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COMPARISON OF BITING MIDGES OF THE EARLY EOCENE CAMBAY AMBER (INDIA) AND LATE EOCENE EUROPEAN AMBERS SUPPORTS THE INDEPENDENT ORIGIN OF EUROPEAN AMBERS

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Comparison of Biting Midges of the Early Eocene Cambay Amber (India) and Late Eocene European Ambers Supports the Independent Origin of European Ambers. Perkovsky, E. E. — Of the three genera of Ceratopogoninae dominant in Late Eocene ambers of Europe, the two known are absent in the Early Eocene Cambay amber (India): the Holarctic genus *Ceratopogon* and the worldwide distributed genus *Culicoides*, known since the Late Cretaceous. Tropical biting midge genera (*Meunierohelea* and *Leptoconops* and genera with feminized male antennae: *Camptopterohelea*, *Eohelea*, and *Gedanohelea*) are abundantly represented in Cambay amber. The proportion of Ceratopogonini with feminized male antennae among all Ceratopogonidae dramatically increases from north to south: from 1.4–2.4 % in unbiased collections of Bitterfeld amber (Humboldt Museum collection) and Baltic amber (the Gieciwicz collection) to 7 % in Danish amber and 12.7 % in Rovno amber; their proportion in Cambay amber is 17 %. The proportion of tropical specimens among specimens Ceratopogoninae in unbiased collections is 6.4 % in Baltic amber, 5.3 % in Bitterfeld amber, 21 % in Rovno and Danish amber, and 58 % in Cambay amber. Strong differences in the proportion of tropical components among Ceratopogoninae from different European ambers are in agreement with data on Cambay amber and so are indicative of origin of the European ambers under different climatic and hence geographic environments.

Key words: Eocene, community structure, Ceratopogonidae, Formicidae, *Paleognoriste*, diversity, amber, climate.

Biting midges (Ceratopogonidae), as well as ants and caddisflies, are among the best-studied groups of amber insect fossils. The nomenclature of Ceratopogonidae in this study follows Borkent (2016), collections acronyms follows Perkovsky (2016)..

In one of my earlier publications (Perkovsky, 2013) the representation of different genera of Ceratopogonidae in unbiased collections of Late Eocene (Priabonian) ambers have been discussed in detail. The recently published data on the tropical Early Eocene (Ypresian) Cambay amber (India) (Strebner et al., 2017 a) makes it possible to compare for the first time the compositions of the Early Eocene and Late Eocene ceratopogonid faunas (Early Eocene Fushun biting midges are still rather scant: Strebner et al., 2016 b). Three ceratopogonid genera are clearly dominant in all four

faunas of European succinites; the fourth genus is dominant in three of the four faunas; 71–82 % ceratopogonid specimens in each of the faunas represent either of the four genera (Perkovsky, 2013, table 2). Three of the four genera, *Ceratopogon* Meigen, *Culicoides* Latreille, and *Brachypogon* Kieffer, belong to the subfamily Ceratopogoninae; one, *Forcipomyia* Meigen, belongs to Forcipomyiinae. *Forcipomyia* is dominant also in Cambay amber; *Brachypogon* (9.7 %, the earliest record of the genus) is a subdominant in the Cambay assemblage; but *Ceratopogon* and *Culicoides* (43–56 % of ceratopogonids in Late Eocene faunas are represented by specimens that belong to either of the two genera), have not been recorded in Cambay amber. The absence of *Ceratopogon* is quite natural, since this Holarctic genus is unknown from the tropics. However, *Culicoides* has been recorded in almost all ambers since the Turonian and has a worldwide distribution. In this case there are not enough data to choose between the two alternative hypotheses, one implying that by the Early Eocene *Culicoides* could not have enough time to have crossed the ocean separating India from Laurasia, and the other one that *Culicoides* was present in the Indian fauna but the pleiade represented by *Culicoides* and caddisflies as defined by Perkovsky and Rasnitsyn (2013) was for some reasons insufficiently represented in Cambay amber. The former hypothesis would be supported if the genus *Austroconops* Wirth et Lee, a living fossil from Western Australia (Szadziewski, 2008: fig. 7), replaced everywhere by the genus *Culicoides* (Borkent, Craig, 2004), is eventually recorded in Cambay amber while *Culicoides* is not recorded there. The Sakhalinian amber is of a similar age and also dominated by *Forcipomyia* (72% of the inclusions studied by Szadziewski (1990) and so could be a test for the first hypothesis, and unfortunately *Ceratopogon* and *Culicoides* are both unknown there. A total of four of the nine ceratopogonid genera recorded in Cambay amber have been recorded to date in Sakhalinian amber (Szadziewski, 1990), but only two species were described (Szadziewski, Sontag, 2013), and the fauna greatly needs in revision.

