

Short communication

Non-aculeate hymenoptera in the Cretaceous ambers of the world

Alexandr P. Rasnitsyn^{a, b, *}, Christoph Öhm-Kühnle^c^a A.A. Borissiak Palaeontological Institute, Russian Academy of Sciences, Moscow 117647, Russia^b Natural History Museum, London, SW7 5BD, UK^c Kirchgasse 11, 71083 Herrenberg, Germany

ARTICLE INFO

Article history:

Received 9 June 2020

Received in revised form

4 January 2021

Accepted in revised form 26 February 2021

Available online 4 March 2021

Keywords:

Amber inclusions

Cretaceous

Hymenoptera symphyta

Hymenoptera parasitica

Biogeography

Biodiversity dynamics

ABSTRACT

A review of non-aculeate hymenoptera recorded in the world's Cretaceous amber assemblages is provided herein. Recorded are 287 species (265 named) representing 47 families in 17 amber assemblages. The richest in family number is the Burmese (Kachin) amber (35), followed by Canadian (19), Spanish (15), Kheta (12), Raritan (11), Charentese (10), Agapa (9) and Levantine (7) ones; hymenopterans in other ambers are less well documented. In the eight mentioned amber faunas, the share of extinct families decreases from 50/53 to 21 percent in a good correlation with their putative age, therefore suggesting a contiguous character of the studied world fauna. This inference is confirmed by the fact that endemic families are not recorded, with the only but prominent exception of the insular Burmese (Kachin) fauna with its 8 endemic families (23% of known hymenopteran families there). The rate of gradual loss of extinct families in succeeding amber assemblages shows that the main transformation took place during the first half of the Late Cretaceous, and not the Cretaceous–Paleogene boundary. As taxonomic revisions, two species are placed in different families than originally ascribed to, namely, *Albiogonalyx elongatus* Nel, Perrichot & Néraudeau, 2003, is transferred to Praeaulacidae, and *Phoriostephanus exilis* Engel & Huang, 2017, is transferred from Stephanidae to Roproniidae.

© 2021 Elsevier Ltd. All rights reserved.

1. Introduction

Hymenoptera with their 155,517 world species and 132 families (Aguilar et al., 2013) are one of four megadiverse insect orders. Non-aculeate Hymenoptera, which we treat herein, form more than half of the above figures, that is, 89,255 species and 100 families or 57% and 76%, respectively (Aguilar et al., 2013). Non-aculeate hymenopterans are well represented in various Cretaceous ambers (Rasnitsyn et al., 2016) and are highly diverse in their biology and environmental ties, therefore, studying their biology and taxonomy has the potential to provide a great amount of diverse information on the past fauna, flora, biocenoses, climate, and landscapes, and a review is of high interest. The review by Rasnitsyn et al. (2016) was less detailed and, despite just having been undertaken a few years ago, already is outdated because of the great amount of new research during the last years, particularly concerning Burmese amber inclusions (Ross, 2019, 2020a,b). We did our best to compile

all taxa of non-aculeate hymenopterans recorded in Cretaceous ambers (SI Table 1). Due to the high amount of world-wide research, however, it might not be possible include every single publication.

2. Material and methods

All data presented are based on the mentioned publications (SI Tables 1 and SI references). Geographic and stratigraphic position of the ambers considered is shown in Fig. 1. For the hymenopteran taxa involved, we rely on the first descriptions/records unless a later publication affects the taxonomic position of respective taxons or adds their new records within different amber deposits (amber group). The taxonomic changes introduced herein are presented in the Systematic paleontology section:

3. Systematic paleontology

Order Hymenoptera Linnaeus, 1758
 Superfamily Evanioidea Latreille, 1802
 Family Praeaulacidae Rasnitsyn, 1972

* Corresponding author. A.A. Borissiak Palaeontological Institute, Russian Academy of Sciences, Moscow 117647, Russia.

E-mail addresses: alex.rasnitsyn@gmail.com (A.P. Rasnitsyn), christoph.oehm@bmx.net (C. Öhm-Kühnle).

