



Phylogeny and biogeography of Philippine bent-toed geckos (Gekkonidae: *Cyrtodactylus*) contradict a prevailing model of Pleistocene diversification

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ABSTRACT

In the Philippines, Pleistocene sea level oscillations repeatedly connected and isolated neighboring islands. Hence, an understanding of the island platforms adjoined during periods of low sea level has led biologists to a suite of expectations that, taken together, represent a paradigm for the process of recent diversification in southeast Asia. We employ statistical tests of phylogenetic topology and population genetic analyses of widespread species of bent-toed geckos (*Cyrtodactylus*) to ascertain whether patterns of inter- and intra-specific diversity can be explained by a Pleistocene aggregate island model of diversification. Contrary to many classic studies of Philippine vertebrates, we find complex patterns that are only partially explained by past island connectivity. In particular, we determine that some populations inhabiting previously united island groups show substantial genetic divergence and are inferred to be polyphyletic. Additionally, greater genetic diversity is found within islands, than between them. Among the topological patterns inconsistent with the Pleistocene model, we note some similarities with other lineages, but no obviously shared causal mechanisms are apparent. Finally, we infer well-supported discordance between the gene trees inferred from mitochondrial and nuclear DNA sequences of two species, which we suspect is the result of incomplete lineage sorting. This study contributes to a nascent body of literature suggesting that the current paradigm for Philippine biogeography is an oversimplification requiring revision.

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1. Introduction

Owing to its complex geological history and exceptionally variable geography, insular Southeast Asia serves as an excellent model for testing the effects of geographical change on phylogenetic processes (Brown and Guttman, 2002; Esselstyn et al., 2009; Evans et al., 2003; Jansa et al., 2006). The Philippines spans the area between the Sundaland-Eurasian and Philippines sea plates (Rangin, 1990; Yumul et al., 2003, 2009; Dimalanta and Yumul, 2004). Beginning in the Mesozoic, various geological processes shaped the distribution of land, including the collision of sea plates, strike-slip fault formation, and volcanic activity (Rangin, 1990; Yumul et al., 2003, 2009; Dimalanta and Yumul, 2004).

In addition to the geological processes that created the island arc system, Pleistocene sea-level fluctuations have caused repeated and dramatic changes in the size and connectivity of islands (Heaney, 1986; Hall, 1996, 1998, 2001; Rohling et al., 1998; Karns et al., 2000; Siddall et al., 2003). During periods of lower sea levels (100–140 m below current levels), nearby islands became con-

nected into island platforms known as Pleistocene Aggregate Island Complexes (PAICs: Brown and Diesmos, 2002, 2009). In the Philippines, landmass amalgamation resulted in the removal of marine dispersal barriers between nearby islands, potentially allowing for biotic exchange between islands of today. As sea levels subsequently rose and inundated these larger islands, aggregate islands were fragmented and marine barriers re-established. This was then followed by later lowering sea levels, aggregate island reformation, and periods of relaxed dispersal barriers (Heaney, 1986; Heaney et al., 1998; Brown and Diesmos, 2009). This cyclic process of aggregate island formation and fragmentation is believed to have generated terrestrial biodiversity and also maintained it in distinct faunistic subprovinces.

The repeated formation and fragmentation of PAICs has served as an elegant explanatory model and heuristic tool for understanding evolutionary processes that may have contributed to the accumulation of biodiversity across the Philippines and Indo-Malayan Archipelago (Brown and Guttman, 2002; Catibog-Sinha and Heaney, 2006; Dickerson, 1928; Dickinson et al., 1991; Delacour and Mayr, 1946; Diesmos et al., 2002; Esselstyn and Brown, 2009; Heaney and Regalado, 1998; Inger and Voris, 2001; Inger, 1954; Kloss, 1929). Four large PAICs are consistently recognized as the major faunal demarcations within the country: the Greater Luzon,

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Greater Mindanao, Greater Palawan, and Greater Negros–Panay Faunal Regions (Heaney, 1985, 1986; Heaney et al., 2005). There also exist many isolated islands surrounded by deep-ocean channels that never shared land-bridge connections to other islands. These include large islands like Mindoro and small islands like the Babuyan and Batanes archipelagos, Dinagat, Siargao, Siquijor, Lubang, Camiguin Sur, and Sibuyan (Fig. 1; Brown and Diesmos, 2002, 2009; Brown et al., 2008). Islands separated by deep-ocean channels tend to hold restricted range endemic species (Brown and Diesmos, 2002; Dickerson, 1928; Heaney et al., 1998; Stepan et al., 2003).

