized character convergently acquired and possibly related to the small sizes of the concerned taxa (viz. *Glossotermes*, *Zophotermes* and *Lukotermes* gen. nov.).

Comparison with *Glossotermes* and *Serritermes*

The head capsules of the imagoes of *Glossotermes* are rounded, strongly different from that of *Lukotermes* gen. nov. that is elongate, much longer than wide (Canello and De Souza, 2005: figure 10). Also the pronotum of *Glossotermes* is narrower than head and with posterior margin slightly emarginate, while *Lukotermes* gen. nov. has a pro-

notum as broad as head with posterior margin strongly emarginate. The head capsule of *Serritermes* is slightly broader than long (Emerson and Krishna, 1975: figure 1). If its pronotum is as broad as head in its anterior margin, its shape is quite different from that of *Lukotermes* gen. nov. in the sides more converging and posterior width along a line passing at median notch that is only 1/3 the width along anterior margin (2/3 in *Lukotermes* gen. nov.). Lastly *Serritermes* has 13-14 antennomeres, instead of 15 in *Lukotermes* gen. nov., but the number of antennomeres can vary among different specimen of the same termite species.

Comparison with the Subfamilies of Rhinotermitidae

Apart for the tibial spur formula of *Lukotermes* gen. nov. that is only shared by *Termitogeton* and *Zophotermes* in the Rhinotermitidae, we compare our new genus with the different subfamilies. Krishna et al. (2013: 70) separated the Psammotermitinae Holmgren, 1911 from the other representatives of the Rhinotermitidae by the following character: 'forewing scale about same size as hind wing scale, not overlapping hind wing scale' (Psammotermitinae) vs. 'forewing scale distinctly overlapping hind wing scale, almost reaching tip of hind wing scale' (other taxa). These characters are clearly erroneous or badly expressed because in *Reticulitermes*, the forewing scales do not reach the tip of the hind wing scales (see Goellner, 1931: figure 1). Maiti (2006: 2) indicated that the 'forewing scale [is] generally large, overlapping the hind wing scale [in the Rhinotermitidae] except in *Reticulitermes* and *Psammotermes*'. The same author (page 14) proposed a different couplet, viz. 'forewing scale not longer than of hind wing scale' (Psammotermitinae) vs. 'forewing scale always longer than of hind wing scale' (other taxa). In *Lukotermes* gen. nov., the forewing scale is clearly longer than the hind wing one and slightly overlaps its base but not its apex. This character excludes the Psammotermitinae. Also the head shape of *Lukotermes* gen. nov. is different from that of *Psammotermes* Desneux, 1902 (see Maiti, 2006: figure 3), with parallel lateral sides and the head capsule longer than wide.

The postclypeus without a nose-like projection excludes affinities with the Rhinotermitinae (Maiti, 2006: figure 144B; Krishna et al., 2013). The Archeorhinotermitinae have the forewing scale overlapping the hind wing one, unlike *Lukotermes* gen. nov. (Krishna and Grimaldi, 2003). The heads of the alate Termitogetoninae (*Termitogeton*) are

quite different from that of *Lukotermes* gen. nov., viz. subtriangular, broader than long, with a capsule distinctly narrower at level of eyes than in posterior part (Bugnion, 1914; Krishna and Grimaldi, 2003; Šobotník et al., 2010: figure 1A; Parmentier and Roisin, 2013: figure 3; Krishna et al., 2013). The Coptotermitinae Holmgren, 1910 and the extant Prorhinotermitinae have wide head capsules with rounded sides (Krishna and Grimaldi, 2003; Maiti, 2006; Krishna et al., 2013). *Zophotermes* has the forewing with scale overlapping hind wing scale, unlike in *Lukotermes* gen. nov.

