

Short notes and reviews

Progress, prospects and pitfalls in primate biogeography

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Review of **Primate Biogeography, Progress and Prospects**, by Shawn M Lehman and John G Fleagle. Development in Primatology: Progress and Prospects Series (Russ H Tuttle, Series Editor). Springer, New York, 2006, ISBN-13: 978-0387-29871-9.

Crustacean Biogeography, The Biogeography of Ground Beetles on Mountains and Islands, Biogeography of Lantern Fish, Island Biogeography of Mammals; some previous titles that deal with the zoogeography of someone's favourite taxa. And then there is Lehman and Fleagle's *Primate Biogeography*, published in the Developments in Primatology: Progress and Prospects series. When seeking an explanation for the distribution of animals, is there a need for this narrow taxonomic focus? And if so, why focus on primates?

There are three main reasons why the primate order is a highly suitable group for biogeographical analysis. First, they are widespread and diverse. They inhabit a number of continents and a large number of islands, with related taxa frequently geographically separated. Nowadays, primates are largely confined to (sub)tropical South America, Africa and Asia, with exceptions being some macaques and langurs ranging a bit further north in Africa and Asia, and of course humans. But, when the Egyptians were building their pyramids, primate distribution extended further into more temperate zones, including parts of Northern Africa, the Caribbean and China, as far north as the Yellow River (Figure 1). In the Eocene and Miocene, they were also found in North America down to the tip of South America, as well as in Europe and the Middle East. Second, primates are a fairly typical order of mammals; their origin dating back some 91 Mya, with anything between 250-350 extant species (Bininda-Emonds *et al.*, 2007), and an estimated 6,500 species that may have existed at one time or another (Martin, 1993). Third, in comparison with

other mammals, most of which are nocturnal, primates are easy to study, providing a detailed picture of their present-day distribution and, given our fascination with our own history, we arguably know more about primate fossil history and lifestyles than any other mammal order.

In this edited volume, Lehman and Fleagle present an efficiently organized selection of topics, covering nearly all aspects of biogeography, drawing upon the expertise of some 30 colleagues (all but six based in North America). This volume is the first biogeographical textbook fully devoted to primates. The editors have taken an approach that resourcefully covers the entire world and crosses vast amounts of time, ranging from biogeographic impacts on primate origins and evolution up to anthropogenic influences on extant primate populations. Lehman has worked on Neotropical and Malagasy primates, while Fleagle has taken a more historical approach in his career, specializing in various aspects of primate origins, adaptations and evolution. Their background has enabled them to write a superb introduction, which gives a thorough overview of the purpose of this book, primate biogeography in general and a brief synopsis of what this book is about. The remainder of the volume is divided into four sections dealing with the Neotropics, Africa, Madagascar and Asia respectively, followed by a section dedicated to paleobiogeography entitled 'Primate biogeography in Deep Time'. Lehman and Fleagle write a 2-3 page introduction to each section, thereby enhancing the unity of the volume.

Despite the individual chapters all having their own merit, arguably some more than others, overall there is an imbalance in the spectrum of topics covered within the five sections. Thus, although from the introductory chapter (Lehman and Fleagle) we learn that the Neotropics is the most species-rich region, two of the three chapters focus just

on Guyana, while the third is restricted to howler monkeys (*Allouatta* spp). All three chapters contain extensive quantitative datasets, cite an extensive range of sources and provide examples of intriguing biogeographical approaches. It would have been nice, however, to see the results applied to a larger biogeographical context. Lehman's 'Nested distribution patterns and the historical biogeography of the primates of Guyana', and Lehman, Sussman, Philips-Conroy and Prince's 'Ecological biogeography of primates in Guyana', both cover the same eight species, but each takes a different biogeography perspective. Lehman presents evidence for the representation of nestedness in this region with support from geographical barriers and interspecific competition to explain species assemblages and distributions in Guyana. Lehman *et al.* interestingly found riparian forests to be of ecological importance for six of the eight species under study. Not surprisingly, they also noted the combined impact of natural and anthropogenic disturbances and interspecific associations on patterns of biogeography. Ellsworth and Hoelzer in 'Genetic evidence on the historical biogeography of Central American howler monkeys', discovered that the black howler monkey, *Alouatta pigra*, did not follow the south-to-north colonization route the other seven howler monkey species seemed to have taken, leading to several speculations regarding the phylogeographic history of howler monkeys in Central America.

