Zoosymposia 24: 057–069 (2023)
https://www.mapress.com/j/zs

Article

ISSN 1178-9905 (print edition)
ZOOSYMPOSIA
ISSN 1178-9913 (online edition)

https://doi.org/10.11646/zoosymposia.24.1.7
http://zoobank.org/urn:lsid:zoobank.org:pub:764C5336-9C40-4701-AECD-3D53C70C28A8

Factors structuring patterns of Ephemeroptera (mayflies) species assemblages in different segments of the Western Ghats of peninsular India—a snapshot

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Abstract

Species assemblage patterns of the mayflies (Ephemeroptera) in different segments of the Western Ghats (WG) of peninsular India including those on "sky islands" are presented. An updated checklist of species of WG mayflies is provided and sorted by traits of individual species and supplemented by personal observations. Comparisons are made in this context with patterns of current distribution of some ancient lineages of myriapods, amphibians and birds from the WG focusing on relative roles of geographical barriers (gaps), paleoclimatic, eco-evolutionary scenarios and anthropogenic impacts. This is to highlight the need to prioritize conservation of this rapidly shrinking precious biological heritage. Future work on molecular aspects of intra- and interspecific diversity of mayflies, which are "sentinels of inland water ecosystem health" should be augmented in tune with current research trends in montane "sky islands" especially from adjacent Oriental tropics.

Key words: trait-based species assemblages, Ephemeroptera, Western Ghats, Geographical barriers, "sky islands"

Introduction

Understanding the importance of interacting factors structuring biodiversity of the communities of freshwater biota in tropical mountains has become a challenging task. It is especially critical in the context of the urgent need to conserve this fragile species-rich ecosystem in the current 'Anthropocene Era' with its alarming levels of imperilment and extinction (Dudgeon 2019). This is primarily due to anthropogenic effects related to climate change and fragmentation and destruction of habitats that disrupts vital ecosystem services and jeopardizes healthy maintenance in the long run (Molur *et al*. 2011; Macadam *et al.* 2022).

Evolution, diversity and distribution of montane biota all over the globe are closely linked with mountain formation, geotectonic activities and topographic complexity (Hrivniak *et al.* 2022). Mountain systems in the Indian Subcontinent itself are an interesting entity with regard to assemblage patterns of its faunal. India simulates a situation as an "island" due to its prolonged isolation in the geological past, before, during and after the uplift of the Himalaya. Besides physical barriers, there is also a climatic barrier that separates India from the rest of Asia (Ramachandran *et al.* 2017). Phylogenetic patterns of several taxonomic groups, scolopendrid centipedes of WG for instance (Bharti *et al.* 2021), particularly those with low dispersal potential reveal endemic radiations as a result of evolution in isolation, and so typical of evolutionary clades that diversify on islands (Karanth 2015). India is endowed with older Gondwanan lineages which the drifting Indian plate carried before colliding with Eurasia. These lineages share African and Malagasy affinity. More recent Pleistocene refuges and other intrusive lineages dispersed within India after collision. Late Cretaceous volcanism resulted in large scale extinction of Gondwanan biota presumably providing new opportunities for occupation of these lineages (Mani 1974).

Submitted: 15 Oct. 2022; Accepted by Steven K. Burian: 1 May 2023; published: 31 Jul. 2023

Inland water fauna of the WG of peninsular India reflects aforementioned unique evolutionary, biogeographical and eco-climatic features contributing to its faunal assemblage pattern in no small measure, being a "hotspot within a hotspot" of biodiversity. Primary objective of this mini-review is to highlight the impact of topographic barriers creating vertically arranged sequence of "ecological belts" viz., 'sky islands' (Gueuning *et al*. 2017) along elevational gradients on species assemblage and distribution patterns of the larvae of Ephemeroptera, a dominant benthic macroinvertebrate group of crucial phylogenetic, biogeographic and ecological significance in montane freshwaters (larval stages) and adjoining riparian zones (alate stages). Mayflies act as "sentinels of ecosystem health" as well as vital links in fish and riparian vertebrate food chains. They also transfer nutrients and energy through the land-water interface, rendering an array of "ecosystem services disproportionate to their richness and abundance in their habitats" (Jacobus *et al*. 2019; Macadam & Stockan 2015). Their intriguing phylogenetic and phylogeographic histories are primarily impacted by tectonic and paleoclimatic activities over space and time (Sivaramakrishnan & Subramanian 2016; Sivaramakrishnan *et al*. 2020).

