An Eocene ectoparasite of bees: The oldest definitive record of phoretic meloid triungulins (Coleoptera: Meloidae; Hymenoptera: Megachilidae)

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Received: 20 May 2005 Accepted: 15 June 2005

> ENGEL M. S. 2005. An Eocene ectoparasite of bees: The oldest definitive record of phoretic meloid triungulins (Coleoptera: Meloidae; Hymenoptera: Megachilidae). *Acta zoologica cracoviensia*, **48B**(1-2): 43-48.

> Abstract. The first definitve fossils of phoretic meloid triungulins are reported in middle Eocene (Lutetian) Baltic amber. Nine minute specimens of a meloid triungulin (perhaps Nemognathinae) were preserved with their host bee, a female of *Protolithurgus ditomeus* ENGEL (Anthophila: Megachilidae: Lithurginae: Protolithurgini). Although a single, putative triungulin was previously reported in Baltic amber, that specimen was found in isolation of a host and its identity was questionable. These Eocene meloid triungulins are the oldest, definitive direct observation of the specialized host-parasite relationship between meloids and bees.

Key words: paleontology, paleobiology, Baltic amber, Polyphaga, Tertiary, Lutetian, An-thophila, Tenebrionoidea.

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I. INTRODUCTION

The fossil record of ectoparasitic arthropods is exceedingly sparse as one might expect based on their habits. Among the beetles, two families are noteworthy ectoparasites on other insects; the Ripiphoridae and Meloidae. Both of these families have evolved highly mobile, rather than grublike, first larval instars, called triungulins. The triungulins permit the immature beetle to locate, grasp, and attack the host. In those species that victimize bees and wasps, the triungulins are morphologically designed to grasp their hosts (typically grasping setae in the same way lice grasp mammal hair) and are phoretic upon them. In order to gain access to the bee's nest, and thereby to the pollen provisions and immature bees contained therein, the triungulins wait on infloresences for adult bees visiting for pollen or nectar. When a female host visits a flower with triungulins, the immature beetles attach themselves to the bee's setae in locations difficult for the bee to groom. The triungulins are then unwittingly transported by the female bee and in this manner successfully infiltrate the host's nest. Triungulins in one species of *Meloe*, however, aggregate and mimic female M. S. ENGEL

Habropoda (Apidae) in an attempt to lure unsuspecting males (HAFERNIK & SAUL-GERSHENZ 2000). The triungulins then transfer to host females while the bees copulate.

While adults of Meloidae and Ripiphoridae are certainly uncommon in the geological record (fossil Ripiphoridae see KAUPP et al. 2001; fossil Meloidae see Table I), their immatures are far more elusive and understandably almost entirely absent as fossils. Putative ripiphorid triungulins in Cretaceous, Burmese amber have been reported by GRIMALDI et al. (2005) and only two meloid triungulins have been previously recorded as fossils, both uncertainly assigned and only one (from the Miocene) associated with a host (LARSSON 1978; POINAR 1992).

Table I

Taxon	Horizon	Reference
ADULTS		
Epicauta	Eocene-Oligocene/Florissant, CO	Wickham, 1914
	Miocene/Shanwang, China	ZHANG, 1989
	Pliocene/Hidalgo, Mexico	ZARAGOZA-CABALLERO & VELASCO DE LEÓN, 2003
	Pleistocene/Rita Blanca, TX	WERNER, 1969
Gnathium	Eocene-Oligocene/Florissant, CO	SCUDDER, 1893
Lytta	middle Eocene/Baltic amber	BURMEISTER, 1832; SPAHR, 1981
	Eocene-Oligocene/Florissant, CO	Wickham, 1914
	Miocene/Germany	HEER, 1847
	Pleistocene/Rita Blanca, TX	WERNER, 1969
Meloe	middle Eocene/Baltic amber	LARSSON, 1978; SPAHR, 1981
	Miocene/Yugoslavia	HEER, 1847
Mylabris	Eocene/France	Piton, 1940
	Oligocene/Germany	HEYDEN & HEYDEN, 1866
	Miocene-Pliocene/France	Piton & Théobald, 1935
Nemognatha	Eocene-Oligocene/Florissant, CO	WICKHAM, 1912
Tetraonyx	Eocene-Oligocene/Florissant, CO	Wickham, 1914
Zonabris	Eocene/France	PITON, 1940
Zonitis	Miocene/Germany	HEER, 1865
Meloidae sp.	Oligocene/Săo Paulo, Bazil	MARTINS-NETO, 1998
	Miocene/Clarkia, ID	LEWIS et al., 1990
TRIUNGULIN		
Meloidae sp.	Early Miocene/Dominican amber (on <i>Proplebeia dominicana</i>)	POINAR, 1992
	middle Eocene/Baltic amber (on <i>Protolithurgus ditomeus</i>)	present paper
?	middle Eocene/Baltic amber (unassociated)	LARSSON, 1978

