POSSIBLE IMPLICATIONS OF TWO NEW ANGIOSPERM FLOWERS FROM BURMESE AMBER (LOWER CRETACEOUS) FOR WELL-ESTABLISHED AND DIVERSIFIED INSECT-PLANT ASSOCIATIONS[1]

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ABSTRACT: Two undescribed flowers in Burmese amber, and additional evidence herein discussed, support the inference that substantially diverse forests, possibly with well-established and diversified insect-plant associations, were already established and preserved by 100 Ma.

KEY WORDS: Lower Cretaceous, fossil, Burmese amber, insect-plant associations, angiosperms, Pseudopolycentropodidae

Cretaceous insect and/or plant fossils are important because they can be used to test various hypotheses regarding the timing of insect-plant associations (Labandeira 2005a, b). Morphological features, detailed elsewhere (Santiago-Blay et al., in preparation), of two different flowers entombed in Burmese amber (circa 115-100 Ma, see references in Santiago-Blay et al. 2004), suggest that insect-plant interactions were well-established and diversified at least 115-100 Ma in southeastern Laurasia. Briefly, those features include the presence of a shallow bowl (sb) at the base of the gynoecium in one flower (Fig. 1) as well as conspicuously abundant pilosity (p), a tubular gynoecium (g), and possible food sources (fs) on the other (Fig. 2). While these flowers do not constitute by themselves definitive proof of entomophilly, they are suggestive of well-established and diversified insect-plant interactions as such specialized morphological features are often associated with entomophillous flowers (e.g. Barth 1985, Endress 1994, Faegri and van der Pijl 1971, Meeuse and Morris 1984, Proctor et al., 1996).

As far as we are aware, only four angiosperms have been (or are being formally) described from Burmese amber (Poinar 2004, Poinar et al., accepted, Santiago-Blay et al., in preparation) based on flowers. Other fossilized botanical inclusions are known for Burmese amber, including "hepatophyte thalli, an archegoniophore of Marchantiaceae, and leafy shoots of *Metasequoia*" (Grimaldi et al., 2002) and additional materials in the collections of authors SRA and RTB (Santiago-Blay et al., in preparation). Specimens lacking reproductive structures can be difficult to identify due to the absence of diagnostic and/or synapomorphic characters as well as their incomplete nature.

Beetles, flies, moths, wasps, and other insects [Antropov (2000), Grimaldi and Engel (2005), Rasnitsyn and Ross (2000), Ross and York (2000), and others] have

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already been documented in Burmese amber, although it is difficult to determine which ones were actual pollinators. In the case of the two flowers illustrated (Figs. 1-2), insects could have used them as feeding stations. The flower with a shallow bowl at the base of the gynoecium (Fig. 1) could have been nectared or pollinated by an anthophilous brachyceran fly (Labandeira 2005c) or by a generalist winged insect. Though not yet proven as a definitive pollinator, members of the Pseudopolycentropodidae (Diptera, Fig. 3) often exhibit an unusually long, slender, and rigid proboscis, suggesting an already established association with plants (thought not necessarily the angiosperms herein illustrated) for imbibition of gymnospermous pollination drops (Labandeira et al., submitted) or nectar probing from flowers (Anderson and Poinar, independent pers. comm. to Santiago-Blay, January 2005). Furthermore, Labandeira (1998, 2000, 2002) has shown that pollination syndromes have a geological record extending as far back as the mid-Mesozoic, well before the sudden diversification of angiosperms (Labandeira et al., submitted).