Western Ghats (WG)—a unique "tropical paradise of Oriental montane biodiversity"

The WG lies almost parallel to India's west coast. It is a chain of mountains with a north-south orientation, extending about 1600 km (8° to 21° N) from Gujarat state in the North to Kerala and Tamil Nadu states in the South (Fig. 1). The WG are geologically more ancient than the Himalaya. There are three significant geological breaks or gaps in these hills. The widest of them is the Palghat Gap (PG) at 11° N about 40 km wide. This gap is located in the state of Kerala with Tamil Nadu on the eastern side. Average annual rainfall is 1838 mm and average maximum and minimum temperature are 23.2 °C–32.4 °C, respectively. The average elevation of PG is approximately 200 m. The gap is a dextral shear zone and formed around 500 million years ago. Another prominent deeper gap around 224 km south of PG is Shencottah Gap (SG) at 9° N. It is a narrow gap 7.5 km wide, apparently older than PG with an elevation around 300 m with an annual temperature range of 23.5°C–31.1°C and an average annual rainfall of 1312 mm. In contrast to these climatically wet gaps, is a climatically drier, geologically younger (65–80 Mya) comparatively shallow Goa Gap (GG) at 15.8° N, situated 550 km north of PG with an elevation around 600 m acting as climatic barrier (Fig. 2). There is a south-north gradient of dry period length along the WG mountain range with the region north of GG experiencing an extended dry period of 6–7 months compared to the other two gaps spanning a dry spell of less than 4 months (Biswas & Karanth 2021).

Interestingly, southern and middle segments of the WG are endowed with extremely isolated chains of five mountain peaks (sky islands) harbouring unique shola forests, patches of evergreen flora and grasslands. They virtually function as "windows into evolutionary biogeographical and ecological processes", presenting a "gradient model of divergence" validated by empirical studies showing elevational diversification of ecologically divergent sibling/cryptic/endemic species as well as population-level divergence in adaptive morphology ultimately acting as "generators of diversity" (McCormack *et al*. 2009). However, the shola forests have experienced 50% loss since 1850, 25 % of which has occurred in the last three decades. Differences in geological, paleoclimatic and ecological history of these unique mountain systems have generated unique patterns and processes of faunal and floral diversification. Multiple hypotheses of such diversification models have been tested in the recent past to understand the relative roles of Quaternary glaciations, ecological gradients and geological processes (e.g. formation of geological barriers in diversification of fauna with ancient lineages) both spatially and temporally (Joshi & Karanth 2013; Vijayakumar *et al*. 2016).

Interacting factors structuring current mayfly species assemblage patterns in the WG

Recent publications on centipedes (*Digitipes* spp.) by Joshi & Edgecombe (2013) and Bharti *et al.* (2021); bush frogs (*Raorchestes* spp.) by Vijayakumar *et al*. (2016); and Shortwing birds (*Brachypteryx* spp.) by Robin *et al*. (2010; 2011; 2017) and a recent review by Biswas & Karanth (2021) have explored the role of Geographical Gaps in the WG for shaping intra- and interspecific genetic diversity in peninsular India. We explore briefly the diversity and distributional profiles of the archaic and charismatic Ephemeroptera (mayflies). Their current species assemblage across the 'sky islands' of the western Ghats hotspot consists of 45 genera in 13 families encompassing around 111 mayfly species (Sivaramakrishnan *et al*. 2020). Interacting factors impacting origin, diversity and distribution of WG mayfly species are primarily (i) geological gaps and sky islands with patchy shola forests; (ii) phylogenetic and biogeographic impacts; (iii) eco-climatic impacts and arrival of Pleistocene refugia in southern WG and their subsequent colonization in central and northern segments; and (iv) elevational "range extension" and "range contraction" due to climate change, habitat fragmentation and current anthropogenic pollution hazards.

Trait-based mayfly species assemblages—Origin, evolution and adaptive diversification in WG sky islands

Intensive studies by Vijayakumar *et al*. (2016) on multiple drivers of diversification of bush frogs in the WG sky islands of WG compare well with patterns of mayfly species diversification patterns published by Gatti *et al*. (2021) especially among Gondwanan derivatives. Interestingly, both mayflies and bush frogs have difficulty in crossing transoceanic barriers and hence more recent species assemblages of both these taxa in WG sky islands are the result of more recent local ecological and historical processes. In fact, endemic species of mayflies and bush frogs of WG sky islands might have evolved as a result of interplay of the three modes of diversification viz., (1) Geographic based mode of some Gondwanan lineages, (2) Paleo-climatic based Refugia mode of "Pleistocene refuges" and (3) Ecology-based mode of microhabitat and trophic specialists at different periods in their remote and immediate past history.

