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ORIGINAL RESEARCH

Dating the Co-evolution Between Bees and Beetle Triungulins (Coleoptera: Cleridae) to the Mid-Cretaceous

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ABSTRACT

Presently, three families of Coleoptera (Meloidae, Ripiphoridae and Cleridae) produce triungulin larvae that parasitize aculeate Hymenoptera, especially various lineages of social and solitary bees, as well as wasps and other insects. The discovery of a fossil bee with associated beetle triungulins in mid-Cretaceous Burmese amber provides the earliest known date for the co-evolution between bees and beetle triungulins, specifically those of the family Cleridae (Coleoptera). The fossil bee has been described in a new family and the beetle triungulins are described in the present work in the form genus and species *Anebomorpha cercorhampha* gen. et sp. nov. (Coleoptera: Cleridae). The description of *Anebomorpha cercorhampha* is based on 21 triungulins of the family Cleridae, five of which are in direct contact with the primitive bee in the amber. The remainder are at various distances behind the bee. This is the earliest fossil evidence of co-evolution between beetle triungulins and a member of the aculeate Hymenoptera.

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Introduction

The first stage larvae (triungulins) of three beetle families (Meloidae, Ripiphoridae and Cleridae) destroy eggs, larvae and provisions of bees around the world (Böving & Craighead, 1931; Lawrence & Britton, 1991; Petersen, 1957). Solitary bees are the prime targets but social bees of the genus *Apis* are also attacked. Additional damage is caused by the triungulins when they congregate on adult honeybees, sometimes to the point of causing irritation and death (Clausen, 1962; Topitzhofer, Marshall, Royce, & Sagili, 2018).

Specific triungulins of the families Meloidae, Cleridae and Rhiphoridae that are parasitic on developing stages of Apoidea are known to assemble on flowers. In this location, they can attach themselves to the bodies of visiting bees or wasps. After being carried back to the hymenopteran's nest, the triungulins initiate development on the immature stages of their host and its stored nest provisions (Clausen, 1962; Clausen, 1976).

The present study describes a new species of checkered beetle (Coleoptera: Cleridae) based on characters observed in twenty one con-specific beetle triungulins in a piece of Burmese amber containing a primitive, stem lineage bee (Fig. 1) (Poinar, 2020a).

It is presumed that originally, all 21 triungulins were attached to the fossil bee and some became dislodged after the bee entered the resin. It is known that when triungulin densities are high on single bees, flight can be disrupted (Pinto & Selander, 1970) and this may be how the fossil bee entered the resin.

Materials and methods

The amber originated from the Noije Bum 2001 Summit Site mine located in the Hukawng Valley southwest of Maingkhwan in Kachin State (26º20´N, 96º36´E) in Myanmar.

Based on paleontological evidence, this site was dated to the Upper Albian of the Early-Mid Cretaceous (Cruickshank & Ko, 2003), placing the age at 97 to 110 MYA. A more recent study using U-Pb zircon dating determined the age to be 98.79 ± 0.62 MYA (Shi et al., 2012).

Fig. 1. Five triungulins (arrows) of *Anebomorpha cercorhampha* coll. gen. et sp. nov., adjacent to a primitive bee in Burmese amber. Scale bar = 663 µm.

Nuclear magnetic resonance (NMR) spectra and the presence of araucaroid wood fibers in amber samples from the Noije Bum 2001 Summit Site indicate an araucarian tree source for the amber (Poinar, Lambert, & Wu, 2007). Observations and photographs were made with a Nikon SMZ-10 stereoscopic microscope and Nikon Optiphot optical microscope (with magnifications up to 650x). Helicon Focus Pro X64 was used to stack photos for better overall clarity and depth of field.

Results

Some of the twenty one triungulins in the amber piece containing a small primitive bee are in close contact with the bee (Fig. 1), while others are positioned some distance behind the bee. Eighteen of the triungulins are complete but orientated in different positions. Some are outstretched (Figs. 2a,b) while others are curved (Figs. 3a,b). Based on morphological comparisons, all of the triungulins are considered to represent a single species.

