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The first fossil Megalopsidiinae (Coleoptera: Staphylinidae) from Upper Cretaceous Burmese amber and its potential for understanding basal relationships of rove beetles

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1. Introduction

With more than 60,000 described species grouped in 32 extant subfamilies, the Staphylinidae (rove beetles) is currently recognized as the most speciose animal family (Solodovnikov et al., 2013). Within Staphylinidae, the monobasic subfamily Megalopsidiinae is a very distinct rove beetle lineage confined to the world (sub)tropics. Currently more than 430 species of Megalopsidiinae are known globally, most of which occur in the Neotropical region, and many in the Oriental region. However, the group is poorly represented in the Afrotropical region and absent from the Pacific islands. Because Megalopsidiinae are being rarely collected, they are usually described from very limited material. Apparently, the actual species diversity of the group is significantly higher than currently known. For example recent studies, especially by Puthz (2012a, 2012b), doubled the number of described species of the subfamily.

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ABSTRACT

The first definitive fossil of the peculiar monotypic rove beetle subfamily Megalopsidiinae is described as a new species *Megalopinus extinctus* sp. n. It represents a stem lineage valuable for the study of the early diversification of Staphylinidae, where sister group relationships of Megalopsidiinae currently remain a big controversy. This discovery corroborates the Mesozoic origin of this subfamily implied by its presumably basal phylogenetic position within Staphylinidae and hitherto available fossil record for the family. Well preserved peculiar mouthparts of *M. extinctus* specialized similarly with recent *Megalopinus* suggest the same mode of feeding in Megalopsidiinae for nearly a hundred million years.

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In spite of such notable species diversity, overall Megalopsidiinae is a rather morphologically conservative lineage, where all species belong to a single genus Megalopinus Eichelbaum, 1915, with the clear morphological diagnosis. Megalopinus has very distinct habitus and can be easily discriminated from other rove beetles by its bulging eyes occupying most of the lateral head margin, short clubbed antennae inserted in front of the level of anterior margin of the eyes, a deeply bifurcate labrum, and 5-5-5 tarsal formula (Newton et al., 2000; Brunke et al., 2011). Biology and detailed life cycle of Megalopinus are still largely unknown. However, at least for some species of the genus we know that they are associated with fungus-infested wood such as branches of dead standing trees, or crevices under rotten fallen logs with fungal growth (Leschen and Newton, 2003). Occasionally, adults of some species were found from fungus-infested leaf litter on the forest floor (Naomi and Nomura, 2015). In spite of the recent progress in the alpha-taxonomic study of the global species diversity of Megalopinus, no phylogenetic hypothesis for this interesting genus has ever been proposed. Puthz (2012a, 2012b), however, abandoned a pre-phylogenetic, obviously artificial subgeneric division of this genus of the earlier authors (Benick, 1917, 1952; Scheerpeltz, 1972) and divided the genus into several informal species-groups instead.







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Similarly to the lack of phylogenetic knowledge about diversification within the genus *Megalopinus*, the origin and sister group relationships of that lineage within the family Staphylinidae are also largely unknown. Megalopsidiinae is believed to be a monophyletic group based on the morphological evidence (Thayer, 2005; Grebennikov and Newton, 2009) that is currently placed in the informal 'Staphylinine group' of rove beetle subfamilies (Lawrence and Newton, 1982, 1995; Newton and Thaver, 1992; Grebennikov and Newton, 2009). However, monophyly or composition of the 'Staphylinine group', as well as the sister group of Megalopsidiinae are controversial issues of rove beetle phylogeny. Hansen (1997) considered Megalopsidiinae as the least derived lineage of his 'Stenine group' that also included sister subfamilies Steninae and Euaesthetinae. In the morphology-based phylogenetic analysis of Leschen and Newton (2003), Megalopsidiinae is a sister group to the clade (Pseudopsinae, (Steninae + Euaesthetinae)). In the taxonand character-wise more inclusive analysis of Grebennikov and Newton (2009), Megalopsidiinae is resolved as an even more isolated lineage of rove beetles that is sister to a clade formed by eight other subfamilies of the 'Staphylinine group', the latter including Solieriinae and Scydmaeninae. In the recent molecular phylogenetic study of Staphyliniformia (McKenna et al., 2015), Megalopsidiinae got a perplexing position as a lineage related to the 'Oxyteline group' of subfamilies far away from any of the subfamilies of the 'Stenine group' or even a more inclusive 'Staphvlinine group'.

