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Phylogeny and microendemism of the New Caledonian lizard fauna

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Abstract. The lizard fauna of New Caledonia is both diverse and highly endemic. Molecular phylogenetic analyses of the diplodactylid geckos and lygosomine skinks reveal that the island supports a minimum of 106 endemic lizard species. New Caledonian diplodactylids are monophyletic, but recognized genera are not, whereas New Caledonian skinks are paraphyletic with respect to New Zealand skinks, although all but one genus is monophyletic. Geological events in the Eocene and Oligocene are likely to have been responsible for initial cladogenesis within both geckos and skinks in New Caledonia, although the lineages themselves may be of different ages. Microendemism is the result of geologically and climatically-mediated fragmentation of habitats throughout the second half of the Tertiary and poses significant problems for conservation management in New Caledonia today.

Introduction

The biota of New Caledonia is noteworthy both for its phyletic and ecological diversity and for its high level of endemism (Holloway, 1979) and the New Caledonian region has recently been identified as one of the world's hotspots of tropical biodiversity (Myers, 1988, 1990; Mittermeier et al., 1996; Myers et al., 2000; Lowry et al., 2004). Although the botanical significance of the island has long been recognized (Morat, 1983; Morat et al., 1986; Jaffré et al., 1998), the uniqueness of the terrestrial and freshwater fauna has only recently been emphasized (Chazeau, 1993; Platnick, 1993; Séret, 1997). Among vertebrates, lizards constitute the most diverse and highly endemic component of the fauna (Bauer, 1989, 1999; Bauer and Sadlier, 2000). A diversity of habitat types within New Caledonia, including humid forest, sclerophyll forest, and both low and high elevation maquis, certainly contributes to the maintenance of high biodiversity, but the ultimate source of the observed patterns of diversity among the reptiles of New Caledonia is the island's long and complex geological and climatic history. The Grande Terre, the main island of New Caledonia, has a land area of 16,648 km2 and is dominated by chains of mountains (to 1600 m elevation) that parallel the long axis of the island. Parts of the Grande Terre have been emergent for at least 100 Ma and were originally adjacent to Australia. The opening of the Coral and Tasman Seas isolated New Caledonia by about 65 Ma, although sporadic connections to New Zealand and other, smaller land masses may have existed (Kroenke, 1996). Perhaps the most important events in the biotic history of New Caledonia occurred in association with the Eocene ophiolitic obduction (39-36 Ma; Lowry, 1998; Lee et al., 2001), which resulted in the overthrusting of peridotite sheets, which today dominate the southern one third of the Grande Terre as well as a series of isolated massifs extending to the north and west as far as the Belep Islands. This was followed by Oligocene marine transgressions, which reduced neighboring New Zealand to an area of about 18% of its current aerial land mass (Cooper and Millener, 1993) and may have submerged the majority of the Grande Terre, and by Miocene marine regression and mountain building, ultimately resulting in the modern, highly-dissected topography of the island.

An intensive series of field trips by the authors and their colleagues during the period 2001-2004 provided material from numerous areas of New Caledonia that had not been previously sampled for lizards, including the northwest ultramafic peaks and numerous northern offshore islands. Combined with more than 20 years of accumulated specimens and tissue samples, the new material provided an unprecedented opportunity to reevaluate the systematics of the New Caledonian herpetofauna and to erect hypotheses of relationship for both of the major lizard groups occurring on the Grande Terre: diplodactylid geckos and lygosomine skinks of the *Eugongylus* group. We here summarize the broader results of molecular phylogenetic studies on the New Caledonian herpetofauna, although both new taxon descriptions and details of phylogenetic hypotheses have been or will be presented elsewhere (e.g., Sadlier, Smith, Bauer and Whitaker, 2004; Sadlier, Bauer, Whitaker and Smith, 2004; Bauer et al., 2006, submitted).

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Materials and methods

Molecular methods

Nucleotide sequences from the mitochondrial ND2 and ND4 genes and five tRNAs, and from nuclear Rag-1 and c-mos genes were obtained from representatives of most genera and species of New Caledonian geckos and skinks, including numerous putatively new species. In total 2286 bp of sequence were generated for 405 diplodactylid gecko samples including 14 outgroup taxa and all 21 recognized ingroup taxa. 1950 bp of sequence were generated for 382 skinks, including 92 taxa, 39 of which were outgroups. Genomic DNA was extracted using the Qiagen QIAmp tissue kit and PCR amplification was conducted under a variety of thermocyler parameters using a diversity of primers (see Sadlier, Smith, Bauer and Whitaker, 2004; Bauer et al., 2006, submitted). Products were visualized via 1.5% agarose gel electrophoresis. Amplified products were purified either using AmPure magnetic bead PCR purification kit or reamplified products were purified on 2.5% acrylamide gels (Maniatis et al., 1982) after being reamplified from 2.5% low melt agarose plugs. DNA from acrylamide gels was eluted from the acrylamide passively over two days with Maniatis elution buffer (Maniatis et al., 1982). Cycle-sequencing reactions were performed using the Applied Biosystems BigDye™ primer cycle sequencing ready reaction kit. The resulting products were purified using SeqClean magnetic bead purification kit. Purified sequencing reactions were analyzed on an ABI 373A stretch gel sequencer or an ABI 3700 automated sequencer. To insure accuracy, negative controls were included in every reaction, complementary strands were sequenced, and sequences were manually aligned by eye using the original chromatograph data in the program SeqMan II. All ingroup sequences are being deposited in GenBank as primary research papers are published.