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lsid:zoobank.org:pub:B8A7F25C-4789-4BB0-8548-1F178A169081

Order Coleoptera Linnaeus, 1758

Family Cleridae Latreille, 1802
Genus *Anebomorpha* collective gen. nov.
lsid:zoobank.org:act:24FF6F19-97A0-4678-B26A-CBFD67C82BEA

Diagnosis: Triungulins campodeiform, with slender, sub-parallel body and distinct narrow legs; head prognathous, stemmata and 3-segmented antennae present; mandibles with blunt tooth positioned in basal half; labial palpi 2-segmented; legs 5-segmented, including elongate, slightly curved tarsungulus often accompanied by 2 long basal setae (broken off in some specimens); pulvilli absent; abdomen composed of nine segments, terga well sclerotized, spiracles placed along outer border of tergites; ninth abdominal segment bearing a pair of short, two-jointed, upward pointed, curved urogomphi.

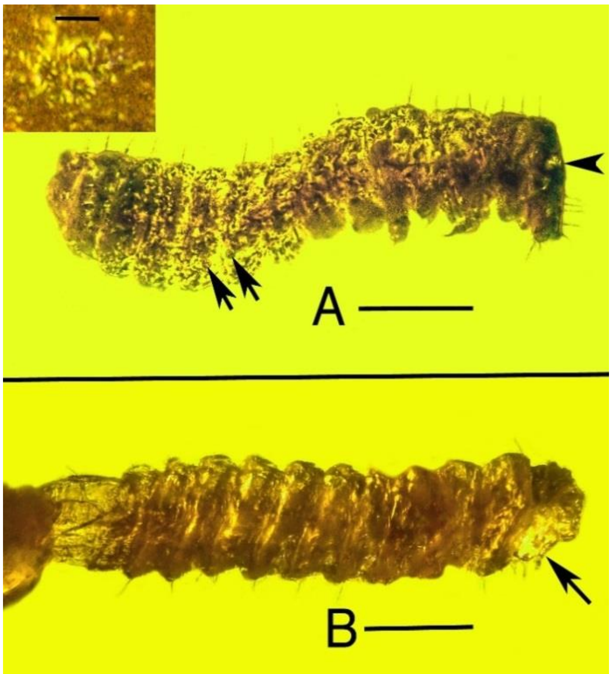

Fig. 2. *Anebomorpha cercorhampha* coll. gen. et sp. nov., in Burmese amber. A. Triungulin with 9 abdominal segments. Arrows show spiracles on tergites 4 and 5. Arrowhead shows stemmata. Urogomphi concealed. Scale bar = 190 µm. Insert shows detail of stemmata. Scale bar = 14 µm. B. Triungulin with exposed right antenna (arrow). Urogomphi concealed. Scale bar= 210 µm.

Etymology*:* The collective generic name is from the Greek "anebos" = immature and the Greek "morpho" = form.

Collective species: *Anebomorpha cercorhampha* collective gen. et sp. nov.
lsid:zoobank.org:act:B6C0C264-9666-4E3A-951A-AA25B93A985C

Etymology: The specific epithet is from the Greek "kerkos" = tail and the Greek "rhamphis" = hook in reference to the 2-segmented curved hooks on the terminal abdominal segment.

Diagnosis: As for collective genus (by monotypy). Specimens deposited in the Poinar amber collection (accession # B-Hy-20) maintained at Oregon State

University, Corvallis, Oregon.

Type locality: Amber mine in the Hukawng Valley, southwest of Maingkhwan in the state of Kachin (26º20´N, 96º36´E), northern Myanmar (Burma).

Comments: In the past, workers of the Meloidae used the comparative morphology of first stage triungulin larvae to form a classification of the family (MacSwain, 1956). If adults were also present, their morphology was added, although the generic classification was based largely on the structure of the larvae, with biological notes included. Rather than continue that tradition in the present work, we have erected a new collective group genus for fossil triungulins that have been identified to an insect family but cannot be placed in any extinct or extant genus. When additional adult material is obtained, the species can be placed in an established or new genus. Collective group genera, as defined in Article 42.2.3 of the code of zoological nomenclature (Ride, 1999), with their respective species, are erected for convenience and are considered independent of the nomenclatural classification used for extant forms. Collective groups have no type species.