Our data (Baranov et al., 2015) support the idea that the source of Sakhalinian amber had a wetland landscape, which could have been the cause of the fauna of this amber being depleted and peculiar. It is possible that some ecological peculiarities of Cambay amber forest were also prohibitive for *Culicoides*.

The fauna of the Cambay amber is the first fossil fauna that includes as many as three genera of biting midges with feminized antenna (Stebner et al., 2016 a, 2017 a). In the tribe Ceratopogonini the male antennae are feminized (totally lacking plume) only in ten extant genera: the Costa Rican *Cacaohelea* Wirth et Grogan, Colombian *Parastilobezzia* Wirth et Blanton, Neotropical *Leptohelea* Wirth et Blanton (Borkent, Picado, 2008), pantropical *Echinohelea* Macfie, Cape Region *Afrohelea* Wirth and *Calcarhelea* Wirth et Grogan, South African *Luciamyia* de Meillon, Afrotropical *Fanthamia* de Meillon and *Stiloculicoides* Wirth et Grogan (one species was described from Vaucluse in southern France), and Oriental *Camptopterohelea* Wirth et Hubert), and in the Eocene genera *Gedanohhelea* Szadziewski and *Eohelea* Petrunkevitch (see below). The genus *Camptopterohelea* also displays a reduced number of segments in male antennae, considered to be a synapomorphy shared by this genus with *Eohelea* (Borkent, Picado, 2008). Remarkably, only two of the 63 species of the above-mentioned extant genera that have feminized male antennae are known from the subtropics of the Northern Hemisphere, and the rest are known from the tropics and the Western Cape area. It was suggested (Perkovsky, 2013) that the abundance and diversity of *Eohelea* in the Rovno amber is possibly associated with a warmer climate of the Rovno amber forest; at least six (fig. 1) *Eohelea* species were recorded from Rovno amber vs. five in the incomparably better studied Batic amber ceratopogonid fauna. The extant *Camptopterohelea* and *Cacaohelea* combine feminized male antennae with modified female wing apices, similar to those of the Sakhalinian amber species of *Eohelea* (Borkent, Picado, 2008) and one of

