Molecular Phylogenetics and Evolution 101 (2016) 163–175

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

A molecular phylogeny of rose chafers (Coleoptera: Scarabaeidae: Cetoniinae) reveals a complex and concerted morphological evolution related to their flight mode

Petr Šípek[c], Silvia Fabrizi[a,b], Jonas Eberle[b], Dirk Ahrens[a,b,*]

[a] Department of Entomology, Natural History Museum, London SW7 5BD, United Kingdom
[b] Centre of Taxonomy and Evolutionary Research, Zoologisches Forschungsmuseum Alexander Koenig Bonn, Adenauerallee 160, 53113 Bonn, Germany
[c] Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, CZ-128 44 Praha 2, Czech Republic

ARTICLE INFO

Article history:
Received 8 December 2015
Revised 28 April 2016
Accepted 7 May 2016
Available online 7 May 2016

Keywords:
Coleoptera
Scarabaeidae
Cetoniinae
Systematics
Flight mode
Elytral base

ABSTRACT

Rose chafers (Cetoniinae) are a large group of flower visitors within the pleurostict Scarabaeidae that are characterized by their distinctive flight mode with nearly closed forewings. Despite their popularity, this is the first study to use molecular data to infer their phylogenetic relationships. We used partial gene sequences for 28S rRNA, cytochrome oxidase I (*cox1*) and 16S rRNA (*rrnL*) for 299 species, representing most recognized subfamilies of Scarabaeidae, including 125 species of Cetoniinae. Combined analyses using maximum parsimony, maximum likelihood and Bayesian inferences recovered Cetoniinae as monophyletic in all analyses, with the sister clade composed of Rutelinae and Dynastinae. Rutelinae was always recovered as paraphyletic with respect to Dynastinae. Trichiini *sensu lato* (*s.l.*) was recovered as a polyphyletic clade, while Cetoniini *s.l.* was recovered as paraphyletic. The inferred topologies were also supported by site bootstrapping of the ML trees. With the exception of Cremastochelini, most tribes of Cetoniinae were poly- or paraphyletic, indicating the critical need for a careful revision of rose chafer classification. Analysis of elytral base structure (including 11 scored characters) in the context of phylogeny, revealed a complex, concerted and rapid transformation of the single trait elements linked to a modified flight mode with closed elytra. This appears to be unlinked to the lateral sinuation of the elytra, which originated independently several times at later stages in the evolution of the group.

1. Introduction

The sclerotization of the forewing (elytron) in Coleoptera and the transformation to a closed protective shield is recognized as one of most crucial factors in driving the success and diversification of beetles (Grimaldi and Engel, 2005; Hunt et al., 2007). The elytra provide mechanical protection as well as protection against dehydration and have enabled them to adapt to a large range of habitats. In most extant lineages the elytra passively participate in supporting flight (Nachtigall, 1964; Le et al., 2010; Johansson et al., 2012). In several cases, however, the latter function has been modified during evolution: flight with closed elytra is one of the most important evolutionary novelties found in the majority of rose chafers (Coleoptera: Scarabaeidae: Cetoniinae) (Fig. 1). In general, the rose chafers are some of the best flyers among beetles (Krikken, 1984); they are able to hover above and land on food resources, such as flowers or fruits, with great control, as well as rapidly escape when threatened by possible predators. One major modification allowing for this flight mode is the lateral (posthumeral) emargination of the elytra. This enables the hind wings (alae) to unfold and slide under the elytra during flight. However, other humeral–thoracic modifications are also involved (Krikken, 1984; Haas and Beutel, 2001; Ahrens, 2006). For example, Eberle et al. (2014) reported that the change of flight mode among rose chafers was also associated with a general dorsoventral flattening of the body.

Cetoniinae are not the only beetles that fly with closed elytra; members of the Scarabaeinae genera *Gymnopleurus*, *Scarabaeus* and *Sisyphus* also exhibit a similar flight mode (Schneider, 1978; Frantsevich, 2012a), along with several representatives of Curculionidae (e.g., *Rhynchophorus* spp.; Weissling et al., 1994) and Buprestidae (Crowson, 1981; Volkovitsh, 2008; Frantsevich, 2012a,b). The origins and evolution of this specialized mode of flight remain unknown. It is presumed that flight with closed elytra

---

[*] Corresponding author at: Zoologisches Forschungsmuseum Alexander Koenig Bonn, Adenauerallee 160, 53113 Bonn, Germany.

