Invertebrate Diversity and Conservation in the Western Ghats, India

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Biogeographic origins and habitat use of the butterflies of the Western Ghats

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Abstract: The butterfly fauna of the Western Ghats of peninsular India, like that of its bird fauna, is strangely unique because it is diverse and yet exhibits low levels of endemism. Although peninsular India shared its plate tectonic history with Africa and Madagascar, most of its fauna is Oriental. Holloway, in his first analysis of the biogeography of Indian butterflies, recognized a few African elements in the butterfly fauna of peninsular India and hypothesized that evergreen forest species had mostly Malayan (Oriental) origins whereas those of drier habitats showed affinities with the African Region. Here this hypothesized link between biogeographic origins and habitat use of butterflies is tested by employing a simplified version of Holloway's method of classifying genera into faunal centres. This analysis shows that of the 164 butterfly genera in the Western Ghats, 129 show affinities to the Oriental and 33 to the African Region, confirming the strong Oriental element in the Western Ghats. Most of the genera inhabiting moist forests are centred in the Oriental region, but the dry habitat butterfly fauna is a mix of Oriental, African and Eremic (Saharan and central Arabian) elements. There are also a few moist forest elements from the African region. Holloway's hypothesis is thus only partly supported. Holloway also believed that the African elements in peninsular Indian butterfly fauna were remnants of the original fauna existing on the Indian plate after it drifted from Africa. Specific examples are discussed here particularly in the face of low endemism and lack of unique biogeographic elements, which suggest that, contrary to Holloway's hypothesis, the African and Eremic elements are relatively recent and there is no evidence of the original Indian plate fauna in the extant butterfly fauna of the Western Ghats. Due to this reason, biogeographic models other than plate tectonics, such as island-hopping, may be more useful in explaining biogeography of the Western Ghats butterflies.

Keywords: Biogeographic affinities, biodiversity hot spots, habitat preference, Oriental butterflies.

Introduction

About 158–160 million years ago (Ma), the ancient continent of Gondwana divided and the Indo-Madagascan plate started separating from Africa. The Indian plate then broke away from Madagascar ca. 84–96 Ma (Briggs 2003), rapidly drifted northward and collided with Eurasia between 55.5 and 66 Ma (Beck *et al*. 1995). Thus, initially the Indo-Madagascan plate was isolated from Africa, and then the Indian plate was isolated from both Madagascar and Africa for extended periods of time. This period of isolation resulted in the evolution of fascinatingly high levels of endemism and unique faunal elements in Madagascar, but biogeographers have largely failed to find such endemic elements in peninsular India, which represents the ancient Indian plate. Some of the very few exceptions are the highly diverse and largely endemic uropeltid snakes and caecilians, which have undergone bouts of speciation in the Western Ghats in isolation (Mani 1974; Das 1996), and the newly discovered frog genus *Nasikabatrachus*, which is a relict from the ancient Indo-Madagascan plate (Biju and Bossuyt 2003; Dutta *et al*. 2004). Simultaneously, some African and north Asian groups are represented in Indian fossils from the time when India is believed to have been isolated from the two larger landmasses. Along with recent stratigraphic and palaeomagnetic data, this indicates that India traversed northward towards Eurasia while maintaining its proximity to the African continent, allowing some faunal exchange (Briggs 2003). This should have further influenced and enriched India's floral and faunal composition with African elements. Despite this plate tectonic history with Africa, it was apparent even from early studies that most of the flora and fauna of peninsular India and the Western Ghats were derived not from the African but from the Oriental Region (Elwes 1873, Wallace 1876).

The Western Ghats are a mountain chain roughly parallel to the western coast of peninsular India. This mountain chain hosts some of the most biodiverse, endangered and unique habitats in peninsular India, including tropical lowland and montane evergreen forests and montane grasslands. The Western Ghats play a crucial role in discussions pertaining to biogeography of peninsular India because practically all of peninsular India's endemic species occur there. Due to their high levels of biodiversity, the Western Ghats have been recognized as one of the only two biodiversity hotspots of South Asia (Myers *et al*. 2000). Given what is known about the plate tectonic history of the Indian peninsula, it has been a challenge for biogeographers to explain the diversity, endemism and relative contributions of African and Oriental Regions to the flora and fauna of the Western Ghats. For example, what are the original African elements in the Western Ghats fauna? Which groups have invaded India from the Malayan region and, in particular, which ones have speciated in the Western Ghats? Has peninsular India contributed any of its original floral and faunal elements to Malayan, Indo-Chinese and other neighbouring sub-regions?

Biodiversity and endemism in the Western Ghats have been prominently highlighted in the past two decades for plants and vertebrates (Gadgil and Meher-Homji 1986; Daniels 1992; Daniels *et al*. 1992; Das 1996; Myers *et al*. 2000; Myers 2003; Dahanukar *et al*. 2004). With a few exceptions, however, the invertebrate fauna of the Western Ghats has been inadequately analysed both for biodiversity dispersion within the Western Ghats and for conservation prioritization (Gaonkar 1996; Kunte *et al*. 1999; Subramanian and Sivaramakrishnan 2005; Kunte 2008). This has hindered progress in understanding the biogeographic origins of invertebrate diversity and its importance to endemism and conservation in the Western Ghats. Some of these aspects of biogeography are also important in light of the recent need to identify areas and habitats of high biodiversity for conservation prioritization (Daniels *et al*. 1991; Das *et al*. 2006; Kunte 2008). As a step towards understanding the diversity and biogeographic patterns of at least a few, relatively well-known invertebrate taxa of the Western Ghats, in this first of a series of four papers, biogeographic affinities of butterflies with other zoogeographic regions are analysed, especially with respect to their habitat use.

Systematic investigations into the biogeographic affinities of butterflies started as late as the 1960s with Jeremy Holloway's work (Holloway and Jardine 1968; Holloway 1969, 1974). Holloway mapped the distributional ranges of select genera of Indian butterflies, identified faunal centres (see Materials and Methods), and analysed affinities of these butterflies to those from Oriental and African Regions. He found that 59% of the Indian butterfly genera were centred in the Oriental Region, 13% were centred in the Palaearctic Region, and only 4% were centred in the African Region. His work was unique for another reason: he also discussed the habitat use of butterflies of peninsular India and its relation to the quantitative patterns of biogeographic affinities he found. Although he did not include all Indian genera in his dataset and did not perform any statistical analyses, he indicated that the extant African butterfly elements in peninsular India were primarily restricted to dry habitats. His explanation for the overall closer affinities to the Oriental Region and the habitat use of African elements, which is summarized below, was based on the plate tectonic history of India. Holloway (1974) pointed out that the Indian plate probably carried its native flora and fauna when it separated from Africa and Madagascar and, owing to its prolonged isolation from any other major landmass, perhaps some of these evolved into unique biogeographic elements. However, the potential of peninsular India as an area for faunal development and endemism was impaired by violent geological activities leading to the formation of the Western Ghats and the Deccan trap, formed from domal uplifting–faulting and laval flows, respectively. Holloway believed that the newly immigrating, highly vagile evergreen forest fauna from the Oriental Region might have replaced whatever original evergreen forest butterfly fauna of peninsular India survived these geologic developments. Hence, the only African elements that remained in peninsular India and the Western Ghats were relicts of dry forests and other dry habitats. Mani (1974) supported this hypothesis with additional observations on vertebrate groups.

