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Laurasian ancestors and "Gondwanan" descendants of Rotoitidae (Hymenoptera: Chalcidoidea): What a review of Late Cretaceous *Baeomorpha* revealed

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ABSTRACT

Baeomorphinae Yoshimoto, 1975, based on *Baeomorpha* Brues, 1937, is transferred from Tetracampidae Förster, 1856 and recognized as a junior synonym of Rotoitidae Bouček and Noyes, 1987 (Hymenoptera: Chalcidoidea) syn. nov. following ICZN (1999) article 35.5. Inclusions in Taimyr amber (84–100 Ma) assigned to *Baeomorpha* are reviewed and the following eleven new species, all of Gumovsky, are described: *B. avamica* sp. nov., *B. baikurenis* sp. nov., *B. bianellus* sp. nov., *B. caeleps* sp. nov., *B. gracilis* sp. nov., *B. ingens* sp. nov., *B. quattorduo* sp. nov., *B. quattoruno* sp. nov., *B. popovi* sp. nov., *B. yantardakh* sp. nov., and *B. zherikhini* sp. nov. The recognized species are differentiated in separate keys to females and males and illustrated through microphotography. Two of four previously described *Baeomorpha* species from Campanian Canadian amber are synonymized: *B. distincta* Yoshimoto and *B. elongata* Yoshimoto under *B. ovatata* Yoshimoto (syn. nov.). One enigmatic rotoitid inclusion, which differs from *Baeomorpha* species in the possession of very short stigmal vein, is described as *Taimyromorpha pusilla* Gumovsky gen. et sp. nov. Inclusions containing specimens identified as *Baeomorpha* and *Taimyromorpha* are found in amber from Taimyr and Canada that originated from Laurasia, not Gondwana. Two Realms are newly proposed to recognize different Cretaceous faunal elements, a more northern *Baeomorpha* Realm that is characterized by a temperate or warm temperate climate and very abundant aphid fossils, and the Isoptera Realm, an opposing southward territory with a warmer climate and common termite but rare aphid fossils. The newly described fossils indicate the southern hemisphere distribution of extant Rotoitidae is relictual with the pattern observed being formed at least in part by extinction events, though distributions of the only two extant rotoitid genera, *Rotoita* Bouček and Noyes, 1987 (New Zealand) and *Chiloe* Gibson and Huber, 2000 (small area in the southern Chile) may have been more extensive in the past. Both of known regions of extant Rotoitidae have highly suppressed ant faunas, which may suggest that their survival there depended on low biocenotic pressure by ants, perhaps as low as is hypothesized for the Late Cretaceous. The Canadian amber genera *Distylopus* Yoshimoto, 1975 (Distylopinae) and *Bouceklytus* Yoshimoto, 1975 (Bouceklytinae) are excluded from Tetracampidae and regarded as Chalcidoidea *incertae sedis*.

1. Introduction

Brues (1937) described *Baeomorpha* Brues, 1937 with a single species, *B. dubitata* Brues, 1937 within the family Scelionidae (currently the family Platygastridae: Murphy et al., 2007; but see McKellar and Engel, 2012) from Upper Cretaceous Canadian amber. The genus was later transferred to Tetracampidae (as the type of the Baeomorphinae Yoshimoto, 1975) by Yoshimoto (1975), who also described three new *Baeomorpha* species and two other fossil tetracampid genera: *Distylopus* Yoshimoto, 1975 (in the subfamily Distylopinae) and *Bouceklytus* Yoshimoto, 1975 (in the subfamily Bouceklytinae).

The placement of *Baeomorpha* in Tetracampidae was not properly substantiated, but largely based on the concept that

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"Tetracampidae are intermediate between Eulophidae and Pteromalidae" (Yoshimoto, 1975) and that the legs of males of *Baeomorpha* were recorded as having 4-segmented tarsi like males of tetracampines. Gumovsky and Perkovsky (2005) suggested that placement of *Baeomorpha* in Tetracampidae was doubtful as part of discussion of the structure of the family.

The initial purpose of this paper was to review Taimyr amber inclusions (Russia, Siberia, Taimyr Peninsula: Upper Cretaceous, 84–100 Ma) that were preliminary identified as representatives of *Baeomorpha*. However, when study revealed that *Baeomorpha* is a member of Rotoitidae rather than Tetracampidae we undertook a more comprehensive review. Prior to our discovery of the proper relationships of *Baeomorpha*, Rotoitidae consisted of just two extant genera, *Rotoita* Bouček and Noyes (1987) from New Zealand and *Chiloe* Gibson and Huber, 2000 mostly from Chiloé Island (Chile), which suggested a Gondwanan origin for the family.

