

A phylogeny of the oil bee tribe Ctenoplectrini (Hymenoptera: Anthophila) based on mitochondrial and nuclear data: Evidence for Early Eocene divergence and repeated out-of-Africa dispersal

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Abstract

The bee tribe Ctenoplectrini, with two genera, comprises nine species in tropical Africa and ten in Asia and Australia. Most of them collect floral oil, pollen, and nectar from Cucurbitaceae, but three species are thought to be cleptoparasites. The unusual morphology of Ctenoplectrini has made it difficult to infer their closest relatives, in turn preventing an understanding of these bees' geographic and temporal origin. We used two mitochondrial and two nuclear markers (4741 nucleotides) generated for most of the species to test the monophyly of the tribe, its relationships to other Apidae, and its biogeographic history. Ctenoplectrini are strongly supported as monophyletic and closest to the Long-horned bees, Eucerini. The presumably cleptoparasitic species form a clade (*Ctenoplectrina*) that is sister to the remaining species (*Ctenoplectra*), confirming the independent evolution of cleptoparasitism in this tribe. Tree topology and molecular dating together suggest that Ctenoplectrini originated in Africa in the Early Eocene and that *Ctenoplectra* dispersed twice from Africa to Asia, sometime in the Late Eocene, 30–40 my ago, from where one species reached the Australian continent via Indonesia and New Guinea in the mid-Miocene, c. 13 my ago. Dry and cool mid-Miocene climates also coincide with the divergence between *Ctenoplectra bequaerti* from West Africa and *Ctenoplectra terminalis* from East and South Africa, perhaps related to fragmentation of the equatorial African rainforest belt.

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1. Introduction

Systematic relationships in bees (Anthophila), a group of more than 16,000 species, remain insufficiently resolved, although molecular phylogenetic data are rapidly improving the situation (Danforth et al., 2006a, 2006b; Cameron et al., 2007). The most diverse of the nine currently accepted families of Anthophila are the Apidae, which comprise Nomadinae, Xylocopinae, and Apinae (Engel, 2001, 2005; Michener, 2007). Each of these three subfamilies is fairly well circumscribed, with only a few taxa not yet clearly assigned as to subfamily. One such taxon is the tribe

Ctenoplectrini, with 19 species in Africa, Asia, and Australia (Eardley, 2003; Engel, 2007; H. Schaefer and M. Engel, manuscript; our Fig. 1). Depending on the interpretation of their relatively short glossa and labial palpi, Ctenoplectrini have variously been placed as a subfamily (Ctenoplectrinae) in the Melittidae, which are short-tongued (S-T) bees (Michener, 1944), as a distinct family (Ctenoplectridae) and sister group to all long-tongued (L-T) bees (Michener and Greenberg, 1980; Alexander and Michener, 1995), or as a tribe (Ctenoplectrini) within the Apidae of the L-T bees (Roig-Alsina and Michener, 1993; Silveira, 1993a). The most recent comprehensive classification of bees assigns Ctenoplectrini to the large L-T subfamily Apinae, which includes 19 tribes, including the commercially important Apini (honeybees), Bombini (bumblebees), and Meliponini (stingless bees) (Michener, 2007). This place-