In his analysis, Holloway (1969, 1974) included a sample of 436 species belonging to 123 genera – a mere 40% of the Indian butterfly fauna (Evans 1932). As mentioned above, he also did not quantify habitat use of butterflies and did not carry out any statistical tests. In the present study a comprehensive dataset that included all 332 species belonging to 164 genera from the Western Ghats was analysed. The dataset included over 95% of the species (including all the endemics) and 100% of the genera of butterflies found in peninsular India. Here, data on distributions and habitat use of the Western Ghats butterflies were combined to test the hypotheses that: (a) although most of the butterfly fauna was derived from the Oriental Region, species of the drier habitats were derived from the African Region, and (b) some of these species may be the original butterfly faunal elements of the Indian plate before it collided with the Eurasian plate. It remains to be seen whether other invertebrates exhibit patterns similar to the ones described below for butterflies. However, butterflies are an excellent group to test the above hypothesis and lead the way for similar studies on other invertebrates, since it is currently the best-studied group in the Western Ghats with respect to taxonomy. The majority of species and subspecies are described, at least some larval host plants of most species have been reported, and distributions and habitat use are fairly well-studied (Wynter-Blyth 1957; Gaonkar 1996; Kunte 2000).

Materials and methods

Butterfly genera and species from the Western Ghats

The list of Western Ghats butterfly species and genera was extracted from Evans (1932), Talbot

(1939), Wynter-Blyth (1957) and Gaonkar (1996), with additional species records of *Appias lalage* (the Spot Puffin) from recent literature (Nalini and Boris 1996; Devy 1998; Kunhikrishnan 1998), and of *Amathusia phidippus* (the Palmking) from unpublished observations (C. Susanth, pers. commun.). Genus placements of species were taken mainly from Pinratana (1981–1996), Larsen (1987, 1988), Corbet and Pendlebury (1992), Gaonkar (1996), Bascombe *et al*. (1999) and Kunte (2000).

Global distribution and centres of diversity

A simplified version of the method used by Holloway (1969, 1974) to identify global distributions and centres of diversity was used. To derive faunal centres, Holloway had classified the Old World into a staggering 48 provinces and used a limited sample of 123 genera of Indian butterflies after excluding monotypic genera and genera in need of taxonomic revisions. He then overlaid distributions of species from these genera onto the provinces, to find the density of species from different genera in various provinces. From this, he identified faunal centres by calculating the number of genera in each province. Although this method is good for identifying faunal centres at a finer spatial scale, it is labour-intensive and less useful for testing broader patterns. Although global distribution of genera and their centres of diversity could be extracted more easily for my broad-level analysis, Holloway's method was simplified so that the complete dataset on the Western Ghats butterflies could be analysed appropriately. Instead of using Holloway's much finer classification of provinces, global distributions to butterfly genera were assigned in terms of zoogeographic regions as follows (Fig. 1): (1) Oriental region (India east and southeast-ward up to Indonesia, Philippines and Taiwan), (2) Australian region (New Guinea–Irian Jaya, Australia, New Zealand and associated Pacific islands), (3) African region (including parts of the Middle East), (4) Palaearctic region (northern Eurasia), (5) Nearctic region (North America including parts of central Mexico), and (6) Neotropical region (southern North America, central and South America). For convenience and borrowing from the Floral Kingdoms (Cox 2001), in Table 1, those genera that have their centres of diversity embracing both Palaearctic and Nearctic regions were classified as 'Holarctic'. Following the distributions of many butterflies in eastern Asia, in addition to these 'Holarctic' and strictly Palaearctic genera, also presented in Table 1 is a breakdown

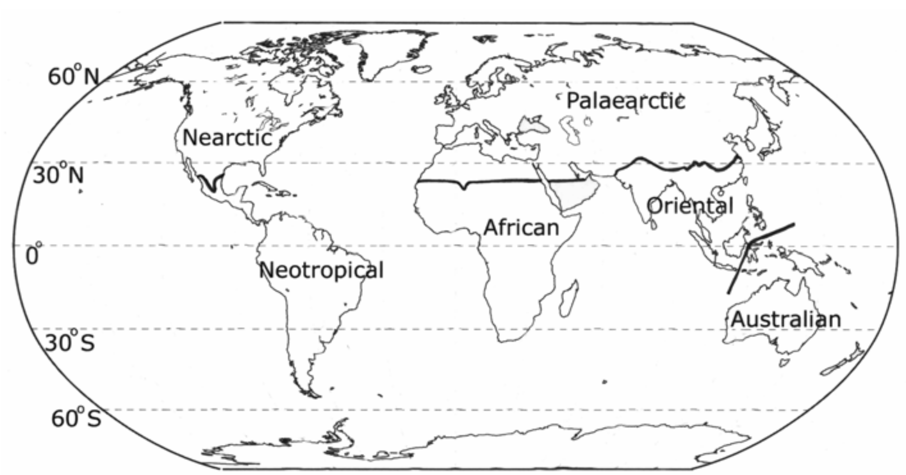

Figure 1. Zoogeographic regions of the world (after Cox 2001).

Table 1. Habitat-wise and centre of diversity-wise breakdown of butterfly genera of the Western Ghats. Numbers of genera with centre of diversity in the Holarctic, Eastern Palaearctic and Palaearctic regions (see Materials and Methods) are presented separately. Nearctic and Neotropical Regions are not represented in the table because none of the Western Ghats genera has its centre of diversity exclusively in these regions although some of the genera included under 'global' have one of their centres of diversity in the two regions.