Depicted as the continent with the largest area of primate inhabited forest, the thoughtful chapter selections representing the whole of Africa will be of interest to primatologists and biogeographers alike. Focussing on three of the most widespread taxa of African primates, this section shows substantial development in the methodologies explored to analyse biogeographic approaches, as well as generalizing results towards a wider perspective. 'Contrasting phylogeographic histories of chimpanzees in Nigeria and Cameroon: A multi-locus genetic analysis' by Gonder and Disotell, is a fine example of how past and present geographical barriers do not necessarily mirror themselves in species. Gonder and Disotell also explore their use of methods in supporting and/or opposing their questions regarding the separation of Western and Central African chimpanzee (*Pan troglodytes*) lineages; discerning which genetic techniques are better suited for calculating large time-scale, phylogeographic questions. Similar methods of analysis used by Kamilar find

support for the current subspecies classifications of baboon populations in his chapter 'Geographic variation in savanna baboon (*Papio*) ecology and its taxonomic and evolutionary implications'. Using an ecological biogeography approach, Kamilar investigates the use of ecological niche separation to determine species differences. Delving into species concepts, Kamilar supports using morphological evidence when classifying species and subspecies and is opposed to the more recent trends of using behavioural and ecological evidence. Finally, McGraw and Fleagle explore species that have already been separated and are assumed to be accurate in 'Biogeography and evolution of the *Cercocebus-Mandrillus* clade: Evidence from the face', revealing morphological evidence that suggests the possibility that relationships need to be redefined within the clade.

Madagascar, for long isolated from mainland Africa and home to the unique lemurs, rightfully occupies an entire section. In consideration of its high levels of diversity and endemism, two of the three chapters explore the biogeographical effects on primate species of Madagascar in its entirety, while one chapter focuses on the continually changing taxonomic status of mouse lemurs, *Microcebus*. As most chapters are directed towards a broader audience, explaining general terms and theories, this section may equally well have been positioned at the beginning of the volume. Also, with 16 or so giant lemur species having gone extinct after the arrival of people on Madagascar around 2000 years ago (some of which were still extant 500-1000 years ago: Burney *et al.*, 2004), these faunas are actually only arbitrary remnants of natural assemblages and a chapter dedicated to this historic theme is unfortunately missing. Two chapters, 'Lemur biogeography' by Ganzhorn, Goodman, Nash and Thalmann, and 'Abiotic and biotic factors as predictors of species richness on Madagascar' by Stevens and O'Connor, take a broad view, of lemur biogeography and speciation. Ganzhorn *et al.* present a qualitative study providing biogeography definitions and theories pertaining to Madagascar's ecogeographical influence on phylogenetic relationships. Stevens and O'Connor use a more quantitative approach, using not only primates but also other vertebrates as model species, taking into account such variables as deforestation and climate change, thereby contributing to a larger conservation plan. Yoder and Heckman's 'Mouse lemur phylogeography revises a

model of ecogeographic constraint in Madagascar', is the only chapter in this section to focus on one genus. As found by Ganzhorn *et al.*, this chapter shows that mouse lemur species do not form eastern and western clades, as ecogeographic evidence may suggest, but rather a separation of species into northern and southern clades.

The Asia section unfortunately comprises only two chapters, one focussing on all mammals in mainland Southeast Asia, and the other concentrating on primates of insular Southeast Asia. This section differs from those on the Neotropics, Africa or Madagascar, as it lacks a chapter on an individual primate species or a primate community. 'The geography of mammals and rivers in mainland Southeast Asia' (Meijaard and Groves), systematically investigates the historic and current effects of ever-changing river systems on species diversification. Well-researched and thorough in its approach, it highlights the asymmetrical effect of large rivers in

determining the distribution of animals (with more species expanding their range in a west-to-east direction than vice versa). Equally suited to this final section, 'Primate biogeography and ecology on the Sunda Shelf Islands: a paleontological and zooarchaeological perspective' (Harrison, Krigbaum and Manser) not only discusses the history of the area in general, but also examines biogeographical influences on the paleontology and zooarchaeology of all extant catarrhine primates found in insular Southeast Asia. This qualitative study is, again, very well researched and leaves little, if any, gaps in the topics discussed.

The last section 'Primate biogeography in Deep Time' deals with exactly that: the biogeography of primates back to the Eocene and Miocene, exploring plate tectonics, timing of biogeographic events and outgroup choice as a means to establish the origin of primates. 'Mammalian biogeography and anthropoid origins' (Beard) suggests an Asian origin of

