An island called India: phylogenetic patterns across multiple taxonomic groups reveal endemic radiations

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Island systems from around the world have provided fascinating opportunities for studies pertaining to various evolutionary processes. One recurring feature of isolated islands is the presence of endemic radiations. In this regard, the Indian subcontinent is an interesting entity given it has been an island during much of its history following separation from Madagascar and currently is isolated from much of Eurasia by the Himalayas in the north and the Indian Ocean in the south. Not surprisingly, recent molecular studies on a number of endemic taxa from India have reported endemic radiations. These studies suggest that the uniqueness of Indian biota is not just due to its diverse origin, but also due to evolution in isolation. The isolation of India has generated some peculiarities typically seen on oceanic islands. However, these patterns might be confined to groups with low dispersal ability.

Keywords: Biogeography, Indomalayan region, intrusive elements, island radiation, molecular data.

Introduction

ISLANDS have long provided an exciting setting for evolutionary research. Darwin[1] was deeply influenced by the peculiarities he observed on the Galapagos Islands, and some of these observations provided the basis for his theory of evolution by natural selection (see chapter XII, *On the Origin of Species*). His contemporary, Wallace was also intrigued by island fauna and has devoted a whole book on this topic[2]. Since then, numerous studies on island systems from around the world have contributed to understanding evolutionary processes such as speciation, diversification and adaptive radiation[3].

An interesting feature of isolated islands is the presence of endemic radiations[4], also referred to as island radiation. Endemic radiation consists of a group of closely related species that are confined (endemic) to an island or island system. Such radiations arise due to colonization of a species from the mainland followed by *in situ* diversification. Often, this diversification occurs due to adaptation to very different niches and are concomitant with extreme morphological divergence among the members of the radiation, a phenomenon referred to as 'adaptive radiation'. As a consequence, the island's biota tends to be unique and distinct from that of the mainland. Endemic radiations have been reported from a range of island systems such as the islands of the Galapagos[5] – which constitutes a few small islands – to large islands such as Madagascar[6]. These radiations span a range of different taxonomic groups. Interestingly, endemic radiations are not confined to islands. For example, the rift lakes of eastern Africa each harbour a radiation of cichlid fishes[7]. These lakes can be considered as 'islands' in a sea of land. Similarly, mountaintops have also been referred to as 'sky islands' as they provide islands of distinct habitats when compared to lowlands[8]. Such mountain-top habitats are also known to harbour endemic radiations[9]. The common theme in all these examples is 'evolution in isolation', i.e. physical isolation of these areas in conjunction with presence of unoccupied niches, which is a consequence of isolation, has provided an ideal setting for diversification.

Indian context

In this context, the Indian subcontinent provides an interesting system to study evolution in isolation. The Indian subcontinent encompasses the large swath of land to the south of the Himalayas and covers Sri Lanka, much of India, and parts of Pakistan and Bangladesh (Figure 1). Much of this landmass, along with Madagascar, was part of the Gondwana supercontinent around 200 million years ago (mya). Subsequently, the break-up of Gondwana resulted in India–Madagascar separating from Africa around 160 mya followed by split between India and Madagascar around 90 mya (refs 10, 11). After separating from Madagascar, the Indian plate drifted across Indian Ocean before colliding with Eurasia. The estimate for initial collision ranges from 50 to 55 mya (refs 12–14) followed by final suturing of India with Eurasia around 35–40 mya (refs 14, 15). Thus the Indian plate was an island for 50–55 million years (my) until it merged with

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Eurasia. The impact of collision caused the uplift of Himalaya[16] and the contact with Asia facilitated faunal exchange between India and Asia[17].