An updated checklist of mayfly species found in the WG is presented in Table 1. A total of 111 species in 13 families are known to occur in the WG. Species are sorted by traits, based mainly after Dudgeon (1999) and other published literature on WG mayfly species up to the end of 2022. This is supplemented by personal observations of authors during periodic field visits spanning several decades. Endemics are categorized herein as paleoendemics that were formerly apparently widespread but now are restricted to a smaller area, in contrast to neoendemics, which are recently evolved through divergence and reproductive isolation. In other words, paleoendemics are considered "museums" of old species whereas neoendemics are considered "cradles" of new species.

The subfamily Ataophlebiinae of the family Leptophlebiidae and the family Teloganodidae are represented by a few species of Gondwanan relictuals in WG sky islands as paleoendemic species. For instance, *Petersula courtallensis* Sivaramakrishnan, 1984, a member of *Kimminsula* complex of genera, might have been a Gondwanan derivative, though Kluge *et al.* (2022) have to wait application of integrative taxonomic study of this taxon to substantiate their gondwanan origin. Gatti *et al*. (2021) has recently studied the Gondwanan breakup scenario under an ephemeropteran perspective, employing molecular tools and concluding that the biogeographic history of Atalophlebiinae is congruent with events that occurred during the second phase of the gradual process of Gondwanan breakup in the Cretaceous and Paleogene. Their results supported the roles of both vicariance and dispersal in the history of diversification prior to the completion of the second phase of Gondwana breakup. This pattern together with natural extinction processes and low dispersal capacity across transoceanic barriers may explain the absence of this Gondwanan lineage in circum-Antarctic regions such as Africa, Malagasy and India (Gatti *et al*. 2021). Hence the paleoendemic species belonging to *Petersula* Sivaramakrishnan 1984 and related genera (Kluge *et al.* 2022) apparently have evolved in WG sky islands more as a result of local ecological and historical processes. The post-quaternary volcanic scenario resulted in the arrival of Afrotropical elements into India. Palearctic spillovers like *Afronurus kumbakkariensis* (Venkataraman & Sivaramakrishnan, 1989) and *Epeorus petersi* Sivaruban, Venkataraman & Sivaramakrishnan, 2013 (Sivaruban *et al*. 2013) might have arrived as per "Route Theory"after post Indian plate and Eurasia collision and contributed to some neoendemic species, which might have recently evolved in WG sky islands presumably through divergence and reproductive isolation. Finally, local species assemblages within montane streams of WG sky islands are fine-tuned by respective microhabitat specialists and trophic specialists exploiting spatio-temporal food availability (Burton & Sivaramakrishnan 1993), eco-climatic changes especially monsoonal vicissitudes, also impacted by periodic landuse changes (Selvakumar *et al*. 2014) and anthropogenic impacts (Dinakaran & Anbalagan 2007) resulting in reduction of species richness and abundance.

TABLE 1. Western Ghats Ephemeroptera species sorted by traits.

Family	Phylogenetic Relictuals			Endemic Species		Specialist Species		
Genus and Species	**Gondwanan derivatives**	**Lauratian Spillovers**	**Pleistocene refuges**	**Paleo-endemic**	**Neo-endemic**	**High altitude**	**Habitat Specialist**	**Trophic Specialist**
Prosopistomatidae								
1. *Prosopistoma coorgum* Balachandran & Anbalagan, 2016				+				
2. *Prosopistoma indicum* Peters, 1967				+				
3. *Prosopistoma someshwarensis* Ramya-Roopa, Selvakumar & Subramanian, 2017				+				
Leptophlebiidae								
4. *Choroterpes* (*Choroterpes*) *petersi* Tong & Dudgeon, 2003			+					
5. *Choroterpes* (*Euthraulus*) *alagarensis* Dinakaran, Balachandran & Anbalagan, 2009					+			
6. *Choroterpes* (*Euthraulus*) *angustifolius* Kluge *et al.* 2022					+			
7. *Choroterpes* (*Euthraulus*) *atelobranchis* Kluge *et al.* 2022					+			
8. *Choroterpes* (*Euthraulus*) *nambiyarensis* Selvakumar, Arunachalam & Sivaramakrishnan, 2013					+			
9. *Choroterpes* (*Euthraulus*) *nandini* Selvakumar & Sivaramakrishnan, 2015					+			
10. *Choroterpes* (*Euthraulus*) *unicolor* Kluge *et al.* 2022					+			
11. *Edmundsula lotica* Sivaramakrishnan				+				
12. *Edmundsula meghamalaiensis* Vasanth, Subramanian & Selvakumar, 2021				+				
13. *Ghatula quadrimaculata* Kluge *et al.* 2022	+							
14. *Ghatula rufa* Kluge *et al.* 2022	+							
15. *Indialis badia* Peters & Edmunds			+					
16. *Indialis kannani* Muthukatturaja & Balasubramanian, 2022			+					
17. *Indialis kodagi* Muthukatturaja & Balasubramanian, 2022			+					