A head with parallel sides, present in *Lukotermes* gen. nov., would characterize the Heterotermitinae (Krishna and Grimaldi, 2003; Krishna et al., 2013). But recent molecular phylogenetic analyses strongly suggest that the Heterotermitinae is paraphyletic to the Coptotermitinae, even with different topologies (Legendre et al., 2015; Dedeine et al., 2016; Bourguignon et al., 2016; Carrijo et al., 2020). Also, Engel et al. (2011: 113) indicated that *Zophotermes* has a 'Head not flattened, narrow oval in shape, with sides somewhat parallel (appears similar to condition in Heterotermitinae but there is some compression which may be obscuring slightly roundish borders)'. Thus the presence of parallel to subparallel sides of head is probably subject to homoplasy. *Lukotermes* gen. nov. also shares with the Heterotermitinae the barely visible ocelli. *Reticulitermes* is separated from *Heterotermes* Froggatt, 1896 after the shape of the labrum of the soldier, tongue-shaped in the former and needle-shaped labrum in the later, and after the structure of the mandible teeth in the alate. Both structures are unknown in *Lukotermes* gen. nov. Nevertheless, *Lukotermes* gen. nov. differs from *Heterotermes* in the presence of pronounced bump above the base of the antenna and the smaller compound eye (Watson et al., 1989: figures 17–19; Maiti, 2006: figures 57A, 60A, 64A, 67A, 70A, 75A, 77A, 78A, etc.), rather similar to that of *Prorhinotermes* (Krishna and Grimaldi, 2003). A similar bump is present in some *Reticulitermes* but clearly less pronounced than in *Lukotermes* gen. nov.; also, in both *Reticulitermes* and *Heterotermes*, the lateral sides of head capsules are less parallel and shorter in parts between the eyes and the postclypeus, than in *Lukotermes* gen. nov. (Goellner, 1931: figures 1, 3; Lash, 1952: figures 1–4; Hsia and Fan, 1965; Tsai et al., 1977, 1980; Ping et al., 1982; Ping, 1985; Takematsu, 1990: fig. 1, 1999: figures 1–4; Clément et al., 2001: figure 1; Lim and Forschler, 2012: figure 3; Ghesini and Marini, 2012: figure 2 A–B). The

shape of the head capsule of *Lukotermes* gen. nov. is more similar to that of a soldier than to an alate in these genera. *Reticulitermes flavipes* (Kollar, 1837) would have also an elongate head capsule, but with the eyes situated closer to the bases of antennae than in *Lukotermes* gen. nov.

The Eocene Baltic amber *Heterotermes eocenicus* Engel, 2008 has much longer setae on head than in *Lukotermes* gen. nov., and its head capsule is rounded, apparently without bumps above the bases of the antennae (Engel, 2008). The head of the Miocene Mexican amber *Heterotermes primae-vus* Snyder, 1960 is deformed and hardly comparable to that of *Lukotermes* gen. nov. (Snyder, 1960; Emerson, 1971). Its redescription, based on better preserved specimens, would be welcome. Numerous Cenozoic fossils are currently attributed to the genus *Reticulitermes* (Nel and Paicheler, 1993; Engel, 2008). *Lukotermes* gen. nov. differs from *Reticulitermes antiquus* in the 15 antennomeres, unlike 17–20 (Germar, 1813). *Reticulitermes minimus* Snyder, 1928 has 14 antennomeres, head and pronotum sizes compatible with those of *Lukotermes* gen. nov., anterior margin of pronotum straight, but an entire body length 6.15 mm contra 3.31 mm in *Lukotermes* gen. nov., and a forewing scale 0.5 mm long contra 0.43 mm in *Lukotermes* gen. nov. (Snyder, 1928; Engel et al., 2007; Engel, 2008). *Reticulitermes minimus* is poorly defined and needs to be revised.

Miniaturization in *Lukotermes* gen. nov.

The alate of *Lukotermes* gen. nov. is very small with a head capsule 0.80 mm long, 0.70 mm wide. These dimensions are comparable to those of *Archeorhinotermes rossi* Krishna and Grimaldi, 2003 (respectively, 0.77 mm and 0.69 mm) slightly smaller than those of the smallest head of alates of *Heterotermes* and *Reticulitermes* (Goellner, 1931; Maiti, 2006). *Termitogeton* has head length to apex of the clypeus mostly larger than *Lukotermes* gen. nov. (Šobotník et al., 2010; Bourguignon and Roisin, 2011). The alate of the Eocene termitid genus *Nanotermes* Engel and Grimaldi (in Engel et al., 2011) has head length to apex of the clypeus 0.30 mm long, making it the smallest termite. Also, the forewing scale of *Lukotermes* gen. nov. is 0.43 mm long, three times as long as that of *Nanotermes* (0.15 mm long for a wing length 2.60 mm), but quite smaller than that of *Archeorhinotermes rossi* (0.64 mm long, for a wing length 4.40 mm). *Lukotermes* gen. nov. had probably short wings but their exact lengths cannot be determined because

the ratio (wing length/scale length) greatly varies among these termites.