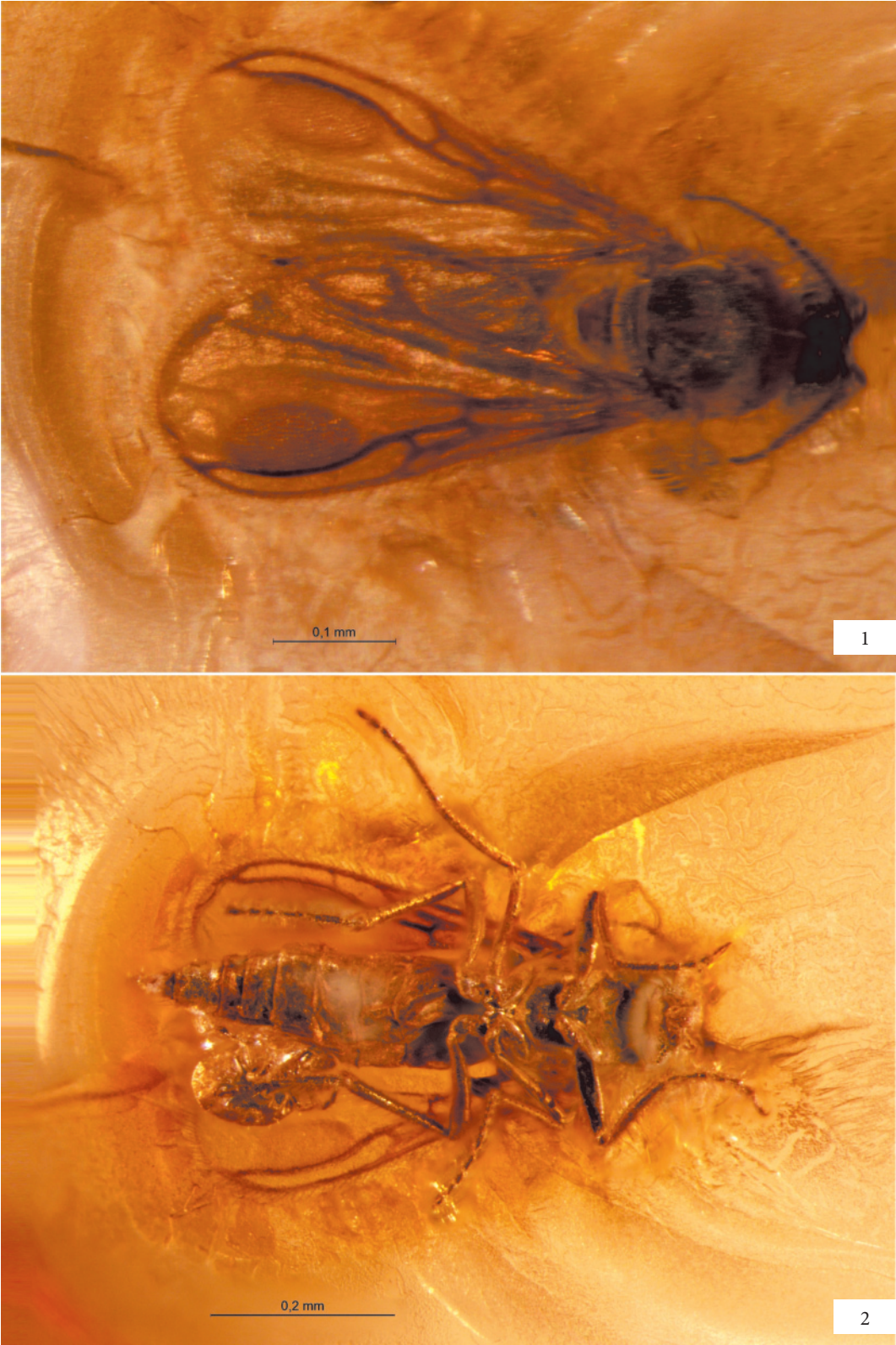


Fig. 1. *Eohelea* sp. with unique structure of wing organ from Rovno amber: 1 — dorsal view, 2 — ventral view.

Priabonian species of this genus (Perkovsky, 2013). Borkent and Picado regard *Camptopterohelea* as a sister group to *Eohelea*; Szadziewski (1988) considered it close to the genus *Gedanohelea*. Very peculiar structures for attracting the males appear in females at least in the Eocene representatives of the genera *Eohelea* (Perkovsky, 2013) and *Camptopterohelea* (Stebner et al., 2016 b). In this study we consider *Eohelea*, *Gedanohelea*, and *Camptopterohelea* as tropical components: *Camptopterohelea* is an extant tropical genus, and *Eohelea* is its closest relative (Stebner et al., 2016 b, 2017 a), not known from any area of temperate climate. The genus *Gedanohelea* is the third most abundant ceratopogonid genus in Cambay amber (and second ceratopogonine one), and *Gedanohelea gerdessorum* Stebner et Szadziewski (12.9 % of all Ceratopogonidae) is the most abundant species in Cambay amber, whereas the proportion of *Gedanohelea* in most European ambers is much smaller than 1 % and nearly reaches 1 % only in one of them, Rovno amber (table 1). In Asia, in addition to Cambay amber, this genus has been recorded from the paratropical Early Eocene Fushun amber (two species: Stebner et al., 2016 b). The thickened vein R_3 found in *Gedanohelea gerdessorum* is unique among ceratopogonids. Interestingly, the proportion of plumeless Ceratopogonini among all Ceratopogonidae dramatically increases from north to south (table 1): from 1.4–2.4 % in unbiased collections of Bitterfeld amber (HMB) and Baltic amber (the Tadeusz Gieciwicz collection) to 7 % in Danish amber and 12.7 % in Rovno amber (Perkovsky, 2013, table 2); their proportion in Cambay amber is 17 % (Stebner et al., 2017 a, table 1; the same proportion, 17 %, is found in Tadkeshwar alone, the site from which the majority of Cambay amber ceratopogonids originate).

