

Out-of-India Gondwanan origin of some tropical Asian biota

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Many hypotheses have been proposed to explain the presence of Gondwanan lineages in tropical Asia including, the out-of-India hypothesis, the Eurasian route hypothesis, long-distance transoceanic dispersal and the boreotropical hypothesis. Recent molecular studies support an out-of-India Gondwanan origin of some tropical Asian taxa. Specifically these studies suggest that ancient Gondwanan lineages survived on peninsular India in spite of dramatic climatic changes and Late Cretaceous volcanism. Under this model, Gondwanan lineages dispersed into Asia when peninsular India collided with Asian plate. These Gondwanan lineages represent the remnants of unique ancient biota that require urgent attention from conservationists if we are to preserve the overall evolutionary history of Indian biota.

Keywords: Disjunct distribution, Eurasian rout, Gondwana breakup, molecular phylogeny.

THE break-up of Gondwana and continental drift in the Early Cretaceous has been cited as one of the reasons for tropical intercontinental disjunctions^{1,2}. One of the peculiarities of this global disjunct distribution is the presence of many Gondwanan forms in tropical Asia. Gondwanan forms are lineages that are distributed predominantly in the southern continents of South America, Africa-Madagascar, and Australia (Figure 1 *a*). As much of Asia was never part of Gondwana, the presence of Gondwanan forms in tropical Asia is intriguing. A variation of Gondwana breakup hypothesis, referred to as out-of-India hypothesis, has been proposed to explain the presence of Gondwanan forms in tropical Asia^{1,3,4}. According to the out-of-India hypothesis, Gondwanan forms from Africa and Madagascar reached Asia by way of rafting on peninsular India after the breakup of Gondwana. The geophysical evidence for this scenario is well known⁵. Peninsular India along with Madagascar was originally part of the Gondwana continent. The split between Indo-Madagascar landmass and Africa was initiated around 160 million years ago (mya). By 130 mya Indo-Madagascar landmass had separated from Antarctica, followed by the split between Madagascar and peninsular Indian around 90 mya. For the next 40 million years peninsular India traversed northward through the Indian Ocean, supposedly in isolation, before slamming into the Asian plate around 50 mya (Figure 1). Thus it is plausible that rafting peninsular India carried with it Gondwanan forms to Asia. Mani³ points out that with the physical contact of peninsular India with

Asia, extensive interchange between peninsular autochthonous and Asiatic Tertiary flora and fauna occurred. The peninsular elements presumably spilled over into Asia and differentiated in the Tertiary mountains of south China, Indo-China, Thailand, and the Malayan peninsula. However, it must be noted the dramatic latitudinal and climatic changes that affected the peninsular India during its journey from Gondwana to Laurasia caused substantial extinctions in its biota^{3,6}. Moreover the massive volcanism (Deccan traps) at the Cretaceous–Tertiary boundary supposedly had a devastating impact on peninsular India biota⁷. Nevertheless, fossil data suggest a Gondwanan affinity for many Late Cretaceous fauna from peninsular India^{8–10}. Additionally, recent molecular studies on a wide range of species, in conjunction with our knowledge of plate tectonics and fossil data support the out-of-India hypothesis for numerous tropical Asian taxa (see Table 1).

In the case of the out-of-India model, the phylogenetic trees of Gondwanan taxa in Asia should mirror the sequence of geophysical events that led to the breakup of the Gondwana. For example, among the cichlid fishes, the branching pattern of the molecular phylogeny based on mitochondrial genes is congruent with the out-of-India hypothesis. Here, species from India and Madagascar branch together to the exclusion of African species consistent with the separation of Indo-Malagasy landmass from Africa around 160 mya, followed by the split between India and Madagascar around 90 mya (Figure 2 *a*). Another important aspect of the out-of-India hypothesis is that the estimated divergence times between Asian/Indian taxa and their counterparts in Africa/Madagascar/Australasia should correspond to the time when these land masses separated from each other. This appears to be the case for

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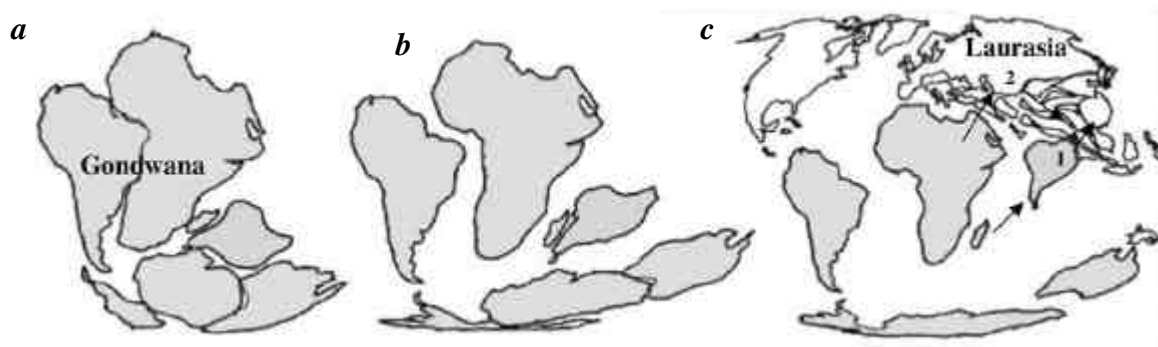