Compression fossils and amber inclusions assigned to Meloidae (most of the compression fossils are of dubious identity and should be restudied)

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Phoretic meloid fossils

A female of *Protolithurgus ditomeus* ENGEL (2001), an extinct relative of the leaf-cutter, mason, and wool-carder bees, was discovered in middle Eocene (Lutetian) Baltic amber with nine meloid triungulins in locations typical of modern ectoparasite attachement. The triungulins were all grasping setae of the bee's body and presumably had attached themselves during one of the bee's final visits for floral resources. Bees themselves are quite uncommon in amber and it is therefore all the more remarkable to have recovered an individual accompanied by meloid parasites. The fossils here provide the most ancient, definitive record of the specialized phoretic morphology and mode of parasitism for meloid beetles.

A c k n o w l e d g e m e n t s. Support for this research was provided in part by the General Research Fund of the Department of Ecology & Evolutionary Biology (#2301360) and a grant from the National Science Foundation (USA) EF-0341724. This is contribution #3423 of the Division of Entomology, Natural History Museum, University of Kansas.

II. SYSTEMATIC PALEONTOLOGY

Meloidae Triungulins

(Nemognathinae?)

Fig. 1

M a t e r i a l. Sex indeterminate; nine specimens in a single piece of amber and on the holotype female of *Protolithurgus ditomeus* ENGEL (Hymenoptera: Megachilidae: Lithurginae). Baltic amber: Eocene, Kaliningrad, Yantarny, AMNH B-W 157 (Amber Collection, Division of Invertebrate Zoölogy, American Museum of Natural History, New York). The piece of amber was epoxy embedded following the protocol of NASCIMBENE & SILVERSTEIN (2000) and then trimmed and polished with a water-fed saw and grinder/polisher prior to study.



Fig. 1. Holotype of *Protolithurgus ditomeus* ENGEL (AMNH B-W 157) (Hymenoptera: Megachilidae), with position of triungulin on gena marked by white box. Inset shows enlarged photomicrograph of triungulin grasping genal seta. Eight additional triungulins are preserved clinging to the venter of the bee (not visible from this aspect).

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D e s c r i p t i v e n o t e s. Total body length ca. 0.65 mm; color light brown; integument well sclerotized and apparently minutely imbricate. Body form navicular, body gently tapering posteriorly. Head prognathous, elongate, gently tapering anteriorly, length approximately 1.5 times length of pronotum; antenna three-segmented, segments slender and elongate (each much longer than wide), basal segment slightly broader than more distal segments which are progressively more thin, apicalmost segment exceedingly long and thin, longer than combined lengths of first and second segments; epicranial cleavage lines not evident (this is challenging to see owing to distortion in the amber and thus their presence should be considered unknown rather than truly absent). Thoracic segments of equal size except prothoracic segment slightly larger in both length and width. Legs five-segmented; pulvilli absent. Abdomen nine-segmented; first abdominal segment with spiracles positioned on segment, not produced on lateral extensions; ninth abdominal segment smallest, without terminal bladder or sucker.

