Early Cretaceous angiosperms and beetle evolution

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INTRODUCTION

The Coleoptera (beetles) constitute almost one-fourth of all known life-forms on earth. They are also among the most important pollinators of flowering plants, especially basal angiosperms. Beetle fossils are abundant, almost spanning the entire Early Cretaceous, and thus provide important clues to explore the co-evolutionary processes between beetles and angiosperms. We review the fossil record of some Early Cretaceous polyphagan beetles including Tenebrionoidea, Scarabaeoidea, Curculionoidea, and Chrysomeloidea. Both the fossil record and molecular analyses reveal that these four groups had already diversified during or before the Early Cretaceous, clearly before the initial rise of angiosperms to widespread floristic dominance. These four beetle groups are important pollinators of basal angiosperms today, suggesting that their ecological association with angiosperms probably formed as early as in the Early Cretaceous. With the description of additional well-preserved fossils and improvements in phylogenetic analyses, our knowledge of Mesozoic beetle-angiosperm mutualisms will greatly increase during the near future.

FOSSIL RECORD

SCARABAEOIDEA

Scarabaeoidea (scarab beetles) is a cosmopolitan monophyletic superfamily comprising around 35,000 described species (Scholtz and Grebennikov, 2005). They are commonly stout-bodied beetles, sometimes with bright metallic colors, measuring between 1.5 and 160 mm long (Bai et al., 2012). Their adult fossils can be distinguished by the following features: distinctive, clubbed antennae; front legs broad and adapted for digging; and meso- and metatibiae commonly with transverse, setose, or spinose keels on an outer surface (Krell, 2006). The earliest unequivocal fossils, represented by several families, are recorded from the Middle Jurassic of Daohugou, China and the Upper Jurassic of Karatau, Kazakhstan (Nikolajev et al., 2011; Bai et al., 2012). The fossil record of Scarabaeoidea has been reviewed by Krell (2006) and Nikolajev et al. (2011). Recently abundant Early Cretaceous fossils have been described and our knowledge of the evolution of beetles has improved greatly. These new fossils, therefore, provide important clues to explore the co-evolutionary processes between beetles and angiosperms. In this paper, we review the fossil record and early evolution of these four Early Cretaceous polyphagan groups, and briefly discuss their probable ecological associations with early angiosperms.
Wang et al. Flowers and beetle evolution

Adult tenebrionoids are distinguished by an aedeagus of heteromerous condition, trochanterofemoral articulations oblique, and tarsal formulae of 5–5–4, 4–4–4, 3–4–4 or rarely 3–3–3 (Lawrence et al., 2010). These characters are not autapomorphies of Mordellidae, but instead these characters suggest Praemordellidae is a stem group of modern Mordellidae which probably includes ancestors of Mordellidae and of other scarab families may have originated in the Cretaceous (Oberprieler et al., 2007). An updated list of Mesozoic fossils provides by Soriano et al. (2008) and Legállov (2012). They are easily recognizable with their elongate body shape and fine pubescence; head deflexed, constricted behind the eyes to form a neck; and abdomen (not pygidium) extending beyond elytra (Liu et al., 2007). These characters are not autapomorphies of Mordellidae, and all can be found in the Ripiphoridae and Scarabaeidae. Instead, these characters suggest Praemordellidae is a stem group which probably includes ancestors of Mordellidae and of other groups, such as Ripiphoridae. The earliest definitive Mordeiliidae are reported from the earliest Cretaceous (Late Cretaceous) (McKenna and Farrell, 2009). Some Early Cretaceous fossils have been attributed to the extinct subfamily “Praemordellinae” which was placed in Mordeiliidae on the following characters: tarsal formula 5–5–4, body wedge-shaped, elongate, and arched with fine pubescence; head deflexed, constricted behind the eyes to form a neck; and abdomen (not pygidium) extending beyond elytra (Liu et al., 2007). These characters are not autapomorphies of Mordeiliidae, and all can be found in the Ripiphoridae and Scarabaeidae. Instead, these characters suggest Praemordellidae is a stem group which probably includes ancestors of Mordeiliidae and of other groups, such as Ripiphoridae. The earliest definitive Mordeliidae are reported from the earliest Cenomanian (Late Cretaceous) (McKenna and Farrell, 2009). The oldest weevils, belonging to the Nemonychidae, occur in the Middle Jurassic of Daohugou, China (undescribed specimens) and Upper Jurassic of Karatau, Kazakhstan (see annotated list of Mesozoic beetle fossils given by Wang and Zhang, 2011).

