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Divergence times and colonization of the Canary Islands by *Gallotia* lizards

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ABSTRACT

The Canary Islands have become a model region for evolutionary studies. We obtained 1.8 Kbp of mtDNA sequence from all known island forms of the endemic lizard genus *Gallotia* and from its sister taxon *Psammodromus* in order to reanalyze phylogenetic relationships within the archipelago, estimate lineage divergence times, and reconstruct the colonization history of this group. Well-supported phylogenies were obtained using maximum parsimony and Bayesian inference. Previous studies have been unable to establish the branching pattern at the base of the tree. We found evidence that *G. stehlini* (Gran Canaria) originated from the most basal *Gallotia* node and *G. atlantica* from the subsequent node. Divergence times were estimated under a global clock using Bayesian Markov Chain Monte Carlo methods implemented by three different programs: BEAST, MCMCTREE, MULTIDIVTIME. Node constraints were derived from subaerial island appearance data and were incorporated into the analyses as soft or hard maximal bounds. Posterior node ages differed slightly between programs, possibly due to different priors on divergence times. The most eastern Canary Islands first emerged just over 20 mya and their colonization appears to have taken place relatively quickly, around 17–20 mya. The subsequent node is consistent with cladogenesis due to colonization of Gran Canaria from the eastern islands about 11–13 mya. The western islands appear to have been colonized by a dispersal event from Lanzarote/Fuerteventura in the east to either La Gomera or one of the ancient edifices that subsequently formed Tenerife in the west, about 9–10 mya. Within the western islands, the most recent node that is ancestral to both the *G. intermedia*/*G. gomerana*/*G. simonyi* and the *G. galloti*/*G. caesaris* clades is dated at about 5–6 mya. Subsequent dispersal events between ancient Tenerife islands and La Gomera are dated at around 3 mya in both clades, although the direction of dispersal cannot be determined. Finally, we show that *G. galloti* is likely to have colonized La Palma more than 0.5 Ma after emergence of the island 1.77 mya, while *G. caesaris* from the same clade may have colonized El Hierro very soon after it emerged 1.12 mya. There are tentative indications that the large-bodied endangered *G. simonyi* colonized El Hierro around the same time or even later than the smaller-bodied *G. caesaris*. This study demonstrates the effectiveness of Bayesian dating of a phylogeny in helping reconstruct the historical pattern of dispersal across an oceanic archipelago.

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1. Introduction

The Canary Islands have become a focal point for evolutionary studies during the past 20 years, largely due to their high rates of endemism (e.g., Juan et al., 2000; Emerson, 2002). They also have a well-known geological history, with times of subaerial appearances established for most islands. This offers a temporal framework within which to examine biological diversification. New Bayesian methods provide a robust statistical framework for such an analysis (Thorne et al., 1998; Yang and Rannala, 2006; Drummond and Rambaut, 2007).

Bayesian estimation of lineage divergence times is superior to current maximum likelihood approaches because maximum and/or minimum limits on the nodes, and the uncertainties associated with them, are correctly incorporated into the analysis through the prior (Yang, 2006, pp. 245–258). Here, island emergence determines the earliest possible time of island colonization allowing specification of an upper limit to the time of between-island divergence. Poor date estimation may occur if a maximal date is unreliable (Ho and Phillips, 2009), which may be difficult to detect when only one node is calibrated. However, incorrect constraints may be detected by comparison of posterior with prior node distributions when multiple calibrations are used (Sanders and Lee, 2007). Successful dating also requires minimal bounds, which may be lacking if only island emergence is used. This problem is avoided for recently-colonized young islands because the ancestral node age will be tightly constrained between zero and the (recent) date of subaerial emergence. Dated phylogenies therefore provide the best method for inferring the historical pattern of dispersal across an

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archipelago, even though this may require several assumptions, particularly in the absence of a fossil record.

The subfamily Gallotiinae within the family Lacertidae comprises two sister lineages that have been assigned to the genera *Gallotia* and *Psammodromus*. The former are endemic to the Canary Islands, while the latter are found in southern Europe and northwest Africa. *Gallotia* originated from a Miocene colonization of the Canaries by an ancestor from southern Europe or northwest Africa (Arnold et al., 2007). Subsequent diversification within the islands has occurred, and most authors recognize seven extant species, each comprising several subspecies (Fig. 1). Previous studies have examined phylogenetic relationships within *Gallotia* using morphology (Thorpe, 1985) or molecular approaches based on RFLPs (Thorpe et al., 1993, 1994), DNA sequence (Thorpe et al., 1994; Gonzalez et al., 1996; Rando et al., 1997; Maca-Meyer et al., 2003; Arnold et al., 2007) or microsatellite DNA (Richard and Thorpe, 2001). There is clear support for two western sister clades with overlapping distributions: the *G. galloti*/*G. caesaris* clade from the islands of La Palma, La Gomera, El Hierro and Tenerife, and the clade containing the larger-bodied endangered lizards *G. simonyi* (El Hierro), *G. gomerana* (called *G. bravoana* by some authors) (La Gomera) and *G. intermedia* (Tenerife) (Rando et al., 1997; Maca-Meyer et al., 2003; Arnold et al., 2007). The latter clade is of considerable interest because it was considered extinct until *G. simonyi* was rediscovered on the island of El Hierro during the 1970s (Böhme and Bings, 1975). This was followed by the relatively recent rediscovery of the Tenerife and La Gomera lizards (Hernandez et al., 2000; Nogales et al., 2001). The existence of subfossils shows that this clade was also found on La Palma (Barahona et al., 2000) but as yet there is no hard evidence to demonstrate its continued survival there. The between-island relationships within the two western clades are well-established and show similarities. In both cases, the Tenerife species (together with La Palma for *G. galloti*/*G. caesaris*) outgroups the (La Gomera, El Hierro) clade (Thorpe et al., 1993, 1994; Rando et al., 1997; Arnold et al., 2007). The two remaining lineages within the *Gallotia* phylogeny are the small-bodied *G. atlantica* from the eastern islands of Fuerteventura and Lanzarote and the large-bodied *G. stehlini* from the central island of Gran Canaria. Previous studies show that these lineages originate from the most basal nodes within the *Gallotia* phylogeny, but their branching order has proved difficult to resolve.