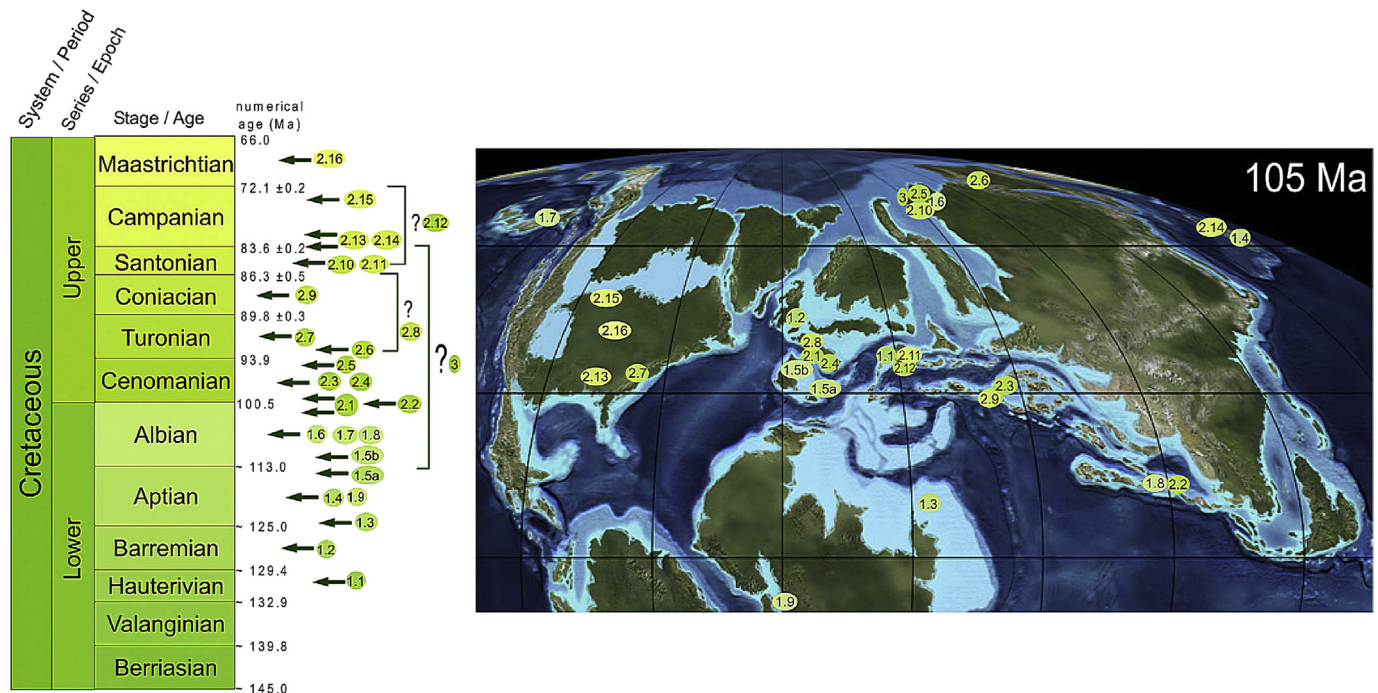


Fig. 1. Geographic and stratigraphic distribution of the Cretaceous ambers studied (modified from Rasnitsyn et al., 2016). Localities: 1. Lower Cretaceous: 1.1. Golling, Austria; 1.2. Wessex Fm., Isle of Wight, U.K.; 1.3. Levantine amber belt (Lebanon, Jordan, Israel); 1.4. Choshi, eastern Honshu Isl., Japan; 1.5.a mainly Escucha Fm. (San Just, Arroyo de la Pascueta, La Hoya) - upper Aptian, 1.5b mainly Utrillas Group (El Caley, El Sopla, Pefiacerrada, Salinillas de Buradón) - Albian, Spain; 1.6. Begichevo Fm. (Zhdanikha, Kresty) Taimyr Peninsula, Russia; 1.7. Arctic Coastal Plain, Alaska, U.S.A.; 1.8. Hkamti amber, Sagaing Region, Myanmar; 1.9. Chéla Formation, Congo. 2. Upper Cretaceous: 2.1. Charentese amber (Archingeay-Les Nouillers, ile d'Aix, Cadeul, Puy-Puy, Fouras, etc.), Western France; location for part of 2.4 (middle Cenomanian Anjou amber) is the same; 2.2. Hukawng Valley, Myanmar; 2.3. Agdzhakend, Azerbaijan; 2.4. (part) Fourtou and Salignac, South-eastern France; 2.5. Agapa, Taimyr Peninsula, Russia; 2.6. Timmerdyakh, Yakutia, Russia; 2.7. Raritan Fm., New Jersey and Maryland, U.S.A.; 2.8. Vendée, Western France; 2.9. Shavarshavan, Armenia; 2.10. Kheta Fm. (Yantardakh, Romanikha, Ugolyak), Taimyr Peninsula, Russia; 2.11. Piolenc and Belcodene, Southern France; 2.12. Ajka, Csinger valley, Hungary; 2.13. Eutaw Fm. (Alabama - Santonian), Neuse River near Goldsboro (North Carolina - Campanian) U.S.A.; 2.14. Kuji group - Campanian and Futaba group - Santonian, northern Honshu Isl., Japan; 2.15. Grassy Lake, Alberta, and Cedar Lake, Manitoba, Canada; 2.16. Hell Creek Formation, North Dakota, U.S.A. 3. Controversially dated locality: Baikura, ? Ognevka Formation, Taimyr Peninsula, Russia.