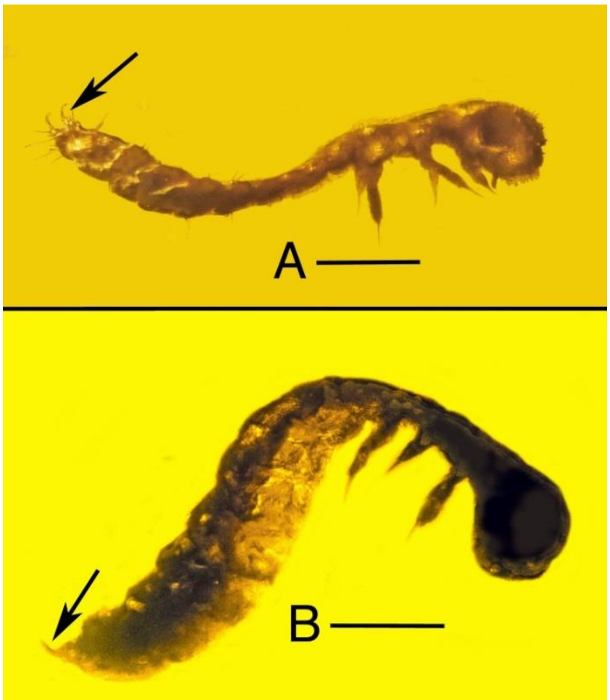

Fig. 3. *Anebomorpha cercorhampha* coll. gen. et sp. nov., in Burmese amber. A. Triungulin showing urogomphi on T9 (arrow). Scale bar = 132 µm. B. Triungulin showing urogomphus on T9 (arrow). Scale bar = 155 µm.

Description: In the present work, we use “urogomphi” as defined by Petersen (1957) to mean “paired processes projecting from the posterior end of the tergum of the 9th abdominal segment that may be jointed and movable by muscles or unjointed and immovable”. While some equate urogomphi with cerci, cerci in general are more flexible, slender and not as sclerotized as urogomphi (Torre-Bueno de la, 1989).

Anebomorpha cercorhampha collective gen. et sp. nov. (Figs. 1-5).

Triungulin campodeiform; tan; lightly sclerotized; elongate, with sub-parallel sides and slender legs. Body length, 670 µm -1100 µm. Maximum width (measured in center of abdomen), 170 µm -230 µm.

Head: Prognathous, oval to elongate, length, 188 µm - 209 µm; epicranial suture obscured; stemmata placed dorsolaterally behind transverse line in middle of head capsule; diameter stemmata, 16 µm -23 µm; antennae 3-segmented, directed anterolaterally, details obscured, length antennae, 48 µm - 58 µm; labrum not visible; mandible with reduced, sub-basal mola; in some specimens mandibles appear to have a horizontal orientation, while in others they show a vertical orientation, length mandibles, 44 µm - 64 µm; labial palps short, 2-segmented, blunt tipped; maxillary palps blunt tipped, cardo and stipes fused; galea and lacinia peg-like (Fig 4a); mushroom-like projections occur on the head of some specimens as well as on the abdomen of other individuals (Fig 5a).

Thorax: Segments transverse, slightly broader than head; margins of each segment usually rounded; length, 178 µm -270 µm; greatest width, 140 µm -162 µm; spiracles obscured; legs slender, lacking major setae, 5-segmented, length, 95 µm -140 µm; femora slightly larger that tibiotarsus; not enlarged in middle; tibiotarsi slightly tapered at apex; extended setae absent on legs; tarsungulus slightly curved, tip pointed, length 38 µm - 63 µm; pulvilli absent.

Abdomen: Elongate; often subparallel sided but not fusiform; dorsoventrally flattened, with 9 segments approximately equal in width, ninth segment suboval; length abdomen, 440 µm - 790 µm, maximum width, 170 µm -220 µm; posterior end of ninth segment bearing a pair of 2- segmented, upward curved, pointed urogomphi (Fig. 5a,b), length urogomphi, 51 µm -97 µm), chalazae not present; abdominal terminus with several straight caudal setae, one of which is often as long as the urogomphi (Figs. 5a,b); spiracles subequal in diameter, positioned along outer border of tergites (Fig. 2a).