Interestingly, *Nanotermes* has also a tibial spur formula 2:2:2, suggesting that this character could be linked to the miniaturization and/or juvenilisation. Indeed, e.g., *Termitogeton* has also antennae generally with 9 to 15 articles and wings without median and radial vein (Bourguignon and Roisin, 2011 and references therein). It seems that this character is subject to many convergences among the termites, as it is also present in some taxa of the termitid subfamilies Apicotermiinae, Termitiinae, and Syntermitiinae.

CONCLUSION

Because of the lack of information on its mandibles, the position of *Lukotermes* gen. nov. between the Rhinotermitidae vs. the Serritermitidae remains problematic. An attribution to the later family is possible because of the spur formula 2:2:2. Nevertheless its shape of head and pronotum is very different from those of the extant Serritermitidae. It can be attributed to the Rhinotermitidae, possibly to the Heterotermitinae, on the basis of the elongate head with parallel lateral sides (but this character is somewhat subject to homoplasy as also present in *Zophotermes*). It does not fit in any of the extant and extinct rhinotermitid genera, and neither corresponds to any of the described Baltic amber Rhinotermitidae. Thus we consider that it corresponds to a new genus and species mainly characterized by an elongate head with lateral margins parallel and a strong bump above the antenna base. We provisionally attribute it to the Heterotermitinae. The discovery of a new alate with the mouthparts and wings better preserved would be welcome to precise its position.

The very particular shape of its head, looking more to a soldier head than to an alate one is surprising (compare with Maiti, 2006: figures 26, 30, 57, etc.), although there are other similar cases, viz. we are currently describing another alate Mastotermitidae from the Cretaceous Crato Formation in Brazil that also shows an elongate head with lateral side strongly parallel similar to that of a soldier (Jouault et al., unpublished data).

All known Ypresian and the single Cretaceous Neoisoptera *Archeorhinotermes rossi* are small (Perkovsky and Vasilenko, 2020); it could reflect a unidirectional decrease in size as a general pattern of termite evolution (Nalepa, 2011). However, as the mating pair still requires a bare minimum of initial metabolic resources to initiate efficient colony foundation and provide biparental care, the com-

bined initial weight of female and male explained 27% of the variation in incipient colony growth (Chouvenc, 2019 and references therein). Study of Chouvenc (2019) was done on a tropical rhinotermitid species introduced to Florida; probably that outside of tropics the initial weight of parents was even more important. It could be the reason why miniaturization was much less expressed in Baltic and Rovno Priabonian amber forest with mesothermal climates with low seasonality and even in Ypresian Oise amber forest with paratropical climate, than in Ypresian Cambay tropical forest (Perkovsky and Vasilenko, 2020). The climate of Rovno amber forest was distinctly warmer than the Baltic one, and it can be the reason of *Lukotermes* absence in the huge amount of Baltic amber inclusions.

Emerson (1971: 257) suggested that 'probably the Termitidae replaced many genera of the Rhinotermitidae in similar habitats in ancient times, as they tend to do at present.' As we do not know any Asian or European descendants of *Nanotermes*, it seems that the first termitid attempts to distribute outside of Africa were 'unsuccessful' (Perkovsky and Vasilenko, 2020 and references therein); at least *Nanotermes*-size termites were too small not only for ecological domination, but even for long-term survival. Earlier African termitids should be much more diverse than first travelers outside of Africa, and their early descendants could have been larger than *Nanotermes*, preventing them from rapid extinction. As there was no termitid 'pressure' on rhinotermitids and styloptermitids (Perkovsky and Vasilenko, 2020), both families

were much more diverse during the Eocene outside of Africa.

Lukotermes as part of this diversity can be especially interesting. It is not only very small for rhinotermitids, it has the smallest forewing scale in Rhinotermitidae and the second smallest forewing scale in fossil termites after *Nanotermes*. In extant Rhinotermitidae, small forewing scale is known only in *Psammotermes*, but this character is found in all Termitidae. We suppose that the characters of *Lukotermes* demonstrate an extreme miniaturization, possible for 'lower' termites without loss of their protist symbionts (see details in Perkovsky and Vasilenko, 2020). As in the recent molecular phylogenetic analyses (e.g., Bucek et al., 2019), the clade (Heterotermitinae + Coptotermitinae) forms the sister group of Termitidae, and as extreme miniaturization was an important step in termitid way to their extant ecological domination (Perkovsky and Vasilenko, 2020), the study of *Lukotermes* and its fossil relatives could be instrumental in the better understanding of higher termites' origin.

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