The phylogenetic relationships among the families of Tenebrionoidea are still poorly understood (Beutel and Friedrich, 2005; Lawrence et al., 2010). The Mordeiliidae are thought to be among the most basal groups of Tenebrionoidea based on molecular analysis (McKenna and Farrell, 2009). Some Early Cretaceous fossils have been attributed to the extinct subfamily “Praemordellinae” which was placed in Mordeiliidae on the following characters: tarsal formulae 5–5–4, body wedge-shaped, elongate, and arched with fine pubescence; head deflexed, constricted behind the eyes to form a neck; and abdomen (not pygidium) extending beyond elytra (Liu et al., 2007). These characters are not autapomorphies of Mordeiliidae, and all can be found in the Ripiphoridae and Scarabaeidae. Instead, these characters suggest Praemordellidae is a stem group which probably includes ancestors of Mordeiliidae and of other groups, such as Ripiphoridae. The earliest definitive Mordeliidae are reported from the earliest Cenomanian (Late Cretaceous) (McKenna and Farrell, 2009). The oldest weevils, belonging to the Nemonychidae, occur in the Middle Jurassic of Daohugou, China (undescribed specimens) and Upper Jurassic of Karatau, Kazakhstan (see annotated list of Mesozoic beetle fossils given by Wang and Zhang, 2011).

The Anthribidae, Attelabidae, Caridae, and Curculionidae are definitely known from the Early Cretaceous (Oberprieler et al., 2007; Kirejtshuk et al., 2009; Cognato and Grimaldi, 2010; Santos et al., 2011). Estimated divergence times indicate that initial diversification of most families occurred on gymnosperms during the Jurassic, and a massive diversification even probably began in the mid-Cretaceous (McKenna et al., 2009; Jordal et al., 2011).

The Nemonychidae, consisting of 21 living genera and 76 known species, is a small, relict family of weevils (Kuschel, 1983; Oberprieler et al., 2007). They are the most primitive weevils, with the most plesiomorphic features of all extant lineages. These beetles are the most diverse in the Australian and Neotropical regions, with fewer species occurring in the Nearctic and Palearctic regions. The Nemonychidae are predominantly associated with conifers, especially the family Araucariaceae, while the Pinaceae provide their common hosts in the northern hemisphere. The Nemonychidae are presumed to retain the ancestral life style of weevils, including their mobile larva living freely (ecophytically) among the sporophylls within dehiscing male conifer strobili (cones), feeding on pollen in open pollen sacs and moving between cones (Oberprieler et al., 2007).

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**CHRYSOMELOIDES**

Most chrysomelid beetles belong to two unusually diverse families: Chrysomelidae (leaf beetles) with more than 35,000 described species, and Cerambycidae (longhorn beetles) with over 20,000 described species (Marvaldi et al., 2009). The Chrysomelidae are typically small to medium-size beetles with an elongate-oval body form, and adults that commonly consume leaves or floral elements (Wilson et al., 2002). Cerambycidae are generally large insects with raised antennal insertions and long antennae (Turnbow and Thomas, 2002). Adult Cerambycidae feed on leaves, meristicatic
Wang et al. Flowers and beetle evolution

is the preservation in fossil angiosperm flowers of specialized lidae (Barth, 1985; Krenn et al., 2005). Bernhardt (1996) reviews partnership which can be traced back to the mid-Cretaceous. offer a compelling argument that the pollination of members of evidence is, however, very scarce due to the rarity of well-preserved subfamilies of Chrysomelidae originated before the beginning of www.frontiersin.org...
CONCLUSION
Scauraboridea, Tenebrionoidea, Curculionoidea, and Chrysomelidae currently are among the common pollinators of the most basal angiosperms. Both the fossil record and molecular analyses reveal that these four groups had already diversified during or before the Early Cretaceous. Their divergence to insects currently identified as the common pollinators of the most basal angiosperms and achieved widespread floristic dominance, suggesting that their ecological association with angiosperms probably formed as early as the Lower Cretaceous. In addition to small beetles, other common pollinator groups were around at this time pollinating basal (ANITA-grade) angiosperms, such as thrips, nematoceran flies, moths, scorpionflies, and small parasitoid wasps (Labandeira, 2005; Labandeira and Currano, 1996). One hundred million years of morphological coevolution in a bark beetle–tree (Cerambycidae–Scleritinae) phylogeny and comparison with other Mesozoic faunas. J. Syst. Palaeontol. 34, 1–18. doi: 10.1016/j.jsp.2018.02.003.

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