

Endemic fishes of the Western Ghats and the Satpura hypothesis

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Starting late in the 19th century till the first half of the 20th century, biogeographers in India were attempting to explain the apparent discontinuity in the ranges of certain plants and animals. The isolated presence of flora and fauna of Malayan origin in the Western Ghats and other south Indian hills led to a lot of speculation on the prehistory of peninsular India. At this time, Sunder Lal Hora, an ichthyologist, proposed the Satpura hypothesis, which over the years has remained unquestioned though not adequately substantiated. Recent advances in systematics and ecology of freshwater fishes and better understanding of peninsular India's geological history have rendered the Satpura Hypothesis untenable.

In a series of papers published between 1937 and 1953, Sunder Lal Hora made an attempt to explain what he considered an 'anomalous' distribution of hill-stream fishes in peninsular India¹⁻⁴. The anomaly was that many species of stream fishes in the hills of peninsular India, especially the Western Ghats, had populations of their kind or of congeneric species, only in the Eastern Himalayas, often extending further east through South-east Asia. He proposed that these fishes migrated from the Assam (Garo) Hills via the Satpura (Rajmahal) Hills and descended into the Western Ghats through Gujarat. The theory proposed by Hora came to be the well-known 'Satpura hypothesis'⁴. The apparent Malayan affinity in the flora and fauna of the Western Ghats had not only intrigued Hora but many other biogeographers, that the Satpura hypothesis soon found wide acceptance^{3,5}.

Hora primarily based his hypothesis on fishes inhabiting torrential hill-streams, as they are bound to have restricted geographical distribution. Their geographical range and ecology are affected by their specialized mouth modifications – sucking discs that enable them to cling to rock surfaces in torrential waters and at the same time limiting their feeding niche and their reduced respiratory organs being inhabitants of oxygen-rich waters. Considering these ecological limitations, Hora opined that hill-stream fishes could not have dispersed through 'normal' water channels, but only through corridors of hill-streams¹.

Hora first studied the patterns of fish distribution in the streams of the Himalayas. He arrived at two broad conclusions. First, the hill-stream fish fauna of the northern face of the Himalayas is strikingly different from that on the

southern face. Second, while species of *Labeo* and *Barbus* (larger barbs now placed under a few different genera, viz. *Barbodes*, *Hypselobarbus*, etc. see Table 1)⁶ that inhabit rather slow-flowing deeper streams, have spread westwards over the Himalayas till about the Siwaliks and Punjab, torrent stream fishes such as *Balitora*, *Silurus* and *Parapsilorhynchus* have not. They however occur in the Western Ghats¹.

Hora suggested that soon after India joined mainland Eurasia (some 45 m.y. BP) in the Eocene (56–35 my BP)⁷, the westward migration of Malayan freshwater fauna began. Dispersal of hill-stream and torrent fishes was enabled by (a) river capture, (b) longitudinal river valleys, and (c) tilting of mountain blocks. Such processes, according to him, may change the course of streams without altering torrential flow¹. Hora then went on to dwell upon the possibility of the prehistoric Indo-Brahm that had its headwaters in Assam, flowing west to Punjab, taking with it the Malayan fish fauna to the Western Himalayas. Large Malayan stream fishes, including *Wallago*, *Silonia*, *Cirrhinus*, etc. have thus entered India during the Eocene¹.

The westward migration of Malayan fish that began in the Eocene, went on through the Miocene (23–5 m.y. BP)⁷. Westward migration of Malayan stream fishes is assumed to have been interfered with in the late Miocene (c. 15–10 m.y. BP) by the Nepal Himalayas. The path of migration was thus deflected southwards over the Satpuras, enabling the hill-stream fishes to eventually reach the Western Ghats^{1,3}. Elsewhere, Hora has also drawn attention to the Garo-Rajmahal Gap, through which the rivers Ganges and Brahmaputra drain. Hora has shown that

the gap was non-existent till in the late Miocene and hence had directly served as a bridge in the movement of Malayan hill-stream fishes through Assam, over the Satpuras and finally down the Western Ghats^{2,4}.

