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Article



## A hypothetical evolutionary history of passalid beetles narrated by the comparative anatomy of the hindgut (Coleoptera: Passalidae)

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## Abstract

When seen as a whole, the hindgut, more than any other section of the digestive tube, provides insights for the taxonomy of higher-level taxa of Passalidae. This comparative cladistics study utilized parsimony analyses, with 57 terminal taxa (including five outgroups) and 18 characters from the ileum of most genera of passalid beetles (Coleoptera: Passalidae), which resulted in a single tree. Based on the results and the topology of the cladogram, the following classification was adopted: (Aulacocyclinae (Solenocyclinae (Proculinae (Passalinae, Macrolininae)))). Three subfamilies (Solenocyclinae, Proculinae, and Macrolininae) are here elevated from the tribal level to the subfamily level. The subfamily Passalinae is redefined and no longer contains any tribes. The family-group name Leptaulacinae is placed in synonym with Solenocyclinae and the family-group name Ceracupedini is placed in synonymy with Aulacocyclinae.

Key words: cladistic analysis, classification, comparative morphology, ileum, intestines

## Introduction

Passalid taxonomy is based on external morphology. Some authors have focused on the head characters (Gravely 1914, 1918), using them as a diagnosis for higher taxa. Other external characters have also been discussed and used for identification (Hincks 1950; Reyes-Castillo 1970). In addition, Bührnheim (1978) showed the taxonomic importance of the aedeagus, opening up the possibility of using internal anatomy as an identification aid. However, Pereira and Kloss (1966) focused their attention "on one anatomic character which with no doubt appears to be closely related to the evolutionary process of that coleopteran". That character was the hindgut, which in Passalidae has been described for 24 species belonging to five genera (Lewis 1926; Patterson 1937; Umeya 1960; Pereira & Kloss 1966).

Very few papers have been concerned with Scarabaeoidea hindgut and histology (Lewis 1926; Becton 1930; Cooper 1938; Umeya 1960, 1974; Miller 1961; Halffter & Matthews 1971; López-Guerrero 2002; Nardi *et al.* 2006). Umeya (1960) did a comparative study, which may help with the understanding of the cladogenesis processes by comparing the anatomical aspects of adult alimentary tracts in order to establish a correlation between the alimentary tract length and feeding behaviour.

There are few papers that utilize a phylogenetic analysis of the higher taxa of the Passalidae (Fonseca 1987, doctoral thesis; Gillogly 2005, PhD dissertation; Boucher 2006). Fonseca (1987) raised Aulacocyclinae to the level of family, which redefined Passalidae as consisting of taxa previously in the subfamily Passalinae according to the classification of Reyes-Castillo (1970). The proposed Aulacocyclidae family was divided into two subfamilies, Aulacocyclinae and Ceracupinae, while Passalidae consisted of Solenocyclinae and Passalinae. The Passalinae was formed for two tribes, Passalini and Leptaulacini: the Passalini was composed of the subtribes Macrolinina and Passalina. In spite of this, the classification proposal was not published and was not followed by any other authors, however it was considered and discussed by Gillogly (2005) and Boucher (2006).