Previous studies involving many vertebrate taxa (e.g., Heaney et al., 2005; Jones and Kennedy, 2008; Roberts, 2006a,b) have explained faunal affinity by evoking geological history, with suites of species said to be endemic to particular groups of historically connected islands (Heaney et al., 1998; Kennedy et al.,

2000; Brown and Diesmos, 2002; Brown and Guttman, 2002; Evans et al., 2003; Esselstyn et al., 2004). This pattern of diversity partitioned by historically connected island groups can be assumed to vary with a species' ability to disperse across terrestrial landscapes and oceanic barriers (Roberts, 2006a,b). Expectations derived from the PAIC model include testable a priori hypotheses that address the predicted distribution of taxonomic diversity (Esselstyn and Brown, 2009): (1) populations from a given island should be more closely related to each other than to populations on different islands within the same PAIC; (2) intra-PAIC populations are expected to be more closely related to each other than inter-PAIC populations; and (3) monophyletic lineages are expected to be found within PAICs, not across PAICs, though incomplete lineage sorting, variation in relative dispersal abilities, and the timing of island colonization could obscure these patterns.

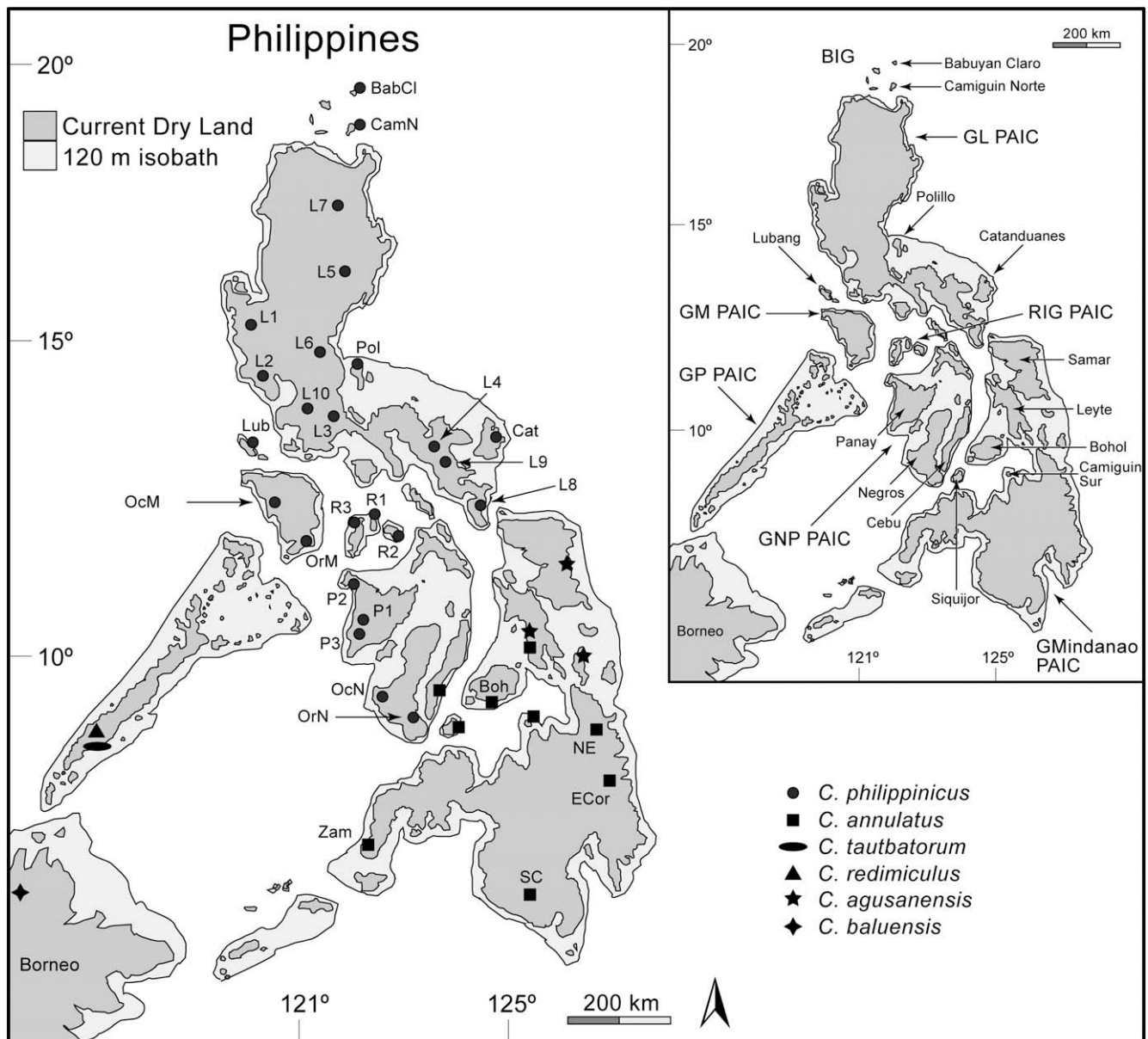


Fig. 1. Distribution of *Cyrtodactylus* samples from the Philippines (see species key at lower right). Locality codes on larger map indicate sampling localities, corresponding to terminals and clades in Figs. 3–5 and Table 3. The inset shows the five recognized major Pleistocene aggregate island complexes (PAICs) and additional deep-water islands. Abbreviated PAIC names are defined in Table 3. Current islands in the Philippines are shown in medium grey; light gray areas enclosed in black 120 m bathymetric contours indicate the hypothesized maximum extent of land during the mid- to late Pleistocene.

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