Even as Hora was gathering all possible evidence in support of the Satpura hypothesis, alternate views on the migration of South-east Asian flora and fauna into peninsular India and the Western Ghats had been proposed. The oldest of these suggested a direct land connection between the South-east Asian and south Indian hills². Whereas Hora has called this 'untenable'², I shall discuss the plausibility of this hypothesis later in the paper.

As early as 1879, Medlicott and Blanford (as cited by Hora²) have commented on the occurrence of temperate flora and fauna on several isolated hilltops in southern India (Eastern and Western Ghats) and Sri Lanka. They have specifically cited the cases of endemic hill-mammals in the Western Ghats such as the Nilgiri Tahr (*Hemitragus hylocrius*) and Nilgiri Marten (*Martes gwatkinsi*), which have congeneric species only in the Himalayas⁸. Medlicott and Blanford have further drawn attention to the Himalayan flora shared by Mt Abu in the Aravalli Range in western India. The Medlicott–Blanford theory suggests that there had been a long history of migration of flora and fauna from South-east Asia into peninsular India, taking advantage of both periods of high humidity and lower temperature.

Hora has in fact acknowledged that the Medlicott–Blanford theory may hold true in case of terrestrial fauna such as birds, mammals and insects. He however maintained that the distribution of aquatic fauna

is governed by other equally important factors².

In his 1953 publication entitled 'The Satpura Hypothesis'⁴, Hora has reiterated that the hypothesis was given a positive

shape by the materials derived from three zoological disciplines – taxonomy, ecology and distribution. In what follows, I wish to discuss how recent advancements in research in taxonomy, ecology and

distribution of India's biological diversity have yielded results that lend little support to the Satpura hypothesis.

During the past half century, fish systematics has undergone considerable

Table 1. Diversity and biogeographical affinity of fishes endemic to the Western Ghats⁶

Genera	No. of freshwater species in India	Geographical distribution		
		Species endemic to Western Ghats	Western Ghats + Indian sub-continent	Western Ghats + eastern Himalayas + SE Asia
Danios, barbs, carps and loaches				
<i>Barilius</i>	15	4	1	0
<i>Salmostoma</i>	10	4	1	0
<i>Chela</i>	4	2	2	1
<i>Danio</i>	12	2	3	1
<i>Esomus</i>	4	1	1	0
<i>Parluciosoma</i>	2	1	1	0
<i>Neolissochilus</i>	2	1	0	0
<i>Tor</i>	5	1	1	0
<i>Osteobrama</i>	5	1	1	0
<i>Barbodes</i>	2	2	1	1
<i>Hypselobarbus</i>	11	10	1	0
<i>Echathalakenda*</i>	1	1	0	0
<i>Puntius</i>	30	11	11	1
<i>Cyprinion**</i>	5	3	0	0
<i>Cirrhinus</i>	5	2	0	0
<i>Labeo</i>	17	5	8	1
<i>Schismatorhynchus**</i>	1	1	0	0
<i>Crossocheilus***</i>	2	1	1	0
<i>Garra***</i>	13	5	2	0
<i>Horallabiosa*</i>	2	2	0	0
<i>Parapsilorhynchus**</i>	2	2	1	0
<i>Botia</i>	7	1	0	0
<i>Pangio</i>	3	1	0	0
<i>Noemacheilus***</i>	47	12	3	0
<i>Homaloptera**</i>	2	2	0	0
<i>Balitora**</i>	2	1	0	0
<i>Bhavana*</i>	1	1	0	0
<i>Travancoria*</i>	2	2	0	0
Catfishes				
<i>Mystus</i>	13	4	5	3
<i>Batasio</i>	3	1	0	0
<i>Pseudobagrus*</i>	2	2	0	0
<i>Ompok</i>	4	1	1	1
<i>Silurus</i>	3	1	0	0
<i>Pseudeutropius</i>	1	1	0	0
<i>Silonia</i>	2	1	0	0
<i>Gagata***</i>	6	1	0	0
<i>Glyptothorax***</i>	21	5	0	0
<i>Clarias</i>	2	1	1	1
<i>Horaglanis*</i>	1	1	0	0
Others				
<i>Horaichthys*</i>	1	1	0	0
<i>Aplocheilus</i>	4	2	0	0
<i>Monopterus</i>	6	3	0	0
<i>Parambassis*</i>	2	2	0	0
<i>Pristolepis</i>	2	1	0	0
<i>Etroplus</i>	3	1	2	0
<i>Pseudosphromenus</i>	2	1	1	0
<i>Macrognaathus</i>	3	1	1	0
<i>Tetraodon</i>	2	1	0	0
Total 48	298	114	52	11