The genus *Leptoconops* Skuse has a pantropical range (Szadziewski, 2008, fig. 6). The absence of this genus in the Baltic amber of the Gdańsk Bay can be explained by climatic factors, as well as the absence in this amber of the equally easily identifiable myrmicine genus *Fallomyrma* Dlussky et Radchenko. The latter genus is very common in Danish amber (6.9 % of all ants: Perkovsky, 2011) and much more abundant and diverse than previously believed in Rovno amber, in which one-third of all myrmicines belong to four species of this genus (Perkovsky, 2016).

The only extant species of *Meunierohelea* Szadziewski is known only from tropical rainforests of extreme northern Queensland (Debenham, 1988; Szadziewski, 1993), suggesting that this genus was strongly thermophilic. Similarly to Ceratopogonini with plumless antennae, *Meunierohelea* is very common and diverse in Cambay amber (Stebner et al., 2017 a). Szadziewski (1988) indicated the almost pantropical distribution of the genus *Nannohelea* Grogan as well. We consider the genus *Fossihelea* Szadziewski as also tropical, because it is very closely related to the monotypic *Congohelea* Wirth et Grogan from the Congo Republic, the only extant genus in Ceratopogonini to possess spines only on the fore femur and sensilla coeloconica on the first flagellar segment. It differs from *Fossihelea* only in all female claws lacking the inner teeth; unequal middle and hind claws were found in Bitterfeld *Fossihelea* (Szadziewski, 1993).

The genera *Ceratopogon* (Szadziewski, 2008, fig. 11) and *Ceratoculicoides* Wirth et Ratanaworabhan, *Atyphohelea* Borkent (*Neurohelea* Kieffer in earlier publication on amber dipterans; Szadziewski, 1988, 1993; Perkovsky, 2013), *Forcipomyia* (*F.*) *costata* group, *Forcipomyia* (*Eurojoannisia*) *borealis* group, *Serromyia crassifemorata* group (Szadziewski, 1988), and the genus *Schizohelea* Kieffer (Szadziewski, 1993) are considered here as Holarctic in the sense of Dlussky, Rasnitsyn (2009).

The results are summarized in table 2 which displays that the ratio of Holarctic to tropical specimens in European ambers (in Cambay amber Holarctic species absent). It is 5.4 in the Gieciwicz collection (TG), 8.4 in HMB (Bitterfeld amber), 1.9 in SIZK (Rovno amber), and 1.6 in ZMUC-S (Danish amber). The ratio of the numbers of Holarctic to tropical species is as follows: 1.5 in TG, 1.4 in HMB, 1.2 in ZMUC-S, and 0.8 in SIZK.

Forcipomyiinae and Dasyheleinae from Rovno amber and Forcipomyiinae from Cambay amber (the monotypic subfamily Dasyheleinae is not known from Cambay amber) have not been identified to species (Perkovsky, 2013; Stebner et al., 2017 a). However, Forcipomyiinae are known to include both Holarctic and tropical species groups; genus *Dasyheleia* Kieffer is cosmopolitan. It is therefore necessary to calculate separately the proportions of the tropical component among biting midges of the other subfamilies (table 3). The proportion of tropical biting midges among ceratopogonid specimens identified to genus, excluding representatives of the subfamilies Forcipomyiinae and Dasyheleinae, is 62 % in Cambay amber (Stebner et al., 2017 a, table 1; 61% in Cambay amber from Tadkeshwar) and 20.9 % in Rovno amber (Sontag, Szadziewski, 2011); 22.3 % in Danish amber (our data), 5.3 % in HMB (Bitterfeld amber), 7.6 % in all Bitterfeld amber (Szadziewski, 1993), and 6.4 % in Baltic amber from the Giecewicz collection (our data). The same proportions for Ceratopogoninae alone are very similar: 58 % tropical components in Cambay amber, 20.7 % in both Danish and Rovno ambers, 5.3 % in HMB, and 6.4 % in the Giecewicz collection. Thus, the proportion of tropical components among the Ceratopogoninae is 2.8 times as high in Cambay amber as in either Danish amber or Rovno amber and 3.2–3.9 times as high in either Danish amber or Rovno amber as in HMB (Bitterfeld amber) or Baltic amber (the Giecewicz collection). The proportions of extant tropical genera in different Eocene ambers display a similar pattern, although Rovno and Danish ambers show a considerable difference, and the differences between Cambay and Danish ambers is comparatively small (table 4): the proportion of extant tropical genera among Ceratopogoninae is 2.8–8.3 times as high in Cambay amber as in Rovno amber or Danish amber and 1.5–17.4 times as high in Danish amber or Rovno amber as in representative collections of Bitterfeld amber or Baltic amber (the Giecewicz collection); the proportion of tropical genera among Ceratopogoninae and Leptoconopinae taken together is 2.9–9.3 times as high in Cambay amber as in Danish amber or Rovno amber and 1.6–18.5 times as high in Danish amber or Rovno amber as in Bitterfeld amber or Baltic amber (the Giecewicz collection).