	EVG	MOI	DEC	WOO	DRY	SCR	MON	GEN	Total
Oriental	57	36	16	12	2	2		3	128
African	2	6	3	7	4	8		3	33
Australian	10	7	2	4		1			24
Holarctic		3					2		5
Eastern Palaearctic	1	1							2
Palaearctic						1	1		2
Global		1		1			1	1	4
Total	70	54	21	24	6	12	4	7	198

EVG: low and mid-elevation evergreen and semi-evergreen forests; MOI: moist forests; DEC: moist and mixed deciduous forests; WOO: woodlands; SCR: scrub, savannahs and grasslands; DRY: wide range of dry habitats; MON: montane habitats (shola forests and montane grasslands).

of genera by their centres of diversity in the 'Eastern Palaearctic' sub-region (mainly China, Japan and Korea). For presentation purposes, in a few cases where a majority of the species from a genus were found in particular zoogeographic region(s) and only a very small number of the species (typically one or two) found marginally outside this region, the former region was assigned as the global distribution of the genus. The following sources were consulted for global distributions of genera: Evans (1932); Larsen (1991); Scott (1986); Lewis (1987); Corbet and Pendlebury (1992); d'Abrera (1997, 2004, 2006); Bascombe *et al*. (1999), and the butterfly section of Markku Savela's database (Savela 2006).

Centres of diversity were assigned to genera simply by evaluating the area where the majority (>70%) of their constituent species were found. If species from a genus were scattered and clustered in different zoogeographic regions and none of the regions had more than 70% of the species of the genus, then all the regions that together contained more than 70% of the species of the genus were assigned as the centres of diversity for the genus. Thus, for example, *Ypthima* (family Nymphalidae) have centres of diversity both in the African and Oriental Regions. Centres of diversity were classified as 'global' if species of the genus were distributed in over four of the six zoogeographic regions. This applied mostly to widely distributed, species-rich genera such as *Papilio* (family Papilionidae) and *Eurema* (family Pieridae). Very widely distributed but highly species-poor genera such as *Zizula, Pseudozizeeria* (both family Lycaenidae) and *Cynthia* (family Nymphalidae) were not assigned a centre of diversity because the concept of centre of diversity is not meaningful for these genera. Localized genera, however species-poor (e.g. *Zesius* (family Lycaenidae) and *Zipaetis* (family Nymphalidae)) were assigned centres of diversity.

It is important to note that centres of diversity of genera (equivalent to Holloway's centres of speciation) are not necessarily centres of origin. This distinction is important because although it is likely that centres of diversity are the regions where the particular genera actually originated and diversified, it is not necessarily true. It is possible that centres of diversity differ from centres of origin for various reasons. For example, if the genus emigrated from the centre of its origin into a previously unoccupied region and diversified there in a niche vacuum and due to lack of competition, the centres of origin and diversity would be quite different. Another example would be a situation where the genus suffered total extinction of its species from its centre of origin due to geological catastrophe, making it appear as if the genus flourished in the current centre of diversity and originated there. These possibilities are not easily known or tested but these are extreme examples, and therefore the centres of diversity will sometimes be used as surrogates for centres of origin in the discussion that follows. Subsequent use of the term 'centres of origin' should be read and understood with the above caveats in mind.

Habitats of genera

Because the main goal of this chapter was to assess whether butterflies from the wetter forests of the Western Ghats have their centres of origin in the Oriental Region and those from drier habitats have centres of origin in the African Region, habitats were classified in broader categories reflecting the precipitation gradient and groups of habitats used by the Western Ghats butterflies as follows:

1. EVG: low and mid-elevation (sea level up to 1200 m, sometimes extending up to 1500 m) evergreen and semi-evergreen forests. Genera assigned to this category were evergreen and semi-evergreen forest specialists.
2. MOI: moist forests including evergreen, semi-evergreen and dense riparian moist deciduous forests. EVG would thus be a subset of MOI, EVG genera being more specialized. Genera assigned to this category usually do not venture into drier and more exposed parts of the deciduous forests.
3. DEC: moist and mixed deciduous forests which may have distinct riparian vegetation that is not very tall and dense and certainly not as moist as the previous category.
4. WOO: genera assigned to this category have species that inhabit a wide range of woodland habitats, from openings in evergreen forests to wooded areas in urban settings. These are woodland generalists.
5. SCR: scrub and savannahs, including grasslands maintained by slight human disturbances.
6. DRY: genera inhabiting a wide range of drier habitats including dry deciduous forests, scrub, savannah and grasslands.
7. MON: montane habitats (above 1800 m) including shola forests and montane grasslands of southern Western Ghats, which share species with temperate habitats.

To facilitate comparisons between various zoogeographic regions and to statistically test the hypothesis, evergreen, semi-evergreen and dense riparian moist deciduous forests were treated as 'moist forests' and dry deciduous, scrub, savannah and grasslands as 'dry habitats'.

Habitat information on individual butterfly species was gathered from Wynter-Blyth (1957), Larsen (1987, 1988), Kunte (2000) and extensive unpublished personal observations taken over the past 15 years throughout the Western Ghats. Genera were assigned a habitat category based on whether the majority of its Western Ghats species use the habitat. If species from a genus were found in many kinds of habitats, habitat type of the majority of the species ('majority rule') or the habitat in which the species were most frequently seen ('abundance rule') was assigned to the genus. Genera were classified as 'GEN' or habitat generalists if many of their constituent species use a diverse range of habitats from moist forests to highly disturbed habitats associated with modern human settlements with similar abundance levels.

The complete list of genera of the Western Ghats butterflies along with their global distribution, centres of diversity, habitat and the number of species in the Western Ghats is given in Appendix 1.

Results

The 332 butterfly species reported from the Western Ghats belonged to 6 families and 164 genera. The breakdown of families by genera and number of species is given in Table 2. The breakdown of genera by their centres of diversity and habitats is given in Table 1. Of the 164 genera, 128 genera (78%) had their centres of diversity in the Oriental region and 33 genera (20%) in the African region, and 24 genera (15%) in the Australian region. Almost all of the genera with Australian centres of diversity only had a few species and shared the centres with the Oriental region. The Holarctic, Palaearctic proper and Eastern Palaearctic regions together contributed only 9 genera (5%), or 12 species (4%), to the Western Ghats. Note that these numbers exceed 164, the total number of Western Ghats genera, because some of those had more than one centre of diversity and have thus been counted more than once. Most of the genera (124 genera or 76%) were found in moist forests whereas few were found in any other habitats: dry habitats harboured only 19 genera (12%) and montane habitats harboured only 7 genera (4%) (Table 1). Given the small proportion of genera contributed by 'global' region and the small proportion of montane and generalist genera, they are excluded from further detailed analysis and are only briefly discussed later.

Table 2. Breakdown of families by number of genera and species of Western Ghats butterflies. Number of species in each genus is given in Appendix 1.

