



## Sequence and scale of changes in the terrestrial biota during the Cretaceous (based on materials from fossil resins)



A.P. Rasnitsyn<sup>a,\*</sup>, A.S. Bashkuev<sup>a</sup>, D.S. Kopylov<sup>a</sup>, E.D. Lukashevich<sup>a</sup>, A.G. Ponomarenko<sup>a</sup>, Yu.A. Popov<sup>a</sup>, D.A. Rasnitsyn<sup>a</sup>, O.V. Ryzhkova<sup>a</sup>, E.A. Sidorchuk<sup>a</sup>, I.D. Sukatsheva<sup>a</sup>, D.D. Vorontsov<sup>b</sup>

<sup>a</sup> Arthropoda Laboratory, Paleontological Institute, Russian Academy of Sciences, 117997 Moscow, Profsoyuznaya ulitsa 123, Russia

<sup>b</sup> Laboratory of Comparative Physiology, Institute of Developmental Biology, Russian Academy of Sciences, 117808 Moscow, ulitsa Vavilova 26, Russia

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This paper is dedicated to the memory of Vladimir Zherikhin, whose contribution to our knowledge of amber arthropods was truly remarkable.

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### ABSTRACT

Comparative analysis of arthropod assemblages found in Cretaceous fossil resins is provided. Arthropod-bearing Cretaceous resin sites are reviewed, and a list of arthropod records (identified to the family level) published up to 2015 is provided. Also, new records of mites, and new arthropod records from the Siberian resins are given. An efficient method for extracting amber from loose sediments in situations of limited infrastructure but easy access to water is described as well.

The sequence of arthropod assemblages in Cretaceous resins according to their evolutionary aspect does not match their geological sequence. This can be only partly explained by taphonomic constraints and inadequacy of the material: there is a deeper difference between somewhat contemporary assemblages than was characteristic of Permian assemblages studied in a similar way in previous studies. Our results confirm the earlier hypothesis that the Palaeozoic–Mesozoic biotic crisis was not so much a mass extinction as a biotic reorganisation that opened the way to diversification. These results might indicate a peculiar feature of the immediate effects of such reorganisations, namely that Mesozoic–Cenozoic communities became differentiated in their compositions much deeper than Palaeozoic ones (i.e., that their constituent groups acquired the ability to evolve much deeper changes while adapting to the ecological specifics of their environments). A transformation of organisms and/or their communities took place, comparable in scope to the rise of skeletal fauna in the Cambrian. The difference between these two transformations is that the later one resulted not from a particular adaptation (the skeleton) but from the ability to specialize more deeply than was possible in the Palaeozoic.

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### 1. Introduction

Fossil resins are well known for their unique property, the ability to preserve remains of living beings with life-like precision. In descriptions of inclusions preserved in ambers—in contrast to other fossils—one can use almost all morphological characters used to describe and classify extant organisms. Fossil resins containing arthropod remains are broadly distributed in space and time. Only one limited assemblage is known to date from the Triassic (Roghi *et al.*, 2006; Schmidt *et al.*, 2012; Sidorchuk *et al.*, 2015), and no reliable records are known from Jurassic resins, but Cretaceous resins containing more or less rich arthropod inclusions are known

from dozens of sites in Europe, Asia, and North America, dated to all stages of the Cretaceous period except the earliest two, the Berriasian and Valanginian (for details, see below). The palaeontological study of biological inclusions in amber has been especially popular over the last few decades, characterised by enormous interest in molecular and morphological taxonomy; this area has been so popular, among other reasons, because of the need to calibrate molecular clocks and date assumed evolutionary events (Dunlop and Selden, 2009; Ronquist *et al.*, 2012), and to test phylogenetic hypotheses (Garwood and Dunlop, 2014). The Cretaceous attracts especially much interest as the period of fundamental transformations in vegetation and of explosive increase in arthropod diversity (Rasnitsyn and Quicke, 2002; Grimaldi and Engel, 2005). Dozens of studies are published annually that contain descriptions of new finds of arthropods and other organisms in Cretaceous ambers (Grimaldi, 2000; Ross, 2000; Perrichot

\* Corresponding author.

E-mail address: [alex.rasnitsyn@gmail.com](mailto:alex.rasnitsyn@gmail.com) (A.P. Rasnitsyn).

and Néaudeau, 2009; for overviews, see Penney, 2010). The taxonomic diversity of some of the assemblages that have already been described is considerable, although they have been studied to very different degrees (see below).

The purposes of this study were to summarize and compare the available data on the compositions of arthropod assemblages within Cretaceous fossil resin sites worldwide at the family level, and reveal the trends of their changes in space and time. We pay special attention to the rates of appearance and disappearance of families in the fossil record, the ratio of these two rates, and the total intensity of such changes; we try to reveal the unevenness of changes in the hope of clarifying the problems of the most important events in taxonomic diversity dynamics during the Cretaceous, such as the reality of mass extinction events. We also assess whether these data can be used for specifying the temporal (stratigraphic) sequence of arthropod assemblages in Cretaceous resins, using a similar approach to that successfully used earlier for Palaeozoic insects (Rasnitsyn, 2012; Aristov et al., 2013; Aristov and Rasnitsyn, 2015; Rasnitsyn et al., 2015). Furthermore, we use the results of this study to estimate whether and how these data match various notions about general patterns of the evolutionary process.