Figure 1. Gondwana breakup and out-of-India hypothesis. *a*, Peninsular India was part of the Gondwana supercontinent 200 million years ago (mya). The split between eastern and western Gondwana was initiated around 160 mya; *b*, By 120 mya Indo-Malagasy landmass was isolated from Africa and Antarctica–Australia landmass; *c*, Around 90 mya India separated from Madagascar and traveled through Indian Ocean for 40 my before colliding with Asian landmass 50 mya carrying with it Gondwanan forms to Asia. The numbers 1 and 2 represent the out-of-India and Eurasian route hypotheses respectively. Figure modified from the Conti *et al.*¹³.

Table 1. Molecular studies that suggest out-of-India dispersal of Gondwana flora and fauna into Asia

Species	Phy	MD	References
Amphibians			
Ranidae frogs	+	+	4
Nasikabatrachidae frog	+	+	20, 22
Caecilians ^a	+	+	23, 24
Reptiles			
Agamid lizards ^a	+	–	17
Fishes			
Asian arowana ^c	–	+	25
Asian cichlids ^c	+	–	26
Aplocheiloid fishes ^c	+	–	27
Birds			
Ostrich ^{c,d}	–	+	28
Plants			
Asian Dipterocarps	+	–	29, 30
Crypteroniaceae ^{a,b}	+	+	13, 18

Phy, Out-of-India hypothesis supported by phylogenetic pattern.

MD, Out-of-India hypothesis supported by molecular data based divergence date.

^aSpecies not distributed in Madagascar.

^bSpecies that went extinct on peninsular India.

^cSee Briggs³¹ for alternative hypotheses for the current distribution of these taxa.

^dAccording to Cooper *et al.*²⁸, ratites entered Indo-Madagascar through the Kerguelen Plateau in Late Cretaceous (~80 mya) from Australia. Later they dispersed out of India and reached Africa via Eurasia before going extinct in Asia.

some studies where the molecular data are available (Table 1).

An alternative explanation for this disjunct distribution is that Gondwanan forms dispersed into tropical Asia from Africa by way of Eurasia during the Oligocene or later, here referred to as the Eurasian route. For example, based on molecular data, Yoder¹¹ postulated that strepsir-

rhines (lorises, galagos and lemurs) dispersed into India/Asia from Africa through Eurasia some time after 39 mya¹². The Eurasian route would predict a phylogeny where the Asian species would branch with African species, suggesting dispersal out of Africa (Figure 2 *b*), but see Conti *et al.*¹³ for geological inconsistencies with respect to this hypothesis. Additionally this hypothesis would predict a more recent Mid to Late Tertiary split between Asian and African forms. Two other hypotheses have been put forward to explain these tropical intercontinental disjunctions particularly among plants. These include the long-distance transoceanic dispersal and the boreotropical hypothesis that suggest immigration from the Laurasian tropics during the Eocene². Again, these hypotheses suggest more recent arrival of Gondwanan elements in Asia, whereas the out-of-India hypothesis argues for an ancient Mid to Late Cretaceous origin.

Thus lineages with Gondwana ancestry have reached peninsular India through several different routes. A subset of these lineages was already present on the Indian plate during Mid to Late Cretaceous period (see molecular data in Table 1) and dispersed out of India when peninsular India made contact with the Asian plate (out-of-India hypothesis). The presence of these ancient Gondwanan lineages on peninsular India can therefore be explained by vicariance event (Gondwana break-up), while other lineages differentiated in Africa and Asia before dispersing into peninsular India when contact between India and Asia was established. Therefore, Gondwanan forms in peninsular India can be divided into two broad categories, ancient Gondwanan lineages from Mid to Late Cretaceous and recent dispersers from the Tertiary.

It must also be noted that in some species convergence among distantly related taxa in widely separated areas might erroneously suggest intercontinental disjunct distribution. For example, the treefrogs (subfamily Rhancophorinae) and burrowing frogs (subfamily Tomopterninae) of Madagascar and South India exhibit disjunct distributions. But molecular phylogenetic studies suggest that

