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Author for correspondence:

Paul M. Oliver

e-mail: paul.oliver@unimelb.edu.au

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Evolutionary biology

Crossing the line: increasing body size in a trans-Wallacean lizard radiation (*Cyrtodactylus*, Gekkota)

Paul M. Oliver^{1,2,3}, Phillip Skipwith⁴ and Michael S. Y. Lee^{5,6}

¹Department of Zoology, University of Melbourne, Parkville, Victoria 3052, Australia

²Department of Sciences, Museum Victoria, GPO Box 666, Melbourne, Victoria, Australia

³Research School of Biology, Australian National University, Canberra 0200, Australia

⁴Department of Integrative Biology and Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA

⁵South Australian Museum, North Terrace, Adelaide, South Australia 5000, Australia

⁶School of Earth and Environmental Sciences, University of Adelaide, South Australia 5005, Australia

The region between the Asian and Australian continental plates (Wallacea) demarcates the transition between two differentiated regional biotas. Despite this striking pattern, some terrestrial lineages have successfully traversed the marine barriers of Wallacea and subsequently diversified in newly colonized regions. The hypothesis that these dispersals between biogeographic realms are correlated with detectable shifts in evolutionary trajectory has however rarely been tested. Here, we analyse the evolution of body size in a widespread and exceptionally diverse group of gekkotan lizards (*Cyrtodactylus*), and show that a clade that has dispersed eastwards and radiated in the Australopapuan region appears to have significantly expanded its body size 'envelope' and repeatedly evolved gigantism. This pattern suggests that the biotic composition of the proto-Papuan Archipelago provided a permissive environment in which new colonists were released from evolutionary constraints operating to the west of Wallacea.

1. Introduction

The region between Wallace's and Lydekker's Lines (Wallacea) demarcates the transition between two geographically proximate but sharply differentiated terrestrial biotas. To the west lies the Sunda shelf, dominated by lineages of Asian origin, and to the east lies the Australopapuan region, characterized by a suite of endemic lineages with varying histories of isolation [1]. While marine barriers have impeded migration across this region, numerous terrestrial lineages have nevertheless successfully dispersed into Australasia from Asia [2,3], or more rarely into Asia from Australasia [4]. However, while there has been a long history of research into distributional patterns within Wallacea [5], there have been comparatively few examinations of the evolutionary consequences of these trans-Wallacean dispersal events [6–8].

Bent-toed geckos (*Cyrtodactylus*) are a very diverse (over 180 species) and widespread lineage of gekkotan lizards that occurs on both sides of Wallacea [9,10]. While the majority of *Cyrtodactylus* diversity occurs to the west (especially southeast Asia and Indochina), a cursory examination of maximum sizes suggests the majority of large species occur to the east (New Guinea and surrounding islands; [9,10]; electronic supplementary material, table S1). Here we use ancestral state analyses to examine whether Australopapuan taxa have independently approached large body sizes, and simulations to test whether species in this region are significantly larger than would be expected under null models of size evolution.

2. Material and methods

Phylogenetic relationships, divergence dates and ancestral body sizes for 87 species of *Cyrtodactylus* including 'Geckoella' (approx. 50% of recognized taxa) and outgroups were all simultaneously co-estimated with BEAST [11] (see the electronic supplementary material, SI_1 for data sources, SI_2 for alignment and SI_3 for BEAST xml file). Maximum recorded snout–vent length (SVL) was used as a proxy for body size (being tightly related to mass in lizards that do not exhibit limb-reduction) [12]. Morphological and sequence data were derived primarily from published work (see the electronic supplementary material for complete details).

We used a parametric bootstrapping approach to test for significant patterns in body-size evolution associated with colonization of the Australopapuan region. First, we estimated the rate of body-size evolution on our dated maximum clade credibility phylogeny under Brownian motion using BAYESTRAITS v. 2.0 [13] (necessary because the rate or 'precision' parameter in BEAST is not straightforward to interpret). Five replicate BAYESTRAITS analyses were run using default settings for 100 000 generations, sampling every 1000 generations and discarding the first 10 000 generations as burnin. Parameter convergence was assessed using TRACER v. 1.5 with effective sample sizes (ESS) of more than 200 being taken as proper mixing of the MCMC. Using the mean rate of evolution for body size inferred by BAYESTRAITS, we used MESQUITE v. 2.75 [14] to simulate the evolution of body size (1000 replicates) on our dated *Cyrtodactylus* phylogeny (see above) using a Brownian motion model with the rate inferred from BAYESTRAITS.

We used the Spearman rank coefficient to test whether *Cyrtodactylus* have larger body sizes than would be expected under a stochastic model in (i) the main clade (see below) in the Australopapuan region and (ii) in the Australopapuan region generally. This non-parametric rank-based value is a conservative test, as it is less sensitive to absolute body-size values (and differences) generated in the simulations. For each simulation replicate, the species were ranked according to body size (largest = highest ranks), and the rank sum for either the main Australopapuan clade or the Australopapuan region determined. The distribution of rank sums from all 1000 simulations was then compared to the observed (actual) value for the relevant groups of taxa. An observed value above the 95% percentile generated in the simulations would indicate that actual body sizes in the relevant group (e.g. main Australopapuan clade) were significantly larger (occupied higher ranks on average) than expected by chance, given a Brownian motion model on our phylogeny.