The absence of the pulvilli (a.k.a., pretarsal bladders or lobes) precludes assignment to Ripiphoridae as does the 9-segmented abdomen (ripiphorids have ten-segmented abdomens, the terminal segment typically tubular). Eight triungulins are clinging to setae of the bee's mesosomal venter while the ninth is attached to a seta of the gena. Unfortunately in none of the nine specimens are details of the mouthparts evident owing to the position of the specimens in the amber and relative to the bee. Similarly the chaetotaxy is challenging to observe in each of the specimens. These are important traits for more definitive, phylogenetic placement within Meloidae. The navicular body form, however, is typical of triungulins in the Tetraonycinae and Nemognathinae. *Tetraonyx*, however, has the first abdominal spiracles produced on lateral extensions and thus the fossils considered herein are likely nemognathines of some kind. Indeed, the body form and shape of the head capsule are reminiscent of some *Zonitis*.

III. DISCUSSION

The geological record of Meloidae is entirely confined to the Tertiary and is principally based on dubiously assigned compression fossils (Table 1). Meloid triungulins have been recorded twice previously – once from a putative specimen in Baltic amber (LARSSON 1978), and once in Dominican amber (POINAR 1992). The first specimen is of uncertain systematic position and was found in isolation of any other insects (e.g., a presumed host). The specimen reported by POINAR (op. cit.) in Early Miocene (ca. 20 Ma) amber from the Dominican Republic was preserved on the pronotal dorsal surface of the extinct stingless bee, *Proplebeia dominicana* (WILLE & CHANDLER) (Apidae: Meliponini). The association was not only noteworthy as it was previously the only known fossil triungulin in association with its presumed host but also because today meloids are not known to victimize stingless bees, suggesting a host-parasite relationship now lost to the modern world. The association is further interesting since even loosely hygenic behaviors in social bees would presumably have made such an association challenging. While for now this record and association is accepted, the figure provided by POINAR (op. cit.) is not suggestive of a meloid and the identity should be confirmed.

Like the meloid-*Proplebeia* association, the meloid-*Protolithurgus* affiliation is a novelty not presently known in the living fauna. Although meloids are indeed ectoparasites of several Megachilidae, they are not currently understood to attack species of the subfamily Lithurginae. There is nothing about lithurgine biology to preclude such an association and it may eventually be discovered that such a host-parasite relationship does exist in our midst. Should this be the case, it would be remarkable that the association was first made known on the basis of paleontological material, as both the hosts and parasites are exceptionally rare in the fossil record.

While the meloid triungulin evolved a single time in the ancestor of Meloinae + Tetraonycinae + Nemognathinae (plesiomorphically absent only in the basalmost subfamily, Eleticinae), phoresy has apparently arisen independently at least seven times (BOLOGNA & PINTO 2001). If the assign-

Phoretic meloid fossils

ment of the various compression fossils is to be trusted, then adults of three of the seven phoretic lineages are known from the mid- to latest Eocene (i.e., *Meloe, Tetraonyx*, and *Nemognatha* + *Gnathium* + *Zonitis*). The oldest fossil bee is from the Late Cretaceous and the bees as a whole arose and diversified in the middle Cretaceous (ca. 120–110 Ma) (ENGEL 2000, 2001, in press; GRIMALDI & ENGEL 2005). The fact that this specialized association was already established by the middle Eocene, as directly evidenced by the fossils discussed herein and suggested by the putative adults described, implies that the relationship between meloids and bees is certainly older, perhaps as old as the Cretaceous. It is likely, however, that the real radiation of Meloidae took place in the Early Tertiary. Several, now-dominant groups such as ants, bees, and termites originated and first diverged into higher lineages (e.g., families of bees, subfamilies of ants, basal families of termites) in the Cretaceous but did not truly become speciose and abundant until the Paleogene (GRIMALDI & ENGEL 2005). The same may be true of the meloids who may have originated in the mid- to Late Cretaceous and then more extensively radiated in the Paleocene.

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