Phylogenetic methods

Phylogenetic trees were estimated using parsimony, likelihood and Bayesian analysis. PAUP* 4.0b10a (Swofford, 2002) was used to estimate parsimony and likelihood trees. Parsimony searches were conducted with 100 heuristic searches using random addition of sequences. Non-parametric bootstrap resampling was used to assess support for individual nodes using 1000 bootstrap replicates with ten random addition searches. For maximum likelihood analyses, ModelTest version 3.5 (Posada and Crandall, 1998) was used to compare different models of sequence evolution with respect to the data. The chosen model was used to estimate parameters on the most parsimonious tree. These likelihood parameters were fixed and the most parsimonious trees were used as starting trees for branch swapping in 25 heuristic searches with random addition of taxa to find the overall best likelihood topology. To estimate a phylogenetic tree with a Bayesian framework MrBayes 3.0 (Huelsenbeck and Ronquist, 2001) was used with the model chosen using ModelTest 3.5. The Bayesian analyses were initiated from random starting trees and run for 2,000,000 generations with four incrementally heated Markov chains. Likelihood parameter values were estimated from the data and initiated using flat priors. Trees were sampled every 100 generations, resulting in 20,000 saved trees. To ensure that Bayesian analyses reach stationarity, the first 5000 saved trees were discarded as 'burn-in' samples.

Results

Diplodactylid geckos

The diplodactylid geckos of New Caledonia form a monophyletic group that has as its sister group the viviparous geckos of New Zealand. This result is strongly supported by Bayesian analysis, although under maximum parsimony, the Australian Pseudothecadactylus is weakly supported as the immediate sister group of the New Caledonian clade. Outgroup relationships and basal ingroup relationships were chiefly supported by Rag-1 sequence data. Although relationships among basal groups was equivocal, all analyses retrieved the same series of strongly supported New Caledonian clades, each deeply divergent from all other such clades. Groupings did not correspond to the three diplodactylid genera currently recognized in New Caledonia. Indeed, only the highly autapomorphic *Eurydactylodes* was unambiguously monophyletic. The monophyly of the giant geckos, *Rhacodactylus*, was falsified, as was that of the morphologically plesiomorphic genus *Bavayia*. Although most described species of *Bavayia* are members of a single clade, other taxa previously assigned to this genus appear in two other basal clades. In addition, a newly discovered species with superficial resemblances to *Bavayia* was found to be the sister group of all other New Caledonian diplodactylids (Bauer et al., 2006). Molecular data, supplemented by morphological traits (discussed elsewhere) also revealed many undescribed species among New Caledonian diplodactlyids. These include cryptic taxa, as well as easily recognized novelties. New taxa identified include one new *Eurydactylodes*, two new "*Rhacodactylus*"(as well as one resurrected from synonymy), and 32 new *Bavayia*, chiefly in the *B. cyclura, B. sauvagii,* and *B. validiclavis* clades.

Lygosomine skinks

The bulk of the New Caledonian skink radiation is part of a single clade withing the Eugongylus group, with only *Cryptoblepharus novocaledonicus* and *Emoia* spp. (limited to the Loyalty Islands within the New Caledonian region) falling outside this clade. The New Caledonian clade also subsumes the New Zealand skinks, which appear to be monophyletic. All of the recognized New Caledonian endemic genera are monophyletic except *Lioscincus*, which is polyphyletic. Most generic level taxa are, however, well supported and have long branch lengths. A new genus and species, *Kanakysaurus viviparous,* has recently been identified and described as one such distinctive clade (Sadlier, Smith, Bauer and Whitaker, 2004). Relationships among skink genera are not as well supported as those among diplodactylids, but there is strong support, chiefly from mitochondrial data, for patterns of species relationships. In two of the most speciose genera, Nannoscincus and *Caledoniscincus*, molecular and morphological data are inconsistent with respect to species boundaries. In the former case, several morphological species appear to be paraphyletic and one pair of morphologically distinctive species are genetically indistinguishable. In the latter genus, molecular data reveals the existence of several cryptic species, but also suggest that not all species previously recognized on the basis of allozyme data (Sadlier et al., 1999) should be recognized. At a minimum, phylogenetic data indicate the existence of six more skink species than are currently recognized, despite the requirement for the synonymization of some nominal species.

Discussion

The monophyly of New Caledonian diplodactylids is consistent with earlier, morphologically based studies (e.g., Kluge, 1967; Bauer, 1990), but the non-monophyly of the constituent genera has not been previously proposed (Bauer, 1990; Vences et al., 2001; but see Good et al., 1997). Among skinks, the current system of generic divisions established initially by Sadlier (1986) has been supported. Although no previous studies have explicitly examined the higher order phylogenetics of New Caledonian skinks, the monophyly of the New Caledonian + New Zealand clade is at odds with at least some earlier conjectures of affinity (e.g., Böhme, 1976; Bauer and Sadlier, 1993).