Family	No. of genera	No. of species
Papilionidae	4	19
Pieridae	14	34
Nymphalidae	45	97
Riodinidae	1	1
Lycaenidae	54	100
Hesperiidae	46	81
Total	164	332

A large number (57 or 35%) of the genera that had their centres of diversity in the Oriental Region were found exclusively in evergreen and semi-evergreen forests in the Western Ghats. Only two genera (*Anthene* and *Hypolycaena*, both family Lycaenidae, Table 3) with centres of diversity in the African region were found exclusively in the evergreen and semi-evergreen forests. Thus, the Oriental region has contributed significantly more number of genera to the Western Ghats butterfly fauna, and particularly to evergreen and semi-evergreen forests, compared to the African region ($\chi^2 = 51.2$, $df = 1$, $P < 0.0001$). When the genera occurring in all the moist forests were pooled, the contribution of the Oriental region was similarly prominent ($\chi^2 = 67.6$, $df = 1$, $P < 0.0001$). Thus, there is strong evidence supporting Holloway's impression that the moist forest butterfly fauna of the Western Ghats has been derived from the Oriental region (Table 1).

If we consider all dry habitats (deciduous forests, scrub, savannah and grassland), contrary to expectations from Holloway's discussion, there was no significant difference between the relative contributions of Oriental and African regions to the Western Ghats (20 and 17 genera, respectively; $\chi^2 = 0.243$, $df = 1$, $P = 0.622$). This was because, compared to African elements, the Oriental elements were strong even in the relatively moist dry habitats (deciduous forests) (3 versus 16 genera, respectively; $\chi^2 = 8.89$, $df = 1$, $P = 0.003$), further underlining the Oriental region's contribution to the Western Ghats butterfly fauna. It was only for the extreme dry habitats (scrub and savannahs) that the African region had contributed 12 genera, significantly more than the Oriental region's four

Table 3. The Oriental and African genera from deciduous forests and dry habitats, and the unusual African elements in the moist forests of the Western Ghats. Habitat abbreviations as in Table 2. The complete list of genera and their habitats is given in Appendix 1.

Elements of Oriental Region		Elements shared between Oriental and African Regions			Elements of African Region		
DEC	DRY/SCR	EVG and MOI	DEC	DRY/SCR	EVG and MOI	DEC	DRY/SCR
Hebomoia	*Castalius*	EVG:	*Caprona*	*Tarucus*	EVG:	*Deudorix*	*Belenois*
Caleta	*Taractrocera*	*Hypolycaena*	*Arnetta*[1]		*Anthene*		*Colotis*
Catochrysops	*Parnara*						*Byblia*
Surendra		MOI:			MOI:		*Azanus*
Catapaecilma		*Graphium*			*Charaxes*		*Euchrysops*
Zesius		*Neptis*					*Apharitis*
Tajuria		*Abisara*					*Sarangesa*
Rapala		*Chilades*					*Gomalia*
Curetis		*Celaenorrhinus*					*Spialia*[2]
Pseudocoladenia							*Gegenes*
Coladenia							*Borbo*
Odontoptilum							
Suastus							
Matapa							

[1]Shared between Oriental Region and Madagascar, not with mainland Africa.
[2]Shared between African and Palaearctic Regions.

genera ($\chi^2 = 4$, $df = 1$, $P = 0.046$). It should be further noted that one of the Oriental genera inhabiting dry habitats (*Tarucus*, family Lycaenidae) had a shared centre of diversity with Africa, and the use of dry habitats by the remaining three genera is probably a secondary adaptation. Thus, the data support Holloway's second impression that the African elements are restricted to dry habitats only if we consider the driest of habitats available in the Western Ghats. Most of these elements are more correctly Eremic (related to deserts or sandy region), not African. Moreover, the difference in African contribution to moist forests (8 genera) and to dry habitats (15 genera) of the Western Ghats was not statistically significant ($\chi^2 = 2.13$, $df = 1$, $P = 0.144$; Table 3).

Discussion

The results presented here, although restricted to the Western Ghats, not only confirm some of the broader patterns of biogeographic affinities of butterflies of entire India presented by Holloway (1969, 1974), but also add useful insights into the association between centres of diversity of genera and habitat use of the constituent species. Major findings of the present study are: (a) The butterfly fauna of the Western Ghats shows strong biogeographic affinities to the Oriental region, and most of the Oriental elements are restricted to moist forests within the Western Ghats, (b) Butterfly fauna of the driest habitats of the Western Ghats shows greater affinity to the African region than to any other biogeographic region; however, Oriental rather than African elements are more conspicuous in deciduous forests, and (c) A very small proportion of butterfly genera has its centres of diversity in Holarctic, Palaearctic and other regions, and these genera typically inhabit montane habitats or moist forests.

Holloway found 72 genera (59%) out of the 123 genera included in his analysis to be centred in the Oriental region (78% in my study), 16 genera (13%) in the Palaearctic region (5% in my study including the Holarctic and Eastern Palaerctic regions) and five genera (4%) centred in the African region (20% in my study). Thus, the proportion of Oriental and African genera was much higher in my study. On the other hand, the biogeographic affinities of the Western Ghats butterfly fauna with the Palaearctic region were weaker than those presented for entire India by Holloway. This was expected since most of the Palaearctic elements in India are restricted to the higher Himalayas. The few species of Palaearctic origin found in the Western Ghats are mostly restricted to higher elevations in the Nilgiri and Anamalai–Palni Hills and other mountains further south, some of which are endemic to those mountains.

The biogeographic affinities of various floral and faunal – particularly vertebrate – groups have been studied, but there has been confusion over whether the original faunal elements of peninsular India that evolved there still exist, and how much they have contributed to faunal compositions of neighbouring areas (Briggs 2003). According to Mani (1974):

> 'Most biologists have, however, failed completely to recognize the dominant place of the Peninsula in the biogeography of India, but have over-emphasized the place and importance of the Indo-Chinese subregion. We thus find that nearly all earlier workers have supposed the Peninsula to have been colonized entirely by genera and species, which were differentiated in Assam–Burma and areas farther east, completely ignoring the fact that the greatest bulk of the true Indian flora and fauna differentiated and evolved in the Peninsula, throughout the Palaeozoic, Mesozoic and Tertiary, right nearly up to the Pleistocene times, and spread extensively into the extra-Peninsular areas during the late Tertiary.'