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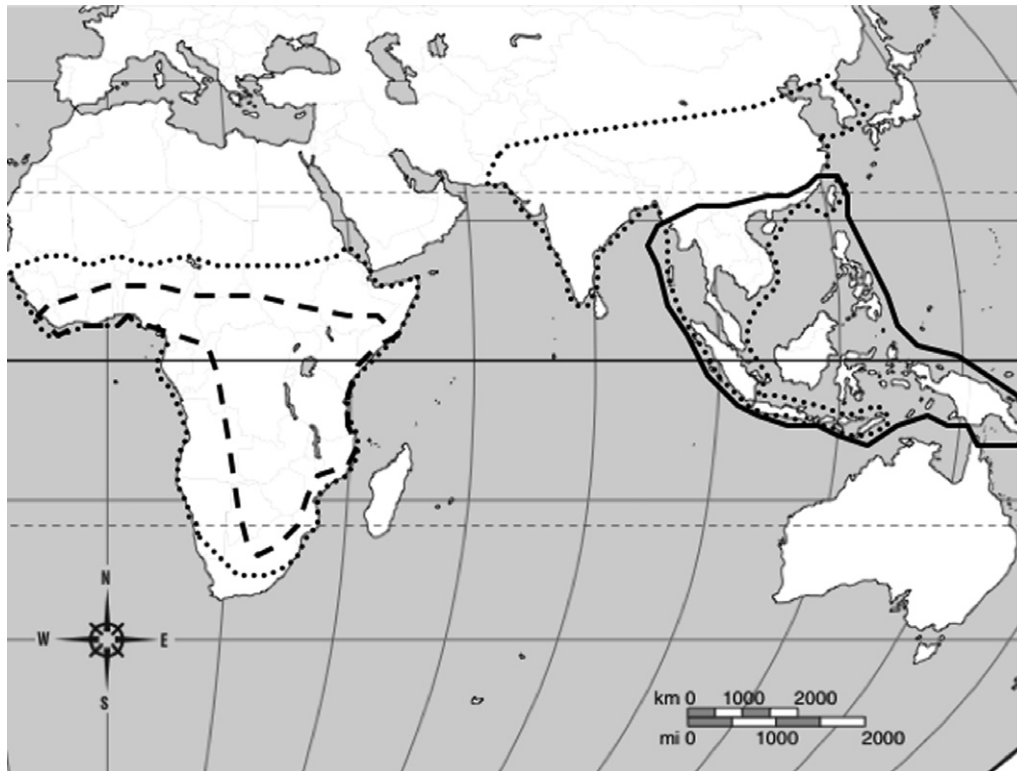


Fig. 1. Distribution map of the oil bee tribe Ctenoplectrini (Apidae): Australian/Asian *C. kelloggi* clade (bold line), *Ctenoplectrina* (broken line), *C. polita* clade in Africa and *C. davidi* clade in Asia (dotted lines). The Australian range of the genus is confined to a very small region of Northern Queensland's Cape York Peninsula.

ment is supported by the morphological study of Roig-Alsina and Michener (1993), who used 131 characters of adult bees. In a recent analysis, Danforth et al. (2006b) added DNA data from five markers to the morphological data set of Alexander and Michener (1995) and found *Ctenoplectra albolimbata* (the only included Ctenoplectrini) nested among the twelve representatives of Apidae sampled.

Ctenoplectrini comprise two genera, *Ctenoplectrina* and *Ctenoplectra*, with the former having three species endemic in Africa, the latter nine species in Asia, one in Australia, and six in Africa (H. Schaefer and M. Engel, manuscript). There are two morphological groups (Vogel, 1990), each spanning Africa and Asia, namely large, metallic bluish-green species and small, brown or black species. *Ctenoplectra* bees are oligolectic on Cucurbitaceae flowers from which they obtain pollen and floral oil as larval food, as well as nectar to cover the energy requirements of the adults (Vogel, 1990; H. Schaefer and S. Renner, unpublished data). *Ctenoplectrina* females have lost the morphological features associated with oil or pollen collection and are therefore thought to be cleptoparasitic, probably on small *Ctenoplectra* species (Rozen, 1978; Michener, 2007; field observations by HS).

As part of a study on the evolution of pollinator relationships in the Cucurbitaceae, we set out to test the monophyly and relationships of Ctenoplectrini and to infer their biogeographic history, focusing on major divergence events

in the tribe. The unclear relationships among the 19 tribes of Apinae required relatively broad sampling of potential outgroups to achieve proper rooting of Ctenoplectrini. We therefore focused on mitochondrial and nuclear markers widely used in bee phylogenetics (Schwarz et al., 2004; Fuller et al., 2005; Danforth et al., 2006a, 2006b; Cameron et al., 2007). A second reason for relatively broad outgroup sampling was the need to include taxa with fossil records to constrain a molecular clock for Ctenoplectrini. Specific questions we wanted to answer were, (i) where and when did Ctenoplectrini evolve and are they monophyletic; (ii) what is the relationship between the Asian and African species and how old are these disjunctions; (iii) what is the phylogenetic relationship of the (presumed) cleptoparasites to their hosts; and (iv) is *Ctenoplectra* diversification temporally correlated with particular climates and the evolution of special biota, such as savannah or dry forest biomes.

2. Materials and methods

2.1. Taxon sampling

Ctenoplectrini are poorly represented in collections, and most museum specimens are too old or too valuable for destructive sampling. DNA sampling therefore relied mostly on specimens collected during the first author's fieldtrips to Africa and Australasia in 2005, 2006, and 2007. Our taxon sampling includes all six African species

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