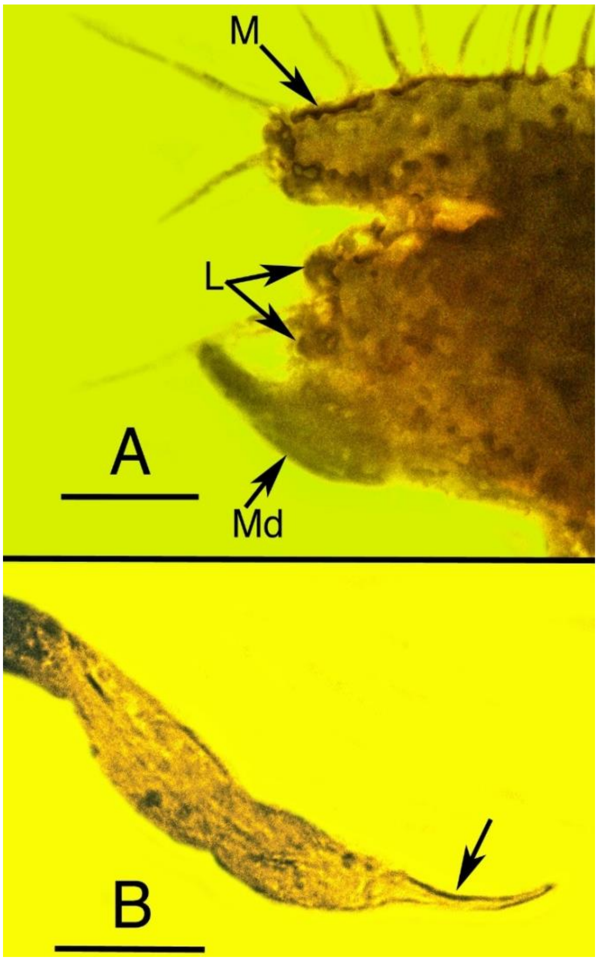

Fig. 4. *Anebomorpha cercorhampha* coll. gen. et sp. nov., in Burmese amber. A.Ventral view of anterior head portion. L = labial palps. M= maxilla. Md= mandible. Scale bar = 36 µm. B. Terminus of anterior leg showing extended, curved tarsungulus (arrow). Scale bar = 38 µm.

Comments: *Anebomorpha cercorhampha* coll. gen. et sp. nov. cannot be placed in the Meloidae or Ripiphoridae since there are no extant or extinct triungulins in these two families with urogomphi and triungulins of the latter group possess disc-like termini on the legs, especially the forelegs (Böving & Craighead, 1931; Petersen, 1957). However extant triungulins of *Trichodes* (Cleridae) possess urogomphi and are predaceous on both solitary and social bees (Roubik, 1989). Triungulins of *Trichodes ornatus ornatus* Say hatch from eggs deposited on flowers, attach themselves to bees and are carried to their nests where they devour the larvae (Linsley & MacSwain, 1943).