Genus *Albiogonalyx* Nel, Perrichot & Néraudeau (2003)

Type species. *Albiogonalyx elongatus* Nel, Perrichot & Néraudeau (2003)

Remarks. The genus was described by Nel et al. (2003) within the family Trigonalysidae (for the correct spelling of the name see Engel, Lelej, 2020) from the Charentese amber. However, its hind wing venation demonstrates free apical section of Cu leaving outer side of cell cua far from A, as well as a short free apex (Nel et al., 2003, fig.4). Both these features are not at all characteristic of Trigonalysidae which have free A lost and that of CuA shifted toward A and mimicking its free apex (Rasnitsyn, 1988). At the same time, the holotype of *A. elongatus* even though being shown dorsally (Rasnitsyn, 1988, fig. 1), shows its metasoma attached high on the propodeum. Additionally, general appearance of the insect with its antennae long and multisegmented, several basal metasomal segments much elongate and legs very long (particularly the hind ones) suggest its evanioid affinities. That is why it is transferred herein to Evaniioidea based on the above features. It is attributed to the family Praeaulacidae because their hind wings possess enclosed cells which is diagnostic of Praeaulacidae, Othniodellithidae and Anomopterellidae and because Othniodellithidae clearly differ in the enlarged and modified head (normal in *Albiogonalyx*), and Anomopterellidae have venation modified (fore wing cells 2- and 3r-m fused on one long cell and hind wing RS fused with M distally) unlike an ordinary venation of *Albiogonalyx*.

Family Gasteruptiidae Ashmead, 1900

Type genus. *Gasteruptia* Latreille, 1797

Remarks. We follow Townes (1950) in treating the family as embracing also Aulacidae (as the subfamily Aulacinae); the same,

contra Engel (2013), concerns the family Baissidae (Rasnitsyn, 2013). The reason most importantly, but not only is the existence of transitional forms which are referred to by Townes (1950) and are particularly abundant among Mesozoic fossils, but also a consideration that, if treating Aulacinae as a full family, the same should hold for Baissidae as well, which in our eyes is an explicitly paraphyletic group (the mother rather than sister one in respect to both Gasteruptiidae and Aulacinae; for details see Rasnitsyn, 2013). Gasteruptiidae in the present wide sense display easily recognizable synapomorphies not shared by Evaniidae (male antenna with 11, female with 12 flagellomeres), which confirm their monophyly (Li et al., 2018).

Family Evaniidae Latreille, 1802.

Genus *Cretevania* Rasnitsyn, 1975

Cretevania sp.

Female evaniid wasp: Bouju, Perrichot (2020), fig. 3A.

Remark. The wasp from the Congo amber displays the unmistakable diagnostic characters of *Cretevania*: large semicircular head tightly appressed to short and high mesosoma, fore wing with incomplete M+Cu, long and narrow cell 3r (marginal), small cell 1mcu with postfurcal 1cu-a, Cu practically straight from cu-a till apex (without usual strong kinks at 1m-cu and 2cu-a), and metasoma with a long petiole which is widened subapically and attached to propodeum at the end of its rather long dorsal surface. These are the reasons why the wasp is attributed to the above genus.

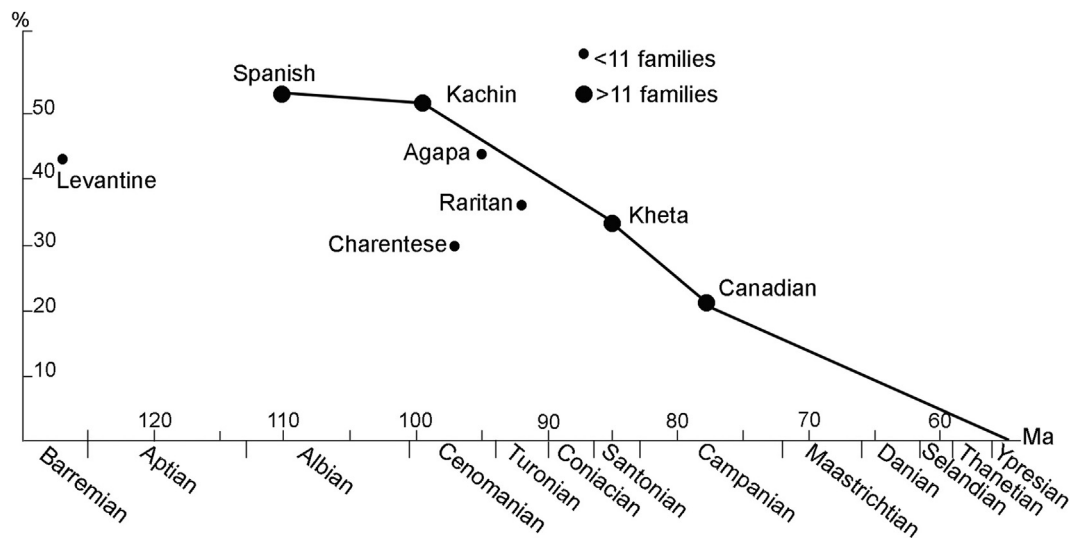


Fig. 2. Share of extinct families of non-aculeate Hymenoptera in more rich Cretaceous amber assemblages. Only assemblages with 10 or more families considered.