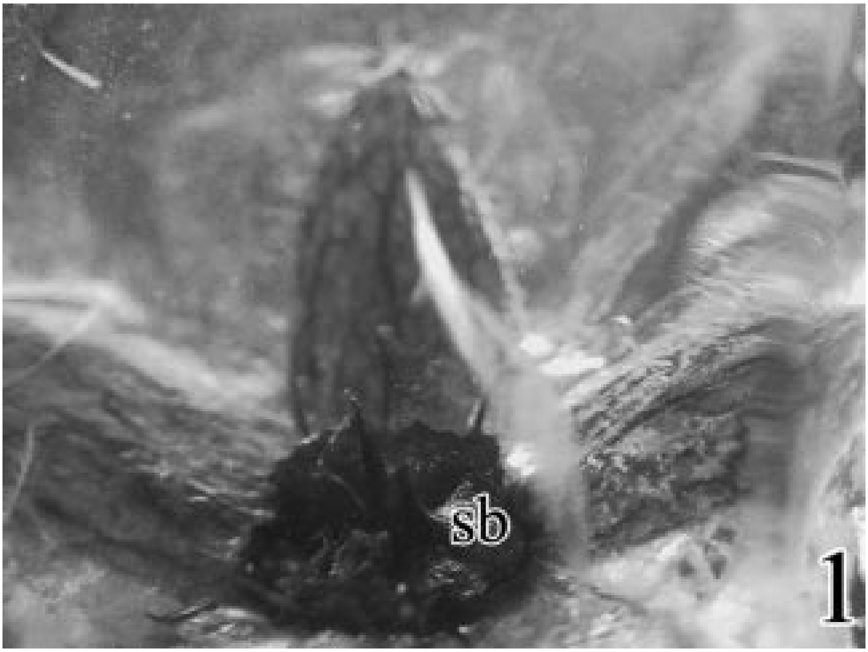
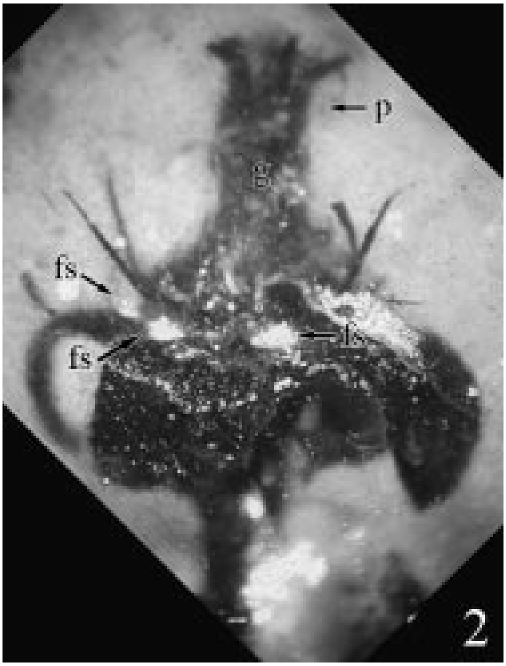


Fig. 1. Flower in Burmese amber showing its possible entomophillous traits. The shallow bowl (sb) at base of the gynoecium may have been a site for insect feeding. Photo taken by author Ronald T. Buckley.

There is a huge body of literature on insect-plant interactions and their presumed connection with the rise of angiosperms. While such interactions probably are partially associated with the geologically sudden diversification of angiosperms, other cases suggest that some insect-plant interactions predate and/or are unrelated to the rise of angiosperms (Gorelick 2001; Labandeira 1998; Labandeira et al., submitted; Lloyd 1992).

As for the botanical source of amber from Burma, Grimaldi et al. (2002) indicated that "*Metasequoia* is possibly the source of the amber" [modern classifications tend to place *Metasequoia* in the Cupressaceae (Judd et al., 2002)]. Studies with solid state nuclear magnetic resonance spectroscopy using the carbon 13 nucleus suggest that burmite and other fossil resins belong to a large, worldwide assemblage (fossil resin Group B, Lambert and Poinar 2002). Some of the Group B resins perhaps belong in the Dipterocarpaceae (modern resins, Group D, Lambert et al., 2002), although this has not been firmly established. Modern geographic sources for Group B fossil resins include Borneo, Sumatra, Australia, Papua New Guinea, India, and North America. Nevertheless, Group B fossil resins are spectroscopically distinct from the partially sympatric *Agathis*-related plants (fossil resins, Group A of Lambert et al., 2002; modern resins, group CA, Cupressaceae and Araucariaceae of Lambert et al., 2005).