In fact the high proportion of extant tropical genera in Danish amber is caused by the abundance of three species of *Meunierohalea* (tables 1, 2; 8.2 % of all Ceratopogoninae, compared to 3.3 % in Rovno amber; the number of *Meunierohalea* species as in Cambay amber). According to Borkent (2000), the ratio of extant male to female

Table 1. Number of specimens of Holarctic and tropical biting midge genera in representative collections of Late Eocene European ambers

Genus	Rovno amber (SIZK)	Bitterfeld amber (HMB)	Baltic amber (TG)	Danish amber (ZMUC-S)
<i>Ceratopogon</i>	225 (33.7 %)	66 (31.0 %)	80 (27.9 %)	59 (25.4 %)
<i>Eohelea</i>	79 (11.8 %)	3 (1.4 %)	5 (1.7 %)	15 (6.5 %)
<i>Meunierohalea</i>	19 (2.8 %)	1 (0.5 %)	4 (1.4 %)	15 (6.5 %)
<i>Nannohelea</i>	3 (0.5 %)	0	2 (0.7 %)	6 (2.6 %)
<i>Gedanohelea</i>	6 (0.9 %)	0	2 (0.7 %)	1 (0.4 %)
<i>Fossihelea</i>	13 (1.9 %)	4 (1.9 %)	3 (1.1%)	1 (0.4 %)
<i>Leptoconops</i>	2 (0.3 %)	0	0	4 (1.7 %)
<i>Atyphohelea</i>	5 (0.8 %)	0	1 (0.4 %)	3 (1.3 %)
<i>Schizohelea</i>	0	0	1 (0.4 %)	1 (0.4 %)
<i>Ceratoculicoides</i>	0	0	0	1 (0.4 %)
Total	668	213	287	232

Table 2. Share of specimens of Holarctic and tropical biting midges in the representative collections of European ambers

Collection	Holarctic	Tropical	Holarctic/ Tropical	<i>F. borealis</i> & <i>F. costata</i> group	Holarctic/Tropical without <i>F. borealis</i> & <i>F. costata</i> group
TG	87 (30.3 %)	16 (5.6 %)	5.4	3 (1 %)	5.25
HMB	67 (31.5 %)	8 (3.8 %)	8.4	-	8.4
ZMUC-S	68 (29.3 %)	42 (18.1 %)	1.6	4(1.7 %)	1.5
SIZK	232 (34.7 %)	121 (18.1 %)	1.9	-	1.9

Ceratopogonidae within one habitat as well as summarized for the whole group is about 2 : 3 and shifts in favor of females with distance from the original habitat because of female dispersal. Taking this observation into account, we can infer that the ratio of males to females 1 : 2 in Danish amber reflects the entrapment of *Meunierohalea* near the site of emergence, and the ratio 3 : 16 in Rovno reflects the remoteness of the Rovno amber forest from the site of emergence. It is noteworthy that 3 : 16 (15.8 % of males) is the lowest ratio of males to females among the Late Eocene genera of Ceratopogonidae represented by 10 or more specimens (Szadziewski, 1988); therefore, the differences between Danish amber and Rovno amber in the proportion of extant tropical genera are caused only by the difference in the distance from the site of emergence of *Meunierohalea* to the amber forest. In addition, it also follows from the same logic that *Gedanohelea gerdessorum* was extremely abundant, since this species is represented exclusively by females and, notwithstanding, dominates in Indian amber (4 of the 19 ceratopogonines; the only species, known in Cambay amber from both Tadkeshwar and Valia).