Superfamily Proctotrupoidea Latreille, 1802
Family Roproniidae Viereck, 1916
Genus *Phoriostephanus* Engel & Huang, 2017
Type species. *Phoriostephanus exilis* Engel & Huang (2017)

Remark. *Phoriostephanus exilis* Engel & Huang (2017) is described as a member of the family Stephanidae (Engel, Huang, 2017). However, the illustrations provided (Engel, Huang, 2017 Figs 1–3) demonstrate clearly that the wasp in question lacks the characters diagnostic of Stephanidae. Its head lacks a crown of teeth around the fore ocellus, and its hind femur is ordinary (not incrassate and with no ventral teeth). At the same time, its wing venation is typical of Proctotrupoidea: 3r cell triangular, 2r-m, 3r-m and 2m-cu crossveins lost, and Cu with weak kinks at 1m-cu and 2cu-a. Within Proctotrupoidea, a combination of the long metasomal petiole with short scape excludes all families other than Roproniidae and Heloridae. *Ph. exilis* is attributed to Roproniidae based on the cell 1mcu which is quadrangular (triangular in Heloridae) and Cu which is weakly but distinctly angular at 1m-cu and 2cu-a and not straight there as in other Proctotrupoidea.

4. Discussion

By January 1, 2021, as many as 287 species of non-aculeate Hymenoptera were recorded from Cretaceous amber assemblages, either named or unnamed but identified up to family level (SI Table 1). This comprises 265 fully described species and 47 families recorded. The most diverse are Evaniidae with 28 species, followed by †Serphitidae (22), Braconidae (20), Scelionidae (18), †Stigmaphronidae (17), Rotoitidae (15), Gasteruptiidae (14), Ichneumonidae (13) and †Maimetshidae (11). However, the above figures also are a result of preferences of researchers interested in certain groups and do not entirely depict the actual diversity.

Information about the relative abundance of various families in different amber assemblages could be more indicative than the total number of identified species, but unfortunately that information is even less reliable due to the inconsistent rate of research done on the different assemblages. A general impression, however, is that in rather well-explored ambers, Scelionidae is the most common family of non-aculeate hymenopterans. In Spanish amber (Ortega-Blanco et al., 2009), Scelionidae comprise 60% and

†Stigmaphronidae 18% of all Hymenoptera. In the collection of Kachin amber at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (Zhang et al., 2018), Scelionidae are the most abundant among the registered specimens, followed by Evaniidae, †Serphitidae, Megalynidae and Gasteruptiidae. In Baikura amber (Rasnitsyn, 1980), Scelionidae are followed in abundance by †Serphitidae, Mymarommatidae and Rotoitidae. Agapa amber is richer in Scelionidae, with less abundant †Stigmaphronidae and Mymarommatidae, and even less †Serphitidae. The Raritan fauna (Grimaldi and Ross, 2017) is equally dominated in number by Scelionidae, followed (with a wide gap) by Braconidae. In the Kheta amber (Rasnitsyn, 1975), Scelionidae are followed by †Serphitidae and, again with a wide gap, by Braconidae, Mymarommatidae and Rotoitidae. A similar structure is found in Canadian amber (McKellar and Engel, 2012, table 2): Scelionidae are followed with a wide gap by †Serphitidae and Mymarommatidae, then by Chalcidoidea (apparently mainly Rotoitidae). Taking into account that in Cenozoic Mymarommatidae and Rotoitidae turned into rare, relict groups, it is possible to conclude that all known rich Cretaceous amber assemblages, even the latest Canadian one, had a half of their dominated families extinct or nearly extinct now. Unlike this, the Cenozoic hymenopteran assemblages, both from amber and rock, included an absolutely negligible share of extinct families (e.g., Rasnitsyn, 1977) and a tiny one of those representing unquestionable relicts, such as Xyelidae (Rasnitsyn, 1995), Blasticotomidae (Zhelokhovtzev and Rasnitsyn,

Table 1
General composition of more rich amber assemblages.^a

Amber	Age	Species	Families		
			Total	Extinct	Endemic
Levantine	Barremian	13	7	3 (43%)	0
Spanish	Albian	42	15	8 (53%)	0
Kachin	mid-Cretaceous	105	35	18 (51%)	8
Charentese	Cenomanian	10	10	3 (30%)	0
Agapa	Cenomanian	10	9	4 (44%)	0
Raritan	Turonian	17	11	4 (36%)	0
Kheta	Santonian	36	12	4 (33%)	0
Canadian	Campanian	44	19	4 (21%)	0

^a Considered are only the assemblages with 10 or more species recorded, including those identified up to genus or family level, or to superfamily level in case of Chalcidoidea.

1972), Mymarommatidae (Ortega et al., 2011), Heloridae (Muona, 2020), Scolebythidae (Brothers, Janzen, 1999), Embolemidae (Olmi et al., 2010), Rhopalosomatidae (Lohrmann et al., 2019).