Several speciose groups, mainly herpeto-faunal groups with high endemism in the Western Ghats, such as the uropeltid snakes and caecilians, are often cited as examples of such indigenous evolution in Peninsular India. It is true that, overall, fish, amphibian and reptilian faunas are diverse with high levels of endemism in the Western Ghats (Daniels 2001). For Mani's impression to be correct, however, we should find at least a few groups of different animals and plants that are diverse in the Indian peninsula but not in other areas. With the few exceptions just mentioned, we do not find such groups among other organisms. As for butterflies, Gaonkar (1996) has pointed out that the butterfly fauna of the Western Ghats has a scattering of endemics from various subfamilies and genera, but unique butterfly faunal elements are almost missing in the Western Ghats in particular, and peninsular India in general. Two genera should be discussed, though. The genus *Arnetta* (family Hesperiidae), with three species endemic to Madagascar (Lees *et al*. 2003), one species (*A. mercara*, the Coorg Forest Hopper) endemic to the Western Ghats (Gaonkar 1996), and one (*A. vindhiana*, the Vindhyan Bob) endemic to Peninsular India (Wynter-Blyth 1957), seems to be a relic of the Indian–Madagascan island that existed between 90 and 160 Ma. This genus has only one species in northeast India and parts of Indo-China, and another species in southeast Asia. Although systematic molecular studies are required to test the monophyly of this genus, the genus as it is currently classified appears to reflect the ancient relationship between peninsular India and Madagascar (David Lees, however, informs me that the Madagascan species of *Arnetta* themselves may be polyphyletic).

Another interesting, monotypic genus is *Parantirrhoea* (*P. marshallii*, the Travancore Evening Brown; family Nymphalidae), which is endemic to the southern Western Ghats. It represents the only genus that is endemic to Peninsular India and the Western Ghats: all other genera have centres of diversity in Oriental, African, Australian and other regions outside India with only a few species represented in the Western Ghats, with even fewer being endemic there. *Parantirrhoea* was named after the South American *Antirrhea* owing to their similar wing venation (Marshall and de Nicéville 1883), which is one of the taxonomically important traits. Its taxonomic affinities, however, are not resolved and biogeographically this should be a remarkable genus. Molecular studies on this genus will be important for future studies of biogeography of the Western Ghats butterflies. In any case, *Arnetta* and *Parantirrhoea*, as prominent exceptions, rather underline the fact that the butterfly fauna of the Western Ghats is mostly derived from other faunal regions and Mani's belief is not supported by data on butterflies. Moreover, it should be noted that: (1) the Western Ghats support relatively few butterfly species – an area of comparable size in southeast Asia or tropical Africa may have twice the number of species, and (2) there is extremely low endemism in the Wetsern Ghats, especially at higher taxonomic levels such as genera. These two facts suggest that the butterfly fauna of the Western Ghats was established fairly recently in comparison to the tectonic history of Indian peninsula, and may not have had enough time to evolve and extensively speciate there.

One notable result from the present analysis is that some of the genera that inhabit moist forests in the Western Ghats and are centred in southeast Asia as far as Borneo and the Philippines or in Sulawesi and New Guinea islands have endemic species in the Western Ghats. Genus *Discophora* and *Troides* are good cases in point. The Australian genera mentioned in Table 1 are mainly from Sulawesi, New Guinea and Irian Jaya. This area has traditionally been classified under the Australian region, although it may deserve a special status (Cox 2001) and it has extensively exchanged faunal groups with the Oriental region. Although the Indian plate was physically closer to Africa than to these deeper southeast Asian islands, the latter have contributed more to extant butterfly fauna than the former. This is probably because India has been well connected to southeast Asia in the recent past *via* almost contiguous evergreen forests. Whatever oceanic gaps faced were easily hopped over by the species with good dispersal ability. On the other hand, the oceanic gaps between India and tropical parts of Africa have been much wider, and more formidable, for over 50 million years. Also, the high, arid mountains to the west of India and the dry landmass in northern Africa have been desiccated and inhospitable for moist forest butterflies for many million years, cutting off that dispersal route. Thus, it is apparent that after the rise of the Western Ghats and other geological disturbances in Peninsular India, extinctions of the original moist forest butterfly fauna of the Indian plate have been widespread and the loss severe, and that the invasions by Oriental moist forest butterfly elements have been overwhelming.

Holloway's initial impression that Oriental butterflies occupy mostly evergreen forests in the Western Ghats is correct, and it is also true that more African genera occupy dry habitats than moist habitats. Given this general pattern, the few genera that do not follow this pattern demand a comment. Table 3 lists genera of Oriental centres of diversity that inhabit dry forests, genera that share centres of diversity between African and Oriental regions, and all African genera that inhabit moist forests and dry habitats. From the table it is immediately apparent that most of the deciduous forest genera from the Western Ghats are exclusively centred in the Oriental region, and those from the dry habitats are exclusively centred in the African region, highlighting their relative contributions to the respective habitats. For example, the genus *Colotis* (family Pieridae) has about 40 African species but less than 5 species that barely penetrate the Oriental region in northern India, most of which are shared with the African region. Similarly, *Borbo* and *Gegenes* (family Hesperiidae) are almost exclusively African genera with a minority of Oriental species. This pattern contrasts markedly with those genera that have African centres of diversity and that inhabit moist forests in the Western Ghats. Six of these eight African genera have two centres of diversity, the other being in the Oriental region. For example, *Graphium* (family Papilionidae) has about 50 Indo-Australian and 25 African species (the African species are classified under subgenus *Arisbe*), and *Neptis* (family Nymphalidae), *Abisara* (family Riodinidae) and *Hypolycaena* (family Lycaenidae) have comparable numbers of species in the African and Oriental Regions. This pattern shows the genera to be at least 30 million years old, dating back to the Oligocene, when evergreen forests ranged from the tropics all the way up to the present-day United Kingdom and Japan. Thus, the genera were widespread and speciated in both the regions extensively, which explains their current dual centres of diversity.

Against this backdrop, two genera – *Anthene* (family Lycaenidae) and *Charaxes* (family Nymphalidae) – inhabiting evergreen and semi-evergreen forests in the Western Ghats deserve special mention. The genus *Anthene* has close to 90 African and less than 10 Indo-Australian species, 2 of which are found in the Western Ghats, and *Charaxes* has over 110 African and close to 10 Oriental species, with 2 Western Ghats representatives. Are these genera the only surviving relicts of the African elements that were carried on the Indian plate after detachment with Africa? Or are these more recent immigrants from Africa into peninsular India with secondary dispersal and further speciation in the Oriental region? Available evidence seems to favour the second possibility. First, if the Western Ghats species represented very old lineages, they should be distinct from the extant African species due to their separation for 50 to 80 million years. Second, we expect these genera to be much more speciose than their current diversity levels in the Oriental region if they had speciated there for 50 Ma. Both these expectations are not met. The peninsular Indian and Oriental species are not sufficiently differentiated from the African species, indicating relatively recent colonization from Africa (perhaps not older than 15–20 Ma), and species-level endemism of these genera in the Oriental region is very low, further supporting the idea of more recent colonization from Africa.