E-mail addresses: sipekpetr80@gmail.com (P. Šípek), ahrens.dirk_col@gmx.de, d.ahrens@zfmk.de (D. Ahrens).

http://dx.doi.org/10.1016/j.ympev.2016.05.012
1055-7903/© 2016 Elsevier Inc. All rights reserved.

Fig. 1. Flight images of rose chafers and their allies (from top left to bottom right): *Melolontha melolontha*, flight mode state (i) (photo: J. Schmidt); *Valgus hemipterus*, flight mode state (ii) (photo: J. Schmidt); *Plectrone borneensis*, flight mode state (iii) (photo P. Šípek); *Goliathus goliathus*, flight mode state (iv) (photo M. Hrdý); *Eupotosia affinis*, flight mode state (iv) (photo H. Poláček); *Taeniodera egregia*, flight mode state (iii) (photo H. Poláček).

is related to the diurnal way of life and to life strategies that depend on unpredictably scattered food resources, represented by the uneven blooming of fruiting trees or distribution of herbivore dung; however, direct evidence is missing. Alternatively, Verdú and Lobo (2008) explain the existence of different flight types in Canthonini (Scarabaeinae) with variable ecophysiological strategies related to their endothermy and body temperature control.

Although the elytra represent a crucial evolutionary novelty among Coleoptera, little information is available about the morphology or biomechanics of their articulation and opening mechanisms (Frantsevich, 2012a,b). Moreover, while the general morphology is similar to the second pair of wings, the terminology applied in different studies is incongruent and in some cases even contradictory (Stellwag, 1914; Herbst, 1944; Doyen, 1966; Ahrens, 2006; Frantsevich, 2011, 2012a, 2012b). Typically, the elytra–thorax articulation consists of a series of four axillary sclerites (AX1–AX4). These are embedded in an elastic membrane which is connected to the basal projection of the elytra (elytral root) with the tergites (i.e., scutum and scutellum) and pleurites (i.e., episternum and epimeron) of the mesothorax. The second axillary sclerite (AX2) is connected with the elytral root and forms a condylar joint with the pleuron and a hinge with the mesoscutum. The other 3 axillary sclerites are attached to direct wing muscles (for an illustrative schema, refer to Frantsevich, 2011, 2012b). Although little is known about the morphology of elytral articulation of most Cetoniinae, Herbst (1944, 1952) showed that in *Cetonia aurata* (Linnaeus, 1761) the axillar sclerites are largely reduced. He attributed this to a loss of function related to a flight mode with closed elytra.

The majority of beetles (including representatives of the Cetoniine tribe Trichiini) open their elytra by a sideward, forward and upward turn (Stellwag, 1914; Herbst, 1944, 1952; Schneider, 1978; Frantsevich, 2012a,b). Frantsevich (2012a) showed that the opening and closing movements of beetle elytra is a result of a double rotation of the elytra axis (abduction-supination/adduction-pronation, respectively) and that the apparent phases of the elytral movements are integral to the circular motion circumscribed by the apex of the elytra. However, a different mechanism has been found among rose chafers (Cetoniini), where the initial elytral movement is a result of a slight supination without abduction (Frantsevich et al., 2005) including a simultaneous elevation and a minute spreading of the elytron (Frantsevich, 2012a).

In the ancestral (i.e., plesiomorphic) state common to most beetles, the opening and closing (abduction/adduction) of elytra is attributed to the direct mesothoracic elytral muscles (Stellwag, 1914; Herbst, 1944). Frantsevich (2012b) argued that, with several exceptions, the elevation of the prothorax might be a superior mechanism that induces the opening and closing of elytra. However, he also noticed that this mechanism is absent in rose chafers.

Rose chafers (Cetoniinae) represent one of the major lineages of phytophagous scarabs. They originated ca 70 Myr ago and diversified throughout the Cenozoic (Ahrens et al., 2014). Among the approximately 4000 described species of Cetoniinae some of the most spectacular and the largest beetles are found, along with a small number of tiny species belonging to the Microvalgini tribe