*Genera endemic to the Western Ghats; **Genera of torrential stream fishes with discontinuous distribution of species that illustrate Hora's 'Satpura hypothesis'⁴; ***Genera of fishes typically inhabiting the streams of the southern face of the Himalayas¹ – *Noemacheilus*, *Garra*, *Glyptothorax* and *Balitora* inhabit torrential streams.

changes worldwide and Indian fishes, especially the freshwater species, have not been spared in this regard. Recent taxonomic revisions in Indian freshwater fishes may be seen in the comprehensive accounts as that of Menon⁶ and Jayaram⁹. Of these accounts, I have for this discussion, chosen that of Menon⁶ for two reasons. First, Menon lists only those species existing within the political limits of India and excludes all estuarine and brackish water-forms. Second, Menon was part of the team led by Hora that undertook field surveys to substantiate the Satpura hypothesis⁴.

I have discussed elsewhere how taxonomic uncertainties can affect studies of conservation¹⁰. Here, I wish to highlight how taxonomic revisions can challenge prevailing biogeographical theories, specifically the Satpura hypothesis (Table 2).

Table 2 suggests that taxonomic revisions have rendered an apparent biogeographic pattern non-existent. Further, Hora² had used the occurrence of *Laguvia*, a genus of torrent catfishes, in the Satpuras and Rajmahal Hills to illustrate his hypothesis. *Laguvia* has since been synonymized with *Glyptothorax*, a genus of hill-stream catfishes⁶. The genus *Glyptothorax* has 21 species within Indian limits, of which the 5 species known from the Western Ghats are endemic (Table 1).

Taxonomic revisions have left just one catfish, *Amblyceps mangois*, known from the Rajmahal Hills, Krishna river system in peninsular India and through eastern Himalayas till Thailand⁶, to substantiate the Satpura hypothesis¹². The two other peninsular species considered 'isolates' of Malayan fish fauna, viz. *Thynnichthys sandkhol* and *Schismatorhynchus nukta*^{1,2,4}

are not strictly species of the Western Ghats. They occur in the east in rivers and associated aquatic systems in the Deccan Plateau, more commonly in the east-flowing river Krishna⁶.

Ecology of freshwater fish communities in India is just beginning to get scientific attention. Very little is known of the autecology of most of the nearly 450 species of fishes treated as freshwater fishes by Menon⁶. Hill-stream fishes are indeed sensitive to certain environmental factors such as the levels of dissolved oxygen, temperature and speed of flow of water. Hence Hora's¹ apprehension about their ability to disperse through normal means, may be partly justified.

Fishes normally disperse through a number of means, particularly taking advantage of rain and floods. Although torrential stream fishes are more specialized in habits, they do survive in slow-moving and stagnant waters, especially when young, as personal experience has shown. For more than thirty years I have collected hill-stream fishes from the Western Ghats and to a lesser extent from Eastern Ghats and Himalayas and transported them alive to my aquarium. For instance, juvenile *Barilius bendelisis* collected from the periphery of Rajaji National Park (Siwaliks), withstood a 72-h train journey within a tin can during summer and survived in my aquarium in Bangalore and later travelled with me to Chennai to live a full two years and become adults. More recently, *Bhavana australis* a typical torrent fish in the Western Ghats, collected from a small stream near the Kudremukh National Park (Karnataka), survived a 24-h train journey to Chennai in half a litre of water inside a 'Bisleri' bottle! I can provide

several examples of this sort involving species of *Garra*, *Noemacheilus* and others. After all, the aquarium trade has in its list a fairly good number of hill-stream loaches and torrent catfishes, both from India and other parts of the world. They have all adapted to stagnant, less oxygenated and sometimes hard water (as that in Chennai), bred in captivity and survived long years. Hora's contention that hill-stream and torrent fishes cannot disperse through normal means is therefore not entirely correct. Irrespective of the Satpuras, over the 12–15 m.y. since Malayan hill-stream fishes began migrating into peninsular India³, melting glaciers, storm waters, etc. could have all aided their dispersal.