However, the formation of the Himalayas had a profound impact on the climate and biogeography of the Indian subcontinent. Today the 5200 km long Himalayan range forms the northern, northwestern and northeastern limits of this landmass, isolating it from rest of Eurasia[16]. To the south, this landmass is surrounded by the Indian Ocean. Thus, even though the Indian subcontinent is currently part of Eurasia, this landmass is cutoff from the rest of Eurasia by high mountain ranges in the north and the ocean in the south (Figure 1). In addition to this physical isolation, there is also a climatic barrier that separates the Indian subcontinent from the rest of Eurasia. To the north and northwest, India is flanked by arid zones that receive low rainfall (Figure 2). With the establishment of these physical and climatic barriers, faunal exchange between the Indian subcontinent and the rest of Eurasia might have been severely limited in more recent times. Thus, the subcontinent witnessed a prolonged period of isolation in the past and is currently largely isolated from much of Eurasia[4]. In this regard, India can be considered as an island that was intermittently connected to Eurasia before the rising Himalayas and associated climate change prevented further biotic exchange. However, faunal links with Southeast Asia might have been maintained through the 'Assam gateway' along the northeastern borders of the subcontinent[17]. This is because the northeastern part of India is climatically contiguous with Southeast Asia and the mountain ranges separating these two regions are not as high as rest of the Himalayas. Given this scenario, does the origin and evolution of Indian biota exhibit signatures of this isolation?

The Indian biota can be broadly classified into the older Gondwanan elements and the more recent intrusive elements that dispersed into India after collision. The Gondwanan elements represent the original biota of India that were present on the drifting Indian plate and have African and Malagasy affinity[17]. However, late Cretaceous volcanism and latitudinal shift that the drifting Indian plate experienced during its northward journey might have caused large-scale extinctions of Gondwanan biota[18–20]. These extinctions could have opened up new niches for the intrusive elements to occupy. Nevertheless, recent molecular studies suggest that some Gondwanan elements did survive these extinction events, and some lineages have dispersed out of India[21,22]. The intrusive elements are largely of Southeast Asian origin, but many African and Eurasian (Palearctic) elements have also reached India after collision[17,22,23].

Island hypothesis

Intrusive elements therefore represent species colonizing the 'Indian island' from the mainland Eurasia or Africa. An important prediction of this island hypothesis is that most intrusive elements would have dispersed into India post-collision when the link between India and Eurasia was established. These lineages would have undergone

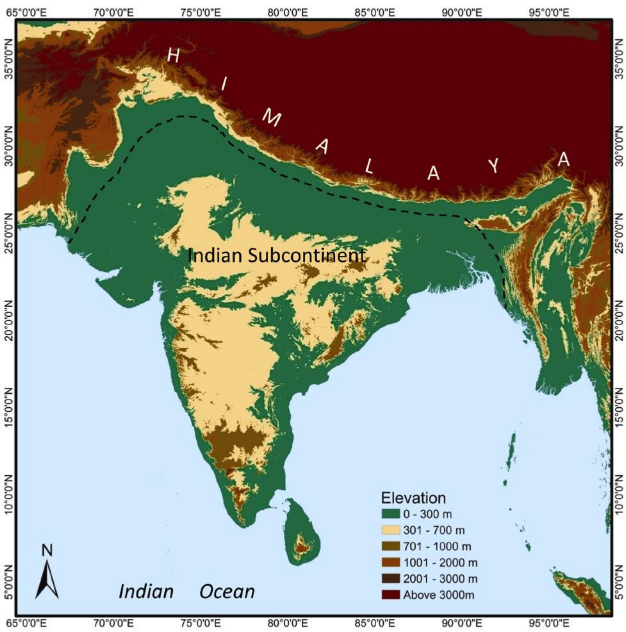

Figure 1. The Indian subcontinent. Dotted line shows the approximate boundary of the Indian subcontinent, which is bounded by the Himalayas in the north and the Indian Ocean in the south. Source: Worldclim–Global climate data[38].

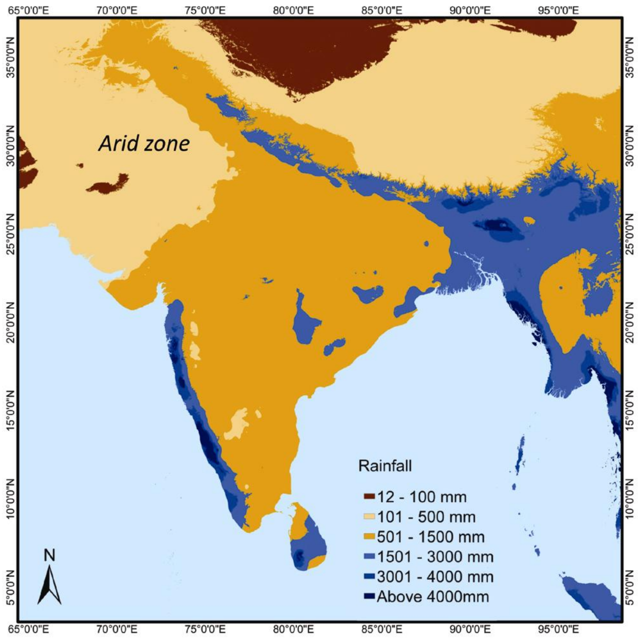

Figure 2. Rainfall map of India. Areas in yellow and brown are arid areas with low rainfall (<500 mm). Source: Worldclim–Global climate data[38].