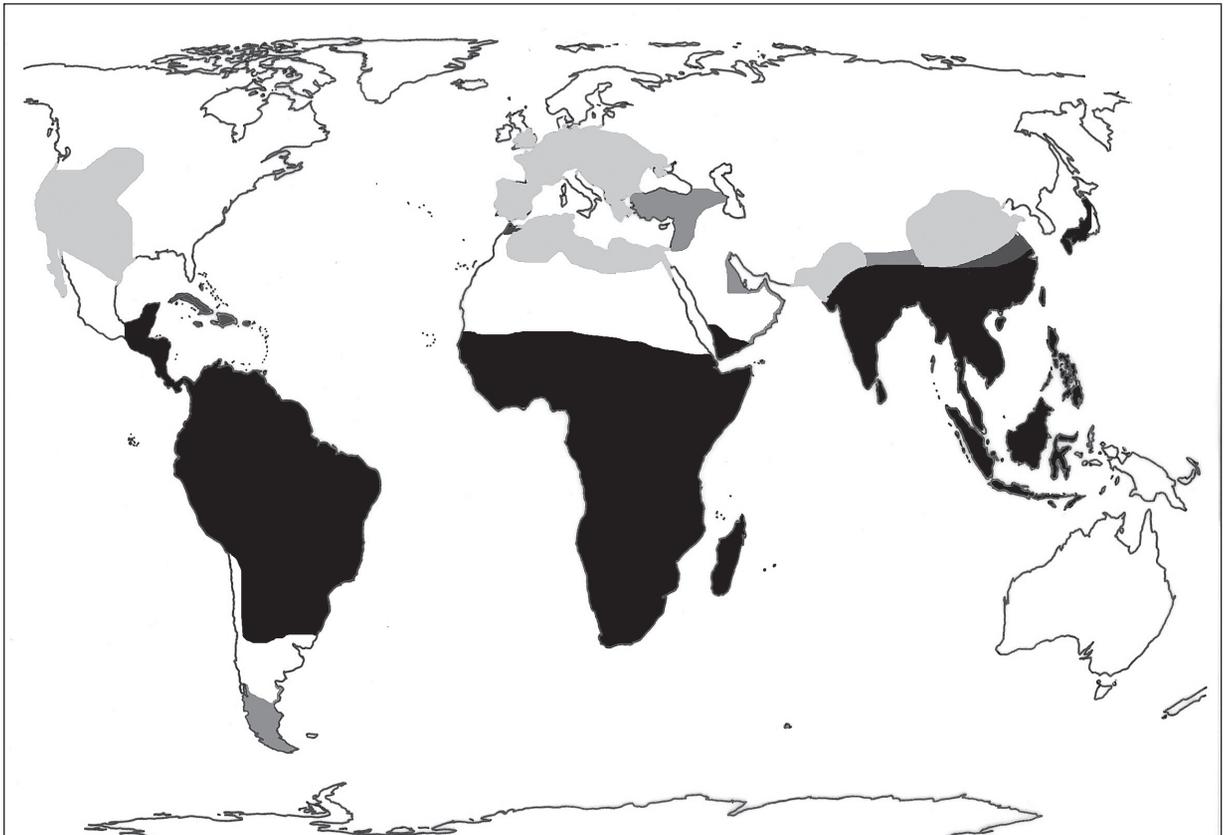


Fig. 1. Distribution of the Order Primates present and past (partially after Fleagle and Gilbert, Chapter 13). Black: Present; Dark-grey: Historic (~1-4 kya); Medium-grey: Miocene Climatic Optimum (~17 Ma); Light-grey: Eocene Climatic Optimum (~40 Ma) with only the Eocene shown when Eocene and Mid-Eocene distributions overlapped.

primates based on fossil evidence and the order being nested firmly within an exclusively Asian branch of the mammalian family tree. However, Heesy *et al.* ('Biogeographic origins of primate higher taxa'), show that outgroup choice in biogeographic reconstructions can have an influence on both tree topology and purported geographic origin of the order, and depending on what outgroup one chooses, primates can originate in Europe, Asia or Africa.

Fleagle and Gilbert's 'The biogeography of primate evolution: the role of plate tectonics, climate and chance', and Rossie and Seiffert's 'Continental palaeobiogeography as phylogenetic evidence', both expose the role of plate tectonics and oceanic dispersal in explaining present-day primate distributions. Fleagle and Gilbert begin the section with a traditional perspective of primate origins and dispersal mechanisms. Rossie and Seiffert introduce the concept of 'chronobiogeographic debt' in phylogeography, adding one step of parsimony debt for any implied dispersal between landmasses. Then again, simply accepting an earlier origin of Primates of at least 90 Mya (based on molecular clock estimates), as opposed to the popular 65 Mya (based on fossils, see e.g. Martin *et al.*, 2007), reduces the need to invoke numerous trans-oceanic dispersal events in explaining primate biogeographical patterns.

Despite numerous typographical errors, imbalance in the depth of concepts, inconsistencies in

writing styles and some inconclusive figures, all of which seem to be a natural component of any edited volume, Lehman and Fleagle have produced a must-read book for all those interested in zoogeography. Primates are intriguing in their past and present relationships to humans and their environment and the numerous authors have succeeded in covering an impressive array of subjects and themes on a diverse, widely distributed and, generally speaking, fascinating Order. We want more, and eagerly await a Lehman and Fleagle *Primate Biogeography Part II*.

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Received: 4 April 2008

Accepted: 16 May 2008