The above results are worth comparing with those concerning ants. Earlier it was found that in the Baltic amber, Holarctic ant species clearly prevail not just in terms of the share of their specimens (by 9.8 to 19.6 times), but also by the number of species (Perkovsky, 2016). In Bitterfeld amber, Holarctic ant species are somewhat less numerous than tropical ones, but their specimens are 6 times more numerous than tropical ones (Perkovsky, 2016). In unbiased collections of Rovno and Danish ambers, the number of tropical ant species is 1.5 to 1.7 times as high as of Holarctic species, but the number of their specimens is 4.9 to 6.9 times less (Perkovsky, 2016). The only difference from the results obtained earlier for ants, apart from the fact that Holarctic biting midges dominate over tropical ones in Danish amber in the number of species is the surprisingly high proportion of Holarctic components in the unbiased HMB collection. In the Manfred Kutsher collection the ratio of Holarctic and tropical biting midge specimens is only 3.6, which is only 0.43 times as high as in HMB. We believe that this difference can have two causes. First, most of the amber pieces containing ant inclusions that have been studied from the HMB collections were very small. The

Table 3. Share of specimens of tropical Ceratopogoninae and Leptoconopinae in the Eocene ambers

Amber	Ceratopogoninae	Ceratopogoninae & Leptoconopinae
Baltic (TG)	16 (6.4 %)	16 (6.4 %)
Bitterfeld	17 (7.6 %)	17 (7.6 %)
Danish (ZMUC-S)	38 (20.7 %)	42 (22.3 %)
Rovno (SIZK)	120 (20.7 %)	122 (20.9 %)
Cambay	9 (58 %)	11 (62 %)

Table 4. Share of specimens of extant tropical genera of Ceratopogoninae and Leptoconopinae in the representative collections of Eocene ambers

Amber	<i>Meunierohelea</i> *	Ceratopogoninae*	Ceratopogoninae & Leptoconopinae
Baltic (TG)	4 (1.6 %)	6 (2.4 %)	6 (2.4 %)
Bitterfeld (HMB)	1 (0.7 %)	1 (0.7 %)	1 (0.7 %)
Danish (ZMUC-S)	15 (8.2 %)	21 (11.4 %)	25 (13.3 %)
Rovno (SIZK)	19 (3.3 %)	21 (3.6 %)	23 (4.0 %)
Cambay	5 (26.3 %)	6 (31.6 %)	8 (38.1 %)

*From Ceratopogoninae only.

pieces containing biting midges from the same collection should also be very small, which is confirmed by the extreme scarcity of syninclusions (Szadziwski, 1993). The size of pieces can be the reason of the overrepresentation of *Culicoides* and *Ceratopogon* in HMB (*Culicoides* and *Ceratopogon* compose 58 % of HMB ceratopogonids vs. 43–50 % in SIZK, TG and ZMUC-S): 65 % of Rovno amber pieces containing *Culicoides* and 71% containing *Ceratopogon* weigh less than 3 g, whereas the proportion of amber pieces of such weight containing *Eohelea* is as low as 32 %. The dependence of the proportion of *Eohelea* specimens on the size of amber pieces is very strong. *Eohelea* compose 31.8 % of all ceratopogonids found in the Rovno sample (Perkovsky et al., 2010: table 5), which consists of big pieces, weighing at least 7 g prior to processing, but only 9.1 % of all ceratopogonids found in smaller pieces, weighing 2–5 g prior to processing (Perkovsky et al., 2010: sample 1). Moreover, *E. sinuosa* has not been found in amber pieces of this sample weighing less than 4.5 g. It is precisely the insufficient representation of *Eohelea*, and hence the difference in mean size of amber pieces, that could explain the overrepresentation of Holarctic component of the HMB collection. If the proportion of this genus in the HMB collection were the same as in the Kutscher collection, the number of Holarctic biting midges in it would have been only 4.3 times as high as the number of tropical biting midges.

Perkovsky (2013) erroneously indicated that males represent 16.7 % of *E. sinuosa* (and 12.5 % of all specimens of the genus *Eohelea*) in HMB; in fact, *Eohelea* males are absent in the HMB collection. In practice, non-specialists can very rarely correctly identify male specimens of *Eohelea* to family; the same is often true of specimens of both sexes of the genus *Brachypogon*. The subgenus *Isohelea* Kieffer of the genus *Brachypogon* is one of the dominants in all other representative Late Eocene amber collections, but it is completely absent in the HMB collection, which appears no less strange than the fact that *E. sinuosa* is represented in that collection by only one specimen, whereas the most abundant species of the same subgenus, *B. (Isohelea) prominulus* (Meunier), is represented in Bitterfeld amber (Perkovsky, 2013) and makes up 3.4 % of all ceratopogonids in the Kutscher collection. As many as 7.8 % of all ceratopogonids in the Kutscher collection and only 0.5 % of all ceratopogonids in the HMB collection belong to this genus. It appears to be promising to try to find more individuals of the genera *Eohelea* and *Brachypogon* in syninclusions in larger amber pieces from the HMB collection and among dipterans identified as “Chironomidae” or “Nematocera indet”.