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TABLE 1. (Continued)

Family Genus and Species	Phylogenetic Relictuals			Endemic Species		Specialist Species		
	Gondwanan derivatives	**Lauratian Spillovers**	**Pleistocene refuges**	**Paleo-endemic**	**Neo-endemic**	**High altitude**	**Habitat Specialist**	**Trophic Specialist**
18. *Indialis payaswini* Muthukatturaja & Balasubramanian, 2022			+					
19. *Indialis rossi* Peters, 1975			+					
20. *Indialis thirparapensis* Muthukatturaja & Balasubramanian, 2022			+					
21. *Isca* (*Isca*) *purpurea* Gillies, 1951								+
22. *Klugephlebia kodai* Selvakumar, Subramanian & Sivaramakrishnan, 2016						+		
23. *Megaglena agasthiya* Vasanth, Subramanian & Selvakumar, 2021						+		
24. *Megaglena sivarubani* Srinivasan & Isack, 2022						+		
25. *Nathanella indica* Demoulin, 1955						+		
26. *Nathanella saraswathiae* Sivaramakrishnan, Venkataraman & Balasubramanian, 1996						+		
27. *Notophlebia ganeshi* Kluge, 2014								+
28. *Notophlebia hyalina* Peters & Edmunds, 1970								+
29. *Notophlebia jobi* Sivaramakrishnan & Peters, 1984								+
30. *Petersula courtallensis* Sivaramakrishnan, 1984	+							
31. *Petersula heptagenoides* Kluge *et al*. 2022	+							
32. *Petersula nathani* Sivaramakrishnan & Hubbard, 1984	+							
33. *Thraulus cuspidatus* Vasanth, Subramanian & Selvakumar, 2022			+					
34. *Thraulus gopalani* Grant & Sivaramakrishnan			+					

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TABLE 1. (Continued)

Family Genus and Species	Phylogenetic Relictuals			Endemic Species		Specialist Species		
	Gondwanan derivatives	Lauratian Spillovers	Pleistocene refuges	Paleo-endemic	Neo-endemic	High altitude	Habitat Specialist	Trophic Specialist
35. *Thraulus malabarensis* Vasanth, Subramanian & Selvakumar, 2022			+					
36. *Thraulus mudumalaiensis* Arumuga-Soman, 1991			+					
37. *Thraulus semicastaneus* (Gillies, 1951)			+					
38. *Thraulus thiagarajani* Balasubramanian & Muthukatturaja, 2019			+					
39. *Thraulus vellimalaiensis* Vasanth, Subramanian & Selvakumar, 2022			+					
Ephemeridae								
40. *Ephemera* (*Aethephemera*) *nadinae* McCafferty & Edmunds, 1973							+	
41. *Ephemera* (*Ephemera*) *annandalei* Chopra, 1937							+	
42. *Ephemera* (*Ephemera*) *diffusa* Chopra, 1937							+	
43. *Ephemera* (*Ephemera*) *distincta* Hubbard, 1982							+	
44. *Ephemera* (*Ephemera*) *exspectans* (Walker, 1860)							+	
45. *Ephemera* (*Ephemera*) *fulvata* Navas, 1935							+	
46. *Ephemera* (*Ephemera*) *immaculata* Eaton, 1871							+	
47. *Ephemera nathani* Hubbard, 1982							+	
48. *Ephemera* (*Ephemera*) *supposita* Eaton, 1883							+	
49. *Eatonigenia trirama* McCafferty, 1973							+	
50. *Anagenesia minor* (Eaton, 1892)							+	
Polymitarcyidae								
51. *Povilla* (*Languidipes*) *taprobanes* Hubbard, 1984							+	
52. *Ephoron indicus* (Pictet, 1843)			+					