A comparison of the richer amber assemblages (with 12 or more families recorded) in their taxonomic composition, as revealed by SI Table 1, shows a pattern of a share of extinct families around 50% during the Earlier Cretaceous that changes with its decrease up to about 20% toward the Campanian age before the end of the Cretaceous period (Fig. 2). The precise date when the decrease started is not clear yet because the meaning of the high share of extinct families in the Kachin assemblage is somewhat equivocal. The established age of amberiferous deposits of Kachin, the earliest Cenomanian (Shi et al., 2012). At the same time, the insular (isolated) nature of the Kachin biota could be a reason why it was enriched with old taxa (Rasnitsyn and Öhm-Kühnle, 2018; Zhang et al., 2018) in contrast to mainland mid-Cretaceous biotas that might have already lost a part of their extinct families. Nevertheless, it is possible to infer that a loss of some 30% of extinct families has started at some time near the boundary between the Early and Late Cretaceous and continued at least for the next some 20 myr up to the Campanian. The remaining 20% have been lost somewhere within the interval of another some 20 myr between the Campanian and Ypresian (earliest Eocene), when the youngest Cenozoic insect assemblages are known that are rich enough for comparison and known to lack any appreciable share of extinct families of Hymenoptera. These are the Oise amber, France (Nel and Brasero, 2010) and Okanagan Highlands, SW Canada and NW USA (Archibald et al., 2018). The precise dating of the above events remains impossible, yet we can conclude that the available information provides no support for the hypothesis of the end-Cretaceous mass extinction or for a stronger decrease than during the within-Cretaceous event.

Another important result implied by Table 1 is a unique abundance of endemic families in the Kachin amber (23% of the families recorded), as opposed to no endemic families found in any other assemblages studied. This further supports the hypothesis of an insular nature of the West Burma plate isolated in the midst of the Tethys Sea (Rasnitsyn and Öhm-Kühnle, 2018; Zhang et al., 2018; Westerweel et al., 2019).

An interesting aspect of the taxonomic composition of non-aculeate hymenopterans in Cretaceous amber is a lack of some taxa that would be expected to be a part of it. The archaic sawfly family Xyelidae is a long-known example for this (Rasnitsyn, 1969, p. 21). Living Xyelidae are mainly (except for the tribe Macroxyelini) and tightly connected with conifer trees (e.g., Taeger et al., 2010). The absence of any Xyelidae and particularly of the genus *Xyela* Dalman from any amber including the Baltic one is paradoxical for many reasons. First, *Xyela* is a pine tree specialist, and *Pinus* L. is well known to be abundant and diverse in the Baltic amber forest and one of possible sources of that amber (Alexeev, 2018). Also, the genus *Xyela* is recorded since the Early Cretaceous (Rasnitsyn, 1965), and not uncommon in the Cenozoic (Rasnitsyn, 1995). Furthermore, *Xyela* wasps are small enough to get trapped in resin and therefore should have been recorded from amber assemblages (Zherikhin et al., 2009). Rasnitsyn (1969) hypothesized that this lack of Xyelidae buried in amber could be due to an abundance of ants, which however is not particularly convincing due to, the first, scarcity of Cretaceous ants and the fact that ants comprise 10% of the sample of contemporary resin containing *Xyela*. So, this enigma remains unsolved.

One more intriguing case is the lack of Proctotrupidae which are absent from all Cretaceous ambers despite their abundance as Lower Cretaceous rock fossils (Rasnitsyn et al., 1998). Unlike Xyelidae, Proctotrupidae are recorded in Baltic amber (Brues, 1940), and their absence in Cretaceous amber is as difficult to explain as in

the case of Xyelidae. There are more families known from Lower Cretaceous rock fossils that would also be expected in Cretaceous amber but are still lacking there, such as Sepulcidae, Archaeocynipidae, Jurapriidae, or Praeichneumonidae. However, these are not as common in the Cretaceous as Proctotrupidae, so their absence from amber is less unusual.

Furthermore, it is worth to mention the case of Bipetiolarida, a group comprising two superfamilies of tiny parasitic wasps, Serphitoidea and Mymarommatoidae, abundant in most Cretaceous ambers (see above), but later (Eocene through now) represented only by the single and very rare family Mymarommatidae. Yet, the Barremian Levantine amber provides only a unique find of two males of the archaic Bipetiolarida *Archaeoserphites* Engel, 2016. This could mean that the Barremian was the very dawn of bipetiolarids.

Concerning the trophic preferences of the non-aculeate hymenopterans recorded from Cretaceous ambers, it is assumed that the majority was carnivorous, with the remaining wasps being apparently pollinivorous (Syspastoxyelidae, an analogue of smaller Xyelidae), xylomycetaphagous (Anaxyelidae, based on habits of the unique living relative), or feeding whilst boring inside living twig tissues (Cephidae, for the same reason) (for the biology of living relatives and analogues see Rasnitsyn, 1969). No folivorous wasps are found, except possibly a single species of the gall wasp Cynipidae.

