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The age and phylogeny of wood boring weevils and the origin of subsociality

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ABSTRACT

A large proportion of the hyperdiverse weevils are wood boring and many of these taxa have subsocial family structures. The origin and relationship between certain wood boring weevil taxa has been problematic to solve and hypotheses on their phylogenies change substantially between different studies. We aimed at testing the phylogenetic position and monophyly of the most prominent wood boring taxa Scolytinae, Platypodinae and Cossoninae, including a range of weevil outgroups with either the herbivorous or wood boring habit. Many putatively intergrading taxa were included in a broad phylogenetic analysis for the first time in this study, such as *Schedlarius*, *Mecopelmus*, *Coptonotus*, *Dactylipalpus*, *Coptocorynus* and allied Araucariini taxa, *Dobionus*, *Psepholax*, *Amorphocerus–Porthetes*, and some peculiar wood boring Conoderini with bark beetle behaviour. Data analyses were based on 128 morphological characters, rDNA nucleotides from the D2–D3 segment of 28S, and nucleotides and amino acids from the protein encoding gene fragments of CAD, ArgK, EF-1α and COI. Although the results varied for some of the groups between various data sets and analyses, one may conclude the following from this study: Scolytinae and Platypodinae are likely sister lineages most closely related to *Coptonotus*; Cossoninae is monophyletic (including Araucariini) and more distantly related to Scolytinae; Amorphocerini is not part of Cossoninae and *Psepholax* may belong to Cryptorhynchini. Likelihood estimation of ancestral state reconstruction of subsociality indicated five or six origins as a conservative estimate. Overall the phylogenetic results were quite dependent on morphological data and we conclude that more genetic loci must be sampled to improve phylogenetic resolution. However, some results such as the derived position of Scolytinae were consistent between morphological and molecular data. A revised time estimation of the origin of Curculionidae and various subfamily groups were made using the recently updated fossil age of Scolytinae (100 Ma), which had a significant influence on node age estimates.

1. Introduction

Weevils are the most diversified group of organisms on this planet with more than 62,000 species known to science (Oberprieler et al., 2007). These beetles are found in a broad range of habitats, from deserts to tropical forests, feeding on fungus and dead wood to seeds and green leaves, and found in all kind of decompositional stages of plant tissues. The greatest diversification occurred within the so-called advanced weevils (Curculionidae), a radiation frequently ascribed to a tight association with the evolution of flowering plants (Farrell, 1998; Marvaldi et al., 2002; McKenna et al., 2009). In this perspective it is particularly interesting that several species rich lineages have reversed the phytophagous life style towards being primary decomposers of dead wood, dominating the forest decomposition guild in forests world wide. Prominent representatives for such wood boring groups include the infamous bark and ambrosia beetles in the subfamilies Scolytinae and Platypodinae where all species construct tunnels for mating and nesting in mainly dead, woody tissue.

Beetle engravings in bark and wood are frequently associated with the inoculation of fungus spores and mycelial growth (Beaver, 1989; Farrell et al., 2001), which often becomes a serious problem for forest health and timber trade (Mathew, 1987; Zwolinski and Geldenhuys, 1988). Considerable scientific efforts have therefore been dedicated to the study of wood boring ecology and pest management. Much less attention has been given to other interesting aspects of wood boring weevil biology such as their highly variable and fascinating patterns of subsocial family structure (Kirkendall et al., 1997). Elaborate care for offspring is a common trait in bark and ambrosia beetles where males and females provide variable support during larval development. Subsociality of this kind (Zablotny, 2003) is found sporadically in several insect orders,

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but is only known from a few weevil groups beyond Scolytinae and Platypodinae, such as members of the cossonine tribes Araucariini (Kuschel, 1966; May, 1993) and Onycholipini (e.g. Mecke, 2002), and from the baridine subtribe Campyloscelina (Conoderini) (Thompson, 1996). Despite considerable efforts in reconstructing the phylogeny and age of weevils (Kuschel, 1995; Kuschel et al., 2000; Marvaldi et al., 2002; McKenna et al., 2009), the origin and evolution of the wood boring habit is still controversial. A more stable phylogeny with predictable relationships between at least some of the most contentious taxa would therefore improve our understanding of weevil classification and the evolution of wood boring and subsociality.

Resolving mega-diverse clades of Cretaceous age (see e.g. Grimaldi and Engel, 2005; McKenna et al., 2009) is frequently impeded by the lack of sufficient molecular and morphological data. Even more problematic is the typically low number of sampled taxa relative to the total diversity in a clade (Franz and Engel, 2010), particularly so when missing taxa are transitional between distantly related lineages and thus may reduce the problems associated with long branches (see e.g. Pick et al., 2010). The phylogenetic resolution in weevils seems particularly limited by the apparently short time frame in which the main curculionid lineages originated (McKenna et al., 2009). Not only are diagnostic molecular changes hard to detect at the base of such ancient rapid radiations, but a correspondingly near continuous variation in morphological characters is equally problematic (Oberprieler et al., 2007). With apparently very little extinction of main lineages since the origin of Curculionidae, the classification of subfamilies and tribes and their relationships is therefore an intricate task to solve.