Brownie [15] was used on the BEAST maximum clade credibility (MCC) tree to test whether the simple Brownian motion model implemented in BEAST, BAYESTRAITS and the simulations (in contrast to a multi-rate model or an Ornstein–Uhlenbeck process) was adequate for the ancestral state reconstructions and parametric bootstrapping simulations.

3. Results

The phylogeny and timeframe for evolution in *Cyrtodactylus* are consistent with previous studies and indicate that two lineages have independently crossed into the New Guinea region: (i) a relatively old clade (approx. 20 million years ago (mya)) including the vast majority of Australopapuan species (25+ species) and ranging in maximum SVL from 71 to 172 mm and (ii) the younger *C. papuensis* group (approx. 5 mya) with only one or two small species (maximum SVL 65–74 mm; figure 1 and electronic supplementary material, figure S1).

Of the 33 species of *Cyrtodactylus* in the Australopapuan region (electronic supplementary material, table S1), 14 are larger (more than 126 mm) than the largest of 145 species found elsewhere, and nine are over two standard deviations

larger (more than 138 mm) than the mean for the genus. Bayesian estimation of ancestral traits also suggests that three largely allopatric Papuan lineages (*C. loriae*, *C. lousiadensis* and *C. noveaguineae* groups) have independently attained very large size (approx. 160 mm; figure 1). At the other end of the size spectrum, five species from the Australopapuan region (all from divergent lineages) are smaller than the mean for the genus and none is outside two standard deviations from the mean (they are of comparable size, but not smaller, than typical 'small' *Cyrtodactylus*).

Comparison of the empirical data with simulations (rate: $\sigma^2 = 1.8 \times 10^{-3}$) indicates that species in the main Australopapuan *Cyrtodactylus* clade ($p = 0.012$) and species in the Australopapuan region ($p = 0.021$) are significantly larger than would be expected due to chance (electronic supplementary material, figure S2).

The simple undirected Brownian motion model appears adequate compared to more complex models tested in Brownie. There is no evidence for different rates of Brownian evolution between the main Australopapuan clade and the remaining 'background' (censored rate results = aaa: insignificant under the three metrics used by Brownie), and no evidence for attraction to different means under an Ornstein–Uhlenbeck model (attraction parameter was the minimum possible Brownie value of 0.001).

4. Discussion

Cyrtodactylus in the Australopapuan region are significantly larger than elsewhere and appear to have undergone repeated independent evolution towards very large size (more than 160 mm). This conclusion holds whether we consider only the older clade, or all taxa in the region (i.e. both clades). Similar shifting patterns of ecological diversification and/or species accumulation following overwater dispersal eastwards into Wallacea have been described in other vertebrate lineages [6,8,16]. For example, another trans-Wallacean gecko lineage (*Gehyra* and allies) comprises a comparatively depauperate fauna of small taxa in Asia, juxtaposed against a younger and morphologically diverse radiation in Australasia—including two lineages that have independently approached large sizes similar to those observed in *Cyrtodactylus* (more than 140 mm) [16]. Likewise, fanged frogs (*Limonectes*) show statistically significant evidence for adaptive radiation following overwater colonisation of Sulawesi from the Philippines [8].

Lowered competitive and/or predatory pressures in isolated and simpler insular biotas are the two most obvious potential hypotheses for these shifts in evolutionary trajectory [7,12].

In *Cyrtodactylus*, we currently lack sufficient data to test these hypotheses but both are at least plausible. The Asian region is the area of origin for *Cyrtodactylus* [9] but is also home to a diversity of other Gekkotan lineages [16,17]. These may have constrained the maximum body sizes. Of particular note is a moderately old lineage (20+ mya) of very large geckos (max SVL 185–191 mm) in the genus *Gekko* that is widespread across Indonesia as far east as Sulawesi and the Lesser Sundas [16,17]. These species are aggressive competitors (and potentially also predators) that use similar microhabitats to the giant Papuan *Cyrtodactylus* (medium to large trees and tree hollows) but do not overlap in distribution [16,17]. The second lineage of *Cyrtodactylus*, which has successfully colonized New Guinea more recently, is also relatively species poor and