Except for Cynipidae, all recorded non-aculeate Apocrita are parasitic. Many of them are expectably xylobiotic judging either by the biology of their living relatives (Orussidae, Stephanidae, Megalyridae) or by characteristic adaptations of the head (a support which aids the enclosed wasp in getting out from the wood). These adaptations support the head directly (the head is armed with teeth in Burmorussidae, Orussidae, Ohlhoffiidae and Stephanidae; Jouault et al., 2020; Zhang et al., 2020) or indirectly, by a fixation of the thorax/mesosoma in the enclosing tunnel (transverse carination or backward inclined toothlets on the mesonotum in Anaxyelidae and many Gasteruptiidae, or desclerotized mesosomal dorsum in Myanmarinidae, permitting the mesosoma to swell and cling firmly in the tunnel; cf. Li et al., 2018). However, there are probably other xylophilous wasps among those, which lack a clear evidence of the above kind.

Hosts of the Cretaceous non-aculeate Apocrita are largely unknown, except a few but important cases. Hosts of xylobiotic parasites most likely were larvae of xylophagous beetles and horntails. Numerous Evaniidae probably were, as their living relatives, acting as a predator within oothecae of cockroaches, which are equally common in many Cretaceous ambers (Ross, 2019, 2020a,b). Minute Bipetiolarida probably parasitized insect eggs (in many cases possibly those of Psocoptera; Rasnitsyn and Öhm-Kühnle, 2020). Judging from their small body size, many Chalcidoidea recorded from amber were egg parasites as well.

5. Conclusions

The Cretaceous fauna of non-aculeate Hymenoptera known as amber inclusions is found to be rich and diverse, comprising 287 species (263265 named) and 47 families recorded in 17 amber assemblages by the end of 2020. The fauna is found unexpectedly coherent in space and time: with the only exception being Kachin amber, the fauna is uniform lacking endemism of the assemblages studied at the family level. A transformation of the fauna during Cretaceous in terms of the gradual loss of ancient, now extinct families, is demonstrated: a share of extinct families was decreasing from 50% till near zero during at most 45 myr (by the beginning of the Eocene). More than half of that amount of extinct families was lost during the first some 20 myr (by the Campanian), that is, well before the end of the Cretaceous. Overall, the presented data shows

a decrease commencing well in the Cretaceous, rather than a sudden mass extinction of non-aculeate Hymenoptera at the Cretaceous–Paleogene boundary.

Acknowledgements

We offer our sincere gratitude to the reviewers for their valuable comments. For APR, this research was supported by the Budget funding within the framework of the State Assignment of the Paleontological Institute, Russian Academy of Science.