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TABLE 1. (Continued)

Family Genus and Species	Phylogenetic Relictuals			Endemic Species		Specialist Species		
	Gondwanan derivatives	**Lauratian Spillovers**	**Pleistocene refuges**	**Paleo-endemic**	**Neo-endemic**	**High altitude**	**Habitat Specialist**	**Trophic Specialist**
53. *Ephoron punensis* Dubey, 1970			+					
Potamanthidae								
54. *Potamanthus subcostalis* Navas, 1931								+
55. *Rhoenanthus distafurcatus* Bae & McCafferty, 1991								+
56. *Rhoenanthus tungaiensis* Balasubramanian & Muthukatturja, 2019								+
Caenidae								
57. *Caenis americani* Sivaruban *et al.*, 2021								+
58. *Caenis maratha* Malzacher, 2015								+
59. *Clypeocaenis bisetosa* Soldan, 1978								+
60. *Clypeocaenis gayathri* Balasubramanian & Muthukatturaja, 2020								+
61. *Clypeocaenis kaveri* Balasubramanian & Muthukatturaja, 2021								+
62. *Clypeocaenis multisetosa* Soldan, 1978								+
63. *Clypeocaenis napoklu* Balasubramanian & Muthukatturaja, 2021								+
64. *Clypeocaenis malzacheri* Srinivasan, Sivaruban, Barathy & Isack, 2022								+
65. *Clypeocaenis sharadhae* Balasubramanian & Muthukatturaja, 2020								+
Neoephemeridae								
66. *Potamanthellus caenoides* Ulmer, 1939		+						
Ephemerellidae								

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TABLE 1. (Continued)

Family	**Phylogenetic Relictuals**			**Endemic Species**		**Specialist Species**		
Genus and Species	**Gondwanan derivatives**	**Lauratian Spillovers**	**Pleistocene refuges**	**Paleo-endemic**	**Neo-endemic**	**High altitude**	**Habitat Specialist**	**Trophic Specialist**
67. *Torleya lacuna* Jacobus, McCafferty & Sites, 2007			+					
68. *Torleya nepalica* (Allen & Edmunds, 1963)			+					
Teloganodidae								
69. *Derlethina tamiraparaniae* Selvakumar, Sivaramakrishnan & Jacobus, 2014					+			
70. *Dudgeodes bharathidasani* Anbalagan, 2015					+			
71. *Dudgeodes palnius* Selvakumar, Sivaramakrishnan & Jacobus, 2014					+			
72. *Dudgeodes sartorii* Srinivasan, Sivaruban, Barathy & Isack, 2021					+			
73. *Indoganodes jobini* Selvakumar, Sivaramakrishnan & Jacobus, 2014	+							
74. *Teloganella indica* (Selvakumar, Sivaramakrishnan & Jacobus, 2014)					+			
75. *Teloganodes dentatus* Navas, 1931					+			
76. *Teloganodes kodai* Sartori, 2008					+			
Tricorythidae								
77. *Sparsorythus gracilis* Sroka & Solan, 2008								+
78. *Sparsorythus nanjangudensis* Muthukatturaja & Balasubramanian, 2021								+
79. *Sparsorythus srokai* Srinivasan, Sivaruban, Barathy & Isack, 2021								+
Heptageniidae								

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TABLE 1. (Continued)