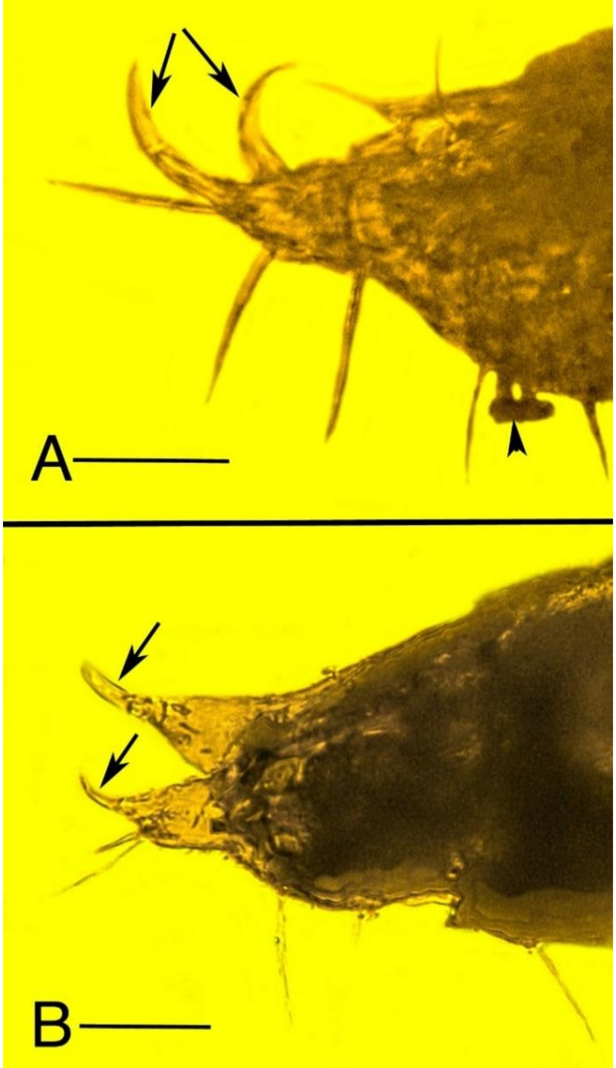

Fig. 5. *Anebomorpha cercorhampha* coll. gen. et sp. nov., in Burmese amber. A. Two-segmented urogomphi (arrows) on tergite 9. Arrowhead shows mushroom- like structures attached to abdominal ventrite. Scale bar = 60 µm. B. Two-segmented urogomphi (arrows) on tergite 9. Note thick first segments. Scale bar = 50 µm.

With the other basic features of clerid triungulins mentioned above, *Anebomorpha* is placed in the family Cleridae (Böving & Craighead, 1931; Petersen, 1957). The life cycle of *Anebomorpha cercorhampha* gen. et sp. nov., is proposed to have been similar to that of extant members of *Trichodes*.

Anebomorpha cercorhampha coll. gen. et sp. nov., can be distinguished from extant clerid triungulins by its two-segmented urogomphi since all presently known clerid triungulins and later larval stages have unjointed urogomphi (Böving & Craighead, 1931; Petersen, 1957). In a previous study, a small meloid triungulin described as *Microentomus epibatus* Poinar (Coleoptera: Meloidae) was attached to the dorsum of the Burmese amber jumping ground bug, *Lumatibialis burmitis* Poinar and Brown (Hemiptera: Schizopteridae). While many of its features were obscured, *Microentomus* did not possess urogomphi (Poinar & Brown, 2014).

Discussion

The discovery of beetle triungulins associated with a bee in Burmese amber shows that beetle triungulins were already well established by the mid-Cretaceous and establishes the earliest known record of co-evolution between beetle triungulins and bees.

The most distinctive diagnostic feature of *Anebomorpha cercorhampha* coll. gen. et sp. nov. are the upward curved, 2-segmented, pointed urogomphi on the 9th abdominal tergite. If and how these urogomphi were used to secure the triungulins to the body of the bee is unknown. In the case of a fossil meloid triungulin attached to a stingless bee (Hymenoptera: Apidae) in Dominican amber, the triungulin was holding on to one of the hairs of the bee with its mandibles (Poinar, 2009). A similar method of transport could have been used by the fossil triungulins by clasping the scopal hairs on the mid and hind legs or possibly the wing margins of the bee.

Some behavioral patterns used by beetle triungulins to reach female bees are quite sophisticated. A study by Saul-Saul-Gershenz and Millar (2006) demonstrated how triungulins of *Meloe franciscanus* Van Dyke (Meloidae) aggregate on plants and release a scent that mimics the sex pheromone of the female solitary bee, *Habropoda pallida* Timberlake (Hymenoptera: Apidae). Male bees attracted to the scent are then boarded by the triungulins. When the male bee later mates with a female, the triungulins shift from the body of the male to that of the female and are carried back to the bee's nest.

The earliest fossil record of the family Cleridae is from the Upper Jurassic of southwestern Mongolia. There are a number of additional Mesozoic records as well (Kirejtshuk, 2012) so the presence of members of this family in mid-Cretaceous Burmese amber is not to be unexpected.

The present study not only represents the earliest record of beetle triungulins associated with Aculeate Hymenoptera but also shows that the predatory behavior of clerid beetle triungulins to bees had already been established by the mid-Cretaceous. One of the triungulins was infected with a microsporidian, thus further illustrating the intricate relationship between a host bee, beetle parasites and microsporidian pathogens (Poinar, 2020b).

Disclosure statement

No potential conflict of interest was reported by the authors.

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