If the moist forest butterfly elements in the Western Ghats that have been derived from African genera are mostly recent invasions in the Indian/Oriental region, do the arid zone butterflies represent the original butterfly fauna of the Indian plate, as Holloway suggested? Even this, unfortunately, does not seem to be the case. Larsen (1984) has shown that most of the arid zone butterflies that occur in peninsular India/Western Ghats (e.g. *Colotis* (family Pieridae), *Byblia* (family Nymphalidae) and *Gomalia* (family Hesperiidae)) are largely African and they have presumably spread to India in the recent past, with no penetration in the Oriental Region east of Bangladesh. Other dry habitat genera such as *Gegenes, Spialia* (family Hesperiidae) and *Tarucus* (family Lycaenidae) are most likely of Eremic (Saharan and central Arabian) origin. These, too, seem to have spread to India relatively recently, certainly long after the initial collision of the Indian plate with the Eurasian plate (Larsen 1984).

Thus, there is no evidence of the original African/Indo-Madagascan elements of the ancient Indian plate in extant butterfly fauna of the Western Ghats. All the African and Eremic elements, which are few, are relatively recent immigrants into the Indian region as evidenced by the lack of unique biogeographic elements in India and by low levels of diversity and endemism. The conclusion of recent invasion into peninsular India holds true for the Oriental contribution as well. Although it is true that all the endemics of the Western Ghats belong to genera that have Oriental affinities, the overall endemism is still very low (Gaonkar 1996).

Appendix 1. List of genera of the Western Ghats butterflies with their global distribution, centre of diversity, habitat types and number of species in the Western Ghats.

	Scientific name	English name	Global distribution	Centre of diversity	Habitat*	No. of spp
	Family Papilionidae (total 19 spp)					
1	*Troides*	Birdwings	Oriental and Australian	Oriental	WOO	1
2	*Pachliopta*	Roses	Oriental, Australian and E. Palaearctic	Oriental	WOO	3
3	*Graphium*	Bluebottles/ Swordtails/Jays	Oriental, African, Australian and E. Palaearctic	African, Oriental and Australian	MOI	5
4	*Papilio*	Swallowtails	Global	Global	MOI	10
	Family Pieridae (total 34 spp.)					
5	*Catopsilia*	Emigrants	Oriental, African and Australian	Oriental, African and Australian	WOO	2
6	*Eurema*	Grass Yellows	Global	Global	WOO	6
7	*Colias*	Clouded Yellows	Global	Holarctic	MON	1
8	*Delias*	Jezebels	Oriental, Australian and Eastern Palaearctic	Australian	WOO	1
9	*Leptosia*	Psyche	Oriental, Afrotroical and Australian	African	WOO	1
10	*Prioneris*	Sawtooths	Oriental	Oriental	EVG	1
11	*Pieris*	Cabbage Whites	Global	Holarctic	MON	1
12	*Cepora*	Gulls	Oriental and Australian	Oriental	WOO	2
13	*Belenois*	Caper Whites	Oriental and African	African	DRY	1
14	*Appias*	Albatrosses and Puffins	Oriental, African, Australian and Neotropical	Oriental	EVG	6
15	*Colotis*	Salmon Arabs/ Little Orange-tips	Oriental and African	African	SCR	7
16	*Ixias*	Large Orange-tips	Oriental and Australian	Oriental	WOO	2
17	*Pareronia*	Wanderers	Oriental and Australian	Oriental	MOI	2
18	*Hebomoia*	Great Orange-tips	Oriental and Australian	Oriental and Australian	DEC	1
Family Nymphalidae (total 97 spp.)						
19	*Discophora*	Duffers	Oriental	Oriental	EVG	1
20	*Amathusia*	Palmkings	Oriental	Oriental	EVG	1
21	*Parantirrhoea*	Travancore Evening Brown	Oriental	Oriental	EVG	1

(*Contd*)

Appendix 1. (*Contd*)

	Scientific name	English name	Global distribution	Centre of diversity	Habitat*	No. of spp
22	*Melanitis*	Evening Brown	Oriental, Australian, African and Eastern Palaearctic	Oriental	MOI	3
23	*Elymnias*	Palmflies	Oriental and Australian	Oriental	MOI	1
24	*Lethe*	Treebrowns	Oriental and Eastern Palaearctic	Oriental and Eastern Palaearctic	MOI	3
25	*Mycalesis*	Bushbrowns	Oriental, Australian and Eastern Palaearctic	Oriental	EVG	11
26	*Orsotriaena*	Nigger	Oriental and Australian	Oriental and Australian	MOI	1
27	*Zipaetis*	Catseyes	Oriental	Oriental	EVG	1
28	*Ypthima*	Rings	Oriental, Australian, African and Palaearctic	Oriental and African	WOO	8
29	*Polyura*	Nawabs	Oriental, Australian and Eastern Palaearctic	Oriental	MOI	3
30	*Charaxes*	Rajahs	Oriental, Australian and African	African	MOI	2
31	*Acraea*	Costers	Oriental, African and Neotropical	African	GEN	1
32	*Cethosia*	Lacewings	Oriental and Australian	Oriental and Australian	EVG	1
33	*Vindula*	Cruisers	Oriental and Australian	Oriental and Australian	EVG	1
34	*Cupha*	Rustics	Oriental and Australian	Oriental and Australian	EVG	1
35	*Phalanta*	Leopards	Oriental, Australian and African	Oriental and African	WOO	2
36	*Cirrochroa*	Yeoman	Oriental and Australian	Oriental	MOI	1
37	*Argynnis*	Fritillaries	Oriental, Australian, African and Palaearctic	Palaearctic	MON	1
38	*Rohana*	Princes	Oriental	Oriental	MOI	1
39	*Euripus*	Courtesans	Oriental	Oriental	EVG	1
40	*Neptis*	Sailers	Oriental, Australian, African and Palaearctic Eastern Palaearctic	Oriental and African	MOI	7

(*Contd*)

Appendix 1. (*Contd*)