in situ diversification due to the availability of unoccupied niches, as much of the local biota was probably extinct during Cretaceous volcanism. Back dispersals out of India are predicted to be rare due to subsequent isolation of India and lack of open niches in rest of Eurasia. Thus, most members of the radiation would be endemic to India (endemic radiation).

The predictions of the island hypothesis can be tested for various Indian taxa in a phylogenetic framework in conjunction with molecular dating[22]. From a phylogenetic perspective, the island hypothesis would predict that the endemic species from India would form a clade that would be nested within a larger phylogeny consisting of species from outside India, i.e. from the rest of Eurasia. Furthermore, the age of the node representing the most recent common ancestor of Indian radiation would be less than 35–40 mya (date for the final suturing of India with Eurasia). This would in turn suggest a single dispersal event into India after its merger with Eurasia, followed by *in situ* diversification.

For example, molecular phylogenetic studies on the langurs (*Semnopithecus*) of South Asia revealed an endemic radiation consisting of at least five species that are distributed across the Indian subcontinent in a range of habitats (Figure 3). This clade is nested within the tree consisting of Asian colobines, suggesting a single dispersal of langurs into India from Southeast Asia[24]. This dispersal event has been dated to around 8–10 mya (ref. 25), which is consistent with their arrival after the collision. Genus *Semnopithecus* is endemic to the Indian subcontinent, suggesting that there has been no back dispersal out of India. Thus, the evolution and diversification of this group in the Indian subcontinent is consistent with the predictions of the island hypothesis. Similarly, molecular phylogenetic studies suggest that India harbours endemic radiations in a range of other vertebrate groups such as lizards[4,26,27], toads[28], as well as invertebrates[29] and plants[30]. In most of these cases, except the lizard genus *Lygosoma*, molecular data support a single colonization of these taxa into India. Secondly, where molecular dates are available, the colonization events were estimated to have occurred

Table 1. List of taxa showing endemic radiation in the Indian subcontinent

	N(*B*)	Age (my)	Reference
Mammals			
Semnopithecus	>5	8–10	24
Lizards			
Hemidactylus	>23(3)	35–40	26
Geckoella	~14	30	39
Eutropis	13(2)	5.5–17	27
*Lygosoma**	7(1)	–	4
Amphibians			
Duttaphrynus	14(4)	>15	28
Snails			
Paracrostoma	>4	–	29
Plants			
Ceropegia	>50	–	30

N, number of species in the endemic radiation, this number will increase for some groups as more species are described; *B*, number of back dispersals. Age (in million years (my)) refers to the estimated time of dispersal into India based on molecular dating. Dashes indicate lack of molecular date estimate. *Two dispersal events in the case of genus *Lygosoma*.

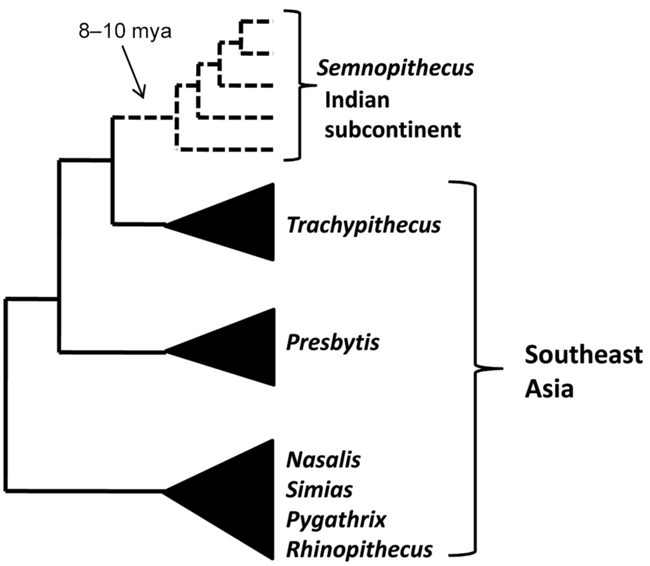

Figure 3. Phylogeny of Asian colobine monkeys based on Karanth *et al.*[24] and Roos *et al.*[25]. Dotted line shows the Indian radiation.

