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An old adaptive radiation of forest dung beetles in Madagascar

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ABSTRACT

Adaptive radiations of mammals have contributed to the exceptionally high levels of biodiversity and endemism in Madagascar. Here we examine the evolutionary history of the endemic dung beetle tribe Helictopleurini (Scarabaeidae) and its relationship to the widely distributed Oniticellini and Onthophagini. Helictopleurini species are dependent on mammals for their resources. We date the single origin of the tribe at 37 to 23 MY ago, indicating overseas colonization of Madagascar. The main radiation occurred concurrently with the main radiations of lemurs. The ancestors of Helictopleurini are inferred to have been coprophagous species inhabiting open habitats. Subsequent evolution has involved a shift into forests, changes in resource use to a more generalized diet, and changes in body size. Four species of the extant 65 species have shifted to use the dung of the recently introduced cattle in open habitats, allowing these species to greatly expand their geographical ranges.

1. Introduction

Much of the biological diversity on Earth has arisen during relatively short periods of time in rapid radiations, which have generated suites of related species from a single ancestor. In the case of adaptive radiations (Schluter, 2000), the new species have evolved to dissimilarly use a range of resources, which has increased the long-term viability of the new taxa. Oceanic islands and archipelagos provide particularly informative situations for the study of adaptive radiations (Emerson, 2002). The high or relatively high species diversity and endemism on large oceanic islands is often the result of adaptive radiations, though multiple colonizations from continents or other islands and speciation due to vicariant events may have further increased diversity. Well-studied examples of adaptive radiations on islands and sets of islands include the Darwin's finches on the Galapagos islands (Sato et al., 2001; Schluter, 1996), the *Anolis* lizards in the Caribbean (Losos, 1990a,b; Losos and Irschick, 1996), Hawaiian silverswords (Baldwin, 1997; Barrier et al., 1999) and Hawaiian *Schiedea* plants (Sakai et al., 1997; Weller et al., 1990).

Madagascar is the world's fourth largest island with a great variety of climates and habitats. Madagascar has been isolated for 160–158 MY from mainland Africa and 80 MY from India (Briggs, 2003; de Wit, 2003), and it has consequently an exceptionally high level of endemism at different taxonomic levels, making it one of the hottest biodiversity hotspots on Earth (Myers et al., 2000). Madagascar's biota includes many examples of apparently adaptive mammalian radiations, involving lemurs (Yoder and Yang, 2004), nesomyine rodents, tenrecs and carnivorans (Poux et al., 2005). These taxa have colonized Madagascar probably only once by overseas dispersal after the break-up from other continents (Poux et al., 2005). Geckos, chameleons and tortoises have radiated in Madagascar and further dispersed to other Indian Ocean islands and mainland Africa (Austin et al., 2004; Palkovacs et al., 2002; Raxworthy et al., 2002), while colubrid snakes and hyperoliid frogs have colonized Madagascar multiple times (Monaghan et al., 2005; Nagy et al., 2003; Vences et al., 2003). Vicariance appears to have led to speciation following the Gondwanian break-up in e.g. boid snakes, podocnemid turtles, iguanid lizards and freshwater fishes (Noonan and Chippindale, 2006; Sparks and Smith, 2004). In contrast, little is known about the evolutionary history of invertebrates in Madagascar. The best studied groups include butterflies (Torres et al., 2001; Zakharov et al., 2004), ants (Fisher, 1997) and small minnow flies (Monaghan et al., 2005), which appear to have colonized Madagascar more than once, though there are no estimates of the time of colonization or radiation. Considering all the Malagasy faunal and floral groups, long-distance dispersal appears to be the most common way of origin (Yoder and Nowak, 2006).

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The dung beetle family Scarabaeidae has a worldwide distribution with some 27,800 described species (Cambefort, 1991a; Jameson and Ratcliffe, 2005). Dung beetles play an important role in many ecological processes, especially in nutrient cycling and fertilization and aeration of soils, but also in seed dispersal and the dynamics of some parasite species (Andresen, 2002a,b; Mittal, 1993). The phylogenetic relationships within Scarabaeidae have been recently studied, but they remain largely unresolved (Browne and Scholtz, 1995, 1998; Cabrero-Sanudo and Zardoya, 2004; Monaghan et al., 2007; Philips et al., 2004; Smith et al., 2006; Villalba et al., 2002). There is only one study of the Malagasy dung beetles (Orsini et al., 2007), examining the molecular evolution of the two main groups of dung beetles in Madagascar.

The ancient isolation of Madagascar is reflected in the composition of its dung beetles, which lack the evolutionarily younger tribes that have become to dominate in abundance the older tribes elsewhere in the world, with the partial exception of the Neotropical region (Davis and Scholtz, 2001). In Madagascar, the vast majority of dung beetles belong to only two tribes, Helictopleurini and Canthonini. The former is completely endemic to Madagascar, while the latter is endemic at the generic level. Helictopleurini has two genera, *Heterosyphus* and *Helictopleurus*, the first of which is monotypic while the second one has 64 species and subspecies (Lebis, 1960; Montreuil, 2005a,b, 2007). The tribe is diverse (Paulian and Cambefort, 1991), and the species have been divided into nine morphological groups (Lebis, 1960; Montreuil, 2005b). The genus *Helictopleurus* was first described within Oniticellini (d'Orbigny, 1915), but it has subsequently been elevated to the level of the subtribe Helictopleurina and to the tribe Helictopleurini (Lebis, 1960; Montreuil, 2005a,b; Paulian, 1986). According to recent phylogenetic studies (Philips et al., 2004; Villalba et al., 2002), Onthophagini, Oniticellini, and Onitini are the closest tribes to Helictopleurini. The current taxonomy and limited molecular evidence (Monaghan et al., 2007) suggest that Oniticellini is the closest taxon to Helictopleurini.