	Scientific name	English name	Global distribution	Centre of diversity	Habitat*	No. of spp
41	*Pantoporia*	Lascars	Oriental and Australian	Oriental	EVG	2
42	*Athyma*	Sergeants	Oriental and	Oriental	EVG	4
43	*Limenitis*	Commanders	Holarctic and Oriental	Holarctic	MOI	1
44	*Parthenos*	Clippers	Oriental and Australian	Oriental and Australian	EVG	1
45	*Tanaecia*	Counts	Oriental	Oriental	MOI	1
46	*Euthalia*	Barons	Oriental	Oriental	MOI	4
47	*Dophla*	Dukes	Oriental	Oriental	EVG	1
48	*Byblia*	Jokers	Oriental and African	African	SCR	1
49	*Ariadne*	Castors	Oriental, Australian and African	Oriental, Australian and African	WOO	2
50	*Cyrestis*	Maps	Oriental and Australian	Oriental	EVG	1
51	*Libythea*	Beaks	Oriental, African, Australian and Palaearctic	None	MOI	2
52	*Junonia*	Pansies	Global	African and Oriental	GEN	6
53	*Cynthia*	Painted Ladies	Global	None	GEN	1
54	*Vanessa*	Red Admirals	Global	Global	MON	1
55	*Kaniska*	Blue Admirals	Oriental and Eastern Palaearctic	Oriental and Eastern Palaearctic	EVG	1
56	*Hypolimnas*	Eggflies	Oriental, African and Australian	African and Australian	WOO	2
57	*Doleschallia*	Autumnleaf	Oriental and Australian	Australian	EVG	1
58	*Kallima*	Oakleafs	Oriental	Oriental	MOI	2
59	*Parantica*	Glassy Tigers	Oriental, Australian and Eastern Palaearctic	Oriental	WOO	2
60	*Tirumala*	Blue Tigers	Oriental, Australian, African and Eastern Palaearctic	Oriental	WOO	2
61	*Danaus*	Tawny Tigers	Global	Global	GEN	2
62	*Euploea*	Crows	Oriental and Australian	Oriental and Australian	MOI	3
63	*Idea*	Tree Nymphs	Oriental and Australian	Oriental	EVG	1
Family Riodinidae (total 1 sp.)						
64	*Abisara*	Judies	Oriental, Australian and African	Oriental and African	MOI	1

(*Contd*)

Appendix 1. (*Contd*)

	Scientific name	English name	Global distribution	Centre of diversity	Habitat*	No. of spp
Family Lycaenidae (total 100 spp)						
65	*Spalgis*	Apeflies	Oriental, Australian and African	African	GEN	1
66	*Logania*	Mottles	Oriental and Australian	Oriental and Australian	EVG	1
67	*Castalius*	Pierrots	Oriental	Oriental	DRY	1
68	*Caleta*	Pierrots	Oriental	Oriental	DEC	1
69	*Discolampa*	Blue Pierrots	Oriental	Oriental	MOI	1
70	*Tarucus*	Pierrots	Oriental, Australian, African and Palaearctic	African and Oriental	DRY	6
71	*Azanus*	Babul Blues	Oriental and African	African	DRY	3
72	*Everes*	Cupids	Oriental, Australian and Holarctic	Holarctic	MOI	1
73	*Udara*	Hedge Blues	Oriental and Australian	Oriental and Australian	EVG	2
74	*Acytolepis*	Hedge Blues	Oriental	Oriental	MOI	2
75	*Celatoxia*	Hedge Blues	Oriental	Oriental	EVG	1
76	*Celastrina*	Hedge Blues	Oriental, Australian and Holarctic	Holarctic	MOI	1
77	*Neopithecops*	Quakers	Oriental and Australian	Oriental and Australian	EVG	1
78	*Megisba*	Malayans	Oriental and Australian	Oriental and Australian	MOI	1
79	*Pseudozizeeria*	Grass Blues	Oriental and Eastern Palaearctic	None	SCR	1
80	*Zizeeria*	Grass Blues	Oriental, Australian and African	None	SCR	2
81	*Zizina*	Grass Blues	Oriental, Australian and African	None	SCR	1
82	*Zizula*	Grass Blues	Oriental, Australian, African and Neotropical	None	SCR	1
83	*Chilades*	Lime Blue	Oriental, Australian, African and Palaearctic	Oriental and African	MOI	3
84	*Euchrysops*	Gram Blues	Oriental, Australian and African	African	DRY	1
85	*Catochrysops*	Forget-me-nots	Oriental and Australian	Oriental and Australian	DEC	2
86	*Lampides*	Pea Blue	Oriental, Australian, African and Palaearctic	None	DRY	1

(*Contd*)

Appendix 1. (*Contd*)

	Scientific name	English name	Global distribution	Centre of diversity	Habitat*	No. of spp
87	*Jamides*	Ceruleans	Oriental and Australian	Oriental	MOI	3
88	*Nacaduba*	Lineblues	Oriental and Australian	Oriental	MOI	6
89	*Ionolyce*	Lineblues	Oriental and Australian	Oriental and Australian	EVG	1
90	*Prosotas*	Lineblues	Oriental and Australian	Oriental	MOI	3
91	*Petrelaea*	Lineblues	Oriental and Australian	Oriental and Australian	MOI	1
92	*Talicada*	Red Pierrot	Oriental	Oriental	GEN	1
93	*Anthene*	Ciliate Blues	Oriental, Australian and African	African	EVG	2
94	*Arhopala*	Oakblues	Oriental, Australian and Eastern Palaearctic	Oriental	EVG	6
95	*Thaduka*	Oakblues	Oriental	Oriental	EVG	1
96	*Surendra*	Acacia Blues	Oriental	Oriental	DEC	1
97	*Zinaspa*	Acacia Blues	Oriental and Eastern Palaearctic	Oriental and Eastern Palaearctic	MOI	1
98	*Iraota*	Silverstreak Blue	Oriental, Australian and Eastern Palaearctic	Oriental	EVG	1
99	*Amblypodia*	Leaf Blues	Oriental	Oriental	EVG	1
100	*Spindasis*	Silverlines	Oriental and African	Oriental and African	WOO	6
101	*Apharitis*	Silverlines	Oriental, African and Palaearctic	African	SCR	2
102	*Catapaecilma*	Tinsels	Oriental	Oriental	DEC	1
103	*Loxura*	Yamfly	Oriental	Oriental	MOI	1
104	*Cheritra*	Imperials	Oriental	Oriental	EVG	1
105	*Rathinda*	Monkey Puzzles	Oriental	Oriental	EVG	1
106	*Horaga*	Onyxes	Oriental	Oriental	EVG	2
107	*Zesius*	Redspot	Oriental	Oriental	DEC	1
108	*Ancema*	Royals	Oriental	Oriental	EVG	1
109	*Creon*	Royals	Oriental	Oriental	EVG	1
110	*Pratapa*	Royals	Oriental	Oriental	EVG	1
111	*Tajuria*	Royals	Oriental	Oriental	DEC	4
112	*Rachana*	Royals	Oriental	Oriental	EVG	1
113	*Hypolycaena*	Tits	Oriental, Australian and African	Oriental and African	EVG	2
114	*Zeltus*	Fluffy Tits	Oriental	Oriental	EVG	1
115	*Deudorix*	Guava Blues/ Cornelians	Oriental, Australian and African	African	DEC	3