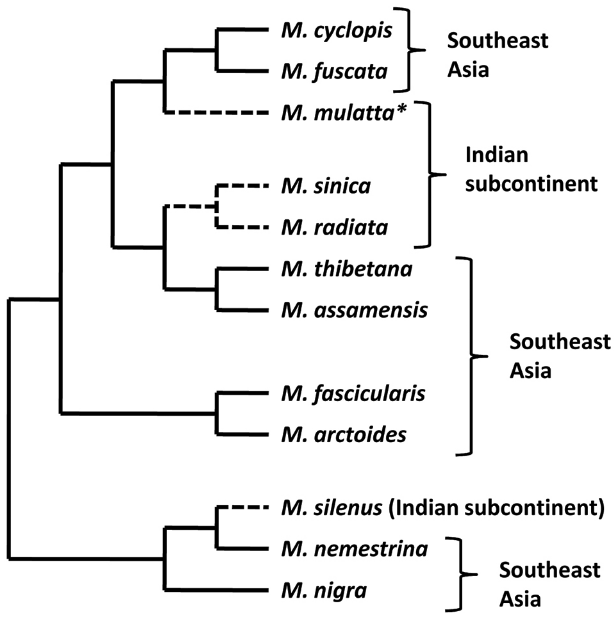

Figure 4. Phylogeny of Asian macaque monkeys (*Macaca*) based on Morales and Melnick[31]. Dotted line shows the Indian lineages. *M. mulatta* is also distributed in Southeast Asia.

less than 50 mya. Additionally, back dispersals are rare with only four groups exhibiting from one to four back dispersals (Table 1). The rarity of dispersals out of India compared to dispersals into the subcontinent suggests that open niches promoted establishment of taxa that dispersed in, whereas competition on the 'mainland' prevented establishment of lineages that dispersed out.

Do all intrusive elements support the island hypothesis? The alternate scenario is the Indian subcontinent was not an isolated insular entity, and that much of the biota of this landmass was assembled through multiple colonization events from Eurasia. The multiple colonization scenario would predict that endemic taxa of the Indian subcontinent are not closely related to each other; instead they are related to species from elsewhere in Asia. The earliest molecular evidence for this scenario comes from the macaques. There are four species of macaques distributed in the Indian subcontinent. The phylogeny of the Indian macaques does not support their monophyly[31]. In the macaque phylogeny shown in Figure 4, the three lineages of Indian macaques: *Macaca mulatta*, *M. silenus* and *M. radiata-sinica*; are more closely related to Southeast Asian macaques than to each other. Thus, the phylogeny supports three independent colonization events rather than one followed by *in situ* diversification. Similarly in butterflies too there is a growing body of evidence suggesting multiple dispersal in and out of India[32,33].

Conclusion

The molecular evidence available thus far largely supports the island hypothesis. These studies suggest that a significant proportion of the Indian intrusive biota might have been assembled through single colonization followed by *in situ* diversification, rather than multiple colonizations from Eurasia. The results of these studies are summarized in Table 1.

From a biogeographical perspective, much of India is placed in the Oriental region[34] or the Indomalayan region[35]. Recently, Holt *et al.*[36] generated a global map of zoogeographical regions based on distributions of and phylogenetic patterns from birds, mammals and amphibians, and retrieved regions similar to those proposed by Wallace. Thus, this assignment of India to the Oriental region has remained stable since 1876 with few minor changes in the boundary. Most zoogeographical classifications further divide the Oriental region into Indian, Indochinese and Sunda subregions, thereby emphasizing the uniqueness of these subregions. In the Indian scenario, the uniqueness of its biota has been attributed to its diverse origin, including Southeast Asia (Oriental), Africa (Ethiopian), Gondwanan and Palearctic. The current review suggests that the uniqueness of Indian biota is not only due to diverse origins, but also due to evolution in isolation. The isolation of India has generated some peculiarities typically observed on large islands. However, it should be noted that these patterns might not be observed in all taxonomic groups. In this regard, vagility of the taxa might be very important[37]. Endemic radiations might not be seen in taxa with high dispersal ability (such as butterflies).