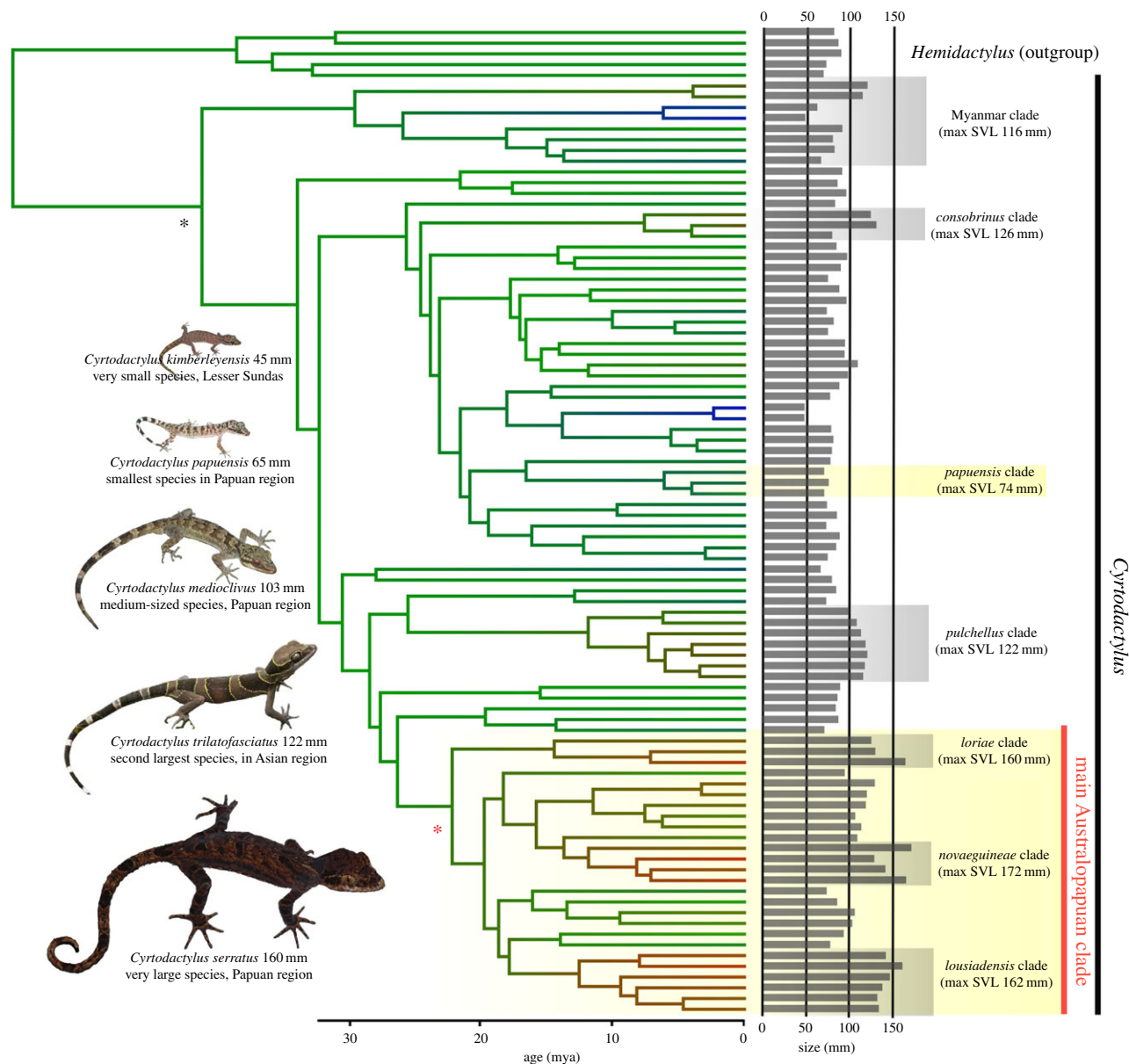


Figure 1. Dated phylogeny (Bayesian MCC tree) for *Cyrtodactylus* estimated with concatenated nuclear and mitochondrial dataset showing divergence dates and ancestral state reconstructions for body length (blue smallest, green intermediate and red largest); taxon names and posterior probabilities are given in the electronic supplementary material, figure S1; exact ages and sizes of all nodes (with 95% highest posterior density (HPD) intervals) are in electronic supplementary material, file S1_4. Yellow shading denotes the two clades occurring in the Australopapuan region. Grey bars at right denote maximum body size for each species (in mm), with grey shading denoting larger-bodied clades in Asian and Australopapuan regions. (Online version in colour.)

sits near the bottom end of the size range of the main Australopapuan radiation (less than 74 mm). This may be further evidence that competition has played a role in shaping the distribution and body size of Australasian geckos.

In addition, all the main predatory mammals of Asia are absent in the Papuan region [18] and recent dating analyses suggest that the sole native group of carnivorous mammals in New Guinea (Dasyuridae) colonized from Australia during the mid-Miocene—after the initial radiation of Papuan *Cyrtodactylus* [9,19]. It has been suggested that the absence or paucity of mammals (especially carnivores) has played an important role in shaping the distribution of clades in Wallacea (especially some radiations of birds) [20]. However, the idea that many trans-Wallacean colonists might also show detectable shifts in patterns of evolution in response to the same factor [6] has not yet been widely tested.

Empirical data suggest that many lineages have undergone ecological release following eastwards dispersal across

Wallacea [6,8,16]. However, despite the extensive literature on the biogeography of Wallacea, *Cyrtodactylus* is currently one of few lineages that provide statistically significant evidence of a shift in evolutionary trajectory related to dispersal into the Australopapuan region. We now need further analyses of additional trans-Wallacean lineages to elucidate the pervasiveness and predictability of ecological shifts, and more detailed ecological data to understand the processes that might be responsible.

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