Family Genus and Species	Phylogenetic Relictuals			Endemic Species		Specialist Species		
	Gondwanan derivatives	**Lauratian Spillovers**	**Pleistocene refuges**	**Paleo-endemic**	**Neo-endemic**	**High altitude**	**Habitat Specialist**	**Trophic Specialist**
80. *Afronurus keralensis* (Braasch & Soldan, 1987)		+						
81. *Afronurus kumbakkaraiensis* (Venkataraman & Sivaramakrishnan, 1989)		+						
82. *Afronurus meenmutti* Balasubramanian & Muthukatturaja, 2021		+						
83. *Thalerosphyrus flowersi* Venkataraman & Sivaramakrishnan, 1987		+						
84. *Epeorus* (*E.*) *gilliesi* Braasch, 1981		+						
85. *Epeorus* (*E.*) *petersi* Sivaruban, Venkataraman & Sivaramakrishnan, 2013		+						
Isonychiidae								
86. *Isonychia moyarensis* Vasanth, Selvakumar & Subramanian, 2019								+
87. *Isonychia radhae* Balasubrmanian & Muthukatturaja, 2021								+
Baetidae								
88. *Acentrella* (*Liebebiella*) *vera* Müller-Liebenau, 1982			+					
89. *Baetis michaelohubbardi* (Selvakumar, Sundar & Sivaramakrishnan, 2012)					+			
90. *Centroptella* (s. str.) *ornatipes* Kluge, 2021			+					
91. *Centroptella* (s. str.) *longisetosa cinerea* Kluge, 2021			+					
92. *Centroptella (Chopralla) ceylonensis* Müller-Liebenau 1983			+					
93. *Centroptella* (*Chopralla*) *ghatensis* Kluge, 2021					+			
94. *Indobaetis microfolius* Kluge & Novikova, 2014					+			

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TABLE 1. (Continued)

Family Genus and Species	Phylogenetic Relictuals			Endemic Species		Specialist Species		
	Gondwanan derivatives	**Lauratian Spillovers**	**Pleistocene refuges**	**Paleo-endemic**	**Neo-endemic**	**High altitude**	**Habitat Specialist**	**Trophic Specialist**
95. *Indocloeon* (*Hindocloeon*) *continentale* Kluge & Suttinun, 2020					+			
96. *Labiobaetis jacobusi* Kubendran & Balasubramanian, 2015					+			
97. *Labiobaetis soldani* Kubendran, Rathinakumar, Balasubramanian, Selvakumar & Sivaramakrishnan, 2014					+			
98. *Nigrobaetis paramakalyani* Kubenderan & Balasubramanian, 2015					+			
99. *Nigrobaetis klugei* Sivaruban, Srinivasan, Barathy & Isack, 2021					+			
100. *Tenuibaetis frequentus* Muller-Liebenau and Hubbard, 1985.					+			
101. *Cloeon bicolor* Kimmins, 1947			+					
102. *Cloeon bimaculatum* (Eaton, 1885)			+					
103. *Cloeon harveyi* Kimmins, 1947			+					
104. *Cloeon kimminsi* Hubbard, 1974			+					
105. *Cloeon marginale* (Hagen, 1858)			+					
106. *Procloeon dipsicum* (Gillies, 1949)			+					
107. *Procloeon* (*Oculogaster*) *malabarensis* Kluge, 2020					+			
108. *Procloeon palmyrae* (Gillies, 1949			+					
109. *Procloeon rubellum* (Navas, 1931)			+					
110. *Symbiocloeon madhyasthai* Subramanian & Sivaramakrishnan, 2009							+	
111. *Waynokiops palifer* Kluge, 2022			+					

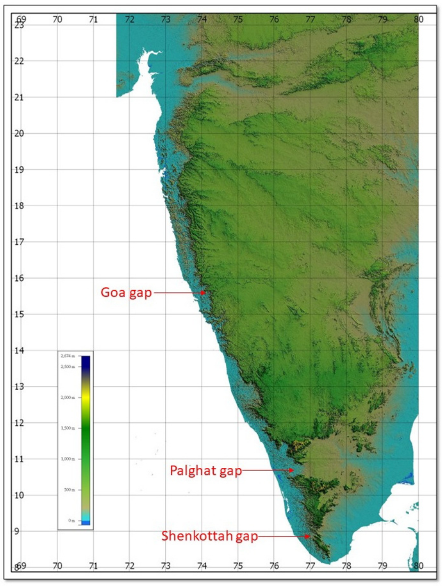

FIGURE 1. Geographical gaps of the Western Ghats in southern India.

