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A first higher-level time-calibrated phylogeny of antlions (Neuroptera: Myrmeleontidae)

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ABSTRACT

In this study, we reconstruct the first time-calibrated phylogeny of the iconic antlion family, the Myrmeleontidae (Neuroptera: Myrmeleontiformia). We use maximum likelihood and Bayesian inference to analyse a molecular dataset based on seven mitochondrial and nuclear gene markers. The dataset encompasses 106 species of Neuroptera, including 94 antlion species. The resulting phylogenetic framework provides support for a myrmeleontid classification distinguishing four subfamilies: Acanthaclisinae, Myrmeleontinae, Palparinae, and Stilbopteryginae. Within Myrmeleontinae, Myrmecaelurini and Nemoleontini are recovered as monophyletic clades; Gepini also appears as a valid tribe, distinct from Myrmecaelurini whereas Myrmecaelurini and Nesoleontini on one hand and Brachynemurini and Dendroleontini on the other hand, appear closely related. Some preliminary information related to generic and specific levels are also implied from our results, such as the paraphyly of several genera. Dating analyses based on thoroughly evaluated fossil calibrations indicate that the antlion family likely originated in the Cretaceous, between 135 and 138 million years ago (depending on the set of fossil calibrations), and that all higher-level lineages appeared during the Early Cretaceous. This first phylogenetic hypothesis will provide a valuable basis to further expand the taxonomic coverage and molecular sampling, and to lay the foundations of future systematic revisions.

1. Introduction

The order Neuroptera (*ca.* 6000 species) consists of small to large holometabolous insects that are considered, together with Megaloptera + Raphidioptera, as a sister group of Coleopterida (i.e. Coleoptera + Strepsiptera) (Misof et al., 2014). Neuroptera are commonly divided into three sub-orders (Hemerobiiformia, Myrmeleontiformia and Nevrorthiformia) and 17 families (Aspöck, 1992, 1993; Grimaldi and Engel, 2005). The higher-level phylogenetic relationships among these groups, as well as the family-level hierarchy of Neuroptera, have been extensively discussed based on both morphological and molecular data, and is now rather satisfactorily resolved (Aspöck et al., 2001, 2012; Aspöck, 2002; Haring and Aspöck, 2004; Aspöck and Aspöck, 2008; Winterton and Makarkin, 2010; Winterton et al., 2010).

Within Neuroptera, antlions (Myrmeleontiformia: Myrmeleontidae) constitute the most species-rich family. In the most recent catalogue, Stange (2004) listed 1522 extant species and about 13 fossil species classified in 14 tribes and 201 genera. Since the publication of Stange's catalogue, numerous new species have been described, and the world antlion fauna is currently estimated at *ca.* 2000 species (Acevedo et al., 2013). Myrmeleontidae occur in most temperate and tropical regions of the world, with the greatest diversity being found in the intertropical area (see Fig. 1 for an excerpt of antlion diversity). Most antlions are psammophylous and live in arid or semiarid environments (Mansell, 1996). Most adults are crepuscular or nocturnal and rest on vegetation during day, but some species are more typically diurnal. Adults in most species retain a predatory diet, which is potentially complemented by pollen in a few species (Stelzl and Gepp, 1990). Although most myrmeleontid species are ambush-hunters (see Miller and Stange, 1985; Stange et al., 2003; Stange, 2004; Badano and Pantaleoni, 2014 for an overview), antlions are well known for the behavior of the species that construct pitfall traps in sandy soil to catch

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Fig. 1. Illustration of antlion diversity. (A) Adult of *Macronemurus appendiculatus* (Latreille) (Myrmeleontinae); (B) Adult of *Palparellus spectrum* (Rambur) (Palparinae); (C) Adult of *Centroclisis* sp. (Acanthaclisinae); (D) Adult of *Stilbopteryx napoleo* (Lefèbvre) (Stilbopteryginae); (E) Unidentified antlion larva; (F) Sand pits of *Myrmeleon inconspicuus* Rambur (Myrmeleontinae).

prey; the pit construction and the pit-dwelling larva behavior have been described in detail (e.g. New, 1986; Mansell, 1988; Devetak et al., 2005; Mencinger-Vračko and Devetak, 2008; Hollis et al., 2011, 2015; Lambert et al., 2011; Scharf et al., 2011). Ambush-hunter larvae live on cliffs, under rocks, on trees or in trunk cavities; their biology is far less well known (Badano and Pantaleoni, 2014). Some species, such as the Mediterranean species *Myrmecaelurus trigrammus* (Pallas), are also facultative pit-builders, either ambushing their prey at surface or constructing pitfall traps (Devetak et al., 2013). Antlions larvae have effective toxins, which are derived from both the insect and bacterial symbionts (Dunn and Stabb, 2005). They also possess potent digestive enzymes, which are used to liquefy the internal components of their prey (Griffiths, 1980, 1982; Van Zyl et al., 1998). In all species with known biology, pupation occurs in a silk cocoon spun by the last larval instar in the same habitat. Overall, reproduction biology has been poorly investigated. Sexual communication relies on pheromones (Baeckström et al., 1989; Bergström et al., 1992; Yasseri et al., 1996; Bergström, 2008) and few studies have investigated in details the morphological structures that are involved in pheromone perception (but see Zhang et al., 2015). Copulation has rarely been observed and it is assumed that in most cases eggs are laid separately on the ground (New, 1986; Miller, 1990; Yasseri and Parzefall, 1996; Yasseri et al., 1996).

Larvae of Myrmeleontidae exhibit several combinations of characters (see Badano and Pantaleoni, 2014 for a very detailed description of antlion larvae). The buccal cavity is closed anteriorly with each mandible and maxillary lacinia elongate and closely united to form complex piercing and sucking tubes, the mid-gut is closed posteriorly and disconnected of the hind-gut, and the Malpighian tubes produce silk to make the cocoon that surround the pupa. They are also flattened dorso-ventrally and covered with dolichasters representing modified setae. Their elongate and apically curved jaws bear generally three mandibular teeth of variable length, but additional teeth are observed in certain species and a few genera have a reduced number, and the head capsule is heavily sclerotized with a convex posterior margin (Aspöck, 1992). Adults are characterized by short and slightly enlarged antennae (clubbed in Stilbopteryginae). Wing venation varies between sub-families, and includes a long hypostigmatic cell (except in Stilbopteryginae) located under the pterostigma. Legs are well developed and variably equipped with stout setae. In some species claws can be folded on the ventral surface of the last tarsomere. Configurations of male and female genitalia exhibit also differential characters (Stange, 1970, 1994; Aspöck and Aspöck, 2008). The phylogenetic significance of external and internal morphological characters was discussed in detail by Aspöck et al. (2001), Aspöck and Aspöck (2008) and Zimmermann et al. (2011).