Figs. 2. A second flower in Burmese amber showing their possible entomophillous traits. Note tubular gynoecium (g), abundant pilosity (p), and possible food sources (fs). Both flowers illustrated in this paper are deposited in the private collection of Ron T. Buckley.

A handful of flowers has been described from younger amberiferous formations, such as those from the Dominican Republic and/or the Baltic region, including the families Araceae (Bogner 1976), Arecaceae (Poinar 2002), Fagaceae (Mai 2003), and Leguminosae (Poinar and Brown 2002). Interestingly, no flowers have yet been described from Lebanese amber (Poinar and Milki 2001), which is Aptian (Grimaldi et al., 1993) to Hauterivan (Roth et al., 1996) in age, approximately 120-135 Ma, although most localities appear to be closer to 120 Ma (Labandeira to Santiago-Blay,

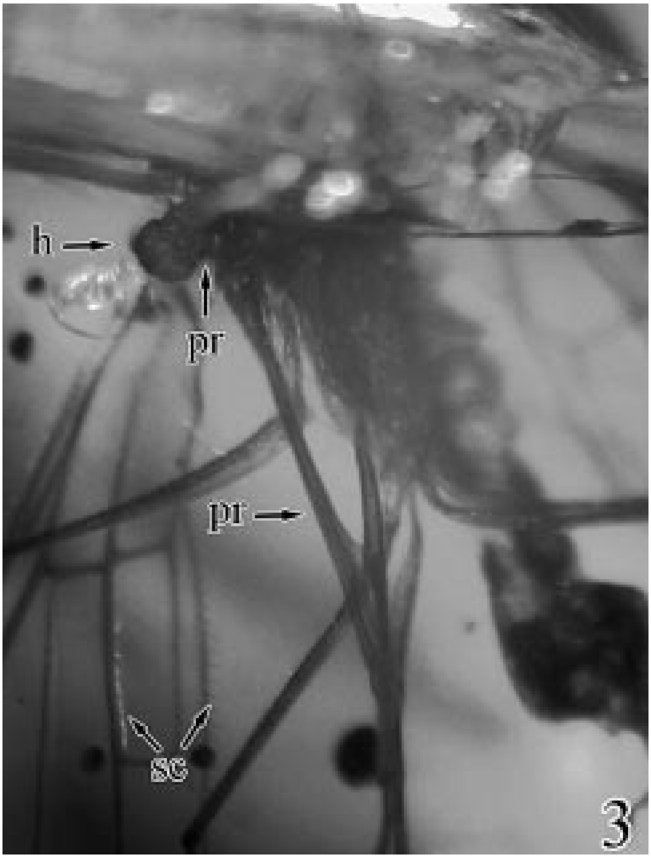


Fig. 3. Pseudopolycentropodid showing elongated, slender, rigid proboscis, (pr) perhaps used to probe nectar/pollen in flowers (Anderson and Poinar, pers. comm. to Santiago-Blay); h, indicates head, and sc, wing scales. The pseudopolycentropodid is deposited in the private collection of Scott R. Anderson. Photos taken by author Scott R. Anderson.

pers. comm., December 2005). Flowering plants preserved in various non-amber matrices have been extensively documented in the Cretaceous throughout the World and they exhibit remarkable diversity (e.g. Archaefructaceae, Sun et al., 2002; Magnoliidae, Dilcher and Crane 1984, Crane and Dilcher 1984; Lauraceae, Drinnian et al., 1990; and other lineages, Friis 1984).

The known diversity of Burmese amber insect and plant inclusions, the inferred morphological specialization of flowering plants, possibly related to entomophilly, and NMR evidence support the inference that substantially diverse forests, possibly with well-established and diversified insect-plant associations, were already established and preserved by 115-100 Ma. The few angiosperms and potential pollinators discovered thus far in Burmese amber are assisting in refining our understanding of the possible connection between insect-plant interactions and the rise of angiosperms.

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