Incongruent results from various phylogenetic analyses of the recent species may indicate, among other possibilities, high rate of extinction for lineages in question, and therefore a necessity to include stem lineages in the studies of the respective deep divergences. Although Cai and Huang (2013) mentioned some compression fossil of Megalopsidiinae from the Lower Cretaceous Lushangfen Formation in China, no any extinct fossil representative of this subfamily has ever been described. Herein, we provide the first formal description of the extinct lineage of Megalopsidiinae that is a remarkable new species based on a single well preserved specimen in Cretaceous Burmese amber (Cenomanian) from Myanmar. Although the newly discovered extinct species is different in some character states from Megalopinus, lack of a comprehensive phylogeny of that species-rich genus, or even of a global overview of its morphological diversity, urged us to describe this species as a member of Megalopinus pending proper phylogenetic study. We also place the new finding in the context of the broader knowledge of megalopsidiine evolution and ecology.

2. Materials and methods

The beetle specimen is embedded in a small, flattened, semicircular piece ($10.1 \times 7.3 \times 3.4$ mm) of clear-yellow coloured Burmese amber (burmite). The sole specimen came from the Hukawng Valley (Fig. 1), southwest of Maingkhwan in the state of Kachin, northern Myanmar (Burma). Recent commercial mining of Burmese amber has been limited to "Noije Bum" (26°15'N, 96°34'E) only, close to Tanai Village (Grimaldi et al., 2002; Shi et al., 2012). Burmese amber was once thought as Eocene-Miocene in age, but it is currently considered as Late Cretaceous (earliest Cenomanian, ca. 99 Ma) based on U–Pb zircon dating (Shi et al., 2012). The palaeofauna of Burmese amber is diverse and reviewed by Grimaldi et al. (2002) and Ross et al. (2010). SY cut and polished the amber piece for observation. The beetle specimen is very well preserved, and observations at multiple angles are possible. The holotype is housed in the American Museum of Natural History (AMNH: D. Grimaldi), New York, NY, USA. Observations and photographies were conducted using two types of stereoscopic compound microscopes (Leica M205C and Leica S8 APO: Leica Microsystems



Fig. 1. Location of the studied amber deposit in Myanmar (red star: Hukawng Valley, Kachin, northern Myanmar). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

GmbH, Wetzlar, Germany), with an attached Canon 7D digital camera (Canon Inc., Tokyo, Japan). Photographs were later stacked using the automontage software CombineZM (Alan Hadley, UK). When photographs were taken, the amber piece was immersed in clove oil (Wako Pure Chemical Industries, Ltd., Osaka, Japan; refractive index: 1.52–1.55). This oil-immersion method reduces extra light reflections on amber surface and increases visibility of an insect specimen inside (Crighton and Carrió, 2007; Penney and Green, 2010). Morphological terminology generally follows Naomi (1986), Thayer (2005), and Naomi and Nomura (2015). The measurements were given in the maximum length.

3. Systematic palaeontology

Order: Coleoptera Linnaeus, 1758 Family: Staphylinidae Latreille, 1802 Subfamily: Megalopsidiinae Leng, 1920

Genus Megalopinus Eichelbaum, 1915

Megalopinus extinctus sp. n. (Figs. 2–6)

Material. Holotype, female, specimen number AMNH Bu-SY2.

Locality and horizon. Myanmar, Kachin State, Hukawng Valley, Burmese amber; Upper Cretaceous, lowermost Cenomanian.

Diagnosis. Distinguishable from all extant species of *Megalopinus* by combination of the following character states: gular sutures moderately separated, sub-parallel-sided basally but divergent anteriorly; pronotum elongate, with two pairs of longitudinal sulci dorsally; elytra with three pairs of longitudinal sulci; mesocoxae

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