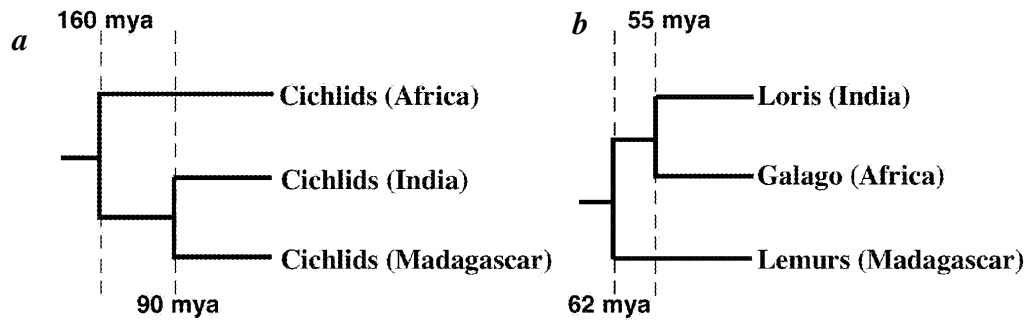


Figure 2. Tree topologies of out-of-India and Eurasian models discussed in the text. *a*, The dates shown in cichlid phylogeny represent the times when Africa split from Indo-Madagascar and India split from Madagascar²⁶. *b*, The dates shown in strepsirrhines phylogeny are based on molecular data^{11,12}.

these subfamilies are not monophyletic. Instead these studies indicate that they are endemic radiations in Madagascar and South India exhibiting convergence of morphological and behavioural characters in adult and larval stages¹⁴. Among plants too there are numerous examples of such intercontinental convergence¹⁵. Therefore the first step in the study of disjunct distributions is to determine if the observed pattern is real and not due to convergence, i.e. an artifact of incorrect taxonomy¹⁶.

Some peculiar distributional patterns of ancient Gondwanan forms in the tropical Old World

Another intriguing aspect of Gondwana biogeography is the patchy distribution of ancient Gondwanan forms in the tropical Old World. For example caecilians are found in South America, Africa, and tropical Asia, but are absent from Madagascar. This is rather unusual given that molecular data supports the out-of-India Gondwana origin of Asian caecilians (Table 1). It is likely that caecilians dispersed into peninsular India after India split from Madagascar and later dispersed into Asia. Recent fossil discoveries suggest that India remained close to Africa during its northward journey towards Asia. As India became detached from Madagascar and moved parallel with Africa, it appears that it continued to pick up invaders among which were frogs, caecilians, and lizards⁵. Therefore it is likely that caecilians never dispersed into Madagascar. Thus, for certain species the out-of-India hypothesis has to be modified to include direct dispersal of African forms into peninsular India, rather than through Madagascar (see refs 17, 18 for more details).

Another interesting distributional pattern of ancient Gondwanan forms in Asia is the complete absence of certain species from peninsular India. For example, Crypteroniaceae (a family of Asian evergreen trees) is not represented in peninsular India, but there is a single species in Sri Lanka and there are many species in SE Asia. Asian arowanas (freshwater fishes) are another example of a Gondwanan form distributed in SE Asia, but not India. If

we are to invoke the out-of-India hypothesis for their distribution in Asia, then how do we explain their current absence in peninsular India? According to Conti *et al.*¹³, this pattern may be explained by the massive extinction of India's Gondwanan elements caused by Late Cretaceous/Early Tertiary climatic changes and limited survival in refugial areas. In this regard, Sri Lanka might have a proportionally higher number of ancient Gondwanan forms than peninsular India. This is because Sri Lanka being an island away from the rest of Laurasia is less likely to have been affected by faunal interchange during Early Tertiary. Thus, the absence of Gondwanan forms from Madagascar can be explained by the relative position of the continental plates during the Late Cretaceous. Whereas, in the case of India, Cretaceous/Early Tertiary extinction of some ancient Gondwanan lineages such as, Crypteroniaceae plants and arowanas fishes, might explain their absence from peninsular India.

Conclusions

As mentioned earlier, much of the peninsular Indian Cretaceous biota has been lost probably due to Late Cretaceous/Early Tertiary climatic changes and volcanism. In addition, the biotic uniqueness of peninsular India was diluted further due to extensive biotic interchange with Asia after the two masses collided. But mounting molecular evidence suggests that some ancient Gondwanan lineages have survived on peninsular India in spite of these events. These Gondwanan lineages from the Cretaceous represent the remnants of a unique ancient biota^{3,19}. Urgent action needs to be taken to identify these ancient lineages through the use of molecular tools. This information can in turn be used for better protection of the overall evolutionary history of Indian biota. Studies done thus far also indicate that many of these ancient lineages, particularly amphibians, are confined to the Western Ghats and Sri Lanka. The fact that such deep evolutionary history is concentrated in a spatially limited forest area stresses the urgent need for revised protection measures for the Western Ghats/Sri

Lanka hotspot^{19–21}. Molecular studies also support the out-of-India Gondwanan origin of some tropical Asian biota. With the establishment of the biotic bridge between peninsular India and Asian plate, some of these ancient Gondwanan forms dispersed into tropical Asia resulting in intercontinental disjunctions. Interestingly, the vertebrate species listed in Table 1 are predominantly amphibians and freshwater fishes or non-volant birds. Given the sensitivity of amphibians and freshwater fishes towards salt water and the inability of non-volant birds to fly, the evolutionary history of these vertebrates is bound to be tightly linked with the geological histories of landmasses. These observations lend further support to the out-of-India hypothesis for these groups. Further studies are needed to determine the proportion of Gondwanan forms in tropical Asia that can be accounted for by out-of-India hypothesis.

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