To foster greater progress in resolving the evolutionary conundrum of weevil relationships, a better integration of all possible data from molecular as well as morphological sources is needed to improve resolution and stability. An important strategy in this respect includes the sampling of critical transitional taxa which have been shown by e.g. Kuschel et al. (2000) to be crucial in establishing character homology between more distantly related taxa. This study therefore aims at combining the strengths of broad taxon and character sampling, by including DNA sequences from four nuclear and one mitochondrial gene, constructing a large and unbiased matrix of 128 morphological characters coded for all three main developmental stages, and by including for the first time in a combined phylogenetic analysis a range of putatively transitional taxa (see Section 2). Perhaps the most enigmatic weevil group is Platypodinae, which has shown higher than average substitution rates and a phylogenetic position which is particularly ephemeral (Farrell et al., 2001; Jordal, 2007; Jordal et al., 2008; McKenna et al., 2009). We will therefore focus more strongly on this group by testing their phylogenetic position with the inclusion or exclusion of taxa such as *Schedlarius*, *Mecopelmus* and *Coptonotus* which are all potentially transitional between Platypodinae and other weevils.

All recent and comprehensive phylogenetic analyses have unambiguously placed Platypodinae and Scolytinae within Curculionidae, with Brentidae as the sister group to all Curculionidae (Kuschel, 1995; Marvaldi, 1997; Marvaldi et al., 2002; McKenna et al., 2009). This seems apparently at odds with the fossil record which indicate that Scolytinae is slightly older than other defined lineages within Curculionidae (Cognato and Grimaldi, 2009; Kirejtshuk et al., 2009). Until lately, the oldest reliable fossil used to date the origin of Scolytinae was from early Tertiary time (London Clay 55 Ma, see also McKenna et al., 2009). However, much older cretaceous scolytine fossils were recently discovered and described from 100 Ma Lebanese and Burmese amber (Cognato and Grimaldi, 2009; Kirejtshuk et al., 2009). These recently discovered fossils are older than all other known Curculionidae fossils (upper Turonian about 90 Ma, see Oberprieler et al., 2007 for detailed review), which raise not only important questions about the age of Scolytinae and other weevils, but also the phylogenetic position of Scolytinae. Nearly doubling the age of one such important calibration point likely involves substantial changes in node age also for other weevil lineages and we will provide new estimates using an updated topology comprehensively sampled for putatively transitional taxa. We will furthermore explore the effect on dating lineages using radically different fossil ages on a single calibration point, to illuminate potential errors associated with biased fossil records.

2. Materials and methods

2.1. Taxon sampling

The classification system of Oberprieler and co-workers (2007) has been followed in this study (Table 1), in which the authors reduce several subfamilies to tribal level, particularly so the many groups now included in Baridinae (e.g. Conoderinae, Ceutorrhynchinae), Molytinae (e.g. Cryptorhynchinae) and use a broader concept of Brachycerinae (includes e.g. Erirhininae). We aimed at sampling the majority of taxa that have been proposed transitional between Scolytinae and Platypodinae, and between Scolytinae and Cossoninae, Molytinae (and Cryptorhynchini/-inae). In relation to the enigmatic status of Platypodinae, we included *Notoplatypus*, *Periommatus*, *Schedlarius* and *Mecopelmus*. While the first two taxa have some minor morphological features deviating from the typical Platypodinae, the last two show a mixture of platypodine and non-platypodine features, which has led several authors to propose that these taxa are transitional between Platypodinae and Scolytinae (Wood, 1973, 1993), with affinities to Cossoninae (Kuschel et al., 2000). With respect to the possible transition between Cossoninae and Scolytinae (see Kuschel, 1966; Kuschel et al., 2000; Marvaldi, 1997; May, 1993), we included several genera of the bark weevils in Araucariini, which have lateral socketed spines on their tibiae similar to many Scolytinae (Kuschel, 1966; Mecke, 2005). *Coptonotus* was retained in Platypodinae (Platypodidae: Coptonotinae) by Wood (1993) irrespective of its previous transfer by Thompson (1992) from Platypodinae to Scolytinae based on the shape of the male sternite VIII and the tarsus shape. This taxon also shows some affinities with Cossoninae and the genera in the scolytine tribe Scolytini in tibial structures; its phylogenetic position is therefore highly uncertain (Jordal and Oberprieler, 2011). Potential affinities between the cryptorhynch *Psepholax* and the cryptorhynch-like scolytine genus *Dactylipalpus* were also tested due to their similarly vestigial rostral channel and the lack of sclerolepidia (Zimmermann, 1994; Lyal et al., 2006). Similarly, the alternative positions of Amorphocerini (*Amorphocerus*, *Porthetes*) were tested with respect to their current placement in Molytinae (Alonso Zarazaga and Lyal, 1999), and previously in Cossoninae (Kuschel, 1966). Furthermore did we include some recently discovered wood boring and subsocial Conoderini to assess their phylogenetic relationship to other weevils.

Sample sizes were distributed relatively equally among the three major wood boring groups Scolytinae (33 spp.), Platypodinae (20 spp.) and Cossoninae (20 spp.) and the other weevil ingroup species combined (32 spp.). The inclusion of more Scolytinae species relates to the uncertain classification of some taxa in Scolytinae, e.g. *Dactylipalpus*, *Phloeoborus*, Scolytini (*Scolytus*, *Camptocerus*, *Cnemonyx*), *Scolytoplatypus*, and the oldest documented fossil of Scolytinae – *Microborus* (see Cognato and Grimaldi, 2009). Outgroups were selected among Brentidae, Anthribidae and Attelabidae. Brentidae is unequivocally established as the sister group of Curculionidae (Kuschel, 1995; Marvaldi et al., 2002; McKenna et al., 2009).