References

- Aguiar, A.P., Deans, A.R., Engel, M.S., Forshage, M., Huber, J.T., Jennings, J.T., Johnson, N.F., Lelej, A.S., Longino, J.T., Lohrmann, V., Mikó, I., Ohl, M., Rasmussen, C., Taeger, A., Yu, D.S.K., 2013. Order Hymenoptera. *Zootaxa* 3703 (1), 51–62. <https://doi.org/10.11646/zootaxa.3703.1.12>.
- Alekseev, P.I., 2018. [The revision of gymnosperm species from Eocene Baltic amber]. *Botanicheskii Zhurnal* 103 (2), 229–245 (in Russian). Available online at: https://www.researchgate.net/publication/325570158_The_revision_of_Gymnosperm_species_from_Eocene_Baltic_Amber.
- Archibald, S.B., Rasnitsyn, A.P., Brothers, D.J., Mathewes, R.W., 2018. Modernisation of the Hymenoptera: ants, bees, wasps, and sawflies of the early Eocene Okanagan Highlands of western North America. *The Canadian Entomologist* 150, 205–257. <https://doi.org/10.4039/tce.2017.59>. <https://www.cambridge.org/core/terms>.
- Bouju, V., Perrichot, V., 2020. A review of amber and copal occurrences in Africa and their paleontological significance. *BSGF - Earth Sciences Bulletin* 191 (17), 1–11. <https://doi.org/10.1051/bsgf/2020018>.
- Brothers, D.J., Janzen, J.-W., 1999. New generic synonymy in *Scolecophoridae*, with redescription of both sexes of *Pristapenesia primaeva* Brues from Baltic amber (Hymenoptera: Chrysidoidea). In: Vršanský, P. (Ed.), *Proceedings of the First Palaeontological Conference, Moscow, vol. 1998. AMBA Projects International, Bratislava, Slovakia*, pp. 17–26, 199+ [2] pp.
- Brues, Ch T., 1940. Serphidae in Baltic amber. With the description of a new living genus. *Proceedings of the American Academy of Arts and Sciences* 73, 259–264. <https://doi.org/10.2307/25130185>.
- Engel, M.S., 2013. A new genus and species of Baissidae in Late Cretaceous amber from New Jersey (Hymenoptera: Evaniidae). *Novitates Paleontologicae* 3, 1–8.
- Engel, M.S., Huang, D., 2017. A new crown wasp in Cretaceous amber from Myanmar (Hymenoptera: Stephanidae). *Cretaceous Research* 69, 56–61. <https://doi.org/10.1016/j.cretres.2016.08.014>.
- Engel, M.S., Lelej, A.S., 2020. On the spelling of family-group names based on the genus *Trigonalys* Westwood (Hymenoptera: Trigonalidae versus Trigonalidae). *Entomologist's Monthly Magazine* 156, 58–60. <https://doi.org/10.31184/M00138908.1561.3989>.
- Grimaldi, D.A., Ross, A.J., 2017. Extraordinary Lagerstätten in amber, with particular reference to the Cretaceous of Burma. In: Fraser, N.C., Sues, H.-D. (Eds.), *Terrestrial conservation Lagerstätten: Windows into the evolution of life on land*. Dunedin Press, Edinburgh, pp. 287–342.
- Jouault, C., Rasnitsyn, A.P., Perrichot, P., 2020. Ohlhoffiidae, a new Cretaceous family of basal parasitic wasps (Hymenoptera: Stephanidae). *Cretaceous Research* 117, 104635. <https://doi.org/10.1016/j.cretres.2020.104635>.
- Li, L., Shih, C., Rasnitsyn, A.P., Li, D., Ren, D., 2018. A new wasp of Myanmarinidae (Hymenoptera: Stephanidae) from the mid-Cretaceous Myanmar amber. *Cretaceous Research* 86, 33–40. <https://doi.org/10.1016/j.cretres.2018.02.009>.
- Lohrmann, V., Ohl, M., Michalik, P., Pitts, J.P., Jeanneau, L., Perrichot, V., 2019. Notes on rhopalosomatid wasps of Dominican and Mexican amber (Hymenoptera: Rhopalosomatidae) with a description of the first fossil species of *Rhopalosoma* Cresson, 1865. *Fossil Record* 22, 31–44. <https://doi.org/10.5194/fr-22-31-2019>.
- McKellar, R.C., Engel, M.S., 2012. Hymenoptera in Canadian Cretaceous amber (Insecta). *Cretaceous Research* 35, 258–279.
- Muona, J., 2020. *Helorus arturi* sp. nov. (Hymenoptera, Proctotrupoidea, Heloridae) from Baltic amber. *Palaeontologia* 3, 347–351. <https://doi.org/10.11646/palaeontologia.3.4.4>.
- Nel, A., Brasero, N., 2010. Oise amber. In: Penney, D. (Ed.), *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester, United Kingdom, pp. 137–148.
- Nel, A., Perrichot, V., Néraudeau, D., 2003. The oldest trigonalid wasp in the Late Albian amber of Charente-Maritime (SW France) (Hymenoptera: Trigonalidae). *Eclogae Geologicae Helvetiae* 96, 503–508. <https://doi.org/10.1007/s00015-003-1104-3>.
- Olmi, M., Rasnitsyn, A.P., Guglielmino, A., 2010. Revision of rock fossils of Dryinidae and Embolemidae (Hymenoptera: Chrysidoidea). *Zootaxa* 2499, 21–38.
- Ortega-Blanco, J., Delclòs, X.I., Peñalver, E., Pérez de la Fuente, R., 2009. Wasps (Insecta: Hymenoptera) from the Early Cretaceous Amber from Spain. In: *Tenth International Symposium on Mesozoic Terrestrial Ecosystems and Biota*. Universidad Autónoma de Madrid, Teruel, pp. 55–57.
- Ortega-Blanco, J., Peñalver, E., Delclòs, X., Engel, M., 2011. False fairy wasps in early Cretaceous amber from Spain (Hymenoptera: Mymarommatidae). *Palaeontology* 54, 511–523.
- Rasnitsyn, A.P., 1965. Notes on the biology, systematics and phylogeny of Xyelinae (Hymenoptera, Xyelidae). *Polskie Pismo Entomologiczne* 35, 483–519 (in Russian, with English keys and summary).