All seven major islands have independent origins and tend to be older in the east and relatively recent in the west (Fig. 1). The oldest islands are Fuerteventura and Lanzarote, with subaerial rocks being dated at 20.4–20.6 million years (Ma) (Coello et al., 1992; Carracedo et al., 1998). The central island of Gran Canaria then emerged 14.5 million years ago (mya) (Carracedo et al., 1998). In the west, the Roque del Conde edifice within the current island of Tenerife and the island of La Gomera emerged about 11.6 mya (Ancochea et al., 1990; Guillou et al., 2004) and 10.5 mya (Ancochea et al., 2006), respectively. Tenerife is also composed of two additional formerly independent islands that appeared after Roque del Conde: Anaga (6.5 mya) and Teno (7.4 mya) (Guillou et al., 2004). The two most recently emerged islands are in the western extreme of the archipelago. La Palma appeared 1.77 mya (Guillou et al., 2001) while the oldest subaerial rocks on El Hierro have been dated at 1.12 Ma (Guillou et al., 1996). Previous phylogenies all suggest a general east–west pattern of colonization as might be predicted from these ages. La Palma and El Hierro were the last islands to be colonized by *Gallotia*. Other lizards (Brown and Pestano, 1998; Carranza et al., 2002) and bats (Pestano et al., 2003) also appear to have colonized these latter islands soon after their appearance.

There have been previous attempts to estimate divergence times in this group. Most recently, Arnold et al. (2007) used maximum likelihood to estimate divergence times in the Lacertini, including the Gallotinae, based on 620 bp of mtDNA sequence and a single calibration point. This analysis was unable to fully resolve the branching order for *G. atlantica* and *G. stehlini* but suggested an initial colonization of the Canaries 12.8 mya, and separation of the two western island clades about 6.9 mya. Here, we aim to provide the most rigorous analysis to date using: (1) Bayesian methods which correctly incorporate constraints derived from multiple island appearance data, (2) all available geological data on island appearance, (3) more DNA sequence, (4) a large number of taxa, including *Psammodromus* to allow estimation of the time of origin of *Gallotia*. In addition, we used the divergence times and the phylogeny to infer the historical pattern of island colonization by *Gallotia*.

2. Materials and methods

2.1. Samples and sequences

Sequences were obtained from 76 *Gallotia* and 13 *Psammodromus* specimens covering all species in these genera (Appendix A). All known island forms of *Gallotia* were included with several specimens available for some islands. Whole genomic DNA was extracted from digested blood and tail-tip samples using phenol/chloroform or spin column (DNeasy tissue kit, QIAGEN) extraction methods. Sequences from four mitochondrial genes were amplified using PCR: cytochrome *b* (cytb), cytochrome oxidase subunit 1 (COI), 12S rRNA, and 16S rRNA (primers are detailed in Appendix B). All sequences were examined carefully to ensure that amplified fragments represented authentic mtDNA rather than numts. Sequences were aligned using ClustalW and manual adjustments made by eye, taking into account 16S rRNA (Brown, 2005) and

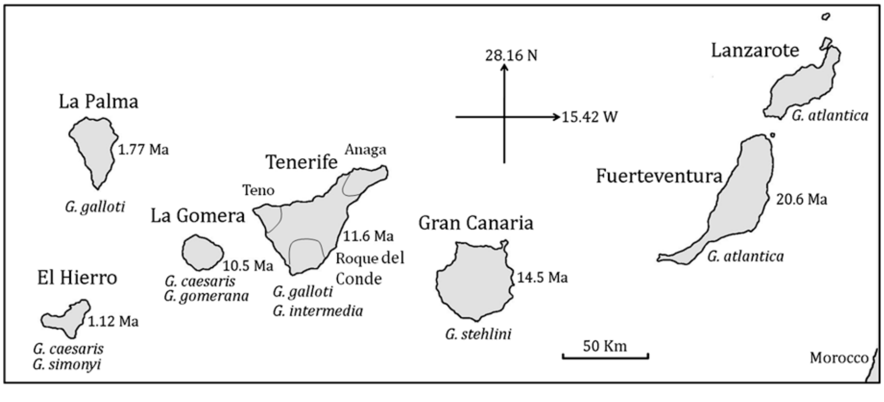

Fig. 1. Canary Island ages and *Gallotia* distribution, by island.

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