1. Darwin, C., *On the Origin of Species by Means of Natural Selection*, Harvard University Press, Cambridge, Massachusetts, 1859, p. 513.
2. Wallace, A. R., *Island Life*, Macmillan and Co, London, 1880, p. 560.
3. Losos, J. B. and Ricklefs, R. E., Adaptation and diversification on islands. *Nature*, 2009, **457**, 830–836.
4. Datta-Roy, A., Singh, M. and Karanth, K. P., Phylogeny of endemic skinks of the genus *Lygosoma* (Squamata: Scincidae) from India suggests an *in situ* radiation. *J. Genet.*, 2014, **93**, 163–167.
5. Sato, A., O'Huigin, C., Figueroa, F., Grant, P. R., Grant, B. R., Tichy, H. and Klein, J., Phylogeny of Darwin's finches as revealed by mtDNA sequences. *Proc. Natl. Acad. Sci.*, *USA*, 1999, **96**, 5101–5106.
6. Karanth, K. P., Delefosse, T., Rakotosamimanana, B., Parsons, T. J. and Yoder, A. D., Ancient DNA from giant extinct lemurs confirms single origin of Malagasy primates. *Proc. Natl. Acad. Sci.*, *USA*, 2005, **102**, 5090–5095.
7. Fryer, G., Endemism, speciation and adaptive radiation in great lakes. *Environ. Biol. Fishes*, 1996, **45**, 109–131.
8. McCormack, J. E., Huang, H. and Knowles, L. L., Sky islands. In *Encyclopedia of Islands* (eds Gillespie, R. G. and Clague, D.), University of California Press, Berkeley, CA, 2009, pp. 839–843.
9. Hughes, C. and Eastwood, R., Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proc. Natl. Acad. Sci., USA*, 2006, **103**, 10334–10339.
10. Chatterjee, S. and Scotese, C., The breakup of gondwana and the evolution and biogeography of the Indian Plate. *Proc. Indian Natl. Sci. Acad. Part A*, 1999, **65**, 397–425.
11. Briggs, J. C., The biogeographic and tectonic history of India. *J. Biogeogr.*, 2003, **30**, 381–388.
12. Beck, R. A. *et al.*, Stratigraphic evidence for an early collision between northwest India and Asia. *Nature*, 1995, **373**, 55–58.
13. Kumar, P., Yuan, X., Kumar, M. R., Kind, R., Li, X. and Chadha, R. K., The rapid drift of the Indian tectonic plate. *Nature*, 2007, **449**, 894–897.
14. Bouilhol, P., Jagoutz, O., Hanchar, J. M. and Dudas, F. O., Dating the India–Eurasia collision through arc magmatic records. *Earth Planet. Sci. Lett.*, 2013, **366**, 163–175.
15. Ali, J. R. and Aitchison, J. C., Gondwana to Asia: plate tectonics, paleogeography and the biological connectivity of the Indian subcontinent from the Middle Jurassic through latest Eocene (166–35 Ma). *Earth-Sci. Rev.*, 2008, **88**, 145–166.
16. Valdiya, K. S., *Dynamic Himalaya*, University Press (India) Limited, Hyderabad, 1998, p. 178.
17. Mani, M. S. (ed.), Biogeographical evolution in India. In *Ecology and Biogeography of India*, Dr W. Junk b. v. Publishers, The Hague, Netherlands, 1974, pp. 698–724.
18. Thewissen, J. G. M. and McKenna, M. C., Paleobiogeography of Indo-Pakistan: a response to Briggs, Patterson and Owen. *Syst. Biol.*, 1992, **41**, 248–251.
19. Conti, E., Eriksson, T., Schönenberger, J., Sytsma, K. J. and Baum, D. A., Early tertiary out-of-India dispersal of Crypteroniaceae: evidence from phylogeny and molecular dating. *Evolution*, 2002, **56**, 1931–1942.
20. Samant, B. and Mohabey, D. M., Palynoflora from Deccan volcano-sedimentary sequence (Cretaceous–Palaeogene transition) of central India: implications for spatio-temporal correlation. *J. Biosci.*, 2009, **34**, 811–823.