- Rasnitsyn, A.P., 1969. *Proiskhozhdeniye i evolyutsiya nizshikh pereponchatokrylykh* [Origin and evolution of lower Hymenoptera]. *Trudy Paleontologicheskogo instituta Akademii nauk SSSR*. Nauka, Moscow (in Russian).
- Rasnitsyn, A.P., 1975. *Vysshie pereponchatokrylye mezozoya* [Hymenoptera Apocrita of Mesozoic]. *Trudy Paleontologicheskogo instituta Akademii nauk SSSR*. Nauka, Moscow (in Russian).
- Rasnitsyn, A.P., 1977. A new family of sawflies (Hymenoptera, Tenthredinoidea, Electrotomidae) from the Baltic amber. *Zoological Zhurnal* 56, 1304–1308 (in Russian).
- Rasnitsyn, A.P., 1980. *Proiskhozhdeniye i evolyutsiya pereponchatokrylykh nasekomykh* [Origin and Evolution of Hymenoptera]. *Trudy Paleontologicheskogo instituta Akademii nauk SSSR*. Nauka, Moscow (in Russian).
- Rasnitsyn, A.P., 1988. An outline of evolution of the hymenopterous insects (order Vespida). *Oriental Insects* 22, 115–145.
- Rasnitsyn, A.P., 1995. Tertiary Sawflies of the Tribe Xyelini (Insecta: Vespida = Hymenoptera: Xyelidae) and Their Relationship to the Mesozoic and Modern Faunas. *Contributions in Science, Natural History Museum of Los Angeles County* 450, 1–14.
- Rasnitsyn, A.P., 2013. *Vectevania vetula* Cockerell, 1922 from the uppermost Eocene of Bembridge Marls, England, and the system of the family Gasteruptionidae s.l. [Vespida (= Hymenoptera), Evaniidae]. *Proceedings of the Russian Entomological Society* 84 (2), 98–106.
- Rasnitsyn, A.P., Bashkuev, A.S., Kopylov, D.S., Lukashevich, E.D., Ponomarenko, A.G., Popov, Yu.A., Rasnitsyn, D.A., Ryzhkova, O.V., Sidorchuk, E.A., Sukatshva, I.D., Vorontsov, D.D., 2016. Sequence and scale of changes in the terrestrial biota during the Cretaceous (based on materials from fossil resins). *Cretaceous Research* 61, 234–255. <https://doi.org/10.1016/j.cretres.2015.12.025>.
- Rasnitsyn, A.P., Jarzembowski, E.A., Ross, A.J., 1998. Wasps (Insecta: Vespida = Hymenoptera) from the Purbeck and Wealden (Lower Cretaceous) of southern England and their biostratigraphical and paleoenvironmental significance. *Cretaceous Research* 19 (3 & 4), 329–391. <https://doi.org/10.1006/cres.1997.0114>.
- Rasnitsyn, A.P., Öhm-Kühnle, Ch., 2018. Three new female *Aptenoperissus* from mid-Cretaceous Burmese amber (Hymenoptera, Stephanidae, Aptenoperissidae): Unexpected diversity of paradoxical wasps suggests insular features of source biome. *Cretaceous Research* 91, 168–175. <https://doi.org/10.1016/j.cretres.2018.06.004>.
- Rasnitsyn, A.P., Öhm-Kühnle, Ch., 2020. *Archaeoserphites engeli* sp. nov., the first archaeoserphitid wasp in Burmese amber and first known archaeoserphitid female (Hymenoptera, Archaeoserphitidae). *Palaeontologia* 3 (3), 235–239. <https://doi.org/10.11646/palaeontologia.3.3.3>.
- Ross, A.J., 2019. Burmese (Myanmar) amber checklist and bibliography 2018. *Palaeontologia* 2 (1), 22–84. <https://doi.org/10.11646/palaeontologia.2.1.5>.
- Ross, A.J., 2020a. Supplement to the Burmese (Myanmar) amber checklist and bibliography, 2019. *Palaeontologia* 3 (1), 103–118. <https://doi.org/10.11646/palaeontologia.3.1.14>.
- Ross, A.J., 2020b. Burmese (Myanmar) amber taxa. <https://doi.org/10.11646/palaeontologia.3.1.14.3> on-line supplement v2020.1. *Palaeontologia*, available online at:
- Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., Li, X., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research* 37, 155–163. <https://doi.org/10.1016/j.cretres.2012.03.014>.
- Taeger, A., Blank, S.M., Liston, A.D., 2010. World Catalog of Symphyta (Hymenoptera). *Zootaxa* 2580, 1–1064. <https://doi.org/10.11646/zootaxa.2580.1.1>.
- Townes, H.K., 1950. The Nearctic species of Gasteruptionidae (Hymenoptera). *Proceedings of the United States National Museum* 100, 85–145.
- Westerweel, J., Roperch, P., Licht, A., Dupont-Nivet, G., Win, Z., Poblete, F., Ruffet, G., Swe, H.H., Thi, M.K., Aung, D.W., 2019. Burma Terrane part of the Trans-Tethyan arc during collision with India according to palaeomagnetic data. *Nature Geoscience* 12, 863–868. <https://doi.org/10.1038/s41561-019-0443-2>.
- Zhang, Q., Kopylov, D.S., Rasnitsyn, A.P., Zheng, Y., Zhang, H., 2020. Burmorussidae, a new family of parasitic wasps (Insecta, Hymenoptera) from mid-Cretaceous Burmese amber. *Papers in Palaeontology* 6, 593–603. <https://doi.org/10.1002/spp2.1312>.
- Zhang, Q., Rasnitsyn, A.P., Wang, B., Zhang, H.C., 2018. Hymenoptera (wasps, bees and ants) in mid-Cretaceous Burmese amber: a review of the fauna. *Proceedings of the Geologists' Association* 129 (6), 736–747. <https://doi.org/10.1016/j.pgeola.2018.06.004>.
- Zhelochovtzev, A.N., Rasnitsyn, A.P., 1972. On some Tertiary sawflies (Hymenoptera: Symphyta) from Colorado. *Psyche* 79, 315–327.
- Zherikhin, V.V., Sukacheva, I.D., Rasnitsyn, A.P., 2009. Arthropods in contemporary and some fossil resins. *Paleontological Journal* 43, 987–1005. <https://doi.org/10.1134/S0013030109090019>.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2021.104805>.