(*Contd*)

Appendix 1. (*Contd*)

	Scientific name	English name	Global distribution	Centre of diversity	Habitat*	No. of spp
116	*Bindahara*	Planes	Oriental and Australian	Oriental and Australian	EVG	1
117	*Rapala*	Flashes	Oriental, Australian and Eastern Palaearctic	Oriental	DEC	4
118	*Curetis*	Sunbeams	Oriental	Oriental	DEC	3
Family Hesperiidae (total 81 spp.)						
119	*Burara*	Awlets	Oriental and Eastern Palaearctic	Oriental	EVG	2
120	*Bibasis*	Orangetail Awl	Oriental and Eastern Palaearctic	Oriental	MOI	1
121	*Hasora*	Awls	Oriental and Australian	Oriental	MOI	4
122	*Badamia*	Awls	Oriental and Australian	Oriental and Australian	MOI	1
123	*Choaspes*	Awlkings	Oriental	Oriental	EVG	1
124	*Celaenorrhinus*	Spotted Flats	Oriental and African	Oriental and African	MOI	3
125	*Tagiades*	Snow Flats	Oriental, Australian and African	Oriental	EVG	3
126	*Gerosis*	Yellow Breasted Flats	Oriental	Oriental	EVG	1
127	*Psuedocoladenia*	Pied Flats	Oriental	Oriental	DEC	1
128	*Coladenia*	Pied Flats	Oriental	Oriental	DEC	1
129	*Sarangesa*	Small Flats	Oriental and African	African	SCR	2
130	*Tapena*	Angles	Oriental	Oriental	EVG	1
131	*Odontoptilum*	Angles	Oriental	Oriental	DEC	1
132	*Caprona*	Angles	Oriental and African	Oriental and African	DEC	3
133	*Gomalia*	Marbled Skipper	Oriental and African	African	SCR	1
134	*Spialia*	Skippers	Oriental, African and Palaearctic	African and Palaearctic	SCR	1
135	*Aeromachus*	Grass/Scrub Hoppers	Oriental and Eastern Palaearctic	Oriental	WOO	2
136	*Ampittia*	Bush Hoppers	Oriental, African and Eastern Palaearctic	Oriental	GEN	1
137	*Halpe*	Aces	Oriental	Oriental	EVG	2
138	*Sovia*	Aces	Oriental	Oriental	EVG	1
139	*Thoressa*	Aces	Oriental	Oriental	EVG	4
140	*Iambrix*	Bobs	Oriental	Oriental	EVG	1
141	*Psolos*	Coons	Oriental	Oriental	EVG	1

(*Contd*)

Appendix 1. (*Contd*)

	Scientific name	English name	Global distribution	Centre of diversity	Habitat*	No. of spp
142	*Notocrypta*	Banded Demons	Oriental and Australian	Oriental	EVG	2
143	*Salanoemia*	Lancers	Oriental	Oriental	EVG	1
144	*Udaspes*	Demons	Oriental	Oriental	MOI	1
145	*Arnetta*	Forest Hoppers/ Bobs	Oriental and African	Oriental and African	DEC	2
146	*Suastus*	Palm Bobs	Oriental	Oriental	DEC	2
147	*Cupitha*	Wax Dart	Oriental	Oriental	MOI	1
148	*Baracus*	Hedge-hoppers	Oriental	Oriental	EVG	1
149	*Hyarotis*	Brush Flitters	Oriental	Oriental	EVG	2
150	*Quedara*	Flitters	Oriental	Oriental	EVG	1
151	*Gangara*	Redeyes	Oriental	Oriental	EVG	1
152	*Erionota*	Redeyes	Oriental	Oriental	EVG	1
153	*Matapa*	Redeyes	Oriental	Oriental	DEC	1
154	*Taractrocera*	Grass Darts	Oriental and Australian	Oriental and Australian	SCR	2
155	*Oriens*	Dartlets	Oriental and Australian	Oriental	EVG	2
156	*Potanthus*	Darts	Oriental and Eastern Palaearctic	Oriental	EVG	5
157	*Telicota*	Palm Darts	Oriental and Australian	Oriental and Australian	MOI	2
158	*Parnara*	Swifts	Oriental, African and Eastern Palaearctic	Oriental	SCR	1
159	*Gegenes*	Swifts	Oriental, African and Holarctic	African	SCR	1
160	*Borbo*	Swifts	Oriental, Australian and African	African	SCR	2
161	*Pelopidas*	Swifts	Oriental, Australian and African	Oriental	EVG	6
162	*Polytremis*	Swifts	Oriental and Eastern Palaearctic	Oriental	MOI	1
163	*Baoris*	Swifts	Oriental	Oriental	MOI	1
164	*Caltoris*	Swifts	Oriental	Oriental	MOI	3

*Habitat types:
EVG: low and mid-elevation evergreen and semi-evergreen forests.
MOI: moist forests including evergreen, semi-evergreen and dense riparian moist deciduous forests.
DEC: moist and mixed deciduous forests.
WOO: woodland generalists.
SCR: scrub and savannahs, including grasslands maintained by slight human disturbances.
DRY: dry deciduous forests, scrub, savannah and grasslands.
MON: montane habitats (above 1800 m) including shola forests and montane grasslands.

From these results and discussion it appears that the traditional framework of plate tectonics may not be useful in explaining presence of the few African and Eremic elements in the butterfly fauna of the Western Ghats. Instead, this could be explained by dispersal of the dry habitat species by land *via* the Eremic region and the Middle East, and of the two moist forest genera by island-hopping model (e.g. Holloway 1974; Larsen 1984).

Further analysis of the biogeography, diversity and endemism of butterfly fauna of the Western Ghats will benefit greatly from the use of molecular data and comparative methods. In recent years the use of molecular data, phylogenetic methods and molecular dating have provided important insights into several biological problems such as the evolutionary origins of various butterfly groups, the spread of taxa and subsequent speciation in relation to major geological events, and better understanding of phylogenetic relationships between major groups of butterflies (Zakharov *et al*. 2004; Wahlberg *et al*. 2005; Wahlberg 2006). These can also be used to test several hypotheses, for example, regarding the timing of arrival of forest-dwelling African and Oriental elements in India, and their subsequent speciation. In the present analysis it was not possible to use a phylogenetically constrained analytical framework to answer the questions discussed since phylogenetic positions of most Indian butterfly genera and species are currently unknown. The rapidly advancing techniques and reduced costs of molecular analysis will remedy this problem in the near future. Several research labs are currently studying phylogenetics of Indian butterflies. The data generated from these studies will enable us to answer in greater detail questions regarding biogeography and phylogeography of the Western Ghats butterflies.

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