The Malagasy Canthonini consists of 13 genera and ca. 170 species (Montreuil, 2006; Paulian, 1975). Other tribes of Scarabaeidae in Madagascar include three genera of Scarabaeini, each with one endemic species, and six species of *Onthophagus* (Onthophagini), two of which are introduced and four are endemic (Davis and Scholtz, 2001; Lebis, 1960).

The primary resource for dung beetles worldwide, large herbivore dung, is very limited in Madagascar, as native ungulates apart from the now extinct hippopotami have been completely lacking and the largest mammals are primates (lemurs). The largest Malagasy herbivores, including gorilla-sized lemurs, hippopotami, giant tortoises and the elephant bird, have gone extinct in the past 2000 years (Burney et al., 2004), but they can be expected to have contributed to the radiation of dung beetles. Most recently, in the past 1500 years, humans have introduced the new resource of cattle dung, which is now plentiful especially in open areas.

In a previous study, Orsini et al. (2007) examined the molecular evolution of all Malagasy dung beetles using 7 gene regions and a sample of 44 species, including 17 Helictopleurini species. Here we focus on the evolutionary history of Helictopleurini with a large sample of individuals, and reconstruct a molecular phylogeny for about half of the described species, representing all the morphological groups (Lebis, 1960). We include in the analysis a representative sample of 24 species of the presumed sister tribes of Helictopleurini. We investigate the adaptive radiation in Helictopleurini by addressing the three criteria listed by Schluter (2000): single origin, one or more periods of rapid speciation, and evolution of traits that facilitate the fit of the species to their environment. Single origin would be supported by monophyly of Helictopleurini. Times of divergence are estimated based on mtDNA sequences, and these estimates are used to describe the temporal pattern of speciation, also in relation to the known times of radiation in the relevant mammalian taxa. Using data on body sizes, resource use and positions and sizes of geographical ranges, we describe the likely pattern of ecological differentiation. Finally, we describe a recent shift of resource use by a small number of species to cattle dung and the apparent ecological and possible evolutionary consequences of that shift.

2. Materials and methods

2.1. Sampling

We have conducted and organized trappings of dung beetles in 40 forest localities across Madagascar in the years 2002–06 (Fig. 1). Beetles were trapped with standard baited pitfall–traps (plastic cups, 1.5 dl), over which a large leaf was placed to prevent rain water entering the trap. The traps were filled up to one third of their volume with water containing some washing-up liquid to decrease water tension. A bait of fish, chicken intestine or primate

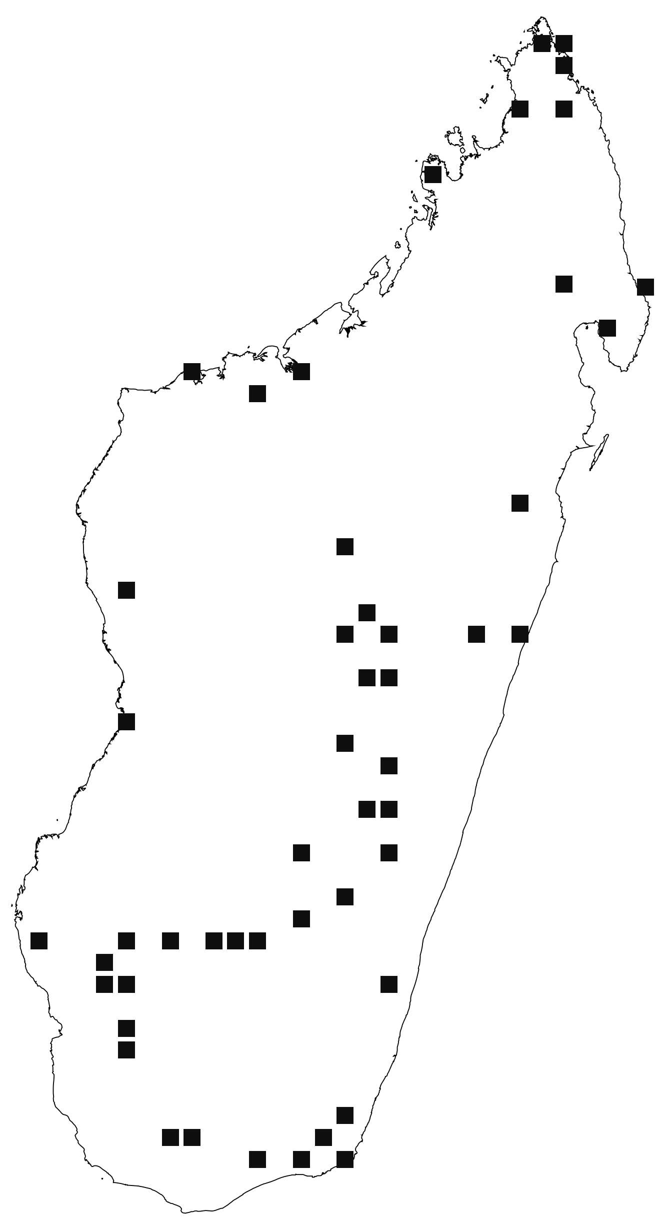

Fig. 1. Trapping localities in the sampling of Helictopleurini.