Hora completely ignored fishes that are not strictly inhabitants of torrents, and yet have migrated from the Malayan Archipelago and largely evolved in the Western Ghats. Forty-eight genera of freshwater fishes have got at least one species endemic in the Western Ghats (Table 1). Fishes in the genera *Labeo*, *Puntius*, *Myristus*, *Pristolepis*, *Monopterus*, *Pseudosphromenus*, etc. do show Malayan affinity. These are however, not typically torrential stream fishes. They could have reached the Western Ghats through 'normal' means.

Ecologically speaking, it is not only the fauna of torrential streams (including species of amphibians such as *Ansonia* and *Pedostibes*) that has migrated onto the Western Ghats from the Malayan Archipelago. Cold-adapted flora and fauna have also colonized these distant southwestern hills. Examples of plants and mammals have been discussed in the Medicott–Blanford theory. I have elsewhere discussed how cold-adapted birds might have reached the hilltops of the Western Ghats¹¹. Such ecological considerations further narrow the scope of the Satpura hypothesis.

Distribution and ecology of biodiversity in peninsular India, especially in the Western Ghats, during prehistoric times are poorly understood mainly due to the lack of fossil evidence¹¹. Nevertheless, thanks to the considerable advances in the science of geology, we now know fairly well the origin and history of both hills and rivers in peninsular India^{12,13}. Starting somewhere in the Cretaceous (150–65 m.y. BP)⁷, there have been volcanic influences leading to uplifts and trap formation over the entire peninsular India. The Western Ghats were uplifted

Table 2. Species of fishes considered by Hora² as shared by Western Ghats and the Malayan Archipelago with their present taxonomic status and geographic distribution as provided by Menon⁶

Sunder Lal Hora	A. G. K. Menon
<i>Pristolepis fasciatus</i>	Occurrence in Western Ghats doubtful
<i>Clarias dussumieri</i>	Endemic to Kerala
<i>Ophiocephalus micropeltes</i>	<i>Channa striatus</i> – widespread in the Indian region, including Pakistan and Sri Lanka
<i>Ambassis thomassi</i>	<i>Parambassis thomassi</i> – endemic to southern Western Ghats
<i>Macropodus cupanus</i>	<i>Pseudosphromenus cupanus</i> – peninsular India and Sri Lanka
<i>Barbus burmanicus</i>	Not listed
<i>Mastacembelus guentheri</i>	<i>Macrogathus malabaricus</i> – endemic to Kerala
<i>Rohtee cotio</i>	<i>Osteobrama cotio</i> – peninsular India, east till Myanmar

Table 3. Endemic vertebrates of the Western Ghats

Class	No. of species	No. endemic	Per cent endemism
Fishes	218	114	52
Amphibians	118	91	77
Reptiles	157	97	62
Birds (resident)	324	19	6
Mammals	120	14	12
Total	937	335	36

Source: Refs 6, 14–17, 19, 20.

during the later half of the Eocene (c. 50 m.y. BP) and the peninsular rivers started flowing east, even before India collided with mainland Asia. It was only during the Pliocene (5–1.6 m.y. BP)⁷ that the Western Ghats came to be known more or less as they are today. Soon after this, during the Pleistocene (c. 1.5 m.y. BP)⁷, river capture, waterfalls and deep gorges gave rise to the present structure of watersheds in the Western Ghats¹³.

The early view that there was a direct land connection between the South-east Asian and south Indian hills, is not entirely untenable. According to Radhakrishna¹², before the uplift of the Western Ghats, there came into being the 67–68 m.y.-old Deccan Traps and the 115–117 m.y.-old Rajmahal Traps in peninsular India¹². These uplifted surfaces together with the Western Ghats and the Deccan Plateau were topographically ideal for a wide network of torrents, streams and rivers in peninsular India, providing conducive conditions for westward and southwestward migration of Malayan fishes. The still young and diversifying carps and catfishes² found extensive habitats, as they were amongst the earliest colonizers invading peninsular India during the Eocene. The torrent fishes, as are found in the Western Ghats today, appeared much later². They are however, more probable products of *in situ* evolution (e.g. *Bhavana*, *Travancoria*, *Parapsilorhynchus*, *Horalabiosa*; see Table 1). Moreover, there is no reason why early ancestors of the torrent species could not have ascended the Western Ghats through the rivers Krishna and Godavari, as evident by their present patterns of distribution⁶.