21. Karanth, K. P., Out-of-India Gondwanan origin of some tropical Asian biota. *Curr. Sci.*, 2006, **90**, 789–792.
22. Datta-Roy, A. and Karanth, K. P., The Out-of-India hypothesis: what do molecules suggest? *J. Biosci.*, 2009, **34**, 687–697.
23. Kurup, G. U., Mammals of Assam and mammal-geography of India. In *Ecology and Biogeography of India* (ed. Mani, M. S.), Dr W. Junk b. v. Publishers, The Hague, Netherlands, 1974, pp. 585–612.
24. Karanth, K. P., Singh, L., Collura, R. V. and Stewart, C.-B., Molecular phylogeny and biogeography of langurs and leaf monkeys of South Asia (Primates: Colobinae). *Mol. Phylogenet. Evol.*, 2008, **46**, 683–694.
25. Roos, C. *et al.*, Nuclear versus mitochondrial DNA: evidence for hybridization in colobine monkeys. *BMC Evol. Biol.*, 2011, **11**, 77.
26. Bansal, R. and Karanth, K. P., Molecular phylogeny of *Hemidactylus* geckos (Squamata: Gekkonidae) of the Indian subcontinent reveals a unique Indian radiation and an Indian origin of Asian house geckos. *Mol. Phylogenet. Evol.*, 2010, **57**, 459–465.
27. Datta-Roy, A., Singh, M., Srinivasulu, C. and Karanth, K. P., Phylogeny of the Asian *Eutropis* (Squamata: Scincidae) reveals an 'into India' endemic Indian radiation. *Mol. Phylogenet. Evol.*, 2012, **63**, 817–824.
28. Bocxlaer, I. V., Biju, S. D., Loader, S. P. and Bossuyt, F., Toad radiation reveals into-India dispersal as a source of endemism in the Western Ghats–Sri Lanka biodiversity hotspot. *BMC Evol. Biol.*, 2009, **9**, 131.
29. Köhler, F. and Glaubrecht, M., Out of Asia and into India: on the molecular phylogeny and biogeography of the endemic freshwater gastropod *Paracrostoma* Cossmann, 1900 (Caenogastropoda: Pachychilidae). *Biol. J. Linnean Soc.*, 2007, **91**, 621–657.
30. Surveswaran, S., Kamble, M. Y., Yadav, S. R. and Sun, M., Molecular phylogeny of *Ceropegia* (Asclepiadoideae) of Indian Western Ghats. *Plant Syst. Evol.*, 2009, **281**, 51–93.
31. Morales, J. C. and Melnick, D. J., Phylogenetic relationships of the macaques (Cercopithecidae: *Macaca*), as revealed by high resolution restriction site mapping of mitochondrial ribosomal genes. *J. Hum. Evol.*, 1998, **34**, 1–23.
32. Kodandaramaiah, U. and Wahlberg, N., Out-of-Africa origin and dispersal mediated diversification of the butterfly genus Junonia (Nymphalidae: Nymphalinae). *J. Evol. Biol.*, 2007, **20**, 2181–2191.
33. Kodandaramaiah, U., Lees, D. C., Müller, C. J., Torres, E., Karanth, K. P. and Walhberg, N., Phylogenetics and biogeography of a spectacular Old World radiation of grass feeding butterflies: the subtribe Mycalesina (Lepidoptera: Nymphalidae: Satyrini). *BMC Evol. Biol.*, 2010, **10**, 172.
34. Wallace, A. R., *The Geographical Distribution of Animals – Part I*, Harper and Brothers, New York, 1876, p. 574.
35. Corbet, G. B. and Hill, J. E., *The Mammals of the Indomalayan Region: A Systematic Review*, Oxford University Press, New York, 1992, p. 488.
36. Holt, B. G. *et al.*, An update of Wallace's zoogeographic regions of the world. *Science*, 2013, **339**, 74–78.
37. Kodandaramaiah, U., Vagility: the neglected component in historical biogeography. *Evol. Biol.*, 2009, **36**, 327–335.
38. Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. and Jarvis, A., Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.*, 2005, **25**, 1965–1978.
39. Agarwal, I. and Karanth, P., A phylogeny of the only ground-dwelling radiation of *Cyrtodactylus* (Squamata: Gekkonidae): diversification of *Geckoella* across peninsular India and Sri Lanka (Squamata: Gekkonidae). *Mol. Phylogenet. Evol.*, 2015, **82**, 193–199.

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