Perhaps most surprising among our findings is that such a large proportion of New Caledonian lizard diversity remained hidden, despite two decades of intensive research on an island of only moderate size. Indeed, based on our current research, the Diplodactylidae is represented on New Caledonia by a minimum of 58 species, whereas there are at least 51 species of New Caledonian lygosomine skinks. Of these, all of the diplodactylids and all but three of the skinks are strictly endemic to New Caledonia and its islands. Thus there are at least 106 endemic lizard species in New Caledonia. This is an increase of 72 (212%) since 1980 and 46 (77%) since 2000 (Bauer and Sadlier, 2000).

Much of the increased diversity, especially among geckos, has been the result of recent explorations of the ultramafic massifs of northwestern New Caledonia (Whitaker et al., 2004). This has revealed that most isolated peaks and plateaus support one or more endemic species. Likewise, increased sampling in central and southern New Caledonia has revealed species breaks that could not have been localized without fine scale sampling and which were not suspected until sample sizes permitted the distinction between minor regional or clinal variation and species-specific differentiation – sometimes a difficult task among morphologically conservative genera such as *Bavayia* and *Caledoniscincus*. This new picture of New Caledonian lizard diversity further emphasizes a previously signalled pattern of microendemism (Sadlier, 1986; Bauer and Vindum, 1990; Bauer and Sadlier, 1993, 2000). In addition to previously recognized areas of microendemism, such as the southern ultramafic block of the Grande Terre and the Panié Massif, our phylogenetic results and recognition of cryptic species suggests that virtually all montane blocks in New Caledonia (Bauer et al. submitted), as well as lowland limestones (Sadlier et al., 1999) and certain vegetation types at all elevations (Bauer et al., 2006) may be considered areas of intra-island endemism.

How has the extreme microendemism seen in New Caledonia evolved? Both diplodactylid geckos and lygosomine skinks are commonly associated with certain substrates or microhabitats. This connection has probably promoted speciation in both groups in association with the fragmentation of once continuous habitat/substrate types over geological time. The Eocene ophiolitic obduction and Oligocene marine transgressions that impacted New Caledonia are candidate historical events that may have played a role in at least basal cladogenesis within the lizard lineages. Indeed, a comparative analysis of the New Caledonian and New Zealand skink and gecko fauna suggest that basal within-island cladogenesis in both taxonomic groups occurred approximately 30 million years ago (Jackman, 2005; Bauer et al., submitted), at a time consistent with the "Oligocene bottleneck" that is credited with the reduction of genetic and phyletic diversity of the New Zealand fauna (e.g., Cooper and Cooper, 1995; Hickson et al., 2000; Chambers et al., 2001). Within the *Bavayia validiclavis* lineage, the most recent speciation events correspond to an age of 5-6 Ma (Bauer et al., submitted) suggesting that cladogeneic events throughout the Mid- to Late Tertiary may have played a role in the fragmentation and speciation of the New Caledonian lizard fauna. Climatic and vegetational changes in New Caledonia during this period were substantial (Lowry, 1998; Lee et al., 2001) and might well be relevant to herpetofaunal diversification, although specific candidate cladogenetic events remain elusive.

Although there is no evidence for divergences compatible with Gondwanan cladogenesis within New Caledonian lizards, their Gondwanan origin is not excluded. These age estimates merely suggest that the modern radiations of lizards date from the Oligocene, but it is plausible to suppose that older lineages may have become extinct, perhaps during the period of Eocene overthrusting or subsequent drowning of much of the Grande Terre, leaving a single surviving lineage which subsequently diversified. Rough dating of the divergence between New Caledonian and New Zealand diplodactylids, as well as that between East Tasman and Australian diplodactylids, is consistent with Late Cretaceous to Early Tertiary geological events occurring along the eastern margin of Gondwanaland (Jackman, 2005). No such evidence exists for skinks and we think it likely that the founders of the New Caledonian/New Zealand skink lineage reached the Grande Terre via overwater dispersal in the mid-Tertiary (Bauer ,1999).

Microendemism poses particular problems for conservation and new data from New Caledonia will necessitate new priorities for conservation management. Based on our results, very few endemic New Caledonian lizards have island-wide distributions, and most are restricted to very localized areas. Many such areas are associated with geological features of economic importance and are subject to exploitation by mining, New Caledonia's most important industry. Small, localized populations are also at greater risk from introduced predators, which are widespread in New Caledonia (Gargomigny et al., 1996), fire ant invasion (Jourdan et al., 2001), and agricultural activities. If most or all endemic lizards in New Caledonia are to receive protection, it will necessitate the establishment of a much more extensive system of protected areas, incorporating much of the remaining forested habitat on many of the Grande Terre's mountains, as well as a diversity of habitats at low and middle elevation.

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