Nine-hundred and thirty-seven species of vertebrates are resident in the Western Ghats. Of these, 335 (36%) are endemic (Table 3). Highest endemism is in amphi-

bians (77%), followed by reptiles (62%) and fishes (52%). A highly diverse family of snakes, viz. Uropeltidae (33 species in the Western Ghats) is endemic to the Western Ghats and Sri Lanka¹⁴. *Nyctibatrachus* (11 species) and *Micrixalus* (7 species), both genera of torrent amphibians, are endemic to the Western Ghats¹⁵. The 114 species of endemic fishes belong to 48 genera (an average of 2.4 species per genus; Table 1). Similarly, 36 genera of reptiles are represented by the 97 endemic species (c. 2.7 species per genus¹⁶). In amphibians, however, the number of genera is only 18 (ref. 17). The average number of endemic species per genus is 5.0.

Fishes and reptiles that are endemic to the Western Ghats are diverse at the generic level, suggesting multiple lineage of evolution. However, unlike in the amphibians, the average number of species per genus is lower. Exceptionally, amongst fishes and reptiles the genera *Hypselobarbus* (fish) and *Uropeltis* (snake) have diversified the most in the Western Ghats. These two genera have no congeneric species in South-east Asia. In amphibians, the genus *Philautus* that has diversified the most (18 endemic species^{15,17}) has congeneric species distributed throughout South-east Asia. Such patterns of vertebrate diversification in the Western Ghats suggest the following:

- Birds and mammals being warm-blooded and more mobile, have not been isolated long enough in the Western Ghats to evolve independently. The cold-blooded and less mobile fishes, amphibians and reptiles have, on the other hand, diversified in isolation.
- Whereas amphibians have diversified much more in isolation from a fewer genera (thereby fewer ecological groups), in fishes and reptiles endemic

species have appeared across a diverse range of ecological groups. It is possible that the bimodal life-history of amphibians limits their niche diversification compared to fishes and reptiles.

- Amphibians and reptiles with specialized ecological traits such as burrowing (*Uropeltis*), direct development (*Philautus*) and parental care (*Philautus* and *Nyctibatrachus*) have diversified much more in the Western Ghats than fishes with specialized traits as the torrential stream fishes. Torrential fishes, as suggested by Hora⁴, appeared in the Western Ghats during the Pleistocene (the ice age) less than 2 m.y. ago and coincident with the creation of torrents and waterfalls in the Western Ghats¹³.
- For every species of fish endemic to the Western Ghats, there is a less than 10% chance that a congeneric species exists in the Eastern Himalayas and South-east Asia. However, the chance that there is a congeneric species elsewhere in peninsular India and throughout the Indian subcontinent (including Pakistan, Nepal and Sri Lanka) is over 45% (Table 1).

The above patterns in the distribution of endemic vertebrates in general and fishes in particular, do not readily substantiate the Satpura hypothesis. Peninsular India has had a long history of human influence too. Since the time that modern humans emerged, there has been a variety of ecological changes that locally shaped the structure and organization of plant and animal communities. Hunter-gatherers of the Palaeolithic age, dating back to 12,000 y BP had started modifying the ecosystem of the Western Ghats, especially along rivers in Goa and Karnataka¹⁸. Human-induced local extinctions and human-aided local colonization of flora and fauna certainly began around this time.

As hunter-gatherers, humans started modifying aquatic ecosystems much before they burnt down forests. Settled agriculture created corridors through canals, enabling fishes to seek fresh habitats. By the time Hora began his surveys, aquatic ecosystems throughout India had been modified by humans. The absence of torrent stream fishes in the hills of Orissa and the Eastern Ghats⁴, may well be a recent phenomenon.

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