The differences between the ant faunas of European ambers appear more reliable and significant than those between biting midge faunas, because the former have been revealed from larger and more diverse materials (Dlussky, Rasnitsyn, 2009; Perkovsky, 2016). The biased representation of ants in the Kutscher collection (Dlussky, Rasnitsyn, 2009) is directly linked to the fact that amber pieces containing rare or big well preserved ants, in contrast to those containing biting midges, are among the favorite collecting

items. It is difficult to imagine the reason why the bias in representation of biting midges in the Kutscher collection being even much less than the bias in representation of ants. The proportion of tropical Ceratopogoninae in the HMB and Kutscher collections together (151 and 71 specimens, respectively) is 7.6 %, and the ratio of Holarctic to tropical specimens is 3.6 (5.4 in Baltic amber: table 2), which confirms that further studies can help to correct the available data on the composition of Ceratopogonidae in the HMB collection.

The combination of Holarctic and tropical elements in one fauna (and even in one syninclusion) is well known for European ambers and explained by equable climate of their origin (see Archibald, Farrel, 2003). Therefore, Priabonian amber Ceratopogonidae faunas, as well as the Formicidae faunas (Perkovsky, 2016), differ from tropical faunas in the strong representation of Holarctic components, many times as abundant as the tropical components. This composition of faunas is incompatible with the assumed Middle Eocene (Lutetian) dating of the succinites, because in the paratropical climate of the latest Early (Lenz et al., 2015) and Middle Eocene of Europe tropical elements had to be at least visibly dominant, as they are in Cambay amber (58 % of all ceratopogonine specimens). At the same time, the proportions of tropical components among ceratopogonines in Baltic amber or Bitterfeld amber (6–8 %) on the one hand, and in Rovno amber or Danish amber (21 %) on the other hand, are considerably different; moreover, the differences between these faunas in the proportion of tropical components are much more pronounced for biting midges than they are for ants. In reality differences can be even bigger: I have not included in this analysis the genus *Mantohoelea* Szadziewski, known from Cambay, Fushun and Late Eocene European ambers and similar in venation and the presence of spines on female forelegs to the tropical *Eukraiohelea* Ingram et Macfie: armed forelegs of both sexes are known only in *Mantohoelea* and extant tropical genus *Heteroceratopogon* Wirth et Grogan (Szadziewski et al., 2007). The genus is very rare in Baltic amber and more common in its southern coeval Rovno amber (at least the first *Mantohoelea* males were found after 103 years of study in Baltic and after 5 years of study in Rovno). In paratropical Fushun it was found in the first five pieces of amber with biting midges determined to genus. In the temperate Sakhalinian amber the genus is not recorded yet. All in all, *Mantohoelea* occurrence in temperate regions seems very unlikely. If *Mantohoelea* is taken in account, tropical components in Cambay amber will equal 63 % of all ceratopogonines (in European ambers *Mantohoelea* is uncommon, so shares of tropical components will be unchanged).

Interestingly, no faunal connections between contemporaneous thermophilic Cambay amber from India and Oise amber from France have been found to date yet, in contrast to numerous affinities recorded between the fossils in Cambay and Baltic ambers (see references in Stebner et al., 2017 b: 3). We suppose that the reason is the earliest Ypresian age of Oise and Cambay amber. Asian communities had no time to establish in islands of Western Europe in Ypresian; easily determinable longbeaked *Paleognoriste* Meunier present in Cambay amber (Stebner et al., 2017 b), but absent even in Ypresian Fushun amber and Middle Eocene Sakhalinian amber (its age is not Paleocene, Baranov et al., 2015), but two species of this genus known from Priabonian Baltic amber. We suppose that there was not enough time in Ypresian for migration of *Paleognoriste* and Asian elements (similar in Baltic and Cambay amber) to Europe. The finding *Paleognoriste* in Priabonian Rovno amber would support this hypothesis.

Strong differences in the proportion of tropical components among Ceratopogoninae from different European ambers are in agreement with data on Cambay amber and so are indicative of origin of the European ambers under different climatic and hence geographic environments.

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