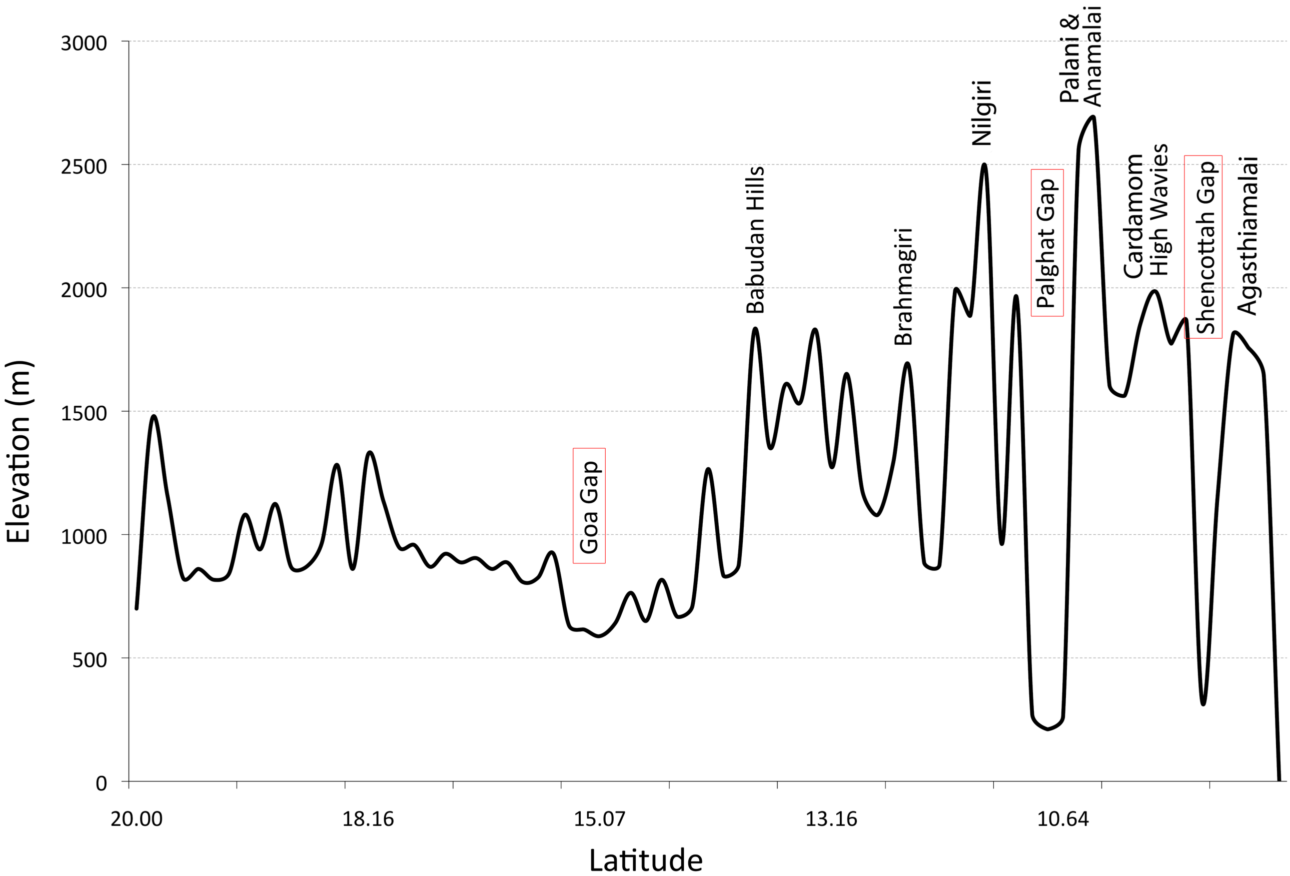

FIGURE 2. Elevational profile of the Western Ghats showing the geographical gaps and sky islands. Modified from Ramesh *et al.* (1997).

Future dimensions

Further explorations of evolutionary and eco-climatic drivers structuring genes and communities of mayflies of WG sky islands adopting a state-of-the-art integrative approach involving molecular ecology, molecular phylogeography and ecogenomics on aspects covered by recent pioneering explorations elsewhere are to be initiated. An example is that of Guening *et al*. (2017) on the mayflies of Sumatran sky islands, a study the first of its kind in aquatic insects of the Oriental tropics.

Acknowledgments

Authors thank reviewer Luke Jacobus and editor Steve Burian for valuable, critical inputs that improved the manuscript. C. Selvakumar is grateful to the Science and Engineering Research Board, Government of India, New Delhi for financial support under the Empowerment and Equity Opportunities for Excellence in Science (F. N. EEQ/2022/000317). He also thanks the Head of the Department of Zoology, Principal and the Management, The Madura College (Autonomous), Madurai for their support and encouragement. K. A. Subramanian and M. Vasanth are grateful to the Director, Zoological Survey of India, Kolkata for providing facilities to conduct this work.

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