2. Material and methods

The Taimyr amber pieces reported in this paper were collected during expeditions of the Paleontological Institute of the Russian Academy of Sciences (Moscow, PIN) in 1970–1977 and 2012, and are deposited in the collection of this institution. Comparative analyses of hymenopteran assemblages of Taimyr and Canadian ambers were provided earlier in corresponding reviews by Rasnitsyn et al. (2016) and McKellar and Engel (2012), respectively. Stratigraphical data for examined amberiferous localities (Fig. 1) are listed in Table 1. Comparative material of Canadian amber hymenopterans (from Cedar Lake in Manitoba and Medicine Hat in Alberta), in particular the specimens studied and described by Carl Yoshimoto, were obtained from the Canadian National Collection of Insects, Arachnids and Nematodes (CNC, Ottawa, ON). Data on the other Canadian amber specimens described by C. Yoshimoto were obtained from the Royal Ontario Museum (ROM, Toronto, ON) and the Museum of Comparative Zoology, Harvard University (MCZ, Cambridge, MA, USA). The pictures of MCZ specimens were taken with a Leica MZ16 stereomicroscope and with an Olympus BH-2 microscope by Ricardo Perez de la Fuente, and kindly provided for the authors because personal examination of the specimens was not possible.

Scanning electron microscopy (SEM) of extant Rotoitidae was carried out in the Mineralogy Department of the Natural History Museum (BMNH, London, UK) using ISI ABT-55 low-vacuum and LEO 1455VP microscopes, which allow imaging of uncoated specimens. Imaging with light microscopy was conducted in the Schmalhausen Institute of Zoology NAS of Ukraine (Kiev, Ukraine, SIZK) using an upright microscope Olympus CX-41, with the images stacked using Helicon Focus Pro software. If the surface of a piece of amber was uneven, the piece was put under water to fill the gaps with water as a medium and covered with cover slip before imaging.

Morphological terminology largely follows that of Gibson et al. (1997) and Heraty et al. (2013). The "funicle" is considered as that part of the flagellum between the anellus or anelli (the proximal most ring-like or distinctly smaller flagellar segments) and the clava (Gibson et al., 1997). The following abbreviations are used:

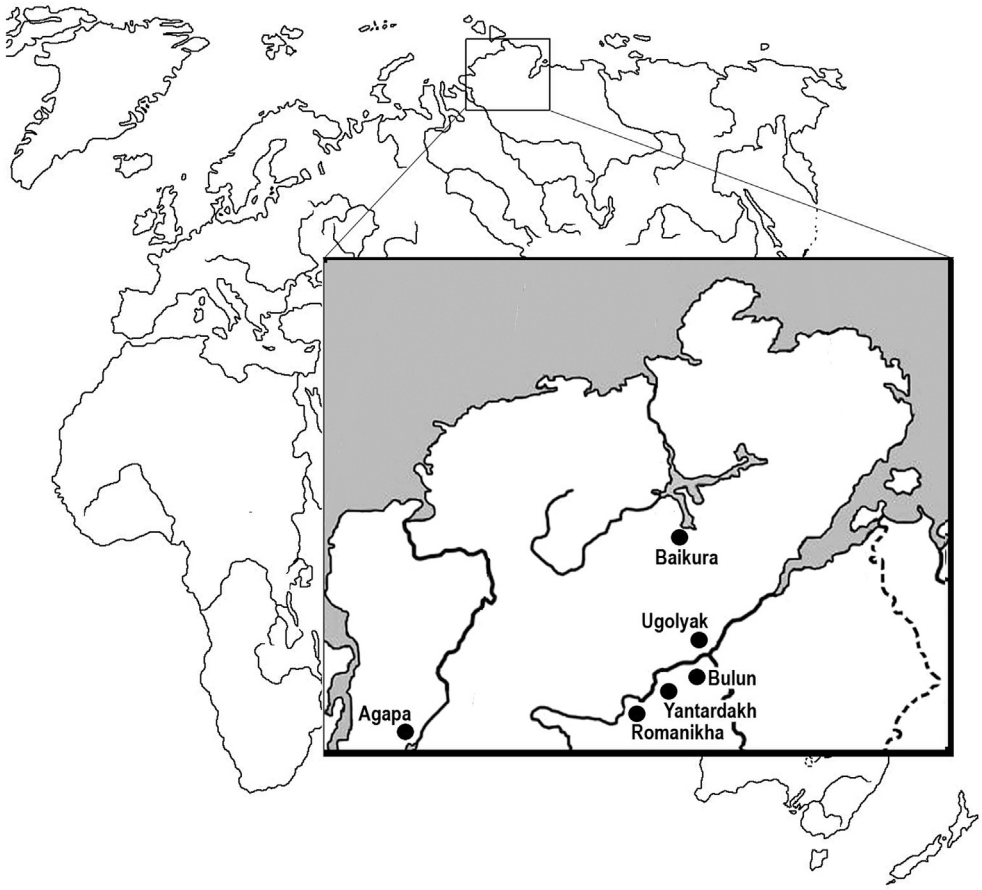

Fig. 1. Yantardakh, Baikura, Agapa, Romanikha, Ugolyak, Bulun localities (Russian Federation, Taimyr), the origin sites of amber inclusions discussed below, marked on the map.