## 2. Material

### 2.1. List of the arthropod families known from Cretaceous resins

Table 1 in Supplementary Information (SI Table 1) contains a referenced checklist of arthropod records from Cretaceous resins worldwide, omitting only those we could not use further in calculations. Data on these localities are summarized in Section 2.2. The records involving fossil resins from Siberia are largely the first publications of identifications based on materials stored in the Arthropoda Laboratory, Borissiak Palaeontological Institute, Russian Academy of Sciences (PIN). Provisional identifications (determined by E.A.S., 2011–2014) of mite records from the following collections are also published for the first time: American Museum of Natural History (AMNH, Burmese and New Jersey amber); Canadian National Collection of Insects, Arachnids and Nematodes (CNC, Canadian amber); Collection of the Department of Geosciences of the University of Rennes, France (IGR, French amber); and private collection of Prof. Dany Azar, temporary housed in the National Museum of Natural History, Paris (AZ-MNHN, Lebanese amber). The table also provides data on occurrences of the same families within deposits before and after the Cretaceous amber records. Records before the Cretaceous, since they are scanty and extremely important for our calculations (see Sections 3 and 4), are cited with references; those after the Cretaceous (most often Recent records), are not referenced, in order to avoid excessive references. Also, the referenced records of these families from non-amber (rock) compression fossil deposits within the interval covered by ambers are noted, if those records are either the oldest (first) or youngest (last) finds of the family in question. Records stemming from other rock units are not mentioned. Arthropods not identified to family (indicated as fam. indet.) are listed only for the sake of comprehensiveness; data on records from deposits earlier and later than the study period are not given. With regards to insect and spider records from sites outside Russia, this checklist is a product of summarizing published data referenced in cells of the table. We equally considered publications containing complete taxonomic descriptions and publications containing only checklists of records, because many widespread and common taxa, such as Chironomidae, are known from some sites, but remain undescribed. In those cases where checklists were corrected based on later reports, we omitted the initial (shown to be incorrect)

identification from the table, such as the record of Culicidae by Poinar and Milki (2001) from Lebanese amber, not confirmed later (D. Azar, pers. comm., April 2015), as well as ‘Tipulidae’ from Burmese amber (Grimaldi et al., 2002), incorrectly identified and actually representing Ptychopteridae (Lukashevich and Grimaldi, 2004). Moreover, Tipulidae sensu stricto remain unknown to date in any Cretaceous ambers, in spite of the several references (Poinar and Poinar, 2008; Grimaldi and Nascimbene, 2010; McKellar and Wolfe, 2010; Ross et al., 2010), because all crane flies described from the Cretaceous ambers (including Raritan and Canadian amber; Krzemiński and Teskey, 1987; Gelhaus and Johnson, 1996) belong to Limoniidae in the system accepted here (not Tipulidae sensu lato of some American authors). The record of Apidae from Raritan amber (Michener and Grimaldi, 1988a, 1988b) was omitted, because of doubts about whether the material originates from Raritan fossil resins (Rasnitsyn and Michener, 1991). Two identifications first published by Zherikhin (1978) were subsequently rejected and hence do not appear in SI Tables: Eomyiidae (recorded from the Begichevo Fm.), because Mostovski (1999: 103) restudied the only specimen (the holotype) from the Jurassic of Karatau and concluded that the family was not identifiable; and Pleciomimidae (recorded from Agapa), because Kovalev (1990: 159), after re-studying the specimens, rejected this identification. Records of Syrphidae from the Ugolyak site (Kheta Fm.; Zherikhin and Eskov, 1999) and Pentatomidae from the Lower Cretaceous Manlay locality in Mongolia (Popov, 1980) have also been shown to be incorrect (G.V. Popov, pers. comm., May 2015, and Yu.A.P. pers. obs., respectively), and are not mentioned in the SI Tables. In those cases where the initial identification was subsequently changed or corrected and repeated together with the correct identification, we cite both the initial publication and subsequent publications (or cite our new data, if the initial identification was corrected by one of us). This is the case with the mite *Rasnitsynella punctulata* Krivolutsky from the Taimyr retinite, initially identified as Plateremaeidae (Krivolutsky and Ryabinin, 1976) and subsequently identified as Archaeorchestidae (E.A.S., pers. obs.), or the wasp *Bryopompilus intersector* Engel et Grimaldi, which was initially assigned to Pompilidae (Engel and Grimaldi, 2006) but does not belong to this family (A.P.R., pers. obs.), and is mentioned as Hymenoptera fam. indet. in SI Table 1.

The closing date for publications on the amber arthropod finds used in our calculations is December 2014.

### 2.2. Cretaceous sites of arthropod-containing resins

Fig. 1 shows the positions of fossil sites with arthropods in Cretaceous resins on a palaeogeographical map of the world (Blakey, 2011), and their dates according to sources cited in the text. Summarized published data on these sites are given below, in accordance with their dates and degrees of studiedness. In this section we try to describe the insect-bearing sites of the former Soviet Union as comprehensively as possible, even those from which few records are known, because little information about such sites is available in English-language literature. We determined the approximate ( $\pm 50$  m) coordinates of such sites from published descriptions and personal communications using Google maps; these are the coordinates given below, unless stated otherwise.

The amber from Alem-Ketema in Ethiopia, originally dated to Cenomanian (Schmidt et al., 2010), is not discussed below, for there is now compelling evidence from new arthropod inclusions (mostly ants) and revised palynomorphs that it is not Cretaceous, but Tertiary, and the paper on this subject is being prepared (V. Perrichot, pers. comm.).

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